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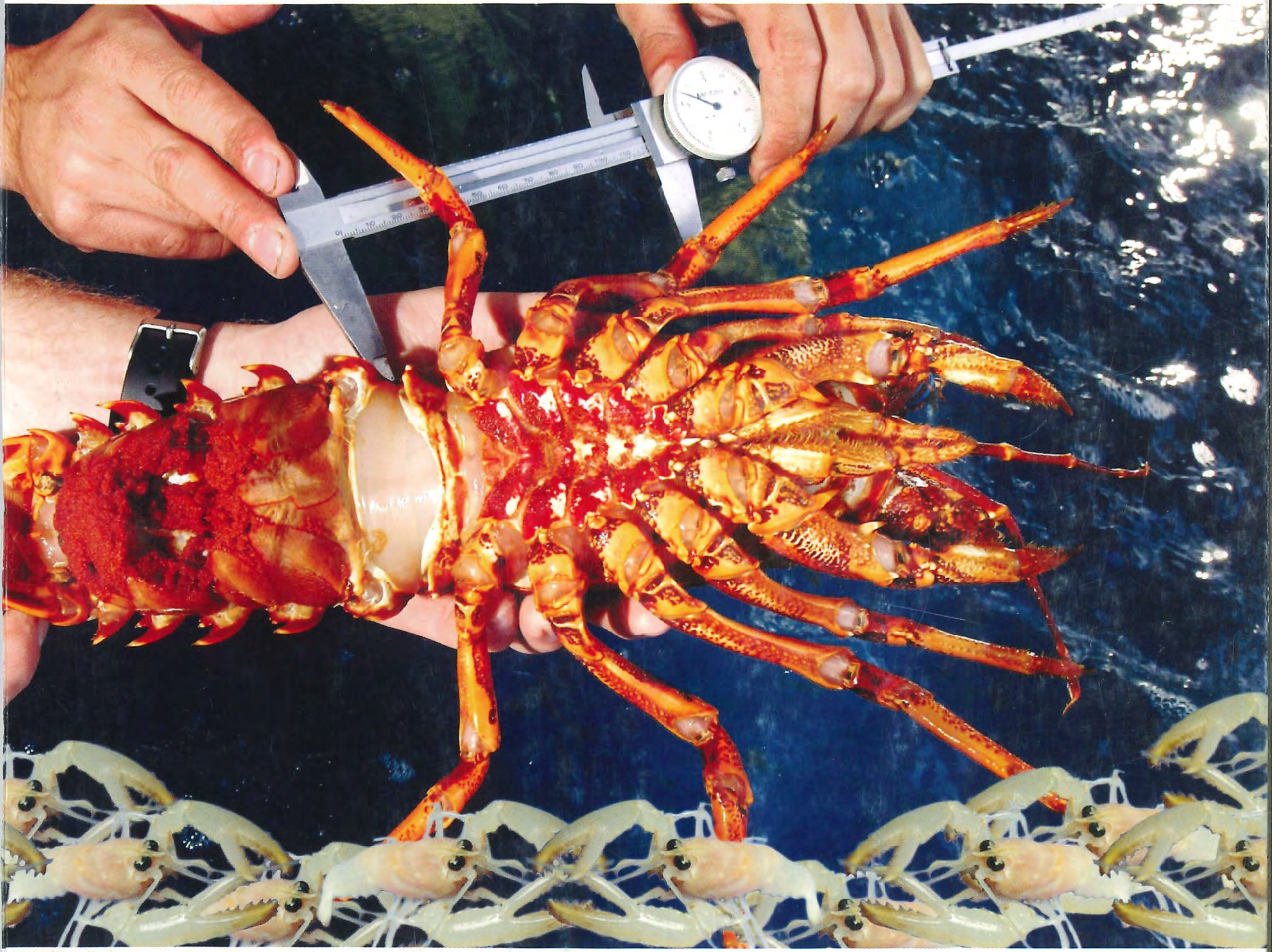

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**Cover: Measuring morphological parameters on the spiny lobster, *Jasus edwardsii*, using vernier calipers. Photo: Bruce Miller. (See Smith & Ritar pp. 317–324.) White hatchery-reared American lobsters (*Homarus americanus*). Photo: M. Tlusty. (See Tlusty pp. 571–580.)**

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## Special issue 2: Lobster biology and management

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# Field estimation of daily ration of Norway lobster (*Nephrops norvegicus*) in the south of Portugal

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**Abstract** Daily ration estimates of Norway lobster (*Nephrops norvegicus*) from field samplings over a 24-h cycle were obtained. Four tows were conducted in the middle continental slope, off the south coast of Portugal. The results from Eggers (1977, 1979) and Elliot & Persson (1978) daily ration models were compared, by the Worobec δ-method (1984), showing no significant differences among them. The estimates of food consumption obtained varied from 1.098 to 1.170 g dry food per 100 g body wet weight in males and 1.642 to 1.755 g dry food per 100 g body wet weight in females. Our results were compared with daily rations reported for other crustaceans. Daily ration values were compared and tested by a two-way ANOVA, with interaction, showing significant differences between sexes. This has been registered for other decapods and may be explained by a period of active growth in females, on the onset of vitellogenesis, increasing their nutritional/feeding needs.

**Keywords** daily ration; *Nephrops norvegicus*; feeding ecology

## INTRODUCTION

The Norway lobster (*Nephrops norvegicus* (L.)), is one of the dominant crustacean species in the continental shelf assemblages in the North Atlantic (Farmer 1975), at bathyal depths in the eastern Atlantic coast (Figueiredo 1988, 1989), the western Mediterranean (Abelló et al. 1988; Cartes et al. 1994), and the eastern Mediterranean (Froglia & Gramito 1995). This is a species that has been widely studied in its different aspects of biology and fisheries (Figueiredo & Thomas 1967; Farmer 1975; Chapman 1980; Sardà 1995) but, as Sardà (1995) pointed out, feeding studies were poorly covered. For this reason the feeding ecology of *N. norvegicus* from the south coast of Portugal has been the subject of several recent studies (Cristo 1998, 2001; Cristo & Cartes 1998; Cristo & Encarnação 2000).

However, daily ration estimates based on field experiments are still lacking for Norway lobster. This field has been widely studied and developed for fish (Worobec 1984; Macpherson 1985; Héroux & Magnan 1996; Pakhomov et al. 1996) and was successfully applied recently for decapod crustaceans from bathyal grounds (Maynou & Cartes 1997, 1998).

These are important studies because the estimation of daily rations in deep-water organisms can be a source of indirect information on the carrying capacity of deep environments to sustain given levels of abundance, biomass, and diversity (Maynou & Cartes 1997).

Decapod crustaceans are significant in this context because they play an important role in the structure of the food webs, making the link between macrofauna and megafaunal top predators (Cartes & Sardà 1992; Cartes 1998).

The present daily ration study is of particular interest for the previously discussed ecological reasons and because it is based on a field study of *N. norvegicus*.

Several authors have developed daily ration models based on field experiments (Eggers 1977, 1979; Elliott & Persson 1978) that have been applied to fish studies and decapod crustaceans.

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Results from feeding studies reveal that *N. norvegicus* feeds on a wide diversity of prey (Thomas & Davidson 1962; Lagardère 1977; Cristo 1998), presents median stomach fullness indices (Mytilineou et al. 1992; Cristo & Cartes 1998), and has lower evacuation rates compared with other decapods (Cristo 2001). The objective of our study was to estimate food consumption by *N. norvegicus* from the south of Portugal, based on daily ration models, as a quantitative complement to the feeding ecology studies of this important species.

## MATERIALS AND METHODS

The water masses in the surrounding area show characteristics of Eastern North Atlantic Water (ENAW) (Relvas de Almeida 1999). However the water in the sampling area, a canyon that runs east-west, shows well marked characteristics of Mediterranean Water (MW) that is known to flow out of this basin through these submarine canyons (Madelain 1970). These water masses correspond to the shallow core of MW, with temperatures that are constant and relatively high throughout the year: 13°C ± 0.5°C (Ambar 1983).

### Data sampling and data treatment

This field experiment was conducted on a commercial trawler, in spring (26–27 April) 1999 at depths of 600 m in the vicinity of 36°45′N, 7°50′E. Four trawls were completed during a 24-h period: dawn, noon, sunset, and night. Table 1 presents the data relative to the samples and sampling sites. Because of the low densities of Norway lobster at these depths and the duration of the fishing operations, tows of 4–5 h were required to guarantee adequate sample sizes.

From each haul, a sample of c. 50 individuals was randomly collected, and preserved on board in 4% buffered formalin. In the laboratory the samples were transferred to 70% ethanol after 48 h. Sex, standard cephalothorax length (mm CL), and wet weight with no claws (WNC), were recorded. This last parameter is important because not all specimens had two claws, so it is preferable to register the weight with no claws and then transform those values to wet weight with claws (WC), through linear regressions—

Female: $WC = 1.1744\ WNC + 0.8898$ ($r^2 = 0.9984$ $n = 30$); and

Male: $WC = 1.4492\ WNC - 3.3001$ ($r^2 = 0.9912$ $n = 44$).

Size varied between 30.2 mm and 48.1 mm CL for females and 31.4 mm and 56.6 mm CL for males.

Stomachs were removed, and the contents carefully washed and dispersed in distilled water and then filtered through a pre-dried and weighed Whatman-GF/C glass microfibre filter, in a vacuum water jet pump system, to guarantee no loss of content. The filters with the stomach contents were then dried for 48 h at 60°C. The stomach content dry weights (DW) were calculated by subtraction of the filter DW.

The gut fullness index is expressed as g dry food weight per 100 g lobster wet weight (%DW/WC). The stomach fullness index (F) was computed for each individual as (Maynou & Cartes 1998):

$$F_{wet} = (\text{g stomach content DW}) \times (100 \text{ g lobster WC})^{-1}$$

A two-way ANOVA with interaction was used to test the effect of sex and time of day on the stomach fullness ($F_{wet}$).

### Daily ration models

The models and methods usually used for the determination of daily ration in fish have been reviewed by several authors (Boisclair & Leggett 1988; Boisclair & Marchand 1993; Bromley 1994; Héroux & Magnan 1996). Maynou & Cartes (1997, 1998) assessed the applicability of fish models to decapod crustaceans.

Daily ration models are based on the assumption that gastric evacuation is an exponential decay

**Table 1** Trawl samples of *Nephrops norvegicus* collected for daily ration determination in the south off Portugal. (*N*, number of individuals analysed; CL, carapace length.)

| Tow | Depth (m) | Start time (h GMT) | End time (h GMT) | *N* | Sex ratio (% females) | Size range (mm CL) | | Mean weight (g) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Females | Males | Females | Males |
| 1 | 578–615 | 5:30 | 9:30 | 52 | 40.4 | 31.5–48.1 | 31.9–53.9 | 36.52 | 58.43 |
| 2 | 578–639 | 10:45 | 15:15 | 51 | 50.9 | 32.8–46.3 | 35.5–56.6 | 35.00 | 68.37 |
| 3 | 547–617 | 17:15 | 21:15 | 52 | 59.6 | 30.2–47.2 | 31.4–51.2 | 33.04 | 52.71 |
| 4 | 594–637 | 22:45 | 4:15 | 49 | 53.1 | 30.8–47.0 | 32.3–52.5 | 35.60 | 56.14 |

function (Eggers 1977; Elliot & Persson 1978) which includes a constant for gastric evacuation rate (R).

The R value can be obtained from the results of field experiments under certain conditions (Héroux & Magnan 1996; Cristo 2001) or by laboratory experiments (Sardà & Valladares 1990, Héroux & Magnan 1996; Cristo 2001).

The R value used in this study is $R = 0.177\ h^{-1}$. This was derived, for the same species, from the results of a field study conducted in the same area (Cristo 2001). As temperature and prey composition are the main factors affecting R (Elliot 1972; Elliot & Persson 1978; Bromley 1994), and assuming these conditions are maintained, this value is appropriate.

The three most widely used models to calculate daily ration in fish are those of Eggers (1977, 1979) and Elliot & Persson (1978). These models were successfully applied to decapod crustaceans by Maynou & Cartes (1997; 1998), and can be expressed as:

Eggers (1977): $C_{(24E)} = F_{24}\ R\ 24$ (1)

where $F_{24}$ is the mean stomach fullness index over 24 h, as $F_{wet}$. This model assumes that the feeding periodicity is such that the fullness indexes at the beginning and at the end of a 24-h period are equal (Eggers 1979; Boisclair & Leggett 1988).

Eggers (1979): when this assumption cannot be met, Eggers (1979; see also Boisclair & Marchand 1993) proposed the corrected model:

$$C_{(24EC)} = C_{(24E)} + (F_{t=24} - F_{t=0}) \quad (2)$$

where $F_{t=24}$ and $F_{t=0}$ are the values of stomach fullness index as $F_{wet}$ at the end and the beginning of the 24-h sampling period.

Elliot & Persson (1978): The food consumed during the time interval $t_i$ is:

$$Ct_i = \frac{(Ft_i - Ft_0 e^{-Rt_i})Rt_i}{1 - e^{Rt_i}} \quad (3)$$

and the daily ration is the summation, over 24 h, of the K time intervals considered:

$$C_{(24E\&P)} = \sum_{t=1}^{K} Ct_i \quad (4)$$

This model assumes, as do the others, that food evacuation is exponential and that the rate of food consumption within each sampling interval is constant. It does, however, have an important limitation: that time intervals should not be greater than 3 h. With longer time intervals estimates of daily ration tend to decrease.

In the calculation of daily ration, we used the fullness index $F_{wet}$ instead of the stomach content DW, after verifying that the relationship between wet body weight and dry stomach content weight is isometric for both sexes (see discussion in Héroux & Magnan 1996).

Following Worobec (1984) the standard error of the Elliott & Persson model was computed, using the $\delta$-method approximation. The same method was used to compute the standard errors of the other two Eggers models. In all examples the standard errors can the considered as overestimated, since covariance was not included in the calculations.

## RESULTS

The results of the two-way ANOVA on stomach fullness indexes, with factors time of the day, sex, and their interaction are presented in Table 2. For both sexes time of the day (TOW) was significant as were differences between sexes. The interaction was not, meaning that males and females exhibit the same trends in stomach fullness during the day but with average values lower for males (Fig. 1).

As there are significant differences regarding fullness index between females and males, all the

**Table 2** Results of two-way ANOVA. Response variable is the stomach fullness index ($F_{wet}$) and the factors are time of the day (TOW) and sex. Interaction factor was also considered.

| Source | d.f. | Sum of squares | Mean square | $F_{wet}$ | $P > F$ |
|---|---|---|---|---|---|
| Model | 7 | 2.41 | 0.34 | 7.72 | 0.0001 |
| TOW | 3 | 1.62 | 0.54 | 12.09 | 0.0001 |
| SEX | 1 | 0.74 | 0.74 | 16.68 | 0.0001 |
| TOW*SEX | 3 | 0.05 | 0.02 | 0.37 | 0.7768 |
| Error | 196 | 8.73 | 0.04 | | |
| Corrected total | 203 | 11.13 | | | |

calculations were done separately by sex. Table 3 summarises the fullness index calculated per haul and for all hauls. Average values are also presented in Fig. 1.

Figure 1 clearly shows that despite the absence of a period of no food consumption, there is an increase in the feeding activity corresponding to noon (2° haul), and that this activity decreases afterwards.

The daily ration estimates calculated by the three models presented are given in Table 4. The Eggers's (1979) model estimates are the highest, and between the other two models, Eggers's (1977) gives slightly higher values than Elliot & Persson's (1978) model. However the values are very similar among sexes, with females showing higher daily ration values than males.

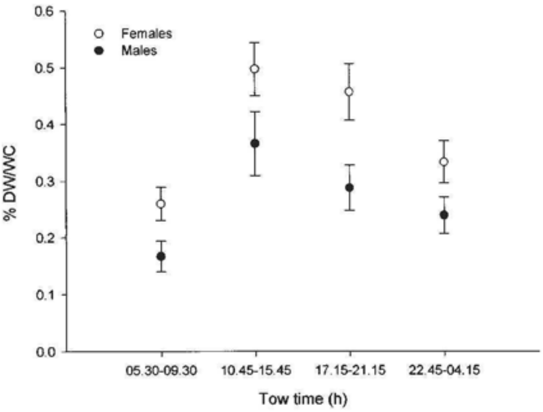

**Fig. 1** Average fullness index values and standard errors for females and males per tow (tow time in h GMT). (DW/WC, g stomach content dry weight per 100 g lobster wet weight.)

**Table 3** Mean stomach fullness ($F_{wet}$) in g stomach content dry weight per 100 g *Nephrops norvegicus* wet weight. Standard error in parentheses.

| Haul | $F_{wet}$ for females | $F_{wet}$ for males |
|---|---|---|
| 1 | 0.260 (±0.029) | 0.167 (±0.027) |
| 2 | 0.497 (±0.046) | 0.366 (±0.056) |
| 3 | 0.456 (±0.049) | 0.288 (±0.039) |
| 4 | 0.333 (±0.037) | 0.239 (±0.032) |
| All hauls | 0.396 (±0.023) | 0.258 (±0.021) |

**Table 4** Daily ration estimates in *Nephrops norvegicus* by three different models: $C_{(24E)}$ (Eggers 1977); $C_{(24EC)}$ (Eggers 1979); $C_{(24E\&P)}$ (Elliott & Persson 1978); R = 0.177 $h^{-1}$ (Cristo 2001). Values of C in g stomach content dry weight per 100 g lobster wet weight (% DW/WC). Standard error in parentheses. Bold indicates the values of daily ration based on theoretical considerations of the models.

| | Daily ration | |
|---|---|---|
| Model | Females | Males |
| $C_{(24E)}$ | **1.682 (±1.032)** | **1.098 (±0.899)** |
| $C_{(24Ec)}$ | **1.755 (±1.058)** | **1.170 (±0.942)** |
| $C_{(24E\&P)}$ | 1.642 (±0.743) | 1.125 (±0.687) |

**Table 5** Comparison of daily ration in %DW/WC (g stomach content dry weight per 100 g lobster wet weight) of *Nephrops norvegicus* with daily rations obtained for other species. (Sources: (1) Cristo & Encarnação 2000; (2) Sardá & Valladares 1990; (3) Maynou & Cartes 1997; (4) Maynou & Cartes 1998; (5) recalculated from Pakhomov & Perissinotto 1996.)

| Species | Daily ration* | Experiment | Source |
|---|---|---|---|
| *Nephrops norvegicus* females | 1.642–1.755 | Field | This study |
| *N. norvegicus* males | 1.098–1.170 | Field | This study |
| *N. norvegicus* (min.–max. values) | 0.40–1.23 | Laboratory | (1) |
| *N. norvegicus* (range of average values) | 0.77–0.86 | Laboratory | (1) |
| *N. norvegicus* (max. food consumption) | 0.86 | Laboratory | (2) |
| *Aristeus antennatus* | 0.130–0.223 | Field | (3) |
| *Munida tenuimana* females | 0.457–1.086 | Field | (4) |
| *M. tenuimana* males | 0.302–0.722 | Field | (4) |
| *Geryon longipes* | 0.054–0.061 | Field | (4) |
| *Polycheles typhlops* | 0.077 –0.096 | Field | (4) |
| *Themisto gaudichaudi* (average value) | 4.5 | Field | (5) |

*Range of daily ration models except were stated.

## DISCUSSION

Daily ration models, originally developed for fish are also applicable to decapod crustaceans (Maynou & Cartes 1997, 1998). The estimates of daily ration resulting from the three models considered give similar values, although they are based on different assumptions (Eggers 1977, 1979; Elliott & Persson 1978).

The limitations were mainly related to the operation procedures of the boat (see Materials and Methods). It was, however, possible to make at least four tows, at critical hours of the day (Farmer 1974). Other authors have obtained reliable results with the same methodology using five tows per 24 h (Maynou & Cartes 1997, 1998).

Given the previously discussed limitations and considerations, the values obtained by the two first models (Eggers 1977, 1979) may be considered more appropriate.

The R value used in the three daily ration models, R = 0.177 $h^{-1}$ (Cristo 2001), is very similar to the value used for daily ration estimates of *Aristeus antennatus* (R = 0.179 $h^{-1}$) (Maynou & Cartes 1997) and is well within the range of the values used for nine other species of deep-water decapods (Maynou & Cartes 1998) (R values between 0.150 and 0.312 $h^{-1}$). The values used by these authors were recalculated from previously published data obtained from laboratory experiments (Sardà & Valladares 1990) or based on the value of $R_{max}$ (Héroux & Magnan 1996) ($R_{max.}$ for *Gerion longipes*: 0.183). However, the important consideration seems to be the fact, as pointed out by Bromley (1994), that whatever method is used, R values are similar because temperature is the limiting factor.

It proved to be important to test sex influence on the index of stomach fullness, since different fractions of the population may have different daily rations. *N. norvegicus* females at this time of the year (April) had a higher daily ration than males. The female reproductive season in this area starts in March and extends to October (Orsi Relini et al. 1998). During this period there is also an increasing percentage of gastroliths (Gramitto 1998), which precludes moulting, occurring once a year before mating. So, this is a high energy-demand period for females that may justify the increase in feeding activity. Maynou & Cartes (1998) observed the same occurrence in *Munida tenuimana*, and made the same justification for the higher metabolic requirements of active growth.

The occurrence of an increase in the feeding activity towards noon was also found by Aguzzi et al. (2004). Coincidentally, those authors found a peak of emergence and a retrieve to their burrows during night time, also observed by Farmer (1975). This emergence cycle does not seem to be coupled to the peaks of endogenous rhythms of metabolism, demonstrated by Atkinson & Naylor (1976) and Aguzzi et al. (2004). Our interpretation is that the ingestion of prey is done outside the burrows and digestion inside, thus justifying the increase in oxygen consumption and cardiac rhythmicity. It is the metabolic process associated with digestion that appears to have an endogenous rhythm, whereas foraging activity is controlled by other factors of a more behavioural nature.

Comparing our daily ration results with previously published data at similar temperature ranges (13°C ± 0.5°) (Maynou & Cartes 1998) (Table 5), we noticed that: (1) field estimates of daily ration for *N. norvegicus* are higher than estimates obtained from laboratory experiments (Cristo & Encarnação 2000); and (2) our daily ration estimates are generally higher than the estimated values found for other decapod crustaceans with a similar ecological niche (benthic, reptant decapods, ex. *Aristeus antennatus*, *Munida tenuimana*, *Geryon longipes*, *Polycheles typhlops*) (Maynou & Cartes 1998).

The first difference may be because studies based on field sampling allow estimates of daily rations based on the natural diets which are, in this instance, very difficult to replicate in the laboratory, because of the natural diversity in the diet of *N. norvegicus* (Cristo & Cartes 1998). The animals are in confined conditions with limited mobility, and under stress which certainly may reduce food consumption.

Relative to the second point, these are values computed from only one survey, which need subsequent studies, since daily rations may vary greatly with season. However the same methodology was followed by Maynou & Cartes (1997, 1998) with consistent results, although somewhat contradictory to our findings. However those authors also compared daily rations from March and July, with consistent results. The question here is, "Does the geographic influence overcome the seasonal effect?" Only with daily ration studies covering all seasons can this question be answered.

According to these authors, reptantian benthic species usually show low daily rations and high trophic diversity. According to our results *N. norvegicus*, though it is considered a reptant species, presents a relatively low trophic diversity (H' = 2.02) (Cristo & Cartes 1998), thus justifying the need of a relatively high daily ration. Maynou & Cartes (1998) proposed a daily ration model at 13°C, the same temperature at which our lobsters were captured (T = 13ºC ± 0.5), that can be expressed as DR = 0.814 + 0.217CL/CW – 0.252H', in which DR is the daily ration, CL/CW the carapace length/carapace width ratio in mm, and H' the Shannon-Weaver trophic diversity. According to this model the *N. norvegicus* daily ration is DR = 0.928, a value that is within the values calculated by the three methods (Table 4).

Further studies must be developed on a wider spatio-temporal scale to give a better picture of the food consumption by deep sea crustaceans and to investigate metabolic rates among benthic crustaceans, as was done for fish (Koslow 1996).

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# Comparative morphology and evolution of the reproductive structures in spiny lobsters, *Panulirus*

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**Abstract** Males and females of the spiny lobster genus *Panulirus* have evolved a range of modifications to the penile process and the thoracic sternum respectively. The pattern of evolution of the reproductive structures confirms the previously presented patterns of speciation in *Panulirus*, based on genetics and on the morphology of adults, larvae, and pueruli. These structures may have themselves helped to initiate speciation in *Panulirus* and may have evolved as a consequence of the longer lasting spermatophoric mass and the delayed use of sperm by the females of some species. During courting, body caresses enable males to assess the size of females. The evolution of different copulatory structures heightens the probability of same-species mating and for the male to confirm a female's size and reproductive status, and ejaculate and correctly position an external spermatophore of the required size.

**Keywords** reproductive structures; evolution; *Panulirus*; mating; external spermatophoric mass; tar spot; delayed fertilisation

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## INTRODUCTION

Unlike the clawed lobsters (Nephropidae), the unspecialised male pleopods of the spiny lobsters (Palinuridae) take no part in sperm transference and there is no deep-pocketed, sperm receptacle on the sternum of the female (Fielder 1964; Phillips et al. 1980). In the Stridentes subgroup of the Palinuridae, across the posterior sternal segments of the female, the male spreads a paired spermatophoric mass ("tar spot") that hardens quickly in sea water (Fig. 1) whereas in the Silentes subgroup of the Palinuridae, the spermatophoric mass is soft and gelatinous and rapidly breaks up in sea water (Berry 1970; Berry & Heydorn 1970; MacDiarmid 1989). The tar spot contains, embedded in its matrix, the convoluted spermatophores that contain the spermatozoa (Berry & Heydorn 1970). In most palinurid genera, the mature female thoracic sternum is a fully calcified surface. Only in some species of *Panulirus* are the posterior segments soft and fleshy (Lindberg 1955) or have sets of round or oval decalcified "windows" (Berry 1970; Chitty 1973; Kagwade 1988; Fig. 1). Berry & Heydorn (1970) noted that for *P. homarus rubellus*, the butterfly-shaped tar spot fully covered the soft windowed area of the female sternum. Berry (1970) suggested that for *P. h. rubellus*, these "soft areas enable the males to locate the correct position for deposition of the spermatophoric mass with his copulatory organs, both of which are supplied with tufts of sensory setae". The outer covering of the tar spot is eventually scraped away by the female, allowing use of the sperm for fertilisation. After all the remnants of the tar spot of *P. polyphagus* were scraped away, Kagwade (1988) observed the soft windows as 3 pairs of dark scars on the sternum (Fig. 1).

While reviewing the taxonomy of *Panulirus*, numerous specimens were examined and the presence or absence of decalcified areas and associated distinct transverse ridges on the female sternum were noted. The variations in the ornamentation and setation of the male copulatory organ, particularly on the penile processes, were also recorded (Fig. 2). This paper reports the results of

**Fig. 1** Ovigerous female *Panulirus polyphagus* from south-west India showing a new tar spot and the anterior pair of soft windows on the third thoracic segment (arrowed).

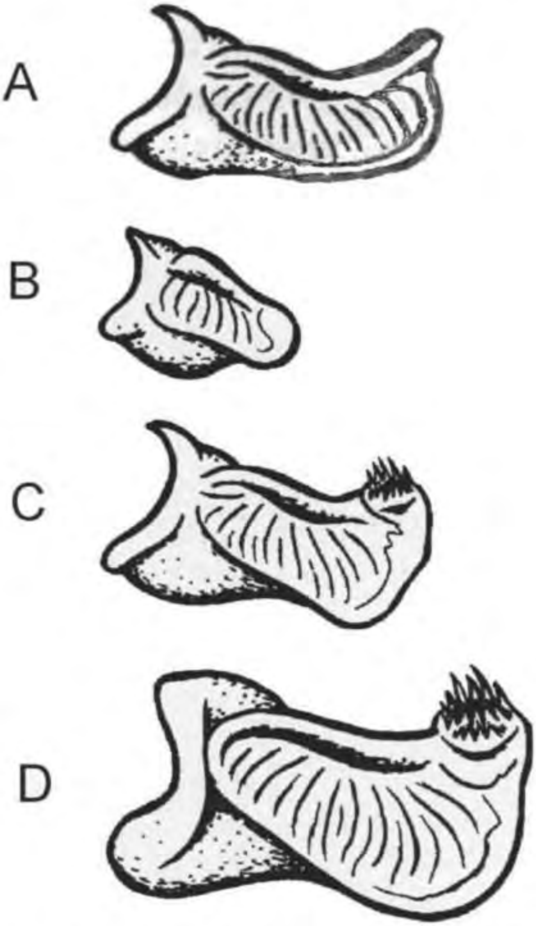

**Fig. 3** Penile process of **A**, mature *Panulirus cygnus*. Development of penile process of *Panulirus homarus rubellus* (after Heydorn 1969); **B**, juvenile; **C**, subadult; **D**, mature.

**Fig. 2** (*left*) Male *Panulirus ornatus* from south-west India showing medial process (arrowed) and serrated tips.

those examinations and makes a phylogenetic comparison with the current evolutionary hypothesis, based on genetics as well as adult, larval, and puerulus morphology (George & Main 1967; Baisre 1994; McWilliam 1995; George 1997; Ptacek et al. 2001; Patek & Oakley 2003).

I discuss the possible evolutionary values of the various reproductive structures in *Panulirus*, including species recognition, size and positioning of the spermatophoric mass, and signalling of the female reproductive status.

## RESULTS

### Development and variation in the male mating organ and the female sternum

In the smaller juvenile males of *Panulirus*, the surfaces of the thoracic sterna are covered in short setae and the gonopores are simple openings on the base of the fifth leg. As the males mature, the sternal setae are lost and a small knob (Fig. 3B) develops at the median anterior corner of the basal joint of the fifth leg. With growth, this knob becomes a prominent penile process, which possesses either a curved smooth crest (Fig. 3A) (for 12 taxa, see Table 1) or a pointed, serrate extension (Fig. 2) that is accompanied by a distinct tuft of setae or "hairbrush" (Fig. 3C, D) (for 11 taxa, see Table 1).

For about one-third of the species of *Panulirus*, no obvious decalcified windows develop on the

**Fig. 4** Sternum of female *Panulirus cygnus* from Western Australia showing pale and non setose fourth and fifth segments and the site of the tar spot.

**Table 1** Sternal windows of fully mature females and the structure of the male penile process in *Panulirus*. Two major lineages and the clades are those identified by Ptacek et al. (2001), Patek & Oakley (2003), and George (unpubl. data). (c , sternal surface fully calcified, without windows.)

| Clade | Species | Pairs of windows on female sterna 5th | 4th | 3rd | 2nd | Penile process and hairbrush |
|---|---|---|---|---|---|---|
| **First Major Lineage** | | | | | | |
| *argus* | *argus* spp. | c | c | c | c | curved, smooth (small) |
| *longipes* | *l. longipes* | c | c | c | c | curved, smooth (nil) |
| ditto | *l. bispinosus* | c | c | c | c | curved, smooth (nil) |
| ditto | *femoristriga* | c | c | c | c | curved, smooth (nil) |
| *japonicus* | *japonicus* | c | c | c | c | curved, smooth (nil) |
| ditto | *marginatus* | c | c | c | c | curved, smooth (nil) |
| ditto | *cygnus* | c | c | c | c | curved, smooth (nil) |
| ditto | *pascuensis* | c | c | c | c | curved, smooth (nil) |
| ditto | *brunneiflagellum*[*] | c | c | c | c | curved, smooth (nil) |
| *echinatus* | *echinatus* | two | one | c | c | curved, smooth (nil) |
| ditto | *penicillatus* | two | two | c | c | curved, smooth (nil) |
| stand-alone | *guttatus* | c | c | c | c | curved, smooth (nil) |
| stand-alone | *interruptus*[†] | "full" | "full" | "full" | c | straight, serrated (small) |
| **Second Major Lineage** | | | | | | |
| *regius* | *regius* | three | one | one | one | pointed, serrated (large) |
| ditto | *polyphagus* | one | one | one | c | pointed, serrated (large) |
| ditto | *laevicauda* | one | c | c | c | pointed, serrated (large) |
| *gracilis* | *gracilis* | two | one | c | c | pointed, serrated (small) |
| ditto | *inflatus* | one | one | c | c | pointed, serrated (large) |
| *homarus* | *h. homarus* | one | one | one | c | pointed, serrated (small) |
| ditto | *h. rubellus* | one | one | c | c | pointed, serrated (large) |
| ditto | *h. megasculpta* | two | one | c | c | pointed, serrated (large) |
| stand-alone | *stimpsoni* | one | one | c | c | pointed, serrated (large) |
| stand-alone | *ornatus* | one | one | one | one | pointed, serrated (small) |
| stand-alone | *versicolor* | one | one | c | c | pointed, serrated (small) |

[*] *P. brunneiflagellum* n.sp. Sekiguchi & George 2005 is the formal name of *P. "aka"* (George 1997).

[†] Decalcified area of *P. interruptus* extends across the mid-line ("full window") to cover the whole of each sternal segment.

**Fig. 5** Development of softened areas of female sternal segments (arrowed) in *Panulirus interruptus*, Laguna Ojo Liebre, Baja California. **A**, juvenile 65 mm carapace length (CL); **B**, immature 86 mm CL.; **C**, mature 137 mm CL.

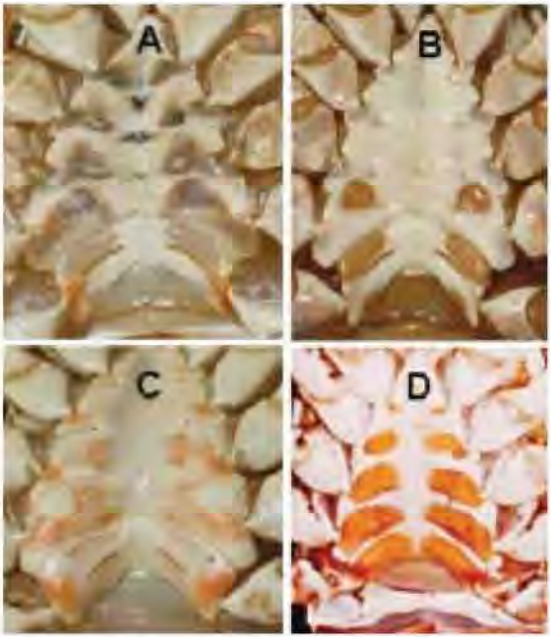

**Fig. 6** **A**, Adolescent; and **B**, mature female of *Panulirus homarus homarus*. **C**, Adolescent; and **D**, mature female of *Panulirus ornatus*. All specimens from south-west India.

female sternum and these were recorded as "fully calcified" in Table 1. However in some of these species, like *P. cygnus*, the future site of the tar spot appears to be marked by the loss of setae on the fifth and part of the fourth sternal segments, forming a distinct smooth, different coloured area (Fig. 4 ).

The condition of the female sternum in *P. interruptus* is unique. In juveniles all the sternal segments are hard but with maturity, the fifth, then fourth and finally the third segments progressively become decalcified "full windows" (Vega 2003; Armando Vega Velazquez pers. comm.; Table 1, Fig. 5).

Mature females for the other two-thirds of the *Panulirus* species possess multiple sets of rounded or oval decalcified areas and hard transverse ridges. At puberty, the first set of ridges and windows develops on the fifth thoracic segment and additional sets subsequently develop forward in sequence (Fig. 6A–B,C–D). In *P. regius* and *P. ornatus* the windows in the fully adult condition are present as far as the second segment (Fig. 6D). Two or three sets of windows can develop on each thoracic segment (Table 1).

## DISCUSSION

### Reproductive combinations

Comparison of the development of the female sternal structures and the shape of the penile process for the 27 taxa of *Panulirus*, suggests that three combinations can be recognised (Table 1). Combination 1 has the female sternum fully calcified (Fig. 4), without obvious soft areas and the male penile process has a curved smooth crest but without a hairbrush, e.g., *P. cygnus* (Fig. 3A). Combination 2 has the female sternum with one or more pairs of soft decalcified windows (Fig. 7) and the male penile process has the curved smooth crest without the hairbrush, e.g., *P. penicillatus*. Combination 3 has the female sternum with one or more soft decalcified windows (Fig. 6B,D) and the male penile process has a pointed serrated crest with a distinct hairbrush, e.g., *P. h. homarus* (Fig. 3D). Combination 1 is considered the basic plesiomorphic condition since the simple, uniformly hard surface of the female sternum and the simple gonopore crest is similar to that of all the other Stridentes genera which are considered to be less specialised than *Panulirus* (George & Main 1967; Baisre 1994; George 1997).

### Phylogeny and reproductive structures

Initially, George & Main (1967) recognised four groups of species in *Panulirus*. However, following the comparative analyses of Baisre (1994),

**Fig. 7** Mature female of *Panulirus penicillatus* from south-west India.

McWilliam (1995), George (1997), Ptacek et al. (2001), Patek & Oakley (2003), and George (unpubl. data), the recognition of only two major groupings, the "First and Second Lineages", are well supported.

In Table 1, the two major lineages are recognised and the order of the species in the list reflects the general order of evolution from the earliest to the most recent. With few exceptions, the three combinations of the reproductive structures echo the previous evolutionary pattern. Except for *P. argus* which has a small penile hairbrush, those species with Combination 1 are the earliest in the First Major Lineage and correlate with Group 1 of George & Main (1967). Those species with Combination 2 are later members of the First Major Lineage and correlate with Group 11 of George & Main (1967). All the species of the Second Major Lineage have Combination 3.

In her comparisons of larval and puerulus morphology, McWilliam (1995) found that several features of *P. interruptus* made it difficult to neatly place that species into the general order, causing her to classify the "stand-alone" *P. interruptus* as an "intermediate". Its reproductive structures shed no further light on its species affiliations. The softened full-windowed sternum of the female allies it to the species in Combination 2 or 3 but its unique, straight, serrated penile process with a small hairbrush approximates the most specialised condition in Combination 3. Its adult maxilliped exopod morphology (George & Main 1967) suggests relationships with the species in Combination 1.

The concept of "ontogeny follows phylogeny" seems to be supported during the development of the sexual copulatory structures of the more specialised species of *Panulirus*. In the males of *P. h. rubellus* for instance (Fig. 3), Heydorn (1969) describes the juvenile mating organs as "small knobs growing inwards from the position of the genital openings", a condition that is similar to the smooth curved condition in the fully mature species of the First Major Lineage. At full maturity, the penile process has developed the specialised features of the medial elongated, serrated protrusion with a large tuft of setae. In the females of the species with Combinations 2 and 3, the subadult condition of fully hardened sternum resembles that of the basic adult condition of the species in the First Major Lineage. With growth through to full maturity, the specialised soft decalcified areas develop increasing numbers of sets of windows from the fifth segment forward.

## Spermatophore deposition and fertilisation delay

It appears that some, and perhaps all, species of *Panulirus* have evolved a more specialised receptive site for spermatophore deposition than for other palinurid genera and the female has the option to delay the use of the longer lived spermatophore if her eggs are not ready to oviposit. For *P. cygnus*, one of the more basic species with Combination 1, spawning takes place 6–8 weeks after mating (Chittleborough 1976, fig. 2) and the deposition of the tar spot is confined to the posterior two sternal segments that can be demarked by the simple loss of setae and fine pitting (Fig. 4). Such a restriction of the spermatophoric mass to that posterior sternal area of the female resembles the situation for *Palinurus* where the paired, rounded spermatophoric masses of *P. gilchristi* are spread broadly over the fifth and part of the fourth segments and overflow onto the arthroidal membrane of the abdomen and the bases of the fifth leg (Berry 1969). Perhaps that somewhat haphazard deposition of a short-lived spermatophoric mass reflects the more primitive reproductive characteristics of the family.

For the other half of the species of *Panulirus*, the more specialised, decalcified windows and hard ridges that may be present as far forward as the second sternal segment of the female, provide a distinctive and a much larger prepared area for the allocation of the tar spot. These species have also developed more elaborate penile processes.

### What are the possible values of these reproductive variations in *Panulirus*?

It is surprising that most research workers have overlooked the variety of reproductive structures in *Panulirus*. Perhaps the morphological changes that develop as the sexes mature were considered as unsatisfactory taxonomic features for species recognition or perhaps the fact that most of the well-studied commercial species have very similar structures of a non-windowed sternum and smooth, curved penile process (Combination 1) did not prompt further investigation. Only a few of the species with soft windows caused the researchers such as Lindberg (1955), Berry (1970), and Chitty (1973) to note their presence and remark on their possible reproductive role. Lindberg (1955) for example, correlated the soft and fleshy nature of the posterior sternal segments of female *P. interruptus* with maturity status and suggested it was "an adaptation for the reception and retention of the sperm case".

Apart from the recent experimental studies by MacDiarmid & Butler (1999) that showed that male *P. argus argus* can control the size of the spermatophoric mass, little information is available to evaluate the reasons for the differences in reproductive morphology between species of *Panulirus*.

The evidence for four potential, though not mutually exclusive, hypotheses are summarised below.

#### *Species recognition*

*Panulirus* is the only genus that has developed prominent penile projections at the bases of the last pair of legs, and soft windows and hard ridges on the female sternum. The species in the First Major Lineage became isolated much earlier than those of the Second Major Lineage and most species have allopatric distributions living in the cooler, subtropical regions where there would be little requirement to reinforce genetic integrity by modification of the copulatory structures. Those species have retained the unspecialised copulatory structures of a curved, smooth penile process and a fully hardened female sternum.

With the proliferation of separate species in the Second Major Lineage that were evolving sympatrically into the newly formed ecological niches in the equatorial tropics (George 1974; George 1997), the genetic integrity of each taxon would have been enhanced by the development of any specialised copulatory structures that would avoid cross-fertilisation. Indeed the evolution of such structures may have helped initiate the genetic isolation of subpopulations. The only instances of cross-species fertilisation in these tropical *Panulirus* species are between geographically overlapping, closely-related taxa like the three subspecies of *P. homarus* (Berry 1974; Hadkirasouliha 1994) and the two subspecies of *P. longipes* (Juinio et al. 1991). George (1997) believed that such hybridisation supported the concept of the relatively recent separation of these taxa.

Recent genetic studies have revealed the presence of three regional subpopulations of *P. interruptus* along the Californian and Mexican coasts of the east Pacific. Each unit has separate seasonal reproductive peaks (Perez et al. 2001). Those discoveries suggest that these units may represent incipient taxa. Future investigations might reveal that the copulatory apparatus of one or both sexes may be different in each area, further reinforcing genetic and regional isolation.

#### *Spermatophore placement*

It may be surmised that as *Panulirus* speciated, larger areas of the female sternum became modified as receptive areas for the tar spot. Perhaps the male of the ancestral *Panulirus* (and maybe the early ancestors of the family) simply deposited a packet of spermatic material directly onto the posterior segments of the female sternum that lay directly below his reproductive openings. Perhaps the initial modification of the basic *Panulirus* ancestor, as represented by *P. cygnus*, was a different coloured and non-setose, pitted area that marks the female's receptive area on the last two sternal segments. The next step might be represented by *P. interruptus* that has the whole of the receptive area marked by a broad softening of the posterior segments.

The male of one of the most recently evolved species, *P. ornatus*, spreads a large spermatophoric mass over almost the entire sternum of large, fully mature females that develop four sets of softened windows to mark the prepared area. The area covered by the tar spot can exceed the sternal prepared area as was observed by Manambrakat Vijayakumaran (pers. comm.) for a female *P. h. homarus* (Fig. 8) that has three sets of windows in the adult condition. To cover the anterior sternal segments of the female, males are apparently able to move forward and shape the spermatophoric mass into a narrower spread during the copulatory embrace.

However, the presence of soft windows is not obligatory for successful breeding since female *P. ornatus* can produce viable broods and hatch phyllosomata before they develop any windows (Manambrakat Vijayakumaran pers. comm.). Presumably these females are early maturers and the sternal feature that marks the prepared area is the pair of rough ridges across the fifth segment (Fig. 6C).

The evolution of a pointed, serrated tip and the sensitive hairbrush on the penile process (Reproductive Combination 3) may have evolved to heighten the male's ability to monitor the size of the prepared area on the female sternum and apply the appropriate shape and amount of spermatic material.

### *Reproductive status of female*

The early signals that reflect the maturity status and the sexual readiness of a female spiny lobster are almost certainly received by the male through a combination of stimuli. For *Jasus*, these include the emission of a male pheromone in the urine that indicates its maturity and size to a female (Raethke et al. 2004). For *Palinurus*, the female alerts the male of her preparedness to mate by producing a mating call that changes as soon as contact is made (Hunter 1999). However, in *Panulirus*, the male detects the readiness of the female to mate by direct contact of her body with his antennules and legs, particularly the elongate third leg (Berry 1970).

If the penile process is as sensitive as Berry (1970) suggests, it is likely that a male would be able to confirm those early signals when he makes direct contact with her sternum. The male could then respond accordingly. A smooth sternum would indicate that mating is required, a spermatophore-covered sternum would indicate that a previous mating had taken place, whereas a setae-covered sternum would indicate that the female was immature and ejaculation was not required.

### *Signalling and assessing female size*

Male *Panulirus* can control the size (MacDiarmid & Butler 1999) as well as the position of the spermatophoric mass on the mature female sternum (Berry & Heydorn 1970). It is likely that the males are able to assess the female's size through a combination of stimuli, including close body contact during the embrace. Berry (1970) found no evidence for a pheromone in the female urine but found strong circumstantial evidence for a female sex attractant that was distributed over many parts of the body, and that physical contacts by antennules or dactyls of legs were necessary for positive recognition of the attractant. It is very plausible to envisage that during the courtship of the receptive female, the male's regular contact by brushing with his sensitive antennules and stroking with the dactyls of his legs made him very aware of her size. This pre-mating assessment of her size could prepare him for the emission of the appropriate amount of spermatic material required. That assessment could be confirmed when direct penile contact with her sternum was made at the time of copulation. That confirmation would be facilitated if the preferred site on her sternum was directly related to her egg production and was physically demarked. As females grow after puberty, the size of the prepared area increases. Perhaps the gradual increase in the size of the internal egg mass with age reflects a hormonal increase that in turn increases the size of the prepared area. Only those species with obvious decalcified areas can be said to have positive demarked areas. More investigation is required to positively identify if a valid prepared area is present on all species and if its size does reflect the brood size of the female.

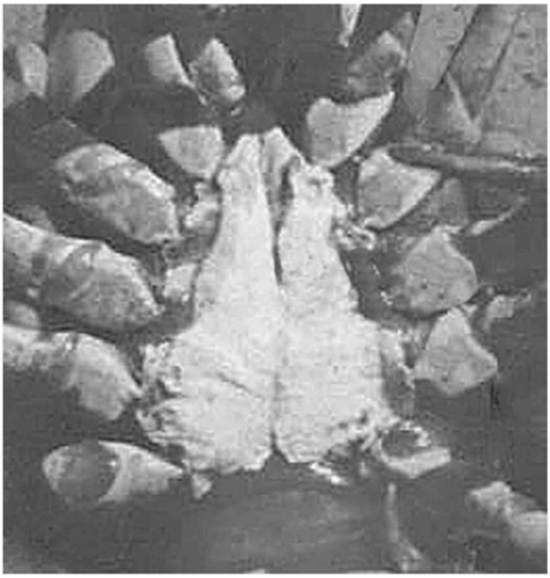

**Fig. 8** Female *Panulirus homarus homarus* from south-west India with exceptionally large tar spot covering whole of sternum.

## CONCLUSION

Unlike other palinurids, it does not appear that female *Panulirus* actively pursue the male, probably because her mating window is much longer and she can delay the use of the sperm until her eggs are fully ripe. In the evolution of *Panulirus*, the development of the longer-lasting spermatophoric mass and the delayed use of sperm by the female have required the development of specialised structures on the female sternum and the male reproductive organ. These structures may have helped initiate speciation in *Panulirus*.

Although the male may first assess the maturity and size of the female during courtship, this is probably confirmed or modified at copulation, when the male's penile processes touch the prepared sternal area of the female. Her overall size and the extent of the prepared area reflect her maturity status and potential brood size, and spermatophores from previous matings can also be detected. The male can then deposit a suitably-sized tar spot or not mate at all. Further research is required to establish whether, in all species of *Panulirus*, females develop prepared areas on the sternum at maturity.

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Review

# Evolution of life cycles, including migration, in spiny lobsters (Palinuridae)

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**Abstract** A comparison of the documented ecology and behaviour of the separate phases in the life cycles is presented. Data gathered during the review show that during the evolution of the family from deeper-water habitats to the more rapidly fluctuating shallower waters, there have been many biological adjustments at each phase in their life cycles. In the more ancient Stridentes genera, like *Puerulus*, the larvae are found well below the surface waters and the pueruli often settle at greater depths than those of the adults. Long incubation times, few larval instars, and year-round spawning are probably their life cycle characteristics. As an "intermediate-evolved" genus of Stridentes, *Palinurus* lives along the outer shelf, grows slowly, matures late, and breeds seasonally once a year. Incubation time is long, the larvae live at depth, the number of larval instars is limited, and the puerulus is a weak swimmer. Settlement is often downstream of the breeding stock. Incubation times are short for the more recently evolved Stridentes *Panulirus*, the larvae pass through many instars in the surface waters to c. 200 m. Some pueruli settle in special coastal habitats, others settle in the same habitat as the adult. Breeding in the cooler water First Major Lineage species is seasonal, one or two broods being produced. Most of the species in the tropical Second Major Lineage are faster growing, breed repetitively over a long breeding season, and have a shorter larval life. For the Silentes, the trend in biological changes from deep to shallower water is comparable with that of Stridentes. Incubation is probably long in the more ancient *Projasus*, the larvae are rare in surface waters and the pueruli settle at depths similar to those of the adults. *Sagmariasus* and *Jasus* breed once during a defined season, incubation time is moderate, and the larvae pass through many instars. The pueruli of *Sagmariasus* settle downstream and exhibit contranatant migration whereas the pueruli of *Jasus* swim strongly to their shallow habitats. In each life cycle phase, migration methods range from vertical paddling in phyllosomata, horizontal swimming in pueruli, and horizontal walking when juveniles move to adult habitats. Adult movements are associated with foraging, searching for shelter, avoiding adverse seasonal conditions, or walking to preferred offshore locations for moulting and reproduction.

**Keywords** evolution; spiny lobsters; Palinuridae; life cycles; migration strategies

## INTRODUCTION

Past tectonic movements, energetic intensification of oceanic and coastal systems, as well as general climate changes have combined to create a multitude of new shallow-water habitats by altering surface water temperatures and enhancing current systems (George 1997). These environmental constraints continually force new biological modifications that are necessary for the successful invasion of these more variable shallow-water environments by the more recently evolved spiny lobsters and ... "life history strategies have evolved in response to this variability, enabling species to avoid extinction during sets of particularly adverse environmental conditions" (Pollock 1995).

The dramatic habitat shift from the cool, dark, calm, deep waters to the warmer, more turbulent, well lit coastal waters by the recent genera (George & Main 1967) have necessitated a whole range of adjustments to these new levels of salinity, turbidity,

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temperatures, currents, and turbulence (wave action) (Pollock 1995), as well as light intensity, surge, and swell action. This paper extends the evolutionary study on three palinurid genera by Pollock (1995) and examines additional lifestyle changes throughout the family in morphology, reproductive characteristics, and migratory behaviour.

## CLIMATE AND EVOLUTIONARY CHANGE

The inhabitants of the broad Tethys Sea would have been subjected to a Mesozoic climate of relatively mild wind systems, generally warm seas, and a gentle oceanic circulation system (Kennett 1982); in both the Stridentes and Silentes, the ancestral habitat of the Palinuridae is considered to be in the more stable, deeper water where, except for *Palinurellus*, the more primitive genera live today (George & Main 1967).

However, opposite views have been expressed by Feldmann & Tshudy (1989) who suggested that *Linuparus* arose in the shallow waters of Antarctica, radiating into deeper water, low latitude habitats, and by Davie (1990) who believed that George & Main's (1967) view may have been too simplistic. Davie (1990) suggested that the shallow water, primitive *Palinurellus* has survived by living in deep dark caves and thus avoiding the competition or predatory pressures which caused members of other genera to retreat into deeper water. Perhaps these opinions are also simplistic since they imply that there were no deeper-water competitors or predators and the "harassed" shallow-water fauna simply marched down into vacant deeper-water habitats unhindered, modifying their biological attributes as they went. It seems more likely that the relatively stable environmental conditions in the deeper waters supported biologically stable, ancestral stocks from which several series of experimental radiations have, over time, temporarily colonised the shallow-water environment.

Throughout geological time, this shallow zone has undergone more rapid changes in currents, temperature, sediment, salinity, wave action, and oxygen levels, all of which have been influential in determining the characteristics of the shallow and geologically-speaking, more recently evolved spiny lobster species. One would expect the shallow regions where primitive relict species abound, such as the Caribbean region, to have had a history of relative environmental stability. *Palinurellus* and *Panulirus argus* could be good examples of spiny lobsters with long survival records.

## EVOLUTION AND MORPHOLOGY IN PALINURIDAE

Within the Stridentes, morphological changes in the adult, in response to the evolution into high energy rocky shelters (*Panulirus*), include the adoption of a well-calcified, cylindrical exoskeleton, strong legs, and elevated eyes that are protected by large, erect, forwardly-curved supraorbital horns. *Palinurus* lives at deeper depths (70–400 m) and is regarded as a part-way genus in the evolutionary pattern (Baisre 1994). The eyes are laterally disposed and protected by large obliquely-elevated supraorbital horns, the legs are moderately strong, and the carapace is cylindrical. The ancestral-like genera that live on soft bottom at depth (*Linuparus*, *Puerulus*, and *Palinustus*) have poorly calcified, subcylindrical bodies, weak legs, and eyes sunken beneath low, flattened supraorbital horns (George & Main 1967). The rare, deepwater *Palibythus* has a cylindrical body, weak legs, and small eyes sunken beneath the rostral plate and is considered by Davie (1990) as an early Stridentes offshoot from a pemphicid ancestor.

The elongated eyestalks of larvae of some of the shallower water genera are considered a more recent specialisation (Baisre 1994) and this may be part of an adaptive response to levels of low light intensity, thus facilitating control by the larvae to retain a desired position in the upper water layers.

Phylogenetic morphological changes are also apparent for the larval stages in the two major lineages of *Panulirus* that have been recognised by Baisre (1994), McWilliam (1995), Ptacek et al. (2001), and Patek & Oakley (2003). The larvae of the deeper-water, more ancestral First Major Lineage, listed in Table 1, have less spinose pereopods (fewer ventral coxal, subexopodal, sternal, and dorsal coxal spines), have a shorter tapered apex to the antenna and a narrow cephalic shield compared with those of the shallower, more specialised, Second Major Lineage (see Table 1) which have spinose larvae with long, spatulate-tipped antennae and wide cephalic shields (McWilliam 1995). For the puerulus stages, McWilliam also concluded that these lineages show a similar specialised trend from less to more spinose (e.g., posterior sternal spines), from short and tapered to long and spatulate antennae and from long to short exopods on both the second and third maxillipeds.

**Table 1** Comparative life cycle attributes of palinurid genera.

| Species | Age (years) hatching to maturity | Egg size index | Broods per year | Incubation period (months) | No. of instars | Larval period (months) | Puerulus period (days) |
|---|---|---|---|---|---|---|---|
| **STRIDENTES** | | | | | | | |
| ***Palinurus*** | | | | | | | |
| *P. elephas* | | | 1(22) | 5–9(11) | 10(22) | 5–12(22)<br>4–5(30) | 11–15(1)$^{*}$ |
| *P. delagoae* | c. 8(39) | 200(37) | 1(11) | 5–6(11) | | 5–6(11) | |
| *P. gilchristi* | c. 8(39) | 200(37) | 1–2(38) | | | | |
| ***Panulirus***—First Major Lineage | | | | | | | |
| *P. a. argus* | | 800(3) | 1–2(5) | 1(27) | | 6–8(25) | 5–10(6) |
| *P. a. westoni* | | | 2(19) | 4(19) | | | |
| *P. interruptus* | 3–6(14) | 400(3) | 1(14) | | | 7.75(1) | 75(9) |
| *P. japonicus* | >3(16) | | 2(16) | 1–2(27) | 29(30) | 9–10(24)<br>12(26)<br>8–13(24)$^{*}$ | >8(1)<br>12–15(1)$^{*}$ |
| *P. marginatus* | | | 2(17) | | | 6–11(1) | |
| *P. cygnus* | 6–7(29) | 400(3) | 1–2(13) | 0.5–2(27) | 15(1) | 9–11(1) | 15(1) |
| *P. l. bispinosus* | | | 1(15) | 2–3(15) | | 9(26) | |
| *P. penicillatus* | 3(32) | | 3–4(5) | 1(27) | | >7–8(1) | |
| *P. guttatus* | | 330(10) | >2(18) | | | | |
| ***Panulirus***—Second Major Lineage | | | | | | | |
| *P. polyphagus* | 3(34) | | 2–5(34) | 2–3(33) | | | >2–4(1) |
| *P. laevicauda* | | | 2(19) | 4(19) | | | |
| *P. gracilis* | c. 2(14) | | 3–4(5) | 1(14) | | 7(14) | |
| *P. inflatus* | c. 2(14) | | 3–4(5) | 1(14) | >25(6) | 7(14) | |
| *P. h. homarus* | <3(35) | 620(35) | 2–4(35) | c.1(36) | 18–19(35) | 4–6 (35)$^{*}$ | |
| *P. h. rubellus* | <3(40) | 800(3) | 1–4(40) | 1–2(40) | | 4–6(7) | |
| *P. ornatus* | 2+(20) | 720(35) | 3(20) | c.1(35) | 18–19(35) | 4–7(21) | |
| *P. versicolor* | | 740(35) | | | 8–19(35) | 4–6(35) | |
| **SILENTES** | | | | | | | |
| ***Sagmariasus*** | | | | | | | |
| *S. verreauxi* | 6–7(29) | 500(3) | 1(12) | 3(4) | 17(4) | 8–12(1) | 25(30)<br>20(1)$^{*}$ |
| ***Jasus*** | | | | | | | |
| *J. lalandii* | 5–6(31) | 500(3) | 1(5) | 4–6(5) | 17(31) | 9–10(1)<br>14–18(8)<br>10(30)$^{*}$ | >31(1)$^{*}$ |
| *J. novaehollandiae* | 3.5–5(29) | 400(3) | 1(5) | 4–6(5) | | 8–22(29) | |
| *J. edwardsii* | 5–11(28) | 300(3) | 1(5) | 4–6(5) | 15–17(30) | 12–22(28)<br>7–9(30)$^{*}$ | >70(2)<br>19(1)$^{*}$ |
| *J. frontalis* | | 400(3) | 1(5) | 4–6(5) | | | |
| *J. tristani* | | 300(2) | 1(5) | 3–4(8) | | | |

$^{*}$Denotes laboratory conditions.

References: (1) Booth & Phillips 1994; (2) Pollock & Goosen 1991; (3) Pollock 1995; (4) Kittaka et al. 1997; (5) Quackenbush 1994; (6) Phillips & Sastry 1980; (7) Berry 1974; (8) Roscoe 1979; (9) Serfling & Ford 1975; (10) Pollock 1997; (11) Berry 1973; (12) Booth 1986; (13) Chubb 2000; (14) Briones & Lozano 2000; (15) Gomez et al. 1994; (16) Minagawa 1997; (17) Polovina et al. 1995; (18) Losado-Tosteson et al. 2001; (19) Soares & Calvacante 1985; (20) Skewes et al. 1997; (21) Dennis et al. 2001; (22) Hunter 1999; (23) Pollock & Augustyn 1982; (24 ) Baisre 1994; (25) Silberman et al. 1994; (26) Inoue & Sekiguchi 2001; (27) MacDiarmid & Kittaka 2000; (28) Booth 2000; (29) Phillips et al 2000; (30) Kittaka 2000; (31) Pollock 1986; (32) Plaut 1993; (33) Kagwade 1988a; (34) Kagwade 1988b; (35) Vijayakumaran pers. comm.; (36) Vijayakumaran 1990; (37) Pollock & Melville-Smith 1993; (38) Groeneveld & Rossouw 1995; (39) Groeneveld 2000; (40) Berry 1971.

Within the Silentes, from *Projasus* through *Sagmariasus* to *Jasus*, morphological changes that parallel those in the Stridentes accompany the evolutionary trend from deeper, calmer waters to shallower, more turbulent waters. The deep-water *Projasus* (175–880 m, Webber & Booth 1988; Baez & Ruiz 2000) is similar to the Stridentes *Puerulus* in having a poorly calcified, spinose ridged, subcylindrical carapace, weak legs, and eyes sunken below flattened supraorbital horns. The shallower-water *Sagmariasus* and *Jasus* have strongly calcified, evenly spinose cylindrical carapaces, strong legs, and moderately elevated eyes protected by moderately elevated supraorbital horns, somewhat similar to *Panulirus* (George & Main (1967). Following phylogenetic reviews of *Palinurellus* by Davie (1990) and Patek & Oakley (2003), *Palinurellus* is included here in the Silentes. The enigmatic *Palinurellus* is considered to represent the palinurid plesiomorphic condition for both the adult and larval characteristics but it lives in a shallow, perhaps relict, habitat (Davie 1990; Baisre 1994). It has a rounded carapace, small eyes, a broad rostrum, the forerunner of a stridulating organ, and moderately sturdy legs. Unfortunately, little is known of its life cycle characteristics.

## SPERMATOPHORIC MASS

Berry & Heydorn (1970) discussed the selective forces that shaped the evolution of the spermatophoric mass. The most specialised condition is found in the most recently evolved Stridentes genus *Panulirus* where the ribbons of spermatophores are surrounded by a putty-like, granular mass that hardens in sea water and can be retained for minutes (10 min for *Panulirus japonicus*) or months (up to 69 days for *Panulirus cygnus*, MacDiarmid & Kittaka 2000) before the surface layers of the protective matrix are scraped away by the female when she chooses to fertilise her ripe eggs. For the more primitive Stridentes genera *Puerulus*, *Linuparus*, and *Palinurus*, the mass is gelatinous, does not disintegrate in sea water, and the female makes deep single scratches in the surface to release spermatozoa within a matter of days after deposition (Berry & Heydorn 1970). Berry & Heydorn concluded that the hardened spermatophoric mass of *Panulirus* is not a prerequisite for its invasion of shallow water but rather a strategy to control or prolong the interval between mating and oviposition. In the shallow waters, the ability of the female to respond to seasonal and annual fluctuations in the environment and thus control the timing of egg-laying and subsequent larval release is a substantial advantage in enhancing the success of a species.

For the Silentes *Jasus*, the gelatinous spermatophoric mass contains a simple thread of spermatozoa that disintegrates in sea water and thus shows an unspecialised level of development that has changed little in the relatively stable environment of the southern temperate zone. Berry & Heydorn (1970) concluded that the spermatozoa are released immediately and are used to fertilise the ripe ova as they are exuded. This conclusion that egg laying immediately follows copulation is further supported by the experiments of MacDiarmid (1988).

## LIFE CYCLE OF STRIDENTES

For the Stridentes, if we use what little natural history information we have on the deep water and primitive *Puerulus* and *Linuparus* as a guide, the ancestral genera probably lived in deep, dark basins where water temperatures were cooler than near the surface and stratification was less intense than today (Kennett 1982). The gelatinous spermatophoric mass remains intact for a few days (Berry & Heydorn 1970) and year-round spawning with prolonged incubation were likely in the constant conditions at those depths.

It is conjectured that the larvae of the deep-water genera circulated at depth since their larvae and pueruli are very rare in epipelagic (<200 m) plankton collections. For the pueruli of the deeper-water genera, Kanciruk (1980) states "The puerulus stages of deep water species such as *Palinurus delagoae* (180–400 m), *Puerulus angulatus* (300 m), and *Linuparus* spp. (300 m) are not reported in shallow inshore areas. Presumably, they settle out at the greater depths characteristic of the adults". This concept of settlement of pueruli over wide distances is supported by the further observations of Berry (1974) and Chan (1997) who recorded pueruli of deep-water genera well outside their adult grounds. To recruit successfully, the juveniles must have the capability to migrate in the right direction to the adult grounds or they would be lost to the next generation.

The genus *Palinurus* is considered to have emerged "part-way" along the evolutionary line of the Stridentes (Forster 1973; Baisre 1994). On the basis of its biological attributes, the following scenario can be proposed. The adults grow slowly, are long-lived (>20 years), mature late (Table 1), and aggregate once a year for seasonal mating (Pollock & Augustyn 1982; Hunter 1999; Groeneveld 2000; Pollock et al. 2000). When the oocytes are fully mature, the females attract the males via a mating call (Hunter 1999) and they receive a short-lived spermatophoric mass (Berry & Heydorn 1970) that almost immediately releases sperm for fertilisation of the ripe eggs (Hunter 1999).

The egg size given in Table 1 is an inverse index of egg size calculated by dividing the number of eggs in the brood by the body weight in grams over a wide range of body sizes (Pollock 1995). These calculations assume a constant weight and a constant size of an egg throughout development but Silberbauer (1971) and Pollock & Augustyn (1982) showed that egg diameter does increase with development for *Jasus lalandii* and *Palinurus gilchristi* respectively and Vijayakumaran (1990) found that the average egg of *Panulirus h. homarus* was c. 35% lighter and 20% smaller in the early stage of incubation than in the late stage. In spite of these possible variations, the egg indices given for the genera in Table 1; 200 for *Palinurus*, 300–500 for *Sagmariasus*/*Jasus* and, except for *Panulirus guttatus*, 400–800 for *Panulirus*, show very significant differences. Species of *Palinurus* produce a relatively low number of large eggs (Pollock & Melville-Smith 1993; MacDiarmid & Kittaka 2000) and incubate the eggs on the pleopods for a long period of 5–9 months (Hunter 1999). The newly hatched phyllosoma are relatively large, have well-formed, multi-spinose appendages and pass rapidly through only 10 instars to the relatively small final stage (Berry 1974; Baisre 1994; Kittaka 2000). Larvae probably inhabit mesopelagic depths (200–1000 m) in totally dark or extremely low light levels for 5–12 months (Berry 1974; Hunter 1999). The heavy, weak-swimming puerulus (Hunter 1999) is little more than a convenient morphological intermediate "transfer" phase from the last pelagic larval stage to their seabed settlement site (Pollock & Melville-Smith 1993) at depths similar to or deeper than that of the adults.

The most recent Stridentes genus, *Panulirus*, lives in the well-lit subtropical and tropical shelf waters in habitats that have been subjected to major environmental changes by tectonic plate movements over the past 20–30 million years. Two major lineages have been recognised (Ptacek et al. 2001). The biological attributes of the cool subtropical zone species (most species of the First Major Lineage) reflect an initial movement by the more primitive species into the seasonally changing shallow environments. They have slower growing (>3–7 years to maturity, see Table 1) long-lived adults and mate seasonally but the spermatophoric mass can be long lasting because of its insoluble outer coating. Females produce one or two batches of eggs each season (Booth 1986; Gomez et al. 1994; Quackenbush 1994). The eggs are smaller than *Palinurus* (Pollock 1995), incubation time is short (1–4 months) (Soares & Calvacante 1985; Gomez et al. 1994; MacDiarmid & Kittaka 2000) and the small sized, first stage larvae pass through many (15–27) instars (Booth & Phillips 1994; Kittaka 2000) over a relatively long time of 6–12 months (Baisre 1994; Booth & Phillips 1994; Inoue & Sekiguchi 2001) to reach the relatively large final stage (Baisre 1994; Table 1). Early stage phyllosomata rise to the epipelagic waters of the shelf even though they are relatively weak swimmers. The mid stages are stronger vertical swimmers and are carried by the prevailing currents into the offshore oceanic waters. The late stages are more abundant closer to the coast and accumulate near the shelf break (Phillips & Sastry 1980). After metamorphosis, the fast-swimming pueruli cross the shelf (Phillips & McWilliam 1986) to settle in their particular habitat which is shallower than that of the adult.

The Second Major Lineage represents a further radiation of *Panulirus* into a variety of shallow habitats in the tropical zone and the much warmer conditions have resulted in faster-growing (c. 3 years to maturity), shorter-lived, multiple-spawning species (2–>4) (Berry 1971; Soares & Calvacante 1985; Skewes et al. 1997: M. Vijayakumaran pers. comm.) with a shortened larval life of 4–7 months (Baisre 1994; Booth & Phillips 1994; McWilliam 1995; Dennis et al. 2001; Table 1).

## LIFE CYCLE OF SILENTES

For the early genera of Silentes, the biological data is even more scanty (Berry 1974; Webber & Booth 1988; Baez & Ruiz 2000) than for the early Stridentes. The general biology of *Palinurellus* is unknown but the following scenario for *Projasus* is proposed.

*Projasus* occurs in all the major oceans at depths of 175–880 m (Baez & Ruiz 2000) on ridges, seamounts, oceanic volcanic islands, and continental slopes (Parin et al. 1997). *Projasus* is considered to be very close to the ancestral Silentes stock that probably originated in the deep, calm waters of the southern Tethys Sea, perhaps in the southern Indo-Pacific region off the northern coast of Gondwana.

The oceanic circulation was weak (Kennett 1982), spawning was probably year-round or very prolonged, the larvae probably lived at depth, and the pueruli probably settled at depth somewhere near the adults, as they do today (Webber & Booth 1988; Baez & Ruiz 2000). Subsequent intensification of ocean current systems has resulted in two widely distributed species. *Projasus bahamondei* inhabits the south-east Pacific, off Chile and *Projasus parkeri* is widespread from the south-east Atlantic, through the Indian Ocean to south-east Australia and New Zealand (Parin et al. 1997). Based on records in the Western Australian Museum, *P. Parkeri* also occurs off south-west Australia from C. Naturaliste (500 m), through C. Riche (400 m) to Esperance (540 m) (D. Jones pers. comm.). Parin et al. proposed that *P. bahamondei* dispersed eastwards across a major Pacific Ocean barrier from its *P. parkeri* ancestor. Just what evolutionary changes in the life cycle morphology and behaviour of these widely distributed *Projasus* populations occurred, as a result of the intensification of the currents must await further discoveries.

The monotypic *Sagmariasus* has been elevated from a subgenus of *Jasus* to a full genus by Booth et al. (2002) and it is considered to be more primitive (Baisre 1994) and more fecund (Pollock 1997) than *Jasus*. It is the largest lobster in the family, also maturing at a large size and producing many small eggs "as strategies to boost egg production" (Pollock 1997). It may have lived in the subtropical region of the south-west Pacific in late Eocene and certainly in the Oligocene, as *Sagmariasus flemingi* (Glaessner 1969; George 1997). Each of the present two subpopulations of *Sagmariasus verreauxii* that live along the Australian and New Zealand east coasts have retained similar life histories despite their probable separation 10 million years ago (George 1997).

Seasonal regularity in both regions triggers a once-a-year spawning by females (Booth 1986) after a spring moulting and mating. Since the spermatophoric mass is probably short-lived, eggs are extruded synchronously and the sperm are used for almost immediate fertilisation. The small eggs (Pollock 1997) are incubated for 3 months in deeper water and the small larvae (Baisre 1994; Kittaka et al. 1997) hatch in summer with well-formed appendages except that the third maxilliped lacks an exopod until the final stages and an exopod bud does not develop on the fifth leg until the 4th instar of the 17 instar progression (McWilliam & Phillips 1987; Kittaka et al. 1997). During their 8–12 month pelagic life, the larvae may exhibit vertical migration to control their direction of transport and are largely retained in the offshore eddies and gyres (Booth 1986). The pueruli swim strongly towards the coast, grasping onto seaweed as they settle along the coast well south of their natal region (Montgomery & Kittaka 1994). Because of this southern displacement, the subadults have evolved regular along-shore migrations up to 1700 km to recruit to the northern adult breeding grounds (Booth 1986). The very high fecundity probably evolved to counteract the high mortality loss of pueruli recruits since they have been carried far to the south of their optimal habitat, added to which are the predator risks associated with the long counter-current migrations to the adult grounds (Pollock 1997).

For *Jasus*, most is known about the *J. lalandii* clade. Males deposit a short-lived spermatophoric mass and the females immediately extrude the ripe eggs (MacDiarmid & Kittaka 2000). The females carry only one brood of small-sized eggs annually and after incubation for 3–6 months (Quackenbush 1994; Kittaka et al. 1997), the larvae begin a 9–22 month pelagic period (Roscoe 1979; Booth & Phillips 1994).

The behavioural attributes of the larvae of the continental species (*J. lalandii* clade) enable them to be retained in current systems that eventually concentrate the surviving late stages near the continental shelf break. For the South African *J. lalandii* and the New Zealand subpopulation of *Jasus edwardsii* (Booth 2000), larvae undergo stage-specific vertical migrations to c. 300 m depth but around Tasmania, Bruce et al. (1996) found "little evidence of a complicated, stage specific, pattern of vertical distribution. Larvae were primarily confined to the upper 100 m and were commonly at the surface, particularly at night.". If this apparent lack of specific vertical movement by Tasmanian larvae is proven, it would support a conclusion that there are specific differences in each of the Australasian transport systems which assisted in the behavioural separation of the two subpopulations through larval evolution. The pueruli of both these continental species swim rapidly across the shelf to settle in shallow water (Booth 2001) and as subadults, they move to deeper water to join the adult stock. Counter-current movements by subadults of *Jasus* are limited and has only been demonstrated for *J. edwardsii* in the southern portion of its New Zealand range, where a small proportion migrate westwards around the Southland coast (Booth 1997).

Such limited movements by larvae and subadults may answer the question of how the southern

Australian subpopulation that stretches from Tasmania westwards across the Great Australian Bight to Cape Leeuwin is maintained. Perhaps the larvae are truly passive in the upper 100 m and simply rely on "random transport" and perhaps the pathways of the relatively weak currents (Bruce et al. 1996) are exceptionally reliable. This concept of reliable return near the point of origin might well be tenable if the complex tracks of the satellite-tracked drifters that remained within 500 km of the Tasmanian coast for 11–19 months, often returning to the point of release (Bruce et al. 1996), truly reflect the prime method of transport of the apparently passive larvae. Perhaps the larvae and pueruli in Tasmanian waters only need to respond weakly to the narrow temperature/salinity characteristics which clearly define the movements of the Subtropic Front (Bruce et al. 1996, fig. 34, 37–39) to effect their desired recruitment pathways via that water body.

For the species in the insular *Jasus frontalis* clade, egg size, incubation time and length of larval life are similar to the *J. lalandii* clade (Table 1) but little is known about their larval transport mechanisms. Their larval behaviour is more likely to be similar to that of the Australian subpopulation of *J. edwardsii* than to the other members of the *J. lalandii* clade since the local currents encompass isolated islands and/or seamounts and there are no wide continental shelves for the pueruli to swim across. The larvae and pueruli are probably passive and rely more on the strong island eddies and the seamount Taylor Columns for their local retention (George 1997).

## EVOLUTION OF MIGRATION

Advantageous movements by palinurids pervade every phase in the life cycle and most movements are associated with the functions of feeding, sheltering, and reproduction. Herrnkind (1980) and Booth (1997) have given terms to the considerable variation in the benthic movement patterns by subadults and adults across the sea floor that may be associated with differing ecological and physiographic conditions. Here I expand their definitions and also consider the quite different transport methods that are used by the phyllosomata and pueruli during their pelagic and natant phases. An evolutionary approach is taken to assist in the evaluation of the importance of migrations at all phases in the life cycle during the evolutionary shifts into the various shallower water habitats, particularly by *Panulirus*, *Sagmariasus*, and *Jasus*.

### Migratory behaviour and adaptive movements

Light intensity appears to be extremely important in controlling the timing and direction of the various movements of palinurids (such as paddling, swimming, or walking) at each phase of their life. Many larvae respond to weak light values and migrate vertically as they paddle up and sink down diurnally; many pueruli swim horizontally near the surface and the benthic juveniles and adults walk along the bottom. The benthic phases mainly wander at night (nomadism) to forage for food or to seek new individual shelters as their life style changes with growth, particularly in the puerulus and early juvenile phases (Norman et al. 1994). Adults sometimes move seasonally for moulting and reproductive purposes or episodically to avoid short-term, adverse environmental conditions; they then return accurately to their original area (homing), often to the same den (Herrnkind 1980). Shelters of spiny lobsters usually consist of natural caves and crevices in firm, mostly rocky, substrates in contrast to the true lobsters that deliberately construct dens in soft substrates (Cooper & Unzmann 1980). Subadults of spiny lobsters may exhibit permanent, one-way movements (either onshore or offshore) from their settlement sites to the adult breeding areas, or longshore migrations against the current that had displaced their larvae downstream (contranatant migration).

Very little is known about the cues for directional migration by spiny lobsters or indeed many invertebrates. However, for *Panulirus a. argus*, after geomagnetic manipulation and experimental displacement up to 30 km, juveniles "are capable of true navigation without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey" (Boles & Lohmann 2003). Boles & Lohmann concluded that the lobsters possess a magnetic map that allows them to "somehow derive sufficient positional information from the Earth's magnetic field to determine the direction towards home". How these displaced *P. a. argus* juveniles could acquire a geomagnetic map of an area they have only experienced as a first stage larvae remains a mystery. Biogenic magnetite has been suggested as a possible magnetoreceptor but the mechanism(s) remain mainly hypothetical (Alerstam 2003).

The following summary deals initially with some of the adaptive advantages of the various types of movements in the habitat shift to shallow water, first presenting the life style of the shallow water coastal and shelf genera (*Panulirus*, *Sagmariasus*, and *Jasus*) and then the life style characteristics of the more ancestral outer shelf and deeper water genera.

## Shallow-water genera

### *Phyllosoma phase*

Like many other planktonic taxa, the larvae of spiny lobsters can move vertically in the water column and attain horizontal transport advantages by utilising the onshore and offshore currents and gyres that operate at those selected depths during their larval life. The directional offshore movement resulting from the behaviour of the early larvae is rapid and is gradually replaced by "circular retention" at deeper levels, in large eddies, mesoscale gyres, or oceanic currents. During the lengthy larval period of many months, each larval stage maintains a particular seasonal position within the dominant offshore current system, feeding on relatively soft-bodied zooplankters, such as fish larvae, cnidarians, salps, chaetognaths, and euphausids (McWilliam & Phillips 1997) from which soft foods can be sucked by a pumping action (MacMillan et al. 1997).

The availability of these food types also varies seasonally and spatially within each current system and Cox & Johnston (2004) have described some of the digestive changes in the foregut that accompany larval growth. Cox & Johnston (2004) showed that the early larval stages of *S. verreauxi* possess simple digestive structures that are only equipped to deal with softer prey items like fish larvae and gelatinous zooplankton. However, the late larval stages develop a more complex filtering, sorting and mixing capacity that extends the range of diet to fleshier prey items like crustaceans. In their study of energy levels of phyllosoma and puerulus, McWilliam & Phillips (1997) concluded that, "For the late larval development and successful metamorphosis of *Panulirus cygnus*, the richest food resources seem to be located in the slope waters adjoining the shelf-break and the higher zooplankton and micronekton biomass found in this region may be related to the presence and strength of the Leeuwin Current.".

### *Puerulus phase*

The immediate post-larval pueruli can be strong horizontal swimmers, deliberately and directionally crossing the shelf. Some species settle very close to the adult grounds even though that may be on seamounts at 30 m depth (*Panulirus marginatus*, Polovina et al. 1995) or 45 m (*Jasus tristani*, Heydorn 1969). Those species live on steep volcanic islands or banks and show limited movements thereafter because of depth limitations between suitable habitats, but other species like *P. cygnus* and *P. a. argus* settle in special shallow water habitats, and migrate offshore to the adult grounds. The successful survival of the non-feeding puerulus depends not only on its accumulated food reserves and its swimming prowess but also its ability to detect and settle in an area that provides individual protection, such as natural crevices or small-sized close-fitting holes that are often left in the solid substrate by dead borers such as pholad molluscs (Yoshimura & Yamakawa 1988; Jernakoff 1990; Norman et al. 1994). Booth (2001) concluded that "puerulus settlement of *Jasus edwardsii* is a process of active searching and habitat choice, at the small scale".

### *Juvenile phase*

Short-distance movements of the fast-growing early post-puerulus are usually foraging forays in search of small food items such as tiny molluscs, worms, crustaceans, and epiphytes such as coralline algae. Following each moult and growth increment, the progressively larger juveniles must also search for and find larger, suitably-sized close-fitting holes or crevices for protection during these nomadic forays. Their survival also depends on the suitability of the environment to provide a range of shelter sizes as well as adequate food size, food quality and quantity. As the juveniles grow, they require larger-sized food items and must migrate to nearby suitable environmental grounds, eventually aggregating as two-year-olds (Kanciruk 1980) in large community dens. These deliberate movements are irreversible and have evolved to accommodate these dramatic changes in their requirements for particular feeding resources, physical habitats, and social characteristics.

### *Subadult phase*

Most shallow water species emigrate from the juvenile habitat at or slightly before maturity (Kanciruk 1980). Only those individuals that deliberately march to the recognised breeding grounds can contribute genetically to the future cohorts of recruits. After an inshore moult, the adolescent "white" phase of *P. cygnus* migrates offshore and to the north-west, to join the adult stock. It is likely that such directional movements by the subadults also help to build up the reproductive stock in the northern regions and thus counteract the net southward transport of larvae (George 1958; Griffin et al. 2001).

If the local current systems consistently carry late stage larvae and pueruli beyond their natal grounds, subadults are naturally selected for their ability to emigrate and join the adult stock. Subadult *S. verreauxi* in both Australia and New Zealand migrate long distances to the north to reposition a recruitment stock upstream of the dominant south-flowing coastal currents which have carried the larvae far to the south of the acknowledged breeding grounds (Booth 1997; Phillips et al. 2000). Only small proportions of immature *J. edwardsii* migrate against the current, mainly in the Southland region (Booth 1997).

Sporadic adverse events associated with depleted oxygen levels along the south-west coast of South Africa force inshore movements of subadult *J. lalandii*, particularly of small females, and can result in devastating mass strandings (Cockcroft 2001).

### *Adult phase*

Once the individuals have reached adulthood, migrations are quite short in distance and time (homing activities) and are associated with moulting in a more protected area, food gathering during nocturnal foraging, or finding a more environmentally comfortable position in another location when external conditions, such as winter storms and summer high temperatures (e.g., *P. a. argus* Herrnkind 1980) or oxygen depletion (e.g., *J. lalandii* Newman & Pollock 1974) force temporary emigration. The timing and extent of these migrations vary in each species and have been evolved in response to the particular characteristics of, and the seasonal changes in, the suite of environmental parameters that have controlled, and now determine its special habitat requirements.

## Deeper-water genera

In some of the outer shelf and slope genera (*Puerulus* and *Palinurus*), their pueruli appear to settle downstream and/or in deeper water, i.e., well outside the preferred range of the adults (e.g., *Puerulus*, Berry 1974; Chan 1997) and the evolution of deliberate subsequent migrations by subadults to the adult grounds must be an obvious selective advantage. Compensatory migrations by subadults from deep to shallower water, as well as alongshore against the prevailing current, to the adult breeding grounds have also been evolved in *Palinurus gilchristi* and *P. delagoae* (Groeneveld 2002; Groeneveld & Branch 2002). In *Palinurus*, short-term offshore-onshore homing movements also facilitate successful individual participation in reproduction, particularly in the processes of mating, incubation, and larval release (e.g., *P. elephas*, Hunter 1999 and *P. delagoae* Cockroft et al. 1995; Groeneveld 2002).

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# Allozyme variation in European lobster (*Homarus gammarus*) throughout its distribution range

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**Abstract** The European lobster, *Homarus gammarus*, is a high value species, which is widely distributed from the northern part of Norway to Morocco in North Africa. It is also found throughout the Mediterranean including the Aegean Sea. Knowledge of the genetic structure is necessary for rational management of exploited species. As part of a comprehensive genetic investigation of European lobster (EU-project "Genetics of European Lobster"), 1514 lobsters from 14 locations were analysed for six polymorphic allozyme loci. Despite generally low levels of genetic differentiation (overall $F_{ST} = 0.016$), the tests for population differentiation revealed highly significant values for all loci investigated. In particular, the lobsters from three areas including northern Norway, the Netherlands, and Aegean Sea in the Mediterranean were genetically different from lobsters from other regions. Lobsters from northern Norway have 30% of the genetic diversity observed in the samples from other areas, and polymorphism was only detected at the *IDHP-1** locus. A new slow-moving allele at the *GPI-1** locus was found in the samples from the Aegean Sea. Pairwise $F_{ST}$ comparisons, as well as a UPGMA dendrogram based on Nei's genetic distance (calculated from allele frequencies across the six loci investigated), confirm the separate main groupings.

**Keywords** European lobster; *Homarus gammarus*; genetic diversity; allozymes; genetic structure

## INTRODUCTION

The European lobster, *Homarus gammarus*, is usually found in shallow waters and most catches are taken with traps in depths of less than 30 m. Lobsters have, however, been found down to 150 m (Holthius 1991; Mercer et al. 1998). The species has a wide geographical distribution extending from the Arctic Circle to Morocco. It is found along the Atlantic coast, including the British Isles and Ireland, but is not found in the Baltic Sea possibly because of lowered salinity and extreme temperatures. The southern limit is c. 30°N (latitude) on the Atlantic coast of Morocco, and lobsters are also distributed in the coastal and island areas of the Mediterranean Sea, although less abundant.

The total annual European landings have varied between 1600 and 4800 t. In the early 1960s, c. 3500 t were harvested, but landings decreased during the 1970s to below 2000 t in the early 1980s. Since then a slow increase to 3200 t has been observed (Browne et al. 2001). The most important lobster fisheries are currently in Ireland, England, Scotland, Wales, and the Channel Islands. Before the 1960s, Norway recorded catches of 600–1000 t annually, but during the subsequent two decades a collapse in the fishery was observed and annual catches are now less than 30 t (Agnalt et al. 1999). Similar declines were also observed in Sweden and Denmark.

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Lobsters are classed as a luxury food and support valuable fisheries, which are of considerable socio-economic importance in many coastal areas. The large variation in annual wild harvest initiated lobster hatchery activities in many countries. In early 1900, a large number of hatchery-produced lobster larvae were released in North America as well as in Europe (Aiken & Waddy 1995; Nicosia & Lavalli 1999). Later, a large-scale lobster hatchery was established in Norway to produce 1-year-old lobster juveniles for release into natural waters (Grimsen et al. 1987). In contrast with earlier release experiments, the development of "coded wire tags" (Jefferts et al. 1963) and their use in lobsters (Wickins et al. 1986), made it finally possible to quantitatively evaluate lobster release programmes. This achievement triggered a number of release experiments in Europe (Addison & Bannister 1994; Burton et al. 1994; Cook 1995; Bannister & Addison 1998; Browne & Mercer 1998; Latrouite 1998; Agnalt et al. 1999).

During recent decades, there has been increasing awareness that aquaculture activities, including stock enhancement and commercial ranching, may have negative impacts on native gene pools. Genetic problems connected to hatchery operations have been discussed (Allendorf & Ryman 1987; Busack & Currens 1995; Campton 1995; Waples 1999), and genetic considerations are also part of the "responsible approach to marine enhancement" proposed by Blankenship & Leber (1995). The main concern is that hatchery production is likely to result in genetic change and that interbreeding between wild and hatchery-produced organisms can result in genetic changes in the wild populations causing reduction in overall fitness and productivity (Utter et al. 1993; Utter 2000). These aspects should also be considered in the evaluation of the potential of enhancement for European lobster, which has been discussed recently (Laurec 1999).

Many marine species are believed to have high potential for pelagic larval dispersal, but there is increasing evidence (Bailey et al. 1997; Benzie 2000; Zane et al. 2000; Sundby et al. 2001) that other oceanic features such as current patterns, sea floor topology, and temperature gradients can provide sufficient opportunities for isolation and differentiation. For European lobster, the first few weeks post-hatching is characterised by a pelagic phase. The duration of this phase is temperature dependent and is variously reported as 14–20 days (Jørstad et al. 2001). Although potentially larvae can drift with currents, it has been increasingly shown for marine fish and other animals that dispersal is much less than might be expected (Sundby et al. 2001). The oceans are much more structured than previously considered, with various subsurface oceanographic fronts and gyres that limit larval dispersal. Also larvae may have behavioural mechanisms such as vertical movements that prevent dispersal (Benzie 2000; Sundby et al. 2001). The general biology of American lobster, *Homarus americanus* (Phillips et al. 1980; Aiken & Waddy 1995) is well known, including pelagic and first bottom stage (Wahle & Incze 1997). For European lobster, this kind of biological information is still lacking (Mercer et al. 2001).

Detailed information about the genetic structure of European lobster has not been available. This contrasts with the situation for the American lobster where Tracey et al. (1975) screened 44 different protein loci in a sample collection from eight geographically different localities on the east coast of North America. Also, by comparing berried females with their offspring, Hedgecock et al. (1975) found that five polymorphic loci (*EST-2**, *IDHP**, *GPI-3**, *GPI-4**, and *PGM-1**) followed Mendelian inheritance. These were also most informative in the population study carried out (Tracey et al. 1975). Comparison of allele frequencies for the different loci, however, suggests very small genetic differences between areas. This was also indicated by analyses using mtDNA (Kornfield & Moran 1990) and RAPD analyses (Harding et al. 1997), and this situation triggered development of more sensitive genetic markers such as microsatellites (Tam & Kornfield 1996).

The early study of Hedgecock et al. (1977) also compared a sample of *H. americanus* ($n = 94$) with a sample of *H. gammarus* ($n = 51$), and found large differences in the number of alleles as well as allele frequencies. New alleles specific for *H. gammarus* were found at several loci, and they estimated genetic distance (Nei 1972) of 0.11 between the two species averaged over all loci investigated. For *H. gammarus* two different samples were included, one from western Norway and one from the Irish Sea. Differences in allele frequencies were found for several loci, including *ME**, *GPI**, and *PGM** (Hedgecock et al. 1977). Mainly based on the loci and allele descriptions in that study, genetic analyses were incorporated in the Norwegian Sea Ranching Program (PUSH) in 1991. In addition, a more detailed study of the genetics of wild lobsters in Norwegian areas was conducted. Samples from 22 different locations (2580 individuals) were screened for four enzymes (ME, GPI, IDHP, and PGM).

Generally, very low levels of variation were found for all loci, but significant genetic differences at all loci were detected in the sample from the most northern population analysed (Jørstad & Farestveit 1999).

Sustainable management of European lobster stocks is dependent on detailed knowledge of the genetic structure throughout the distribution range, and this is especially important considering future enhancement strategies. A larger genetic study "Genetics of European Lobster" (GEL) was initiated in 1998 and funded by the European Commission. The main objective was to conduct a large-scale genetic characterisation of lobster stocks throughout the geographic range in Europe and evaluate the results in relation to future lobster stock management and enhancement/ranching approaches. Large-scale sampling was carried out mainly for analyses by new methods such as microsatellite DNA techniques (Estoup & Angers 1998) and mtDNA analyses, and a general description of the work carried out is available (Ferguson 2002, www.qub.ac.uk/bb/prodohl/GEL/gel.html). As part of this work, tissue samples were also collected from selected areas and analysed for allozyme variation. The results from the allozyme analyses are presented in this study.

## MATERIALS AND METHODS

Initially within the GEL project, a sampling protocol for tissue collection for genetic analysis was established together with biological data collection procedures. The collection of samples was dependent on fishery practices, abundance of lobsters, and the local marketing practice in various areas. Except for the samples from northern Norway, the samples were collected through direct contact with fishers and/or at landing harbours and live lobster storing facilities.

Samples for allozyme analyses had the proximal segment of one of the walking leg removed. These were frozen as soon as possible and kept on dry ice during transport to the laboratory. Because of lack of a commercial fishery in the northern part of Norway, several research vessel surveys were organised using the small RV *Fangst*. Sampling was carried out in this region over a number of years. Details about the overall sampling (locations, number of specimens, year of sampling) are given in Table 1 and the geographical distribution/locations are shown in Fig. 1. For the overall comparison, two earlier samples, NorwaySW1 and NorwaySE, were included (Jørstad & Farestveit 1999). In total, samples from 1514 specimens were analysed, representing 15 samples from 14 different localities (one repeated sampling—NorwaySW1 and NorwaySW2) throughout the lobster distribution range. All samples were transported to the laboratory in Bergen where the tissues were stored at –80°C until analyses.

The genetic analyses were based on earlier described polymorphic loci present in white muscle tissue of American lobsters (Tracy et al. 1975), which were also found in European lobster (Hedgecock et al. 1977; Jørstad & Farestveit 1999). Muscle extracts from each individual sample were run on starch gel electrophoresis (histidine buffer pH = 7.0; 100–130 V; running time 90–110 min) and the allozymes were identified by traditional selective staining methods. The allozymes included four enzymes: glucosephosphate isomerase (GPI), isocitrate dehydrogenase (mIDHP), phosphoglucomutase (PGM), and malic enzyme (sMEP), representing six loci (Jørstad & Farestveit 1999; Table 2). Although different tissues were used, the two loci designated *GPI-1** and *GPI-2** in this paper possibly correspond to the *GPI-3** and *GPI-4** in Hedgecock et al. 1975.

The statistical treatment of the genetic data was undertaken in the computer package GENEPOP (Raymond & Rousset 1995), version 3.3. The exact tests in GENEPOP were used for testing for Hardy-Weinberg equilibrium and population differentiation, including 100 iterations per batch and 100 batches. Pairwise linkage disequilibria were tested by the LINKDOS program (Garnier-Gere & Dillman 1992) available in GENEPOP. *F* statistics were calculated according to Weir & Cockerham (1984) as implemented in GENEPOP. Estimates of Nei's genetic distances (Nei 1972) between the samples and construction of UPGMA dendrogram were performed using the TFGPA programme of Miller 1997. The bootstrapping was conducted with 1000 permutations.

## RESULTS

The gene diversity estimates are summarised in Table 1 and confirmed the low levels of polymorphism that have been earlier observed for the same allozyme loci (Tracey et al. 1975; Jørstad & Farestveit 1999). Overall, the observed heterozygositiy varied from 0.004 (NorwayNW) to 0.091 (IrelandENE). In general, the samples from northern

**Table 1** Sample collection details and gene diversity estimates based on six polymorphic loci. Percentage of maximum value of heterozygosity is related to the sample from Irish Sea (=100%). Sample locations are shown in Fig. 1.

| Map no. | Area | Locality | Year | Sample size | Heterozygosity (obs.) | Alleles / locus | *FIS* | % maximum |
|---|---|---|---|---|---|---|---|---|
| 1 | NorwayN3 | Tysfjord/Stefjord | 2000 | 157 | 0.023 | 1.17 | 0.023 | 15 |
| 2 | NorwayN4 | Tysfjord/Mannfjord | 2000 | 45 | 0.028 | 1.33 | 0.030 | 33 |
| 3 | NorwayNW | Nordfolda | 2000 | 93 | 0.004 | 1.17 | 0.004 | 4 |
| 4 | NorwaySW1 | Bjørnafjorden | 1995 | 96 | 0.055 | 1.67 | 0.066 | 73 |
| 5 | NorwaySW2 | Bjørnafjorden | 2000 | 93 | 0.061 | 1.83 | 0.061 | 67 |
| 6 | NorwaySE | Oslofjorden/Drøbak | 1995 | 189 | 0.073 | 1.83 | 0.074 | 81 |
| 7 | SwedenSW | Kattegat | 2000 | 94 | 0.062 | 2.00 | 0.062 | 68 |
| 8 | Netherlands2 | Oosterschelde | 2001 | 100 | 0.069 | 1.83 | 0.069 | 76 |
| 9 | ScotlandN | Orkney/Westray | 1999 | 100 | 0.084 | 2.00 | 0.084 | 92 |
| 10 | EnglandSW2 | Scilly Island | 1999 | 100 | 0.069 | 2.00 | 0.069 | 75 |
| 11 | IrelandENE | Irish Sea/Newcastle Bay | 2000 | 81 | 0.091 | 2.00 | 0.091 | 100 |
| 12 | IrelandW | Kerry | 2000 | 100 | 0.062 | 1.83 | 0.062 | 68 |
| 13 | FranceW | Brittani/Brest | 2000 | 94 | 0.060 | 1.83 | 0.060 | 65 |
| 14 | AegeanNE | Alexandroupolis | 1999–2000 | 98 | 0.068 | 2.00 | 0.068 | 75 |
| 15 | AegeanN | Toronaios | 1999–2000 | 74 | 0.058 | 2.00 | 0.058 | 63 |

Norway (samples 1–3) have a much lower diversity compared with the other samples in the present sample collection. Taking the sample (IrelandENE) as a reference, the diversities for the northern Norway samples were only 4–33% compared with the reference sample. This reduction was also seen comparing the number of alleles per locus in the various samples. The allozyme data for the northern samples have also been compared with the mtDNA and microsatellite analyses based on the same samples, and the compiled genetic information as well as biological characteristics provides evidence (Jørstad et al. 2004) for genetic distinct subarctic lobster populations in this region.

The extreme low levels of gene diversity in most northern samples were mainly a result of monomorphism (Table 2) at five of the allozyme loci analysed. Only the *mIDHP-1** locus was polymorphic in the northern lobster samples, and the highest frequency of *mIDHP-1*120* allele was actually found in sample NorwayN3, which agreed with earlier estimates obtained in samples from the same locality in 1995 (Jørstad & Farestveit 1999). In the sample analysed here, the starch gel electrophoresis revealed both triple and single banding patterns in this sample, corresponding to heterozygotes and homozygotes for the rare allele *mIDHP-1*120*. Overall, the allele frequency ranged from 0.005 (Netherlands2) to 0.089 (NorwayN). A similar situation was found at the *PGM-2** locus, where the frequencies of the 90 allele ranged from 0.000 (NorwayN3 and NorwayNW) to the relatively high value of 0.114 (Netherlands2).

The collections also included two samples from the Aegean Sea in the Mediterranean (Table 1; Fig. 1). The analyses detected a new slow-moving allele at the *GPI-1** locus. The typical banding patterns observed in the samples included both triple and single banding patterns corresponding to heterozygotes and homozygotes for the rare allele (*GPI-1*80*). This allele has not been found previously (Jørstad & Farestveit 1999) and is present in the Aegean samples at a frequency of c. 0.05 (Table 2). In contrast, only one single heterozygote was detected in one sample (IrelandENE) in the samples collected from the Atlantic region of Europe (Table 2). For both Aegean samples the *GPI-2** locus was found to be monomorphic.

Tests for Hardy Weinberg (Genepop, exact tests) proportions revealed only a few departures from expected values. In all, 57 tests were conducted and significant departure from Hardy Weinberg was found in five instances. These are indicated in bold

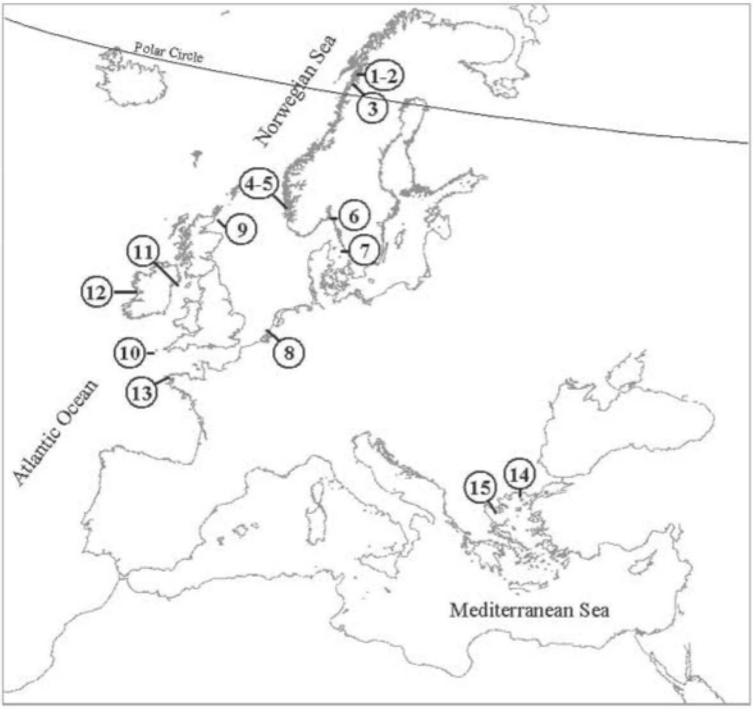

**Fig. 1** Sampling localities of European lobster (*Homarus gammarus*) throughout the distribution range. (See further details in Table 1.)

in Table 2 for the loci and samples in question. When using the most conservative Bonferroni correction, this number was reduced to only one sample—Netherlnd2 and for the *GPI-2** locus. The tests for linkage disequilibria between loci revealed only five significant values, which were not specific to any combination of loci.

The tests for population differentiation (Raymond & Rousset 1995b) based on allele frequencies, revealed highly significant values ($P < 0.001$) for each of the loci tested across all collections, as well as across all loci and samples ($P < 0.0001$). This indicates genetic structuring in the European lobsters despite generally low levels of genetic variation. The pairwise tests for population differentiation demonstrated a number of significant differences, and these are mainly a result of the samples from northern Norway (NorwayN3, NorwayN4, NorwayNW), the Netherlands2, and AegeanNE/AegeanN. The *P* values obtained in the tests based on six loci are summarised in Table 3. With reference to the discussion of Ryman & Jorde (2001), the values presented have not been corrected for significance level (Rice 1995).

All samples from northern Norway were significantly different from the other samples with three exceptions—NorwayN4 against EnglandSW2, IrelandW and FranceW—which is possibly because of the small sample size. Except for a few instances (NorwaySW1 and SwedenSW) the Netherlands2 sample was significantly different from all the other samples. Finally the AegeanNE and AegeanN samples were significantly different from the rest of the samples, mainly based on the variation found at the *GPI-1** and *GPI-2** loci. The same results were essentially obtained when conducting the testing based on genotype frequencies (data not shown).

Table 3 also summaries the $F_{\mathrm{ST}}$ values obtained in pairwise comparisons. The largest value (0.098) was found between the sample from NorwayN3 and Netherlands2, whereas the value was as high as 0.048 between the two samples from northern Norway (NorwayN3 and NorwayNW). Table 4 shows the *F* statistics and genetic differentiation of different sample groups according to geographic areas. The estimates are based on all six loci and the highest $F_{\mathrm{ST}}$ value (0.016) was found, as expected, in the total sample group. Excluding the most divergent samples (B) reduced the value of $F_{\mathrm{ST}}$ but still the global test for genetic differentiation was significant ($P = 0.014$). Based on the samples analysed here, there was no indication for genetic

**Table 2** Allele frequencies for six polymorphic allozyme loci in European lobster (*Homarus gammarus*) samples. Values given in bold indicate deviation from Hardy Weinberg (without Bonferroni corrections; see Ryman & Jorde 2001). (NA, not analysed.)

| | | *sMEP** | | *IDHP-1** | | *GPI-1** | | *GPI-2** | | *PGM-1** | | | *PGM-2** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sample | *N* | 100 | 120 | 100 | 120 | 80 | 100 | 80 | 100 | 80 | 100 | 120 | 80 | 90 | 100 |
| NorwayN3 | 157 | 1.000 | 0.000 | 0.911 | 0.089 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 1.000 |
| NorwayN4 | 45 | 1.000 | 0.000 | 0.922 | 0.078 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.011 | 0.989 |
| NorwayNW | 93 | 1.000 | 0.000 | 0.989 | 0.011 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 1.000 |
| NorwaySW1 | 96 | 0.934 | 0.066 | 0.971 | 0.029 | 0.000 | 1.000 | **0.087** | **0.913** | 0.017 | 0.983 | 0.000 | NA | NA | NA |
| NorwaySW2 | 93 | 0.909 | 0.091 | 0.973 | 0.027 | 0.000 | 1.000 | 0.038 | 0.962 | 0.027 | 0.973 | 0.000 | 0.000 | 0.033 | 0.967 |
| NorwaySE | 189 | 0.937 | 0.063 | 0.965 | 0.035 | 0.000 | 1.000 | 0.050 | 0.950 | 0.024 | 0.974 | 0.003 | 0.000 | 0.063 | 0.938 |
| SwedenSW | 94 | 0.952 | 0.048 | 0.979 | 0.021 | 0.000 | 1.000 | 0.059 | 0.941 | 0.005 | 0.995 | 0.000 | 0.011 | 0.051 | 0.938 |
| Netherlands2 | 100 | 0.941 | 0.059 | 0.995 | 0.005 | 0.000 | 1.000 | **0.104** | **0.896** | 0.005 | 0.995 | 0.000 | 0.000 | 0.114 | 0.886 |
| ScotlandN | 100 | 0.911 | 0.089 | 0.931 | 0.069 | 0.000 | 1.000 | 0.045 | 0.955 | 0.030 | 0.970 | 0.000 | 0.005 | 0.045 | 0.950 |
| EnglandSW2 | 100 | 0.924 | 0.076 | 0.924 | 0.076 | 0.000 | 1.000 | 0.020 | 0.980 | 0.005 | 0.995 | 0.000 | 0.005 | 0.047 | 0.948 |
| IrelandENE | 81 | 0.920 | 0.080 | 0.920 | 0.080 | 0.006 | 0.994 | **0.049** | **0.951** | 0.031 | 0.969 | 0.000 | 0.000 | 0.049 | 0.951 |
| IrelandW | 150 | 0.952 | 0.048 | 0.931 | 0.069 | 0.000 | 1.000 | 0.052 | 0.948 | 0.007 | 0.993 | 0.000 | 0.000 | 0.030 | 0.970 |
| FranceW | 94 | 0.947 | 0.053 | 0.947 | 0.053 | 0.000 | 1.000 | 0.032 | 0.968 | 0.005 | 0.995 | 0.000 | 0.000 | 0.059 | 0.941 |
| AegeanNE | 98 | 0.959 | 0.041 | 0.949 | 0.051 | 0.046 | 0.954 | 0.000 | 1.000 | 0.010 | 0.990 | 0.000 | **0.015** | **0.093** | **0.892** |
| AegeanN | 74 | **0.953** | **0.047** | 0.958 | 0.042 | 0.047 | 0.953 | 0.000 | 1.000 | 0.020 | 0.973 | 0.007 | 0.000 | 0.065 | 0.935 |

**Table 3** Pairwise tests for population differentiation (below) based on allele frequencies at six polymorphic allozyme loci. *P* values are given ranging from 0.05 to 0.001. NS, not significant ($P > 0.05$). Pairwise $F_{ST}$ comparisons are also given (above).

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | NorwayN3 | | –0.006 | 0.048 | 0.055 | 0.053 | 0.040 | 0.050 | 0.098 | 0.038 | 0.028 | 0.035 | 0.019 | 0.029 | 0.048 | 0.039 |
| 2 | NorwayN4 | NS | | 0.056 | 0.037 | 0.031 | 0.022 | 0.027 | 0.060 | 0.020 | 0.014 | 0.018 | 0.009 | 0.013 | 0.024 | 0.017 |
| 3 | NorwayNW | <0.001 | 0.016 | | 0.049 | 0.047 | 0.033 | 0.040 | 0.083 | 0.049 | 0.048 | 0.054 | 0.032 | 0.037 | 0.052 | 0.041 |
| 4 | NorwaySW1 | <0.001 | <0.001 | <0.001 | | 0.003 | 0.001 | –0.001 | –0.002 | 0.005 | 0.014 | 0.006 | 0.005 | 0.007 | 0.027 | 0.023 |
| 5 | NorwaySW2 | <0.001 | 0.002 | <0.001 | NS | | –0.000 | 0.003 | 0.021 | –0.001 | 0.003 | 0.001 | 0.006 | 0.003 | 0.020 | 0.009 |
| 6 | NorwaySE | <0.001 | 0.001 | <0.001 | NS | NS | | –0.002 | 0.010 | 0.001 | 0.004 | 0.001 | 0.003 | –0.001 | 0.011 | 0.007 |
| 7 | SwedenSW | <0.001 | 0.007 | <0.001 | NS | NS | NS | | 0.007 | 0.006 | 0.008 | 0.006 | 0.003 | –0.001 | 0.014 | 0.010 |
| 8 | Netherlands2 | <0.001 | <0.001 | <0.001 | NS | 0.005 | 0.010 | NS | | 0.020 | 0.028 | 0.019 | 0.025 | 0.017 | 0.025 | 0.028 |
| 9 | ScotlandN | <0.001 | 0.006 | <0.001 | NS | NS | NS | NS | <0.001 | | –0.002 | –0.005 | 0.001 | –0.000 | 0.014 | 0.008 |
| 10 | EnglandSW2 | <0.001 | NS | <0.001 | 0.006 | NS | NS | NS | <0.001 | NS | | –0.003 | 0.001 | –0.002 | 0.010 | 0.006 |
| 11 | IrelandENE | <0.001 | 0.025 | <0.001 | NS | NS | NS | NS | <0.001 | NS | NS | | –0.000 | –0.001 | 0.012 | 0.007 |
| 12 | IrelandW | <0.001 | NS | <0.001 | NS | NS | NS | NS | <0.001 | NS | NS | NS | | –0.001 | 0.018 | 0.012 |
| 13 | FranceW | <0.001 | NS | <0.001 | NS | NS | NS | NS | 0.002 | NS | NS | NS | NS | | 0.006 | 0.003 |
| 14 | AegeanNE | <0.001 | 0.012 | <0.001 | <0.001 | <0.001 | <0.001 | 0.001 | <0.001 | <0.001 | 0.007 | <0.001 | <0.001 | 0.014 | | –0.003 |
| 15 | AegeanN | <0.001 | 0.017 | <0.001 | <0.001 | 0.005 | 0.002 | 0.003 | <0.001 | 0.004 | 0.016 | 0.018 | <0.001 | 0.040 | NS | |

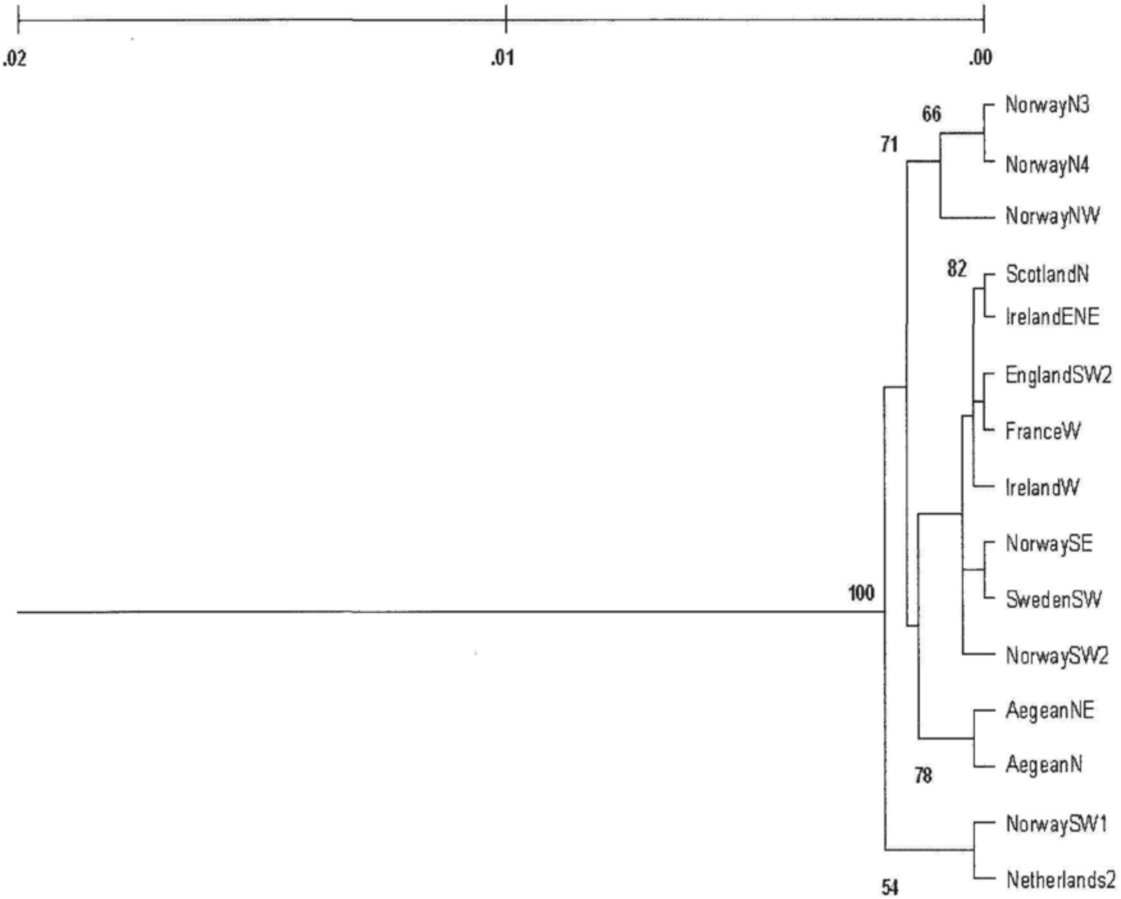

**Fig. 2** UPGM dendrogram based on genetic distance (Nei 1972), calculated from allele frequencies at six polymorphic allozyme loci by using the TFPGA program of Miller (1997). Bootstrap values (more than 50%), estimated from 1000 permutations, are given for the most divergent groups.

**Table 4** *F* statistics of lobster sample collections from different areas. *P* values are estimated from global test of genetic differentiation. (A, all samples; B, all samples except NorwayN3, NorwayN4, NorwayNW, Netherlands2, AegeanNE, AegeanN; C, Aegean Sea (AegeanN and AegeanNE); D, British Isles (ScotlandN, IrelandENE, IrelandW and EnglandSW2); E, North Sea.)

| Areas | $F_{IS}$ | $F_{ST}$ | $F_{IT}$ | $P$ |
|---|---|---|---|---|
| A | 0.084 | 0.016 | 0.098 | <0.0000 |
| B | 0.051 | 0.002 | 0.052 | 0.014 |
| C | 0.174 | –0.003 | 0.171 | 0.847 |
| D | 0.043 | –0.001 | 0.042 | 0.257 |
| E | 0.051 | 0.001 | 0.052 | 0.260 |

differentiation within the Aegean Sea, British Isles, and North Sea. As expected, the genetic distances (Nei 1972) between the samples based on six loci were small, ranging from 0.000 to 0.006. The UPGMA dendrogram based on the genetic distances (Fig. 2) confirmed, however, the main separate groupings as described above.

## DISCUSSION

The 15 samples of European lobster analysed for allozyme variation are distributed throughout a large area, ranging from north of the Arctic Circle in

Norway to the warmer environment of the East Mediterranean. It would be surprising if lobsters at the edges of environmental tolerance for the species, such as northern Norway and Aegean Sea, had not adapted to some degree to these conditions. Certainly, environmental parameters such as variation in temperature and daylight through different seasons are very different in northern Norway compared to the Aegean Sea. Details of life history characters, especially for reproduction and early life stages are unknown (Mercer et al. 2001).

The level of genetic differentiation, however, among the European lobster samples as estimated from six polymorphic allozyme loci, was relatively low. The overall $F_{ST}$ value of 0.016 is in agreement with findings for other marine species (e.g., Buonaccorsi et al. 2001; Stamatis et al. 2004). The various tests for population differentiation and $F_{ST}$ comparisons, and to some degree the UPGMA dendrogram of genetic distance (Nei 1972), suggest four main groups: northern Norway (bootstrap value = 71), Netherlands (bootstrap value = 54), Aegean (bootstrap value = 78), and the other samples in the Atlantic group. Testing of population differentiation after excluding the samples from the three mentioned areas still suggest some genetic variation (Table 4B), whereas no structure was indicated in the samples from the British Isles (D), in the North Sea (E), and Aegean Sea (C).

The genetic differentiation observed was mainly associated with minor difference in allele frequencies. Especially for the northern Norway group, the gene diversities in the different samples were low owing to monomorphism (Table 2) and no unique alleles were detected. The number of alleles per locus also confirmed this. The samples from Netherlands and Aegean Sea have c. 20–30% reduction in observed heterozygosity compared with the reference samples from IrelandENE. This reduction could be a result of recent bottleneck events in these areas. For the Mediterranean samples the obvious differences were a result of the new variation detected in the *GPI-1** locus (Table 2). Also, in contrast with the other samples, no polymorphism was found for the *GPI-2** locus.

The data obtained in this study confirm the existence of a genetically distinct population in the Tysfjord system (NorwayN3/NorwayN4) as reported in an earlier allozyme study from Norway (Jørstad & Farestveit 1999). The samples collected 5 years apart from this area were shown not to be significantly different, suggesting temporal stability. In this investigation, the adjacent fjord system Nordfolda (NorwayNW) was also sampled. Comparisons of allele frequencies revealed significant differences between the two populations even though there is only 142 km shoreline distance between the two fjord systems. In a more detailed comparison (Jørstad et al. 2004) of the two subarctic lobster populations, the differences detected in allozymes were confirmed by microsatellite and mtDNA analyses. Further, differences in biological parameters like size distributions and mean lengths were documented.

Recently, genetic variation among European lobster was investigated using RAPD (Randomly Amplified Polymorphic DNA) technique (Ulrich et al. 2001). They found significant differences among eight samples, but samples sizes were small, especially from some of the areas investigated. The RAPD technique has, however, several limitations for using population genetic studies (for discussion see Ferguson & Danzmann 1998). On the other hand, a more comprehensive genetic study of European lobster based on mtDNA has recently been published (Triantafyllidis et al. 2004). In this study a large number of samples (with reasonable sample sizes) were analysed, and the results confirm the main conclusions from this allozyme investigation. Further, more detailed genetic differentiation was found on the micro geographic level, such as within the Mediterranean Sea.

Indeed, it might be expected that in species such as lobsters, given the patchiness and limited depth-distribution of suitable habitat, there would be strong selection for any mechanism that limited dispersal, since dispersal could easily carry the larvae to areas unsuitable for benthic settlement. The genetic differences between Tysfjord and Nordfolda suggest limited gene exchange, which can be explained by the complex circulation system in the larger, open fjord system (Vestfjorden) adjacent to Tysfjord and Nordfolda (Mitchelson-Jacobs & Sundby 2001). Also the genetics of the Aegean Sea lobsters is not surprising since similar differentiation of Mediterranean marine species populations from Atlantic has earlier been reported (e.g., Zane et al. 2000).

In contrast with the Tysfjord and Nordfolda region and the Mediterranean Sea where hydrographic barriers are possibly preventing gene flow, the sample from Netherlands was collected in a physically isolated area, the Oosterschelde. Because of damming and construction of a storm surge barrier, the Oosterschelde area has very limited exchange with the North Sea, and the genetic differences observed could be a result of geographic isolation and/or bottlenecking. In addition to a reduction in the gene diversity as discussed above, relatively high frequencies of the two allozyme variants (*GPI-2*80*: 0.104; *PGM-2*90*: 0.114) were detected in these lobsters.

Allozyme studies have also been carried out on other crustacean species with pelagic larval stages. A low level of variation was also found for Norway lobster (*Nephrops norwegicus*) samples from the Aegean Sea and Scotland (Passamonti et al. 1977) but despite low sample sizes, significant differences were found at several allozyme loci. As in our study on European lobster, the values for $F_{ST}$ and genetic distances were low. The above results were also confirmed with a mitochondrial DNA analysis of Norway lobster across its distribution (Stamatis et al. 2004). Even for a pelagic species like *Meganyctiphanes norwegica* some genetic structuring has been observed (Zane et al. 2000). The most striking example, however, is from the Isle of Man in the Irish Sea were two different species of spider crabs have been studied (Weber et al. 2000). Both species have a relatively long larval period (40–80 days). Allozyme analyses of samples collected from localities separated by only 40 km revealed significant genetic differences in several loci for both species.

The genetic data obtained through this study fit an island model consisting of discrete populations with little or limited interchange. This means that management should be based on local populations, i.e., self-recruiting stocks. Genetic differences alone are insufficient for this purpose as the level of genetic differentiation is quite low, and large sample sizes and many loci are necessary to detect significant differences. Assessment and management need to be based on a combination of biological, hydrographical, and genetic information.

For the local stock enhancement and ranching, it would be wise to apply the precautionary principle to movements of lobsters for release purposes. This principle has been well elaborated for movement of salmonids such as Atlantic salmon (e.g., Cross 1999). Use of local stocks is preferred to reduce risks both from genetic and health points of view. In instances where releases are planned in areas without any lobsters, the broodstock should come from the nearest wild lobster stock(s). In many European countries the lobster stocks are at very low levels, and any restocking should be based on local stocks and strict management approaches. Transplantation of lobster stocks over larger distances should be avoided until much more detailed information on fitness-related differences is available. Where enhancement is carried out, local hatcheries should be established, which provide juveniles based on local stock, rather than larger "centralised" hatchery facilities.

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# Changes in vertebrate-type steroids and 5-hydroxytryptamine during ovarian recrudescence in the Indian spiny lobster, *Panulirus homarus*

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**Abstract** Vertebrate-type steroids (estradiol-17β and progesterone) and 5-hydroxytryptamine (5-HT) were examined during the different stages of ovarian maturation in the Indian spiny lobster *Panulirus homarus*. Estradiol-17β and progesterone in the haemolymph and ovary were quantified by radioimmunoassay. Estradiol-17β was not detectable in the haemolymph when the oocytes were in stage I. It appeared in the haemolymph only as the oocytes attained stage II. Subsequently, a sharp increase in the level of estradiol-17β was observed in the haemolymph of lobsters with stage III oocytes; it then showed a significant fall when the ovary was full of stage IV oocytes. Although progesterone was also not detectable in the haemolymph when the oocytes were in stage I, it gradually increased during stages II and III and reached a peak level during stage IV. Surprisingly, both estradiol-17β and progesterone were detectable in the ovary from stage I onwards. In the ovary, estradiol-17β and progesterone showed peak levels during stages III and IV, respectively. A stage-dependent change in the activity and distribution of 5-hydroxytryptaminergic neurons in the brain and thoracic ganglia was also observed immunocytochemically in relation to ovarian recrudescence. Furthermore, HPLC-EC conducted on the level of 5-HT in the brain and thoracic ganglia indicated similar changes in relation to ovarian maturation. These results strongly suggest that 5-HT is involved in ovarian development through certain inhibitory/stimulatory factors present in the X-organ-sinus gland complex of the eye-stalk in the spiny lobster *P. homarus*.

**Keywords** estradiol-17β; progesterone; 5-hydroxytryptamine; ovary; brain ganglia; thoracic ganglia; *Panulirus homarus*

## INTRODUCTION

5-Hydroxytryptamine (5-HT) is a well documented mediator of a great variety of functions in invertebrates because of its ubiquitous nature (Fingerman et al. 1994). 5-HT and the rate limiting enzymes involved in its synthesis are found in measurable levels in several regions of the central nervous system (CNS) of decapod crustaceans indicating 5-HT activity. Some of the major tissues that exhibit high 5-HT activity are the optic ganglia, cerebral ganglia, circumoesophageal connectives, stomatogastric ganglia, and thoracic ganglia (Aramant & Elofsson 1976; Beltz et al. 1984). 5-HT has now been established as a neuroregulator in crustaceans since it modulates several physiological processes (Fingerman 1997a).

Different types of influences of 5-HT have been reported in decapod crustaceans: a strong elevation in the level of glucose in *Carcinus maenas* (Luschen et al. 1993), increase in heart rate (Listerman et al. 2000), assertiveness and aggression during social interaction (Huber et al. 1997), regulation of crustacean hyperglycemic hormone activity in *Procambarus clarkii* (Escamilla-Chimal et al. 2001, 2002), pigment dispersing responses in the dwarf crayfish *Cambrarellus shufeldti* (Rao & Fingerman 1975) and in the fiddler crab *Uca pugilator* (Fingerman & Rao 1970), and stimulation of gonad through brain

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and thoracic ganglia (Richardson et al. 1991). The information available on a possible role of 5-HT in crustacean reproduction mainly deals with the stimulatory role of exogenous 5-HT through *in vivo* and *in vitro* studies during ovarian maturation (Richardson et al. 1991; Kulkarni & Fingerman 1992; Kulkarni et al. 1992). Invariably all the studies conducted earlier have uniformly agreed that 5-HT induced ovarian maturation could only be possible through certain inhibitory and/or stimulatory factors present in the CNS. However, some earlier reports on the occurrence of vertebrate type steroids in decapod crustaceans in relation to ovarian maturation provide much impetus to the steroidal control of gonadal maturation in invertebrates (Burns et al. 1984; Quinitio et al. 1994; Shih & Tseng 1999). Evidence of the ability of crustaceans to produce these steroids from cholesterol endogenously (Watson & Spaziani 1985; Shih & Liao 1998) further reiterate the possibility of steroid regulation of ovarian maturation in crustaceans similar to vertebrate models. Physiological doses of progesterone have increased yolk protein synthesis in ovaries of penaeid shrimps (Yano 1987; Quackenbush 1992). In the present study, we examined the quantitative and qualitative changes of 5-HT in the brain and thoracic ganglia during the different phases of ovarian maturation of the Indian spiny lobster, *Panulirus homarus*. In addition, we analysed changes in the levels of estradiol-17β and progesterone in the haemolymph and ovary during the different phases of ovarian recrudescence.

## MATERIALS AND METHODS

### Collection and maintenance of animals

Female Indian spiny lobsters *P. homarus* with different stages of gonadal maturation, weighing 275 ± 20 g, were procured from the local lobster holding centres around Chennai, India. The animals were brought to the seafront laboratory at Neelankarai and were acclimatised to laboratory conditions at least 2 weeks before analysis. During the period of acclimatisation they were maintained in filtered sea water with suitable water quality parameters such as salinity (35 ppt), pH (8.1), dissolved oxygen (4.6 mg litre$^{-1}$), ambient temperature (24–27°C), ammonia (1.2 mg litre$^{-1}$), nitrate (1.4 mg litre$^{-1}$), and nitrite (1.4 mg litre$^{-1}$) and fed with *Perna viridis ad libitum.* Following acclimatisation, the animals were anaesthetised using MS 222 (100 mg litre$^{-1}$) for a period of 10–15 min. First, haemolymph was withdrawn from the intra-arthroidal space for radioimmunoassay (RIA) of estadiol-17β and progesterone using an appropriate anticoagulant (7.5% sodium citrate solution) and 24 G needle fitted disposable syringes. Later the animals were killed, and the brain and thoracic ganglia were dissected out immediately and stored at –70°C until further use for the estimation of 5-HT by High Pressure Liquid Chromatography with Electrochemical Detector (HPLC-ECD). Similarly, another set of animals was also killed and both ganglionic tissues were dissected out and fixed in Bouin's fluid for immunocytochemical investigation of 5-HT. The paired ovaries of all corresponding individuals were removed. One ovary was processed for ascertaining the stage of the ovary histologically by fixing in Bouin's fluid and the other to estimate the estradiol-17β and progesterone by RIA.

### Histological investigation of ovary

Bouin's-fixed ovaries were dehydrated in an ethanol series and cleared in xylene before infiltrating with paraffin. Six microns paraffin sections were cut using a Leica microtome (RM 2125 RT) and stained with haematoxyline and eosin. Photographs were taken using a Zeiss microscope (Axioskop 2).

### RIA of steroids

*Extraction of steroids from haemolymph and ovary*

Five hundred microlitres of haemolymph were taken in a stoppered test tube and triple distilled water was added to make up the volume to 2.0 ml. To this, 5.0 ml of HPLC grade diethyl ether were added and vortexed for 3 min. Diethyl ether was aspirated and dried under $N_2$ gas. Later, 1.0 ml of phosphate buffered saline (PBS, 0.01*M*, pH 7.0) was added and from this, 500 µl were taken for the assay of estradiol-17β and progesterone after maintaining the tubes at 4°C for 30 min. The extraction of estradiol-17β and progesterone from the ovary was carried out by following the procedure of Shih (1997).

### RIA of estradiol-17β and progesterone

The levels of estradiol-17β and progesterone in the extracts of haemolymph and ovary were measured by RIA following the method developed and validated by Lamba et al. (1983). Five hundred microlitres of reconstituted serum extract were taken in an assay tube and 100 µl of anti-estradiol or anti-progesterone (both gifted by G. D. Niswender, Colorado State University, United States) and 10 000–10 500 counts per min (cpm) of $H^3$-estradiol (2, 4, 6, 7– $H^3$) or $H^3$-progesterone (1, 2, 6, 7– $H^3$)

(both from New England Nuclear, United States; Sp. Act.: 71 Ci/mmol and 104 Ci/mmol for estradiol and progesterone, respectively) in 100 µl of PBS were added. The reaction mixture was vortexed and left at room temperature for 1 h and then incubated overnight at 4°C. Following the incubation, 200 µl of ice-cold dextran-coated charcoal were added and vortexed briefly before leaving for 20 min to adsorb the free steroids. The tubes were centrifuged at 1000*g* for 10 min at 4°C and the supernatant was decanted to a scintillation vial containing 10.0 ml of scintillation fluid (Amersham, Hisafe 2). The vials were vortexed gently and counted for 1 min using a liquid scintillation counter (Wallac 1409 DSA) after maintaining in darkness overnight. The detectable limit of the present assay system was 10 pg/ml. Standard curves were obtained by processing tubes containing 0–1000 pg of unlabelled estradiol-17β or progesterone (Sigma, United States) in a similar manner as described for unknown samples, after selecting the antibody titre for 50% binding. For non-specific binding, 100 µl of $H^{3-}$estradiol or $H^3$-progesterone (c. 10 000 cpm) were added to an assay tube containing 0.6 ml of PBS and the tubes were processed in the same manner as the standards. Total counts were obtained by directly adding 100 µl of $H^3$-estradiol or $H^3$-progesterone to 10.0 ml of scintillation fluid. The levels of hormones of unknown samples were calculated using the standard curve.

### HPLC-EC analysis of 5-HT

HPLC analysis was performed using a Shimadzu HPLC apparatus consisting of a pump (LC–10AD VP), Rheodyne injector, System controller (SCL–10A VP) and EC detector (Antec–Leyden). A glassy carbon-working electrode was set at 0.45V versus Ag/AgCl reference electrode. Separation was performed isocratically using a reverse phase $C_{18}$ column (Phenomenex 250 × 4.6 mm, particle size 3 µm) preceded by an appropriate guard column.

### Mobile phase

Citric acid (Molecular weight 210.14; 32 m*M*; 13.448 g), $Na_2PO_4$ (Molecular weight 141.96; 3.54 g), EDTA (Molecular weight 372.24; 0.037 g), and octyl sodium sulphate (Sigma, United States, 0.236 g) were added to 2 litres of triple distilled water and mixed well. The pH of the above solution was adjusted to 4.2. To this, 265 ml of methanol were added and the entire solution was filtered using a 0.2 µ nylon filter (Pall Gelman, United States) and then degassed just before use.

### Sample preparation

Sample preparation and 5-HT quantification were carried out according to the procedure of Kim et al. (1987). Dissected out brain/thoracic ganglia were weighed before homogenising at 0°C with perchloric acid (0.1*M*). The homogenate was centrifuged at 0°C for 20 min at 20 000*g*. The supernatant was collected and filtered through a 0.2 µ Acrodisc filter (Pall Gelman, United States) before injecting into the HPLC system, using a Hamilton syringe, for the estimation of 5-HT.

### Preparation of standard solutions

Perchloric acid (0.1*M*; 0.859 ml) was made up to 10 ml. To this, 38.74 mg of 5-HT (Sigma, United States) was added and mixed well. Further dilutions were made using mobile phase up to 1 ng/µl concentration and filtered through a 0.2 µ Acrodisc filter (Pall Gelman, United States) before use. Different concentrations were injected by maintaining the volume of injection at 20 µl and a standard graph was prepared to quantify sample values after authenticating the retention time of 5-HT. Percentage recovery was also calculated and the sample values were adjusted accordingly. The entire protocol, which includes storage, sample preparation, and preparation of standards, involved only polypropylene disposable wares.

### HPLC-EC detection of 5-HT

HPLC-EC detection of standard 5-HT was made at 5.678 min as we maintained the following working conditions: isocratic elution; mobile phase (32 m*M* citrate buffer in methanol with EDTA and octyl sodium sulphate); phenomenex column (Reverse phase C18, particle size 3 µ, 250 × 4.6 mm); flow rate (1 ml/min); glassy carbon working electrode (+0.45 V versus Ag/AgCl electrode).

### Immunocytochemical localisation of 5-HT in brain and thoracic ganglia

The brain and thoracic ganglia were fixed in Bouin's fluid for 24 h and processed for paraffin embedding on gelatin-coated slides. The sections were hydrated and processed for PAP staining as described earlier (Joy & Kirubagaran 1989). Rabbit anti-5-HT (Sigma, United States) was used as the first antibody (1:4000 dilution, incubation at 4°C for 72 h). Goat anti-rabbit serum was used as second antibody (Sigma, United States; 1:200 dilution, incubation at room temperature for 1 h). After the immunoreaction, sections were incubated in a medium

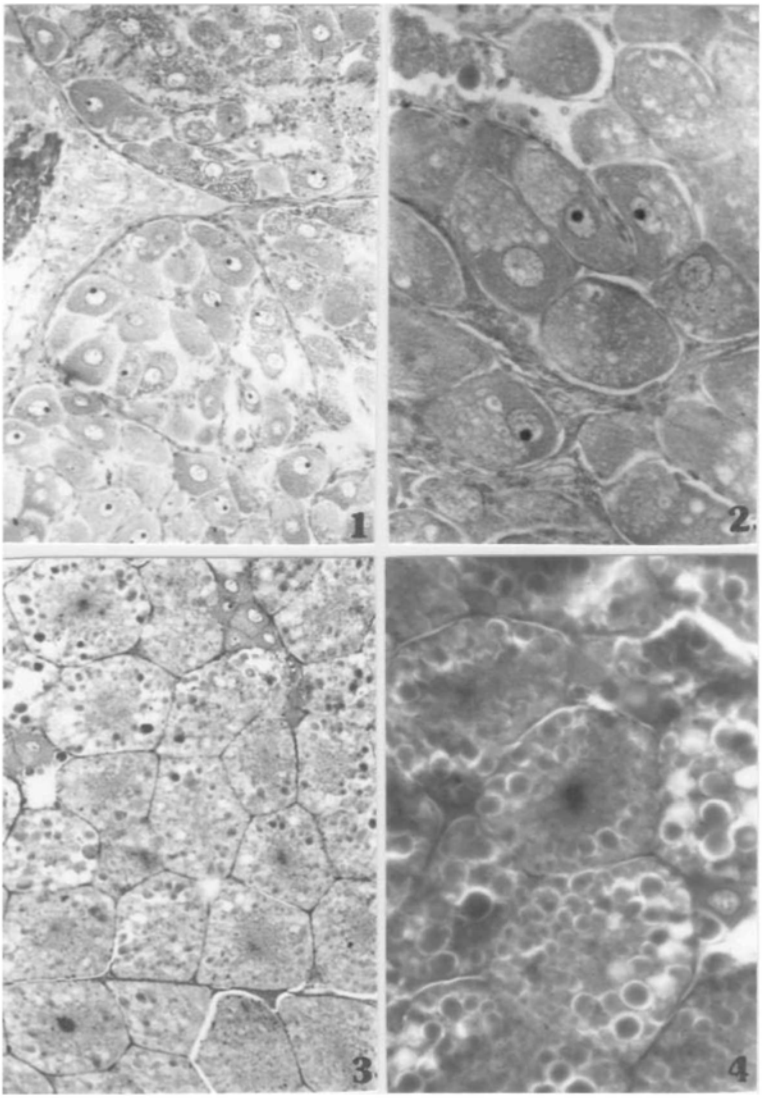

**Fig. 1–4** Cross-sections of ovaries showing: **Fig. 1** immature stage I; **Fig. 2** maturing stage II; **Fig. 3** vitellogenic stage III; and **Fig. 4** post-vitellogenic stage IV oocytes in *Panulirus homarus*. Haematoxyline-Eosin staining. × 240.

consisting of diaminobenzidine (Sigma, United States; 5 mg in 10 ml Tris-HCl and 0.01% fresh $H_2O_2$ for 5 min at room temperature). After immunostaining, the slides were rinsed in distilled water and hydrated through a graded alcohol series, cleared in xylene, and mounted with DPX. The specificity of the immunoreaction was tested with non-immune rabbit serum in the place of antiserum and with the centrifuged supernatant of 5-HT saturated antiserum. In both examples, there was no immunoreaction. Non-specific staining because of the activity of endogenous peroxidase was checked by conducting the histochemical reaction in hydrated sections or in sections pretreated with 0.5–1.0% $H_2O_2$ for 10 min. The endogenous peroxidase activity was negligible and did not interfere with immunostaining in the brain and thoracic ganglia of this species.

### Statistical analysis

Data were expressed as means ± standard error of means (SEM.). All the data obtained on the levels of estradiol-17β, progesterone and 5-HT during different phases of ovarian maturation were subjected to one-way analysis of variance (ANOVA) followed by Multiple Newman-Keuls' test (MNK) and the significance was tested at $P < 0.001$ and $P < 0.05$ levels, respectively.

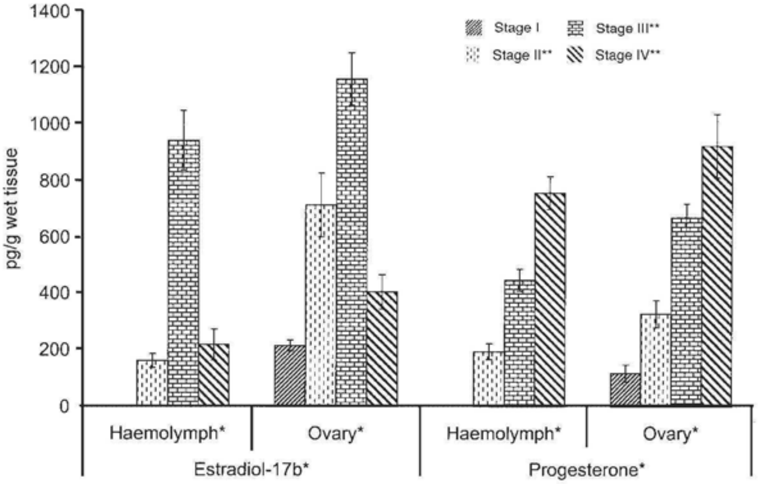

**Fig. 5** Changes in the levels of estradiol-17b and progesterone in the haemolymph and ovary during various stages of ovarian maturation in *Panulirus homarus*. (Values are means ± SEM; $n = 6$; $*P < 0.001$ (One-way analysis of variance), and $**P < 0.05$ (Multiple Newman-Keuls' test).)

## RESULTS

### Changes in the ovarian histology

During the period of ovarian recrudescence, several histological changes were noticed in stage I, II, III, and IV oocytes (Fig. 1–4). The oocyte diameter progressively increased from 120 to 800 μm as the oocytes were transformed from stage I to stage IV. Because of the gradual accumulation of vitellogenic materials during ovarian maturation, a remarkable increase in the diameter of oocytes was detected. The ovary of stage I (Fig. 1) female lobsters was mostly filled with immature oocytes with a large nucleus, whereas in stage II (Fig. 2) the ovary mainly contained maturing oocytes (pre-vitellogenic) with considerably larger ooplasm. Vitellogenic and post-vitellogenic oocytes (with totally invisible nucleus) were most prominently observed in stage III (Fig. 3) and stage IV (Fig. 4) lobsters, respectively.

### Changes in the level of estradiol-17β

Changes in the levels of estradiol-17β in haemolymph and ovary are depicted in Fig. 5. The estradiol-17β in haemolymph was below the detectable limit when the oocytes were mainly filled with stage I oocytes. Estradiol-17β started appearing in haemolymph during stage II of oocytes (162.17 pg/ml) and reached a peak level (943.73 pg/ml) during stage III after which it started declining sharply as the oocytes attained stage IV (219.22 pg/ml). In the ovary, however, estradiol-17β was detectable during immature stage I oocytes (215.65 pg/g). The level increased steadily during stage II oocytes (716.24 pg/g) and showed a peak (1160.25 pg/g) as it attained stage III. As with haemolymph, the level dropped significantly when the oocytes attained stage IV (406.82 pg/g). An overall significant variation was observed in the level of estradiol-17β in the haemolymph ($F = 132.68$; d.f. $= 20$; $P < 0.001$) and ovary ($F = 69.26$; d.f. $= 20$; 69.26; $P < 0.001$) during ovarian recrudescence. MNK test conducted between the groups also indicated that the observed changes were significant at 5% level.

### Changes in the level of progesterone

Changes in levels of progesterone in haemolymph and ovary are depicted in Fig. 5. The progesterone level of haemolymph was also below detectable limits as with estradiol-17β in the haemolymph, when the oocytes mainly contained stage I oocytes. Progesterone started appearing in the haemolymph during stage II oocytes (194.30 pg/ml) and a progressive increase in the level was observed throughout the remaining stages. The observed levels of progesterone during stages III and IV were 448.56 and 759.04 ng/ml, respectively. In the ovary, however, the progesterone was detectable during immature stage I oocytes (118.25 pg/g) as with estradiol-17β in the ovary. The level increased steadily during stage II (327.82 pg/g) and stage III (671.04 pg/g) oocytes. Stage IV oocytes showed a peak level of progesterone (924.11 pg/g) as observed with progesterone level in the haemolymph. The level of progesterone also exhibited a significant variation in the haemolymph ($F = 105.12$; d.f. $= 20$; $P < 0.001$) and ovary ($F = 102.39$; d.f. $= 20$; $P <$

0.001) during ovarian maturation and subsequently-conducted MNK test also showed significant ($P < 0.05$) changes between different stages.

### Variation in the level of 5-HT in brain and thoracic ganglia

The brain and thoracic ganglia of the female lobsters were divided into four types after authenticating the stage of ovarian maturation through the ovarian histology carried out from the corresponding individual. HPLC-EC analysis conducted on the levels of 5-HT in the brain and thoracic ganglia of female *P. homarus* clearly indicated a gradual increase from the immature stage I oocytes to post-vitellogenic stage IV oocytes (Fig. 6). The level of 5-HT in the brain ganglia was at first 201.53 ng/g when the ovary was seen with only immature stage I oocytes. During the progressive changes of oocytes, i.e., from stage II maturing oocytes to stage III vitellogenic oocytes and stage IV post-vitellogenic oocytes, the level of 5-HT was also elevated significantly to 455.04, 706.11, and 942.30 ng/g, respectively. A similar trend was noticed in the level of 5-HT in the thoracic ganglia. The levels of 5-HT observed in the thoracic ganglia during stages I, II, III, and IV were 115.27, 374.15, 665.53, and 1042.20 ng/g, respectively. An overall significant variation was observed in the level of 5-HT in the brain ($F = 93.64$; d.f. = 20; $P < 0.001$) and thoracic ($F = 146.24$; d.f. = 20; $P < 0.001$) ganglia during different phases of ovarian development. Following this the data were subjected to MNK test and the observed levels were significantly different between the groups at 5% level.

### Immunocytochemical changes of 5-HT neurons in the brain and thoracic ganglia

Changes in the distribution pattern of 5-HT immunopositive cells and neurons in the brain and thoracic ganglia were analysed using an antibody against 5-HT during the different phases of ovarian maturation. A distinct difference was noticed in both the regions throughout the four stages examined in this study (Fig. 7–14). During stage I immature ovarian stage, there were few immunoreactive cell bodies and some of them were inactive in some areas of brain and thoracic ganglia (Fig. 7 and 11). The abundance of immunopositive cell bodies was gradually increasing during stages II (Fig. 8 and 12), III (Fig. 9 and 13), and IV (Fig. 10 and 14) correlating with the advancement of ovarian maturation. Many somata and neurons were found active at the ovulatory phase of oocytes maturation.

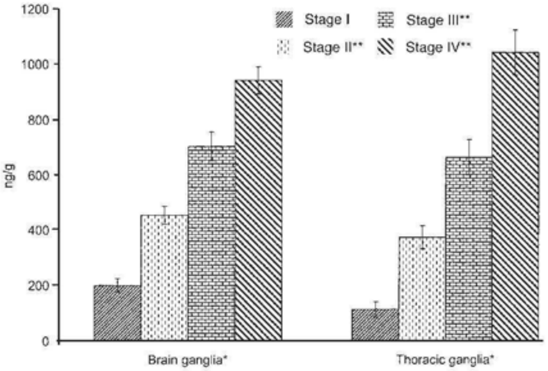

**Fig. 6** Changes in the levels of 5-hydroxytryptamine in brain and thoracic ganglia during various stages of ovarian recrudescence in *Panulirus homarus*. (Values are means ± SEM; $n = 6$; $^{*}P < 0.001$ (One-way analysis of variance), and $^{**}P < 0.05$ (Multiple Newman-Keuls' test).)

## DISCUSSION

The results of the present study demonstrate progressive changes in the level and activity of 5-HT in the brain and thoracic ganglia of the spiny lobster *P. homarus* during the different phases of ovarian maturation. An overall positive correlation was also observed with the levels of estradiol-17β and progesterone in both haemolymph and ovary. These changes appear to be brought about through some other factors like inhibiting/stimulating neuropeptides present in the XO-SG complex of the eyestalk and/or through the action of vertebrate-type of steroid hormones synthesised locally in the ovary.

In lower vertebrates like fishes, ovarian maturation is regulated in two phases. During the first phase the proliferation of oogonial cells and yolk accumulation are controlled by estradiol-17β. Following this, progesterone plays a major role in bringing out the final oocyte maturation as a maturation-inducing steroid (Nagahama et al. 1982). We also observed such changes in the haemolymph and ovary of *P. homarus* as reported in fishes.

Endogenous steroid production in crustaceans remained doubtful despite earlier reports on the occurrence of vertebrate type steroids in the haemolymph, mandibular organ, hepatopancreas, and ovary (Couch & Hagino 1983; Couch et al. 1987; Shih 1992, 1993, 1997) and its physiological response in relation to ovarian maturation (Yano 1987; Quackenbush 1994). However, a study conducted by Shih & Liao (1998) has clearly confirmed

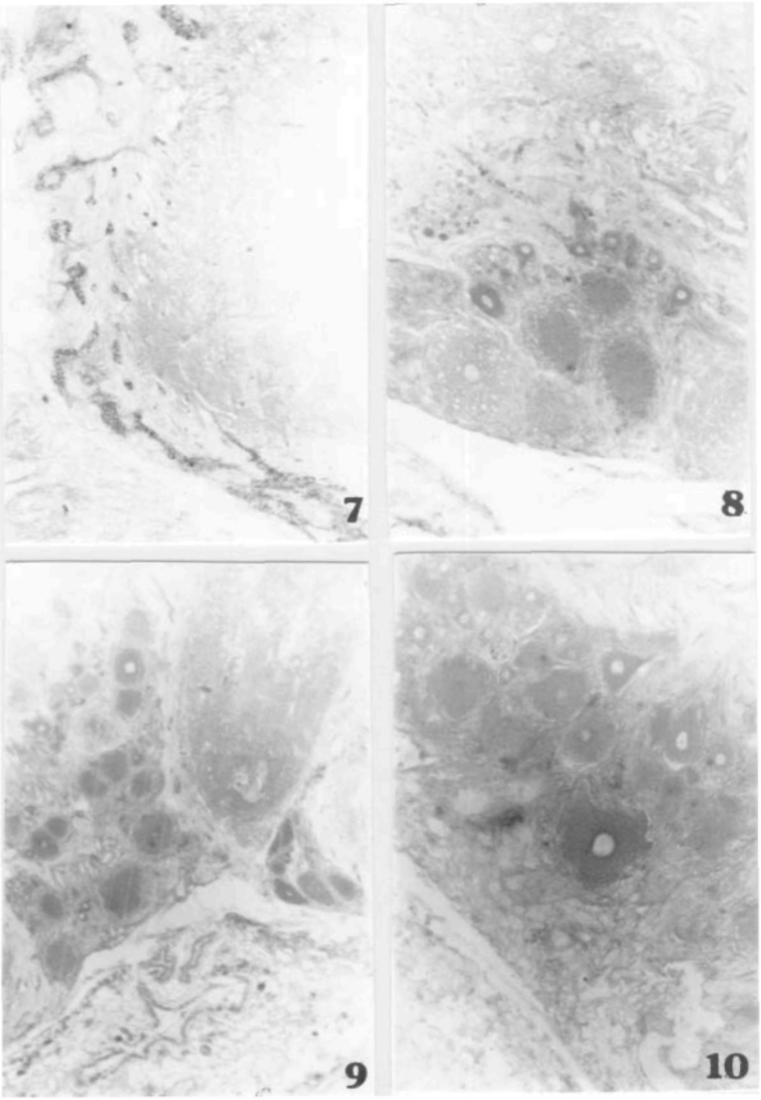

**Fig. 7–10** Cross-sections of brain ganglia showing immunoreactively progressive changes in the distribution and activity of 5-hydroxytryptaminergic neurons when the oocytes were in: **Fig. 7** immature stage I; **Fig. 8** maturing stage II; **Fig. 9** vitellogenic stage III; and **Fig. 10** post-vitellogenic stage IV oocytes in *Panulirus homarus*. × 400.

the conversion ability of cholesterol to sex steroid-like substances in the crab *Micytris brevidactylus*.

Hence, the steroid biosynthesis which occurs locally in the gonadal tissue is responsible for the proliferation of oocytes, accumulation of yolk material through its action on the hepatopancreas by active transport in haemolymph, and finally in the induction of maturational processes. However, the active synthesis of these steroids is initiated by other factors located centrally.

The XO-SG complex is a conglomeration of over 120 neurons in the eyestalk (Beltz 1988; Garcia & Arechiga 1988) that are known to secrete at least two major groups of neuropeptides, namely, the crustacean hyperglycemic hormone (CHH) family and chromatophorotropins. The primary physiological roles of the CHH family, which includes the gonad inhibiting hormone (GIH), moult inhibiting hormone (MIH), and mandibular organ-inhibiting hormone are now well established. Nevertheless, a multifunctional role of these peptides has also been proven in several studies. With regard to regulation of moulting, MIH acts mainly by inhibiting the synthesis of ecdysteroids by the Y-organ, but CHH also has an inhibitory effect on the synthesis of this hormone, although CHH was much less effective than MIH in this respect. It may be because of the sharing of a high degree of homology observed

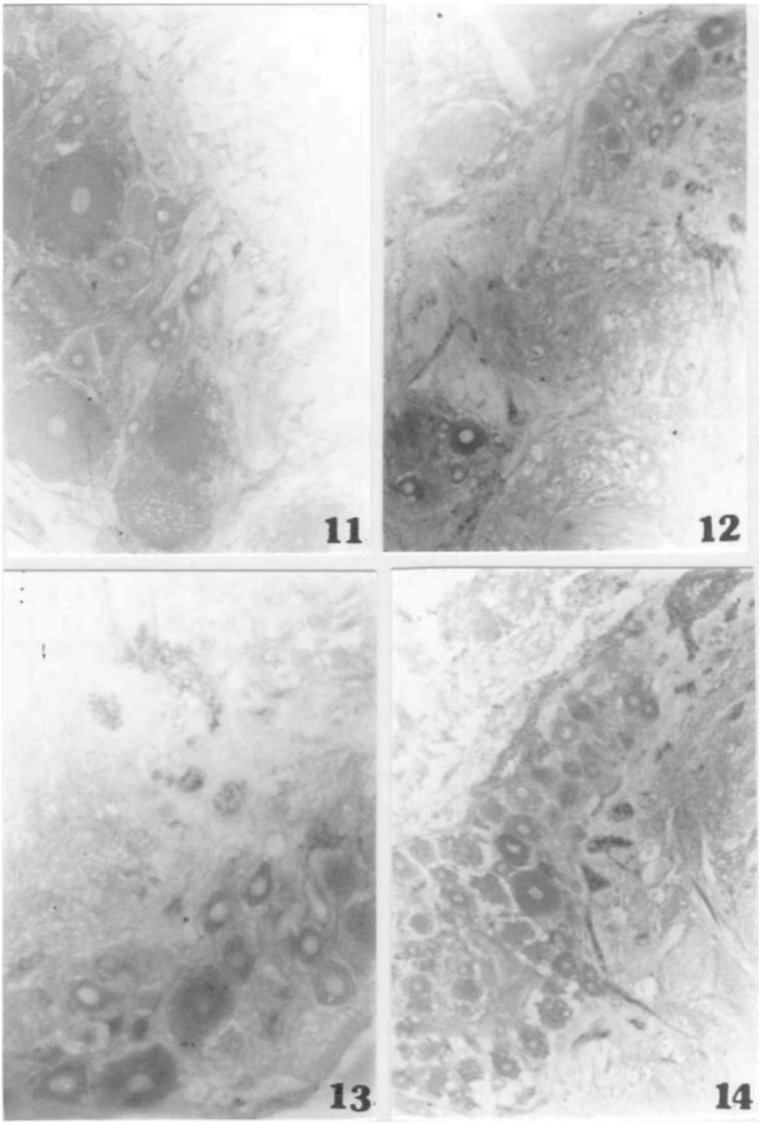

**Fig. 11–14** Cross-sections of thoracic ganglia showing immunoreactively progressive changes in the distribution and activity of 5-hydroxytryptaminergic neurons when the oocytes were in: **Fig. 11** immature stage I; **Fig. 12** maturing stage II; **Fig. 13** vitellogenic stage III; and **Fig. 14** post-vitellogenic stage IV oocytes in *Panulirus homarus*. × 400.

within the CHH family of neuropeptides, which consist of 72–78 amino acids with six conserved cysteine residues.

Similarly, red pigment concentrating hormone (RPCH), a chromatophorotropin, exhibits a variety of physiological roles in various crustacean species apart from promoting the retraction of the pigmentary matrix in tegumentary erythrophores; as a central neurotransmitter in the crab and lobster stomatogastric network (Nausbaum & Marder 1988; Dickinson & Marder 1989) and in the swimmeret system of crayfish (Sherff & Mulloney 1991), and as a stimulator of gonadal maturation (Fingerman 1997a).

An approach to induce ovarian maturation and spawning was proposed by Fingerman (1997b) based on the observation that 5-HT induces ovarian maturation both *in vivo* and *in vitro* in *Procambarus clarkii* by acting to simulate release of a gonad stimulating hormone (GSH) from the brain and thoracic ganglia. Whereas GSH release is stimulated by 5-HT and RPCH, GSH release is inhibited by dopamine (DA) and methionine enkephalin. Meanwhile, GIH release itself is stimulated by methionine enkephalin and DA. However, in this regard, the structure of GSH is yet to be identified. In the present investigation, we observed uniform growth of oocytes which were well synchronised with the activity and level of 5-HT in the brain and thoracic ganglia. However, the data on the level of estradiol-17β in the ovary did not show any modulation in the 5-HT level during stage IV. Therefore, such a refined activity of this steroid hormone, which was observed several times lower than 5-HT, suggests only the occurrence of a temporal modulation of 5-HT production in the CNS during gonadal maturation. This aspect requires further elucidation at the receptor level.

Several physiological studies conducted recently indicated functional evidence for the existence of more than one receptor type for 5-HT, which was subsequently confirmed through radioligand binding techniques (Tierney 2001). Information on invertebrate 5-HT receptors has been augmented by the cloning of 5-HT receptor genes from insects, mollusks, and nematodes. The 5-HT-dro receptor was the first invertebrate 5-HT receptor to be sequenced (Witz et al. 1990). So far, 11 additional receptor genes have been cloned from *Drosophilla*, *Lymnaea*, *Aplysia*, *Caenorhabditis*, and *Ascaris*. 5-HT receptor studies began with the recognition that 5-HT had potent actions on invertebrate tissues, that it mediated many functions in the CNS and periphery, and that the effects of the transmitter were likely to be a result of multiple receptor subtypes (Hen 1992).

The possibility of a non-central action of indoleamines is suggested by high levels of 5-HT and melatonin in birds and mammals, including humans (Sirotkin & Schaeffer 1997). Bodis et al. (1992) noticed a high concentration of 5-HT in follicular fluid which changes in association with the ovulatory cycle. More interestingly, Vasela et al. (2003) have reported the existence and expression of functional 5-HT (5-HT 1D) receptor in mice. Stricker & Smythe (2001) have also demonstrated earlier that 5-HT can cause immature oocytes to undergo an increase in cAMP, which stimulates rather than inhibits meiotic maturation in marine nemertean worms. A cAMP-mediated stimulation of germinal vesicle breakdown (GVBD) during 5-HT triggered maturation is further supported by the fact that protein kinase A inhibitors effectively block 5-HT induction of GVBD. Although the present study is the first one to demonstrate a synchronisation of ovarian maturation with steroidal hormone profile and changes in the level and activity of 5-HT, the occurrence of 5-HT receptors in the ovary should be elucidated further to confirm the direct/indirect role of 5-HT during ovarian maturational processes in *P. homarus*.

## CONCLUSIONS

The ovary of *P. homarus* underwent a progressive change during different phases of maturation. The changes in the levels of vertebrate-type steroids (estradiol-17β and progesterone) observed in the haemolymph and ovary indicated their involvement at the time of ovarian recrudescence. HPLC-EC analysis of 5-HT showed a gradual increment in the brain and thoracic ganglia implying its major role in differentiation of oocytes from the immature stage to the fully ovulated stage. The presence of several immunopositive 5-HT cell bodies seen in the brain and thoracic ganglia support this view. Thus, a direct positive correlation was observed for the first time between gonadal steroids levels and the 5-HT level and activity in the brain and thoracic ganglia as the oocytes progressed towards the advanced stage of maturation. Further studies on the localisation of 5-HT receptors in the ovary of *P. homarus* would be helpful to understand the maturational processes more efficiently.

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# Growth and moulting of captive *Panulirus homarus homarus* in Kenya, western Indian Ocean

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**Abstract** *Panulirus homarus homarus* is the most widely distributed of the three *P. homarus* subspecies and is the second most important spiny lobster in the Kenyan lobster fishery after *Panulirus ornatus*. Growth and moulting of lobsters held in concrete tanks with a flow-through sea-water system and at ambient temperatures, were monitored for 18 months (October 2001 – March 2003). Both moult increment and moulting frequency were inversely correlated with size. Mean moult increment ranged from 4 mm in the 36–45 mm carapace length (CL) size class to 0.6 mm in the 86–95 mm CL size class. Mean intermoult period increased from 49 days in the 46–55 mm CL size class to 66 days in the 76–85 mm CL size class. Growth rates were 19% and 46% higher for males and females, respectively during the south-east monsoon (low temperature) season than during the north-east monsoon (high temperature) season. A shift in energy use from growth to reproduction rather than the influence of temperature was responsible for the variation in the growth rates between the two seasons. Marking-induced injury caused a significant 65% growth reduction in the affected individuals. Mean moult increments calculated for most size classes of uninjured lobsters were comparable to those observed in the subtropical *P. homarus rubellus* reared in the laboratory in South Africa but smaller than those reported in the Indian *P. homarus* under similar conditions.

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## INTRODUCTION

The scalloped spiny lobster *Panulirus homarus homarus* (Linnaeus 1758) is the most widely distributed of the three subspecies of *P. homarus* and is found throughout the Indo-Pacific region with pockets of high concentrations in East Africa and Indonesia (Berry 1974; Pollock 1993). The other two subspecies, *P. homarus megasculptus* and *P. homarus rubellus*, are restricted to the Arabian Sea and the south-east coasts of Madagascar and Southern Africa, respectively. All three subspecies inhabit shallow waters mostly between 1 and 5 m depth among rocks, often in the surf zone and sometimes in highly turbid estuarine areas (Holthuis 1991). However, they respond to different environmental conditions that prevail in their respective areas (George 1997).

Populations of *P. homarus homarus* on the East African coastline occur between those of *P. homarus megasculptus* (to the north) and *P. homarus rubellus* (to the south) with respective populations overlapping at the flanks. Hybrids are common in areas where the subspecies overlap (Pollock 1993). Successful interbreeding suggests that these subspecific separations are fairly recent (George 1997). *P. homarus homarus* is the second most important spiny lobster in the Kenyan lobster fishery after *P. ornatus* and accounts for c. 32% of the total landings (Kulmiye 2004). The Kenyan lobster fishery is artisanal in nature and represents one of the few activities from which local fishers derive a good return since spiny lobsters fetch far higher prices per unit weight than finfish and other crustaceans.

Despite its wide distribution and local importance, an in-depth study on many fundamental aspects of the biology, ecology, and fishery of *P. homarus homarus* is lacking in the western Indian Ocean. Previous studies on *P. homarus* have either exclusively dealt with the other two subspecies

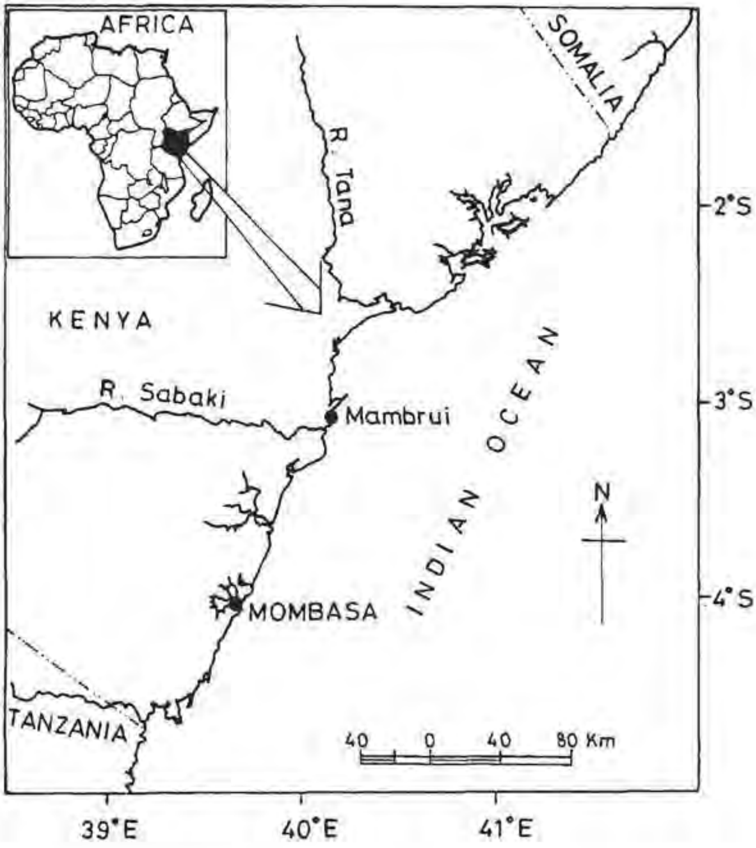


**Fig. 1** Map of the Kenyan coast showing location of the live lobster collection site (Mambrui) and the rearing experimental station (Mombasa).

(Heydorn 1969; Berry 1970, 1971a,b; Smale 1978; Al-Abdulsalaam 1989; Johnson & Al-Abdulsalaam 1991; Liss et al. 1994; Fielding 1997; Mohan 1997; Fielding & Mann 1999) or addressed *P. homarus homarus* populations outside the region (De Bruin 1962, 1969; Jayawickrema 1991; Jayakody 1989, 1993; Thuy 2000). In this paper we present and discuss the growth and moulting of male and female *P. homarus homarus* monitored for 18 months in captivity.

## MATERIALS AND METHODS

### Specimen collection and laboratory conditions

This experiment was performed at the Mombasa Station of the Kenya Marine and Fisheries Research Institute. Lobsters were hand-collected at night by wading fishers from the reefs at Mambrui (Fig. 1) and were immediately put in large polythene bags with aerated sea water. They were brought to the laboratory and released into four outdoor, sheltered concrete tanks (193 × 103 × 106 cm) with a flow-through sea-water system and good aeration. After a 5-day acclimatisation period, each lobster was measured (carapace length (CL) ± 0.1 mm) and tagged by punching coded holes in the uropods and telson with a sterile leather punch for easy identification (Chittleborough 1976; Plaut & Fishelson 1991). Lobsters were provided with artificial shelters using flat coral rocks and asbestos tubes. All the size classes dealt with in the experiment were stocked in each tank at a density of 10 individuals per m$^2$. Mortalities were occasionally replaced with wild captures of similar sizes. The animals were fed daily *ad libitum* on a diet of deck mussel (*Septifer bilocularis*), clam (*Anadara antiquata*), and chopped fish (mostly reef fish). Food was supplied in the late afternoon and any uneaten food items were removed the following morning. Tanks were cleaned thoroughly once a week.

Although no complications were reported for captive *P. cygnus* and *P. penicillatus* tagged in the same manner (Chittleborough 1976; Plaut &

Fishelson 1991), *P. homarus homarus* developed deteriorating necrotic wounds, which resulted in the complete loss of both telson and uropods for some individuals. All lobsters were quarantined in a recirculating anti-bacterial solution (1 ml Sera Baktopur to 20 litre sea-water ratio) for 3 days while holding tanks were thoroughly cleansed with antiseptic solutions. Except for a few animals with advanced injuries, the majority of the affected lobsters were successfully treated. Subsequent markings of both wild replacements and newly moulted animals were made by tying a numbered Dymo Scotch tape to the base of an antenna with a nylon monofilament line. Growth measurements of newly moulted lobsters were made 3 days after ecdysis when the carapace was hard enough to ensure precise measurements. Carapace length (CL ± 0.1 mm) was measured mid-dorsally from the transverse ridge between the frontal spines to the posterior margin of the cephalothorax using a vernier caliper.

### Temperature and salinity

The rearing experiment was run for 18 months (October 2001 – March 2003) under ambient conditions of sea-water quality and temperature. Measurements of temperature and salinity of holding tanks and the adjacent Tudor Creek (pumping station) were simultaneously made once daily with a portable probe (Aanderaa S/T/D Sensor 3230/ Aanderaa Dupley Unit 3315). Since no marked differences were observed between temperature and salinity readings recorded from the tanks and those from the creek, the daily data were combined and mean monthly readings calculated for both temperature and salinity.

### Analytical methods

For statistical purposes, data sets for injured and uninjured lobsters were treated separately and compared for differences using Students' *t*-test and ANOVA. Data for uninjured lobsters were further used to estimate growth parameters as well as to assess the effect of temperature on growth and the intermoult period. For interpretation of moult increment and intermoult period, size class averages were taken. The von Bertalanffy growth function (von Bertalanffy 1938) was used to estimate growth rates:

$$L_t = L_\infty \left(1 - e^{(-K(t - t_0))}\right) \qquad (1)$$

where $L_t$ is the predicted carapace length at age $t$, $L_\infty$, the asymptotic CL (mm), $K$, the growth constant (year$^{-1}$), $t$, the age (year), and $t_0$, the age at zero length. Growth parameters were estimated using Fabens' method (Fabens' 1965) by fitting a rearranged function of Equation 1 to the data on moult increment and intermoult period using FISAT software (Gayanilo et al. 1996):

$$L_2 = L_1 + (L_\infty - L_1) * \left(1 - e^{(-K(t_2 - t_1))}\right) \qquad (2)$$

where $L_1$ is the CL at the marking (initial moult), $L_2$ is the CL at the remarking (following moult), and $t_1$ and $t_2$ are the corresponding dates.

## RESULTS

### Growth in captivity

The mean moult increments of males and females separated into injured and uninjured lobsters are presented in Fig. 2A,B. In the smallest (36–45 mm CL) size class, uninjured males and females attained almost similar moult increments (4 mm CL). Moult increment of uninjured males steadily decreased to 0.6 mm CL in the 86–95 mm CL size class. Female moult increment also decreased to 1.1 mm CL in the 46–55 mm CL size class before recovering and stabilising at 1.6 mm CL in the 66–75 and 76–85 mm CL size classes. There were no significant differences in the mean moult increments among size classes and within sexes of uninjured lobsters except in the 46–55 and 56–65 mm CL female size classes ($P < 0.05$, multiple comparisons among pairs of means, Tukey Honest Significant Difference (HDS) test). Variability in moult increment was high between individual lobsters and between moults of the same individual.

Moult increments of injured male and female lobsters ranged between 0.6 and 1.8 mm CL with no significant differences observed among size classes and within sexes ($F = 1.2695$, $P > 0.05$, one-way ANOVA). The effect of injury on growth was examined by comparing the moult increments of injured and uninjured lobsters (Table 1). Injury significantly affected the moult increment of lobsters, regardless of size, depressing it by an average of 1.06 mm CL (range 0.77–1.16 mm CL) amounting to 65% reduction.

### Growth parameters

By directly fitting Fabens' method (Equation 2) to the data on moult increment and intermoult period for the uninjured male and female lobsters, growth parameters, $L_\infty$ and $K$, were estimated (Table 2). However, the theoretical $L_\infty$ values estimated for the

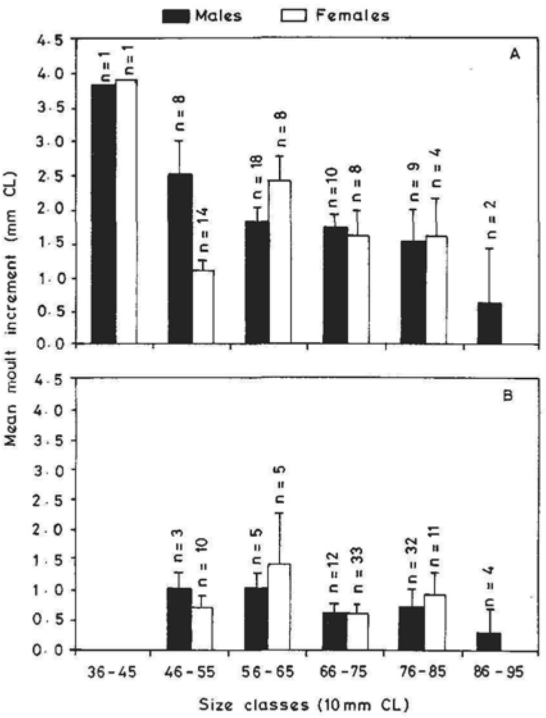


**Fig. 2** Mean moult increment of **A**, uninjured and **B**, injured male and female *Panulirus homarus homarus* in captivity. Bars indicate standard error (+ SE).

captive lobsters were smaller than the maximum sizes observed in the commercial catch for both males and females (115 and 105 mm CL, respectively; Kulmiye 2004). This indicates that $L_\infty$ was underestimated and $K$ was overestimated because the two growth parameters are inversely related (Pauly 1979). Misleading values of $L_\infty$ can be obtained when high variability in moult increment is observed among individual captive lobsters, as was the case in this study.

In an attempt to obtain more realistic growth parameters, the data were recalculated by running the growth routine again with fixed $L_\infty$ values (i.e., 115 and 105 mm CL, for males and females, respectively) employing Munro's Method (Munro 1982) and the resulting parameters are given in Table 2. The estimated parameters were in turn used to plot the growth curves (Fig. 3). The predicted growth patterns are very similar for both sexes until a CL of 72 mm is attained, after which females grow more slowly than males.

## Moulting in captivity

Intermoult periods of injured and uninjured animals that moulted twice or more in captivity are summarised in Table 3. Intermoult period increased with increase in size in both injured and uninjured lobsters. This pattern was, however, more pronounced for the uninjured animals where there were significant differences among the size classes and within sexes ($F = 7.492$, $P < 0.05$; one-way

**Table 1** Comparison of the moult increment between injured and uninjured lobsters within four size classes. (CL, carapace length.)

| Size class (mm CL) | Status | No. of observations | Mean (± SE) moult increment (mm CL) | *t* (d.f.) | *P* level |
|---|---|---|---|---|---|
| 46–55 | Injured | 13 | 0.76 ± 0.12 | 2.3676 (33) | 0.0239* |
| | Uninjured | 22 | 1.53 ± 0.23 | | |
| 56–65 | Injured | 10 | 0.88 ± 0.27 | 4.5226(34) | 0.0001* |
| | Uninjured | 26 | 2.04 ± 0.18 | | |
| 65–75 | Injured | 45 | 0.56 ± 0.12 | 4.0627 (61) | 0.0014* |
| | Uninjured | 18 | 1.57 ± 0.19 | | |
| 76–85 | Injured | 43 | 0.67 ± 0.13 | 2.9798 (55) | 0.0042* |
| | Uninjured | 13 | 1.51 ± 0.32 | | |
| Overall mean: | Injured | 111 | 0.66 ± 0.07 | 4.8560 (188) | 0.0003* |
| | Uninjured | 79 | 1.72 ± 0.11 | | |

*Significant.

ANOVA). The intermoult period of smaller uninjured lobsters (46–55 mm CL) was c. 50 days, whereas that of the larger uninjured ones (76–85 mm CL) was 66 days. For the injured lobsters, the corresponding intermoult period of the smaller and the larger individuals was 57 and 67 days, respectively. On an annual basis, the smaller uninjured lobsters (46–55 mm CL) potentially undergo an average of 7.4 moults compared with 5.5 moults for the larger ones (76–85 mm CL). The effects of sex and injury on intermoult period were examined using two-way ANOVA (Table 4). Injury affected the intermoult period with injured animals moulting less frequently than uninjured lobsters. However, this effect progressively diminished as size increased. Overall, the intermoult period of injured lobsters was 8 days longer than that of uninjured individuals. The intermoult period was not affected by sex ($P > 0.05$), though females tended to have slightly longer intermoult periods than males, especially those below 66–75 mm CL size class.

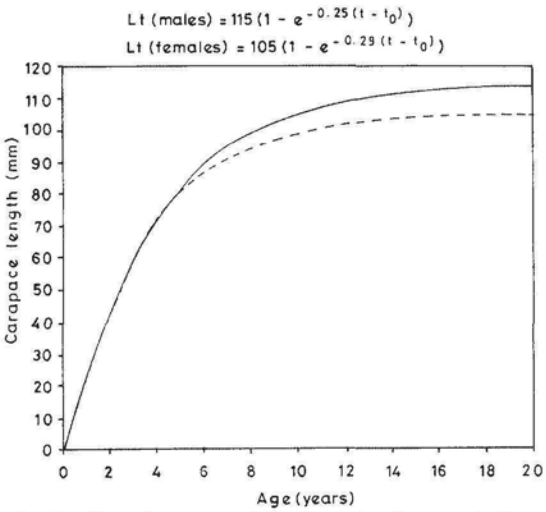


**Fig. 3** Growth curves of the Bertalanffy growth function for uninjured male and female *Panulirus homarus homarus* in captivity. (*Lt*, predicted carapace length at age $t$; $t_0$, age at zero length.)

**Table 2** Growth parameters for captive uninjured male and female *Panulirus homarus homarus* estimated with "fixed" and "unfixed" $L_\infty$ routines using two different methods. (CL, carapace length.) ([a] represents values used to fix male and female $L_\infty$ which correspond to the largest animals encountered in the commercial catch.)

| | | Method | |
|---|---|---|---|
| Sex | Parameter | Fabens (unfixed $L_\infty$) | Munro (fixed $L_\infty$) |
| Males | $L_\infty$ (mm CL) | 95.90 | 115.00[a] |
| | $K$ (year $^{-1}$) | 0.49 | 0.25 |
| Females | $L_\infty$ (mm CL) | 93.10 | 105.00[a] |
| | $K$ (year$^{-1}$) | 0.40 | 0.29 |

**Table 3** Intermoult period of injured and uninjured male and female *Panulirus homarus homarus* in captivity. (CL, carapace length.)

| Size class | | No. of observations | | Mean (± SE) intermoult periods (days) | | Mean annual moulting frequency | |
|---|---|---|---|---|---|---|---|
| (mm CL) | Sex | Uninjured | Injured | Uninjured | Injured | Uninjured | Injured |
| 46–55 | males | 7 | 2 | 49 (2.3) | 55 (4.9) | 7.4 | 6.6 |
| | females | 11 | 8 | 52 (2.7) | 58 (2.5) | 7.0 | 6.3 |
| 56–65 | males | 12 | 5 | 50 (2.3) | 57 (2.7) | 7.3 | 6.4 |
| | females | 7 | 2 | 57 (1.9) | 60 (3.5) | 6.4 | 6.1 |
| 66–75 | males | 7 | 4 | 61 (3.0) | 59 (1.5) | 6.0 | 6.2 |
| | females | 6 | 26 | 64 (2.5) | 66 (2.0) | 5.7 | 5.4 |
| 76–85 | males | 8 | 31 | 66 (2.5) | 67 (3.6) | 5.5 | 5.4 |
| | females | 3 | 10 | 66 (4.0) | 67 (2.8) | 5.5 | 5.4 |
| 86–95 | males | 1 | 3 | 81 | 71 (6.4) | – | 5.1 |
| Combined | | 93 | 61 | 57 (1.3) | 65 (1.4) | 5.6 | 6.4 |

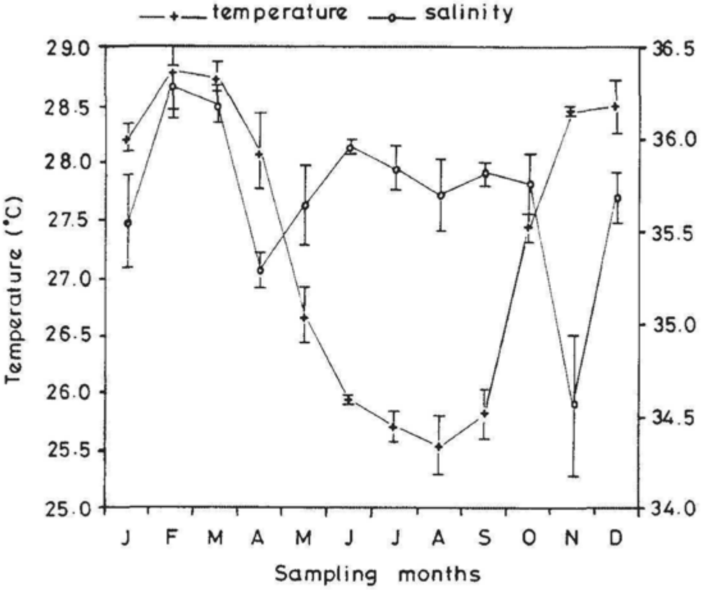


**Fig. 4** Seasonal trends of water temperature and salinity measured as mean monthly temperature and mean monthly salinity (data for all holding tanks and adjacent Tudor Creek pooled). Bars indicate standard deviation (± SD).

**Table 4** Results from two-way ANOVA of the effects of sex and injury on intermoult periods of *Panulirus homarus homarus* in captivity. (NS, not significant.)

| Source of variation | d.f. | SS | MS | *F* | *P* level |
|---|---|---|---|---|---|
| Sex | 1 | 6.848 | 6.848 | 0.430 | 0.836 NS |
| Injury | 1 | 1963.123 | 1963.123 | 12.321 | 0.001* |
| Sex × Injury (interaction) | 1 | 31.302 | 31.302 | 0.196 | 0.658 NS |
| Within groups (error) | 146 | 23263.015 | 159.336 | | |

*Significant.

## Temperature and salinity

The mean monthly water temperature and salinity pooled from the rearing tanks and the adjacent Tudor Creek (from which sea water was pumped) are shown in Fig. 4. Temperature showed a seasonal trend with high values during the north-east monsoon season (November–March) and low values between May and October (south-east monsoon season). There was a 3.2°C difference between the month with the highest temperature (February, 28.7°C) and the one with the lowest temperature (August, 25.5°C). A clearly defined seasonal trend for salinity was absent except for the marked drop in values in both April and November, which correspond to the long and short rains, respectively.

## Growth and temperature

The relationship between temperature and growth was investigated by plotting moult increments of uninjured males and females against sea-water temperature at which the animals moulted (Fig. 5). The moult increment is inversely correlated with temperature, with both males and females attaining higher moult increments at lower temperatures than at higher temperatures. However, the moult increment for females shows a stronger correlation with the sea-water temperature ($r^2 = 0.57$, Fig. 5). Analysis of covariance (ANCOVA, with season as the independent factor, moult increment as the dependent factor, and size as the covariate), also reveals that the difference in the mean moult increment between the south-east

**Fig. 5** Relationship between sea-water temperature and moult increment of uninjured male and female *Panulirus homarus homarus* in captivity.

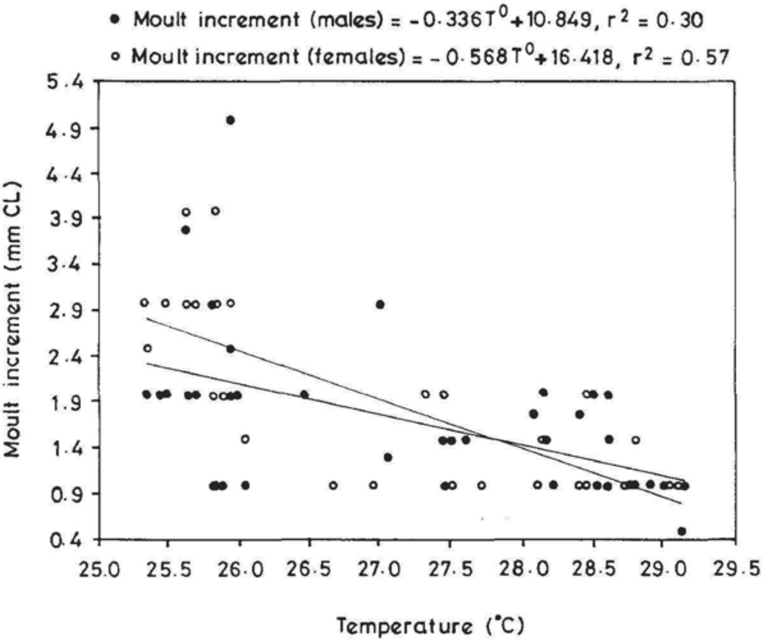
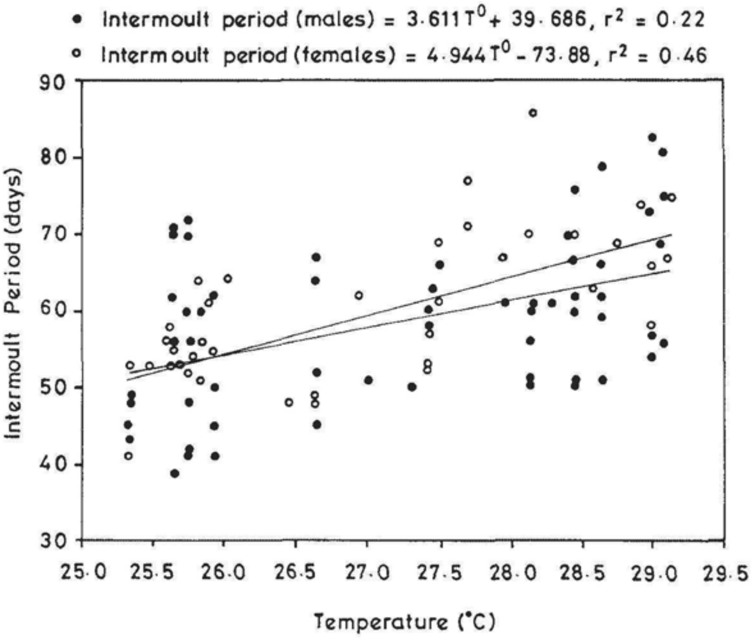


**Fig. 6** Relationship between sea-water temperature and intermoult period of uninjured male and female *Panulirus homarus homarus* in captivity.



monsoon (low temperatures) season and the north-east monsoon (high temperatures) season is significant for females ($P = 0.001$) but not for males ($P = 0.321$). On average, males and females exhibited 19% and 46% larger CL increment per moult, respectively, during the south-east monsoon season in comparison with the values recorded during north-east monsoon season.

### Moulting and temperature

The relationship between temperature and moulting was investigated by plotting intermoult periods of uninjured males and females against the average sea-water temperatures that prevailed during the respective intermoult periods (Fig. 6). The intermoult period is positively correlated with sea-water temperature, with rising temperature resulting in prolonged intermoult periods for both males and females. This correlation is again more pronounced for females ($r^2 = 0.46$) than for males ($r^2 = 0.22$). Analysis of covariance (ANCOVA, with season as the independent factor, intermoult period as the dependent factor, and size as the covariate), also reveals that the difference in the mean intermoult period between the south-east monsoon (low temperatures) season and the north-east monsoon (high temperatures) season is significant for females ($F = 48.026$, $P = 0.000$) but not for males ($F = 0.6614$, $P = 0.4211$). The mean intermoult periods (days) of males and females were 5% and 21% shorter, respectively, during south-east monsoon season in comparison with the values recorded during north-east monsoon season.

## DISCUSSION

### Growth and moulting of uninjured lobsters

The mean moult increment of uninjured *P. homarus homarus* calculated for most size classes in the present study is comparable to that observed in captive *P. homarus rubellus* in South Africa (Berry 1971b) but is noticeably smaller than that reported by Nair et al. (1981) in the Indian *P. homarus* held under laboratory conditions (Table 5). The theoretical maximum sizes ($L_\infty$) predicted for both sexes from growth increment data by the Fabens' method were also relatively smaller than the largest animals observed in the commercial catch (Table 2). Laboratory studies do not always reflect growth under natural conditions, and although all the factors that have been described to influence growth of palinurid lobsters (see Aiken 1980 for review) were either provided in excess (food, shelter, etc.) or taken care of by the tropical climate (temperature, photoperiod, etc.), there were several occasions when oxygen levels in the water gradually dropped from 90% down to 60% saturation as a result of power failure that interrupted both aeration and water inflow. Chittleborough (1975) working with *P. cygnus* reported that low oxygen availability not only lessened size increase at moulting but also increased risk of death if the saturation level dropped to between 47% and 50% during ecdysis. It is therefore possible that the growth rates observed in captive *P. homarus homarus* may have been lower than those in nature as a result of low oxygen availability during power interruptions. Another factor that cannot be ruled out, as a possible cause of low growth rates, is the effect of pathogens on uninjured lobsters in the early part of the study when serious bacterial infection overwhelmed the experiment. Lobsters may have shifted some energy to defensive purposes that would have otherwise been available for growth, resulting in low growth rates.

Despite the possible anomaly between laboratory and natural growth, both moult increment and intermoult period of *P. homarus homarus* followed the general growth pattern of palinurids where the moulting frequency and percentage size increase at moult tend to decrease gradually with increasing size. However, the absence of significant differences in the mean moult increments among the four size classes tested could be attributed to the narrow size range of the lobsters studied, the majority of which were mature and well past their rapid growth phase. The mean moult increments of mature specimens between the size range of 46 and 85 mm CL were more-or-less similar except for the notable decrease in the females of 46–55 mm CL size class. This is also discernible in the predicted growth curves which are very similar for both sexes until a CL of 72 mm is attained. The growth rate of another subspecies, *P. homarus rubellus*, was reported to remain constant throughout much of the sexually mature size range until the upper extremes were attained

**Table 5** Comparison of mean moult increments between populations of *Panulirus homarus* subspecies from three different areas of the Indian Ocean. (CL, carapace length.)

| Source | Location | Subspecies | Sex | Size class (mm CL) | | | |
|---|---|---|---|---|---|---|---|
| | | | | 40–49 | 50–59 | 60–69 | 70–79 |
| Berry (1971b) | South Africa | *P. h. rubellus* | males | – | 2.2 | 2.3* | 2.3* |
| | | | females | – | 2.1 | 2.0* | 2.1* |
| Nair et al. (1981) | India | *P. homarus* | males | 3.5 | 3.1 | 2.9 | – |
| | | | females | 2.5 | 3.0 | 2.3 | – |
| Present study | Kenya | *P. h. homarus* | males | 2.4 | 2.2 | 1.9 | 1.7 |
| | | | females | 1.6 | 1.7 | 2.5 | 1.3 |

*Slightly modified.

(Berry 1971b). The marked drop in female moult increment in the 46–55 mm CL size class signifies the onset of sexual maturity and resource allocation to reproductive activity instead of growth. It is around this size class that females of the other two *P. homarus* subspecies also reach sexual maturity and start reproducing (Heydorn 1969; Berry 1971b; Fielding & Mann 1999).

Although the maximum variation in water temperatures between the south-east and north-east monsoon seasons is only 3.2°C, the growth rate of *P. homarus homarus* is distinctly seasonal and appears to be optimal at the lower limit of the prevailing temperatures in the East African coastal waters. Laboratory held lobsters grew faster at lower temperatures than at higher temperatures because of both increased moult increments and shortened intermoult periods. However, the stronger positive correlation observed to exist between the female intermoult period and temperature as well as the ovipositing of three captive females in February suggest that a shift in energy use from growth to reproduction rather than the influence of high temperature was responsible for the lower growth rates achieved during the north-east monsoon season. Similarly, the higher growth rates attained during the south-east monsoon period are undoubtedly a manifestation of increased energy apportioned to growth since little spawning activity was observed both in the field and in the laboratory. In field conditions, the main mating and egg-bearing season of this subspecies falls within the north-east monsoon period (Kulmiye 2004).

The alternating cycles of high growth rates and spawning activity in line with the changing monsoon seasons suggest a trade-off between reproduction and growth subject to the prevailing environmental factors. The incidence of high temperatures, relatively calm seas, and light winds as well as ocean-bound currents during the north-east monsoon season (McClanahan 1988) seem to be the ideal conditions for the dispersal and survival of larvae. It is therefore advantageous for the animals to invest energy in reproductive activity during this period rather than during the south-east monsoon season when the prevailing conditions are unfavourable.

## Growth and moulting of injured lobsters

Mean moult increments were significantly smaller and mean intermoult periods were longer for injured lobsters than for uninjured individuals kept under the same holding conditions. The observed reduction in the mean moult increment of injured lobsters stemmed mainly from numerous moults with zero growth at moulting during and even after the infection period. It is not unusual for crustacean species to register zero or even negative growth at ecdysis owing to a variety of factors (Aiken 1980; Cockcroft & Goosen 1995). Moults with negative or zero growth seem to signify a shift in energy use from growth to other importunate needs such as reproductive activity, fighting disease, or simply maintenance of basic metabolic requirements in times of hardship. Affected individuals may sacrifice growth altogether at ecdysis but still compensate for the missed growth by markedly increasing in size at subsequent moultings when conditions improve (Travis 1954; Fielder 1964; Thomas 1972). In the present study, several large lobsters showed growth patterns similar to the above observations with zero increase in size at moulting during the infection period and high growth rates at successive moultings following treatment.

Several studies have shown the negative effects of injury on the growth rates of spiny lobsters. Smale (1978) reported lower growth rates for *P. homarus rubellus* similarly tagged and recaptured with necrotic wounds in a field study in comparison with laboratory-held individuals of the same subspecies on the east coast of South Africa (Berry 1971b). Davis (1981) reported that moult increment was 0.5 mm CL smaller and intermoult period 5 weeks longer for injured juvenile *P. argus* than for uninjured ones. Hunt & Lyons (1986) also observed that injury caused a 39% reduction in growth of small *P. argus* (≤60 mm CL) returned by fishers to the sea in Florida. Brown & Caputi (1985) noticed an inverse relationship between growth increment of injured *P. cygnus* and the number of missing limbs.

The implications of injury-induced lobster growth reductions on onset of sexual maturity and fecundity have been discussed (Davis 1981; Brown & Caputi 1985; Hunt & Lyons 1986). Injury-induced fishery yield losses are reported to be significant in both the Western Australian and Floridian lobster fisheries (Davis 1981; Brown & Caputi 1985). In the Kenyan lobster fishery, where divers catch lobsters with spears and other sharp objects, a large but as yet unquantified number of traumatised and injured lobsters are left behind holed up in narrow crevices after divers fail to flush them out during fishing expeditions owing to complexity of the coral reef habitat and/or the crude nature of the catching methods. However, the fate of the affected lobsters and the actual loss to the fishery as a direct result of injuries are not known.

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Short communication

# Conservation of unique patterns of body markings at ecdysis enables identification of individual spiny lobster, *Jasus edwardsii*

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**Abstract** Southern temperate rock lobsters (*Jasus edwardsii*) develop complex body markings and spines that vary uniquely among individuals. These markings are retained after moulting allowing individuals to be recognised without capture or handling in the field. This enables the impact of capture, handling, and tagging procedures on subsequent movements to be more confidently evaluated. Recognition of individuals by natural markings allows post-moult lobsters that were externally tagged and held in large communal tanks to be correctly retagged. Distinctive markings on the pedate processes and on the epistoma, as well as the number and placement of small spines on the antennular plate are particularly useful for recognising individuals. It is highly likely that the other *Jasus* species and the brightly patterned and coloured *Panulirus* species have similar body markings and spine patterns that would aid recognition of individuals.

**Keywords** tagging; pattern; individual; rock lobster

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## INTRODUCTION

Consistent recognition of individuals is a basic requirement in many field and laboratory experiments to determine growth and movement, for example. This requirement is usually satisfied by capturing animals and tagging them with uniquely coded tags. However, the very act of capture and handling can itself lead to stress, injuries, or changes in behaviour and movement that compromise the objective of the tagging programme (Broderick & Godley 1999; Kenward et al. 1999; Cappo et al. 2000; Makinen et al. 2000; Winger & Walsh 2001; Jepsen et al. 2002). Tagging crustaceans can be problematic because they periodically shed their exoskeleton to grow. Any externally applied tag is thus lost along with the exoskeleton. To get around this problem; internally anchored tags are used. One type comprises an internal anchor and an external spaghetti tubing carrying a code. Alternatively, wholly internal tags that are detected visually or by an external electronic detector can be used. Both types of tag can compromise survival or growth (e.g., Benzie et al. 1995; Courtney et al. 2001; Jerry et al. 2001).

The effect of capture and handling on subsequent behaviour and movement can be properly determined only by having a control group that can be recognised by independent means without having to capture animals. In many species some individuals can be recognised by distinctive natural markings or body or fin shape or by scars or other injuries (e.g., Leum & Choat 1980; Stevick et al. 2001; Hillman et al. 2003). MacDiarmid et al. (1991) described the effect of capture and handling on the behaviour and movement of tagged southern rock lobster *Jasus edwardsii* (Hutton) by comparing their behaviour to a subgroup of 30 lobsters that were identified by unique patterns of markings on their pedal processes around the central rostral spine (Fig. 1A). Likewise MacDiarmid & Butler (1999) used the retention of markings after ecdysis to identify and then retag 150 southern rock lobsters used in laboratory experiments. In neither instance were these patterns and

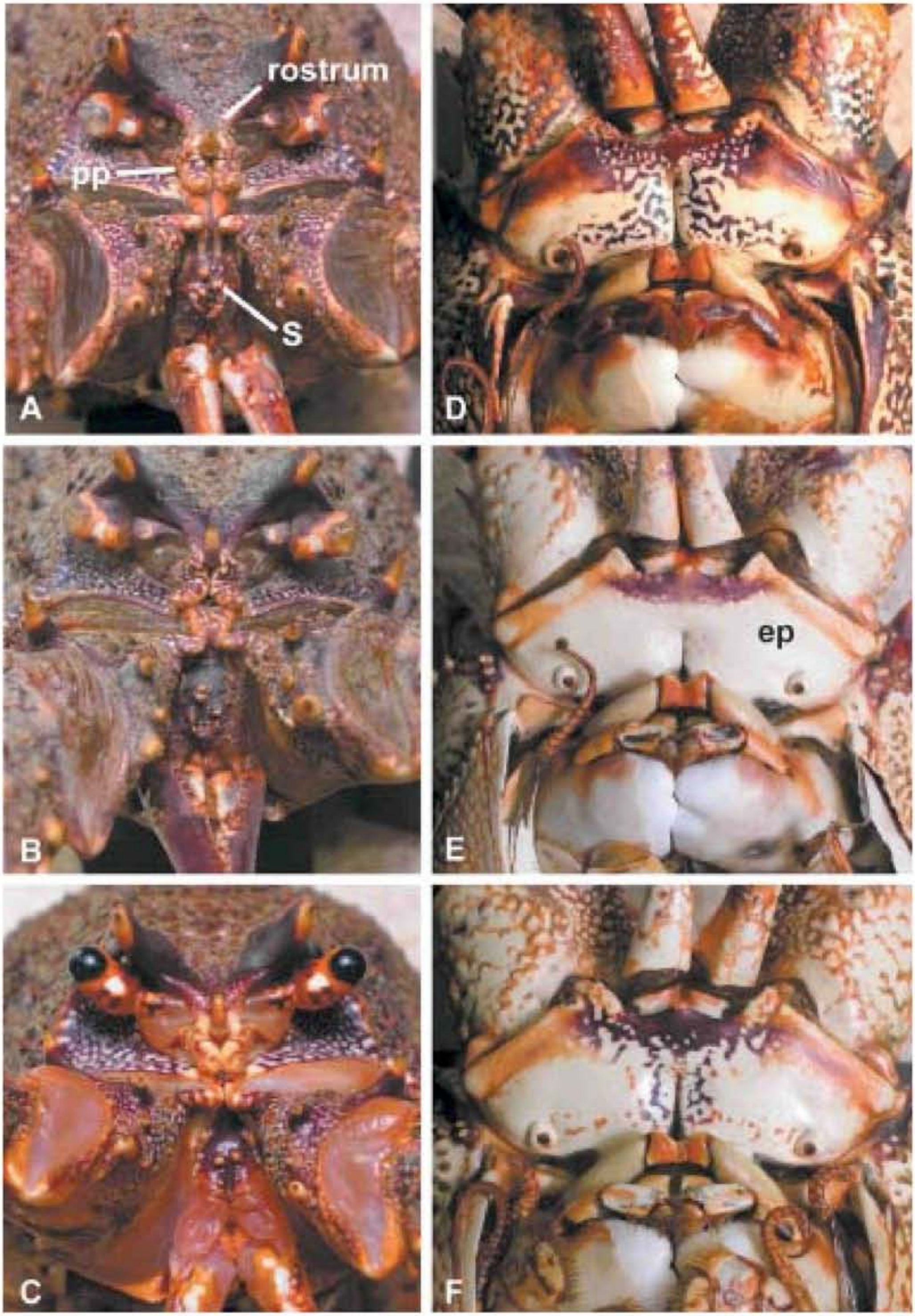

**Fig. 1** Variation in the placement and number of small spines (s) on the antennular plate and in the pattern of markings on the pedate processes (pp) around the rostrum (**A**, **B**, **C**) and on the mid portion of the ventral facing plate-like epistoma (ep) (**D**, **E**, **F**) in three different *Jasus edwardsii*.

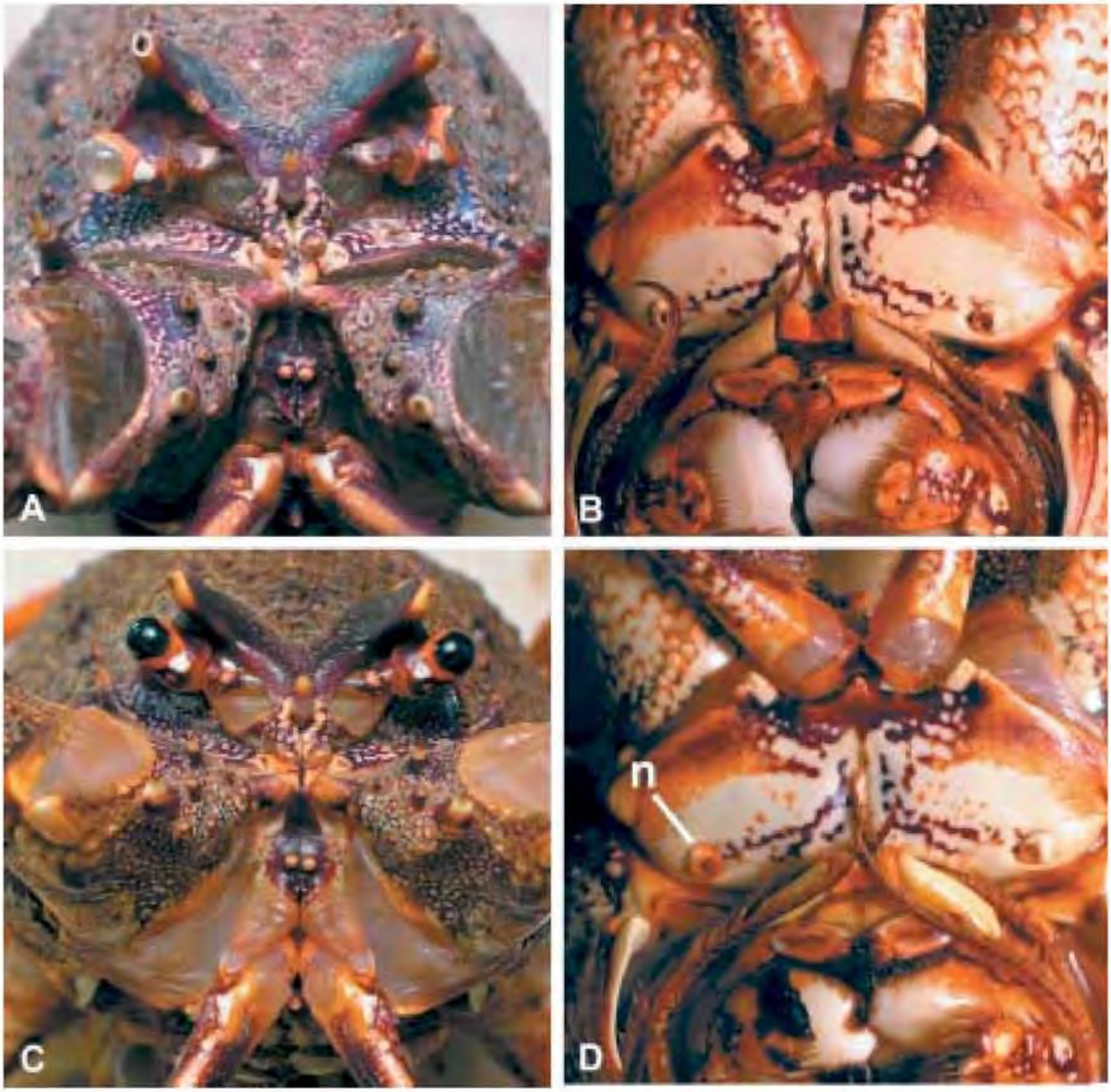

**Fig. 2** Anterior and ventral views of spines and patterns of an individual (**A**, **B**) pre-moult and (**C**, **D**) post-moult *Jasus edwardsii*. (n = nephropore.)

their variation among individuals described or illustrated. Here we describe the patterns and how they vary among individuals, and provide evidence that they are retained through ecdysis.

## METHODS

Fifteen mature male and female *J. edwardsii* were obtained from around the Chatham Islands east of New Zealand and the Wellington coastline at the southern tip of North Island, New Zealand and held in a flow-through sea water system on the shore of Wellington Harbour. Lobsters were measured (carapace length, CL), individually marked with colour coded antennae tags, and distributed to separate 1.8-m diameter, 0.6-m deep concrete holding tanks. The lobsters had continuous access to live food (blue mussels, *Mytilus galloprovincialis*) and were provided shelter from direct light.

The lobsters were checked at least once every day and each newly cast moult was removed and dried. A few days later when the moulted animal was hard enough to handle without injury it was retagged with the same unique colour code and humanely killed by lowering its body temperature to 0°C by placing it in air inside a minus 20°C freezer for c. 1 h. Both the moult and the post-moult animal were then photographed to record the particular unique body features. Routine identification of lobsters using unique body patterns does not require the lobster to be killed or photographed; this was only necessary to obtain high quality photographs suitable for publication. Animal Ethics approval was obtained for all procedures described in this study (NIWA Animal Ethics Committee Approval No. 33).

In addition, juvenile *J. edwardsii* were inspected to determine at what body size the markings and spines could be easily observed with the naked eye.

## RESULTS

Several well-defined features helped to distinguish with the naked eye all individual *J. edwardsii* larger than c. 55 mm CL. First was the number and placement of small blunt spines on the antennular plate that lies on the anterior body wall immediately above the basal connection of the antennules to the body (Fig. 1A–C). These spines can range in number from zero to six and vary in their alignment with one another. Although they are only a few mm high they are conspicuous, even to a diver, as lighter coloured protuberances raised above a darker red or purple background. More varied are the patterns of markings on the pedate processes, bean shaped protuberances either side of the medially positioned rostrum (Fig. 1A–C), and markings on the mid portion of the ventral-facing plate-like epistoma (Fig. 1D–F). Some individuals have very complex patterns (e.g., Fig. 1A,D) whereas others have very few (e.g., Fig. 1C,E).

On juveniles smaller than c. 55 mm CL the patterns of markings on the pedate processes, as well as the number and placement of small spines on the antennular plate, are too small to be easily distinguished by the naked eye but are apparent using a handheld magnifying glass or a low powered binocular microscope. The patterns on the epistoma, however, are visible on juveniles as small as 25 mm CL.

Examination of all 15 lobsters before and after moulting indicated that every individual retained a very similar pattern of markings (Fig. 2). Close examination of these patterns reveals some subtle changes that over successive moults may slowly bring about their transformation. For instance, comparison of the pre- and post-moult epistoma (Fig. 2B and D) shows that on this individual there was an increase in the number of small pale orange dots leading diagonally forward and medially of the nephropore.

## DISCUSSION

The body patterning of *J. edwardsii* varies considerably among individuals. Whereas some individuals have rather bland features others have complex patterns of marks. Comparison of patterning over large areas of the body is difficult because there are few easily recognisable reference points. However, comparison of patterns on small, well-defined, body areas such as the pedate processes and the epistoma reveals considerable variation. Moreover, these patterns are largely retained after moulting though slight modification and elaboration of patterns through successive moults is highly likely. On very small immature *J. edwardsii*, patterns of markings and spine placement can be distinguished only with the aid of magnification but their presence does suggest that the individual markings are present from the earliest benthic phase.

Patterns on the pedate processes and the number and placement of the small spines on the antennular plate have proved particularly useful in the field as they are easily observable by divers without capturing the lobster. These individuals can then serve as controls for determining the effects of capture, handling, and tagging (MacDiarmid et al. 1991). Both these features as well as the patterns on the epistoma have proved useful in quickly and correctly identifying hundreds of post-moult lobsters held in communal tanks (e.g., MacDiarmid & Butler 1999) even though these lobsters have varied considerably in intensity of background body colour from dark red to light purple/pink and pale yellow/orange.

It is highly unlikely that lobsters themselves use these differences in patterning to recognise individuals. The features on the pedate processes are reasonably small and those on the epistoma would not usually be visible to other lobsters. Moreover, recent laboratory experimentation by Raethke (2005) to test for either chemosensory or visual recognition of previous sparing partners by male *J. edwardsii* indicates that after an interval of 24 h there is no recognition.

We have not found any other published reference to patterns allowing identification of individual crustaceans. It is likely, however, that as all the spiny lobsters in the genus *Jasus* have a very similar external morphology (Patterson 1968; George & Kensler 1970) that all species have similar patterns of markings. Moreover, given that many spiny lobsters in the genus *Panulirus* are brightly coloured and highly patterned, individuals of these species may also have unique patterns of markings that would allow recognition. Investigation of these patterns in other species may be fruitful.

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# Visual assessment of the reproductive condition of female western rock lobsters (*Panulirus cygnus*)

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**Abstract** An important issue when surveying the reproductive condition of large numbers of female *Panulirus cygnus* in the field is that each animal must be assessed quickly and accurately on the basis of only a few easily discernable criteria. The four biological criteria most commonly recorded for each lobster are: (1) ovigerous setae condition (not present, partially developed, and fully developed); (2) the presence (unused or eroded) of a spermatophore mass; (3) the presence and developmental stage of external ova; and (4) the visual appearance of the ovaries through the dorso-thoracic musculature. Using the above criteria each female can then be assigned to a reproductive state, i.e., immature, inactive breeder, single breeder, or double breeder. This study compared external assessments with internal cellular development of the ovary (via histology) and elucidated the shortcomings of the external technique. This has resulted in the production of a modified set of criteria that, if applied to samples collected during the peak of the breeding season, enables the breeding state of a female western rock lobster to be more accurately determined in the field without causing it any damage. The height of the breeding season is the optimum time for stock egg production assessment.

**Keywords** lobster; *Panulirus cygnus*; visual assessment; reproductive condition; double breeding

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## INTRODUCTION

The fishery for western rock lobster (*Panulirus cygnus* George) is Australia's most valuable single-species fishery: the average harvest of 11 000 t each year is worth c. AU$350 million. The sustainability of this valuable fishery has consequently been a focus of research since the 1970s, with the legal minimum size (76–77 mm carapace length) being below the size at first maturity in most regions of the fishery (Chittleborough 1976; Grey 1979). The western rock lobster is thus vulnerable to recruitment over-fishing. In recent years, egg production has been closely monitored during an annual survey to check if the fishery is sustainable (Melville-Smith et al. 1998; Hall & Chubb 2001; Caputi et al. 2003). The annual egg production survey is conducted independently of commercial fishing over a 10-day period that spans the last new moon before the start of the commercial fishing season on 15 November. Since collection of all females for dissection in the laboratory is not practical or very sustainable (over 5000 females are sampled each year), the reproductive state of each female is assessed quickly and accurately using external characteristics, thereby allowing them to be returned to the water unharmed.

Studies have generally assumed that female palinurids with ovigerous setae are sexually mature and thus likely to spawn within the breeding season (George 1958; Fielder 1964; Montgomery 1992); however, Chittleborough (1976) showed that, in the laboratory, female *P. cygnus* did not necessarily breed once they developed ovigerous setae. More recently, Chubb (1991) used a combination of external characteristics, namely the stage of external ova, presence or absence of a spermatophoric mass, and ovary condition (assessed through the dorso-thoracic musculature), to determine whether a female is mature and if so, whether she will produce either one or two batches of eggs over that breeding season. However, the assessment of ovary condition used by Chubb (1991) was not confirmed histologically by that author and as such, has the potential to miss-assign maturity state.

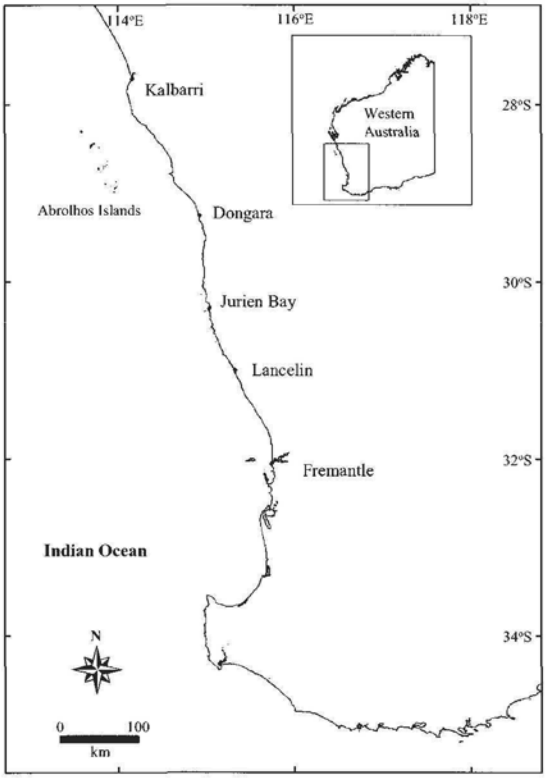

**Fig. 1** Map showing the locations of the fishery-independent egg production surveys in October/November 2002.

The present study was initiated to confirm, at a cellular level using light microscopy, the developmental condition of an ovary and how this relates to the accuracy of the non-invasive visual stage as described by Chubb (1991) and currently employed in the analysis of the annual egg production surveys in this fishery.

## METHODS

### Data sources

A total of 8541 female *P. cygnus* were collected by trapping during the western rock lobster fishery-independent egg production surveys at the Abrolhos Islands, Kalbarri, Dongara, Jurien Bay, Lancelin, and Fremantle on the Western Australian coast (Fig. 1) in October/November 2002, which corresponds with the peak of egg extrusion and fertilisation by female *P. cygnus* (Chubb 1991). All traps were set for a fixed period of time (24 h) in areas used by this species for breeding (Chubb 1991).

For every female lobster, the carapace length (CL), i.e., from the anterior edge of the carapace between the preorbital spines down the mid-dorsal line to the posterior edge of the carapace, was measured to the nearest mm. The state of ovigerous setae on the endopodites of the pleopods was recorded as either "not present", "immature setae" (partially developed), or "mature setae" (fully developed) (Gregory & Labisky 1981). The absence or presence and developmental stage of external ova attached to the setae were recorded as "absent", "early phase" (bright orange ova, no visible eye spots), "mid phase" (dark/dull orange ova, visible eye spots), "late phase" (dark/grey ova, visible eye spots), or "post hatching" (egg shells still attached). The absence or presence of a spermatophoric mass on the sternum was recorded as "no spermatophoric mass present", "unused spermatophoric mass present", or "eroded/used spermatophoric mass present". The colour of the ovaries, determined *in situ* through the dorso-thoracic musculature between the carapace and dorsal ridge of the first abdominal tergite, was used to assign the lobster's ovary to one of two stages: a transparent or white ovary was recorded as "undeveloped", and a faint pink to orange ovary was recorded as "developing". Since it has been suggested that limb loss has the potential to influence the reproductive behaviour of female *P. cygnus*, all individuals that were missing limbs or possessed regenerated limbs were excluded from the analysis.

On the basis of reproductive characteristics, females were classified as either a "single breeder", a "double breeder", an "inactive breeder", or "immature" using two sets of criteria, those developed during this study (see Fig. 3) and those described by Chubb et al. (1989); this latter criteria identified a double breeder as a female carrying eggs or bearing an eroded spermatophore, while possessing bright-orange ripe ovaries.

### Histological examination

Since almost all mature female *P. cygnus* had the distinctive reproductive characteristics that confidently indicated they were either single or double breeders, i.e., possessed both external eggs and an unused spermatophore or both late stage external eggs and obviously developing ovaries, only 10 lobsters in this condition, which covered the full size range, were selected for histological examination. A further 35 females that proved difficult to assign an ovarian condition on the basis of an external examination were selected to determine histologically their

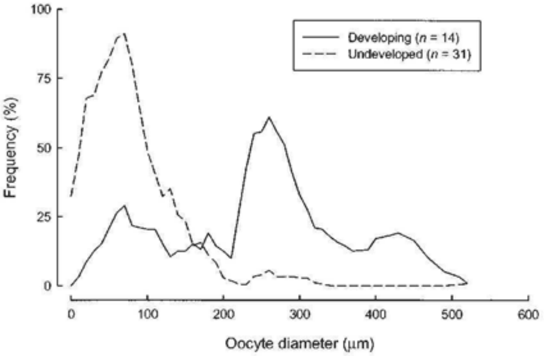

**Fig. 2** Oocyte diameters of *Panulirus cygnus* ovaries that were classified as "developing" (yellow/orange) or "undeveloped" (white/translucent) when viewed through the dorso-thoracic musculature.

true ovarian status. The ovaries of each *P. cygnus* selected for histological examination were assessed externally (through the dorso-thoracic musculature) before they were anaesthetised and had their ovaries removed and fixed in 4% glutaraldehyde in 0.025*M* phosphate buffer (pH 7.0) for 24 h. Glutaraldehyde was used as it had previously been shown to be a good fixative for decapod ovarian tissue (de Lestang et al. 2003). Once fixed, the ovaries were dehydrated in a series of increasing concentrations of ethanol and embedded in paraffin wax. Transverse sections (6 µm thick) of the gonad tissue were cut and stained with Mallory's trichrome and examined under an Olympus CH binocular microscope. The thickness of ovary walls and the diameters of 100 randomly selected oocytes from each of the developing ovaries ($n = 10$), as well as the ovaries that were difficult to stage visually ($n = 35$), were measured to the nearest µm using the imaging software Leica IM1000, which acquired the image via a Leica DC300 digital camera attached to a Leica MZ7.5 dissecting microscope.

## RESULTS

### External and histological determination of ovarian development

A comparison of the ovaries from 45 female *P. cygnus* that had been assessed both externally through the dorso-thoracic musculature and histologically in the laboratory, showed that the ovaries of all 14 lobsters classified through the dorso-thoracic musculature as developing contained numerous small oocytes, as well as large proportions of oocytes >170 µm in diameter (Fig. 2). Since early yolk granular oocytes, i.e., oocytes which are well on their way to developing, have a diameter of c. 150 µm (data not shown), the visual assessment of the ovaries of *P. cygnus* through the dorso-thoracic musculature appears incapable of detecting the presence of any oocytes in the yolk vesicle and early yolk granule stages of development, and thus the early to mid stages of ovarian maturation. Thus, external assessment of the ovaries through the dorso-thoracic musculature underestimates the proportions of female *P. cygnus* that have developing ovaries.

Further histological examination showed that the ovaries of all females in our samples that had recently spawned (i.e., those that had early phase external ova) and that had their ovaries externally classified as developing, contained immature oocytes and remnant mature oocytes (late granular) undergoing atresia. Therefore, these ovaries were clearly not developing. Moreover, the ovary walls of all ovigerous *P. cygnus* in our samples were 2–8 times thicker than those of females that had not yet extruded their ova. A very thick ovary wall, which can remain thick until the ovary begins to mature a second time, can add a yellow tinge to the exterior of the ovary. As a result, these ovaries appear similar to developing ovaries, which increases the likelihood of an externally assessed just spawned ovary being misclassified as developing.

### Assessment of reproductive stage

Although the visual assessment of an ovary's stage of development can be misleading, when this technique is combined with other external observations during the peak of the breeding season, i.e., when the maximum proportion of females are ovigerous, the results can more accurately determine the reproductive stage of a female *P. cygnus*. For example, the presence of an eroded spermatophore mass and early phase external ova suggest that an ovary classified as developing is in fact undergoing atresia after histological examination. Under the criteria which are currently in use in this fishery these lobsters would have been designated as double breeders, whereas, with the correct classification of their ovaries now known, they have been reclassified as single breeders.

The modified combinations of the external characteristics and their resultant reproductive classifications of an individual have been simplified by way of a flow diagram (Fig. 3) to enable researchers to easily and quickly classify a female *P. cygnus* as either immature, an inactive breeder, single breeder, or double breeder.

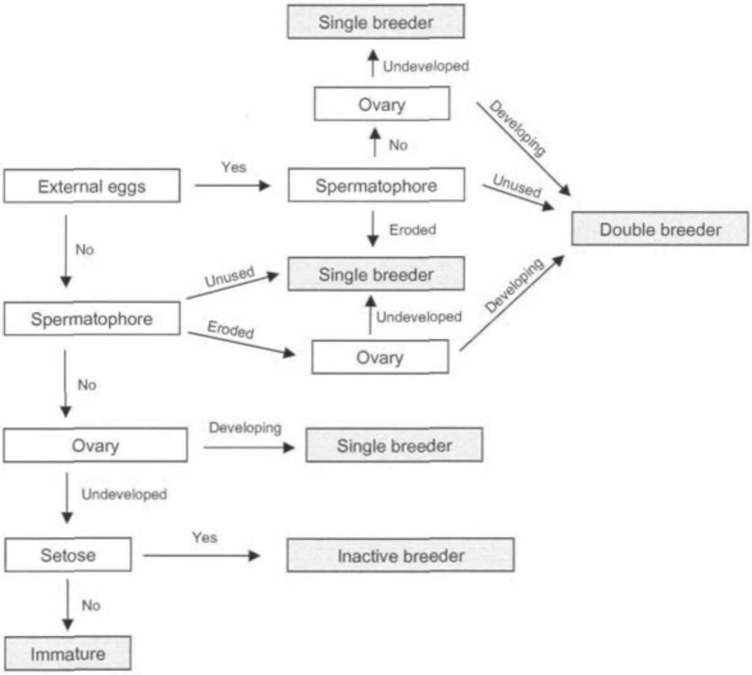

**Fig. 3** Flow chart showing the various combinations of external characteristics which, when combined, classify a female *Panulirus cygnus* as immature, inactive breeder, single breeder, or double breeder.

## Comparison between the classifications of single and double breeders using two different sets of criteria

During the 2002 survey, 8541 female *P. cygnus* were collected and a record made of the condition of their setae, spermatophore mass, external ova, and the stage of development of their ovaries (the last assessed through the dorso-thoracic musculature). From these data the lobsters were sorted twice, based on two sets of criteria, into immature, inactive, single, or double breeders. The first sorting of lobsters was based on the modified set of criteria (Fig. 3) whereas the second was based on the unmodified criteria currently in use in the fishery.

Combinations of external characteristics that would result in a lobster being classified as a double breeder by the modified criteria and a single breeder by the unmodified criteria are either: an eroded spermatophore mass with a developing ovary and no external eggs, or an unused spermatophore mass with external eggs and an undeveloped ovary. A lobster would be classified as a single breeder by the modified criteria and a double breeder by the unmodified criteria if it had an eroded spermatophore mass with external eggs and a developing ovary.

Although in many instances both sets of criteria classified each lobster as either a single or double

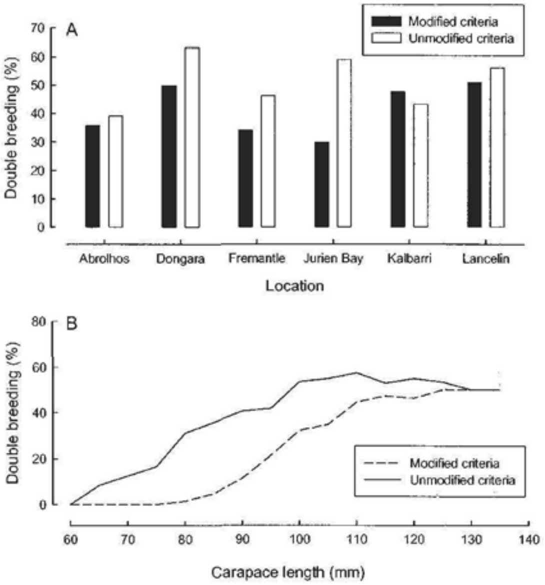

**Fig. 4** Comparison between the proportions of *Panulirus cygnus* classified as double breeders at **A**, six locations and **B**, in different carapace length (CL) classes collected at Fremantle, Western Australia, determined from modified criteria (see Fig. 3) and the unmodified criteria (see Chubb et al. 1991). CL classes have been smoothed with a three-point moving average.

breeder, 9.1% and 44.5% of lobsters classified by the unmodified criteria as single and double breeders, respectively, were classified by the modified criteria as double and single breeders, respectively.

Furthermore, comparisons between the proportions of female *P. cygnus* at six different sites that were classified as double breeders by both sets of criteria during the 2002 survey, showed that at five of the six sites, the unmodified criteria classified between 2% and 32% more lobsters as double breeders in that year than did the modified criteria (Fig. 4A). The modified criteria classified 4% more double breeders than the unmodified technique at Kalbarri (Fig. 4A). The main difference in the proportions classified as single/double breeders at the different sites, was because of the far greater proportions of small lobsters classified as double breeders by the unmodified criteria. For example, in the samples collected from Fremantle, where the females had the largest size range, both sets of criteria classified similar proportions of lobsters above 110 mm CL as double breeders. However the unmodified criteria classified a far greater proportion of the lobsters below 95 mm CL as double breeders than did the modified criteria (Fig. 4B).

## DISCUSSION AND CONCLUSIONS

The histological study confirmed that external features can be employed to classify female *P. cygnus* as either a single or double breeder (as well as an immature or inactive breeder), whether one uses modified or unmodified criteria. However, the visual ovarian assessment is not, on its own, always reliable and when incorporated with other external characteristics in the format described by Chubb et al. (1989) has the potential to misclassify single and double breeders. Therefore, by identifying histologically the instances in which the ovary can be misclassified and modifying the relationships between the various criteria to account for this, this study has substantially improved the assessment of reproductive state without needing to sample each "doubtful" ovary histologically.

The criteria used for assigning females into a particular reproductive state are strongly influenced by the sampling period within the breeding season. In the early stages of the breeding season before egg extrusion, it is not possible to predict whether a female will carry more than one brood; neither is it possible to establish late in the season, whether a female carrying eggs but with criteria assigning it to be a single breeder, might have carried an earlier brood. The method described is therefore only effective during a period when the maximum proportion of the breeding females are ovigerous, i.e., the peak of the breeding season and, even then, cannot, by itself, be used as a definitive indicator of an animal's recent spawning history or future spawning potential.

Newly matured females of spiny lobsters that repetitively spawn during a single season produce fewer broods than their larger conspecifics (Chubb 2000), with newly matured *P. cygnus*, *P. longipes longipes*, and *P. guttatus* all producing only one batch of eggs during a spawning season (Chubb et al. 1994; Gomez & Bermas 1994; Sharp et al. 1997). Thus, the fact that the criteria currently in use in this fishery classified a large proportion of small females, i.e., 18% of those below the size at first maturity at Fremantle, as double breeders, indicates that this set of criteria is probably misclassifying a significant proportion of these lobsters. The modified criteria however did not classify any lobster below the size at maturity as double breeders, suggesting that, at least for smaller females, the modified criteria produce more realistic results. The proportion of double breeders spawning by size is important when determining egg production indices, because the generally larger size of these animals makes the contribution of each brood substantial compared with the smaller single spawning females.

Because there is a short period between the extrusion of ova by breeding females and the redevelopment of external criteria indicating a presumptive second spawning (i.e., an unused spermatophore mass and developing ovaries) it is likely that the modified criteria will slightly underestimate the proportion of double breeding female *P. cygnus*. However, since MacFarlane & Moore (1986) reported that mating occurred shortly after ovulation in *P. ornatus*, and given that most of the females sampled in the survey that had early phase I external ova (<3 weeks old) also had unused spermatophoric masses, it appears likely that only a few females would have been sampled between ovulation and mating.

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# Description of *Panulirus brunneiflagellum* new species with notes on its biology, evolution, and fisheries

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**Abstract** The new species is distinguished from its nearest relatives by the colour and patterning of the anntennual rami. *Panulirus brunneiflagellum* is morphologically close to *P. japonicus* and is restricted to the subtropical Ogasawara Islands in the west Pacific. It probably became isolated from the *P. japonicus* stock with the development of the unique Ogasawara oceanic circulatory system as a result of the deflection of the Kuroshio subgyre as the Iwo-Jima Ridge uplifted. Over 90% of the annual production of c. 5 t is frozen and transported to the Tokyo market, Japan.

**Keywords** *Panulirus brunneiflagellum*; evolution; new species *Panulirus*; fishery

## INTRODUCTION

A review of the *Panulirus japonicus* species complex was published by George & Holthuis (1965) in which keys, descriptions, and figures distinguished the geographically restricted species *P. japonicus*, *P. marginatus*, *P. pascuensis*, *P. cygnus*, and the widespread, and subsequently proven to be confusing, *P. longipes* (see George 1997 and Chan & Ng 2001, for details of taxa related to *P. longipes*, and debate over their nomenclature). George & Holthuis (1965) recognised two subspecies of *P. longipes*, the nominate *P. longipes longipes* with spotted legs of the Indian Ocean and a striped-legged form (called by them *P. longipes femoristriga*) inhabiting the western and central Pacific Ocean. George (1972), Sekiguchi (1991), and Chan & Chu (1996) recognised that *P. l. femoristriga* comprised more than one taxon and, as part of a study of evolution of *Panulirus*, George (1997) concluded that three taxa, all possessing striped legs, have been identified commonly as *P. l. femoristriga*. The key distinguishing features allowing separation of these three taxa with striped legs is the coloration and patterning of the antennular flagella.

Two of the striped-legged taxa were described and figured by Sekiguchi (1991) who used the local Japanese names at Ogasawara Islands of "Aka-ebi" (brown whisker) and "Shirahige-ebi" (white-banded whisker) to distinguish them. *Panulirus femoristriga* sensus strictu is recognised by the distinctive one white and one darl ramus of each antennule and is known as "Shironuke" (plain white whisker) by Japanese fishers. According to Chan & Ng (2001) who examined the nomenclature of *P. l. femoristriga*, *P. bispinosus*, and *P. albiflagellum*, "Shirahige-ebi" is identical to *P. l. bispinosus* and "Shironuke" to *P. femoristriga* sensus strictu (synonym *P. albiflagellum*). Thus, we believe a new *Panulirus* name should be given to Aka-ebi.

In December 1998, the two authors visited Chichi-Jima in the Ogasawara Islands to gather first hand data. This paper formally describes Aka-ebi as the new taxon and provides notes on its speciation,

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habitat, and fishing importance. Measurements are of median carapace length from between the rostral horns and the posterior margin of the carapace.

## SYSTEMATICS

### *Panulirus brunneiflagellum* sp. nov.

(Fig. 1, 2A–C, 3A)

Aka-ebi: Sekiguchi 1991; Chan & Chu 1996
*Panulirus* "aka": George 1997

### Material examined

**Holotype** Ogasawara, Mukojima Chain, in trap, 21–27 November 1997, male, 105.9 mm (Western Australian Museum, WAM C23504).

**Paratypes** Ogasawa, Mukojima Chain, in trap, 21–27 November 1997, 1 male, 90.5 mm (WAM C23507), 2 females, 98.4 and 102.2 mm, with spermatophores (WAM C23505 and C23506). Chichi-Jima, in commercial holding tanks 12 December 1998, 3 females each with spermatophore and 4 males, 95.5–108 mm.

### Description of male holotype

Antennular plate with two principal anterior spines and two posteriorly diverging rows of three spinules behind the principal pair of spines; ventral surfaces of distal two segments of antennal peduncle without spinules, distal segment with central pair of major spines, second segment with central pair and basal pair of major spines (Fig. 3A); exopod of third maxilliped with multi-articulate flagellum reaching half length of merus of endopod (Fig. 2C); exopod of second maxilliped with multi-articulate flagellum reaching well beyond endopod (Fig. 2B); posterior margin of thoracic sternum with distinct pair of posteriorly directed teeth; male reproductive opening with curved, raised chitinous ridge without setal tuft; outer margin of triangular plate (plate D) on first abdominal somite with very slight indentation; anterior margin of second abdominal pleura nearly straight with one very minute spinule (Fig. 2A); transverse grooves of second to fourth abdominal somites uninterrupted, very slightly medianly indented; lateral end of second transverse groove does not join pleural groove, lateral end of transverse groove of third somite on right side only, does not join pleural groove, remainder join corresponding grooves; all grooves covered by fringe of setae; apart from setae along posterior margin of the somites and those along the transverse grooves, abdominal terga entirely naked; male pleopods without endopods.

### Colour

Antennule peduncle blackish-purple with white spot at distal articulations and lateral white irregular line; antennular flagella uniformly brownish without crossbands; antennular plate blackish-purple with a large central triangular white spot; antennal peduncle blackish-purple with pale spots and orange tips to dark spines; antennal flagella uniformly dark gray; supraorbital horns blackish-purple with orange tips and large baso-ventral white spot; dorsal carapace blackish-purple anteriorly, brownish centrally and posteriorly, laterally more orange with pale spots, many spines white and orange tipped; continuous mid lateral stripe on carapace, ventral stripe broken and spotted; posterior carapace margin blackish-purple with 13 distinct white spots; cervical groove with fine white spots and stripes; dorsal abdomen blackish-purple with many white and orange dots and laterally, small white spots and larger spots especially on plate D, behind each somite articulation and on abdominal pleura; pereiopods purplish, merus longitudinally streaked with five irregular, narrow white lines; carpus and propodus with dorsal orange stripe, articulations orange; pleopods bordered white with basal spot; telson bordered yellowish.

### Variations in paratypes

In the series examined, the rows of diverging spinules behind the principal pair on the antennular plate ranged from 1 to 5; the exopod of the third maxilliped of the smallest male and in two females reaches only one third of endopod and in another female the exopod reaches only the base of the merus of the endopod; four of the five males have the distinct pair of spines on the thoracic sternum like the holotype, but in one male there is only one very small spinule on the right side; in two females (one with and one without spermatophore) it is reduced to two tiny spinules, and in the remaining mature three females (with spermatophores) the teeth are absent. For two of the four males and for three of the five females in the paratypical series, the transverse groove of the second abdominal somite does not join the pleural groove, for the other two males and one female this transverse groove does join the pleural groove (as is the situation for a specimen described by Sekiguchi (1991) from Hachijo Island), the joining of the transverse groove and pleural groove in the remaining female is very

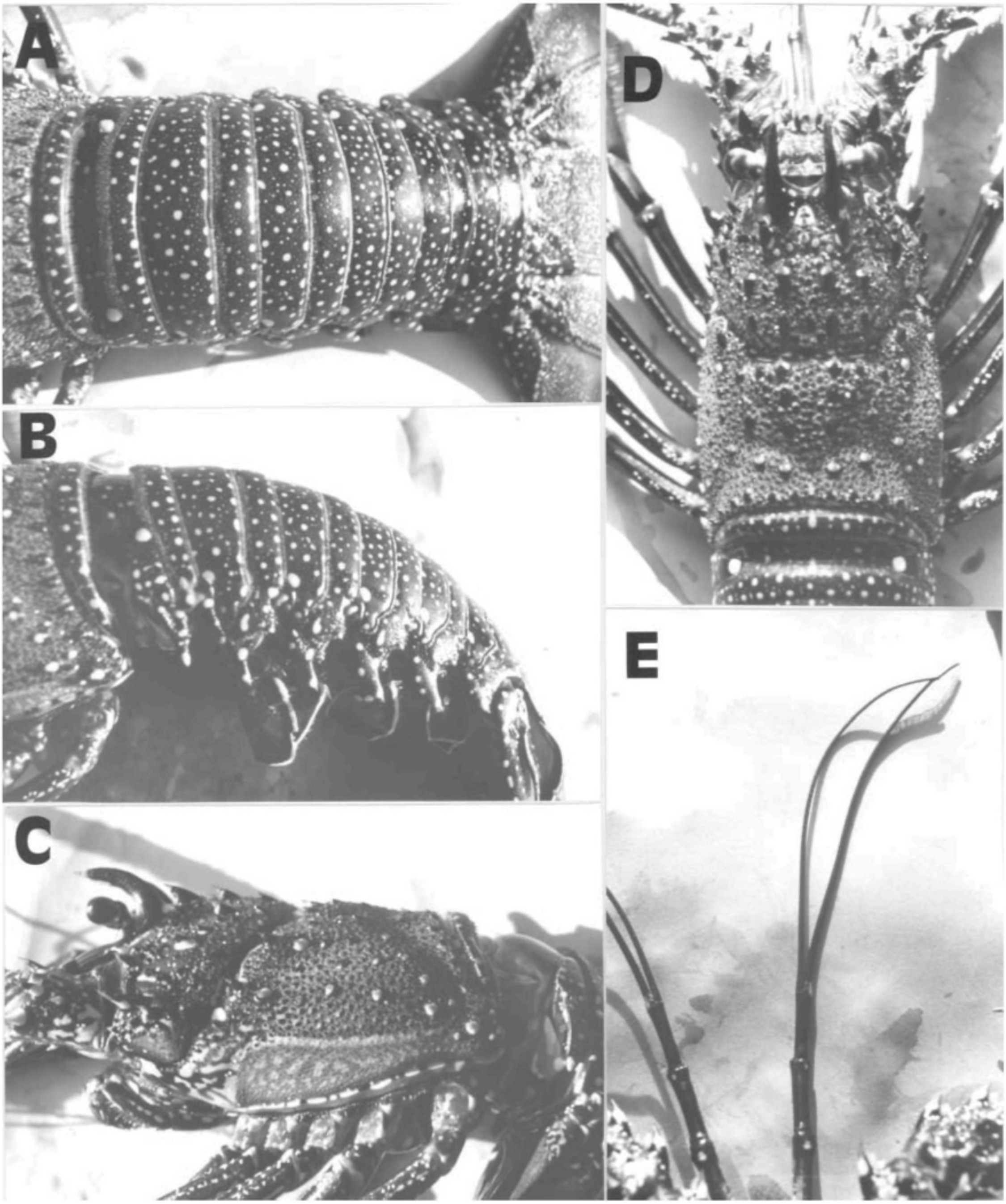

**Fig. 1** *Panulirus brunneiflagellum*. Female with spermatophore from Ogasawara Islands, 120 mm carapace length. **A**, dorsal view of abdomen; **B**, lateral view of abdomen; **C**, lateral view of carapace; **D**, dorsal view of carapace; **E**, antennular flagella (after Sekiguchi 1991).

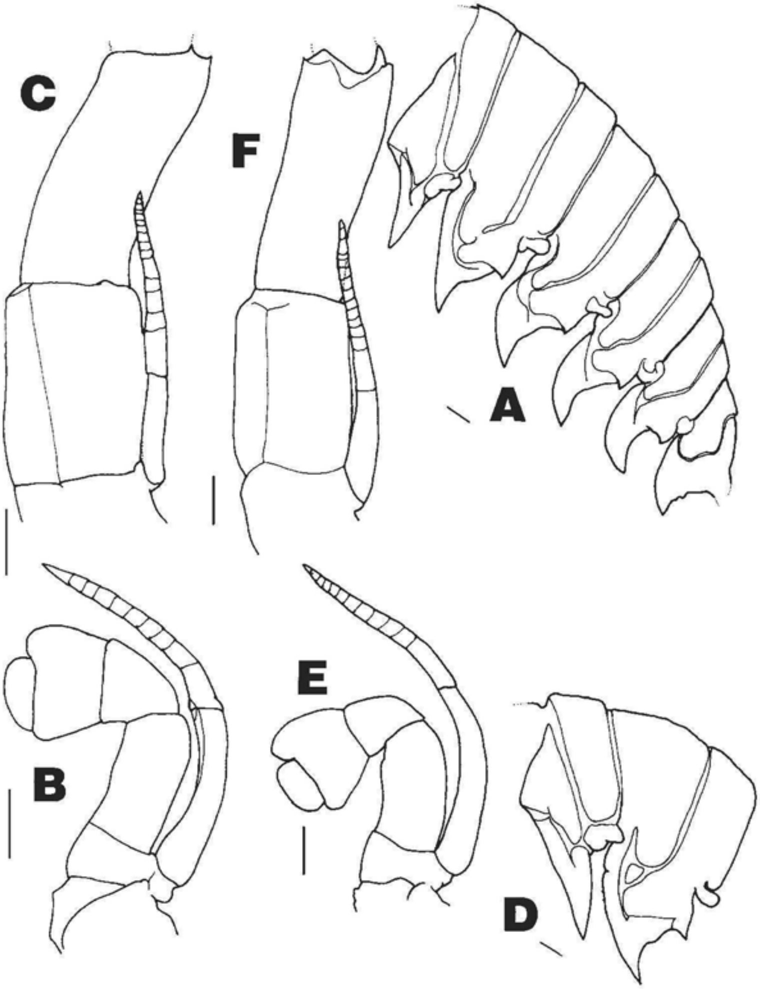

**Fig. 2** **A–C**, *Panulirus brunneiflagellum*. **D–F**, *Panulirus longipes bispinosus*. **A** and **D**, lateral view of abdomen; **B** and **E**, second maxilliped; **C** and **F**, third maxilliped. Short hairs along transverse and pleural grooves of abdomen and spines of second and third maxillipeds are omitted. Scale = 10 mm for A and D, and 5 mm for B, C, E, and F (after Sekiguchi 1991).

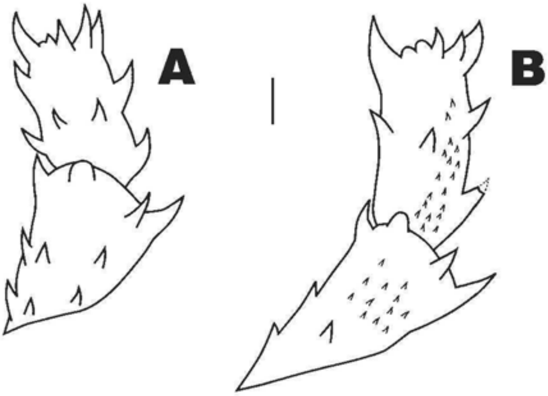

**Fig. 3** Ventral view of distal two segments of antennal peduncle. **A**, *Panulirus brunneiflagellum* holotype male, WAM23504; **B**, "Shirahige-ebi"(*Panulirus longipes bispinosus*). Scale = 10 mm.

indistinct. Thus six of the 10 have the condition as described for the holotype. For the females the small white spots and orange dots on the dorsal and lateral surfaces of the abdomen are larger and provide a more even cover than for the males.

## Distribution

*Panulirus brunneiflagellum* is the dominant species in the southern islands of the Izu Ridge at the Ogasawara Islands (Bonin Is.). These islands are c. 1000 km south of Tokyo, Japan and 1500 km north of Saipan, Mariana Islands. It has also been recorded from Hachijo Island at the northern end of the Izu Ridge, c. 300 km south of Tokyo (Sekiguchi 1991).

*Panulirus l. bispinosus* (referred to in Sekiguchi 1991 as *P. l. femoristriga*), the other less abundant taxon from Ogasawara Is., has been recorded from two separate subtropical regions of the west Pacific. It occurs in the north-west Pacific (10–35°N) at the near-Asian islands of Japan, Ryukyu Archipelago, Taiwan, and Philippines and the offshore islands of Ogasawara and Hachijo (Sekiguchi 1991). Another population occurs in the south-west Pacific (15–32°S) on the moderate sized islands of Cook, Fiji, Vanuatu, and New Caledonia as well as the mid east coast of Australia (George & Holthuis 1965; George 1972; Sekiguchi 1991; Chan & Chu 1996).

## Habitat

*Panulirus brunneiflagellum* lives in open caves, down steep volcanic slopes from surface to 90 m in clear oceanic waters. It usually occupies the entrance of the caves, occasionally sharing the cave with *P. l. bispinosus*, however *P. l. bispinosus* usually shelters singly or in small groups in the deep recesses at the back of the cave (Nishikiori & Sekiguchi 2000). In the spawning season the two species form separate groups in separate caves. Tides at the Ogasawara are semidiurnal with a spring range of 1.5 m. Currents can run strongly between islands but swells are minimal. Surface water temperatures range from 19 to 29°C.

In contrast, habitat records of *P. l. bispinosus* are as follows: Coral reef (Fiji and Heron Island), speared or netted in shallow water (Japan, Philippines, and New Caledonia) and taken in lobster traps to 130 m (Vanuatu and Australia) (George & Holthuis 1965; George 1972; Juinio et al. 1991). In the Ogasawara Islands, *P. l. bispinosus* usually shelters singly or in small groups in the deep recesses at the back of the cave (Nishikiori & Sekiguchi 2000).

## Fishery

Nishikiori & Sekiguchi (2001) report that Japanese fishers have taken lobsters ever since the Ogasawara Islands were occupied more than 150 years ago. They are usually caught between 10 and 40 m depths in steel-framed rectangular traps covered with plastic mesh. Each trap measures c. 1 m × 0.5 m × 0.5 m and has a funnel entrance at each end. The buoyed traps are set singly each day on the volcanic rock slopes, baited with fresh fish.

Twenty fishing boats work out from Chichi-Jima Island and two to four boats from Haha-Jima Island, catching an average of c. 5 t annually, 90% of which is frozen and transported to the Tokyo market. *P. brunneiflagellum* makes up 98% of the catch and the remainder is *P. l. bispinosus*, except for a few *P. penicillatus*. The catch was 6 t in 1997 and 9 t in 1998. The fishery is regulated by Tokyo Metropolitan Fisheries; a closed season operates from June to August to protect berried females.

## Species relationships and distinguishing features among the *Panulirus japonicus* species group

*Panulirus brunneiflagellum* and *P. l. bispinosus* belong to the *P. japonicus* group (Group 1 of George & Main 1967) because they possess multi-articulate flagella on the exopod of both the second and third maxillipeds (Fig. 2B,C,E,F). Like all Indo-West Pacific Group 1 they also have uninterrupted dorsal transverse grooves across the abdominal segments and have one major pair of spines on the antennular plate thus separating them from the East Pacific *P. interruptus* and the West Atlantic *P. argus* which have medianly interrupted abdominal transverse grooves and two pairs of major spines on the antennular plate.

*Panulirus brunneiflagellum* is distinguished from *P. marginatus*, *P. cygnus*, and *P. femoristriga* in having the transverse groove on the second abdominal segment not joining the corresponding pleural groove, whereas the grooves on all abdominal segments join the corresponding pleural grooves in these other species. In this character *P. brunneiflagellum* is closest to *P. japonicus* and *P. pascuensis*. However, *P. japonicus* also has the third and fourth abdominal transverse grooves not joining the pleural grooves and the males of *P. japonicus* are unique in usually having simple or bifid endopods of the pleopods of the second to fifth abdominal segments (George & Carlberg 1995). In *P. brunneiflagellum*, antennular flagella are plain and the abdomen spotted whereas in *P. pascuensis* antennular flagella are banded and pale bands are present on the abdomen.

The two subspecies of *P. longipes*, *P. l. longipes* and *P. l. bispinosus*, together with *P. femoristriga* form a close group sharing the basic morphological characteristics of Group 1—multiarticulate flagella on the endopods of the second and third maxillipeds (Fig. 2E,F), medially uninterrupted absomenal transverse grooves that all join laterally with the pleural grooves (Fig. 2D) and one pair of major spines on the antennular plate. In the past, positive identification of preserved specimens was often very difficult when colour patterns had been obliterated or modified. The colours of fresh material make positive identification possible by combinations of patterns. *P. l. longipes* and *P. l. bispinosus* have banded antennal and antennular flagella (Fig. 4E), a distinct "bow" mark behind the cervical groove, and a single pale stripe along the lateral carapace (Fig.

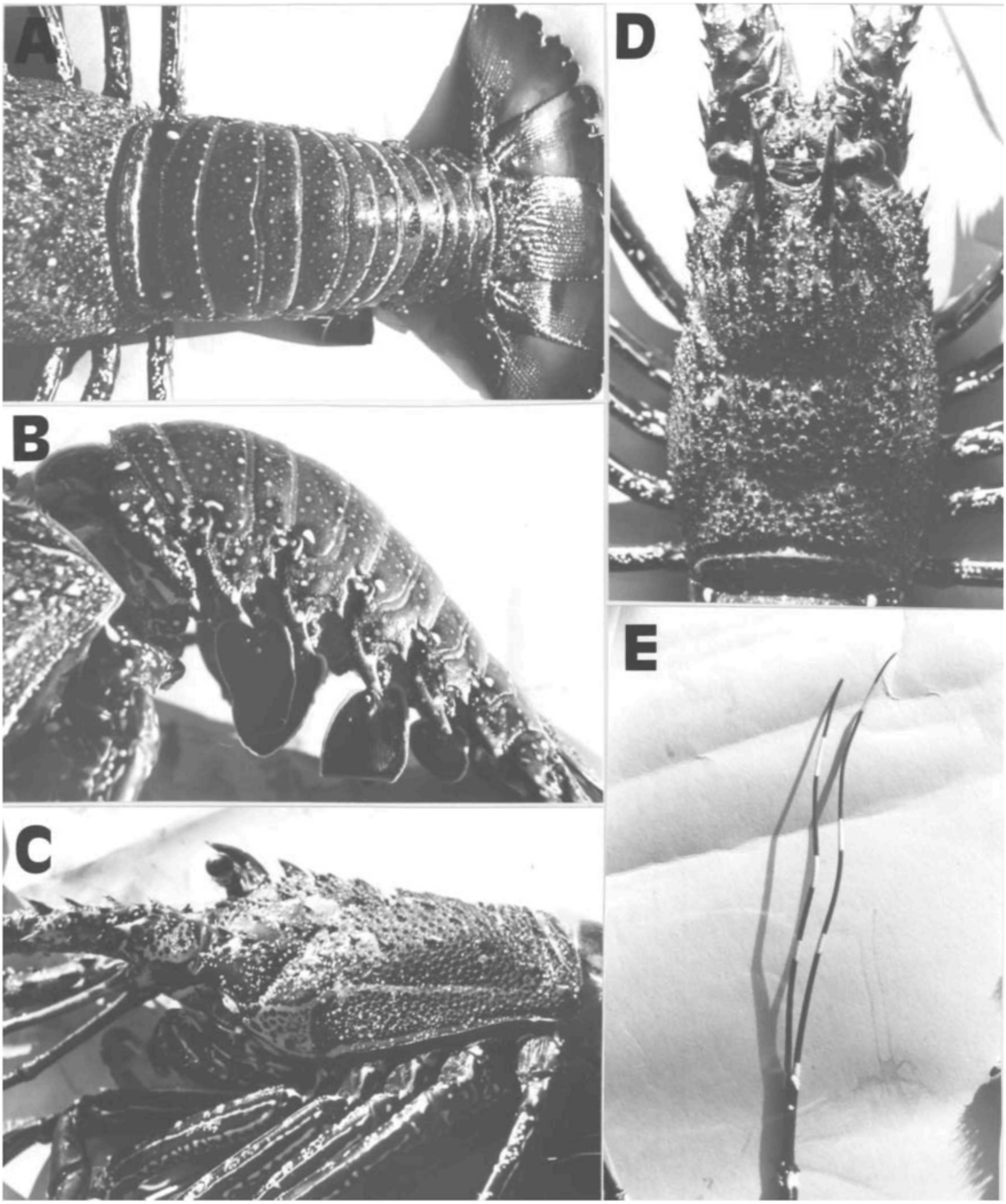

**Fig. 4** "Shirahige-ebi" (*Panulirus longipes bispinosus*). Male from Ogasawara Islands, 145 mm carapace length. **A**, dorsal view of abdomen; **B**, lateral view of abdomen; **C**, lateral view of carapace; **D**, dorsal view of carapace; **E**, antennular flagella (after Sekiguchi 1991).

4C,D); they are distinguished by the broad pale stripe along the legs of *P. l. bispinosus* and the broad pale stripe broken by three white spots along the legs of *P. l. longipes*. *P. femoristriga* has plain (one white, one dark ramus) antennular flagella, a "wishbone" mark behind the cervical groove, two pale stripes along the lateral carapace, and narrow white stripes along the legs.

As mentioned above, *P. brunneiflagellum* is morphologically close to *P. japonicus*. However, as part of his study of the phyllosoma larvae of all the species in the *P. japonicus* group that occur in the Kuroshio subgyre, Dr T. Yoshimura (pers. comm.) used the Internet web DNA database for identification and concluded that *P. brunneiflagellum* has the closest genetic affinity with *P. femoristriga*. It is not apparent at this time whether the morphological or the molecular data provide a better appraisal of the true relationships of *P. brunneiflagellum*.

## SPECIATION

When suggesting possible evolutionary processes to explain the isolation of *P. brunneiflagellum*, volcanic ridge uprisings in the north-west Pacific are important events contributing to their subsequent geographic separation.

According to Kennet (1982), from late Oligocene (30 Ma) a major pulse of volcanism occurred near the continental margin of Japan, peaking about middle Miocene (12 Ma) and this was followed in late Miocene (9 Ma) by a dramatic cold water upwelling and increased oceanic turnover, indicated by the high productivity and altered composition of diatoms. It was into this environment that *P. japonicus* evolved as it moved north from its equatorial origin which it had shared with the incipient *P. cygnus*, and it biologically responded to the Kuroshio subgyre which is the dominant oceanic current system of the region (Sekiguchi 1991).

According to Springer (1982), in the middle Miocene a period of volcanism along the Palau-Kyushu Ridge resulted in the formation of the eastward moving West Mariana Ridge. Sundering along the West Mariana Ridge c. 5 Ma years ago formed the Mariana Trough and produced the volcanically active Mariana Island Ridge to the east. The Iwo Jima Ridge which contains the Ogasawara Islands is a Pliocene (2 Ma) volcanic extension of this Mariana Trench system. The fact that *P. brunneiflagellum* is the clearly dominant species of *Panulirus* around the Ogasawara Islands, that no *P. japonicus* have ever been recorded there and that only a few larvae of *P. l. bispinosus* and even fewer larvae of *P. penicillatus* settle from the nearby west Philippine Basin suggest that a discreet current system circulates around the volcanic island chain (Sekiguchi 1991). This current system probably developed from a major deflection of the Kuroshio subgyre by the elevation of the Iwo Jima Ridge and it is now responsible for the transport and circulation of *P. brunneiflagellum* phyllosoma larvae away from and back to the Ogasawara Islands. Although the Ogasawara Islands may have become subaerial only c. 2 Ma, a significant deflection of the oceanic currents and the subsequent genetic separation of *P. brunneiflagellum* may have been possible at an earlier time since both *P. brunneiflagellum* and *P. japonicus* would be capable of living on any of the ridges or seamounts as they gradually came closer to the surface at depths of at least 90 m.

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# Use of digital colour analysis to assess variation within individual adult American lobsters (*Homarus americanus*) and the process of addition of colour in white lobsters

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**Abstract** A relatively low-cost method using digital macro-photography was developed to assess *in vivo* colour of American lobsters (*Homarus americanus*). Both R*G*B and Commission Internationale de l'Eclairage (CIE) L*a*b systems of colour analysis were used to investigate animal coloration over 11 body locations within each animal. Assuming that lightness (CIE-L) is biologically important for American lobsters, this species was counter shaded and paired comparisons showed that different colour parameters were all highly correlated among all body locations with the exception of the ventral claw. Using a multiple forward stepwise regression of the five hues on CIE-L, the hue Green was the most significant parameter accounting for 97% of the variation of CIE-L. This methodology was then used to assess how dietary white American lobsters add colour to their shell when switched to a diet containing carotenoid. The rate of colour addition was proportional to the amount of carotenoid in the diet, and to the body location. This digital photographic method of colour analysis was useful in that a wide size range of samples could be assessed. All body areas were suitable for colour analysis although relatively flat and smooth locations were most practical.

**Keywords** *Homarus americanus*; astaxanthin; crustacyanin; crustochrin; artificial diet

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## INTRODUCTION

The colour of any crustacean is produced by a combination of morphological and physiological mechanisms (Rao 1985). Morphological colour includes the quantitative and qualitative adjustments of pigments within the exoskeleton, whereas physiological colour includes the dispersion or concentration of pigment granules within chromatophores (Rao 1985). The relative importance of these two mechanisms varies between species. Chromatophores occur in peripheral tissue or deep surrounding organs, and thus are more likely to occur in animals with thin, translucent exoskeletons (Ghidalia 1985). Given their thick calcified exoskeletons, the coloration of Panularid and Homarid lobsters is morphological (Ghidalia 1985; Mellville-Smith et al. 2003) with a significant genetic component (Phillips et al. 1980). Thus, colour change in these species occurs over longer time intervals than in species that rely on physiological colour mechanisms.

It is this lack of short-term colour change that has limited the interest in examining Panularid and Homarid lobster colour. Research to date on American lobsters (*Homarus americanus*, Milne-Edwards 1837) generally has fallen into the category of either determining the structure of specific pigments or as a function of changes in diet. The coloration of American lobsters is a function of the carotenoid astaxanthin. This pigment occurs in the epidermis (Mackenthun et al. 1979) in an esteric form which adds a red hue to overall animal colour. Two astaxanthin molecules combine with two carotenoid binding proproteins to form β-crustacyanin, (Chayen et al. 2003), while α-crustacyanin is formed from an octamer of β-crustacyanin dimers (Buckwald & Jenks 1968). In both β- and α-crustacyanin, the carotenoid conformation is altered resulting in a bathochromatic shift in its absorption spectrum and thus providing a purple and blue hue respectively (Cianci et al. 2002). Finally, in the epicuticle, 20 astaxanthin are packed like a pile of plates resulting in a hypsochromic shift and thus imparting a yellow hue (Buchwalkd & Jencks 1968; Salares et al. 1977; Young & Williams 1983).

The research attempting to find suitable artificial foods for American lobsters observed a shift towards blue coloration in animals fed experimental diets lacking in carotenoids (D'Agostino 1980; D'Abramo et al. 1983; Lim et al. 1997). Many of these observations tended to be ancillary to the main objective of finding suitable diets, and thus the analysis of colour shifts in these experiments tends to rely primarily on qualitative data (D'Agostino 1980; Lim et al. 1997). However, there have been a few studies that quantitatively examined the role of carotenoids as a source of pigmentation in American lobsters (D'Abramo et al. 1983; Floreto et al. 2001). Unfortunately, their methods required extraction of pigments from denatured shell, and thus could not be conducted *in vivo*.

Recently, Melville-Smith et al. (2003) quantitatively measured colour of western rock lobsters, *Panulirus cygnus*, *in vivo* using a Minolta chroma meter. The benefit of the chromameter was that intact cuticle could be utilised and thus changes in a single lobster's colour over time could be addressed. The one drawback to the commercially available chroma meter was that it measured an area 8 $mm^2$. Although this sample size was suitable for larger animals, it was not appropriate for larvae or small juveniles. Thus, in beginning investigations of functional colour shift in the American lobster, a first priority was to evaluate a cost-effective system for analysing colour that could be used on all sizes of animals. Fourth stage lobsters have measurable surface areas of c. 0.5–1 $mm^2$, and thus methodology needs to be able to sample an area at least this small. Second, the units of colour measure need to be determined. Melville-Smith et al. (2003) used the Commission Internationale de l'Eclairage (CIE) L*a*b mode to analyse the colour of western rock lobsters. The CIE system of colour assessment was developed to parallel the sensitivity of the human eye. This system measured the colour's value (lightness), hue, and chroma (saturation). The value, represented by L, ranged from pure black (0) to pure white (100). Hue distinguished opposing colours, and was represented by two axes, a (red/green) and b (blue/yellow). Chroma was the amount of positive or negative hue, where +a indicated red, –a indicated green, +b indicated yellow, and –b indicated blue. The other commonly used colour measurement system for animals was RGB (Hancz et al. 2003). The RGB colour system returned values for the percentage of Red, Green, and Blue in a sample. The three colours vary independently from values of 0–100%. A pure colour was 100% of one colour and 0% of the other two. Samples that were 0% for all three colours were black, whereas white was a value of 100% for all three colours. Thus animals were measured using both systems, and the subsequent analysis indicated which of these six parameters best indicated colour. To accomplish these two tasks, digital photographic techniques were identified and used to assess *in vivo* colour of adult American lobsters over different body locations.

Finally, this new methodology was used to investigate colour shifts in 6-month-old hatchery reared American lobsters. The difference in this study was that as opposed to duplicating the previous efforts in examining the loss of colour, animals were grown having been fed a diet that had little to no carotenoid. Thus, these animals initially appeared white (D'Abramo et al. 1983, Fig. 1). Therefore, this experiment was an *in vivo* analysis of the pattern of colour addition to previously white shell in living animals.

## METHODS

Five wild-type coloured adult American lobsters were purchased from a local wholesaler. These animals were from the inshore Gulf of Maine, but further information of their origin could not be ascertained. The animals were taken back to the New England Aquarium, United States and held in a flow through sea-water system for one week before being photographed. One genetically blue adult animal was also examined. This animal originated from the southern Gulf of Maine, United States, in inshore waters, and was donated to the aquarium. It was photographed on the day of receipt.

Each animal was photographed in 11 different body locations, including the exopodite (EXO), endopodite (END), telson (TEL), last abdominal segment medial (LAM), first abdominal segment medial and lateral (FAM, FAL), the dorsal carapace (cranial medial CCR, caudal medial CCA, and the mid lateral CML) and the dorsal and ventral surfaces of the claw (CLD, CLV, Fig. 2). In this notation, the lateral distinction was used to differentiate samples taken on the dorsal shell, but toward the ventral side as opposed to a truly ventral sample (Fig. 2).

Photographs were taken with a Nikon Coolpix 5000 digital camera with a Nikon SL1 Macro Cool Light attached by a UR-E6 step down ring adapter. The camera was set to macro operation with a focal length of 2 cm and the Best-Shot Selector set to "on". Under these conditions, pictures were taken at a

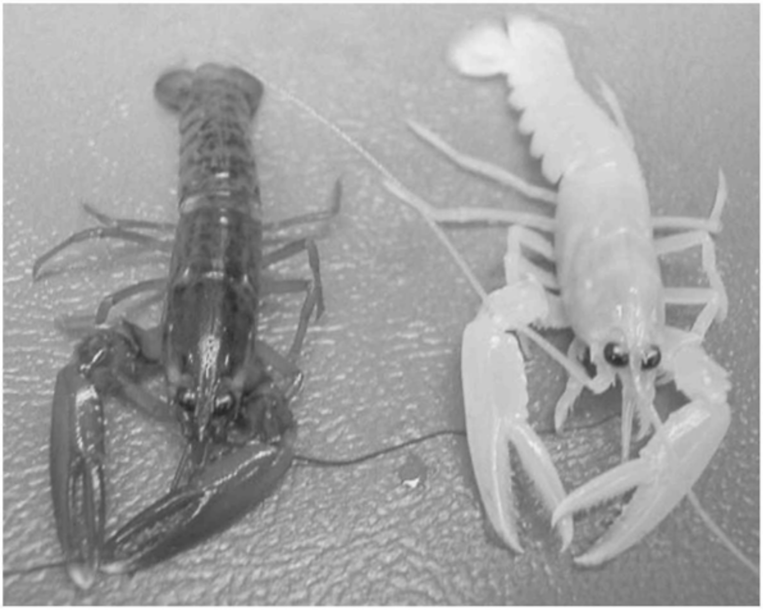

**Fig. 1** White hatchery-reared American lobster, *Homarus americanus* (right) used in the diet portion of this study. A wild-type, coloured American lobster is next to it for comparison.

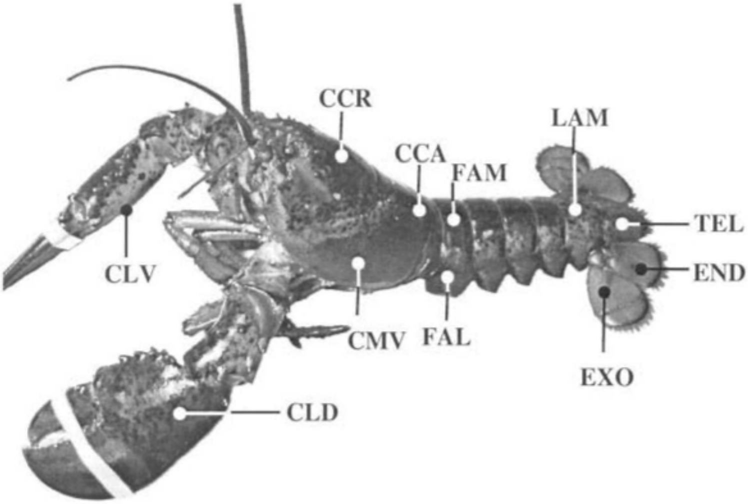

**Fig. 2** Eleven body locations of American lobsters, *Homarus americanus*, examined in this study. Identified locations include the exopodite (EXO), endopodite (END), telson (TEL), last abdominal segment medial (LAM), first abdominal segment medial and lateral (FAM, FAL), the dorsal carapace (cranial medial CCR, caudal medial CCA, and mid lateral CML), and the dorsal and ventral surfaces of the claw (CLD, CLV).

shutter speed of 1/15 to 1/30 with an aperture of F3.6. The section of the lobster was prepared for the photograph by wiping excess water off the shell and placing a white reference square onto the shell. The Macro Cool Light was then lowered into position touching the shell, resulting in a constant focal length. The camera angle was adjusted to minimise the reflective surface, and the image was captured. Pictures were stored in a 1280 × 960 pixel format on a "high" quality setting (jpeg compression of 1/4 the original file size).

Each image and the associated control white square were analysed for both RGB and Commission Internationale de l'Eclairage (CIE) L*a*b values using Adobe Photoshop 6.0. The white squares were used to assess proper lighting within each picture. As a precaution, this white square was used to correct for deviation for pure white (100, 100, 100) for RGB, or 100, 0, 0 (for L*a*b) by standardising the samples by the values obtained for the white squares.

Data for all six colour measures at the 11 separate body locations were analysed as a one-way repeated measures ANOVA with the factor being body location, and the repeated measure being the individual lobster. Paired comparisons were made using Tukey's test. Non-normal data were analysed using a repeated measures ANOVA on ranks. The coloration of the ventral claw appeared significantly different from the 10 other body locations in terms of colour score, and scaling between different colour scores. Thus, this location was removed, and a forward stepwise regression was then calculated for each hue value's (R, G, B, a, b) contribution to lightness (L). Parameters were added provided $F = 4.00$ and removed if $F = 3.90$.

### Diet study

As a practical test of analysing colour differences, 6-month-old white lobsters were assessed for changes in colour as they were switched to diets containing carotenoid. The animals used in this portion of the study were hatched and reared at the New England Aquarium. Beginning at the fourth stage, all animals in the hatchery were held individually to prevent cannibalism, and to facilitate observation. The white animals were created by feeding a group of siblings a commercially available *Artemia* replacement diet (Economac 4, Aquafauna Bio-marine Inc, Hawthorn, CA, United States) beginning at the fourth stage. Although they were white by the seventh stage, diets were not switched until the animals were 6 months old.

From a group of 70, 24 white lobsters were randomly selected. These animals were randomly divided into four groups, and each group was fed a diet differing in the amount of carotenoid. The first diet, L, contained little carotenoid, and was made up of 100% Economac mixed in gelatin. The next two diets were also gel based, and contained a moderate amount of carotenoid (diets M1 and M2). The carotenoid sources in M1 were from krill meal (14.5% by weight), fish meal (14.5%), frozen adult *Artemia fanciscas* (33.7%), and spirulina (4.6%), whereas M2 was the same as M1 with 0.008% Naturose® added in (1.5% carotenoid, Cyanotech Corporation, Kailua-Kona, HI, United States). The last diet, H, had a high level of astaxanthin and consisted of live selco-enriched *Artemia* nauplii, and omega-3 enriched frozen adult *Artemia*. On days 0, 14, 28, and 58, each animal was photographed twice. One picture was of the tail (including the exopodite, endopodite, telson, and last abdominal segment). The second was of the dorsal claw. Data were analysed as a four-way repeated measures ANOVA, with day, diet, body location, and colour measure being the four factors, with the individual lobster as the repeated measure. There were significant three and four-way interactions, and thus the data set was analysed separately by each colour. Because of the importance of CIE-L, this colour was primarily investigated. The reduced data set still had significant three-way interactions (day × diet × body), and thus it was further reduced and reanalysed as a two-way repeated measure (day and diet) ANOVA separated by body location. The continued presence of a significant interaction term made it necessary to analyse simple effects of each diet with Tukey's test. The H diet solely influenced animal colour. To fully understand how the animals responded to this diet, the influence of body location and day on CIE-L were analysed as a two-way repeated measures ANOVA. Furthermore, a detailed analysis of the claw was conducted by examining the influence change in the hues Red, Green, and Blue over the course of the experiment (two-way repeated measures ANOVA). Non-normal data were analysed as ranked data as transformations did not increase normality. For ease of interpretation, all presented values are of unranked data.

## RESULTS

Although taking the photographs was simple, the local properties of the shell influenced the subsequent quality of the image. Shell parts that were highly curved (dorsal carapace, abdominal segments) or an uneven texture (telson) resulted in compromised images that had a high amount of light reflection. Thus, the endopodite, exopodite, and the claws offered the best surfaces for photographs uncompromised by reflection. Although the difficulty of reflection limited the total amount of picture area that could be used for the colour analysis, it never precluded an image from being analysed. The handling of small lobsters occasionally results in claw loss, however no animals dropped claws during this experiment.

A one-way repeated measures ANOVA for the six different colour measurements indicated that the ventral claw was very different than the other 10 body locations (Fig. 3). This body part was singularly greater than any other body part for the Red (repeated measures ANOVA, $F_{10,40} = 33.59$, $P < 0.001$, for all pair-wise comparisons, Tukey's test $q > 8.66$, $P < 0.001$), and CIE-b (repeated measures ANOVA, $F_{10,40} = 34.36$, $P < 0.001$, for all pair-wise comparisons, Tukey's test $q > 7.56$, $P < 0.001$)

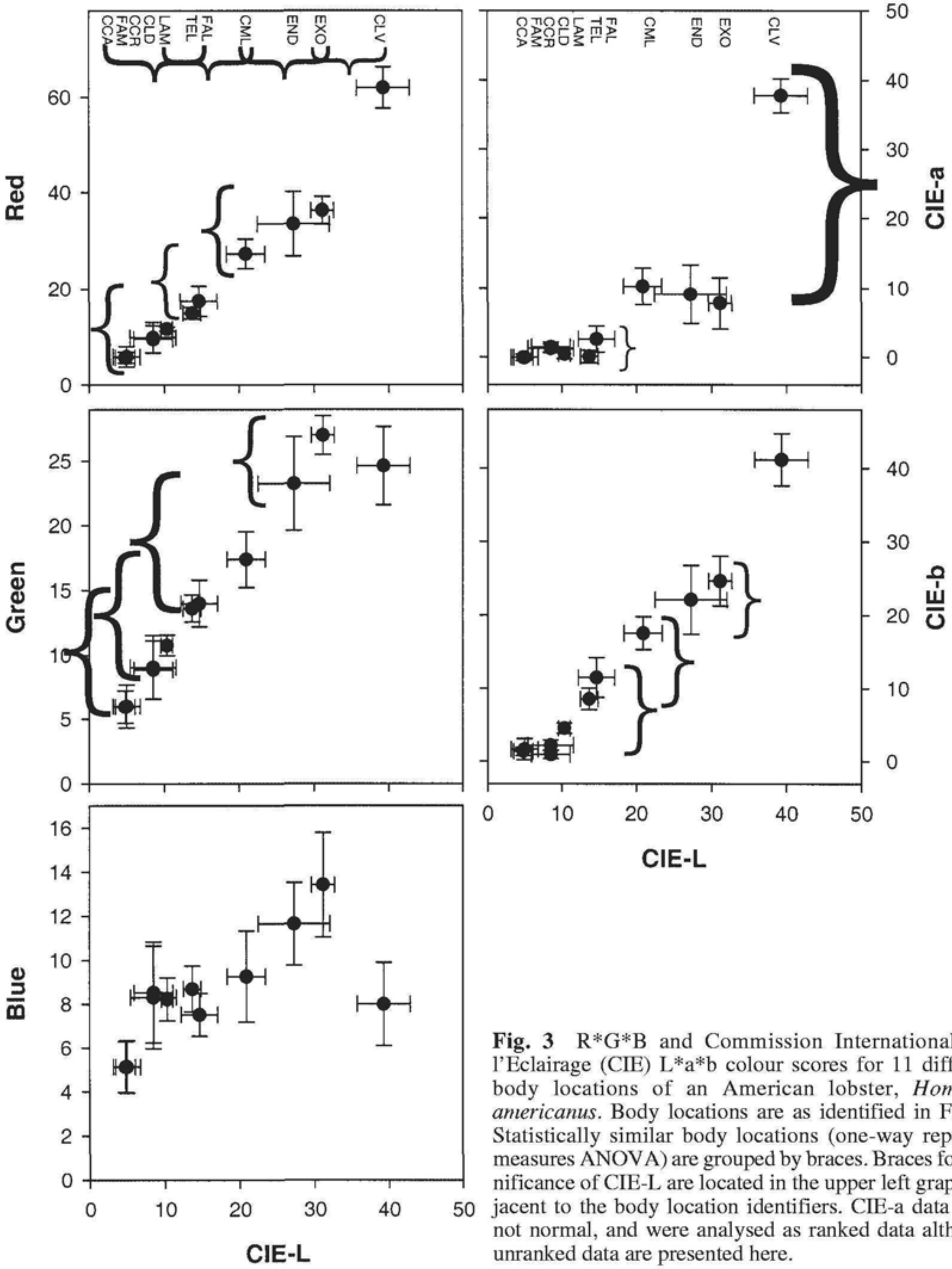

**Fig. 3** R*G*B and Commission Internationale de l'Eclairage (CIE) L*a*b colour scores for 11 different body locations of an American lobster, *Homarus americanus*. Body locations are as identified in Fig. 2. Statistically similar body locations (one-way repeated measures ANOVA) are grouped by braces. Braces for significance of CIE-L are located in the upper left graph adjacent to the body location identifiers. CIE-a data were not normal, and were analysed as ranked data although unranked data are presented here.

measures of colour. The ventral claw was grouped within the largest values for Green (repeated measures ANOVA, $F_{10,40} = 12.78$, $P < 0.001$, for all pair-wise comparisons, Tukey's test $q > 6.18$, $P < 0.001$ except CML, END, and EXO), CIE-L (repeated measures ANOVA, $F_{10,40} = 22.67$, $P < 0.001$, for all pair-wise comparisons, Tukey's test $q > 4.88$, $P < 0.05$ except EXO $q = 3.31$, $P > 0.40$)

and CIE-a (repeated measures ANOVA on ranked data, d.f. = 10 $\chi^2 = 36.46$, $P < 0.001$, for all pairwise comparisons, Tukey's test $q > 4.72$, $P < 0.05$ except FAL, END, EXO, and CML). The only measure for which it was not an extreme was Blue, where there was no significant colour difference between body locations (one-way repeated measures ANOVA, $F_{10,40} = 1.94$, $P > 0.06$).

The Red and Green colours measured in the digital images of American lobsters were highly correlated, and scaled at a rate of 1 Red to 1.5 Green (regression calculated without the ventral claw data):

$$\text{Red} = -2.932 + (1.48^{*}\text{Green}) \qquad r^2 = 0.889$$

The ventral claw was below this line, indicating a significantly predominant red coloration compared to any other part of the body. Because the ventral claw did not coalesce with the colours measured in the other 10 body parts, it was omitted from further analyses.

Removing the ventral claw from the analyses, there were still significant colour differences between the different body locations, and the patterns of significance for the remaining body locations did not differ from the patterns identified in Fig. 3. The dorsal locations (CLC, CCA, CCR, FAM, LAM) were darker in colour than the latero-ventral locations (Fig. 3). Locations including EXO, END, and CML tended to be lighter for most colour measures. FAL and TEL tended to be intermediate in grouping to the dorsal and ventral components, and did not consistently group with either dorsal or latero-ventral locations.

Conducting a forward step regression for the importance of hue components (R, G, B, CIE-a, CIE-b) on value of the sample (CIE-L), Green was the first and most significant factor ($F_{1,48} = 999.99$, $r^2 = 0.977$). Even with a highly significant first component, Red and CIE-a also significantly accounted for variation in CIE-L. These two colours entered the model with $F = 1067.91$ and 4.56 respectively. This three-component model accounted for nearly all of the variation in CIE-L ($F_{3,46} = 99.99$, $P < 0.001$, $r^2 = 0.999$). The poor lack of fit of CIE-a and CIE-b in this model can be explained by lack of variation when CIE-L was <15 (Fig. 3).

The overall pattern of coloration in the genetically blue animals was similar to that of the wild-type animals, but of different numerical value. Within the genetically blue animal, each body location had a similar relative value with respect to the other locations as observed for the wild-type animals, and the ventral claw was an outlying point. There was a general positive correlation ($r^2$) comparing the genetically blue animal with the wild coloured animals for the different colour hues (Red = 0.68, Green and CIE-a = 0.43, CIE-b = 0.12, and Blue = 0.03) and value (CIE-L = 0.60). For all colour parameters except Red, there was a significant colour score difference between genetically blue and wild-type animals. Body locations of genetically blue animals had greater colour scores for Green, Blue, and CIE-L (for all examples, paired $t$-test, d.f. = 10, $t < -4.98$, $P < 0.001$) than wild-type animals. CIE-a and CIE-b were greater in wild-type animals than genetically blue (for all examples, paired $t$-test, d.f. = 10, $t > 4.36$, $P < 0.001$). The Red measurement across body locations was not different for genetically blue compared with wild-type animals (paired $t$-test, d.f. = 10, $t = -0.83$, $P > 0.40$).

Examining the *in vivo* pattern that white lobsters add colour to their shell, the full effects model exhibited significant four-way interactions (diet, day, body location, colour). Thus, analyses were conducted on the colour value (CIE-L) separately for each of the five body locations. In this reduced model, there was still significant diet × day effects (for all body locations, two-way repeated measures ANOVA, $F_{9,42} > 7.25$, $P < 0.001$). Simple effects analysis showed that CIE-L did not change over the course of the experiment for animals fed the L, M1, and M2 diets. However, the CIE-L scores of the animals fed the H diet significantly decreased. Reanalysing just the animals fed H, a two-way repeated measures ANOVA on ranked data showed that all body locations added colour (day factor $F_{3,60} = 39.91$, $P < 0.001$) at the same rate (interaction $F_{12,60} = 1.059$, $P > 0.40$, Fig. 4). These results further confirm the adult analysis in that the CLD, TEL, and LAM were darker than EXO and END (body location, $F_{3,60} = 26.44$, $P < 0.001$. Fig. 4).

To assess how the functional hue of the lobster shell colour changed in the H diet, changes in Red, Green, and Blue were also assessed in the CLD of these animals. These three colour measures varied in their response during the course of the experiment, as there was a significant day × colour interaction (two-way repeated measures ANOVA on ranks, $F_{6,30} = 9.947$, $P < 0.001$). The Red colour score did not significantly drop during the first three measurement periods (for all comparisons, Tukey's test, $q < 0.80$, $P > 0.90$, Fig. 5), whereas the last measurement period was significantly lower than the previous three (for all comparisons, Tukey's test, $q > 10.50$, $P < 0.001$, Fig. 5). For Green and Blue, only the middle two measurements were equivalent

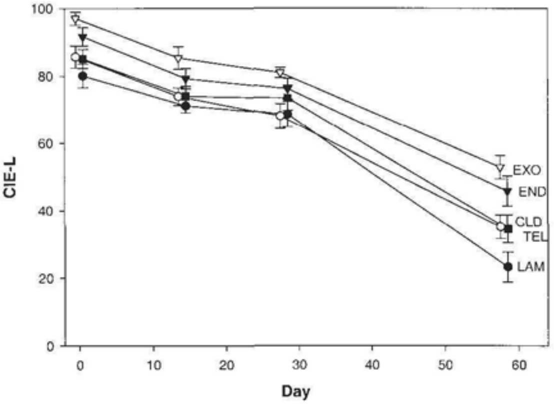

**Fig. 4** Change in Commission Internationale de l'Eclairage -L over the course of the diet experiment for five different body locations in white American lobsters, *Homarus americanus*, fed a high astaxanthin diet. All diets added colour at the same rate as there was no significant interaction. Exopodite (EXO) and endopodite (END) body locations were significantly greater than the other three body locations.

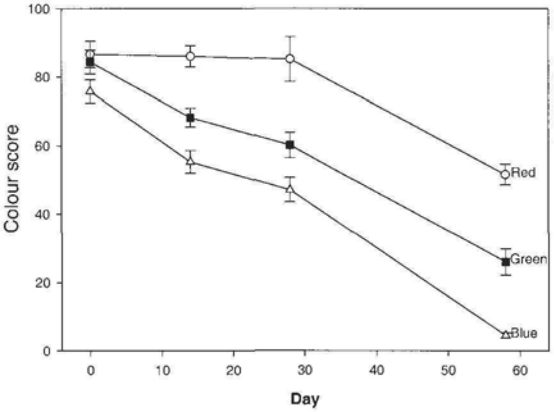

**Fig. 5** Change in Red, Green, and Blue hues in the dorsal claw over the course of the diet experiment in white American lobsters, *Homarus americanus*, fed a high astaxanthin diet. There was a significant day × diet interaction, and simple effects analysis showed that the value of Blue and Green decreased faster than did that of Red.

(Tukey's test, Green, $q = 2.83$, $P > 0.20$, Blue, $q = 2.10$, $P > 0.45$, Fig. 5), whereas all other comparisons were significantly different from each other (for all comparisons, Tukey's test, $q > 5.20$, $P < 0.005$, Fig. 5). This indicated that the animals were initially red in colour before darkening and becoming wild coloured.

## DISCUSSION

The colour of American lobsters, as with any animal, promotes increased survivorship and reproduction within their natural habitat. Thus this study first considered the long-term colouring of adult animals. American lobsters tend to be active in lower light environments (nocturnal, or deep and/or cloudy water, Lawton & Lavalli 1995). Their eyes operate efficiently at low light levels and, having a single receptor type, they do not have true colour vision (Atema & Voigt 1995). Thus their body colour will promote camouflage from predators, and intraspecific signaling given these constraints. The habitat and physical properties of lobster vision suggest that the luminosity of animals, as opposed to specific hues, may govern expression of colour. This analysis of variation in coloration within adult animals demonstrated that American lobsters are counter shaded. Their ventral areas are of higher luminosity than their dorsal areas which are darker. This is a colouring scheme common to a variety of aquatic animals (Saidel 1988), both predators and prey.

All hues were positively correlated to the luminosity (CIE-L) of the body location. The single colour parameter Green accounted for 97% of the variation of CIE-L, although Red and CIE-a were forced in a forward stepwise regression, and ultimately accounted for 99% of the variation in CIE-L. Hues CIE-a and CIE-b were less likely to contribute in the stepwise regression as they exhibited little variation when CIE-L was approaching 0, primarily a result of dorsal (medial) locations. Whereas CIE-L*a*b scoring was utilised in a study of visual properties of lobsters as it relates to acceptability for human consumption (Melville-Smith et al. 2003), the R*G*B colouring system appeared to be a better indication of natural coloration within American lobsters. Part of this was because hue is not uniquely defined by either CIE-a or CIE-b, and changing the saturation (the value of CIE-a or CIE-b) does not necessarily change the perceived colour (Ihara Electronic Industries 2000, CIE Colour Specification, http://www.ihara-group.com/colour/theory4.html#13, accessed 5 January 2004). The utility of RGB in measuring colour is that the changes in the three values track the colour as humans perceive it. The green colour score from the RGB measure was most significantly correlated to the overall lightness (CIE-L) of the adult lobsters. This was a result of the differential importance each component colour had in shifting between the various RGB colour states. A dark red colour (R:G:B 80:10:10) lightens more rapidly when green is added compared with an equal allotment of blue. To the naked eye, blue has to increase approximately twice as much as green before a lightening of the colour becomes visually apparent.

However, within each lobster, one area, the ventral surface of the claw, was aberrantly coloured compared with the close correlations of the other 10 body parts. The ventral claw was shifted towards a reduced number of pigments, with red being predominant. The lack of blue and yellow pigments was apparent in the genetically blue lobster, where the ventral claw was virtually white. The significance of the different colour scheme of the ventral claw has yet to be ascertained. It is likely that the coloration of the ventral claw is important in intra-specific signaling. This surface remains hidden for a majority of the time, save when animals encounter each other and perform a meral spread as part of an assessment of size before a physical encounter (Atema & Voigt 1995). This display is visual, as blindfolded lobsters utilise mechano- and chemo-reception to a greater extent in agonistic encounters than do lobsters that can see (Kaplan et al. 1993).

A number of animals utilise short-term colour shifts. Although some crustaceans demonstrate short-term colour changes, lobsters do not exhibit chromatophore mediated colour alterations. Intra-individual colour variation in American lobsters is only through quantitative and qualitative adjustments of pigments within the exoskeleton. One of the most common observations of this trait is the loss of colour in American lobsters when fed artificial diets (D'Agostino 1980; D'Abramo et al. 1983; Lim et al. 1997; Floreto et al. 2001). The methodology developed here was used on a preliminary assessment of how white lobsters "coloured-up" when fed a diet containing low or high levels of carotenoid. Animals decreased the CIE-L hue only when fed a diet high in carotenoid. Different body locations did exhibit minor differences in the degree in which colour was added, but this was likely a result of the body location. Ventral body locations were light brown-reddish in colour, and lacked the darker overlying pigmentation common to the dorsal group. The similarities between body locations in the rate of colour addition indicate that lobsters do not differentially partition resources to one body location over another. Colour change is a byproduct of protein-carotenoid interactions, and colour is added in proportion to the final body colour, with dorsal components receiving more pigmentation than ventral components. It is possible that overall pigment concentration is a function of shell thickness, and thus the thicker shell sections are concomitantly darker.

The animals on the high carotenoid diet initially shifted to a pure red before darkening. This was likely a result of the excess carotenoid in this diet which amassed in the epidermis in a form yielding a red colour. Although not observed in this experiment, other animals fed low carotenoid diets were observed to initially shift to a blue colour before red was added to finish in the wild-type coloration. Thus the colour shift of the white lobsters may be able to elucidate the binding affinities of the proteins responsible for crustacyanin. It is also possible that the form of the carotenoid fed to the lobsters will influence the rate of mobilisation of carotenoids (D'Abramo et al. 1983). In this experiment, in addition to different levels of carotenoid, the diets utilised carotenoid from different sources. The high carotenoid treatment was made by feeding a combination of frozen adult and live nauplii *Artemia fanciscas*. The medium carotenoid diet 2 was made by mixing commercial astaxanthin (Naturose®) into a mixed diet including 22% frozen adult *Artemia*. Thus the results of the colour-up study can only be considered preliminary, and rates of colour addition need to be compared when animals are fed different concentrations of a carotenoid from the same source.

One of the overarching goals of this study was to develop a relatively low-cost method to examine colour in any size lobsters. The equipment used here, a Nikon Coolpix 5000 digital camera, a Nikon SL1 Macro Cool Light, and image analysis software (Adobe Photoshop) were sufficient to examine the coloration of virtually any sized lobsters. As for the area of the body best suited to examine colour, there is a linear relationship of colours for all locations except the ventral claw. In studies of variation between populations, the ventral areas may be best. In the RGB colour scheme, they have greater values than the dorsal components, and being further from a terminal boundary (black in the RGB scheme is 0,0,0), it may be easier to detect any subsequent variation in colour. Avoiding a terminal boundary was not necessary in the colour-up study since the animals were initially white, the opposite of the terminal boundary. Thus when investigating the addition of colour to white animals, all body locations have the same potential utility given the equal rate of colour addition. The ventral claw is differentially coloured than the other body locations, and additional work is needed to assess if this deviation in coloration is adaptive. Multiple handling of animals can lead to claw loss, and this would be one reason to avoid using the claws if a study relied on repeated measurements. As for the colour to measure, all six parameters scaled linearly amongst the body locations. CIE-L was likely to be biologically important to American lobsters given their visual system and their crepuscular/nocturnal habits. In addition, Green was the hue most significantly correlated to CIE-L, and accounted for 97% in this value. One of these two measures will be of greatest utility in future examinations of the colour of American lobsters.

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Review

# Diverse larval recruitment strategies within the Scyllaridae

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**Abstract** Scyllarid lobsters, together with the palinurids, have a long-lived, planktonic phyllosoma larval phase in their early life history followed by a much briefer postlarval phase which at settlement completes the planktonic period of their life cycle. Information on scyllarid larval biology and recruitment mechanisms is fragmentary. Scyllarid species exhibit a wide range of larval recruitment strategies and durations, from entire larval and postlarval phases being completed in just a few weeks within lagoons, through to species that become widely dispersed in ocean basins over many months. In contrast, the phyllosomas of all palinurids so far investigated invariably, over many months, become widely dispersed in the open ocean well beyond the continental shelf. Among scyllarid species a general relationship is apparent between adult size and the extent of larval dispersal. During the planktonic period currents, in combination with larval vertical migratory behaviour, probably play an important role in larval dispersal and return. Although varying greatly in size, the postlarval nisto of most scyllarids appears to be similar in behaviour to the puerulus of palinurids. Nistos are usually (if not always) non-feeding and appear to alternate between swimming at night and resting on the bottom during the day as they move inshore to regain adult grounds before settling and metamorphosing to the first juvenile lobster instar. Those scyllarids with a somewhat abbreviated larval duration and mainly coastal larval distribution—the "flat" species of *Ibacus* and *Thenus*—appear to have succeeded in exploiting local currents and biotic systems to restrict larval dispersal and maintain their place. Based on the characteristics of the larvae and their recruitment mechanisms, there is support for the present division of the Scyllaridae into its four subfamilies, but also backing for revision, particularly of the Ibacinae.

**Keywords** Scyllaridae; slipper lobster; phyllosoma; nisto; larval recruitment

## INTRODUCTION

Slipper lobsters (family Scyllaridae) are widespread in shallow temperate, and particularly tropical, seas (Baisre 1994), and are also increasingly being reported from deeper waters (>300 m) (e.g., *Scyllarus* sp., NORFANZ 2003, www.oceans.gov.au/norfanz). Scyllarids are particularly distinctive in having the second antenna modified to a closely hinged series of five flat plates, quite without the whip-like flexible flagellum of other decapods—but at the same time they are a very diverse group in terms of size, habitat, and distribution. They range from <50 mm to half a metre long, are found at shallow depths down to habitats beyond natural light, and are known by a wide range of common names (see Holthuis 1991).

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Four subfamilies are recognised, containing c. 80 species: the Ibacinae (genera *Evibacus*, *Ibacus*, and *Parribacus*), Arctidinae (*Arctides* and *Scyllarides*), Scyllarinae (*Acantharctus*, *Antarctus*, *Antipodarctus*, *Bathyarctus*, *Biarctus*, *Chelarctus*, *Crenarctus*, *Eduarctus*, *Galearctus*, *Gibbularctus*, *Petrarctus*, *Remiarctus*, *Scammarctus*, and *Scyllarus*), and Theninae (*Thenus*) (Holthuis 1985, 1991, 2002). New species continue to be reported, mostly among the Scyllarinae, a subfamily of small lobsters that includes well over half the known scyllarids and which is represented in tropical lagoons, on continental shelfs and slopes, and on deep sea ridges and seamounts. Since much of the world's oceans remain unexplored, further new species—and taxonomic revisions—can be expected. Few scyllarids form significant fisheries, which is why much less research, particularly into recruitment, has been directed towards them than spiny lobsters.

Understanding larval recruitment processes in marine species requires, among other things, information on the extent of larval distributions. Early reports on scyllarid larval distributions came mainly from wide-ranging plankton sampling expeditions in which catches were often small (e.g., Gurney 1936; Saisho 1966; Johnson 1971a,b). Some of this material is frustratingly obscure because of difficulties with larval identity. Incorrect or unresolved identifications are a common problem with field-caught larvae of marine species and are particularly evident in this early scyllarid literature (Holthuis 1985). Gurney (1936), for example, reported the distributions of a number of *Scyllarus* spp. extending into ocean basins, but in many instances the species he described remain unidentified or unconfirmed. Unusual features of scyllarid larvae were identified in this early work. Some larvae, probably being *Parribacus* spp., become "giants" reaching 80 mm in total length. Also, the phyllosomas of several scyllarid species become closely associated with other zooplankton, particularly medusae.

Most of the detailed distributional data are for larvae collected as bycatch where other crustaceans were the primary focus (e.g., Phillips et al. 1981; Rothlisberg et al. 1994; Webber & Booth 2001). Studies targeting scyllarid larval distribution and recruitment mechanisms have been undertaken (e.g., Yeung & McGowan 1991), but such information on the Scyllaridae has more often surfaced from studies of palinurid recruitment (e.g., Coutures 2000; Inoue et al. 2001).

There are many similarities in larval development and behaviour between the very closely allied Scyllaridae and Palinuridae. Both families produce large numbers (thousands to hundreds of thousands) of small eggs (c. 1 mm diam.) that are carried for a short period (weeks), and both have a long larval phase (weeks to months). Early development in the Scyllaridae comprises a "prelarva" (naupliosoma) in some, perhaps all species (e.g., Harada 1958; Crosnier 1972; Lesser 1974; Phillips & Sastry 1980; Martins 1985); a larval phase (the phyllosoma); and a postlarval (nisto) phase. The naupliosoma is a short-lived (hours) and small prezoea (1–2 mm long). The phyllosoma is a leaf-like, transparent, and long-lived planktonic zoea which passes through a number of instars and reaches 10–83 mm total length (TL) depending on species (e.g., Robertson 1968a; Ito & Lucas 1990; Baisre 1994). After weeks or months developing in coastal or more distant waters, phyllosomas metamorphose to the nisto. The nisto is a short-lived, transparent, lobster-like megalopa that reaches 20 mm carapace length (CL) in some species. Metamorphosis signals the end of the planktonic phase when the nisto, after assuming the role of returning the lobster to the benthic habitat of the adult, moults to the first-instar juvenile lobster.

More detailed information on scyllarid larval development and behaviour, and confirmation of their identity, has come about through larval culture. Species cultured through most or all their larval stages include *Ibacus ciliatus*, *I. novemdentatus*, *I. peronii*, *Scyllarus americanus*, *S. depressus*, *Petrarctus* (as *Scyllarus*) *demani*, *Thenus orientalis*, and *Thenus* sp. A short larval life and the hardy nature of the larvae have aided in the culture of commercial species (e.g., *Thenus* spp., Mikami & Greenwood 1997a).

Scyllarid phyllosomas are widely represented in plankton collections. For example, there are descriptions of at least 57 scyllarinid (formerly *Scyllarus*) species of phyllosoma, although no more than 20 of them have been given names of known species (Webber & Booth 2001). Indeed, scyllarinid species are often the dominant scyllarid larvae collected from coastal and near-shelf waters (e.g., McWilliam et al. 1995), and are frequently the most abundant of all phyllosomas in those areas (e.g., Berry 1974; Sekiguchi 1986a; Rothlisberg et al. 1994). This has been attributed to either prolonged egg-bearing and hatching periods or to repetitive breeding in a single year, or both (Baisre 1994).

This paper reviews scyllarid larval and postlarval recruitment strategies and knowledge of the life history phases involved.

## SCYLLARID EARLY LIFE HISTORY

### Phyllosoma biology

Our knowledge of aspects of the biology essential to an understanding of larval recruitment is fragmentary. These aspects include larval identity, morphology, food and feeding, behaviour (including swimming ability), predators, sensory systems and, very importantly, larval duration.

There are numerous descriptions of scyllarid larval morphology and development (for examples see Holthuis 1985, 2002 and references therein), but few are comprehensive in their description of the number of instars and the relative development of morphological structures. Many identities are unconfirmed and most scyllarid larvae collected, even those described recently, remain unclassified beyond the level of genus (e.g., McWilliam et al. 1995). It is clear, however, that the morphological characteristics of scyllarid phyllosomas are generally very similar to those of palinurids (see Baisre 1994). Moulting and growth in phyllosomas is accompanied by the progressive development of some appendages and functional changes in others. To analyse these changes, the instars of some species have been grouped into stages, often with a single instar in early stages and more than one in later stages. An interesting feature of scyllarid phyllosomas is that they lack an exopod on the third maxilliped, which is present in all palinurids except for *Jasus* spp. This difference may indicate a phylogenetic separation in feeding strategy between those with and without this exopod, or it may simply stem from a reduced requirement for swimming appendages. An important division within the scyllarids is that *Ibacus* and *Thenus* species hatch at a more advanced level than other species (Baisre 1994).

Tank studies (e.g., Robertson 1968b; Ito & Lucas 1990; Marinovich et al. 1994; Mikami & Greenwood 1997a; Mikami & Takashima 2000) suggest that phyllosomas of most, if not all, scyllarids are primarily predators and use their pereopods to fix and hold food items. The mouth and foregut structures also suggest consumption of soft fleshy foods (Mikami et al. 1994). Foods such as *Artemia*, fish larvae, bivalve gonad, and jellyfish have therefore been useful in phyllosoma culture, particularly of the early stages. In nature, such food items are more abundant in areas of high primary production near land, at upwellings, and along water mass boundaries, than in offshore oligotrophic waters. Nevertheless, appropriate foods necessarily occur offshore, where many scyllarid larvae are found.

There have been several reports of scyllarid phyllosomas, usually late and particularly final stages, being closely associated with—sometimes "riding"—medusae (and possibly salps and ctenophores). Several scyllarid genera have been observed associating with gelatinous zooplankton in this way, including *Ibacus* (Thomas 1963; Shojima 1963, 1973; Booth & Matthews 1994), *Scyllarides* (Shojima 1963), *Thenus* (Barnett et al. 1986), *Scyllarus* (Shojima 1963; Herrnkind et al. 1976; Barnett et al. 1986), and *Petrarctus* and *Eduarctus* (both previously *Scyllarus*) (Barnett et al. 1986). Medusa-riding does not appear to be accidental or entirely intermittent: Herrnkind et al. (1976) observed 80 *Scyllarus* sp. larvae on 402 individual *Aurelia aurita* examined; and Barnett et al. (1986) found 49 out of 51, mostly final stage phyllosomas of *Thenus orientalis*, *P. demani*, *Eduarctus martensii*, and a *Scyllarus* sp. collected, to be closely associated with medusae.

It is not known if this phyllosoma-zooplankton relationship is for food, protection, transport, or a combination of these. Nematocysts in the faeces of a giant phyllosoma (possibly a *Parribacus* sp.) and of other (unnamed) phyllosomas suggested a feeding association to Sims & Brown (1968), and Shojima (1963) observed *Scyllarus* and *Scyllarides* larvae carrying hydromedusae as if for food. Indeed, Kittaka (2000) concluded that medusae may be nutritionally satisfactory for palinurid phyllosomas in laboratory culture. Nematocysts of medusae, which the phyllosomas appear to be unaffected by, may confer some protection from predation to the phyllosomas. Gelatinous zooplankton is more common inside the shelf break than beyond it, and in areas of high primary productivity; association of phyllosomas with this zooplankton may therefore play a role in controlling larval dispersal in some species.

Phyllosoma swimming behaviour appears to differ between species. Some, such as *Thenus orientalis*, appear to be weak swimmers, even in late stages (Barnett et al. 1984). Other species display swimming ability at least as strong as that of palinurids found in the same water masses (see below). In none, however, is swimming strong enough to enable escape from larger predators such as tuna and for the most part phyllosomas seem to rely on their virtual transparency to avoid predation. Also, horizontal swimming alone is insufficient to effect a return to shore of species that become widely distributed. It is likely that shoreward transport is achieved more passively with larvae swimming vertically and occupying particular strata in the water column—this is discussed later. Specialised sensory systems have been suggested as the mechanism by which palinurids orientate shorewards, but this has not been investigated in scyllarids.

## Spatial and temporal scales of larval recruitment mechanisms

Scyllarids have a planktonic development period which is far more variable between genera than is seen among the palinurids, from a few weeks to at least 9 months (Table 1). Consistent with this is a similar variation in the number of instars—from a low of about four in *Thenus* spp. to at least 13 estimated for an *Arctides* sp. (see Table 1).

Much of the early life of most scyllarid lobsters is spent in waters away from parent grounds but, like the duration of larval life, the extent of dispersal varies widely between species (Table 1). For example, *Parribacus*, *Scyllarides*, and *Arctides* spp. have larval distributions generally far further from shore than those of *Evibacus* and many scyllarinid species. Indeed, it has been recently shown that some scyllarinids complete their larval development within the lagoons formed by coral island barrier reefs (Coutures 2000). Even more spatially restricted recruitment mechanisms may exist: Coutures (unpubl. data) has observed that some New Caledonian scyllarinid phyllosomas, regardless of their stage of development and including nistos, are commonly caught in barrier reef crest nets but seldom taken within or beyond the adjacent lagoon waters. But even among the scyllarinids, the smallest of all lobsters, the phyllosomas of some species can still be found hundreds to thousands of kilometres from shore (e.g., *Antipodarctus* (previously *Scyllarus*) *aoteanus*, Webber & Booth 2001). Such wide dispersals among these scyllarinids, and of *Parribacus*, *Scyllarides*, and *Arctides* spp., means that the rule of thumb for palinurids that their larvae are seldom taken beyond the latitudes of the adult distribution (George & Main 1967) does not necessarily apply to all scyllarids.

## Interaction of ocean processes and larval behaviour

In species whose phyllosomas do not become widely distributed in ocean basins, mechanisms must exist to enable larvae to stay close to parent grounds. Even those species with the shortest larval development period (c. 4 weeks, Table 1) have the potential to become widely dispersed without them. Recent work has helped clarify the role of ocean processes such

**Table 1** Scyllarid reproductive and larval parameters. For larvae, [a] denotes data based on wild lobsters; [b] denotes data based on cultured lobsters; d, day; wk, week; mo, month; TL, total length; CL, carapace length. Number of instars given only if an estimate is available (otherwise it is at least the number of stages). Female size suggests the scale of upper estimated breeding size. For extent of offshore distribution: coastal, mainly over continental shelf; intermediate, within but also beyond shelf break; oceanic, mainly well beyond shelf break, including within ocean basins.

| Subfamily/species | Female size (mm CL) | No. instars | No. stages | Length of larval life | Size of final phyllosoma (mm TL) | Extent of offshore distribution of late stages | Nisto duration | Nisto size (mm CL) |
|---|---|---|---|---|---|---|---|---|
| **Ibacinae** | | | | | | | | |
| *Evibacus princeps* | 130[2] | | 11[a, 24] | | 32[a, 8, 24] | Coastal & intermediate [8, 24] | | |
| *Ibacus alticrenatus* | 43[17] | | 7[a, 38] | 4–6 mo[a, 38] | 36–44[a, 38] | Intermediate[38] | | 12–15[a, 38] |
| *Ibacus ciliatus* | 80[2] | 7–8[b, 15, 19] | | 54–76 d[b, 15, 19] | 40–46[a, b, 15, 19, 26] | Coastal & intermediate[4] | | 16–20[a, b, 15, 19, 26] |
| *Ibacus novemdentatus* | 70[2] | 7[b, 19] | 7[a, 4] | 65 d[b, 19] | 21–33[a, b, 4, 19, 26] | Coastal & intermediate[4] | | 13–15[a, b, 4, 19, 26] |
| *Ibacus peronii* | 70[2] | 6[b, 36] | 7[a, 25] | 71–97 d[b, 36] | 39[a, 25] 25[b, 36] | Intermediate & oceanic[25, 35, 39] | 17–24 d[a, b, 25, 36] | 11–12 [a, b, 25, 36] |
| *Parribacus antarcticus* | 80[2] | | >11[a, 30] | c. 9 mo[a, 30] | 75–83[a, 14, 30] | Oceanic[29, 30] | | 20[a, 30] |
| *Parribacus scarlatinus* | 70[2] | | | | | | | 21[a, 9] |
| **Arctidinae** | | | | | | | | |
| *Arctides guineensis* | 50[2] | | 13[a, 34] | c. 8–9 mo[a, 34] | 59[a, 34] | Oceanic[34] | | |
| *Scyllarides aequinoctialis* | 110[2, 22] | | 11[a, b, 13] | c. 8–9 mo[a, b, 13] | 36–48[a, 13] | Oceanic[13, 37] | | 13[a, 22] |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Scyllarides nodifer* | 100[2, 22] | | 12[13] | 9 mo[13] | 37[a, 13] | Oceanic[13] | | 9–11[a, 22] | |
| *Scyllarides herklotsii* | 130[2] | | 11[a, 23] | | c. 25[a, 23] | Oceanic[23] | | 13[a, 23] | |
| *Scyllarides astori* | 100[2] | | | | 44[a, 8] | Oceanic[8] | | | |
| *Scyllarides squammosus* | 130[2] | | | | 48[a, 10] | Oceanic[29, 30, 39, 43] | | 15[a, 10] | |
| **Scyllarinae** | | | | | | | | | |
| *Petrarctus demani* | 28[16] | 8[b, 20] | 6[a, b, 41] | 42–53 d[b, 20] | 10–11[a, b, 20, 41] | Coastal & intermediate [41] | 5–6 d[b, 20] | 4–6[a, b, 20, 32] | |
| *Petrarctus rugosus* | 22[16] | | 12[a, 28, 29] | | 15–19[a, 28, 29] | Coastal & intermediate [28] | | | |
| *Antipodarctus aoteanus* | 30[1] | | 10[a, 3] | Several mo[a, 3] | 19–31[a, 3] | Intermediate & oceanic[3] | | 6.5 [a, 3] | |
| *Scammarctus batei* | 33[16] | | 10[a, 28] | | 26–29[a, 28] | Coastal & intermediate [28] | | | |
| *Crenarctus bicuspidatus* | 25[16] | | | 4 mo[a, 35] | 21[a, 35] | Coastal, intermediate & oceanic[35, 39, 40, 42] | | | |
| *Galearctus timidus* | 27[16] | | 9[a, 30] | | 23[a, 30] | ?Intermediate & oceanic[30] | | 8[a, 16] | |
| *Galearctus kitanoviriosus* | 36[16] | | | | 17–21[a, 27] | Coastal & intermediate[40, 42] | 2 wk[a, 27] | 4–5[a, 27] | |
| *Eduarctus martensii* | 14[16] | | 8–10[a, 6, 18, 28] | 2–3 mo[b, 18] | 11–15[a, 6, 28, 29] | Coastal & intermediate [18, 28, 40, 43] | | 7–9 d[a, 32] | 3[a, 6] |
| *Eduarctus modestus* | 14[16] | | 8[a, 30] | | 13[a, 30] | ?Intermediate & oceanic[30] | | | |
| *Chelarctus cultrifer* | 31[16] | | 11–12[a, 28, 29] | | 25–33[a, 28, 29] | Coastal & intermediate [28, 29, 40, 42] | | | |
| *Biarctus sordidus* | 24[16] | | 8[a, 41] | | 14[a, 41] | Coastal & intermediate[41] | | 3.5[a, 16] | |
| *Scyllarus americanus* | 25[22] | 6–7[a, b, 5] | 6–7[a, b, 5, 33] | 32–40 d[b, 5] | 8–13[a, b, 5] | Coastal & intermediate [5, 33, 37] | | 3[a, b, 5, 22] | |
| *Scyllarus depressus* | 26[22] | | 9–10[a, b, 7] | 2.5 mo[a, b, 7] | 24–27[a, 7] | Coastal, intermediate & oceanic [7] | | 6–7[a, 7, 22] | |
| *Scyllarus chacei* | 25[22] | | | | | Coastal & intermediate [37] | | 3–4[a, 22] | |
| *Scyllarus planorbis* | | 8[b, 12] | 8[b, 12] | 54 d[b, 12] | 8[b, 12] | | | | |
| **Theninae** | | | | | | | | | |
| *Thenus orientalis* | 80[2] | 4[b, 11, 21] | 4[a, b, 11, 21, 31] | 27–45 d[b, 11, 21] | 20[a, 31] 16–20[b, 11, 21] | Coastal[31] | 7 d[b, 11] | 8[a, 31] 7–8[b,11, 21] | |
| *Thenus* sp. | 80[2] | 4[b, 21] | 4[b, 21] | c. 27–45 d[b, 21] | 13–19[b, 21] | | | 7–9[b, 21] | |

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[1]Powell (1949), [2]Holthuis (1991), [3]Webber & Booth (2001), [4]Shojima (1973), [5]Robertson (1968b), [6]Phillips & McWilliam (1986), [7]Robertson (1971), [8]Johnson (1971a), [9]Coutures et al. 2002, [10]Michel (1968), [11]Mikami & Greenwood (1997b), [12]Robertson (1979), [13]Robertson (1969a), [14]Baisre (1994), [15]Mikami & Takashima (1993), [16]Holthuis (2002), [17]Holthuis (1985), [18]Rothlisberg et al. (1994), [19]Takahashi & Saisho (1978), [20]Ito & Lucas (1990), [21]Mikami & Greenwood (1997a), [22]Lyons (1970), [23]Crosnier (1972), [24]Johnson (1968), [25]Ritz & Thomas (1973), [26]Dotsu et al. (1966), [27]Higa & Saisho (1983), [28]Prasad et al. (1975), [29]Berry (1974), [30]Johnson (1971b), [31]Barnett et al. (1984), [32]Barnett et al. (1986), [33]Olvera Limas & Ordonez Alcala (1988), [34]Robertson (1969b), [35]Phillips et al. (1981), [36]Marinovich et al. (1994), [37]Yeung & McGowan (1991), [38]Atkinson & Boustead (1982), [39]McWilliam & Phillips (1983), [40]Inoue et al. (2001), [41]Ritz (1977), [42]Sekiguchi & Inoue (2002), [43]Coutures (2000).

as local eddies, gyres, and counter currents in limiting the dispersal of palinurids (Booth & Phillips 1994). These findings are also likely to apply to scyllarids, as suggested by such workers as Johnson (1971a), Berry (1974), Sekiguchi (1986a,b), Lee et al. (1992, 1994), Fiedler & Spanier (1999), Inoue et al. (2000, 2001), and Sekiguchi & Inoue (2002). Further, eddies can transfer larvae into new regions (McWilliam & Phillips 1983), whereas attachment to gelatinous zooplankton may provide late phyllosoma stages with an indirect way of exploiting water movement to remain relatively near to shore.

The vertical distribution of larvae appears crucial to their retention near shore, with their horizontal direction of movement presumably being affected by their position in the water column. Vertical migration is possibly triggered by positive or negative phototactic responses, a behaviour which also undergoes ontogenetic change. Most scyllarid phyllosomas appear to make diel vertical migrations. *Crenarctus* (previously *Scyllarus*) *bicuspidatus* larvae, for example, occur near the surface at night but during the day concentrate at 40–100 m depth, the early stages being shallowest (Phillips et al. 1981). (Moonlight causes the mid- and late-stage larvae to be deeper by 15–25 m at night.) The extent of diel vertical migration may also be influenced by hydrological conditions. For example, *Chelarctus* (previously *Scyllarus*) *cultrifer* phyllosomas were observed by Minami et al. (2001) to be near the surface at night, within the mixed layer, whereas during the day their upper distribution was at the base of the mixed layer (c. 60 m depth). Typically, because they are smaller and more limited in swimming ability, earlier stages show less extensive vertical migration than later stages (Phillips et al. 1981; Wada et al. 1985; Yeung & McGowan 1991). For early larval stages, and for species whose larvae at all stages migrate little, small vertical migrations may lead to more restricted larval dispersal, as suggested by Yeung & McGowan (1991). Clearly, different scyllarid species migrate vertically to different extents but until more is known about how this relates to local water movements it is not possible to pinpoint any further how these interactions translate into the dispersal or retention of larvae.

## Postlarval phase

Larval recruitment is complete at settlement of the nisto. The postlarval nisto provides the link between the planktonic and benthic life-history phases in scyllarids, as does the puerulus in palinurids. However, Barnett et al. (1986) suggest that in some species (e.g., *T. orientalis*) the nisto is much closer to the adult form than is the nisto of other scyllarid species (or the puerulus of palinurids), and its functional role may not, therefore, be identical in all species. The great range in nisto size (3–21 mm CL; Table 1), not in direct proportion to the size of the final phyllosoma instar, would be consistent with this.

The duration of the nisto has been estimated for few scyllarids (Table 1) and little is known of its biology because nistos are less commonly caught than pueruli and also they have not been the same focus of fishery-directed settlement research as palinurids. Nistos appear to have the same plankton-to-benthos function as pueruli, which swim shorewards from or beyond the continental shelf break. However, because some species of final-stage scyllarid phyllosomas are found much closer to shore before metamorphosis than are final-stage palinurid larvae, the stimulus for metamorphosis and behaviour may not be identical between the two families. Scyllarids which may occur only within the shelf break include *Thenus* spp.

Nistos have been taken reasonably often in plankton tows and in the water column under lights indicating that at times they are pelagic. The nistos of some species have, like pueruli, been observed to forward swim (behaviour associated with time spent up in the water column), in addition to backward swimming to escape threats (Robertson 1968b; Lyons 1970; Higa & Saisho 1983; Barnett et al. 1986). However, variable swimming ability—perhaps more variable than among pueruli—is suggested by a marked difference in size between the pleopods of different species. The nisto of *T. orientalis* has poorly developed pleopods and is a poor swimmer (Barnett et al. 1984), and may not be morphologically equipped for active dispersal or site selection, whereas the nisto of *A. aoteanus*, for example, has well developed pleopods with prominent appendix interna and has been found many kilometres from shore (Webber & Booth 2001).

Sand-burying appears to be common among scyllarid postlarvae (and is becoming increasingly evident in pueruli as well). Nistos of *T. orientalis* and *E. martensii*, for example, were found by Barnett et al. (1986) to be active at night but to bury in sandy substrates during the day. It is likely that most, if not all, nistos repeat this cycle as they move towards settlement areas. Thus the nisto is neither completely planktonic nor entirely benthic and, although ability varies between species, all are probably capable of some swimming. This is supported by the finding that all nistos described to date are almost completely transparent, a feature of the highly motile pueruli of palinurids in which this characteristic has undoubtedly evolved to help them avoid predation as they migrate inshore.

The nisto appears to be largely a non-feeding stage. If nistos do feed, their diet is probably confined to small, soft materials, judging by observations of those cultured in the laboratory, histological examination of the proventriculus, and examination of mouthparts (e.g., Barnett et al. 1986; Mikami & Takashima 1993; Mikami & Greenwood 1997a).

Nistos have only occasionally been reported on collectors deployed for pueruli (e.g., Phillips & Booth 1994), suggesting that in most scyllarids, settlement requirements are different from those of palinurids (holes and crevices in hard substrates or structurally complex growths of algae and sedentary invertebrates). Interestingly, some species change colour diurnally (Barnett et al. 1986), presumably to retain their cryptic colouring against changing backgrounds.

### Behaviour associated with reproduction

There appears to be little published on scyllarid reproductive behaviour that may be crucial to the recruitment mechanism. There are examples of scyllarids—like several palinurids—migrating inshore-offshore in concert with their reproduction periods (Martins 1985). Further, in at least one species, *Ibacus chacei* (Stewart & Kennelly 1998), changes in vertical swimming of larvae may not be the only mechanism required to enable recruitment back to adult grounds. Significant proportions of lobsters >30 mm CL of this species migrate northwards along the coast of New South Wales in the same way as *Sagmariasus verreauxi* lobsters approaching maturity are believed to do (Montgomery 1992). It is thought that this is a contranatant migration to counter larval drift: unless some animals migrate upstream against the current, the centre of distribution of the species may be displaced in the direction of the water flows which transport the larvae. Interestingly, co-occurring *I. peronii* do not make this migration.

## DISCUSSION

Scyllarid recruitment strategies involve the production of a large number of small eggs from which larvae hatch at an early stage of development after a brief period attached to the adult, and an extended, free-living larval life phase which, in some species, is long enough to allow very wide dispersal. During this phase their behaviour, adjusted to take advantage of ocean currents, is thought to effect larvae some control over their distribution. Thus, scyllarid recruitment has many characteristics in common with that of palinurids.

Perhaps the most obvious difference between the two families is in the length of larval life and the concomitant extent of phyllosoma dispersal. Those palinurids for which there are data invariably disperse well offshore, reflecting long larval durations, but in the Scyllaridae there is a wide range of larval life-spans. Many small scyllarid species have much shorter, inshore development whereas other, mostly larger, species have far greater offshore dispersal, sometimes even greater than is seen in palinurids. A second difference, perhaps less significant but nevertheless noteworthy, is the close association of some scyllarid phyllosomas with medusae which, as far as we know, has not been found in palinurids. Finally, the remarkable variety in size of nistos (3–21 mm CL), far more variable than is seen among pueruli, suggests a productive area for further research into the behaviour and role of the nisto stage and the taxonomic relationships among genera.

The planktonic cycle of relatively few scyllarid species has been investigated in detail but some early conclusions can be drawn concerning larval recruitment strategies among the subfamilies. We place emphasis on evidence from the wild rather than from larval culture because it has been shown in palinurids that larval duration and other biological parameters may be different under culture (e.g., see Booth & Phillips 1994 and Table 1). In the Ibacinae, adult females are relatively large (most >70 mm CL). In most species with data, the larval development period is of medium duration (most 2–3 months), consists of at least seven stages (and therefore at least seven instars), and results in large phyllosomas (>30 mm TL) and large nistos (at least 12 mm CL). In one genus, *Ibacus*, larvae hatch at a relatively advanced level of development. For example, *I. alticrenatus* hatches at a level equivalent to the third to fourth phyllosoma stage of scyllarinids such as *A. aoteanus* (Atkinson & Boustead 1982; Webber & Booth 2001). It appears that because of this, *Ibacus* larvae generally do not disperse great distances offshore. Within the Ibacinae, *Parribacus* species are exceptional in having a long-lived larval phase (perhaps 8–9 months) that becomes widespread in ocean basins, and in having phyllosomas reaching a massive 80 mm TL and nistos of up to more than 20 mm CL.

Adult female Arctidinae are large (most >100 mm CL) and the larval development period is long (at least 8 months) with many stages (at least 11), resulting in large phyllosomas (most at least 35 mm TL) and large nistos (at least 10 mm CL). As this might imply, arctidinid larvae disperse great distances offshore, well beyond the shelf break.

In the Scyllarinae, adult females are small (most <30 mm CL) and although there are usually numerous instars (at least 6–12), other parameters are highly variable. Larval development durations range from 1 to 4 months, the final phyllosoma from c. 10 to 30 mm TL, and the nisto a corresponding 3–8 mm CL. Scyllarinids exhibit a wide range of late-stage larval distributions, from being confined close to shore to becoming widely dispersed, beyond the shelf break.

In the Theninae, adults are relatively large and larvae hatch at an advanced stage of development. There are few instars (c. 4), a short larval development period (c. 1 month), and development is inshore. However, most available information on the two theninid species, *T. orientalis* and *Thenus* sp., is from cultured larvae and it is not clear how representative this period of development is of those in the wild.

There appears to be a general relationship within the scyllarids between adult size (and at the same time fecundity) and larval recruitment strategy, the larvae of the larger species tending to have longer, more offshore development than larvae of the smaller ones. In most scyllarids, eggs are small (c. 0.6 mm diam.) and the larger species have larger broods, smaller species smaller broods. (*Ibacus* and *Thenus* are considered separately below because they have much larger eggs—c. 1.2 mm diameter—consistent with the more advanced stage of development of their larvae at hatching.) *Scyllarides* spp. are large and fecund lobsters and their larvae are oceanic (Table 1). For example, female *S. latus* and *S. squammosus* reach more than 110 mm CL, the eggs are 0.6–0.7 mm in diameter, and egg numbers reach over quarter of a million (Martins 1985; DeMartini & Williams 2001). Similarly, *Parribacus caledonicus* are large (females to at least 70 mm CL) and fecund (156 000–211 000) (Coutures 2003), and *Parribacus* spp. larvae are also found well offshore (Table 1). The high fecundity of *Scyllarides* and *Parribacus* spp. is presumably an adaptation to offset high larval losses in oceanic waters. In contrast, the much smaller *Scyllarus americanus* and *Petrarctus demani* (females <30 mm CL; egg diam. 0.5–0.6 mm; brood size c. 8 000–9 000) are generally found closer to shore (Robertson 1968b; Ito & Lucas 1990). (Some unidentified scyllarinid larvae reported from well offshore may be those of yet undiscovered, offshore, deep-water species.)

*Ibacus* and *Thenus* spp. are generally large lobsters that also have large eggs (e.g., *I. peronii* and *T. orientalis* females reach 70–80 mm CL; eggs are 1.1–1.2 mm diam.; broods are 5 500–37 000 and 5 000–50 000 respectively—Jones 1988; Stewart & Kennelly 1997), the advanced larvae apparently being adapted to be retained until settlement near or within coastal waters.

It seems likely that shorter larval durations among the scyllarinid species have evolved so that at least some larvae are not carried too far from shore by currents. It is thought that scyllarids with larval lives lasting several months, such as *Scyllarides*, *Parribacus*, and *Arctides* spp. are similar to palinurids in their dispersal because mid- and late-stage larvae are rarely found close to shore. Such species with more widespread larval dispersal might be expected to recruit more widely geographically than those with more restricted larval dispersal. As a result, post-larval recruitment of these widespread species may be more irregular from year to year, depending on long-term hydrological and ocean climate cycles.

Retention inshore means that larvae develop in more productive waters than if they were transported offshore. It also means that in enclosed waters, particularly in the tropics, they must sometimes tolerate wide variation in such factors as temperature and salinity (Rothlisberg et al. 1994). Those going further offshore enter waters with lower productivity, and although predation losses may be less, growth rates are probably slower, leading to a longer larval life.

It has often been reported how surprisingly large the numbers of scyllarid larvae caught have been, on occasions the numbers appearing to be well out of proportion to the catches of co-occurring palinurids (e.g., Berry 1974; Phillips & McWilliam 1989; Rothlisberg et al. 1994; McWilliam et al. 1995; Sabater & Sais 1998; Sekiguchi & Inoue 2002). This can be explained, however, by the fact that the adults, particularly of the scyllarinids, are often small and cryptic, probably being much more abundant than meets the eye; there are often prolonged egg-bearing and hatching periods or repetitive breeding in a single year, or both, among the scyllarids, and the larvae of some scyllarid species remain relatively close to shore, which is where plankton sampling is usually easier and often more frequent. Further, some species of scyllarid larvae seem to be particularly hardy and so may survive better: much greater proportions of *A. aoteanus* phyllosomas stayed alive longer on board ship than those of *Jasus edwardsii* cultured at the same time (J. Booth unpubl. data).

Baisre (1994) examined the phylogeny of palinuroidean lobsters with emphasis on larval characters. He concluded that the larval characters of scyllarids were fully supportive of Holthuis's (1985) proposal that *Parribacus* is more closely related to *Ibacus* and *Evibacus* than to *Scyllarides* and *Arctides*. Baisre (1994) also distinguished three groups in scyllarid evolution typified by the larvae; a *Scyllarides-Arctides-Parribacus* group and an *Ibacus-Evibacus* group, both of which appeared to have developed early in scyllarid evolution, and a third, *Thenus-Scyllarus* group of more recent origin. Our own reading of the larval literature generally supports these conclusions, although the subfamily Ibacinae (genera *Ibacus*, *Evibacus*, and *Parribacus*) clearly includes some very much more disparate developmental features compared with those that exist in the other subfamilies, including the relatively advanced stage of hatching in *Ibacus* and the extremely large larvae of *Parribacus*. These disparities suggest revision of the Ibacinae may be necessary in future although it is quite evident that there is still much to learn of both larval and adult biology of these, and almost all scyllarid species.

It would seem that both scyllarid and palinurid phyllosoma larvae have evolved at the same time as the prevailing current systems have evolved, so enabling them to exploit the plankton for food and the currents for transport and dispersal. We have observed that adult size in those scyllarids with small eggs may relate to the extent of dispersal (and that palinurids invariably disperse beyond the shelf break), but that some scyllarinids in particular appear to break this generalisation. Indeed it is possible that there are relationships yet to be revealed between length of larval life/recruitment mechanism and the generic composition of the newly established Scyllarinae subfamily (Holthuis 2002), but there are too few data available at present to enable this. However, adaptation to current regimes as different as those within lagoons and in the deep sea, among a group of very similar lobster species indicates a plasticity not immediately evident in their larger relatives.

It is interesting that the genera with the larger eggs and with a somewhat abbreviated larval duration and mainly coastal larval distribution are the "flat" species of *Ibacus* and *Thenus*, which inhabit sedimentary substrates. The relatively small spatial separation between their benthic and planktonic populations may mean that both the phyllosomas and the nistos of these genera need not have particularly well-developed swimming abilities. These scyllarids appear to have succeeded in exploiting local currents and biotic systems to restrict larval dispersal and maintain their place. Abbreviated development such as this is not, so far, apparent among scyllarids that live on rough ground.

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# Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand

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**Abstract** The rock lobster *Jasus edwardsii* forms the basis of important fisheries in south-eastern Australia and New Zealand. Their long pelagic larval phyllosoma phase (12–24 months) raises many questions as to how the larvae are retained and/or recruited into local populations. Recent attempts to model the dispersal of *J. edwardsii* phyllosoma have had mixed success at reconstructing settlement patterns. However, these models have either ignored vertical distribution or have used that of the western rock lobster, *Panulirus cygnus*. We report on the vertical distribution and migration of *J. edwardsii* phyllosomas, collected in March/April 2003 from the Wairarapa Eddy off the east coast of the North Island, New Zealand, and provide a model to describe their vertical distribution. *J. edwardsii* phyllosoma were primarily recorded within the upper 100 m over similar depth ranges to those reported for other palinurid and scyllarid species. Well-defined changes in diel vertical distribution were restricted to late-stage larvae. Mid-stage phyllosomas were concentrated in the upper 20 m both day and night. Late-stage phyllosomas were concentrated in the upper 20 m during the night, but they were absent from the upper 20 m during the day and distributed primarily between 20 and 100 m. Future modelling will benefit from using larval distribution and behaviour patterns specific to *J. edwardsii*.

**Keywords** *Jasus edwardsii*; rock lobster; *Antipodarctus aoteanus*; scyllarid; vertical distribution; diurnal vertical migration; Wairarapa Eddy; phyllosoma

## INTRODUCTION

The Palinuridae (spiny/rock lobsters) are found throughout the world's major oceans between c. 45°N and 45°S and form the basis of several important commercial fisheries (Lipcius & Eggleston 2000). *Jasus edwardsii* occurs from Dongara, Western Australia (29°15′S) around the south coast of Australia, including Tasmania, to Coffs Harbour, New South Wales (30°18′S) (Phillips et al. 2000), on seamounts and banks in the Tasman Sea, around mainland New Zealand, and at the Chatham Islands 800 km to the east of the South Island (Booth et al. 1990). In Australia, the commercial fishery for *J. edwardsii* is concentrated about the south-eastern region. In New Zealand, the main commercial fishery is along the east coast of the North Island south of East Cape, around Stewart Island, and in the south-west of the South Island.

Together with the Scyllaridae (slipper lobsters) and Synaxidae (coral lobsters), rock lobsters have a planktonic larval phase, the phyllosoma, remarkable in form and longevity (Phillips & Sastry 1980). The phyllosoma is dorso-ventrally flattened, leaf-like, and transparent. The phyllosoma of *J. edwardsii*

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passes through c. 17 instars (Kittaka 2000), grouped into 11 stages (Lesser 1978), and takes c. 18 months (Bruce et al. 2000) to reach metamorphosis. Phyllosomas of stages V and above are almost exclusively distributed in waters seaward of the continental shelf and have been recorded up to 900 km from the shore (Booth et al. 1990). The post-larval puerulus is the transitional phase between the pelagic larval phase and benthic juvenile to adult phase.

During this extended offshore larval phase, there is the potential for widespread dispersal caused by currents and wind-driven flows. Since metamorphosis needs to take place within the swimming range of the puerulus to the coast (c. 200 km or less, Jeffs et al. 1999, 2001), there must be some means to prevent phyllosomas from dispersing too far from land. One such means may be to take advantage of different flow regimes between depths via diel vertical migration (DVM). For species that display DVM, the most common form is to rise to the surface layer at night and descend to deeper waters during the day. This pattern in DVM has been recorded for several lobster species (*Panulirus interruptus*, Johnson 1960; *P. cygnus*, Rimmer & Phillips 1979; *P.* [*argus*], Yeung & McGowan 1991; *P. argus*, Hernandez et al. 2000; *P. longipes*, *Scyllarus cultrifer*, Minami et al. 2001). Diel vertical migration has also been reported for *Jasus lalandii* (Pollock 1986) and is believed to take place in *J. edwardsii* (Lesser 1978; Booth 1994; Bruce et al. 2000).

The extent of vertical migration can also differ between developmental stages. For example, early-stage *P. cygnus* phyllosomas perform relatively shallow DVMs as compared with late-stage phyllosomas (Rimmer & Phillips 1979). It is this behaviour that aids dispersal offshore of the early-stage phyllosomas, and return shoreward of the late-stage phyllosomas and pueruli (Rimmer & Phillips 1979; Griffin et al. 2001) because of differences in the direction of current regimes at different depths. Although DVM is thought to occur in *J. edwardsii*, the stage-specific details of this behaviour have not been reported.

The exact role that DVM, and changes in behaviour between stages, would play in *J. edwardsii* dispersal and recruitment is not clear. Deep DVM would effectively take larvae out of the wind-driven (Ekman) layer during the day, and/or bring them into the Ekman layer during the night. Deep migration to below the wind-driven layer may aid in retaining larvae within mesoscale eddies. Alternatively, surface wind-driven drift may occasionally facilitate recruitment via the transport of larvae towards the coast (Booth et al. 2000).

The Wairarapa Eddy, off the east coast of the North Island of New Zealand, is one of three large (100 km diam.) anticyclonic eddies appearing to be permanent features of the circulation in the region. In the mean, the eddy is centred near 41°S, 178°30′E, c. 180 km offshore. A detailed dynamical analysis of the eddy has not yet been made. However, it is probably formed by retroflection of the East Cape Current as it hits the Chatham Rise.

The Wairarapa Eddy is believed to be important to the distribution of *J. edwardsii* phyllosomas in New Zealand as it is believed to entrain phyllosomas (Booth & Stewart 1992; Chiswell & Roemmich 1998; Chiswell & Booth 1999). Both historical larvae catches (Booth & Stewart 1992; Booth et al. 1998) and models of dispersal (Chiswell & Roemmich 1998; Chiswell & Booth 1999) show higher levels of larvae within the eddy than outside. Indeed, without the Wairarapa Eddy system it is possible that *J. edwardsii* would not be able to sustain a population off the south-east coast of the North Island.

Understanding the vertical pattern of distribution of phyllosomas is an important prerequisite for understanding and modelling transport processes, yet this remains unclear for *J. edwardsii* (Bruce et al. 2000). The aim of the present study was to examine the vertical distribution and DVM of *J. edwardsii* by analysing vertically stratified samples collected from the Wairarapa Eddy system off the east coast of New Zealand. New Zealand, and the Wairarapa Eddy in particular, were chosen for this study because of the availability of a suitable vessel, and because of the historic consistency of being able to locate high-density patches of phyllosoma. The results are compared with existing knowledge of *J. edwardsii* DVM both in New Zealand and in Australia.

## METHODS

Sampling took place between 17 March and 2 April 2003 from the 70 m RV *Tangaroa* off the east coast of the North Island of New Zealand (Fig. 1).

The voyage was timed to coincide with the presence of two cohorts of *J. edwardsii* phyllosomas in the plankton within the region of the Wairarapa Eddy (Chiswell & Booth 1999), the oldest cohort from the spring 2001 (October–November) egg hatching and the more recent from the spring 2002 egg hatching.

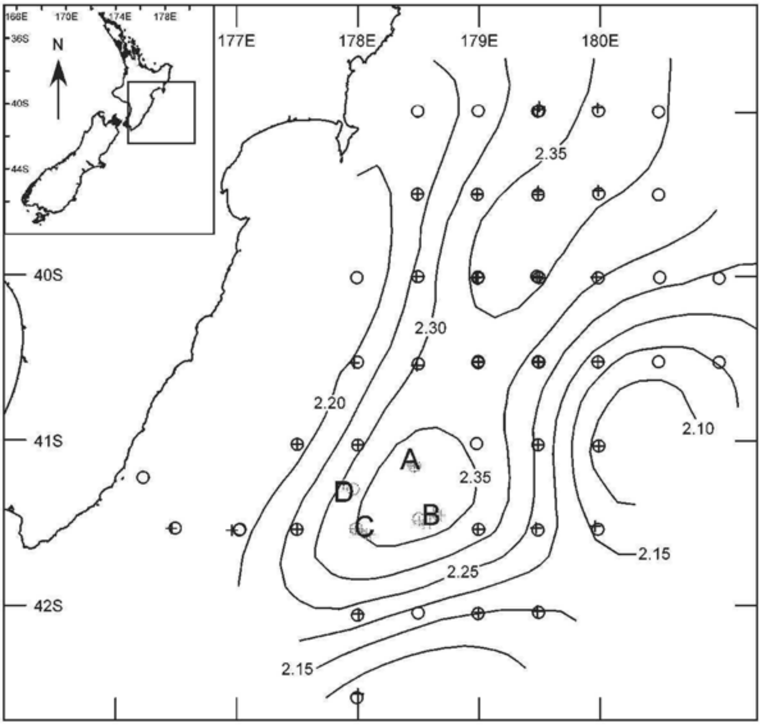

**Fig. 1** Region of study off the east coast of the North Island, New Zealand in relation to the physical oceanography as derived from sea surface height anomalies derived from Conductivity-Temperature-Depth (CTD) data. (o, CTD casts; +, surface net stations; A, B, C, and D denote the locations of the 24-h sampling stations.)

The oldest cohort would be expected to be at or close to final stage (stages X–XI), whereas the younger cohort would consist of mid-stage (V–VIII) larvae.

### Physical oceanography

A Seabird CTD (conductivity-temperature-depth) profiler, in a 12-place rosette with 1.2 litre Niskin bottles, was used to make continuous vertical profiles of temperature and salinity at each station. Water samples were collected to calibrate the conductivity sensor. CTD data collection and processing methods were the same as those detailed in Chiswell et al. (1993) and Walkington & Chiswell (1998). Temperature and salinity were processed to 2 dbar bins. Temperature was estimated to be accurate to 3 mK and salinity to $5 \times 10^{-3}$. CTD casts were made to within 20 m of the sea floor in a grid with nominal spacing of 0.5° in latitude and longitude.

### Net collections

Two net systems were used to sample the zooplankton. Surface macrozooplankton (animals at least 2 mm; Omori & Ikeda 1984) were sampled with a square surface net (mouth area 1 m$^2$; mesh size 1000 μm) fitted with a General Oceanics mechanical flowmeter. The surface net was typically deployed following each CTD cast, and concurrently with the start of a midwater trawl from the midship A-frame.

Macrozooplankton, including phyllosomas, greater than c. 1 cm in the water column were sampled with an Engel fine-meshed (12 mm stretch) midwater trawl (FMMWT) fitted with an opening/closing codend (MIDOC; Pearcy et al. 1977). The FMMWT was 60 m long with a nominal mouth area of 70 m$^2$. The MIDOC contained six codends with a mesh size of 500 μm. An electronic timer triggered codends at pre-defined time intervals to give a 20 min sampling period per depth stratum. Probes concurrently collected data on depth, temperature, and light (relative) levels. FMMWT depth, headline height, and wing spread were monitored acoustically.

Prospecting tows (c. 30 min at a headline depth of 30 m) with the FMMWT were used to locate the first high-density patch of phyllosomas and thereby initiate the first 24-h sampling series. The trigger was ≥60 phyllosomas in a tow. A drogue, with the parachute set at a depth of 5 m, was deployed at the start of each series to mark the start position for each subsequent tow. Tows were made into the wind.

Three night tows and three day tows were taken during each 24-h sampling series (except for Series

D, see Fig. 1). Tows were not made within 1 h either side of dawn or dusk. A standard tow consisted of a 30 min oblique tow to 300 m followed by oblique tows for 20 min each through strata of 200–300, 100–200, 50–100, 20–50, and 20 m to the surface. Despite the discrete depth sampling provided by the opening/closing MIDOC system, phyllosomas from one sampling strata may become temporarily entangled in the net ahead of the codend and provide a source of contamination for subsequent strata (Dennis et al. 2001). To reduce the amount of contamination between strata, the final 5 min of each stratum's tow was held at the upper boundary of that stratum. On two separate occasions the sampling pattern was altered to allow us to explore to a greater depth (500 m).

Samples were sorted immediately after each tow. Phyllosomas were removed and at the same time catches rough sorted into the major groups—fish, euphausiids, cephalopods, prawns, gelatinous material, and amphipods/pteropods/isopods. Phyllosomas were further sorted into species. *J. edwardsii* phyllosomas were then staged according to Lesser (1978) as modified by Booth (1994). Phyllosomas were subsequently either frozen at –30°C, preserved in 100% ethanol, or preserved in 10% buffered formalin in sea water.

### Data analyses

Larval counts were standardised to larval density (number per 1000 $m^3$) by dividing the number of larvae caught by the volume of water filtered by each net. Volume filtered was calculated from the equation $V = D \times A$; where D is distance travelled (derived from the flowmeter reading for the surface net, or from ship's speed ($m\ s^{-1}$) × tow duration (s) for the FMMWT) and A = net mouth area (1 $m^2$ for the surface net, headline height × wing spread for the FMMWT). Because of the MIDOC codend design we were unable to close net 6 while the FMMWT was being brought back onto the deck of the ship. Tow duration for this net was estimated from the depth reading of the MIDOC timer. A stabilised depth reading indicated that the codend was on the surface and was taken to be the end of fishing for net 6.

A Poisson generalised linear model (GLM) (McCullagh & Nelder 1989) was used to model larval counts in terms of depth and time of day while controlling for both volume filtered per tow and regional variability in abundance. The typically patchy nature of zooplankton was accounted for by allowing for overdispersion of the Poisson model.

Data analyses were complicated by the failure of the closing device for net 5 on four of the 22 midwater tows. For these four tows, net 6 failed to open and the net 5 data represents the combined net 5 and 6 counts for the upper 50 m of the water column. Three separate approaches were taken to account for the failures: (1) the net 5 and 6 data from the failed tows were excluded from the analysis; (2) the net 5 and 6 data were amalgamated for all tows, reducing the depth resolution to the upper 50 m of the water column; and (3) the missing individual net 5 and 6 counts were imputed via the EM algorithm (Tanner 1996).

The Poisson distribution is an exponential family (McCullagh & Nelder 1989), and so the EM algorithm for imputing the missing counts takes a particularly simple form (Tanner 1996). Given the totals of the missing net 5 and 6 counts from the failed tows: (1) initial estimates of the missing values are constructed by dividing the known totals equally between nets 5 and 6, and the Poisson GLM fitted to this augmented data set; and (2) improved estimates of the missing values are constructed by dividing the known totals in the proportion predicted by the model, and the model refitted.

Step 2 was repeated until there were no more changes in the fit. Except for where the degree of significance differed such that it provided an alternative conclusion, we report only the results of the imputation approach.

## RESULTS

### Physical oceanography

An analysis of the dynamic height, derived from hydrographic observations, identified two lobes in dynamic height (Fig. 1). The northern lobe was centred near 39°40′S, 179°30′E, whereas the

**Table 1** Depth of mixed layer by day and night for each of the 24-h sampling series estimated from the depth at which the maximum change in temperature occurred, recorded by the electronics unit of the MIDOC codend on the FMMWT (fine-meshed midwater trawl).

| 24-h vertical series | Depth of mixed layer (m) | |
|---|---|---|
| | Day | Night |
| A (25–26 Mar 2003) | 43–61 | 39–71 |
| B (27–28 Mar 2003) | 41–56 | 55–60 |
| C (29–30 Mar 2003) | 36–50 | 32–50 |
| D (31 Mar–1 Apr 2003) | 34–78 | 27–37 |

southern lobe was centred near 41°40′S, 178°30′E. The southern lobe was centred near the mean of the Wairarapa Eddy as defined by Roemmich & Sutton (1998), but was somewhat smaller than suggested by the mean analysis.

Wind speeds were relatively consistent over the first three of the four 24-h sampling series. Over all 24-h sampling series, wind speeds averaged 15.1 ± 1.3 (SE) knots. However, during the final 24-h sampling series wind speeds during the night tows were relatively high, resulting in a deeper mixed layer during the following day tows (Table 1).

### Net collections

Sampling was conducted within the lower lobe of the dynamic height field identified from the hydrographic observations (Fig. 1). A total of 51 surface net tows and four vertical FMMWT series, comprising 22 (10 day, 12 night) tows, were taken. Total phyllosoma captures were dominated by *J. edwardsii* (930) with lower numbers of *Antipodarctus aoteanus* (193) and *Ibacus alticrenatus* (3) also recorded. No phyllosoma of the second commercially fished palinurid, *Sagmariasus verreauxi*, were recorded. The standardised number of *J. edwardsii* phyllosomas per FMMWT sample ranged from 0 to 1.65 per 1000 $m^3$ ($\bar{X} \pm SE = 0.05 \pm 0.015$). The majority (90%) were mid-stage (V–VIII) phyllosomas, with the remainder being late-stage (VIIIA–XI) phyllosomas. A total of 161 ($\bar{X} = 0.11$ per 1000 $m^3$) *J. edwardsii* phyllosomas were collected during the day, whereas 769 ($\bar{X} = 0.55$ per 1000 $m^3$) were collected at night.

### Data analyses

The three methods used to analyse the data, given the missing values, gave similar results with only minor differences in the degree of significance. Where confidence intervals and estimates of relative abundance are given, these are derived from the imputation model. Typically the EM algorithm used to derive imputed net 5 and 6 counts converged within eight iterations. For all models fitted, the residual deviance exceeded the residual degrees of freedom by at least a factor of three, justifying the choice of an overdispersed Poisson model.

Total catches of *J. edwardsii* phyllosomas were significantly ($F_{1,17} = 14.1$, $P < 0.002$) higher at night for all strata combined than during the day (Fig. 2A: mid-stage phyllosomas; Fig. 2B: late-stage phyllosomas). Based on the model, the 95% confidence interval for the ratio of day to night counts was 1.8–12.2. It was noted that one tow in particular had an extremely high catch. Even with this tow excluded from the analyses, the day–night difference remained significant ($F_{1,16} = 20.6$, $P < 0.001$) although the 95% confidence interval was reduced to 1.8–5.8.

There was, however, no significant ($F_{4,97} = 1.6$, $P = 0.17$) difference in the pattern of vertical distribution of phyllosomas (all stages combined) between day and night, after controlling for the observed day–night difference in total abundance. Phyllosomas were most abundant in the upper 50 m of the water column (and particularly the upper 20 m) regardless of time of day.

Although there was no difference in the pattern of vertical distribution of all phyllosoma stages combined, several lines of reason lead us to analyse the data separately for mid-stage (V–VIII) and late-stage (VIIIA–XI) phyllosomas. First, on a series-by-series basis there was a difference in the spatial distribution of mid- and late-stages. Late-stage phyllosomas were almost exclusively found in tows from series C and D, located towards the inshore side of the eddy (Fig. 3). Second, differences in the pattern of vertical distribution between stage groups have been reported within the Palinuridae for what is perhaps the best documented species, *Panulirus cygnus* (Chittleborough & Thomas 1969; Rimmer & Phillips 1979).

There was no significant ($F_{4,97} = 0.3$, $P = 0.8$) difference in the vertical distribution of mid-stage phyllosomas between day and night. Nor was there any evidence of a difference in the vertical distribution of mid-stage phyllosomas between the "inshore side" (series C and D) and "central" (series A and B) regions of the eddy ($F_{4,93} = 0.17$, $P = 0.9$). Mid-stage larvae occurred primarily (96% of the total recorded) within the upper 50 m both day and night (Fig. 4), with 75% of larvae occurring in the upper 20 m of the water column.

Too few late-stage phyllosomas were present in series A and B to permit analyses. However, there was a significant ($F_{4,34} = 10.5$, $P < 0.001$) difference in the vertical distribution of late-stage phyllosomas for series C and D between day and night. During the night, late-stage phyllosomas were concentrated in the upper 50 m (95%) with the majority (68%) recorded in the upper 20 m (Fig. 5). During the day, late-stage phyllosomas were absent from the upper 20 m; 58% of the total collected were recorded in the 20–50 m stratum, 23% in the 50–100 m stratum, and the remaining 19% of phyllosomas were recorded below 100 m.

Two deep FMMWT tows to 500 m were made during the day to determine if phyllosoma were

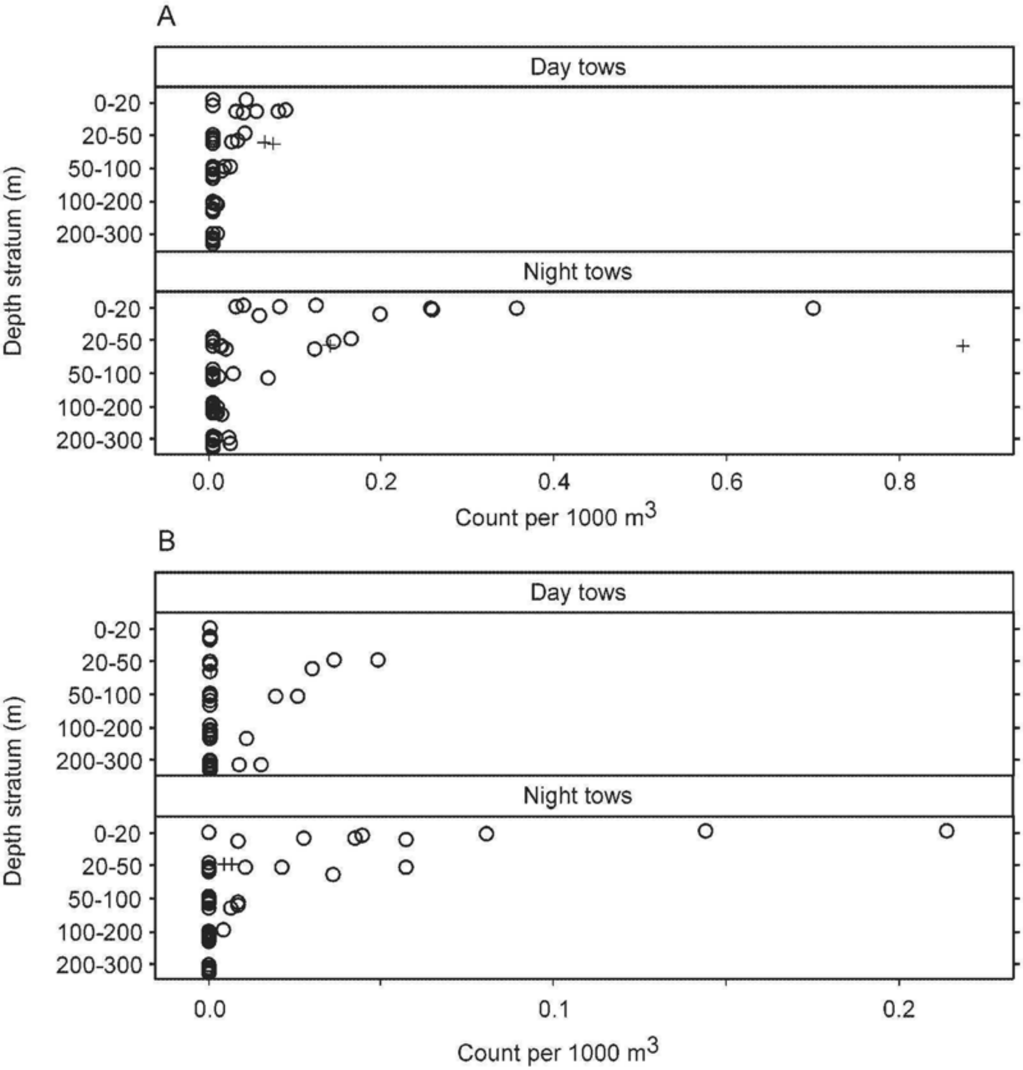

**Fig. 2** Distribution of catch between day and night fine-mesh midwater trawl tows, as measured by abundance (count per 1000m$^3$) for **A**, mid-stage and **B**, late-stage *Jasus edwardsii* phyllosomas, off the east coast of the North Island, New Zealand. Crosses (+) indicate failure of net 5 to close and therefore represent combined counts for nets 5 and 6.

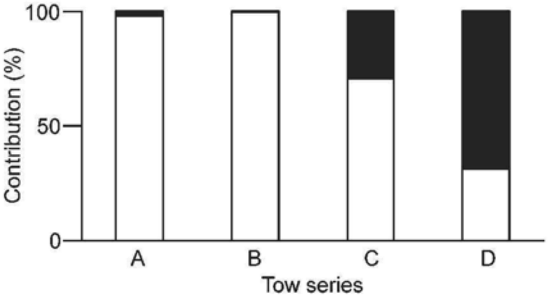

**Fig. 3** Contribution of mid-stage (open bars) and late-stage (closed bars) *Jasus edwardsii* phyllosomas to each of the four 24-h sampling series off the east coast of the North Island, New Zealand.

descending to depths outside the 300 m range of our standard 24-h series. In both tows, *J. edwardsii* phyllosomas were again concentrated in the upper 100 m, with virtually none below 200 m (Fig. 6).

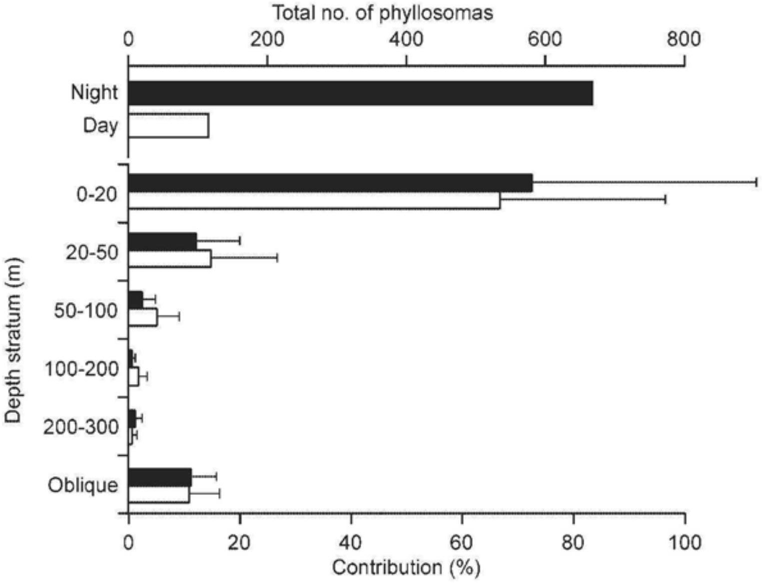

**Fig. 4** Day/night comparison of mid-stage *Jasus edwardsii* phyllosomas caught by the fine-mesh midwater trawl net off the east coast of the North Island, New Zealand. Top axis provides total numbers (unstandardised). Lower axis indicates the percentage of phyllosomas contributing to either day (open bars) or night (closed bars) tows for each depth stratum, based on standardised abundance (per 1000 m$^3$ ± 1 SE).

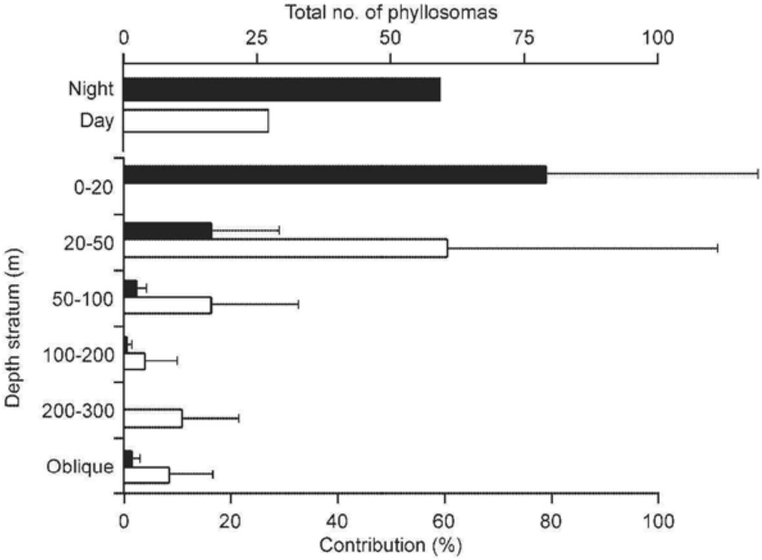

**Fig. 5** Day/night comparison of late-stage *Jasus edwardsii* phyllosomas caught by the fine-mesh midwater trawl net off the east coast of the North Island, New Zealand. Top axis provides total numbers (unstandardised). Lower axis indicates the percentage of phyllosomas contributing to either day (open bars) or night (closed bars) tows for each depth stratum, based on standardised abundance (per 1000 m$^3$ ± 1 SE).

## DISCUSSION

*Jasus edwardsii* phyllosomas were primarily recorded within the upper 100 m and over similar depth ranges to those reported for other palinurid and scyllarid species. Diel differences in vertical distribution were recorded for late stage phyllosomas only. However, a confounding result of the present study was the large difference in total phyllosoma abundance between day and night across all strata combined. In an ideal sampling scenario, we would expect the combined abundance of phyllosomas to be similar both day and night, with differences occurring between strata resulting from changes in vertical distribution. In addition, the patchy distribution of phyllosomas and the relatively low counts observed reduced the overall statistical power of our analyses. The extent of this is difficult to quantify, given both the over-dispersion of the data and the failure of net 5 to close on four occasions.

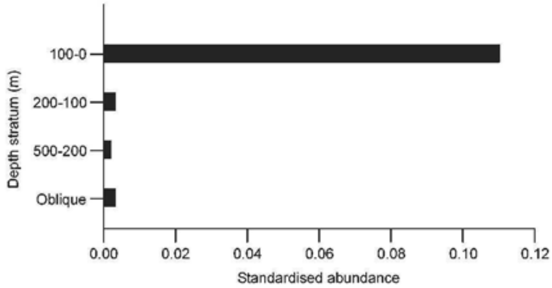

**Fig. 6** Vertical distribution of all *Jasus edwardsii* phyllosomas collected from two tows between the surface and 500 m during daylight hours off the east coast of the North Island, New Zealand.

Several possible explanations for the difference in abundance between day and night tows were considered and each of these are discussed in turn.

(1) Phyllosomas may have migrated out of the depth range sampled, leaving day catches comprised mainly of stragglers. This would suggest that the primary day habitat for *J. edwardsii* phyllosoma was below 300 m (the limit of most of our sampling) and that they were able to ascend/descend to and from that depth during the 2-h period around dawn and dusk where no sampling occurred. The diel vertical movements of phyllosoma of all species for which data are available have been primarily restricted to within the upper 100 m of the water column. Although *Jasus* phyllosoma have been recorded to at least 300 m (Pollock 1986; Booth 1994; Bruce et al. 2000) and thus perhaps the deepest so far for phyllosoma, the number of larvae recorded below 150 m is extremely low. No *J. edwardsii* larvae were recorded below 300 m during our daytime sampling. This suggests that the deep distribution of *J. edwardsii* larvae may be the result of either low frequency events rather than a regular diel pattern or represent net contamination from upper strata. Furthermore, a vertical swimming rate in excess of 4 cm $s^{-1}$ would be required for larvae to move between the surface and 300 m within the time period between our day and night tows. This is nearly 8 times the rate calculated for *P. cygnus* larvae (c. 0.45–0.56 cm $s^{-1}$) by Rimmer & Phillips (1979) and 4 times that suggested for *J. edwardsii* by Chiswell & Booth (1999). Therefore it is unlikely that *J. edwardsii* phyllosomas were descending below our 0–300 m sampling range such that only stragglers were collected during the day.

(2) Phyllosomas may be avoiding the net during the day. Visual net avoidance has been demonstrated in a variety of planktonic taxa and mesopelagic species (e.g., Pearcy & Laurs 1966). However, this response is generally restricted to the more mobile species. Phyllosomas are relatively poor swimmers (Chiswell & Booth 1999; Yeung & Lee 2002 (<1 cm $s^{-1}$)) and, given its 70 $m^2$ mouth opening, it would seem unlikely that they would be able to avoid the FMMWT.

(3) Horizontal aggregation of phyllosomas at night may result in a tendency towards higher night catches. Phyllosomas of *P. cygnus* have been found to actively aggregate at night in areas of increased micronekton biomass (Ritz 1972). It is also possible that phyllosomas moving closer to the surface at night may aggregate because of physical forces such as Ekman surface slicks. Indeed, high variability in night catches of *P. cygnus*, even when replicate hauls were taken at a single station, were observed by Ritz (1972). Furthermore, higher overall night versus day catches of *P. cygnus* appear to have taken place in two separate studies (Rimmer & Phillips 1979; Phillips & Pearce 1997). These studies suggested that night-time horizontal aggregation may result in a bias towards higher night catches.

(4) The sampling strategy utilised may have increased the bias towards higher night-time catches if larvae were migrating to the upper strata during that period. If vertical migration were occurring, we would expect there to be a difference in the number of phyllosoma caught between day and night because of the strata sampling design. Deeper strata covered a wider depth range than the more shallow strata sampled, and thus sampling effort was greater in these shallow strata. Any migration towards the surface at night would thus result in an increase in the overall number of phyllosoma caught at night. Nevertheless, it seems unlikely that this alone would account for differences as large as those observed. Nor can this difference be attributed to the extremely high catch in one trawl, as the ratio between day and night remained large even with this trawl excluded from the analyses.

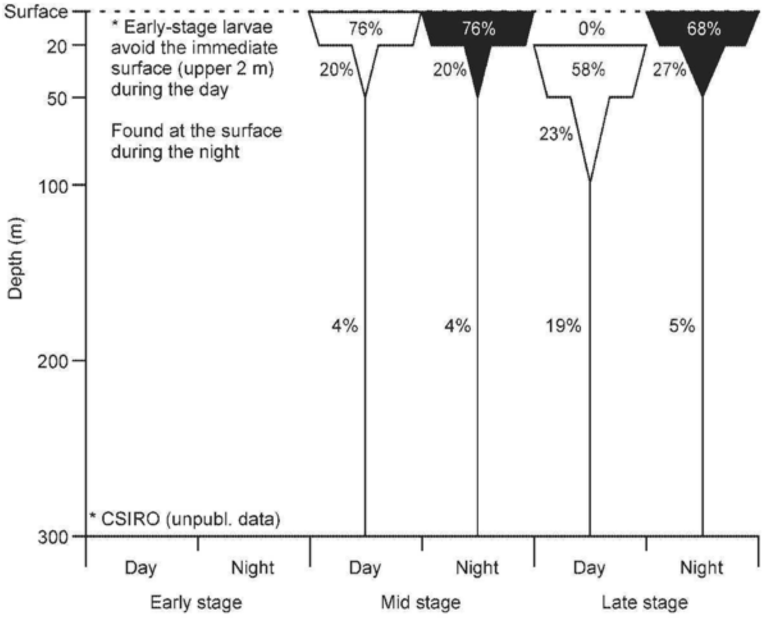

**Fig. 7** Vertical distribution model for early-, mid-, and late-stage *Jasus edwardsii* phyllosomas collected in vertically-stratified tows to 300 m off the east coast of the North Island, New Zealand. Numbers refer to percentage of phyllosoma within the depth stratum whereas the vertical lines indicate the remaining percentage (each column sums to 100%). Data for early-stage phyllosomas is from CSIRO unpubl. data for the south-east region of Australia.

(5) The net design may have resulted in a bias towards collecting more phyllosomas within the upper 20 m if phyllosomas were concentrated in this stratum at night as a result of vertical migration. The overall fishing efficiency of the FMMWT is affected by both the length of time the net fishes and by the area of the mouth. Because the codend of net 6 cannot be closed, it continues to fish while the net is brought onboard, thus increasing the length of time the net fishes in the 0–20 m stratum. However, counteracting this increase in fishing time, the effective mouth area of the net decreases as it begins to collapse on approach to the surface. A slight increase in overall fishing efficiency may bias the data towards greater night-time catches if phyllosomas were more concentrated in the upper 20 m at night as compared to day.

The significant difference between day and night catches prompted us to examine the vertical distribution of *Antipodarctus aoteanus* phyllosomas to see if similar confounding patterns in total abundance were repeated. *A. aoteanus* phyllosomas showed a similar tendency to concentrate in the 0–20 m stratum during the night. However, there was no evidence for a bias towards higher overall night-time catches, with roughly equal numbers being caught during the day and night. Thus, it is unlikely that net design or sampling strategy contributed to the difference observed between day and night catches in *J. edwardsii* and the most plausible reason for the observed differences was perhaps the influence of horizontal aggregations at night as suggested by Rimmer & Phillips (1979) and Phillips & Pearce (1997).

Although we were are unable to fully account for the significant difference in overall abundance of *J. edwardsii* phyllosomas between day and night tows, we found no evidence to reject our conclusions regarding the diel vertical behaviour of mid and late stages.

## Comparisons with other patterns of vertical distribution

The vertical distribution and diel migration of phyllosomas are, in general, poorly understood despite the significance of such data for the modelling of transport processes. Published data exist for only a small number of species (Table 2). Generally, phyllosomas are reported to concentrate in the upper 30–50 m during the night and below 30–50 m during the day. Furthermore, the diel pattern did not appear to change between developmental stage for any of the species except *P. cygnus* (Rimmer & Phillips 1979).

The vertical distribution of *J. edwardsii* phyllosomas has been less well studied. Lesser (1978), Booth (1994), and Bruce et al. (2000) reported that *J. edwardsii* phyllosomas may undergo vertical migrations at least as extensive as those of the other

**Table 2** Summary of vertical distribution for phyllosomas indicating the depth of the main concentration of phyllosomas. (S, south of Matanzas, Cuba; N, north of Matanzas, Cuba.)

| | Depth (m) | | Depth (m) | | |
|---|---|---|---|---|---|
| Species | Day | Stage(s) | Night | Stage(s) | Reference |
| *Panulirus argus* | 50 | all | surface | all | Buesa Mas (1970) |
| | 10–20 | all | surface | all | Austin (1972) |
| | 25–50 | all | 0–100 | all | Baisre (1976) |
| | 40–90(S) | all | 10–50(S) | all | Hernandez et al. (2000) |
| | 30–70(N) | | dispersed(N) | | |
| *P. cygnus* | 30–60 | early | 0–30 | early, late | Rimmer & Phillips (1979) |
| | 50–120 | mid, late | 0–20 | mid | |
| *P. longipes* | 50–80 | | 10–50 | | Minami et al. (2001) |
| *Scyllarus cultrifer* | 50–80 | | 10–50 | | Minami et al. (2001) |
| *Jasus lalandii* | 0–100 | | 0–300 | | Pollock (1986) |
| *J. edwardsii* | | | 0–5 | early | Lesser (1978) |
| | | | 5–40 | mid (VI) | |
| | | | 40–60 | late (XI) | |
| | 30–310 | | 0–30 | | Booth (1994) |
| | 0–20 | mid | 0–20 | mid | Present study |
| | 20–50 | late | 0–20 | late | |

species. However, these studies did not use nets capable of discrete depth sampling and this precluded a more detailed examination of vertical distribution.

Lesser (1978) reported on the night vertical distribution of *J. edwardsii* phyllosoma from samples taken off the east coast of the North Island, New Zealand. He indicated that at around stage V, *J. edwardsii* phyllosomas shift from a predominantly near-surface habit to one in deeper waters. Lesser (1978) found that later stages of *J. edwardsii* phyllosomas remained deeper in the water column, with stage VI phyllosomas largely in the 5–40 m depth stratum and Stage XI phyllosomas in the 40–60 m depth stratum.

Booth (1994) reported on the vertical distribution of *J. edwardsii* phyllosomas from the east coast of the North Island, New Zealand. He indicated that during the day phyllosomas vacated the upper 30 m of the water column, and could be found to depths of at least 310 m. During the night the highest concentrations of mid- and late-stage phyllosomas were within the upper 30 m.

Bruce et al. (2000) reported on the vertical distribution of *J. edwardsii* phyllosomas off south-eastern Australia. They indicated that phyllosomas showed a tendancy to move away from the surface (0–5 m) during the day. Although Bruce et al. (2000) had vertically stratified samples using a similar configuration to that of the present study, the width of depth strata was too large and phyllosoma numbers too low to permit rigorous statistical analyses.

The present study has built upon these previous studies to refine our understanding of DVM for *J. edwardsii* phyllosomas and a model summarising this behaviour is proposed in Fig. 7. We are able to confirm that *J. edwardsii* phyllosomas undergo vertical distributions at least as extensive as other lobster species. Phyllosomas were primarily located within the upper 100 m of the water column with low level abundances recorded to 300 m. Diel vertical migration was restricted to late-stage phyllosomas which avoided the 0–20 m surface layer during the day.

Vertical migration has either been ignored in previous attempts to model the transport and recruitment processes of *J. edwardsii* phyllosomas, or has been based upon that of *P. cygnus*. The current study highlights the need to use species-specific information on vertical distribution when modelling larval transport pathways.

## ACKNOWLEDGMENTS

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# How do spiny lobster post-larvae find the coast?

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**Abstract** The larvae or phyllosomes of many species of spiny lobsters (Palinuridae) are known to complete their development in offshore oceanic waters. Phyllosomes metamorphose to non-feeding, nektonic post-larvae or pueruli, which move into shallow coastal waters where they settle to become benthic dwelling juveniles. There is growing evidence that the movement of pueruli is directed toward the coast rather than a process of random dispersal. The migration inshore by the non-feeding pueruli is likely to be one of the more extreme examples of onshore orientation among marine organisms, but is still poorly understood. This article provides a synthesis of the current state of knowledge of the possible cues and sensory mechanisms that might be used by pueruli of spiny lobsters for orienting toward the coast from offshore waters. The review is used to identify the potential cues that would benefit from future research efforts.

**Keywords** Palinurid; post-larvae; puerulus; underwater sound; magnetic sense; onshore movement

## INTRODUCTION

Spiny lobsters of the family Palinuridae are found throughout tropical and temperate seas, where they are of considerable ecological and economic importance (Lipcius & Eggleston 2000). The life cycle of these lobsters includes a transition from an oceanic planktonic larval phase (phyllosome) through a single-stage nektonic post-larva (puerulus) that moves inshore to settle in shallow coastal waters and then moults to become a benthic dwelling first-instar juvenile. The biology of lobsters during this period of their life cycle is poorly understood, especially the ecology of the puerulus stage (Butler & Herrnkind 2000). The larval phase in spiny lobsters is extensive, lasting up to 18 months in some species, and usually involving 7–13 distinct phyllosome stages, with each stage represented by one or more instars (Phillips & Sastry 1980). This long larval period is unusual among marine invertebrates as only c. 5% of benthic invertebrates have a larval phase that lasts more than 12 weeks (Thorson 1950). The early phyllosome developmental stages that follow from the hatching of eggs have limited swimming abilities and consequently, they are eventually dispersed widely offshore by currents (Phillips & Sastry 1980; Bruce et al. 2000). As a result, the later phyllosome stages in most palinurid species are most commonly found inhabiting oceanic waters beyond the continental shelf, as much as 1500 km from the coast (Berry 1974; Serfling & Ford 1975; Phillips et al. 1979; Booth et al. 1998).

The location and trigger for the metamorphosis from the final stage phyllosome to the puerulus is uncertain because of difficulties obtaining direct

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observational or experimental evidence. An early review of the available evidence for the Western Australian lobster, *Panulirus cygnus*, suggested that salinity changes near the continental shelf edge were likely to be responsible for triggering the metamorphosis for the pueruli that were encountered in this area of the ocean (Phillips & McWilliam 1986). A subsequent review concluded that metamorphosis in the final stage larva only occurred after it had reached a critical, specific, level of stored energy reserves (McWilliam & Phillips 1997). However, only three studies provide any firm evidence of the location of metamorphosis for pueruli and hence the starting point for the onshore migration. Ritz (1972) inferred the location of metamorphosis from 19 cast exuviae of final stage phyllosomes of *P. cygnus*, all caught more than 161 km (ranging from 215 to 400 km) from the shore of Western Australia. Yoshimura et al. (1999) caught three metamorphosing final stage phyllosomes of *Panulirus japonicas* in the Kuroshio Current at 54 and 63 km from the nearest land. Jeffs et al. (2001) inferred the location of metamorphosis for pueruli of *Jasus edwardsii* based on the presence of soft carapaces in 33 out of 260 pueruli caught in an extensive offshore survey east of New Zealand. These recently metamorphosed pueruli were captured between 24 and 216 km offshore (mean of 92.4 km ± 7.8 SE), and had widely varying energy stores (total lipid of 21–39.5% of dry body mass), suggesting that a specific critical level of stored energy was not required for triggering metamorphosis (Jeffs et al. 2001). The locations where newly metamorphosed pueruli were caught were not reliably associated with any of the variables that have previously been suggested as the trigger for metamorphosis, i.e., sea surface temperature, salinity, depth, distance offshore, ocean primary productivity.

Once final stage phyllosomes have metamorphosed to non-feeding pueruli, the mechanisms by which they move inshore into shallow waters to settle is also unclear, but it is likely to involve a combination of active onshore swimming and the use of natural onshore advection or passive processes, such as wind-driven surface currents (Butler & Herrnkind 2000). However, the evidence supporting mechanisms of onshore movement is mostly circumstantial. For example, evidence for active onshore swimming is largely inferred from measured short-distance swimming speeds and rates of energy consumption (Lemmens 1994; Jeffs et al. 1999, 2001; Jeffs & Holland 2000). Likewise, the only evidence for passive onshore transport comes from correlations between the timing of arrivals of settling pueruli and natural phenomenon such as onshore winds, rainfall, and current patterns (Phillips & Pearce 1991; Caputi & Brown 1993; Caputi et al. 1995a,b; Acosta et al. 1997; Eggleston et al. 1998; Yoshimura et al. 1999). These studies have consistently shown relatively weak correlations between onshore advective physical processes and the arrival of settling pueruli on the coast, or have produced conflicting results. For example, the abundance of *Panulirus argus* pueruli arriving in the Florida Keys over an 8-year period were only marginally correlated with onshore windforcing of surface waters (Acosta et al. 1997). Wind speed and direction only explained around half of the variation in *P. argus* pueruli arrivals at three sites at Lee Stocking Island in the Bahamas during a 6-year study (Eggleston et al. 1998). A subsequent 2-year study found pueruli abundance at two sites in the Florida Keys was not correlated with wind patterns (Yeung et al. 2001). However, pueruli abundance was correlated with either the magnitude or frequency of onshore and long shore currents (accounting for c. 60% of variation) which in turn tended to be generated by the presence of mesoscale eddies offshore. However, it was not clear if pueruli were being transported onto the coast directly by these currents, or if the increased pueruli abundance was a result of the presence of the mesoscale eddies which had transported water masses containing pueruli from the Gulf of Mexico to offshore of the Florida Keys. Correlations between the abundance of pueruli on the coast and weather and/or current patterns have been found in other Palinurid species, but in all instances they fail to provide the high level of correlation that would be expected should pueruli be behaving as purely passive particles in the ocean environment (Pearce & Phillips 1988; Hayakawa et al. 1990; Caputi & Brown 1993; Caputi et al. 1995b; Booth et al. 2000).

The distribution of pueruli in a number of offshore surveys strongly suggests that their movement is directed onshore rather than dispersing at random (Ritz 1972; Chiswell & Booth 1999). For example, in the most common species of spiny lobster in New Zealand, *J. edwardsii*, late-stage phyllosomes are most often caught beyond the edge of the continental shelf (>44 km offshore), whereas pueruli prefer to settle in coastal waters of less than 15 m depth (Booth et al. 1991; Bruce et al. 2000). Comparisons among the distributions of mid- and late-stage phyllosomes, and pueruli of *J. edwardsii* sampled over a series of offshore transects from New Zealand demonstrated that the distribution of mid-stage phyllosomes was consistent with passive drift via measured ambient ocean currents (Chiswell & Booth 1999). In comparison, the distribution of late stage phyllosomes was significantly displaced inshore, consistent with shoreward directed movement of 4–6 cm $s^{-1}$, which was inconsistent with the ocean gyre which dominates this ocean region. Pueruli were found significantly more inshore again than late stage phyllosomes, consistent with shoreward directed movement of 8–10 cm $s^{-1}$. These findings suggest that both pueruli and late stage phyllosomes are capable of orienting shoreward from considerable distances offshore (>50 km).

Orientation cues used by late stage phyllosomes and pueruli during this shoreward movement from offshore waters are unknown. Unfortunately, there are no useful parallels to be drawn from fishes, as there has been very little research on the larval movement of the very few groups of fishes which have extended offshore larval development, such as the Cheilodactylids, Bovichthyids, and Anguillidae (B. Bruce, CSIRO, Hobart pers. comm.). The aim of this article is to review the possible cues and sensory mechanisms that might be used by early life stages of spiny lobsters for orienting toward the coast from offshore waters. This review serves to identify those potential orientation cues and methodologies that will be most useful for directing future research endeavours.

## UNDERWATER SOUND

Underwater sound has long been recognised as one of the strongest candidates for onshore orientation by pelagic organisms because it is conducted long distances offshore and it can also carry biologically significant information about distant coastal locations, such as reefs (Myrberg 1978; Hawkins & Myrberg 1983; Kingsford et al. 2002). A number of researchers have suggested that underwater sound, such as waves breaking on the coast, may provide a shoreward orientation cue for the pueruli of spiny lobsters (Phillips & Penrose 1985; Phillips & Macmillan 1987; Macmillan et al. 1992).

Coastal reefs of New Zealand and Australia where pueruli are known to settle have ambient underwater noise with high amplitude sound between 1200 and 1600 Hz (Tait 1962; Cato 1978). This noise originates from rocky coastlines and increases markedly for c. 3 h after sunset. Tait (1962) measured a 7–10 dB directional increase in ambient noise at a point 5 km off shore and a 6 dB fall-off with distance doubled. Attenuation is only 0.1 dB $km^{-1}$ at these frequencies, so the directional noise would be detectable at least 10 km offshore. Cato (1978) reported detecting reef noise that would be louder than surface wind noise at up to 25 km in Australian waters. Based on assumptions of the sensory modality of mechanoreceptors observed on the antennae of pueruli of *P. cygnus*, Phillips & Penrose (1985) concluded that pueruli of this species would only be able to effectively detect directionality of reef noise above 1750 kHz. Furthermore, they estimated that the attenuation of reef noise at this frequency would prevent it from being detected beyond 40 km away from the source. Although 1750 Hz is slightly beyond the band of high intensity reef noise described by Tait (1962), the estimate of 40 km could provide a useful indication of the maximum range for reef noise to be a directional cue. However, if pueruli are capable of detecting lower frequencies, then it is possible that this estimated range could be extended considerably because of greatly reduced attenuation at lower frequencies.

Underwater sound was implicated as a possible cause for more than 4000 pueruli of *J. edwardsii* being caught in the seawater intake of a power station on the west coast of New Zealand where pueruli collectors placed on the adjacent coast failed to collect any individuals (Booth 1989). Subsequent underwater sound recordings indicated that the power station generates a sound signature that can be detected above background ambient noise for some considerable distance offshore and is in the same frequency range as natural reef underwater sound sources (Jeffs unpubl. data).

To date, no behavioural experiments with orientation to underwater sound by pueruli or phyllosomes have been reported, although experiments to test if pueruli of *J. edwardsii* can be attracted to collectors associated with artificial sources of underwater sound have been attempted (Jeffs unpubl. data). The results of these field experiments were inconclusive because of low catches of pueruli in the experimental collectors. However, a number of recent field studies have used a range of techniques to confirm underwater sound as an important orientation cue in larval and post-larval crabs and fishes (Tolimieri et al. 2000, 2004; Leis et al. 2002; Jeffs et al. 2003; Simpson et al. 2004). Diver observations suggested that the swimming behaviour of larval fishes changed in response to the presence of some artificial sources of underwater sound (Leis et al. 2002). Floating light traps associated with and without artificial sound sources produced significantly different catches of crab and fish larvae and post-larvae (Tolimieri et al. 2000; Jeffs et al. 2003; Simpson et al. 2004). Larval reef fish placed in experimental choice chambers in the sea demonstrated a choice toward artificial sources of pre-recorded reef sound (Tolimieri et al. 2004).

There is, however, some debate over the sensory mechanisms that might be used by larval fishes and especially decapod crustaceans (Budelmann 1992; Popper et al. 2001). In general, the sensory structures found in fishes can be compared and related to those well described in many other vertebrate species. However, such comparisons are not possible for crustaceans because the presence of an exoskeleton necessitates different sensory arrangements. Decapods have a wide variety of sensory structures which have attracted considerable research interest, but their sensory and behavioural functions are often still poorly understood (Popper et al. 2001). A variety of receptors have been identified that may have the ability to respond to parameters of underwater sound such as particle motion, pressure changes, and hydrodynamic movement, but their operation, sensory thresholds, range of sensitivity, and especially their behavioural significance is not well defined (Popper et al. 2001).

Investigations of the antennal sensory structures of the early lifecycle stages of several species of spiny lobster found an almost continuous array of pinnate setae along the flagella of the antennae of both pueruli and early juveniles, but absent from late stage phyllosomes (Phillips & Penrose 1985; Phillips & Macmillan 1987; Macmillan et al. 1992; Jeffs et al. 1997). Similar arrays of sensory setae are seen in other decapods without a shoreward migrating lifecycle phase, but it has been speculated that they may also be used for detecting low frequency water vibrations (Ball & Cowan 1977; Denton & Gray 1985). Electrophysiological recordings from such setae have produced conflicting results. Pinnate setae of the antennae of both *Palinurus elephas* and *P. japonicus* are known to have only limited sensitivity, and can only detect gross water movement or act as proprioceptors (Tazaki & Ohnishi 1974; Vedel 1985). However, the pinnate setae on the antennae of some freshwater crayfish are coupled with neighbouring sensory setae and consequently are highly sensitive to low frequency vibrations (Tautz et al. 1981; Masters et al. 1982; Bender et al. 1984). Regardless, the absence of an array of pinnate setae from late stage phyllosomes would prevent them from sensing and responding to underwater sound via this mechanism (Nishida & Kittaka 1992) despite their apparent ability to orient shoreward from offshore (Chiswell & Booth 1999). It has also been suggested that statocysts and chordotonal organs associated with joints of flexible body appendages may also play a role in sound reception in crustaceans. However, there is very limited information on these structures in the early life history stages of Palinurids (Budelmann 1992; Popper et al. 2001). The statocyst of pueruli of *J. edwardsii* are different to the highly developed statocysts of other decapods because they lacked sensory hairs, secretory pores, and fluid within the statocyst cavity (Sekiguchi & Terazawa 1997). Overall, these studies would suggest that although aquatic crustaceans in general appear to have some capacity to detect water-borne sound and vibration, the role of underwater sound in the orientation of the early stages of Palinurids remains unclear. Further work is required to identify the sensory mechanisms, sensitivities, and behavioural importance of this sensory modality for natural sound cues in these early life history stages.

## WATER CHEMISTRY

Crustaceans have highly developed chemosensory abilities which have been shown to play a key role in the settlement behaviour of a number of species, especially crabs (O'Connor & Gregg 1998; Forward et al. 2003; Keller et al. 2003). Consequently, it has been suggested that subtle changes in water chemistry may be instrumental in triggering metamorphosis in final stage phyllosomes and provide some guide to subsequent inshore movement (Phillips & McWilliam 1986). There is limited evidence for chemotaxis to be a mechanism for onshore orientation in early Palinurids. Post-larvae of the American lobster *Homarus americanus* can swim toward odours from adult conspecifics and organisms typically found in settlement habitat, whilst avoiding odours from a fish predator (Boudreau et al. 1993). Post-larvae did not orientate in response to inshore or offshore water, but did toward water conditioned by a rocky substratum versus a sandy substratum. Boudreau et al. (1993) concluded from Y-maze trials that distance chemoreception may play a role in locating settlement habitat by clawed lobster post-larvae. Observations of the post-larvae "zigzagging" through the zone of mixing in the flume, as well as the active movements of the chemosensory antennules and chelipeds would support the role of chemotaxis in these experiments.

Despite these encouraging results, the experimental flume was under a metre in length and it remains unclear on what ecological scale this behaviour may take place.

Among fish there is good evidence that chemical signals can be used over long distances, e.g., the olfactory homing of salmonids (Dittman et al. 1996). Pre-settlement coral reef fishes orient toward lagoon water versus ocean water in a Y-maze apparatus inferring that these settling stages may be orienting to plumes of lagoon water that were present over much larger scales (up to 4 km from the reef) (Atema et al. 2002). Orientation to reefs over these larger scales could help to be achieved by the larvae being guided by directional information contained in the fine scale eddy structure of lagoon-flavoured water carried beyond the lagoon by tidal currents. This sensory modality is known as eddychemotaxis (Atema 1996)

An extensive number and range of chemosensory sensilla are found in various locations on the exoskeleton in the early lifecycle stages of spiny lobsters, especially associated with the antennae and antennules of phyllosomes and pueruli (Nishida & Kittaka 1992; Jeffs et al. 1997; Cox & Bruce 2002). The exact chemosensory and behavioural roles of these structures, however, are yet to be determined. Mechanoreceptor sensilla on the antennae of adults of the spiny lobster *P. japonicus* have also been implicated in osmoreception, which may also provide another source of water-borne chemical information about coastal locations (Tazaki & Tanino 1973; Tazaki 1975). Newly hatched larvae of the Caribbean spiny lobster, *P. argus*, can detect and avoid low salinity waters (Scarratt & Raine 1967). More recently there is evidence that pueruli of this species will actively move toward coastal water versus oceanic water in an experimental choice chamber (J. Goldstein, Old Dominion University, Virginia pers. comm.).

Clearly, further work is required to identify the sensory mechanisms, sensitivities, and behavioural importance of the sensory modality for natural olfactory cues in these stages.

## MAGNETIC FIELDS

Magnetic orientation abilities have been reported in a wide range of animal groups, including spiny lobsters (Wiltschko & Wiltschko 1995). Benthic juvenile spiny lobsters posses an ability to detect and orient using magnetic fields, and parts of their bodies retain ferromagnetic material (Lohmann 1984, 1985; Lohmann et al. 1995; Boles & Lohmann 2003). Early experiments demonstrated that *P. argus* was sensitive to, and used magnetic field polarity, for some direction-setting behaviour (Lohmann 1985; Lohmann et al. 1995). A magnetic sense is thought to be involved in true navigation in this species, i.e., can determine their position relative to a goal without relying on familiar surroundings, cues emanating from the destination, or information collected on the outward journey (Boles & Lohmann 2003). This was based on a series of experiments where heading direction of tethered juvenile lobsters was measured after they had been displaced considerable distances from their home territory (>5 km) whilst deprived of external cues in transit. Artificial magnetic fields were also used to experimentally "displace" captive juvenile lobsters and a significant proportion responded by adjusting their heading direction appropriately.

Despite these intriguing initial experiments it is unclear which features of the Earth's magnetic field spiny lobsters are able to detect; inclination, direction, and/or localised variation in field intensity. The use of some of these features of magnetic fields, such as localised variation in field intensity, for orientation at an ecologically meaningful scale requires a high level of magnetic sensitivity and specific behavioural algorithms that rely on a previous and detailed knowledge of the arrangement of the magnetic field.

We are not aware of any research on the orientation of pueruli or phyllosomes of Palinurids in relation to magnetic cues, or to any attempts to identify a magnetic receptor in these earlier life stages. Such research is likely to be logistically difficult given that actively swimming pueruli require large experimental arenas and tethering pueruli has been found to markedly alter their behaviour (Jeffs & Holland 2000).

## CELESTIAL CUES

A wide variety of arthropod species have been shown to make very effective use of celestial cues for long distance orientation (Giroud & Balvay 1999; Horváth & Wehner 1999; Ugolini 2003). In particular, a number of insect species make extensive use of tracking the movements of celestial bodies, as well as the spectral, intensity, and polarisation gradients of celestial light sources for deriving directional information (Rossel & Wehner 1984; Horváth & Varjù 1997). For some crustacean and insect species the eye structure has become highly developed for detecting positional information from light fields. For example, in some species of stomatopods, cladocerans, desert ants, and bees the morphology of the compound eye has become highly specialised for discriminating the polarisation angles of sky-light so that it can be used for orientation (Mote & Wehner 1980; Wehner 1997; Marshall et al. 1999; Flamarique & Browman 2000).

Given the importance of celestial cues in other arthropods, it would be reasonable to assume that celestial cues could play a significant role as a cue for shoreward orientation in phyllosomes and pueruli. However, there is no evidence to support the use of celestial cues for onshore orientation in the early stages of the lifecycle of Palinurids, although there are indications that ambient light levels may help to determine the scale of vertical movements in the water column and that this in turn may affect passive offshore and onshore movement by oceanographic water movements (Rimmer & Phillips 1979). Among the pelagic stages of other crustaceans only the megalopae of several crab species swim in the direction of the sun's bearing. However, it was unclear how this orientation behaviour might assist with onshore migration (Shanks 1995).

The eyes of adults and pueruli of *P. cygnus* show a very marked change from an apposition- to a clear-zone type of compound eye (Meyer-Rochow 1975a,b) and the overall structure of the eyes of pueruli indicated they are very efficient for the perception of polarised light. Excellent abilities to detect polarised light have been confirmed from electrophysiology recordings from other decapod crustaceans with similar eyes (see Meyer-Rochow 1975a,b). However, the atypical arrangement of the axons of the retinula cells found in the pueruli eye may interfere with this level of sensitivity to polarised light. Meyer-Rochow (1975a) concluded that behavioural assays would be required to determine the true functioning of eyes in pueruli. Regardless, an ability to detect the angle of polarisation of sky-light could provide a useful basis for setting a consistent swimming orientation for pueruli, but would provide no information about the direction of the coast in offshore waters.

## HYDRODYNAMIC CUES

In crustaceans, a wide variety of external sensilla as well as internal sensory organs such as statocysts and proprioreceptors have been identified as potentially important in detecting hydrodynamic stimuli and body movements created by hydrodynamic forces such as waves (Sekiguchi & Terazawa 1997; Popper et al. 2001). A small number of studies have investigated hydrodynamic behaviour in juvenile and adult spiny lobsters, but very little has been reported for pueruli or phyllosomes. Spiny lobsters can localise discrete hydrodynamic stimuli around their bodies (Vedel & Clarac 1976; Wilkens et al. 1996). It was thought this sensitivity was important for the detection and defence against swimming predators rather than for any long distance orientation behaviour. However, hydrodynamic cues, especially wave surge, have been implicated in longer distance orientation behaviour of *P. argus* and *Panulirus guttatus* moving around benthic reef habitats (Herrnkind & McLean 1971; Walton & Herrnkind 1977; Nevitt et al. 1995; Lozano-Álvarez et al. 2002). The direction of ocean swells is a potentially useful orientation cue for pueruli. Because large waves require fetch to develop, they are less likely to be heading shoreward than offshore (Lewis 1994; Kingsland & Macky 1999; Montgomery et al. 2001). Rheotaxis, the orientation and movement in relation to water currents, may also be important in long distance orientation of benthic spiny lobsters (Walton & Herrnkind 1977). However, rheotaxis behaviour was not observed for the pueruli of *J. edwardsii* in small seawater flume trials (Jeffs & Holland 2000). Attempts to establish whether pueruli orient to orbital accelerations associated with wave motion using tethered animals in experimental chambers also failed (Jeffs & Holland 2000; Jeffs unpubl. data).

## ELECTROSENSE

Ocean currents and animals moving through the Earth's magnetic field generate electrical fields that have the potential to be detected and used for orientation by aquatic animals. A relatively small number of fishes are known to be able to detect weak electric fields which for some may provide directional information (Kalmijn 1987; Paulin 1995). However, there is no corresponding evidence for marine invertebrates.

## BEHAVIOURAL OBSERVATIONS

Although there has been little direct experimentation on the orientation cues in spiny lobster phyllosomes and pueruli, it is possible that some of their behaviours that have been observed might provide clues about their orientation. Pueruli have only been observed active at night at or near the surface, most often actively swimming in straight lines (Phillips & Olsen 1975; Serfling & Ford 1975; Calinski & Lyons 1983; Jeffs & Holland 2000). Pueruli of most species have been observed at times swimming within centimetres of the surface or on occasions with their antennae emergent. Likewise, zooplankton net studies have caught pueruli in their greatest abundance near the surface at night and they appear to be in deeper waters or absent from the water column during the day (Phillips et al. 1978; Phillips & Pearce 1997; Yoshimura et al. 1999). However in *P. cygnus*, there is an indication for zooplankton net data that the initial onshore movement of pueruli is undertaken at greater depths, later moving to surface waters once well within shelf waters (Ritz 1972; Phillips et al. 1978). During periods of rough sea conditions the pueruli of some species are more concentrated in surface waters (Ritz 1972; Phillips et al. 1978). The pueruli of a number of species are almost exclusively found during the dark new moon period probably to avoid detection by predators (Acosta et al. 1997; Acosta & Butler 1999), whereas the pueruli of other species have no lunar periodicity to their activity (Hayakawa et al. 1990). Returning to surface waters at night would be required for establishing a compass bearing that was reliant on celestial cues, because the key features of light with the potential to be used for orientation are lost with depth because of absorption and scattering (Lythgoe 1987; Nilsson 1997). However, it is unlikely that those species that are active only during the new moon phase would be able to access any celestial orientation cues given the absence of moonlight. Visiting the surface at night may also allow for better use of wave orientation cues because orbital acceleration from waves is more intense closer to the surface, and dominates the upper 30 m of the ocean (Cook 1984). Some of the behavioural observations of wild pueruli indicate that they are highly sensitive to water movements and are capable of detecting the difference between turbulence and reflected waves (Calinski & Lyons 1983). If pueruli are highly sensitive to wave motion as this observation would suggest, it should be possible for them to discriminate wave interference caused by reflected and refracted waves emanating from coastal and reef features. Reflected waves from the coast may be capable of travelling up to a few kilometres offshore and the direction of these reflected waves when taken in relation to the direction of prevailing onshore waves would provide a very reliable directional heading toward the coast. Again, this may help to explain the numerous observations of pueruli travelling close to the surface of the ocean. In this location pueruli would be well placed to detect waves reflected and refracted from the coast or shallow reefs. In contrast, surface waters are unlikely to be an ideal position in the water column for detecting and orienting toward underwater sound sources. Reflection and scattering of sound from the air/water interface and bubble noise from any breaking waves would potentially obscure the ability to detect more distant acoustic sources.

## DISCUSSION

Overall, there is very little evidence for any long distance orientation cue playing a role in the directed shoreward movement of the pueruli of Palinurids (Table 1). Reliable compass bearings could be derived by magnetic sense and the use of celestial cues, but this is insufficient for pueruli of many species seeking the coastal water from a complete range of compass bearings. It could be that these omnipotent cues are used to provide an ongoing compass bearing that is set in conjunction with a more reliable shoreward cue such as underwater sound. Ambient underwater sound does have the potential to provide an onshore orientation cue for pueruli. However, the potentially effective range for this cue may be limited to less than 40 km offshore (Phillips & Penrose 1985). Other known potential shoreward orientation cues generally have major limitations, particularly in relation to their potential to provide a reliable cue over the longer distances traversed by pueruli (>50 km). Water-borne chemical cues are unlikely to provide a reliably direct shoreward orientation cue from offshore locations, especially for a post-larval stage with limited energy reserves to expend on circuitous routes. However, chemical cues may play a role in locating suitable settlement habitats in the coastal zone, as they have been found to do in other crustaceans such as crabs (Boudreau et al. 1993; Welch et al. 1997; Forward et al. 2003; Keller et al. 2003). Hydrodynamic cues such as wave and current directions would be unreliable sources of information for locating the coast from offshore, although in shallower waters wave direction, including the direction of reflected and refracted waves, could help to locate key coastal features such as reefs.

It is likely that the pueruli of spiny lobsters use an integrated mix of orientation cues that may change in importance with increasing proximity towards inshore settlement areas or with changing circumstances. A similar model for the use of multiple orientation cues has recently been proposed for hatchling turtles and is well established in migratory birds (Avens & Lohmann 2003). A mix of cues is illustrated in the way that lunar phase modulates the orientation behaviour of larval crab stages toward underwater sound (Jeffs et al. 2003). The behavioural significance of this may be to make use of onshore tidal movements, or to avoid times of strong tidal currents.

Research progress in identifying the important shoreward orientation cues in late stage phyllosomes and pueruli are unlikely to come from conventional laboratory experimental approaches because these pelagic stages are extremely difficult to manipulate without modifying their behaviour (Jeffs & Holland 2000). Field research is also problematic given the highly cryptic behaviour and the relatively low abundance of these life history stages in most locations. Large-scale tank experiments or contained field experiments may be sufficient to yield useful results. Additionally, detailed examination of the morphology and sensory capabilities of these stages may also provide useful clues to understanding their full orientation capabilities. Although it will be difficult to reveal the basis and extent of the

**Table 1** Estimated effective ranges for various shoreward orientation cues in pueruli of Palinurids and closely related taxa.

| Shoreward orientation cue | Potential range of operation | Limitations | Existing evidence |
|---|---|---|---|
| Acoustic | <100 km | Effectiveness reduced in rough sea conditions | No evidence in Palinurid pueruli.<br>Crab larvae and post-larvae moved toward reef sounds—Jeffs et al. (2003). |
| Chemical | <100 km | Poor directional resolution over long distances | Pueruli of *Panulirus argus* observed to move toward coastal water—Goldstein (unpubl. data).<br>Post-larvae of *Homarus americanus* chemically mediated behaviour in Y-maze—Boudreau et al. (1993).<br>Chemically mediated behaviour in post-larvae of decapod crab species, e.g., Welch et al. (1997); Forward et al. (2003); Keller et al. (2003). |
| Magnetic field | >100 km | Requires prior knowledge of location of the coast, or magnetic field | No evidence in Palinurid pueruli.<br>Juvenile and adult *P. argus* shown to have magnetic sensitivity and magnetic navigation—Lohmann (1984, 1985); Lohmann et al. (1995); Wiltschko & Wiltschko (1995); Boles & Lohmann (2003). |
| Celestial | >100 km | Requires prior knowledge of location of the coast | No evidence in Palinurid pueruli.<br>Crab post-larvae shown to orient in relation to the sun position—Shanks (1995).<br>Evidence from a variety of other crustaceans, e.g., Giroud & Balvay (1999); Ugolini (2003). |
| Hydrodynamic —waves | <100 km | Wave direction unreliable, unless using reflected or refracted waves | No evidence in Palinurid pueruli.<br>Adult *P. argus* and *P. guttatus* shown to orient in relation to waves—Herrnkind & McLean (1971); Walton & Herrnkind (1977); Nevitt et al. (1995); Lozano-Álvarez et al. (2002).<br>Evidence from other crustaceans and marine arthropods, e.g., Nishimoto & Herrnkind (1978); Rudloe & Herrnkind (1980). |
| —current | >100 km | Requires prior knowledge of location of the coast | No evidence in Palinurid pueruli.<br>Adult *P. argus* shown to use water current direction in orientation—Walton & Herrnkind (1977). |
| Electrosense | >100 km | Requires prior knowledge of location of the coast | No evidence in Palinurid pueruli.<br>No evidence in any crustacean. |

orientation behaviour of late stage phyllosomes and pueruli, a greater understanding of this most extreme example of onshore orientation among marine invertebrates is of wide biological significance.

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# Distribution and abundance of recruits of the eastern rock lobster (*Jasus verreauxi*) along the coast of New South Wales, Australia

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**Abstract** In the mid 1990s, the New South Wales government introduced management measures to increase the size of the population of the eastern rock (spiny) lobster, *Jasus verreauxi*. A fully orthogonal sampling design was begun in July 1995 to test, amongst others, the hypothesis that the relative abundance of recruits (stages of peuruli to early juveniles combined) to the eastern rock lobster population will change over space and time. In the design for the full sampling strategy were the factors of Year (eight levels) and Location (four levels). Three replicate collectors at each of three sites at each location were sampled during the first quarter of each lunar month between August and January between 1995–96 and 2002–03 (inclusive). Recruits occurred on collectors between September and January each year. Results of the two-factor ANOVA showed a significant interaction between Year and Location, meaning that differences in mean relative abundance of recruits between years will depend upon the location. Comparison of means (SNK test) show that in each year the relative abundance of recruits was greatest at the southern locations, but no pattern in mean relative abundance between years for each location was apparent. Management measures introduced in the mid 1990s to increase population size have not to date resulted in increasing levels of recruitment. Considering this, levels of recruitment to the population appear to be influenced most by variation in environmental factors rather than levels of egg production from the stock.

**Keywords** lobster; recruitment; distribution; abundance

## INTRODUCTION

Knowing about the distribution and abundance of larvae of marine organisms enhances understanding about: (1) the survival of individuals during the early stages of their life-cycle; (2) when recruitment to the population occurs; (3) the preferred habitat of recruits; (4) the stock-recruit processes; and (5) the effects of managerial decisions on recruitment. Where all individuals in the population cannot be measured, recruitment to the population is calculated as the catch taken per unit of sampling effort (catch per unit effort) (e.g., Sissenwine 1984) and is referred to as an index of relative abundance. Sampling is usually done at the earliest stage of the species' life-cycle after hatching, when it is practical to catch the organisms. In spiny lobsters, this is commonly the post-larval stage known as the puerulus, a transparent, free-swimming animal that in shallow water species moves from offshore waters towards shore and settles in shallow habitat (Phillips & Sastry 1980).

Scientists have commonly used devices referred to as collectors, to survey the relative abundance of the puerulus stage (for a review see Phillips & Booth 1994). Studies on several species have shown that pueruli occur on collectors year round with one or two times of peak settlement (for reviews see Herrnkind et al 1994; Butler & Herrnkind 2000). Months of peak settlement for the same species may vary between places (e.g., Booth 1994; Briones-Fourzan 1994) and patterns in annual catches of pueruli of the same species and population may vary

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between locations (e.g., Booth & Tarring 1986; Booth 1989, 1994). Catches of pueruli may vary also over small as well as large spatial scales (e.g., Marx 1986; Herrnkind et al. 1994).

Recruitment to a population may vary over time because of changes in environmental factors or in egg production. Little is known about the environmental factors that affect the survival of larval spiny lobsters before settlement, but those that are thought to affect recruitment include changes in the strength and direction of currents and winds assisting phyllosomes and pueruli toward shore (MacDonald 1986; Pollock 1986; Harris et al. 1988; Pearce & Phillips 1988; Caputi & Brown 1993; Polovina & Mitchum 1994; Caputi et al. 1995), changes in abundance of predators, and the width of the continental shelf (Briones-Fourzan 1994). If environmental factors and not the size of the spawning stock determine the level of recruitment to the population, then management measures that aim to increase the size of the population by increasing levels of spawner abundance, may be ineffective. The long duration of the larval phase of spiny lobsters (Phillips & Sastry 1980) increases the probability that any relationship between abundance of spawners and recruits will be obscured by variability caused by the effects of environmental factors upon the survival of larvae (e.g., Caputi & Brown 1993; Caputi et al. 1995).

The eastern rock (spiny) lobster *Jasus verreauxi* (Milne-Edwards 1851) occurs in waters off the east coast of Australia from Tweed Heads (28°S) to Tasmania (42°S), and as far west into Bass Strait as Port MacDonnell (140°E) (Fig. 1 insert). It is also found in New Zealand waters, principally off the North Island. The commercial fishery for this species in waters off New South Wales (NSW), Australia is by international standards small, with landings of around 150 t per annum, but it is one that targets a highly priced (c. AU$ 45.00 per kg) species that is considered a "boutique" seafood. The fishery became restricted in 1994 and management measures including entry criteria to the fishery, individual catch quotas, and a legal maximum size were put in place, with the objective to increase the size of the *J. verreauxi* population.

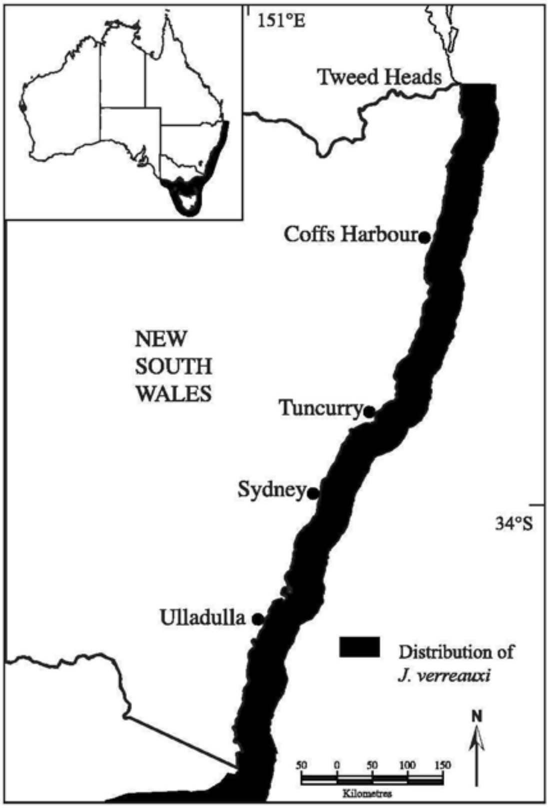

**Fig 1** Distribution of *Jasus verreauxi* off Australia (insert) and New South Wales (NSW). Map of NSW shows the locations where collectors were set at three sites to survey the relative abundance of *J. verreauxi* recruits.

Little is known about the distribution and abundance of *J. verreauxi* recruits. Pilot studies (Montgomery & Kittaka 1994; Montgomery 2000; Montgomery & Craig 1997, 2003) considered the effects of many of the factors, apart from the abundance of animals, that may influence the catch of *J. verreauxi* recruits on collectors; namely collector type, position, soak-time, time of sampling, and levels of replication. Results from these studies led to the development of a standardised methodology and experimental design that was used in full-scale surveys to study the distribution and abundance of *J. verreauxi* recruits. Also, Montgomery (1998) suggested that unlike other palinurids, *J. verreauxi* may settle at only one time (between September and January) each year. This pattern needs to be tested with data collected over a greater number of years than available during the pilot studies, to ensure that the pattern in settlement remains consistent against variation caused by fluctuations in environmental factors and in egg production.

This paper describes the results from the full-scale surveys done to test the hypothesis that the distribution and abundance of *J. verreauxi* recruits changes over space and time. For the purposes of this paper, pueruli have been grouped together with first instar and early benthic juveniles into the term "recruits" to refer to those stages of *J. verreauxi* occuring on collectors and that are assumed to be the current year's recruitment to the population (Montgomery 2000). The data collected allow the hypothesis above to be tested and also provide information about the sizes of recruits and contribute towards assessing whether the objectives of management are being met.

## MATERIALS AND METHODS

In the full-scale experiment were the fixed factors of Year and Location. Three replicate collectors were set at each of three sites at each of four Locations (Coffs Harbour, Tuncurry, Sydney, and Ulladulla), along the coast of NSW (Fig. 1). Locations were chosen from among those where there was the infrastructure to support the sampling programme (e.g., vessels of appropriate size and storage facilities) and so that these were approximately equidistant from each other.

Sea-weed-type collectors of the design described by Montgomery & Craig (1997) were sampled every 4 weeks during the first quarter of the lunar month (Montgomery & Craig 2003). The first quarter was defined as being from three days before the night of first quarter to the third day after the night of first quarter (inclusive).

With the exception of Sydney, the sampling season went from the first quarter of the lunar month falling in late July or early August ($t_0$) to the first quarter in the lunar month of late January or early February inclusive ($t_6$), the time when Montgomery (1998) had shown recruits to settle on collectors (see also Fig. 2). At the first quarter immediately before $t_0$, collectors were placed on moorings at sea to provide "conditioning" (Montgomery & Craig 2003). At $t_0$, collectors were cleared of recruits by using the sampling process described below and were placed back on the moorings. Hence, the first time of sampling was the first quarter moon-phase in late August or early September ($t_1$) and the last sampling time was the latest first quarter in January or the earliest one in February ($t_6$). At Sydney, sampling was done on the first quarter in each lunar month throughout the year to verify the pattern shown by Montgomery (1998).

At all locations, collectors were sampled aboard chartered commercial fishing vessels or research vessels by assistants stationed at each location. Collectors at each site were sampled by the procedure detailed in Montgomery & Craig (2003). One-at-a-time, collectors were removed from the mooring, placed between bearings at either end of a tumbler, and turned briskly through 30 revolutions in each direction to dislodge any recruits. Recruits were collected from the bottom of the tumbler, placed in jars coded for the particular collector, and then immersed in a drum containing 250 litres of salt water.

Sampling was based upon a system of rotating collectors so that each collector was moored at sea for no longer than 3 months at a time (Montgomery & Craig 2003). Experience gained during pilot experiments taught that collectors left at sea for more than 3 months became so encrusted with macroinvertebrates that they were too heavy to sample efficiently. The system of rotating collectors meant that at each site and sampling time there was a collector that had been at sea for 1 month, another for 2 months, and a third for 3 months.

Lobsters in the coded jars were later identified to species, staged according to the criteria of Montgomery (2000), and measured (carapace length, CL). Data were summed to give the number of recruits caught per collector per year at each location and then used in a fully orthogonal two-factor ANOVA to test the hypothesis. Patterns in occurrence of recruits on collectors off Sydney were investigated by plotting means and standard errors.

### Length composition

Data were for the 6 lunar months starting with the earliest first quarter in September each year between 1995–96 and 2002–03 (inclusive) i.e., these excluded the catches from Sydney taken at times other than during the sampling season for the other locations. Lengths of recruits caught on collectors were grouped into 1 mm length classes (e.g., lengths of 7.6–8.5 mm CL were grouped as 8.0 mm CL). Data within locations were pooled across years and treated in two ways. First, the ranges and means of the length distributions of puerulus, first instar juveniles (stage 5), and early benthic juveniles (stage 6) were compared. Second, data for each stage and year were combined as length distributions to test the null hypothesis that there are no differences in the lengths of *J. verreauxi* recruits caught on collectors between locations. Differences in the mean lengths were tested in a one-factor ANOVA using a randomly chosen subset of data ($n$ = 338) from each of Tuncurry, Sydney, and Ulladulla to balance with data from Coffs Harbour. The Kolmogorov-Smirnov test was used on the whole data set from each location to test for differences in the shape of the length distributions.

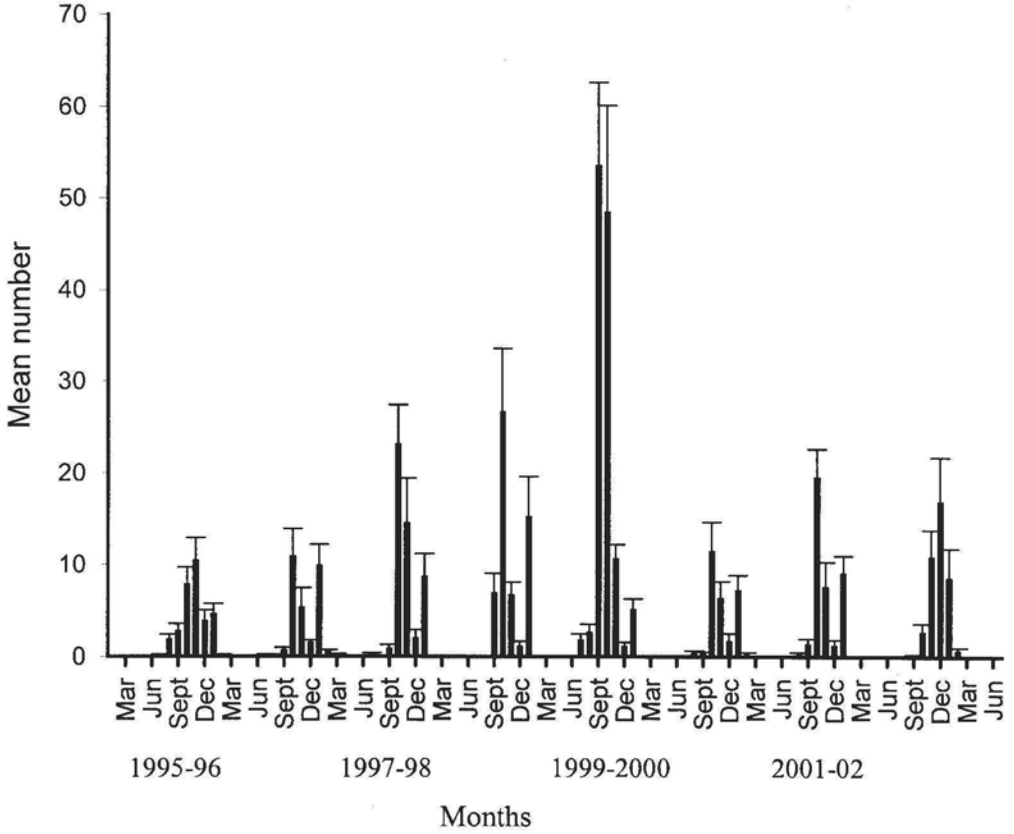

**Fig. 2** Mean number (+standard error) of *Jasus verreauxi* recruits caught on collectors off Sydney from 1995–96 to 2002–03.

## RESULTS

Recruits settled on collectors at sites off Sydney only during the spring-summer period in each of the eight years from 1995–96 to 2002–03 (Fig. 2).

In testing for annual and spatial differences in mean relative abundance of recruits, results of analysis of variance showed a significant interaction between Year and Location indicating that the mean relative abundances of recruits varied a great deal among these factors (Table 1; Fig. 1). This implies that differences in mean relative abundance among years (the main effect which quantifies increases or decreases in abundances of this species over time) depends upon the particular location in question. Student-Newman-Keul's comparison of means (Table 2) however, failed to identify any logical patterns in annual mean numbers per collector for data from each location except Sydney. At Sydney, mean relative abundance was greater in 1999–2000 than in other years, but there were no other patterns in means between years. There were patterns though in mean relative abundance between Locations within Years. In each SNK comparison, the means for the southern Locations (Ulladulla and Sydney) were greater than those for the northern Locations (Coffs Harbour and Tuncurry) (Table 2).

### Length composition

Lengths of pueruli ranged from 9 to 16 mm CL, first instar juveniles from 10 to 22 mm CL, and early benthic juveniles from 11 to 30 mm CL (Fig. 4). Lobsters increased in size by up to 2 mm CL between the puerulus and first instar stages and then between c. 3 and 6 mm CL between the first instar and early benthic juvenile stages; the last stage perhaps included more than one instar.

Mean lengths of recruits differed between Locations (Table 3). Variances of the samples remained

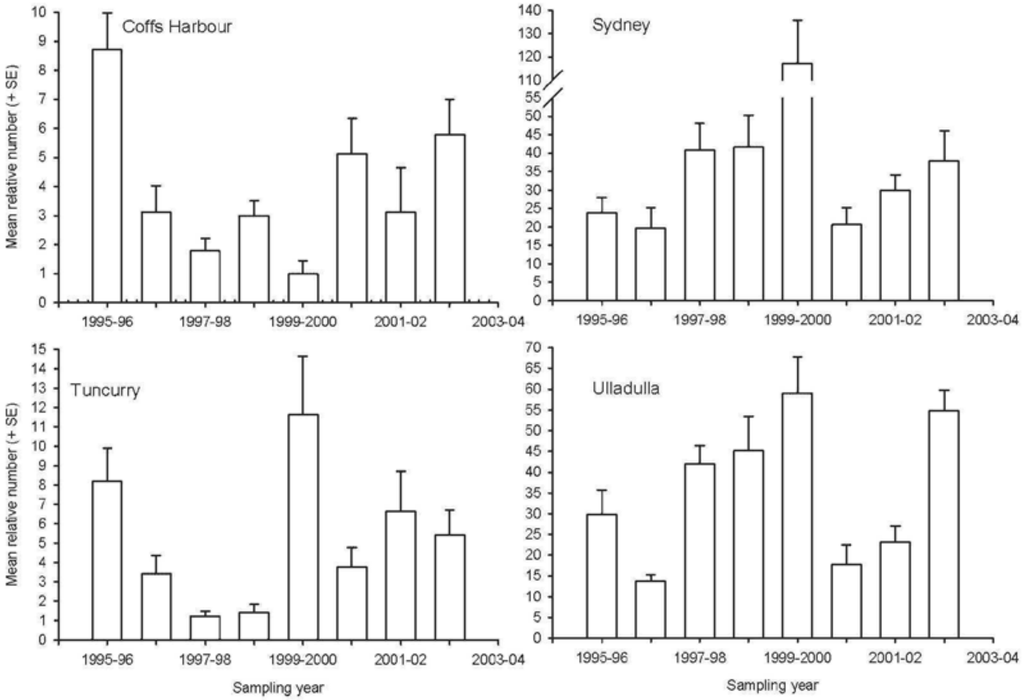

**Fig. 3** Fluctuations in mean number (+ standard error) of *Jasus verreauxi* recruits caught per year at each location.

heterogeneous, but this is thought to have had little effect on the test (Underwood 1997). The mean length of recruits was largest off Coffs Harbour and larger also at Tuncurry than off Sydney and Ulladulla (SNK test, Table 4). There were differences also in the shapes of the distributions of lengths between locations (Table 5). The greatest differences in shape between length distributions occurred between the cumulative proportion of recruits in the length classes from 11 to 13 mm CL.

**Table 1** Analyses of numbers of recruits of *Jasus verreauxi* on collectors between eight Years (Y) and four Locations (L) over the period 1995–96 to 2002–03. Data were transformed by $\log_e (x+1)$ to stabilise variances. (NS, not significant $P > 0.05$; Cochran's test, C = 0.0815 NS.)

| Source of variation | d.f. | MS | *F* | *P* |
|---|---|---|---|---|
| Year = Y | 7 | 3.37 | 8.09 | <0.01 |
| Location = L | 3 | 95.46 | 229.25 | <0.01 |
| Y×L | 21 | 2.65 | 6.35 | <0.01 |
| Residual | 256 | 0.42 | | |
| Total | 287 | | | |

**Table 2** Student-Newman-Keul's comparisons of mean numbers (standard error) of *Jasus verreauxi* recruits per collector at each Location within each Year. (CH, Coffs Harbour; Tu, Tuncurry; Sy, Sydney; Ul, Ulladulla. =, equal; >, greater than; <, less than.)

| | Locations | | | | | | |
|---|---|---|---|---|---|---|---|
| Years | CH | | Tu | | Sy | | Ul |
| 1995–96 | 8.72 (1.26) | = | 8.22 (1.71) | < | 23.89 (4.00) | = | 29.78 (6.01) |
| 1996–97 | 3.11 (0.92) | = | 3.44 (0.93) | < | 19.61 (5.65) | = | 13.67 (1.56) |
| 1997–98 | 1.78 (0.43) | = | 1.22 (0.28) | < | 40.78 (7.32) | = | 42.00 (4.45) |
| 1998–99 | 3.00 (0.50) | = | 1.44 (0.41) | < | 41.67 (8.65) | = | 45.22 (8.24) |
| 1999–00 | 1.00 (0.44) | < | 11.67 (3.01) | < | 117.33 (18.36) | > | 59.11 (8.69) |
| 2000–01 | 5.11 (1.23) | = | 3.78 (1.02) | < | 20.56 (4.72) | = | 17.78 (4.73) |
| 2001–02 | 3.11 (1.53) | < | 6.67 (2.04) | < | 29.89 (4.20) | = | 23.22 (3.77) |
| 2002–03 | 5.78 (1.22) | = | 5.44 (1.27) | < | 38.00 (7.96) | = | 54.78 (5.09) |

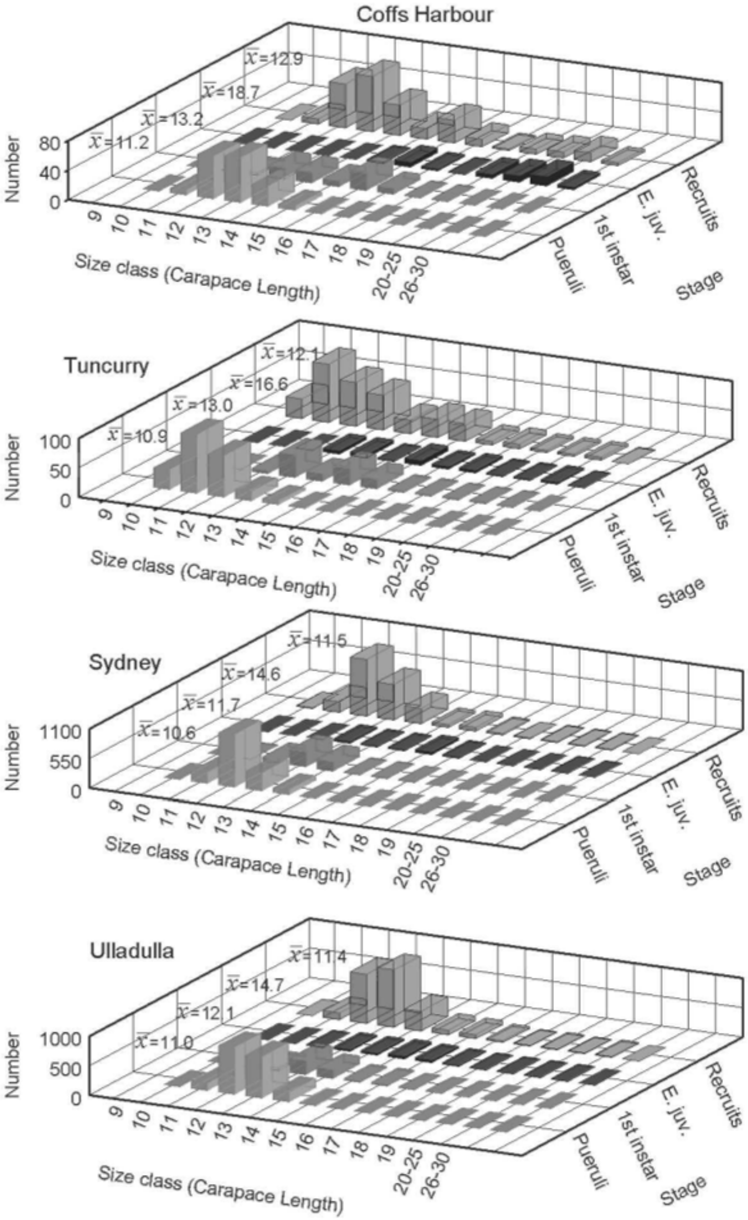

**Fig. 4** Length distributions of *Jasus verreauxi* pueruli, 1st instar juvenules, early benthic juveniles, and recruits (all stages combined) caught on collectors from 1995–96 to 2002–03 at each of the four locations sampled. Mean length ($\overline{x}$) for each category is also shown.

**Table 3** Analyses of mean lengths of recruits of *Jasus verreauxi* on collectors between four Locations (L) over the period 1995–96 and 2002–03. Data were transfomed by $\log_e$ (x+1) to stabilise variances. (*, significant $P < 0.05$ Cochran's test, C = 0.38 *.)

| Source of variation | d.f. | MS | *F* | *P* |
|---|---|---|---|---|
| Location = L | 3 | 186.09 | 28.25 | <0.01 |
| Residual | 1348 | 6.59 | | |
| Total | 1351 | | | |

**Table 4** Student-Newman-Keul's comparisons of mean lengths (standard error) of *Jasus verreauxi* recruits caught on collectors at each location over the period 1995–96 to 2002–03. (Co, Coffs Harbour; Tu, Tuncurry; Sy, Sydney; Ul, Ulladulla. =, equal; >, greater than; <, less than.)

| Locations: | Co | | Tu | | Sy | | Ul |
|---|---|---|---|---|---|---|---|
| | 12.89 (0.17) | > | 12.13 (0.17) | > | 11.51 (0.04) | = | 11.42 (0.04) |

**Table 5** Kolmogorov-Smirnov tests to compare distributions of lengths of *Jasus verreauxi* between Locations for pooled years 1995–96 to 2002–03. Shown are the calculated $D_{max.}$ values and the sample sizes for *m* and *n*. Critical *P* values have been bonferronised to allow for six pair-wise comparisons at a nominal probability of Type I error, $P < 0.05$ (Miller 1966). (Co, Coffs Harbour; Tu, Tuncurry; Sy, Sydney; Ul, Uladulla.)

| | Co versus Tu | Co versus Sy | Co versus Ul | Tu versus Sy | Tu versus Ul | Sy versus Ul |
|---|---|---|---|---|---|---|
| $m,n$ | 338,377 | 338, 2382 | 338,2499 | 377, 2382 | 377,2499 | 2382,2499 |
| $D_{m,n}$ | 0.25 | 0.38 | 0.37 | 0.16 | 0.15 | 0.16 |
| $P$ | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 |

## DISCUSSION

Results showed that *J. verreauxi* settle to collectors only from September to January (inclusive) each year and that along the coast of NSW, relative abundance is greatest at southern locations. Mean annual relative abundance differed between years within each study location but overall there were no discernible patterns.

Considering that *J. verreauxi* spawn between September and January each year (Montgomery 1992) and if it is assumed that *J. verreauxi* caught on collectors during a sampling season are from the previous year's spawning, then the duration of this species' larval phase is c. 8–12 months. This duration is typical of many palinurids (Booth & Phillips 1994) and is supported for *J. verreauxi* by results from laboratory experiments (Kittaka 1994) that recorded a larval phase for this species of c. 8 months. Generally, studies done on culturing larvae in the laboratory achieve shorter larval phases than found from studies on wild populations. For instance, Kittaka (1994) found that the larval phase of *J. edwarsii* in the laboratory had a duration of c. 322 days whereas Booth (1994) found that the larval phase in the wild may last for up to 2 years. In the wild there may be greater differences in the rate of development between individual larvae, and/or delays in metamorphosis from phyllosomata to pueruli (Kanciruk 1980). If so, the larval phase of *J. verreauxi* in the wild may be longer than suggested from laboratory studies.

Results in this study confirmed the temporal pattern shown earlier by Montgomery (1998) of a single annual pulse of *J. verreauxi* recruits to nearshore waters each year. This is an unusual pattern for a species of the family Palinuridae since it is more common for palinurids to recruit throughout the year and to have one or more peaks in relative abundance within a year (Booth 1994; Briones-Fourzan 1994). *Panulirus cygnus* also has a single spring peak in relative abundance each year, but there is continual low-level recruitment of the species throughout the year (Phillips 1986; Caputi et al. 1995).

It would appear that management measures introduced in the mid 1990s have not resulted in increased levels of recruitment to the *J. verreauxi* population, because recruitment to collectors has not increased over recent years. However, it may be that the size of the spawning stock in the mid 1990s was not as low as first thought, that the spawner recruit relationship for *J. verreauxi* is such that small changes in spawning stock do not produce large changes in numbers of recruits, or that there is no relationship between levels of recruitment and the size of the spawning stock. The impacts upon levels of recruitment may not be seen until lobsters spawned in the years immediately after the management measures were introduced live to an age (c. 8 years, Montgomery unpubl. data) to recruit to the spawning stock. Consequently any impact upon recruitment to the population may not be evident until years after 2002–03.

The spatial variability in the relative abundance of recruits of *J. verreauxi* found in this study is typical of patterns found for other spiny lobster species (e.g., MacDonald 1986; Marx 1986; Booth 1994; Briones-Fourzan 1994). However, few studies have described a pattern where relative abundance declines latitudinally within the one palinurid population. The greater relative abundance of recruits at the southern locations sampled is consistent with patterns of relative abundance of *J. verreauxi* juvenile and subadults off NSW (Montgomery 1995) and New Zealand (Booth 1986), suggesting that these southern regions of Australia and New Zealand are important nursery areas for the two palinurid populations. Studies on this species off New Zealand have shown tagged lobsters to move in a northerly direction towards spawning grounds (Booth 1984, 1986) and similar movement patterns have been recorded off NSW (Montgomery unpubl. data). The main spawning areas for *J. verreauxi* off NSW are thought to be in waters north of around 33°S (MacIntyre 1967). It can be hypothesised therefore that *J. verreauxi* are a unit stock along the coast of NSW and that lobsters move from the main nursery areas in southern waters to northern regions to join the bulk of the spawning population.

Temporal and spatial patterns in recruitment of spiny lobsters are a product of changes in levels of egg production or the influence of environmental factors (MacDonald 1986; Pollock 1986; Booth 1994; Booth & Phillips 1994). Considering that the management measures introduced in the mid 1990s to increase the size of the population have not transpired yet into a pattern of increased levels of recruitment to the population, it is likely that at the current level of spawning stock, environmetal factors determine the level of recruitment to the *J. verreauxi* population. Environmental factors of current strength and water temperature have been shown by Caputi et al. (2001) to most influence the level of settlement of *P. cygnus* pueruli. Caputi et al. (2001) hypothesised that the Leeuwin Current which is driven by ENSO events, influenced lobster larval life by first promoting greater survival and growth through warmer water temperatures brought at times of strong current flow and second by greater retention and transportation of larvae across the continental shelf when current flows were strongest. Strong currents were also associated with higher levels of puerulus settlement in southern areas of the species' distribution. Briones-Fourzan (1994) found that *P. argus* pueruli settled along the coast of Mexico where the width of the continental shelf was narrowest and so postulated that the width of the continental shelf may influence the level of settlement. Such factors are perhaps the primary environmental factors influencing the distribution and abundance of *J. verreauxi* recruits to nursery areas.

The coast of NSW is home to a western boundary current, the East Australian Current (EAC), that flows southwards to c. 32–36°S, then veers eastwards and either flows toward New Zealand or splits into anticyclonic eddies that flow at variable speeds southwards (Hamon 1965; Nilsson & Cresswell 1981; Cresswell & Legeckis 1986). It is possible that larvae spawned off the north coast of NSW are transported from the spawning area by the EAC to more southern areas, such as off Sydney and Ulladulla, where the width of the continental shelf is narrower and the current not as strong as further north. Under these conditions, the chances of pueruli reaching the shoreline off NSW in large numbers may be greater in southern waters than further north. During years of strong current flow higher levels of puerulus settlement would be expected because of greater larval survival and growth and greater retention rates and transportation of larvae. For these reasons also, greater levels of puerulus settlement in the southern extremeties of the species' distribution may be expected; as occurred in waters off Tasmania (42°S) in 1999–2000 (Gardner et al. 2000). By continuing the surveys described in this paper and collecting information about spawner abundance and environmental parameters we will, at some future time, be in the position to test the hypothesis that patterns in recruitment of *J. verreauxi* are most influenced by environmental factors rather than the size of the spawning stock and egg production.

Recruits of *J. verreauxi* as long as 30 mm CL were caught on collectors, but most were shorter than 13 mm CL. The length range of pueruli and recruits recorded in this study were greater than those reported by Booth & Phillips (1994) as being common for species of the family Palinuridae that inhabit shallow waters. Differences in the mean length and shape of the length distributions for recruits between locations suggested that recruits in northern locations may grow faster than those in southern areas. Factors that may be influencing these patterns in growth are water temperature, food, and/or density of animals (Hernkind & Butler 1994). Notwithstanding that there is little information about food supply and density of *J. verreauxi* recruits along the coast of NSW, generally rates of growth of palinurids are faster in warmer than in cooler waters (Chittleborough 1975; Lipcius & Herrnkind 1986). Certainly the oceanic water is warmer in the lower latitudes off NSW (Cresswell & Legeckis 1986) where the largest recruits were found than in the higher latitudes where recruit size was smaller.

The sampling strategy implemented in surveys described in this study has been successful in providing mean estimates of the relative abundance of recruits with standard errors that were less than 10% of the mean. There is no evidence to date, to suggest that the management measures introduced in the mid 1990s have impacted upon recruitment to the population. Rather, recruitment seems to be influenced by environmental factors. The southern waters of NSW appear to be important nursery areas for *J. verreauxi* and the environmental factors which influence this distribution need to be investigated. It is generally acknowledged that such investigations require at least 10 years of data before associations between environmental factors and recruitment can first be made (e.g., Pearce & Phillips 1988; Caputi et al. 1995, 2001). The present information on the relative abundance of recruits is the first step in what should be an ongoing sampling programme to collect data that can be used to ascertain whether: (1) environmental factors influence levels of recruitment; (2) management has affected recruitment to the population; (3) there is a relationship between relative abundances of spawners and recruits; and (4) there is an association between the level of recruitment and the level of catch in future years.

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# Can additional abundance indices improve harvest control rules for New Zealand rock lobster (*Jasus edwardsii*) fisheries?

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**Abstract** Although New Zealand rock lobster (*Jasus edwardsii*) fisheries can be assessed with a sophisticated Bayesian length-based model, these assessments are expensive and time consuming; they cannot be conducted for each area every year. Harvest control rules are increasingly important management tools in New Zealand rock lobster fisheries. Recent work has developed and evaluated procedures for rebuilding or maintaining lobster stocks based on criteria agreed by stakeholders. Most management procedures depend on a single abundance index, often catch per unit of effort (CPUE). When management procedures react slowly to changes in vulnerable biomass, allowable catches get out of phase with the stock, causing large oscillations in both catches and CPUE. Lags between data and management actions and "latent years" are features of rules that reduce responsiveness. This study explores ways to improve the responsiveness of harvest control rules by using additional data to predict changes in vulnerable biomass. Four data sets are examined: CPUE trends, pre-recruit indices, puerulus settlement indices, and size frequencies. Only pre-recruit indices, which were explored with a simple delay-difference model based on parameter estimates from recent assessments, appeared to have immediate potential for use in improving management procedures.

**Keywords** decision rules; management procedures; abundance indices; pre-recruit indices

## INTRODUCTION

Red rock lobsters, *Jasus edwardsii* (Hutton 1875), support a large and valuable inshore fishery in New Zealand, with recent annual landings of 2600 t (Sullivan 2003). Since 1990 the fishery, divided into nine quota management areas (QMAs) (Fig. 1), has been managed with individual transferable quotas and input controls such as minimum legal size (MLS) and protection of berried (ovigerous) females.

The fishery is managed by a Management Group established by the Minister of Fisheries and comprising representatives from all stakeholder groups. In an unusual but successful arrangement, the contract to collect fishery data and perform assessment work is held by the NZ Rock Lobster Industry Council. They subcontract the assessment-related work to several research providers including the authors.

Data collection is also conducted by the industry. In some areas fishers count, sex, and measure their catch from a few pre-selected pots (Starr & Vignaux 1997); in others they use their own catch samplers or subcontract sampling to the National Institute of Water and Atmospheric Research Limited (NIWA). Tagging and recapture is conducted by industry primarily to measure growth but also to provide information on movements (Kendrick & Bentley

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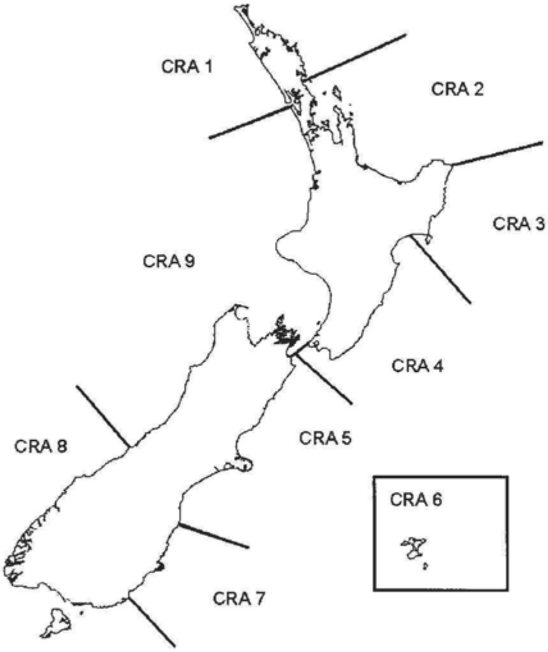


**Fig. 1** Map of New Zealand showing quota management areas (QMAs) referred to in the text. Chatham Islands, CRA 6, are shown south and west of their true location.

2003). Compulsory catch and effort data are also collected by the Ministry of Fisheries. To guide future data collection, trade-offs between cost of data collection and the need for data in assessments for the catch sampling and tag-recapture data have been explored (Bentley et al. 2002a,b).

In New Zealand, rock lobster management relies on a mixture of assessments and agreed "management procedures" (Butterworth & Punt 1999). In this paper we describe work that we conducted to explore the possibility of using additional data sources to guide harvest control rules.

## Assessment

Formal stock assessment of rock lobsters is conducted annually in New Zealand. Over time the spatial scale of assessment has decreased: the first assessments addressed the whole of the North and South Islands combined (Breen 1989); later this "stock" was subdivided into three substocks—northern, central, and southern (Booth & Breen 1992); recent assessments have focused on individual QMAs (Starr et al. 2003; Kim et al. 2004).

Assessment models have evolved from a simple biomass-dynamic model, fitted only to catch and catch per unit of effort (CPUE) (Breen & Kendrick 1998a), through "age"-structured models (Breen & Kendrick 1998b), to a complex length-based model (Starr et al. 2003) of the type described by Punt & Kennedy (1997). This integrated model is fitted to CPUE, older abundance indices, tag-recapture data, and size observations from catch sampling; it estimates recruitment, mortality, growth, maturity, selectivity, and seasonal vulnerability parameters simultaneously. The high complexity is required both to use the data fully and to address changing management and fishing patterns, especially a shift from summer to winter fisheries in the mid 1990s. The approach is Bayesian, in line with evolving assessment practice worldwide (Walters & Ludwig 1994; Punt & Hilborn 1997).

Because assessments are now complex and very time-consuming, recent assessments address only one or two areas each year, so each area can be assessed only once in three or four years. Consequently, New Zealand management has turned to using decision rules and management procedures.

## Decision rules and management procedures

These pre-specify how management changes will be made based on some fishery data. A decision rule specifies what data will be examined, what will "trigger" the rule, and what will then happen. A management procedure is "a fully specified feedback control system applied as part of a fishery management system" (McAllister et al. 1999) and specifies what data will be collected, how they will be collected and processed, what estimates will be made from the data, and how those estimates will determine harvest controls. Good reviews are provided by Butterworth & Punt (1999) and McAllister et al. (1999).

For the northern and central substocks, New Zealand rock lobster management uses simple decision rules that mandate a stock assessment when CPUE falls below a specified base level. A more sophisticated management procedure is used for the southern substock, CRA 7 and 8 (Starr et al. 1997), designed through extensive simulation trials to ensure that the stock will rebuild to a target biomass level in a reasonable period (Bentley et al. 2003a). This procedure is not necessarily suitable for maintaining biomass at a target level or to deliver other goals.

Designing good management procedures demands an understanding of what management is trying to do. An obvious management trade-off, for instance, is between average catch and stability: to maximise mean catch requires frequent catch changes;

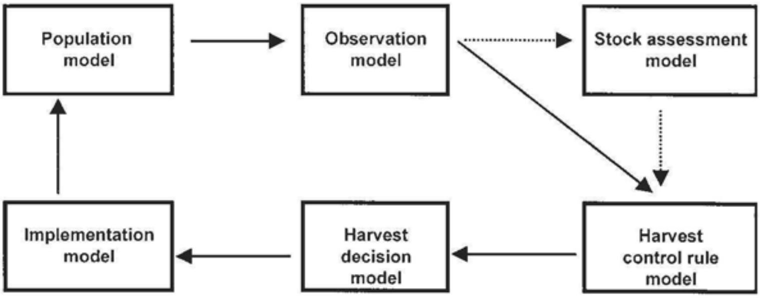


**Fig. 2** Main components in a quantitative fishery management system evaluation (from McAllister et al. 1999).

sustainably stable catches are lower catches. Another is between risk and catch: higher mean catch implies higher risk. Yet another is between mean catch and CPUE: higher CPUE implies greater ease and lower costs of catching. One strategy may produce high catches from a low abundance, another may result in higher abundance but lower catches; the choice between alternatives depends upon the relative importance of each goal.

The relative importance of competing objectives such as yield, safety, abundance, and stability should be clearly defined, we believe, by stakeholders and certainly not by fisheries scientists. In a workshop held in New Zealand, lobster fishers placed importance on stability in catch quotas, maintenance of high CPUE (high abundance), and maintenance of a wide size range of lobsters so that fishers could respond to changes in market demand (Bentley et al. 2003b). Fishers stated clearly that they were willing to trade some potential catch for stability and abundance goals.

## Management procedure design and evaluation

Evaluation of management strategies since the 1970s (Hilborn 1979) has been called management strategy evaluation (MSE), decision analysis framework, simulated adaptive control analysis, and harvest strategy evaluation. The management procedure approach was developed in South Africa (Butterworth et al. 1997; Cochrane et al. 1998), was adopted by the International Whaling Commission (Kirkwood 1997), and is now widespread.

We have tested management procedures for New Zealand goals, using a variety of harvest control rules, with a simulated feedback system (Fig. 2) (Breen et al. 2003). Many rules develop unstable oscillations; our results suggest that constant-exploitation rate strategies are, relative to others, well-behaved. They also showed that lags between observation and action degrade the performance of harvest control rules. When some catch components are not limited by the rule, such as illegal or recreational catches, catch tends to move from controlled to uncontrolled components, with poor results. This is a serious problem for some areas in New Zealand, where recreational or traditional lobster fishing take considerable catch.

Most harvest control rules rely on a single index of abundance, usually CPUE: an imperfect index that may be affected by changes in seasonal and spatial fishing patterns, may not be a linear index (Hilborn & Walters 1992), and may be inflated by technological change (Caputi et al. 2000). Reliance on CPUE also ignores the wealth of other data and stock assessment results.

In this study, we explore what other information could be used in a management procedure. Especially valuable would be the ability to predict future abundance, which would reduce lags and should improve performance. In Western Australia, puerulus settlement is used as a predictor of future recruitment to the fishery (Phillips et al. 2000). We describe several possible approaches to predicting future abundance: looking at trends in CPUE, pre-recruit indices, puerulus settlement, and size frequencies.

# METHODS

## CPUE indices

For each of the nine QMAs, CPUE was obtained from the mandatory catch and effort returns. These were groomed and standardised using a Generalised Linear Model framework (GLM: McCullagh & Nelder 1989). Statistical area (a smaller unit than QMA), month, year, and vessel were used as explanatory variables.

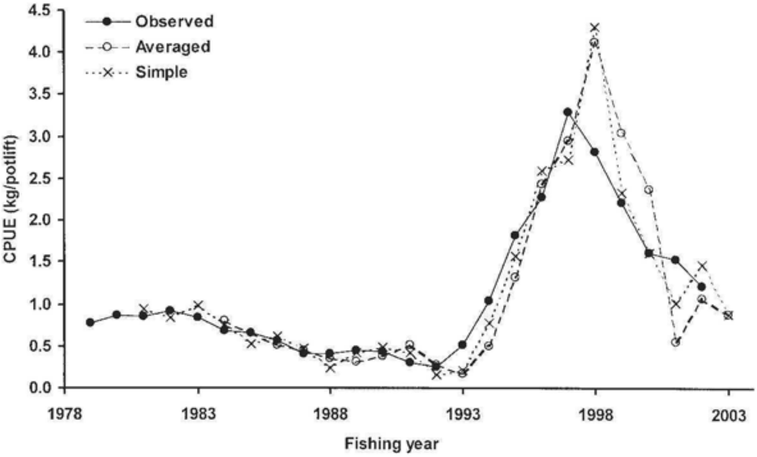


**Fig. 3** Observed CRA 3 catch per unit of effort (CPUE) (filled circles) and CPUE predicted by the simple CPUE trend method (crosses) and the averaged method (open circles).

For most areas (e.g., Fig. 3), CPUE in adjacent years is highly autocorrelated ($r = 0.56–0.96$); this may result from a combination of low annual variation in catchability and fisheries based on several cohorts of recruits, where the effects of annual recruitment variation are smoothed out. This high degree of autocorrelation suggests that it may be possible to predict CPUE based on recent trends.

To test predictive power of CPUE we used two methods, "simple" and "averaged". The first calculates the slope, $\delta_t$, of the CPUE trajectory as the difference in CPUE between years, and predicts future CPUE one year ahead, $\hat{I}_{t+1}$, from the current CPUE, $I_t$, and the slope:

$$\delta_t = I_t - I_{t-1} \qquad (1)$$

$$\hat{I}_{t+1} = I_t + \delta_t = 2I_t - I_{t-1} \qquad (2)$$

The averaged method uses a 3-year running mean of CPUE:

$$\bar{I}_t = \frac{(I_t + I_{t-1} + I_{t-2})}{3} \qquad (3)$$

and calculates the first and second differences of the trajectory:

$$\bar{\delta}_t = \bar{I}_t - \bar{I}_{t-1} = \frac{I_t - I_{t-3}}{3} \qquad (4)$$

$$\varphi_t = \bar{\delta}_t - \bar{\delta}_{t-1} = \frac{I_t - I_{t-1} - I_{t-3} + I_{t-4}}{3} \qquad (5)$$

which are used to predict CPUE in the following year:

$$\hat{I}_{t+1} = \bar{I}_t + 2\bar{\delta}_t + \varphi_t = \frac{4I_t + I_{t-2} - 3I_{t-3} + I_{t-4}}{3} \qquad (6)$$

## Pre-recruit indices

Pre-recruit indices (PRI) were obtained from size data from the combined voluntary logbook and observer catch sampling data sets. For each potlift we determined the number of lobsters below the sex-specific and area-specific size limits. Berried females were not included, because in most areas much of the catch is taken in winter when berried females cannot be taken.

A standardised annual PRI was obtained using depth (treated as a categorical variable in 20 m bins), statistical area, source of the data (logbook or catch sampling), month, and year as explanatory variables. Because many potlifts had no pre-recruits, we used a two-part GLM in which the presence of pre-recruits was regressed against the explanatory variables with a binomial (logit) model. The numbers of pre-recruits in those pots which had pre-recruits was regressed against the same variables with a log-normal model. The two regressions were combined into a single standardised index using the method of Vignaux (1994).

We used a delay-difference model (Deriso 1980; Schnute 1985), tuned with values from the assessment process, to predict CPUE one year ahead from the PRI. This is a simple model based on growth, survival, and recruitment, with a basic premise that biomass in year $t$ is the sum of surviving biomass from year $t-1$, biomass added by growth and biomass of new recruits.

The model assumes that all recruited fish are equally vulnerable to fishing, that natural mortality rate $M$ is constant in time and the same for all recruited fish, and that growth in mean body weight of recruited fish is linear:

$$w_a = \alpha + \rho w_{a-1} \tag{7}$$

where $w_a$ is mean weight at age $a$ and $\alpha$ and $\rho$ are constants. In this description, subscripts for management area are suppressed. The form suggested by Schnute (1987) and Fournier & Doonan (1987) is:

$$B_t = \gamma_{t-1} B_{t-1} + w_R R_t \tag{8}$$

where $B_t$ is the vulnerable biomass in year $t$, $R_t$ and $w_R$ are the number and mean weight of recruits, and $\gamma_{t-1}$ is the growth-survival factor from the previous year:

$$\gamma_{t-1} = \rho A_{t-1} + \frac{A_{t-1}\alpha}{\overline{w}_{t-1}} \tag{9}$$

where $\overline{w}_{t-1}$ is the mean weight of recruited vulnerable lobsters and $A_{t-1} = e^{-M}\,(1-U_{t-1})$ is the survival rate in year $t-1$.

Parameters for each area (Table 1) are based on the most recent assessment for each area. We calculated the annual change in a lobster's weight using the assessment's growth model to calculate the expected weight after 1, 2, 3, 4, and 5 years of growth past the MLS: an example is shown in Fig. 4. From the mean expected weights-at-time-after-recruitment for males and females we regressed $w_{k+t+1}$ on $w_{k+t}$ to estimate $\alpha$ and $\rho$. Growth in weight appears to be linear over this period.

Mean weight of legal-sized lobsters was calculated from logbook and catch sampling data, excluding berried females:

$$\overline{w}_t = \frac{\sum_g \sum_s N_t^{g,s} w^{g,s}}{\sum_g \sum_s N_t^{g,s}} \tag{10}$$

where $N_t^{g,s}$ is the number of lobsters of size $s$ and sex $g$ in year $t$ and $w^{g,s}$ is their mean weight.

We assumed a direct proportionality between CPUE and vulnerable biomass and thus substituted CPUE, $I_t$, for $B_t$ in the delay-difference equation. Exploitation rate $U_t$ was calculated from commercial catch, $C_t$, and the catchability, $q$, estimated in the last assessment for the area:

$$U_t = \frac{C_t q}{I_t} \tag{11}$$

We used the PRI as the basis for recruiting biomass, $R_t$. A coefficient is necessary to scale the PRI to $R_t$ because of pot selectivity (pre-recruits are only partially selected by pots) and growth variability (only some pre-recruits will recruit in 1 year):

$$R_t = \beta^{PRI}\, O_{t-1} \tag{12}$$

where $O_{t-1}$ is the PRI and $\beta^{PRI}$ is estimated (it is the only parameter estimated in this model, although many inputs are estimated by the assessment model). This estimation is made by minimising the least-squares comparison of $I_t$ and $\hat{I}_t$. The revised delay-difference model is:

$$\hat{I}_t = \gamma_{t-1} I_{t-1} + w_R \beta^{PRI}\, O_{t-1} \tag{13}$$

## Puerulus indices

New Zealand puerulus collection has been described by Booth et al. (2001). We developed standardised indices for each area with collectors to reduce the effects of changes in sampling (Bentley et al. 2004a).

Standardisation was based on the number of recent settlers caught in each collector sample. Explanatory variables other than year effect—site, group, collector, and month—were added to the model in a stepwise process, and we used the Akaike Information Criterion to decide when the final model had been reached.

Based on experimentation with a variety of distributions, assumption of Poisson distributed data appears to be appropriate for some areas, but not for areas with a high proportion of zero counts. For some areas, especially where trends differed among sites and where collecting effort had shifted, standardised and raw indices were substantially different; in others they were similar. Error envelopes in some areas with low catch rates of puerulus were very large.

Because growth varies, not all lobsters within a cohort will recruit to the fishery at once. Some juvenile growth information is available from modal progression analysis (McKoy & Esterman 1981; Annala & Bycroft 1985; Breen & Booth 1989), but is not available for all areas and does not have accompanying estimates of growth variability. Thus for each area we assumed an average lag, $k$, between settlement and recruitment, and assumed that 50% of each cohort recruits after the average lag time, 25% recruits 1 year earlier, and 25% 1 year later:

$$R_t = \beta^S\,(0.25 S_{t-k-1} + 0.5 S_{t-k} + 0.25 S_{t-k+1} \tag{14}$$

where $S$ is the standardised puerulus index and $\beta^S$ is estimated as described for $\beta^{PRI}$. This was used to predict CPUE 1 year later using the delay-difference equation as described for pre-recruits (Equation 13).

We assumed different average lags: for CRA 7, we used 3 years, for CRA 3, 4 years, and for the remainder, 5 years. Thus, for CRA 5 it is assumed

**Table 1** Parameters used in calculating parameters for the delay-difference and size-frequency projections models. Assessment sources are: CRA 1 and CRA 2, Starr et al. (2003); CRA 3, Breen et al. (2002); CRA 4 and CRA 5, Kim et al. (2004); CRA 8, Bentley et al. (2001). Parameters for CRA 6 and CRA 9, for which assessments have not been done, were set equal to those for CRA 8 and 1 respectively. (CV, coefficient of variation.)

| Parameters | CRA 1 | CRA 2 | CRA 3 | CRA 4 | CRA 5 | CRA 6 | CRA 7 | CRA 8 | CRA 9 |
|---|---|---|---|---|---|---|---|---|---|
| Logarithm of catchability | –6.87 | –6.92 | –6.05 | –7.63 | –7.63 | –7.90 | –6.50 | –7.90 | –6.87 |
| Size at maximum selectivity (female) | 55.16 | 60.33 | 60.00 | 60.00 | 60.00 | 57.00 | 46.00 | 57.00 | 55.16 |
| Size at maximum selectivity (male) | 53.38 | 53.69 | 52.00 | 54.00 | 54.00 | 54.00 | 46.00 | 54.00 | 53.38 |
| Shape for left-hand selectivity (female) | 3.06 | 5.10 | 8.41 | 20.60 | 20.60 | 10.33 | 5.00 | 10.33 | 3.06 |
| Shape for left-hand selectivity (male) | 7.01 | 3.03 | 2.85 | 19.80 | 19.80 | 19.20 | 5.00 | 19.20 | 7.01 |
| Growth increment at size 50 mm (female) | 4.77 | 4.28 | 3.06 | 1.79 | 1.79 | 3.48 | 3.48 | 3.48 | 4.77 |
| Growth increment at size 50 mm (male) | 3.83 | 3.77 | 1.77 | 1.56 | 1.56 | 1.90 | 1.90 | 1.90 | 3.83 |
| Growth increment at size 80 mm (female) | –0.86 | –0.72 | –1.48 | –0.34 | –0.34 | 1.03 | 1.03 | 1.03 | –0.86 |
| Growth increment at size 80 mm (male) | 0.19 | 0.70 | –0.58 | 0.27 | 0.27 | 1.64 | 1.64 | 1.64 | 0.19 |
| Growth CV (female) | 0.60 | 0.81 | 0.86 | 0.69 | 0.69 | 0.37 | 0.37 | 0.37 | 0.60 |
| Growth CV (male) | 0.28 | 0.43 | 0.86 | 0.69 | 0.69 | 0.37 | 0.37 | 0.37 | 0.28 |
| Growth minimum standard deviation | 1.69 | 2.47 | 1.50 | 0.59 | 0.59 | 1.00 | 1.00 | 1.00 | 1.69 |
| Natural mortality rate *M* | 0.180 | 0.140 | 0.280 | 0.137 | 0.137 | 0.098 | 0.098 | 0.098 | 0.180 |
| Size at 50% maturation rate | 48.9 | 54.4 | 45.7 | 52.8 | 52.8 | 61.9 | 61.9 | 61.9 | 48.9 |
| Size difference between 50 and 95% maturity | 11.0 | 11.0 | 5.9 | 11.6 | 11.6 | 8.0 | 8.0 | 8.0 | 11.0 |
| Intercept for female length-weight | 1.30E-05 | 1.30E-05 | 1.30E-05 | 1.00E-05 | 1.00E-05 | 1.00E-05 | 1.04E-05 | 1.04E-05 | 1.30E-05 |
| Intercept in male length-weight | 4.16E-06 | 4.16E-06 | 4.16E-06 | 4.00E-06 | 4.00E-06 | 1.00E-05 | 3.39E-06 | 3.39E-06 | 4.16E-06 |
| Slope in female length-weight | 2.545 | 2.545 | 2.545 | 2.545 | 2.545 | 3.000 | 2.632 | 2.632 | 2.545 |
| Slope in male length-weight | 2.935 | 2.935 | 2.935 | 2.935 | 2.935 | 3.000 | 2.967 | 2.967 | 2.935 |

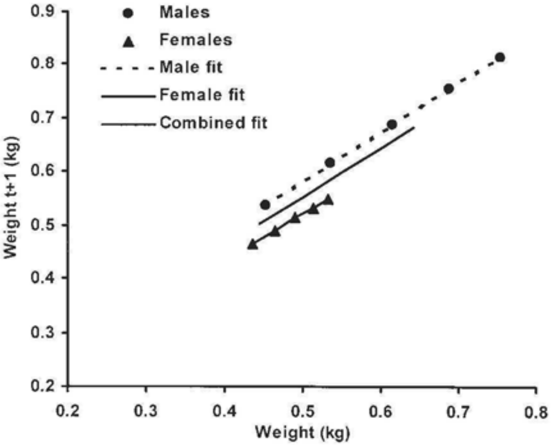


**Fig. 4** Growth in weight for CRA 3 lobsters (*Jasus edwardsii*) based on estimated tail width growth parameters and tail width-to-weight parameters (Table 1).

that 25% of settlers recruit to the fishery in 4 years, 50% in 5 years, and 25% in 6 years. Because there is uncertainty in these lags, for each area we also examined alternative lags by adding and subtracting 1 year from these lags.

### Size-frequency projections

This approach was similar to that of the delay-difference model but involved more detailed information on lobster size, growth, and vulnerability to fishing. Observed size frequencies were projected forward one year using the dynamics of the assessment model (Starr et al. 2003) and predicting change in CPUE from the size and sex structure of the fished population. Parameters used are shown in Table 1.

For this method, the time step was 6 months, but for simplicity we show equations as if the time step was 1 year. The sex and size structure of the fished population can be derived from catch sampling data by adjusting for the selectivity of the fishing gear:

$$N_0^{g,s} = \frac{P_0^{g,s}}{T^{g,s}} \tag{15}$$

where $N_0{}^{g,s}$ is the relative number of sex $g$ and size $s$ at $t = 0$, $T^{g,s}$ is the relative selectivity, and $P_0{}^{g,s}$ is the observed proportion-at-size. When $T^{g,s}$ is small, a few observed individuals translate to a very large number in the population, so $T^{g,s}$ was restricted to 0.05 and greater.

This population structure is projected forward one year under assumptions about growth, maturation, natural mortality, and fishing mortality (see Starr et al. 2003). The growth transition matrix is calculated by the assessment model for each sex based on the growth parameters for each sex.

For males the population after growth and natural mortality is:

$$\dot{\mathbf{N}}_{t+1}^{1} = \mathbf{N}_{t+1}^{1}\mathbf{G}^{1}\, e^{-M} \tag{16}$$

where $\mathbf{N}_{t+1}^{1}$ and $\dot{\mathbf{N}}_{t+1}^{1}$ are the vectors of male numbers-at-size before and after growth and mortality respectively, and $\mathbf{G}^1$ is the growth transition matrix for males. For females, maturation is addressed:

$$\dot{\mathbf{N}}_{t+1}^{2} = \mathbf{N}_{t}^{2}\,(1\text{–}\mathbf{Q})\mathbf{G}^{2}\, e^{-M} \tag{17}$$

$$\dot{\mathbf{N}}_{t+1}^{3} = (\mathbf{N}_{t}^{3} + \mathbf{N}_{t}^{2}\mathbf{Q})\mathbf{G}^{3}\, e^{-M} \tag{18}$$

where the superscripts 2 and 3 index immature and mature females respectively and $\mathbf{Q}$ is the maturation vector. For simplicity, handling mortality and non-commercial catches are ignored.

Exploitation rate, $U_t$, is calculated as in Equation 11. For each area, $q$ was estimated by minimising the mean relative error of the CPUE predictions (see below). Mature females are assumed to be ovigerous and thus invulnerable in autumn and winter period. We used the proportion of the catch taken in spring and summer to adjust the relative vulnerability of mature females.

$$V_t^{1,s} = \begin{cases} 0 & l^s < L_1 \\ 1 & l^s \geq L_1 \end{cases} \quad V_t^{2,s} = \begin{cases} 0 & l^s < L_2 \\ 1 & l^s \geq L_2 \end{cases}. \quad V_t^{3,s} = \begin{cases} 0 & l^s < L_2 \\ Y_t & l^s \geq L_2 \end{cases} \tag{19}$$

where $l^s$ is length indexed by $s$, $L_g$ is the MLS for sex $g$, and $Y_t$ is the proportion of the catch taken during spring and summer. The population size structure in the following year is then predicted by applying fishing mortality:

$$N_{t+1}^{g,s} = \dot{N}_t^{g,s}\left(1 - U_t V_t^{g,s}\right) \tag{20}$$

Based on the relative numbers in each sex and size class the relative vulnerable biomass at $t$+1 can be calculated:

$$B_{t+1} = N_{t+1}^{g,s} w^{g,s} V_{t+1}^{g,s} \tag{21}$$

$B_{t+1}$ is only a relative index of vulnerable biomass because $N$ is originally derived from proportions-at-size, rather than number-per-potlift-at-size, but the change in relative vulnerable biomass can be used to predict the change in CPUE:

$$\hat{I}_{t+1} = I_t \frac{B_{t+1}}{B_t} \tag{22}$$

Predicted proportions-at-size can also be calculated from numbers-at-size:

$$\hat{P}_t^{g,s} = \frac{N_t^{g,s}}{\sum_{g=1}^{g=3}\sum_{s=1}^{s=31} N_t^{g,s}} \qquad (23)$$

### Comparing predicted and observed CPUE

For each of the methods described above, CPUE trends, pre-recruit indices, puerulus indices, and size-frequency projections, we summarised the predicted versus observed CPUE vectors with three statistics. The mean relative error (MRE), as a percentage, is:

$$\%MRE = \left(\frac{100}{n}\right) \sum_{t=1}^{n} \left| \frac{\hat{I}_t - I_t}{I_t} \right| \qquad (24)$$

where $n$ is the number of years of data. A "baseline" MRE was calculated for each area by predicting, for all years, $\hat{I}_{t+1} = I_t$ (i.e., that CPUE next year will be the same as this year). This produces an MRE between 12% and 32% (Table 2). A useful prediction method should at least provide lower MREs than this. Second, average relative bias is:

$$Bias = \left(\frac{100}{n}\right) \sum_{t=1}^{n} \frac{\hat{I}_t - I_t}{I_t} \qquad (25)$$

Third, the direction success rate statistic (DSR) measures the tendency of predictions to change in the correct direction, i.e., whether the predicted and observed values both increased or decreased:

$$DSR = \left(\frac{1}{n}\right) \sum_{t=1}^{n} \left( \begin{array}{l} 100 \left( I_{t+1} < I_t \text{ and } \hat{I}_{t+1} < I_t \right) \\ 0 \left( I_{t+1} < I_t \text{ and } \hat{I}_{t+1} > I_t \right) \end{array} \right.$$

$$\left. \begin{array}{l} \text{or} \left( I_{t+1} > I_t \text{ and } \hat{I}_{t+1} > I_t \right) \\ \text{or} \left( I_{t+1} > I_t \text{ and } \hat{I}_{t+1} < I_t \right) \end{array} \right) \qquad (26)$$

For this indicator a perfect score would be 100; a random process would give a score near 50.

For the delay-difference predictions from the PRI and puerulus indices, the MRE statistic was tested for significance with a randomisation test. We generated 500 series of random numbers by sampling from a lognormal distribution with the same mean and standard deviation as the PRI or puerulus index. For each of the 500 series we ran the delay-difference model, including estimating $q$, calculated the MRE and compiled the distribution of the random-index MREs. Each MRE was compared with the distribution of the random-index MREs and its percentile calculated (MREP). A percentile less than 5% indicates that the observed index predicted CPUE better than 95% of the random series, and suggests that the observed index contains information about recruitment. This test does not measure the performance of the delay-difference method itself but provides a way of comparing indices used by the method.

For the DSR statistic, the direction success probability (DSP) is the binomial probability of the DSR given a sample size of $n$ and a $P$ of 0.5. A DSP less than 0.05 indicates that the directions of predictions were significantly better than they would be from a random process.

## RESULTS

### CPUE indices

Nearly all MREs from both the simple and averaged methods were higher than the baseline MRE (Table 2). The DSR for both methods was low, between 40.9% and 68.2%, and was not significantly higher than 50% in any area. There was little systematic difference between the simple and averaged methods.

Both the CPUE trend methods performed adequately when CPUE had followed a consistent trend of decline or increase for several years (e.g., Fig. 3). But neither method was able to predict sudden changes in trend (e.g., 1997 in CRA3, Fig. 3).

These results suggest that CPUE cannot be predicted one year ahead from recent CPUE trends.

### Pre-recruit results

CPUE predicted from the PRI with the delay-difference method is illustrated for CRA 3 in Fig. 5: in this example, the direction of change of CPUE is correctly predicted, although the magnitude of change is often underestimated. The low percentile of the actual MRE in the randomised distribution means the result is significant for this area.

For four of the six areas with PRIs (Table 2), the MRE was lower than the baseline MRE, and in three areas (CRA 2, 3, and 7) the MRE was significant. Bias was small in all areas. The DSR was higher than 50% in all areas, ranging from 56% to 100%, and the DSP was significant in CRA 2, 3, and 7.

**Table 2** Prediction statistics for 1-year catch per unit of effort (CPUE) predictions made from CPUE trends, delay-difference, and size-frequency projection methods for each CRA area. (MRE, mean relative error; MREP, mean relative error randomisation probability; DSR, direction success rate; DSP, direction success binomial probability.) Bold indicates results significant at the 0.05 level before the Bonferroni correction is made. For each CRA area, the method with the lowest MRE less than the baseline MRE is italicised.

| Area | Method | Lag | %MRE | MREP | %Bias | %DSR | DSP |
|---|---|---|---|---|---|---|---|
| CRA 1 | Baseline | – | 11.1 | – | – | – | – |
| | CPUE Simple | – | 15.7 | – | 1.3 | 40.9 | 0.857 |
| | CPUE Averaged | – | 12.8 | – | –10.4 | 57.9 | 0.324 |
| CRA 2 | Baseline | – | 15.8 | – | – | – | – |
| | CPUE Simple | – | 20.5 | – | 0.3 | 59.1 | 0.262 |
| | CPUE Averaged | – | 20.5 | – | –12.8 | 52.6 | 0.500 |
| | *Delay-diff pre-recruit* | – | 13.1 | **0.002** | –3.5 | 100.0 | **0.002** |
| | Size-frequency | – | 20.4 | – | – | 66.7 | 0.254 |
| CRA 3 | Baseline | – | 21.6 | – | – | – | – |
| | CPUE Simple | – | 21.8 | – | –2.1 | 68.2 | 0.067 |
| | CPUE Averaged | – | 28.5 | – | –12.1 | 57.9 | 0.324 |
| | *Delay-diff pre-recruit* | – | 10.2 | **0.004** | –1.3 | 100.0 | **0.002** |
| | Delay-diff puerulus | 3 | 14.9 | 0.100 | 3.1 | 88.9 | **0.020** |
| | Delay-diff puerulus | 4 | 20.9 | 0.530 | 4.6 | 88.9 | **0.020** |
| | Delay-diff puerulus | 5 | 24.5 | 0.816 | 6.1 | 77.8 | 0.090 |
| | Size-frequency | – | 23.6 | – | – | 55.6 | 0.500 |
| CRA 4 | Baseline | – | 10.8 | – | – | – | – |
| | CPUE Simple | – | 9.8 | – | –1.2 | 54.5 | 0.416 |
| | CPUE Averaged | – | 14.0 | – | –10.7 | 52.6 | 0.500 |
| | Delay-diff pre-recruit | – | 11.8 | 0.192 | 2.3 | 66.7 | 0.254 |
| | *Delay-diff puerulus* | 4 | 7.0 | **0.008** | –0.3 | 77.8 | 0.090 |
| | Delay-diff puerulus | 5 | 7.6 | **0.024** | 0.6 | 77.8 | 0.090 |
| | Delay-diff puerulus | 6 | 11.9 | 0.198 | 2.8 | 77.8 | 0.090 |
| | Size-frequency | – | 16.8 | – | – | 55.6 | 0.500 |
| CRA 5 | Baseline | – | 13.8 | – | – | – | – |
| | CPUE Simple | – | 15.1 | – | –0.7 | 54.5 | 0.416 |
| | CPUE Averaged | – | 14.6 | – | –13.4 | 52.6 | 0.500 |
| | Delay-diff pre-recruit | – | 16.4 | 0.442 | –2.0 | 77.8 | 0.090 |
| | Delay-diff puerulus | 4 | 16.2 | 0.404 | 8.3 | 44.4 | 0.746 |
| | Delay-diff puerulus | 5 | 21.2 | 0.868 | 13.1 | 22.2 | 0.980 |
| | Delay-diff puerulus | 6 | 25.9 | 0.988 | 17.4 | 22.2 | 0.980 |
| | *Size-frequency* | – | 10.8 | – | – | 88.9 | **0.020** |
| CRA 6 | Baseline | – | 9.5 | – | – | – | – |
| | CPUE Simple | – | 15.1 | – | –0.3 | 50.0 | 0.584 |
| | CPUE Averaged | – | 12.7 | – | –10.5 | 42.1 | 0.820 |
| CRA 7 | Baseline | – | 33.6 | – | – | – | – |
| | CPUE Simple | – | 44.0 | – | 0.2 | 68.2 | 0.067 |
| | CPUE Averaged | – | 59.8 | – | –13.4 | 47.4 | 0.676 |
| | *Delay-diff pre-recruit* | – | 20.3 | **0.020** | –0.9 | 88.9 | **0.020** |
| | Delay-diff puerulus | 3 | 25.7 | 0.396 | 4.8 | 44.4 | 0.746 |
| | Delay-diff puerulus | 4 | 28.2 | 0.952 | 5.1 | 44.4 | 0.746 |
| | Delay-diff puerulus | 5 | 30.1 | 0.996 | 4.8 | 33.3 | 0.910 |
| | Size-frequency | – | 22.5 | – | – | 44.4 | 0.746 |
| CRA 8 | Baseline | – | 12.8 | – | – | – | – |
| | CPUE Simple | – | 18.7 | – | –0.8 | 50.0 | 0.584 |
| | CPUE Averaged | – | 19.3 | – | –11.5 | 42.1 | 0.820 |
| | *Delay-diff pre-recruit* | – | 10.6 | 0.626 | 2.7 | 55.6 | 0.500 |
| | Delay-diff puerulus | 4 | 10.9 | 0.674 | 4.1 | 55.6 | 0.500 |
| | Delay-diff puerulus | 5 | 12.9 | 0.906 | 5.4 | 33.3 | 0.910 |
| | Delay-diff puerulus | 6 | 13.7 | 0.950 | 5.3 | 33.3 | 0.910 |
| | Size-frequency | – | 21.5 | – | – | 55.6 | 0.500 |
| CRA 9 | Baseline | – | 13.6 | – | – | – | – |
| | CPUE Simple | – | 22.3 | – | –0.3 | 27.3 | 0.992 |
| | CPUE Averaged | – | 15.5 | – | –11.9 | 52.6 | 0.500 |

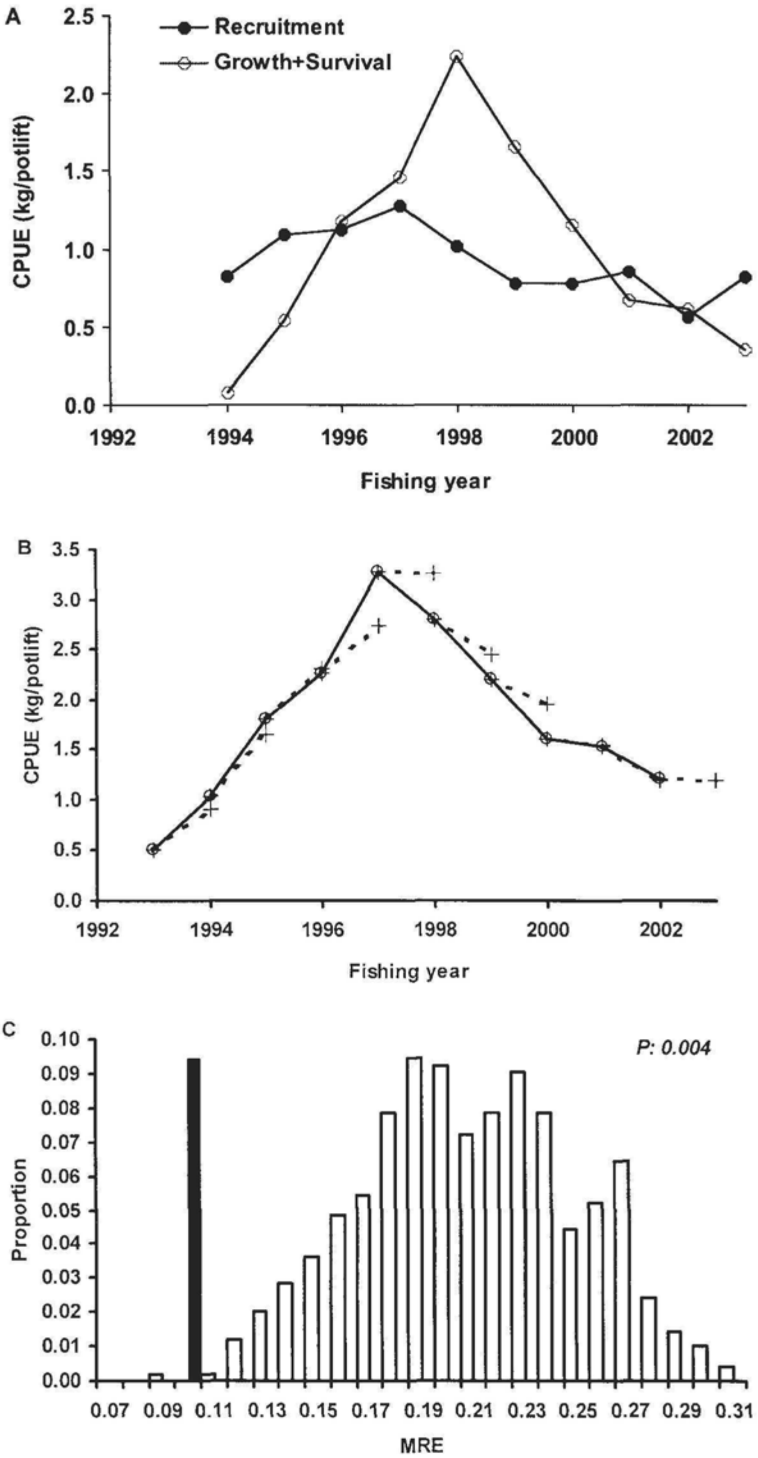
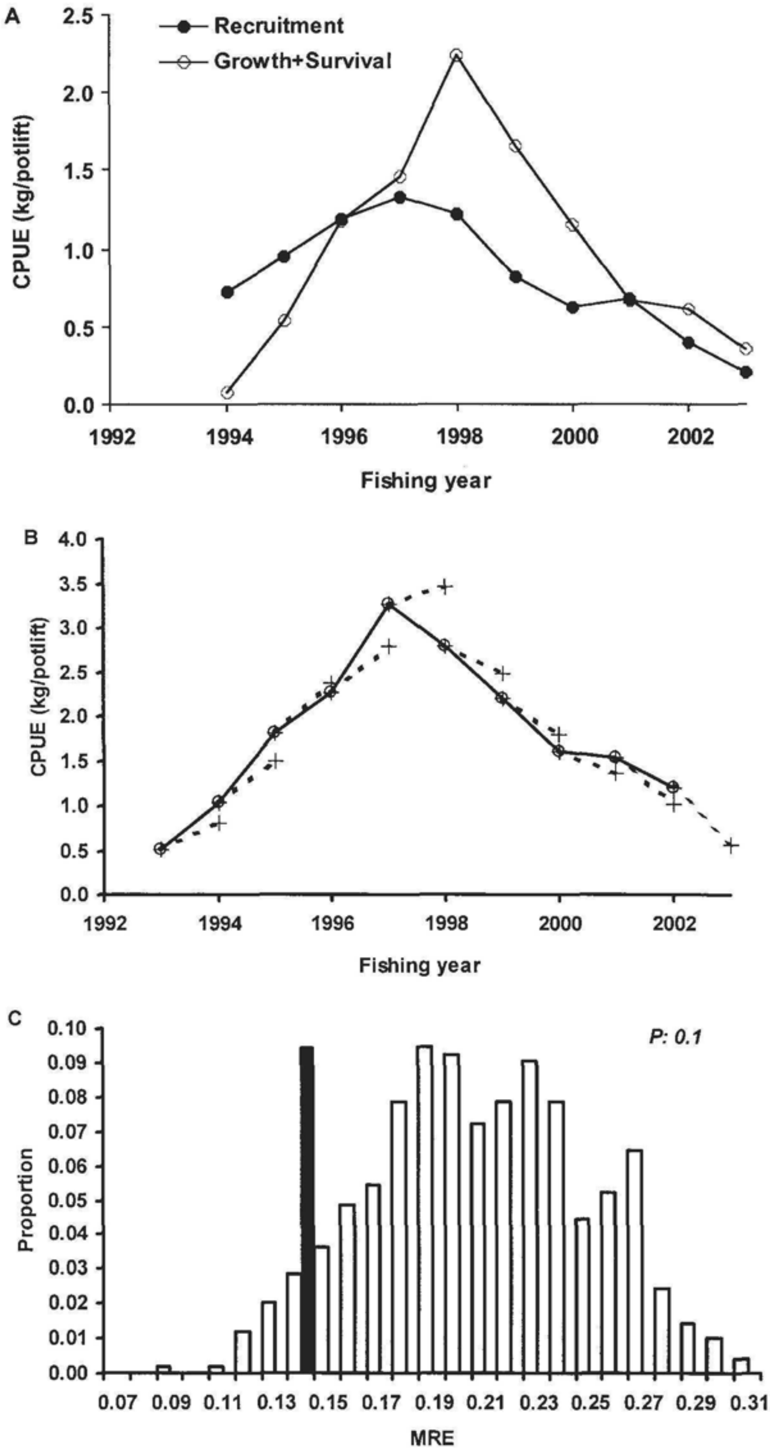


**Fig. 5** Results from the delay-difference method for CRA 3 using pre-recruit index. **A**, Estimated growth plus survival (open circles) and recruitment contributions (closed circles) to catch per unit of effort (CPUE). **B**, observed (open circles) and predicted (crosses) CPUE. **C**, Frequency distribution of mean relative errors (MREs) from 500 random pre-recruit indices (open bars) and the MRE obtained with the actual pre-recruit index (solid bar) (*P* shows the percentile of the actual MRE).

**Fig. 6** Results from the delay-difference method for CRA 3 using the puerulus index. **A**, Estimated growth plus survival (open circles) and recruitment contributions (closed circles) to catch per unit of effort (CPUE). **B**, Observed (open circles) and predicted (crosses) CPUE. **C**, Frequency distribution of mean relative errors (MREs) from 500 random pre-recruit indices (open bars) and the MRE obtained with the actual pre-recruit index (black bar) (*P* shows the percentile of the actual MRE).



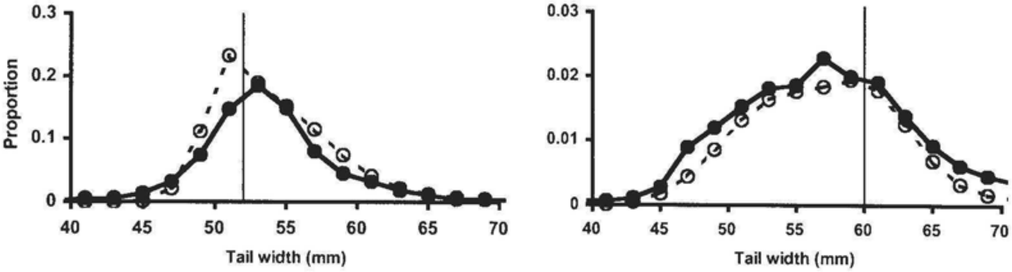


**Fig. 7** Example of observed (closed circles) and projected (open circles) proportions-at-size: CRA 3 in 1998. Left: males, right: mature females; immature females are not shown because their proportions are very low. Vertical lines indicate the minimum legal size.

These results suggest that pre-recruit indices contain information that can be used to predict CPUE one year ahead in three of the six areas with PRI data.

### Puerulus indices

CPUE predicted for CRA 3 using the puerulus indices with a 3-year lag (Fig. 6) shows, as for the PRI index, that direction of change is predicted correctly for all but one year, but the magnitude is underestimated for much of the series. The 3-year lag gave the best results for CRA 3 (Table 2).

The MREs were better than the baseline in some areas (e.g., CRA 7) but not in others (CRA 5). The MREs were significant for the 4- and 5-year lags in CRA 4, but not in other areas. Bias was <6% except for CRA 5, where it peaked at 17%. DSRs were >50% in some areas, lower in others, ranging from 22% to 89%. These were significant in CRA 3 for both the 3- and 4-year lags.

Because three different values are assumed for lag in each area, the chance of rejecting the null hypothesis when it is true is higher than 0.05 for the puerulus indices. The Bonferroni correction reduces the critical value for hypothesis testing based on the number of related comparisons, *m*:

$$\alpha' = 1 - (1-\alpha)^{(1/m)} \qquad (27)$$

where $\alpha$ is the desired risk and $\alpha'$ is the new critical value. With three trials the critical value is 0.017. Thus only the MREP for a 4-year lag in CRA 4 is significant.

### Size-frequency projections

Projected size structure was often similar to that observed: an example from CRA 3 is shown for males in Fig. 7 (we are concerned only with those sizes above the MLS), but CPUE predictions were not very accurate (Fig. 8).

MREs were smaller than baseline values only in CRA 5 and 7; these were not significant (Table 2). DSRs were higher than 50% except in CRA 7; the highest was 89% for CRA 5, which was significant.

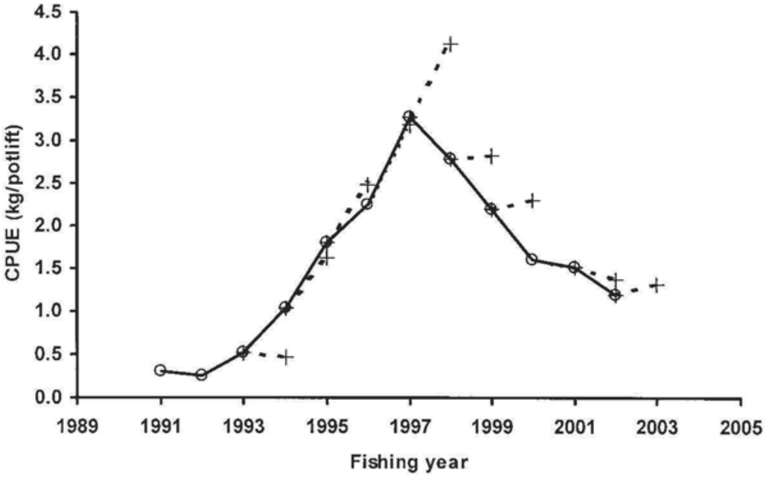
Thus for CRA 5 the MRE was lower than baseline and the DSR was significant, suggesting that the size-frequency data and assessment model contained information for this area. However, the method showed little promise for other areas.

## DISCUSSION

In this study we explored the information content of four data sets with respect to making 1-year predictions of CPUE. A common approach is to calculate the correlation between index and future CPUE, with appropriate lags (e.g., Gardner et al. 2001 for puerulus indices). That implicitly assumes that annual recruitment to the fishery is the main determinant of abundance. In most New Zealand rock lobster fisheries, several cohorts contribute to the vulnerable biomass and changed levels of catch may also have strong effects on abundance: decreases in catch quotas allow stock to remain in the water and to increase abundance.

In a previous study (Bentley et al. 2004b), we addressed this by using the assessment model in two ways to explore the utility of incorporating puerulus and climatic indices. Estimates of annual recruitment to the model were compared with the indices with appropriate lags, and we used the indices to drive a simplified model, then compared the model's fit with a randomised fit distribution. In that study, we could not find any significant relation between those indices and the assessment model results.

**Fig. 8** Observed catch per unit of effort (CPUE) in CRA 3 (open circles) and CPUE predicted (crosses) by the size-frequency projection method.



For puerulus and pre-recruit indices this study used the delay-difference equation, which is much simpler than the assessment model, but which still accounts for changes in catch and carry-over in abundance that are ignored by the correlation method. Only the PRI index showed substantial promise for predicting CPUE one year ahead.

Predictions made from the PRI index were significant, for both the MRE and DSR statistics, in three of the six areas with data and gave the best reduction of MRE in a fourth. This result suggests that the PRI could be used to improve the performance of harvest control rules in at least those areas. Pre-recruit indices have also been used to improve catch predictions in Western Australia (Caputi et al. 1995; Phillips et al. 2000). This study used all lobsters below the MLS as an index of pre-recruit abundance. Further work will be done to examine whether a more limited size range definition provides a better index.

Predictions based on the puerulus index were significant, for different diagnostic statistics, in two areas but had uneven performance in the rest. This result is disappointing in light of the high apparent predictive ability of puerulus in Western Australia (Phillips et al. 2000) and Tasmania (Gardner et al. 2001). There are several possible reasons for this result. The puerulus indices may be imprecise through natural and sampling variability. Survival or growth may vary among cohorts, weakening the puerulus-recruit relation. The period between settlement and recruitment to the fishery is 3–4 years in Western Australia (Caputi et al. 1995), but may be longer in New Zealand (Booth et al. 2001), increasing the time during which growth and survival variability can dampen the relationship. Density-dependence of growth or survival would also tend to attenuate any signal provided by puerulus indices.

Uncertainty in the rate and variability of growth between settlement and recruitment to the fishery is a serious problem for using puerulus indices. In this study we used multiple lags and a distribution of time to recruitment around each lag. It seems likely that puerulus cohorts recruit over several years. Bentley et al. (2004b) used modal progression of juvenile lengths (Annala & Bycroft 1985; Booth & Breen 1989 for CRA 8; McKoy & Esterman 1981 for CRA 3), combined with tag-recapture estimates of growth variability, to estimate that most lobsters recruited over 4 years, with stragglers over a larger range.

By contrast, pre-recruits become recruits in only 1–2 years, giving a more immediate signal than is possible with puerulus indices. The best available information on growth of New Zealand rock lobsters is for pre-recruits, with thousands of tag recaptures available from many areas (e.g., Starr et al. 2003). These data provide greater certainty on what proportion of pre-recruits will recruit in each subsequent year.

Although CPUE series have high auto-correlation, CPUE trends appear to have little information about the direction of change for the next year. It is unlikely that control rules can be improved by incorporating estimates of the recent slope in any simple way.

Although size frequencies could be used to predict proportions-at-size one year ahead, these predictions did not translate successfully into CPUE predictions. This method may be too sensitive to variations in proportions-at-size caused by sampling variation; it may magnify the variations when projecting the size-frequency distribution ahead. Further, this method is very complex, which would probably limit its utility for use in control rules.

Further work is in progress to incorporate PRIs into simulated management procedures. Based on the simple delay-difference results reported here, we expect behaviour of these procedures to improve. The delay-difference method is a good compromise between simplicity and realism: there is also room for experimentation to introduce more biological detail by addressing the different vulnerabilities and growth rates of the sexes. By separating changes in CPUE into recruitment versus growth and survival components, the delay-difference approach also provides a clear way of explaining to stakeholders the causes of recent changes in their stock.

## ACKNOWLEDGMENTS

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# Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery

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**Abstract** The American lobster, *Homarus americanus*, is the most important fishery in the north-east United States. Over the last 20 years, the Collie-Sissenwine (catch-survey) model has been used in estimating fishing mortality in the fishery. This is then compared with a biological reference point derived from an egg-per-recruitment model for determining the status of the stock. However, the complexity of the fishery and population biology for American lobster, data limitations, and uncertainty about underlying parameters call for the development of stock assessment models with more biological detail. Complex and simple modelling approaches are complementary and both are likely to remain useful for such an important and complex fishery. The objective of this study is to develop a size-structured stock assessment model for the American lobster. The proposed stock assessment model includes a set of size-structured, seasonal, and sex-specific population dynamics models and a statistical approach incorporating data of different sources. Using a fishery simulation based on the information on the lobster fishery in the Gulf of Maine, we evaluated the performance of the proposed model in the presence of biased errors in various model variables. This study suggests that the proposed stock assessment model performs well in retrieving the population dynamics of the simulated lobster and is rather robust to the biased errors in growth, fishing selectivity, and landings. Future studies need to focus on the evaluation of the model performance under different scenarios with both biased and random errors.

**Keywords** *Homarus americanus*; size-structured model; biased error, simulation; Gulf of Maine

## INTRODUCTION

The American lobster, *Homarus americanus*, supports the most valuable commercial fishery in the north-east United States (NEFSC 1996; Steneck & Wilson 2001). The majority of landings have occurred in the state of Maine. The Maine landings have increased steadily since the early 1970s and fishing effort is intense (Fig. 1). Currently, the American lobster fishery is assessed using the Collie-Sissenwine (catch-survey) model which estimates fishing mortality from catch and an abundance index derived from the National Marine Fisheries Service (NMFS) trawl survey programme (Collie & Sissenwine 1983; Conser 1995; NEFSC 1996). The status of the fishery is then determined by comparing the estimated fishing mortality with the biological reference point $F_{10\%}$ which is the rate of the fishing mortality that reduces the expected egg production for a cohort of female lobsters to 10% of that produced in the absence of a fishery and is estimated from an egg-per-recruit model (Fogarty & Idoine 1988).

Previous assessments had suggested that the stock had been over-exploited for the last 20 years and had been vulnerable to collapse (NEFSC 1995; Chen & Wilson 2002). Many studies and field observations, however, suggested that recruitment into the fishery, total potential egg production, and stock abundance had increased in recent years. The complexity of the fishery and population biology for American lobster

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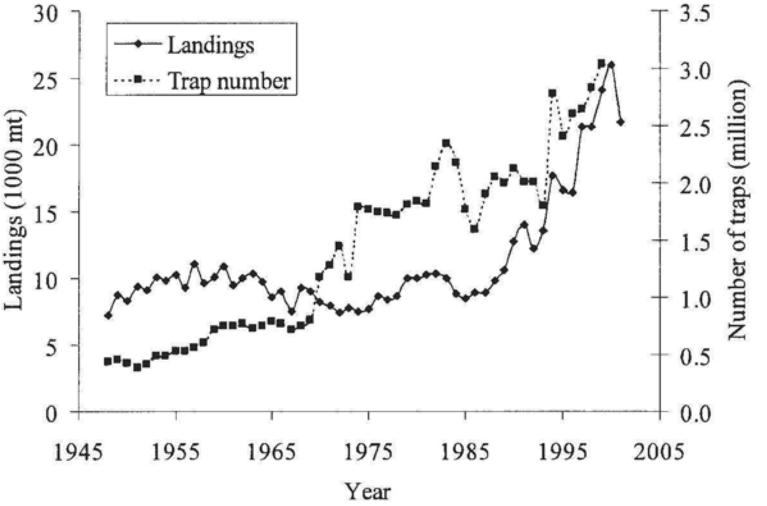


**Fig. 1** American lobster (*Homarus americanus*) fishery history in Maine, United States.

and uncertainty about underlying population dynamics and stock status called for the development of alternative approaches to assessing the lobster fishery (e.g., ASMFS 2000). The development of biologically detailed stock assessment models seems desirable. This is also consistent with the recent calls by National Research Council (NRC) (1997, 1999) for applying multiple stock assessment models of different complexities in assessing fisheries resources.

The objective of our study is to develop a size-structured stock assessment model for the American lobster. This paper includes two components: (1) the description of the proposed size-structured stock assessment model; and (2) evaluation of the performance of the proposed model using a simulated fishery based on the information from the Gulf of Maine lobster fishery in the presence of biased errors in different variables of input data.

## METHODS AND MATERIALS

The proposed model is part of the Bayesian stock assessment framework developed for the lobster fishery (Fig. 2) which includes four components: (1) a size-structured population model describing the dynamics of the lobster population; (2) input data including fishery-dependent and fishery-independent data; (3) a Bayesian estimator which fits the population model to data for estimating key parameters for the lobster population and fishery; and (4) a decision-making component which uses posterior distributions derived in the Bayesian analysis for determining the status of the stock and for risk analyses and exploration of alternative management strategies. This study deals with the first component, the size-structured population model and part of the 2nd (i.e., input data except for priors) and 3rd components (i.e., likelihood function). The AD Model Builder was used to code the model which is detailed below.

### Size-structured stock assessment model

The stock assessment model developed in this study includes a stochastic size-structured, sex-specific model describing the dynamics of the lobster population and fishery (referred to as population dynamics model) and a series of observational models used to relate the population dynamics models to observations made in surveys and fishery. The population dynamics model includes a series of submodels describing various processes of the lobster life history and fishery. The modelling time step is a season, starting from spring (April–June) and ending in winter of the next year (January–March). The key submodels are described below.

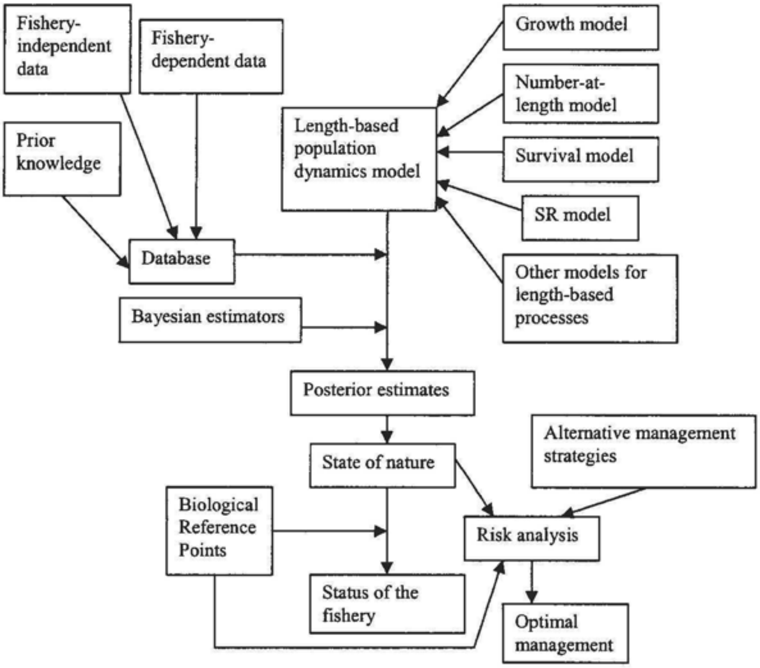
#### *Recruitment model*

Because of a lack of information, we assume no functional relationship between spawning stock biomass (SSB) and subsequent recruitment (Sheehy 2001). We estimate an average recruitment for all the years considered in the assessment ($\bar{R}$), and thus the recruitment of a given year can be estimated as:

$$R_t = \bar{R}\ \exp(R_{dev_t} - 0.5\sigma^2_{R_t}) \qquad (1)$$

where $R_t$ is the recruitment for year $t$, $R_{dev_t}$ is the recruitment deviation from the mean value for year $t$ and can be calculated as:

**Fig. 2** Flowchart of the proposed Bayesian stock assessment framework.



$$R_{dev_t} = \sqrt{R_h}\, R_{dev_{t-1}} + \sqrt{1 - R_h}\ eps_t \tag{2}$$

and $\sigma_{R_t}$ is the standard deviation of the estimated recruitment for all the years included in the assessment, and $eps_t$ describes the part of the variation in $R_t$ with other part described by $R_{dev_{t-1}}$ of previous year. The relative contribution of $eps_t$ and $R_{dev_{t-1}}$ in describing the variation in $R_t$ depends on $R_h$ (Breen et al. 2000). The mean values of $eps_t$ should approach zero. Parameter $R_h$ is an autocorrelation coefficient describing the degree of autocorrelations of recruitment of one year with the recruitment of previous year. Its values range from 0 to 1, respectively, indicating no autocorrelation and perfect autocorrelation of the recruitment in years $t$ and $t$–1. Negative autocorrelation of the recruitment in years $t$ and $t$–1 is not likely, thus not considered. For a given fishing year, recruitment occurs in summer and autumn, associated with major and minor moulting events respectively. The minor moulting occurs to a defined (33%; ASMFC 2000) proportion of small individuals that have their second moult after the major moult.

### Modelling population dynamics

The lobster fishery started in 1800, but reliable information is not available from the early stage of the fishery. Thus we cannot model the lobster population dynamics from the time when they can be treated as a virgin population. We need to include parameters that describe size composition of the lobster stock in the first year defined in the assessment ($p^i_{k,1}$) and initial population size ($N^i_1$), where $i$ indicates sex and $k$ indexes size class. These parameters defining the size-specific abundance of the initial year in the assessment need to be estimated. Thus, the number of lobsters in size class $k$ in the first assessment season (i.e., spring, 1st year) can be calculated as:

$$N^i_{k,1} = p^i_{k,1} N^i_1 \tag{3}$$

Thirty-five size classes are defined, starting from 53 mm carapace length (CL) with a width of 5 mm. We used CL of 53 mm as the starting size of the 1st size class to let the starting value of the 7th size class be 83 mm which is the minimum legal size. The choice of 5 mm for size-class width is determined by the minimum moulting increment (6 mm; ASMFC 2000). Without sex-specific natural mortality before the first size class, we assume a sex ratio of recruitment to the model of 0.5. The recruitment, defined as all the lobster entering into the first three size classes in a given year, is equally divided among the first three size classes, considering the maximum increment in a moult can reach 16 mm. Thus, we have:

$$N^f_{1,t} = N^m_{1,t} = N^f_{2,t} = N^m_{2,t} = N^f_{3,t} = N^m_{3,t} = \frac{R_t}{6} \tag{4}$$

The recruits only come into the fishery in summer when the major moult occurs and in autumn when the double moult (i.e., lobsters that moult in summer moult again in the following autumn) occurs.

The pre-season total biomass, $B_t^{total,i}$, and pre-season legal biomass, $B_t^{legal,i}$, in year $t$ for sex $i$ can be estimated as:

$$B_t^{total,i} = \sum_k N_{k,t}^i w_k^i \tag{5A}$$

$$B_t^{legal,i} = \sum_k N_{k,t}^i P_{k,t}^i w_k^i \quad i \in \{\mathrm{f}, \mathrm{m}\} \tag{5B}$$

where $w_k^i$ is the weight of the lobster in size $k$, and $P_{k,t}$ is a switch (0 for size classes below the minimum legal size or above the maximum legal size, and 1 for legal size classes). The exploitation rate, $U_t^i$, can then be calculated as:

$$U_t^i = \frac{LC_t^i}{B_t^{legal,i}} \quad i \in \{\mathrm{f}, \mathrm{m}\} \tag{6}$$

where $LC_t^i$ is the landings in year $t$ observed in the fishery. No size impact is considered in calculating the overall exploitation rate using Equation 6. If this exploitation rate is used for each size class, it implicitly assumes that the fishing effort is uniformly applied to lobsters of all sizes. This assumption is rather unrealistic because the spatial distribution of lobsters tends to be size-dependent and/or fishing effort is targeted to and selective for certain sizes of lobsters. Thus, we need to estimate size-specific exploitation rates.

The following approach was used for estimating size-specific exploitation rate $U_{k,t}^i$. Taking into consideration various size-specific selectivity processes, the overall selectivity for lobsters of size $k$ in time $t$, $S_{k,t}^i$, can be estimated as:

$$S_{k,t}^i = S_{k,t}^{gear,i}(1 - S_{k,t}^{cons,i}) S_k^{other} P_{k,t} \quad i \in \{\mathrm{f}, \mathrm{m}\} \tag{7}$$

where $S_{k,t}^{gear,i}$ is the gear selectivity coefficient describing the proportion of lobster in size $k$ time $t$ encountering and then retained in traps, $S_{k,t}^{cons,i}$ is the selectivity resulting from the conservation measures such as V-notching and protection of egg-bearing lobsters (ASMFC 2000) and describes the proportion of the lobsters in size $k$, sex $i$, and time $t$ caught in traps, but thrown back to waters because of the conservation measures, and $S_k^{other}$ is the selectivity resulting from reasons other than gear selectivity, conservation measures, and legal sizes for lobsters in size $k$ to the fishery. The values of $S_{k,t}^{gear,i}$ and $S_{k,t}^{cons,i}$ vary with time, and are provided as input data (ASMFC 2000). The $S_k^{other}$ is assumed to be the same over time and between sexes and described by a normal function $N(\mu_S, \sigma_S^2)$. The values of the normal distribution function are standardised to range from 0 to 1 for $S_k^{other}$. The $\mu_S$ and $\sigma_S^2$ determine the shape and location of $S_k^{other}$, and subsequently determine this selectivity coefficient for different sizes of lobsters. They are parameters being estimated in modelling. In this study, to evaluate the potential impacts of $S_k^{other}$ on modelling, we assumed $S_k^{other}$ having a "true" value of 1 in the lobster simulator, but fixed $S_k^{other}$ value to 0.75 in the parameter estimation (see Table 1).

Because the overall selectivity $S_{k,t}^i$ is the product of four selectivity coefficients and the legal switch has values of 1 for legal sized lobsters and 0 for lobsters outside legal size ranges, the impacts of $S_{k,t}^{gear,i}$, $S_{k,t}^{cons,i}$, and $S_k^{other}$ on overall selectivity $S_{k,t}^i$ are limited to lobsters of legal sizes ($S_{k,t}^i$ is 0 for all other size classes because of $P_{k,t}$). All these three selectivity coefficients have values from 0 to 1. Thus, the exploitation rate for lobsters of sex $i$ in size class $k$ in year $t$, $U_{k,t}^i$, can be estimated as:

$$U_{k,t}^i = U_t^i S_{k,t}^i \tag{8}$$

**Table 1** Simulation scenarios considered in evaluating the impacts of biased errors on the performance of the proposed model.

| Scenario | Descriptions of errors |
|---|---|
| I (base case) | No biased errors, only random sampling errors in random Bernoulli trials |
| II | Lack of inshore survey data in the model fitting |
| III | Positive biases in moulting increment and its variance mean moult increment is 2.5 mm larger than the "true" one, and variance increased by 30% |
| IV | Negative biases on the fishery-stock encountering coefficient $S_{k,t}^{other}$ true value = 1, whereas 0.75 was used in the first 10 and last 5 size classes |
| V | Negative biases in landings first 5 years of landings underestimated by 20% |
| VI | Combined errors listed in Scenarios II–V |

where $U^i_t$ is calculated from Equation 6. The use of the above equation ensures the predicted and observed catches are the same (i.e., $\sum_k C^i_{k,t} = LC^i_t$). Thus the size-specific exploitation rate $U^i_{k,t}$ is calculated as the proportion of the total stock biomass removed from size class $k$ in year $t$. The exploitation rate derived in Equations 6–8 is a biomass-based exploitation rates. By using the lobster catch in number and legal stock abundance in Equation 8, we can estimate abundance-based (i.e., number-based) exploitation rates. The survival rate from fishing, $SV^i_{k,t}$, can then be calculated as:

$$SV^i_{k,t} = 1 - U^i_{k,t} \tag{9}$$

The number of lobsters in size class $k$ in year $t$, $N^i_{k,t}$, is calculated as:

$$N^i_t = SV^i_{t-1}\, N^i_{t-1}{}'G^i\, e^{-M^i} \tag{10}$$

where $G$ is the size-specific growth transition matrix (Quinn & Deriso 1999) and $M$ is the instantaneous rate of natural mortality. Because of the complexity of the framework, growth transition matrix is determined outside the framework based on size-specific moulting frequency and moulting increment defined in ASMFC (2000). Equation 10 is used in projecting the change in the number of lobsters in the stock from one year to the next year.

### *Model predictions*

Using the above population dynamics models we can simulate a model lobster fishery. The following predictions can be made from the simulated model fishery—

legal-sized lobster biomass:

$$B^{legal,i}_t = \sum_k P_{k,t} N^i_{k,t} w^i_k \tag{11}$$

fishery CPUE:

$$I^{pred,i}_t = q^i_1 \left(B^{legal,i}_t\right)^{\gamma} \tag{12}$$

abundance index for survey programme $j$: (13)

$$IS^{pred,i}_{j,t} = q^i_{2,j} \sum_k y_{k,j}\ B_{k,j}$$

$j \in$ inshore and offshore

size composition of catch in the fishery:

$$Cp^{pred,i}_{k,t} = \frac{S^i_{k,t} N^{pred,i}_{k,t}}{\sum_k S^i_{k,t} N^{pred,i}_{k,t}} \tag{14}$$

size composition of catch in the survey:

$$p^{pred,i}_{k,j,t} = \frac{N^{pred,i}_{k,t} \psi_{k,j}}{\sum_k N^{pred,i}_{k,t} \psi_{k,j}} \tag{15}$$

where $q$ is catchability coefficient and is assumed to be different among seasons and between sexes, but the same for a given season among different years. This results in eight $q$s to be estimated for the fishey (four seasons for two sexes), four $q$s for the NMFS survey (two seasons for two sexes), and four $q$s for the Maine DMR inshore survey (two seasons for two sexes). Parameter $\gamma$ in Equation 12 is a density-dependent parameter and is assumed to be different among seasons and between sexes, but the same for a given season among different years (eight $\gamma$s for four seasons and two sexes). Parameter $\psi_{k,j}$ in Equation 15 is the selectivity coefficient for lobster in size class $k$ and survey programme I, and can be described by the following logistic curve:

$$\psi_{k,j} = d_j + (1 - d_j) / (1 + \exp(a_j(\mathrm{l}_{k,j} - \mathrm{l}_{50,j})))$$
$$j \in \text{inshore and offshore surveys} \tag{16}$$

The value of $\psi_{k,j}$ ranges from d to 1, and is determined by three parameters $d$, $a$, and $l_{50}$ in Equation 16. These parameters are all estimated in modelling. Because it is likely that inshore and offshore survey programmes have different survey selectivity coefficients, the parameters are estimated separately for the inshore and offshore surveys, resulting in six parameters to be estimated. Past studies have suggested that small lobsters are more likely to be found in inshore areas and large lobsters tend to stay in offshore areas, therefore the sign of parameter $a$ in Equation 16 should be different for the inshore and offshore programmes with the inshore programme having a positive $a$ (thus more likely to pick up lobsters of small sizes in the survey) and the offshore survey having a negative $a$ (more likely to pick up large lobsters in the survey).

### *Observational models*

A group of observational models are developed to relate the predictions from the above dynamics models with the observations made in the fishery. The differences between the predicted and observed output variables in the observational models are assumed to be random and follow certain statistical distributions, which are then used to formulate the likelihood functions needed in the Bayesian parameter estimation. The following observational models are developed—

catch per unit of effort in the fishery: $$I_t^{obs,i} = I_t^{pred,i} \exp(\varepsilon_t) \tag{17}$$

survey abundance index: $$IS_t^{obs,i} = IS_t^{pred,i} \exp(\varepsilon_t) \tag{18}$$

size composition of catch in the survey: $$p_{k,t}^{obs,i} = p_{k,t}^{pred,i} + \varepsilon_t \tag{19}$$

size composition of catch in the fishery: $$Cp_{k,t}^{obs,i} = Cp_{k,t}^{pred,i} + \varepsilon_t \tag{20}$$

Error terms $\varepsilon$ in Equations 17 and 18 are assumed to follow normal distributions, and error terms $\varepsilon$ in Equations 19 and 20 are assumed to have multinomial distributions (Fournier et al. 1990).

*Likelihood functions*

Three different likelihood functions used in Chen et al. (2000) are considered: normal (A), robust normal (B), and *t*-distribution (C) functions. The following likelihood functions are formulated based on the observational models listed above:

$$p(I_t^{obs,i} \mid I_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1}{\sqrt{2\pi}\hat{\sigma}_{I_t^{obs,i}}} \exp\left\{ -\frac{\left(1\mathrm{n}(I_t^{obs,i}) - 1\mathrm{n}(I_t^{pred,i})\right)^2}{2(\hat{\sigma}_{I_t^{obs,i}})^2} \right\} \right] \tag{21A}$$

$$p(I_t^{obs,i} \mid I_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1}{\sqrt{2\pi}\hat{\sigma}_{I_t^{obs,i}}} \exp\left\{ -\frac{\left(1\mathrm{n}(I_t^{obs,i}) - 1\mathrm{n}(I_t^{pred,i})\right)^2}{2(\hat{\sigma}_{I_t^{obs,i}})^2} \right\} + 0.01 \right] \tag{21B}$$

$$p(I_t^{obs,i} \mid I_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1.329}{\sqrt{4\pi}} \left\{ 1 + \frac{\left(1\mathrm{n}(I_t^{obs,i}) - 1\mathrm{n}(I_t^{pred,i})\right)^2}{4(\hat{\sigma}_{I_t^{obs,i}})^2} \right\}^{-2.5} \right] \tag{21C}$$

$$p(IS_t^{obs,i} \mid IS_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1}{\sqrt{2\pi}\hat{\sigma}_{I_t^{obs,i}}} \exp\left\{ -\frac{\left(1\mathrm{n}(IS_t^{obs,i}) - 1\mathrm{n}(IS_t^{pred,i})\right)^2}{2(\hat{\sigma}_{I_t^{obs,i}})^2} \right\} \right] \tag{22A}$$

$$p(IS_t^{obs,i} \mid IS_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1}{\sqrt{2\pi}\hat{\sigma}_{I_t^{obs,i}}} \exp\left\{ -\frac{\left(1\mathrm{n}(IS_t^{obs,i}) - 1\mathrm{n}(IS_t^{pred,i})\right)^2}{2(\hat{\sigma}_{I_t^{obs,i}})^2} \right\} + 0.01 \right] \tag{22B}$$

$$p(IS_t^{obs,i} \mid IS_t^{pred,i}) = \prod_i \prod_t \left[ \frac{1.329}{\sqrt{4\pi}} \left\{ 1 + \frac{\left(1\mathrm{n}(IS_t^{obs,i}) - 1\mathrm{n}(IS_t^{pred,i})\right)^2}{4(\hat{\sigma}_{I_t^{obs,i}})^2} \right\}^{-2.5} \right] \tag{22C}$$

$$L(Cp_{k,t}^{obs,i} = \prod_t \prod_k \frac{1}{\sqrt{2\pi Cp_{k,t}^{obs,i}(1 - Cp_{k,t}^{obs,i}) + 0.1/\Omega}} \exp\left[ -\frac{-N_{k,t}^i (Cp_{k,t}^{obs,i} - Cp_{k,t}^{pred,i})^2}{2\left\{ Cp_{k,t}^{obs,i}(1 - Cp_{k,t}^{obs,i}) + 0.1/\Omega \right\}} + 0.01 \right] \tag{23}$$

$$L(p_{k,t}^{obs,i}) = \prod_t \prod_k \frac{1}{\sqrt{2\pi p_{k,t}^{obs,i}(1 - p_{k,t}^{obs,i}) + 0.1/\Omega}} \exp\left[ -\frac{-N_{k,t}^i (p_{k,t}^{obs,i} - p_{k,t}^{pred,i})^2}{2\left\{ p_{k,t}^{obs,i}(1 - p_{k,t}^{obs,i}) + 0.1/\Omega \right\}} + 0.01 \right] \tag{24}$$

$\Omega$ in Equations 23 and 24 is the number of the size classes. Equations 23 and 24 are multinomial likelihood functions that are robust to possible outliers and can handle $p$ value of 0 or 1 as suggested by Fournier et al. (1990) and Chen et al. (2000). $\sigma$s used in Equations 22 and 23 were estimated from the standard deviations of observed log CPUE and survey abundance indices, respectively. The $t$-distribution method tends to have the best performance in the presence of outliers, the normal distribution method is best in the absence of outliers, and the performance of the robust normal method is ranked in the middle in the absence and presence of outliers (Chen et al. 2000)). In this study, the robust normal likelihood is used in the estimation.

### *Estimation of $F_{10\%}$*

Under the equilibrium, the egg production (EGG) at fishery mortality ($F$) can be calculated as:

$$EGG(F)=\sum_{k} N^{f}_{b,k}(F)\alpha_{fec}(l_k)^{\beta_{fec}} \tag{25}$$

where $N^{f}_{b,k}(F)$ is the number of female lobsters at fishing mortality of $F$ estimated from the population model for an equilibrium population simulated using the parameters estimated in the population model with the average recruitment ($\bar{R}$, Equation 1). $F_{10\%}$ is then estimated, iteratively, from the following equation:

$$EGG(F)\Big|_{F=F_{10\%}} = 0.1EGG(F)\Big|_{F=0} \tag{26}$$

## Input data

The information required by the stock assessment model described above comes from two sources: fishery-dependent and fishery-independent. The fishery-dependent data include a time series of landings by season and sex, a time series of CPUE by season and sex, and a time series of size composition of catch by season and sex. The fishery-independent data include a time series of abundance index and size composition of survey catch.

Information about the lobster growth is needed to develop the growth transition matrix which describes the probability of a lobster in a given size class growing into other size classes in a given season. Because moult only occurs in summer and autumn, two growth transition matrices need to be developed, one for summer and the other for autumn. The moult frequency of female lobsters is influenced by their maturation (see Fig. 3). Thus, growth transition matrices need to be sex-specific. The growth transition matrix is determined by the moult probability, size increment per moult, and for mature female, impacts of maturation. Because of the complexity of lobster growth (Fig. 3) and lack of tagging information that covers the whole range of lobster sizes, the growth transition matrix was determined outside of the population model. The average seasonal size increment decreases with lobster sizes (Fig. 4), reflecting the decreases in moult frequency for lobsters of large sizes. Males tended to have a higher average seasonal size increment in summer than females (Fig. 4). This results from a reduced moult frequency of females after reaching maturation.

Other information required includes data describing the relationship between length and maturation, length-weight relationship, size-specific selectivity including $P_{k,t}$, $S^{gear,i}_{k,t}$, and $S^{cons,i}_{k,t}$, length-specific fecundity, and maximum and minimum legal sizes.

## Parameters to be estimated in modelling

The model parameters to be estimated include 16 catchability coefficients $q$ consisting of eight $q$s to be estimated for the fishery (four seasons for two sexes), four $q$s for the NMFS survey (two seasons for two sexes), and four $q$s for the inshore survey (two seasons for two sexes); 8$\gamma$s (for four seasons and two sexes; Equation 12); six parameters determining the selectivity of the two surveys (two sets of $d_j$, $a_j$, and $l_{50,j}$ for NMFS survey and Maine DMR inshore survey; Equation 16), sex-specific number of lobsters in each size class (35 for each sex, total = 70), average recruitment $\bar{R}$, one recruitment deviation from the mean value $R_{dev_t}$ for each year (16 parameters for 16 years), standard deviation of the estimated recruitment $\sigma_{R_t}$, autocorrelation coefficient describing the degree of autocorrelation between the two consecutive years $R_h$ (Equations 1 and 2), and natural mortality M. Although the fishing selectivity $S^{other}_{k}$ is determined by two parameters which can be estimated in modelling (i.e., $\mu_S$ and $\sigma_S^2$; Equation 7), this study fixed its value in estimation to test its impacts on the estimation of lobster population dynamics. Thus, for a simulated fishery with 16 years of data, there are altogether 120 parameters to be estimated.

## Simulation study to evaluate the model performance

This study is focused on the evaluation of the proposed stock assessment model using data from a simulated lobster fishery described below. Because the properties of the simulated fishery are known,

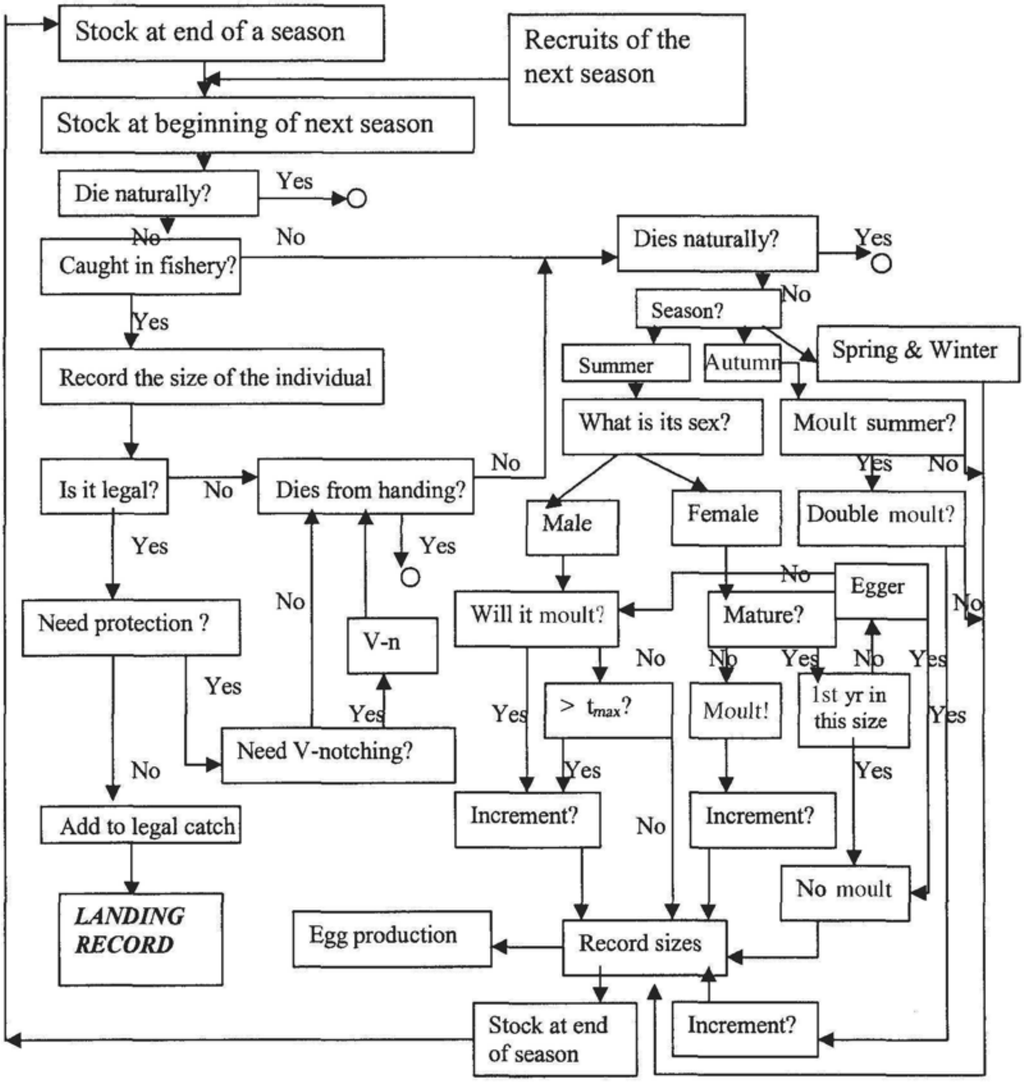


**Fig. 3** Flowchart for the individual-based lobster simulator.

we can compare the parameters estimated using the proposed model with the built-in "true" parameters used in simulating the fishery. For this comparison purpose, we only use maximum likelihood estimators to estimate the model parameters, which excludes the impacts of priors on the parameter estimation.

For simulating the lobster fishery, instead of using the models for aggregate dynamics of a lobster stock, we used a probabilistic approach to simulate the lives of individual lobsters. This can be done by expressing various components of the model equations as random Bernoulli trials. For example, rather than calculating the number of lobsters that survive natural mortality by:

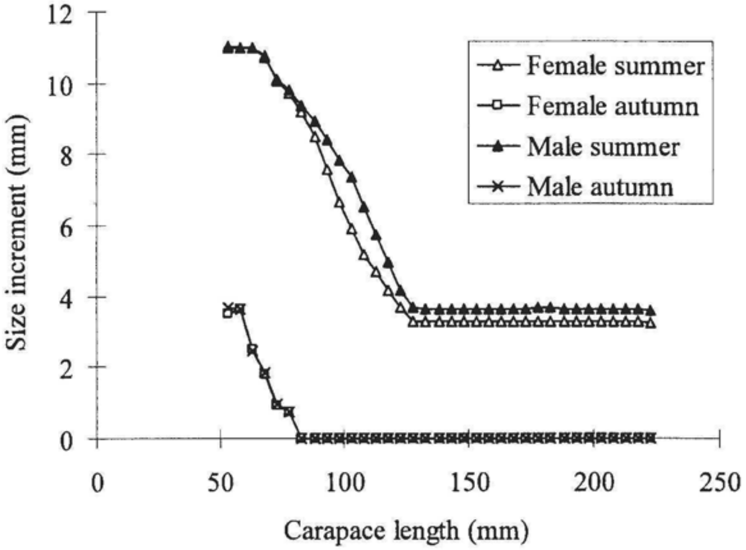
$N_t+1 = N_t e^{-M}$

where $M$ is the instantaneous rate of natural mortality, we simulate natural mortality acting on $N_t$ individual lobsters:

for *1* to $N_t$: if $U(0,1) \le 1-e^{-M}$ then $N_{t+1} = N_t - 1$

where $U(0,1)$ is a uniform distributed random number between 0 and 1. Detailed life and fishery history of an individual lobster is tracked throughout

**Fig. 4** Average seasonal size increment derived from size-specific moulting frequency and moulting increment for male and female American lobsters (*Homarus americanus*). Size increment is 0 for winter and spring because lobsters tend not to moult in these two seasons.



the life span of the lobster in the simulation, and is stopped only after the individual died of natural or fishing mortality rates. We refer to this approach as the lobster simulator. The details of this simulator are described in a flow chart presented in Fig. 3.

For each time step (spring, summer, autumn, and winter), each lobster has probabilities of being caught in the fishery, dying of natural mortality, growing and maturing, and for females, being V-notched. When a lobster is caught in the fishery, its sex and size is recorded to generate catch and size-frequency data. CPUE is generated as a constant proportion of the total weight of legal lobsters in the population.

To simulate a realistic fishery, the simulator was initially run for 60 years with constant recruitment but without fishing to let the lobster population achieve equilibrium. This was then followed by 40 years of fishing with various recruitment mimicking those that occurred in the Gulf of Maine lobster fishery. We used the last 16 years of data for the simulation.

No observation or process errors were included in the simulation aside from the random sampling associated with the Bernoulli random trials. The data simulated by the simulator were then analysed using the proposed model. This is referred to as base case. For this paper, we considered the base case and five other scenarios with biased errors in growth, $S_k^{other}$, and landings, and missing inshore data (Table 1). The key fishery parameters estimated for each of these scenarios were then compared with the true values from the simulated fishery.

## RESULTS

The estimated stock abundance by size for the beginning of the simulation (i.e., spring, 1st year) could mimic the "true" size composition (Fig. 5). For some scenarios (e.g., II and VI), however, large differences were observed in some size classes. The percentage of bias, which was calculated as the difference between the estimate and true values divided by the true value, averaged over all the 35 size classes was –9.5%, –17.6%, –28.5%, –8.8%, –37.1%, and –63.8% for the six scenarios, respectively. Scenario VI had the highest percentage of bias followed by scenarios V and III.

The percentage of bias for the total stock abundance estimates was small for both female and male lobsters in most seasons (Fig. 6), indicating that the proposed model performs well in retrieving the true female and male lobster abundances. The percentage of bias had a strong seasonal pattern for females with the highest estimation bias often occurring in summer. The seasonality of abundance estimation bias was weak for males (Fig. 6). There was virtually no yearly trend in the estimation bias for scenarios I, III, IV, and V with the percentage bias fluctuating near 0, but some yearly trend was observed for scenarios II and VI in which the bias for both the female and male abundance estimates tended to change in negative value to position value. This suggests for these two scenarios the model underestimated the true values in early years, and then overestimated abundance in late years. For most

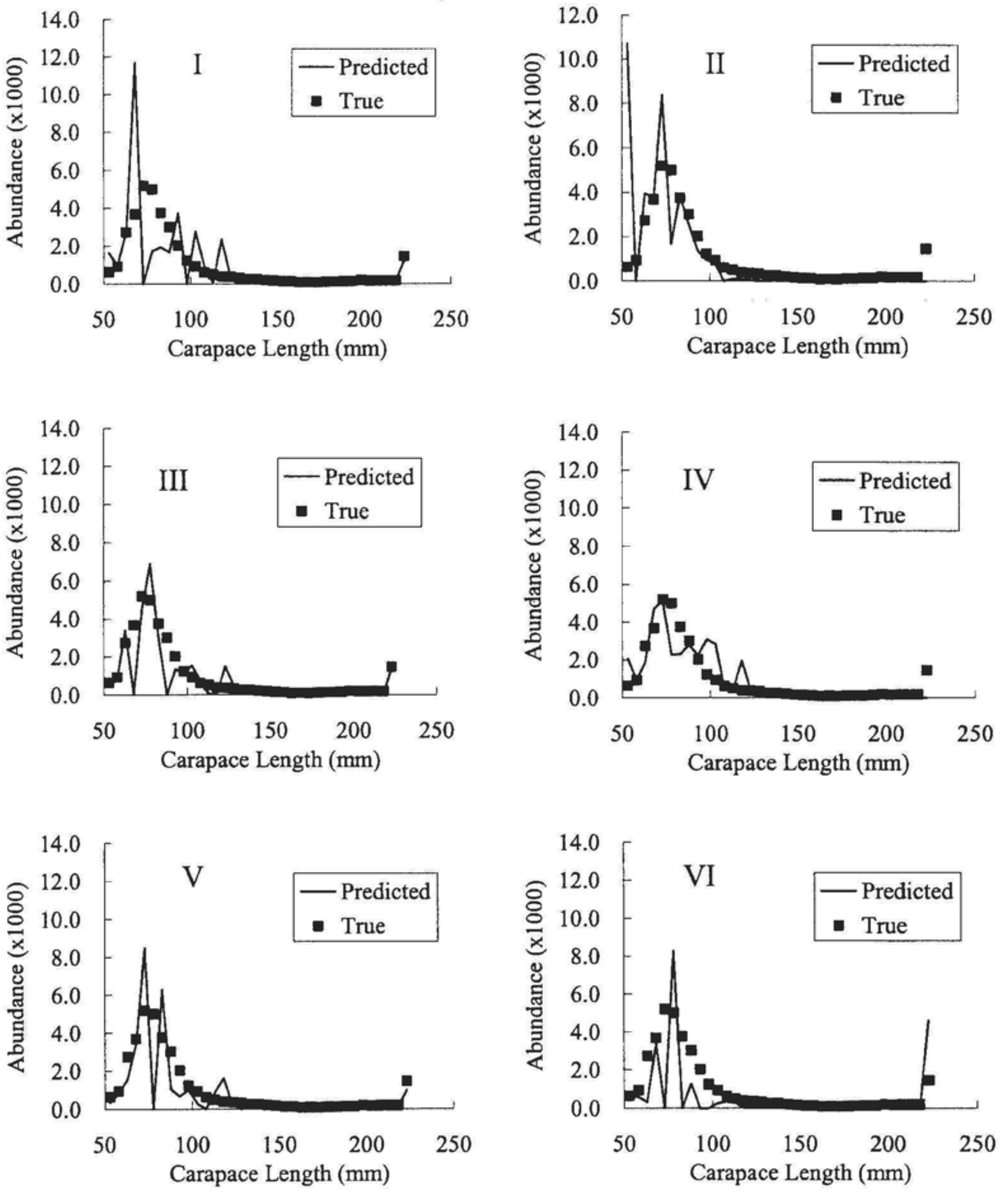


**Fig. 5** True and estimated stock abundance by size class in the beginning of the simulation (i.e., beginning of spring, 1st year) under different simulation scenarios.

seasons, females tended to have higher estimation biases compared with males (Fig. 6). Similar patterns could be observed for the legal stock abundance for female and male lobsters (Fig. 7). Similar temporal patterns and magnitudes in estimation biases between total and legal abundances implied that the stock size structure was well estimated for both females and males.

The percentage of bias was also estimated for legal biomass, exploitation rate, and natural mortality (Table 2). For these key fisheries statistics, scenarios II, III, and VI tended to have large biases compared with other three scenarios, except males for legal biomass and exploitation rate.

Annual recruitment was well estimated by the proposed model (Fig. 8). For scenarios II and VI,

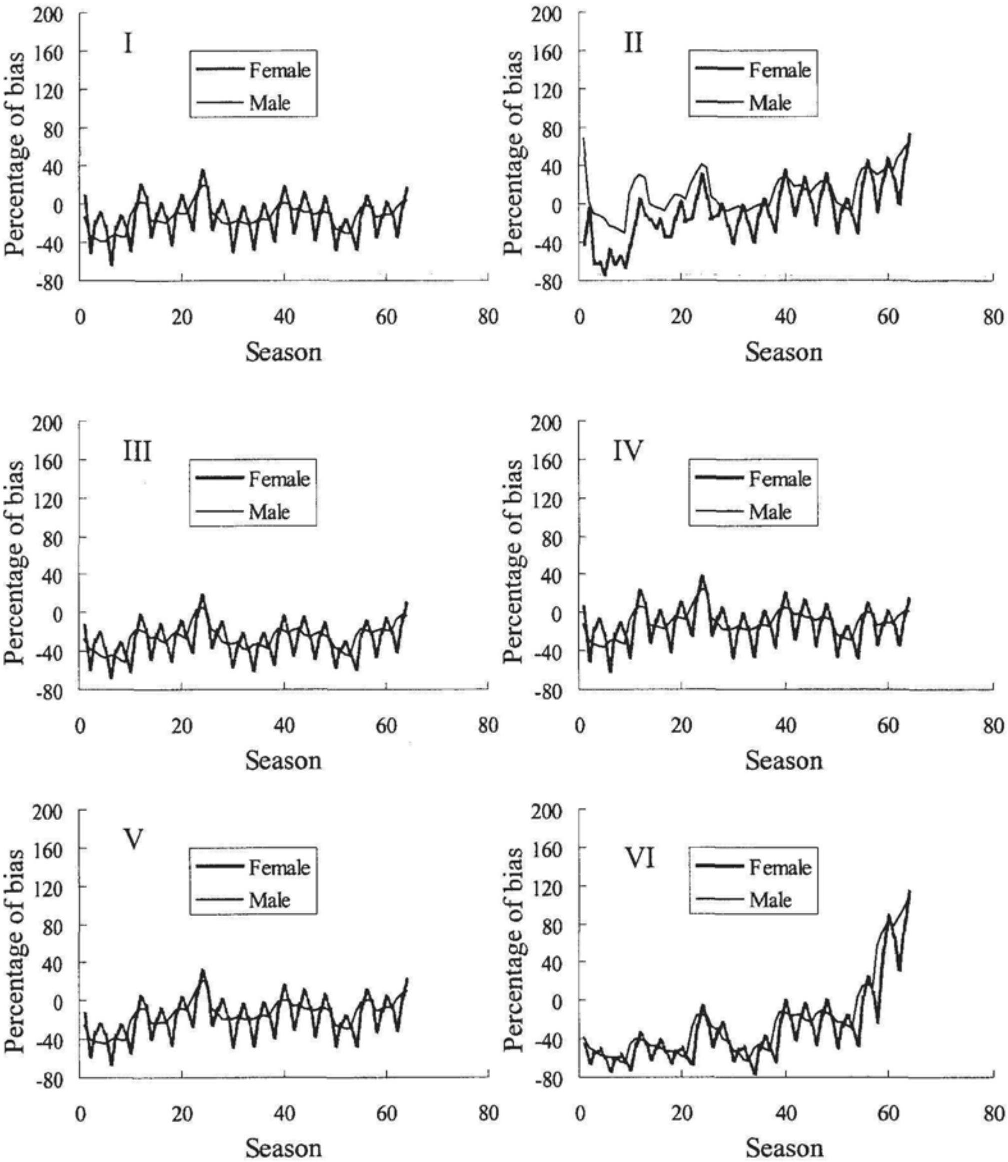


**Fig. 6** Percentage of bias in estimating total stock abundance by sex in different seasons (1, spring, 1st year; 2, summer, 1st year; 3, autumn, 1st year; 4, winter, 1st year; 5, spring, 2nd year; etc.) for different scenarios. Percentage bias is calculated as $\frac{Estimate - True}{True}100\%$.

however, differences arose in the last few years. For other scenarios, the temporal patterns of estimated recruitments mirrored those of the true recruitments. The percentage of biases averaged over all years were smaller than 15% for all scenarios, indicating the proposed model can replicates the recruitment under the biased errors considered in this study.

The logistic curves defined by Equation 15 describe the size-specific selectivity of the two survey programmes. For all the scenarios, selectivity curves for the offshore survey, which targeted lobster of large size classes, were well estimated, whereas large errors occurred in estimating selectivity curves for the inshore survey (Fig. 9), which targeted lobster

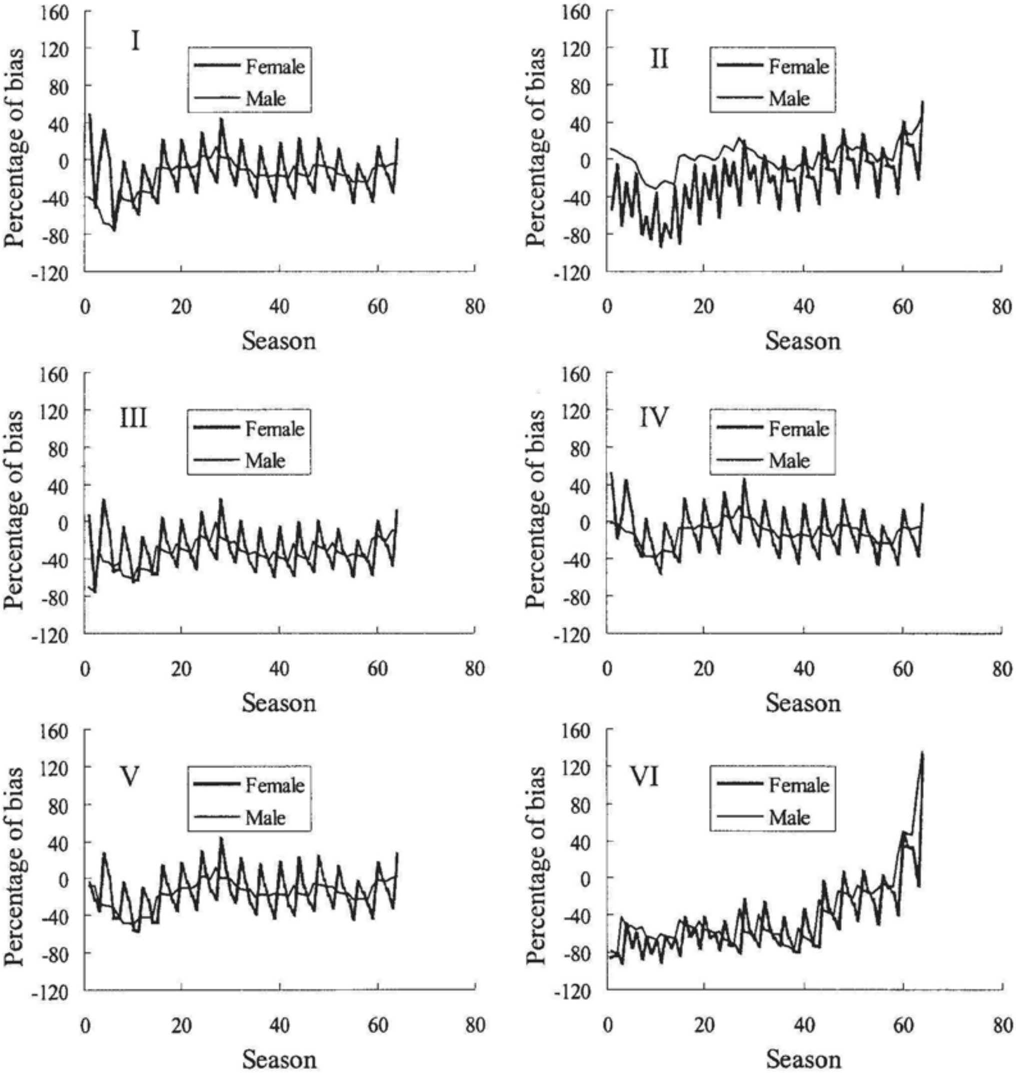


**Fig. 7** Percentage of bias in estimating legal stock abundance by sex in different seasons for different scenarios. Percentage bias is calculated as $\frac{Estimate - True}{True}100\%$.

**Fig. 8** "True" and estimated annual recruitment for the six simulation scenarios.

➤

of small size classes. Because both sets of parameters were estimated in the same phase in the parameter estimation with the program coded with the AD Model Builder, the difference was unlikely related to the way of how these selectivity curves were estimated. Instead, such a difference might reflect lack of information on size structure of small lobsters in data. The size structure for large lobsters was reflected in size composition data of both surveys and catch data, whereas the size structure of small lobsters (sublegal) was only reflected by the survey data.

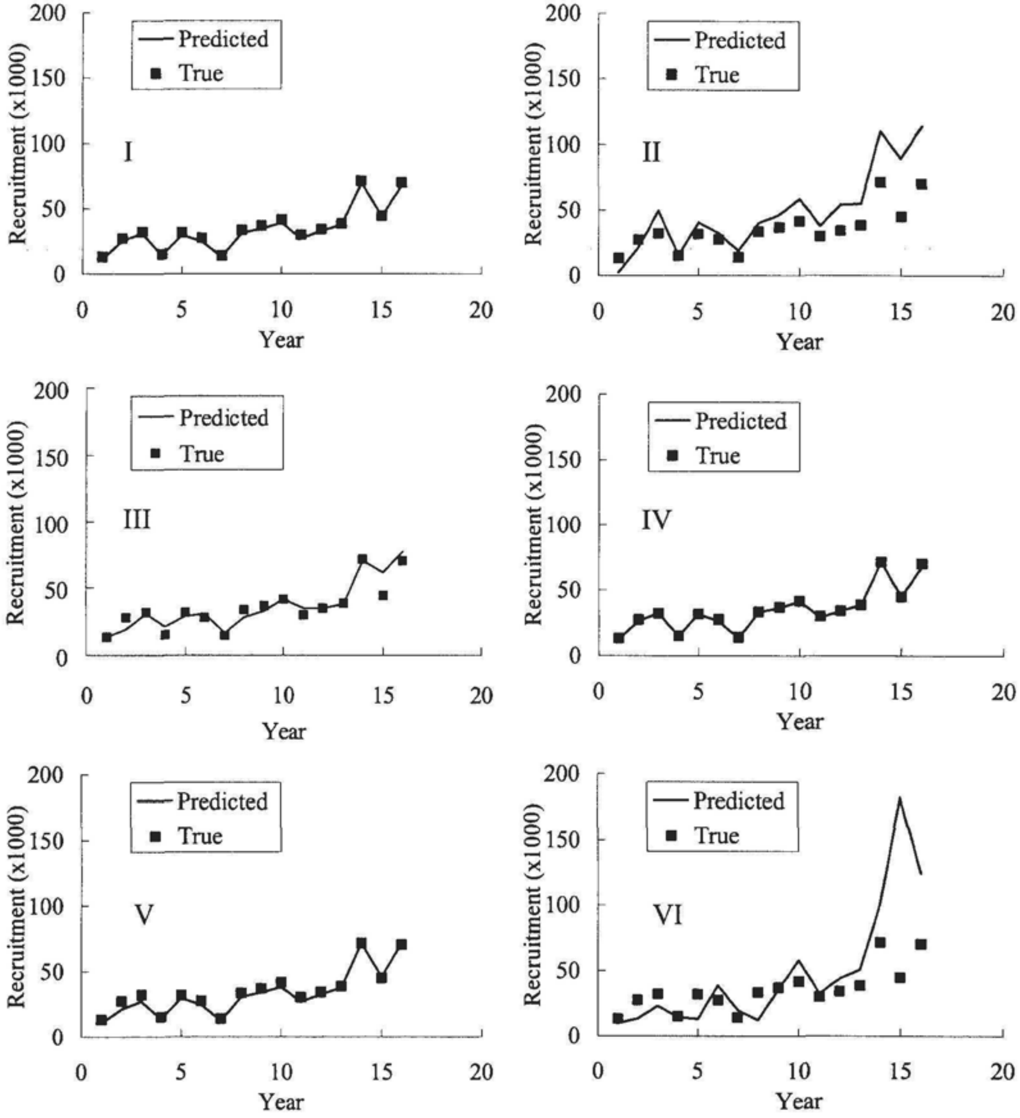


**Table 2** Percentage of biases (PB) for some key fisheries parameter estimates that are not shown in figures. PB is calculated as $PB = \frac{Estimated - True}{True} 100\%$. For a time series of fisheries statistics such as legal biomass and exploitation rate (i.e., catch over legal abundance), the percentage of estimation bias was calculated as PBs averaged over all seasons and years. M = natural mortality.

| | Legal biomass | | Exploitation rate | | |
|---|---|---|---|---|---|
| Scenario | Female | Male | Female | Male | M |
| I | –6.1 | –18.7 | 28.4 | 32.1 | –10.0 |
| II | –33.6 | 1.7 | 97.1 | –0.1 | 53.1 |
| III | –24.1 | –33.7 | 60.4 | 60.2 | 43.0 |
| IV | –3.1 | –12.2 | 20.5 | 15.2 | 0.2 |
| V | –8.8 | –16.7 | 25.8 | 23.6 | –15.9 |
| VI | –47.5 | –39.7 | 196.3 | 113.5 | 38.6 |

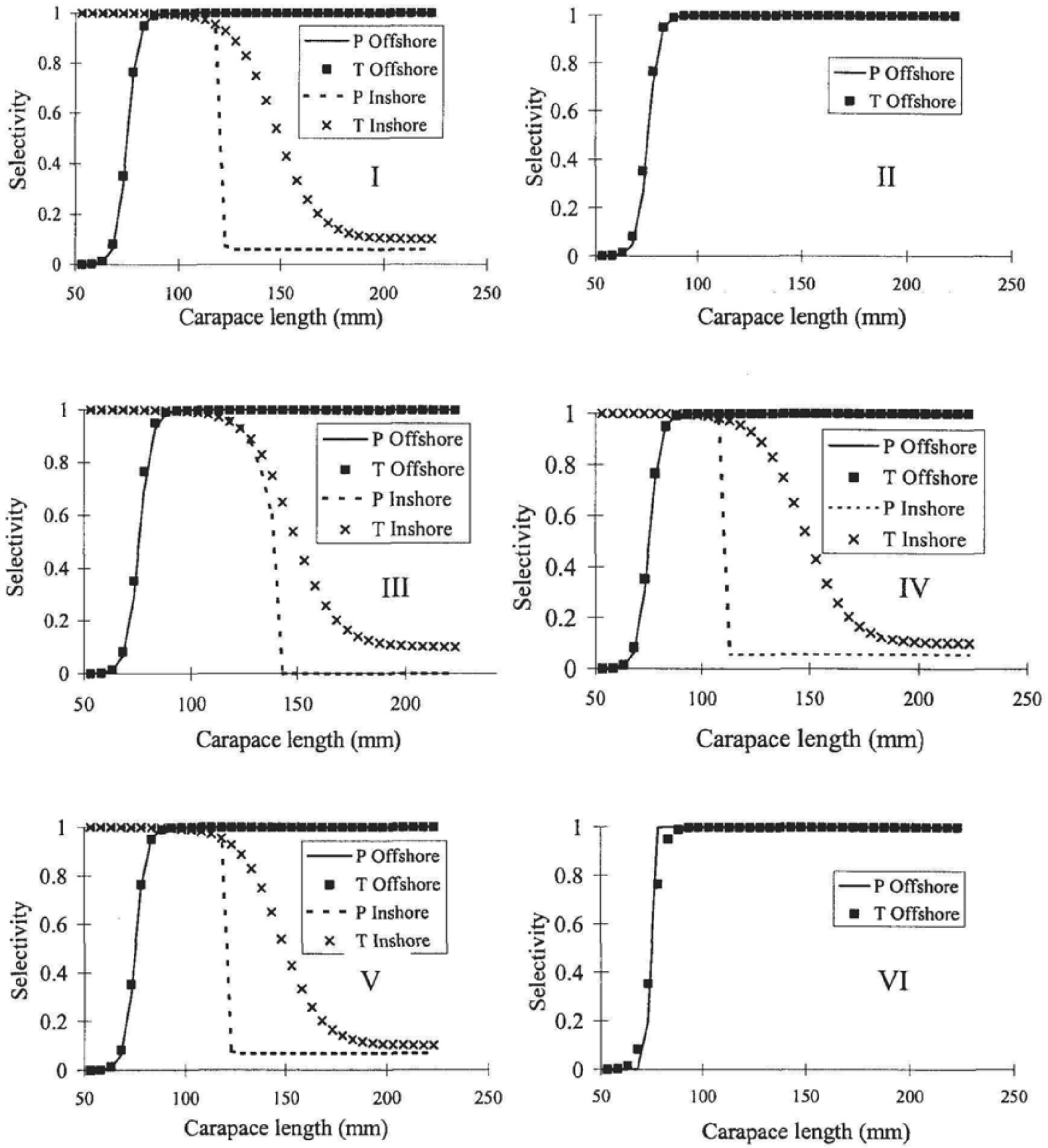


**Fig. 9** "True" and estimated size-specific availability of the stock to inshore and offshore surveys (proportion of survey coverage).

## DISCUSSION

Using the lobster simulator, we simulated lobster fisheries with different scenarios of biased errors for different key input data. The proposed model can retrieve the "true" temporal patterns of stock biomass and abundance, exploitation rate, and recruitment in the simulated lobster fishery with small estimation errors. These key fisheries statistics characterise the lobster population dynamics and are critical in determining the status of the stock and projecting the stock trends under different management scenarios. This suggests that the proposed model can perform well in determining the status of the lobster stock and in quantifying the lobster stock dynamics. However, this conclusion is reached based on a limited number of simulations with biased errors and small random sampling errors involved in simulating the lobster fishery. More extensive simulations that consider large random observation errors and process errors, together with biased errors, need to be done to evaluate the sensitivity of the model performance to errors of different distributions and data quantity. This study should be considered as a first step in developing and testing the proposed model. Our next step is to conduct an extensive simulation study to evaluate the impacts of various observation errors and process errors on the performance of the model, followed by a study to evaluate the performance of the overall Bayesian stock assessment framework in assessing the lobster fishery. This work is currently under way.

Previous studies indicated that the performance of a model might be influenced by the temporal pattern of recruitment with the model performing better for a fishery with large fluctuating recruitment (thus large contrasts in abundance) (Hilborn & Walters 1992). Thus, we need to simulate fisheries with different recruitment patterns in the model evaluation to identify potential limits the proposed model has.

We presented results only for the six simulation scenarios for testing biased errors. The application of the proposed model to the data from the actual lobster fishery and subsequent interpretation and risk analysis need to be detailed in a separate paper because of the sensitivity of the issue and its management and economic implications.

The results derived for Scenario II in this study suggest that lack of inshore survey data only have some impacts on the assessment of small lobsters (e.g., large errors in the first size class for scenario II, Fig. 5), but do not have a large negative impact on the assessment. This, however, needs to be interpreted cautiously. In this paper, offshore survey data are well defined without observation errors. With a defined size-specific availability of lobsters to the offshore survey programme, offshore survey data may be sufficient in providing the information on the lobster population dynamics. If the offshore data are not well defined, and have large observation errors as in actual field data, lack of the inshore data is likely to result in large errors in the assessment.

The estimation results in the simulation are robust to the initial values used in starting the estimation. This may result from lack of random errors in data. An increase in random errors for input data is likely to make the estimation less robust to the initial values starting the estimation process. In this example, different sets of initial values need to be tried to identify their possible impacts and to converge the estimation at the global maximal in the maximum likelihood estimation.

There is a concern that the structure of the Collie-Sissenwine model currently used in assessing the American lobster in the Gulf of Maine may be too simple to describe the complex life history and fishing process of the American lobster (ASMFC 2000). Concerns have also been raised in comparing biological reference point $F_{10\%}$ and fishery fishing mortality rate, which are derived from separate estimations. Recent stock assessment has repeatedly called for the development of other stock assessment models for alternatives and for comparisons (ASMFC 2000). Although the proposed model provides an alternative approach to assessing the American lobster stock in the Gulf of Maine and tries to mimic the complex life history and fishing processes, this does not necessarily mean the performance of this complex model is better than the relatively simple Collie-Sissenwine model. This also does not mean we need to replace one model with another. The use of multiple stock assessment models has been advocated by NRC (1997, 1999), which allows for the comparison of results derived from different models with different biological implications, and different model structure and assumptions. Such a stock assessment approach can allow us to identify potential problems associated with different models and identify potential impacts of model structure and assumptions on the stock assessment. Because different models require different input information, the comparative studies can also help understand the impacts of different data on modelling the population dynamics. For an important fishery like the American lobster fishery, it is certainly inappropriate for its assessment to solely depend on one type of model. A multiple modelling approach with an incorporation of comparative study of different models is more appropriate. We suggest that the proposed model be considered as an alternative approach to assessing the American lobster fishery.

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# Impact of minimum legal size increases on egg-per-recruit production, size structure, and ovigerous females in the American lobster (*Homarus americanus*) population off the Magdalen Islands (Quebec, Canada): a case study

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**Abstract** In the mid 1990s, American lobster (*Homarus americanus*) from Canadian waters was considered overfished based on estimated levels of egg-per-recruit production (EPR). In 1997, the Department of Fisheries Oceans responded by adopting a goal of doubling the level of EPR from its 1996 level. In the Magdalen Islands (Quebec), results from a simulation model indicated that doubling EPR could be reached by increasing the minimum legal size (MLS) from 76 mm to 83 mm carapace length. This was done at a pace of 1 mm per year from 1997 to 2003. Following the increase of MLS, the size structure, mean size, and the abundance of ovigerous females improved significantly in the catches. However, levels of fishing effort are still very high. This could cause undesirable effects such as altering sex ratios and size structure of males, which could lead to sperm limitation, and reducing the contribution of multiple spawners to egg production, which could become an issue if egg quality is important. Consideration of these issues leads to the recommendation of a multidimensional approach to lobster conservation.

**Keywords** American lobster; *Homarus americanus*; egg-per-recruit production; management; conservation

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## INTRODUCTION

The American lobster (*Homarus americanus* Milne Edwards, 1837) has supported an important commercial fishery in eastern Canada since the middle of the 19th century. In the mid 1970s, following a 20-year decline in landings (Fig. 1), Canadian scientists expressed their concerns about the general state of the lobster resource and recognised that most lobster populations were overfished (Anon. 1977). However, despite clear signs of growth and recruitment overfishing, landings increased continuously from the mid 1970s to the early 1990s and this allayed much of the conservation concern. The increase was attributed mainly to an increase in lobster abundance, and the geographical scale of the increase suggested common underlying environmental/ecological factors operating over broad regions (Elner & Campbell 1991; Pezzack 1992; Drinkwater et al. 1996; Fogarty & Gendron 2004). In some areas, increase in fishing effort and efficiency is thought to have also contributed to the increase in landings (Fogarty 1995).

Concerns among scientists and within the fishing industry about a potential overfishing problem, were revived in the early 1990s by a sharp decline in landings (Fig. 1). In Québec, landings totalled 3800 t in 1992 but fell below 3000 t in 1994. In the Québec region, up to 65% of the landings come from the Magdalen Islands, a 100-km long archipelago located in the southern Gulf of St-Lawrence, which constitutes one of the 41 lobster fishing areas (LFAs) of Atlantic Canada (Fig. 2). Landings in the Magdalen Islands decreased from a record high of 2800 t in 1992 to 2000 t in 1994, a decrease of almost 30% over a period of 2 years (Fig. 1). To address the problem, the Canadian Department of Fisheries and Oceans (DFO) requested that the Fisheries Resource Conservation Council (FRCC) review the current approach to lobster management and propose guidelines and tools for improving conservation of the lobster stocks. The FRCC, an advisory committee regrouping people from the industry, management, and scientific communities, was

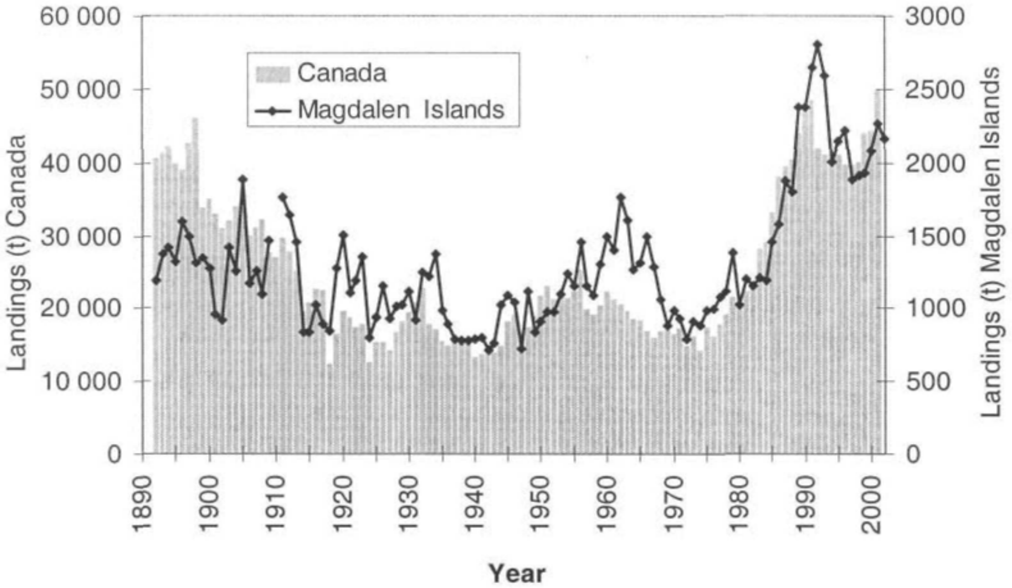


**Fig. 1** American lobster (*Homarus americanus*) landings in Canada and in the Magdalen Islands, Quebec, Canada from 1892 to 2002.

created by DFO in 1994 to advise the Minister on conservation strategies.

In Canada, management of the lobster fishery is based on effort controls, minimum legal size, and restriction on landing ovigerous females. In the Magdalen Islands, the number of licenses is currently limited to 325, the number of traps is limited to 300 per license, and traps cannot exceed 81 cm in length, 61 cm in width, and 50 cm in height. The use of escape vents for sub-legal lobsters started in the beginning of the 1990s and became mandatory in 1994. The fishing season is limited to 9 weeks, starts in spring at ice-break-up, and ends before the summer moulting season. There are no trap hauls on Sundays. The minimum legal size was increased to 76 mm carapace length (CL) in 1957 and was still enforced at the time of the FRCC review. Effort regulations provided no form of control on the increase in fishing efficiency brought about by a number of technological changes over the last 2–3 decades (Gendron & Archambault 1997).

The FRCC (1995) report on lobster conservation reiterated the observations made by scientists that lobster stocks were overfished. It clearly stated that exploitation rates in the majority of LFAs were very high, up to 85% in some LFAs, and still increasing, and that the fishery was based on new, mostly immature, recruits. In most areas, it was concluded that few lobsters reach maturity before becoming vulnerable to the fishery. The FRCC recommended that egg production be increased, the stock size structure improved, and that fishing effort be reduced.

The science and industry response to FRCC recommendations was to focus on increasing egg production and for this goal, discussions centered around the concept of a limit or threshold for egg-per-recruit production (EPR). In the United States, a threshold has already been adopted, and a reduction of EPR to 10% of the unexploited state is considered as a management limit (NEFMC 1995; ASMFC 2000a,b). Preliminary estimates of EPR for the Canadian lobster stocks revealed that the level of EPR was as low as 1–2% of a virgin stock (Pezzack & Maguire 1995) and the FRCC recommended an increase to 5% for all lobster stocks of Atlantic Canada. However, uncertainties in the determination of growth, mortality, and reproduction processes in a virgin population caused some difficulty for the calculation of EPR for an unexploited population. Recognising this difficulty, the goal of doubling EPR was adopted instead of a limit reference point expressed relative to a virgin population. Measures for doubling EPR relative to 1996 levels, over a

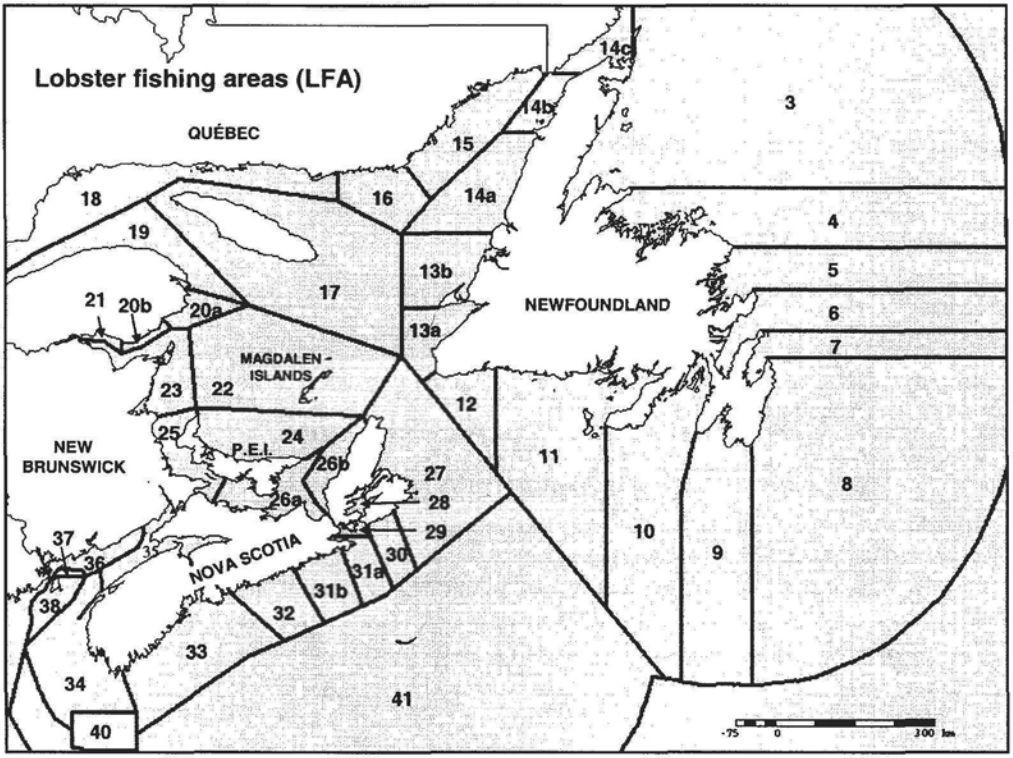
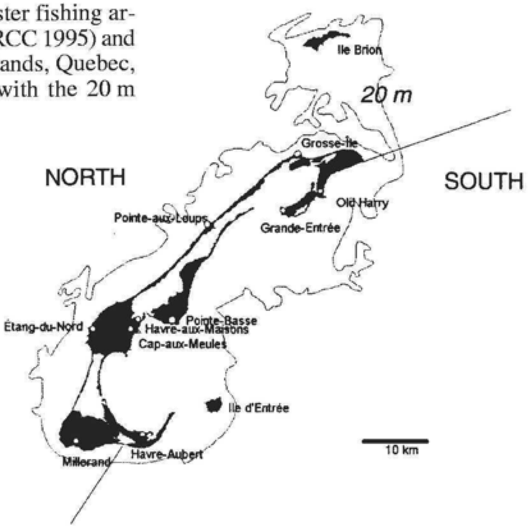


**Fig. 2** Map of Atlantic Canada showing the 41 lobster fishing areas (LFAs) (from FRCC 1995) and of the Magdalen Islands, Quebec, Canada (LFA 22) with the 20 m isobath line.



period of 4–8 years, were developed by fisher's associations throughout eastern Canada and were implemented in 1997 or 1998.

Here I present the results of a simulation model that was used to determine the EPR level in the Magdalen Islands lobster population in 1996 and to assess the effectiveness of different potential management measures for increasing EPR. The choice of increasing minimum legal size (MLS) to reach the target of doubling EPR was taken based on the results of the simulation model, industry acceptance, and ease of enforcement. Changes in the lobster population that resulted from the increase in MLS from 76 mm CL in 1996 to 82 mm CL in 2002 are reported and discussed.

## MATERIAL AND METHODS

### Egg-per-recruit calculation

#### *Simulation model*

The model used to determine EPR values in the Magdalen Islands is an extension of the biological model developed by Fogarty & Idoine (1988) for United States lobster fisheries and is fully described in Gendron & Gagnon (2001). The model captures many facets of the lobster's life cycle including natural mortality, moult increment and frequency, size at sexual maturity, female fecundity, and timing of spawning, moulting, and hatching events. Calculations reported here are for the female component only. In the model, the year starts with the fishing season. Fishing mortality is applied only to non-ovigerous females. After the fishing season, the majority of surviving females will either moult (immature and post-hatching females) or spawn (mature females). The model can, however, account for deviations from the generally accepted 2-year cycle with spawning and moulting in alternate years, such as moulting and spawning in the same year or spawning in successive years. The ovigerous females will incubate their eggs for almost 1 year. After the eggs hatch, females moult and return into the population component of non-ovigerous females, and thus become vulnerable to fishing in the following year. Egg production is calculated at the time the eggs hatch.

This new model was adapted from the former to better reflect the main biological characteristics of lobster in the Magdalen Islands and the distinctive features of the fishery in this region. The model requires the definition of 19 different variables, which may be described by a constant, or a probability function to account for uncertainty in biological processes and parameter measurements. Uncertainty is then propagated to the final estimates of EPR, using Monte Carlo simulation which iteratively assigns various values to the parameters, chosen randomly within the defined probability distribution. For each management scenario, 100 iterations were performed. Final values of EPR were then expressed relative to the 1996 values of EPR as a ratio referred to as the increment factor. For each scenario, the mean of the EPR increment factor values from the 100 iterations was computed and compared with the target value of 2, which represents a doubling of EPR. As explained in Gendron & Gagnon (2001), the cumulative frequency distribution of the 100 EPR values may then be produced to assess the management risk, i.e., the probability of not reaching an increment factor of 2. The program is a DOS executable written in FORTRAN. An application written in Visual Basic 6.0 allows the model to be run under Windows.

Lobster from the southern and northern parts of the Magdalen Islands (see Fig. 2) have a different size at sexual maturity (Dubé & Grondin 1985) and are subject to different levels of fishing mortality (Gendron & Savard 2003a). Calculations reported here are for the southern part of the Magdalen Islands only. The simulations examined the impacts of increasing MLS from the reference size of 76 mm CL in 1996 to 84 mm CL. The model was run by keeping constant all other biological and fishery parameters.

#### *Input data*

The biological data used in the model are described in detail in Gendron & Gagnon (2001). The data on moult increment were taken from the results of mark/recapture campaigns conducted in the Magdalen Islands by Dubé (1985). An average moult increment of 10 mm was reported for commercial-sized lobsters but to account for uncertainty and variability, values were chosen from a uniform distribution ranging from 8 to 12 mm.

Moulting probability was determined from observations on the proportion of post-moult lobsters obtained from a trawl survey carried off the Magdalen Islands in September 1995, after the moulting period (L. Gendron unpubl. data). For each 1-mm size class, the number of lobsters in a post-moult condition was determined. The number was then assigned to the corresponding pre-moult size class, based on data on moult increment from Dubé (1985). The numbers were added to those that did not moult. The proportion of animals that moulted was then computed for each 1-mm size class. The probability of moulting as a function of size was represented by a logistic equation with the inflexion point at 90 mm, and with an interval of 25 mm between the 25 and 75 percentiles. In the model, values for the inflexion point were chosen from a normal distribution characterised by a mean of 90 mm and a SD of 4 mm. The values for the interval between the 25 and 75 percentiles were chosen from a uniform distribution of values ranging between 20 and 30 mm.

Maturity ogives determined by Dubé & Grondin (1985) were used to determine the probability that a non-ovigerous female will spawn in a given year. In the southern Magdalen Islands, the size at which 50% of the females are mature is 79 mm CL. The inflexion point was considered to be distributed inside a normal distribution with a mean of 79 mm and a SD of 3 mm. The interval between the 25 and 75 percentiles of the maturity ogives was considered to be distributed uniformly between 6 and 8 mm.

Fishing mortality values (F) were chosen from a normal distribution with a mean of 1.12 and a SD of 0.11. Values of F are based on the computation of an annual mortality rate index (Z) (Gendron & Savard 2003a). The calculation method is taken from Miller et al. (1987) and compares the abundance of the first moult class recruited to the fishery to the abundance of the second moult class one year later. Fishing mortality (F) is then obtained by subtracting natural mortality ($M = 0.15$) from total mortality (Z). Based on unpublished observations by M. Comeau and M. Mallet (DFO, Gulf Fisheries Centre, Moncton, New Brunswick), the annual rate of natural mortality (M) was taken to be 0.15, of which 0.1 was attributed to moulting and the remainder to other events. For the model, the portion of M associated with moulting could vary uniformly between 0.08 and 0.12 and the portion of M associated to other events could vary between 0.04 and 0.06. Size-specific fecundity of females was obtained from the relationship $Y = 0.00256 \times CL^{3.409}$ described by Campbell & Robinson (1983), where Y is the number of eggs.

## Population trends

### *Field sampling*

The impact of the MLS increase on the population was based on the analysis of data from a fishery-dependent sampling programme, performed annually since 1985 off the Magdalen Islands. Sampling is done three times during the 9-week fishing season, at the beginning (first and second weeks), middle (fifth week), and end (last 2 weeks of the fishing season). At each period, the catch from the whole set of traps of four different fishing boats (out of a total of c. 150) is characterised at-sea. All lobsters (legals, sub-legals) are sexed and CL is measured. Each year, between 5000 and 8000 trap-caught lobsters are measured. Although sampling was also done in 2003, data were excluded from the present analysis because the size of the escape vents was modified by law and therefore trap selectivity changed.

Abundance indices of the different components of the population are expressed in terms of catch-per-unit-effort (CPUE), i.e., the number of lobster caught per trap. Size of traps does not vary among fishers and sampling is limited to traps with a soak time of 24 h. A value of CPUE is obtained for each of the three sampling periods by dividing the sum of trapped lobster by the sum of trap hauls. A mean value for the whole season is obtained by averaging the three values, after weighting them by their respective contribution to the total fishing season (3 weeks for the beginning of the fishing season, 4 weeks for the middle, and 2 weeks for the end).

For each year, the size structure of the population is obtained by two different methods, depending on the population component. For the commercial fraction of the population (males and non-ovigerous females ≥MLS), the overall size structure is obtained by grouping the size-frequency distributions obtained at each sampling period, after weighting them for landings recorded during each sampling period, i.e., landings of weeks 1–3 for the beginning of the fishing season, landings of weeks 4–7 for the middle of the season, and landings of weeks 8–9 for the end of the season. This allows the determination of the total number of lobster landed during a given year, as a whole, or in each size class. Size-frequency distribution of ovigerous females is obtained by grouping together all ovigerous females caught during the three sampling periods. The numbers are then divided by the total number of traps hauled.

### *Data analysis*

The impact of MLS increase on the abundance of ovigerous females was assessed by comparing the changes in annual CPUEs. Comparisons were done for all ovigerous females, for ovigerous females between 76 and 81 mm CL, which corresponds to the newly protected size classes and includes mainly primiparous females, and for large ovigerous females (≥90 mm CL) considered to be multiparous females. Mean CPUE were computed for three different periods: the period of 1994–96, before the increase in MLS, the transition period of 1997–99 corresponding to the first years of MLS increase, and the period 2000–02 corresponding to the recent increases in MLS. Mean CPUE values were compared using one-factor ANOVA after conditions of normality and homocedasticity were confirmed. When significant differences were detected ($P < 0.05$), a Tukey *a posteriori* multiple comparison test was carried out (Sokal & Rohlf 1995). An index of egg production was also computed for each period by combining the size structure of ovigerous females weighted by the index of abundance (CPUE) and the size-specific fecundity.

## RESULTS

### Egg-per-recruit production

Table 1 shows the means and SDs for the 100 absolute values of EPR and increment factors relative to 1996 calculated for each scenario of MLS increase. In 1996, with a MLS of 76 mm CL, EPR averaged 3636 ± 1199 eggs in the southern Magdalen Islands. From the simulation model, the objective of doubling EPR relative to 1996 levels (increment factor of 2) was expected to be achieved by increasing MLS to 83 mm CL.

The risk of not doubling EPR was considered to be 100% up to 81 mm CL. Raising the minimum size to 82 mm CL reduced the risk to 86%, and raising the size to 84 mm CL reduced the risk to only 24%. Increasing MLS to 83 mm CL results in a risk of 50% (Gendron & Gagnon 2001).

### Population trends

*Size structure of the lobster population*

The increase in MLS caused a gradual shift in the size-frequency distribution of commercial lobsters (Fig. 3). The 2002 size-frequency distribution differs markedly from that of 1996. The mean size of lobster caught in 1996 was 83.5 mm CL compared with 88.7 mm CL in 2002. This represents a 22% increase in mean individual weight, from a mean of 471 g in 1996 to 581 g in 2002. Both size distributions are highly truncated and landings are mainly composed of lobsters from the first moult class recruited to the fishery.

In both years, males were slightly more abundant than females. Sex ratios (M:F) were 1.12 : 1 in 1996 and 1.13 : 1 in 2002. Males were larger than females in both years. In 1996, the mean CL was 84.8 mm for males compared with 82.2 mm for females. In 2002, mean CLs were 90.2 and 87.3 mm for males and females, respectively. The total number of lobsters caught was 3.0 and 2.7 million for 1996 and 2002, respectively. Although the numbers were lower in 2002, weight of landings was higher, because of the larger size of lobsters, reaching 1563 t compared with 1479 t in 1996.

*Ovigerous females*

From 1985 to 2002, the number of ovigerous females per trap fluctuated between 0.06 and 0.21 (Fig. 4). In the period preceding the increase in MLS, the abundance of ovigerous females reached relatively high levels in 1991 and 1992, during a period when the abundance of lobster was greatest. This is reflected by the CPUE of commercial lobsters (≥MLS) (see Gendron & Savard 2003a) which are considered to approximate abundance well. From 1993 to 1996, the abundance of ovigerous females dropped markedly, despite a slight increase in lobster overall abundance between 1994 and 1996. From 1997 to 2002, as MLS was increased at a pace of 1 mm per year, the abundance of ovigerous females increased steadily, reaching its maximum value in 2002.

**Table 1** Mean and standard deviation (SD) of egg-per-recruit production and increment factor from the simulation model at different minimum legal sizes (MLS) in the southern part of the Magdalen Islands, Quebec, Canada. Reference size for the increment factor is 76 mm carapace length.

| | Egg production per recruit (no. of eggs) | | Increment factor | |
|---|---|---|---|---|
| MLS | Mean | SD | Mean | SD |
| 76 mm | 3636 | 1199 | – | – |
| 78 mm | 4147 | 1286 | 1.15 | 0.05 |
| 79 mm | 4555 | 1361 | 1.27 | 0.07 |
| 80 mm | 5059 | 1446 | 1.41 | 0.10 |
| 81 mm | 5734 | 1481 | 1.60 | 0.14 |
| 82 mm | 6320 | 1616 | 1.78 | 0.18 |
| 83 mm | 7167 | 1639 | 2.02 | 0.24 |
| 84 mm | 7850 | 1753 | 2.24 | 0.30 |

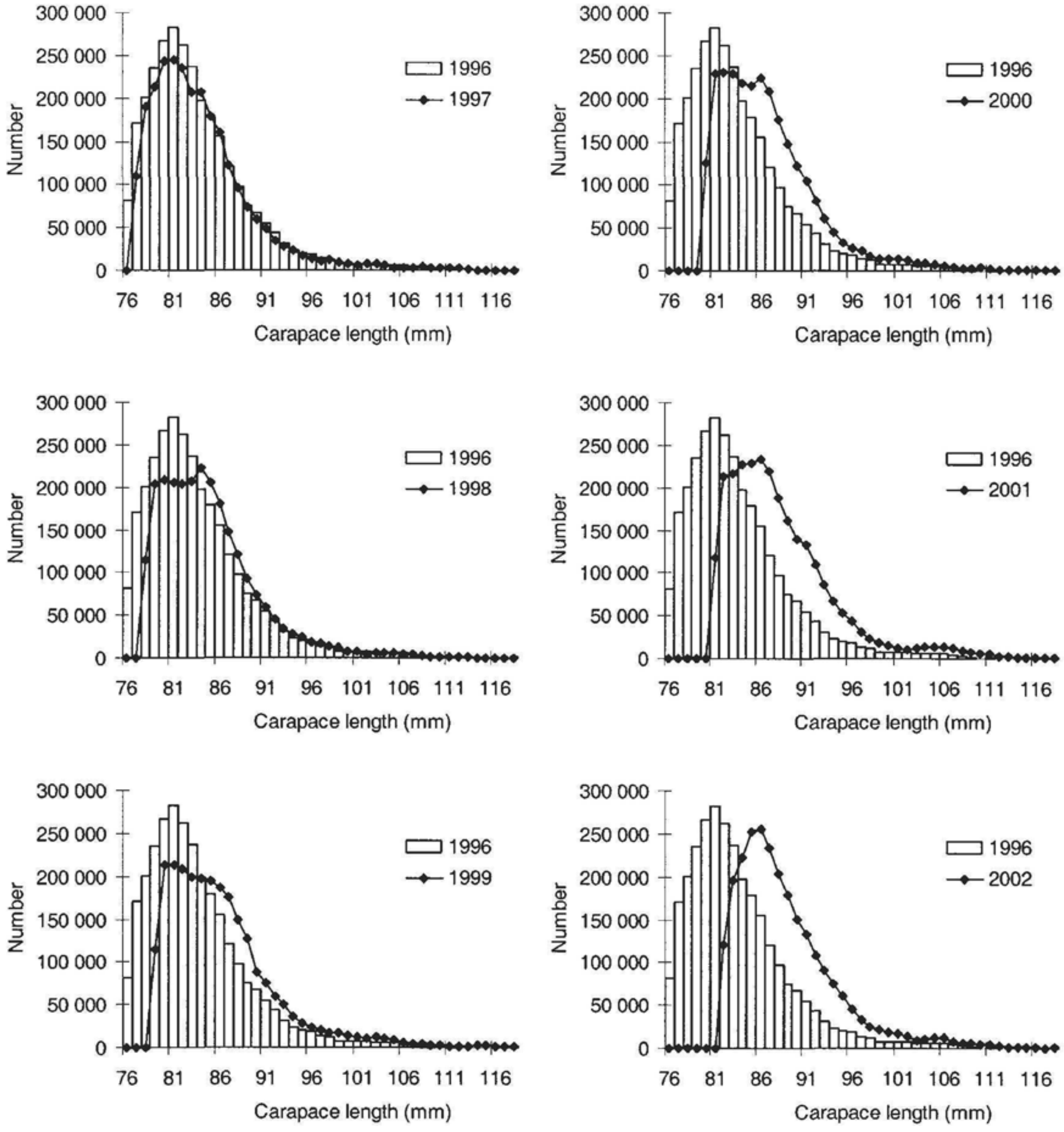


**Fig. 3** Size-frequency distributions of commercial lobsters (males and non-ovigerous females) in numbers weighted by the landings for the southern part of the Magdalen Islands, Quebec, Canada from 1996 to 2002.

The abundance of ovigerous females (all sizes), expressed as the mean CPUE in number of ovigerous females per trap changed significantly between the three periods ($F = 19.70$, $P = 0.0023$, d.f. = 2). Abundance in recent years (2000–02) was significantly higher than the abundance recorded during the 3-year period (1994–96) preceding the increase in MLS and during the first years (1997–99) of the increase in MLS (Fig. 5A). The abundance of ovigerous females observed during the transition period (1997–99) showed intermediate values that did not vary significantly from the preceding period (1994–96).

Significant differences were also noted when comparing the abundance of ovigerous females of 76–81 mm CL among the three periods ($F = 30.88$,

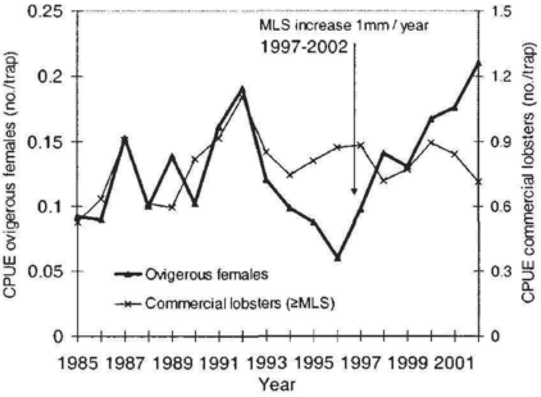


**Fig. 4** Abundance of ovigerous females expressed in catch-per-unit-effort (CPUE) in number of ovigerous females caught per trap, in the southern part of the Magdalen Islands, Quebec, Canada from 1985 to 2002. Line in background represents the CPUE of commercial lobsters, minimum legal size (MLS) for this area for the same period.

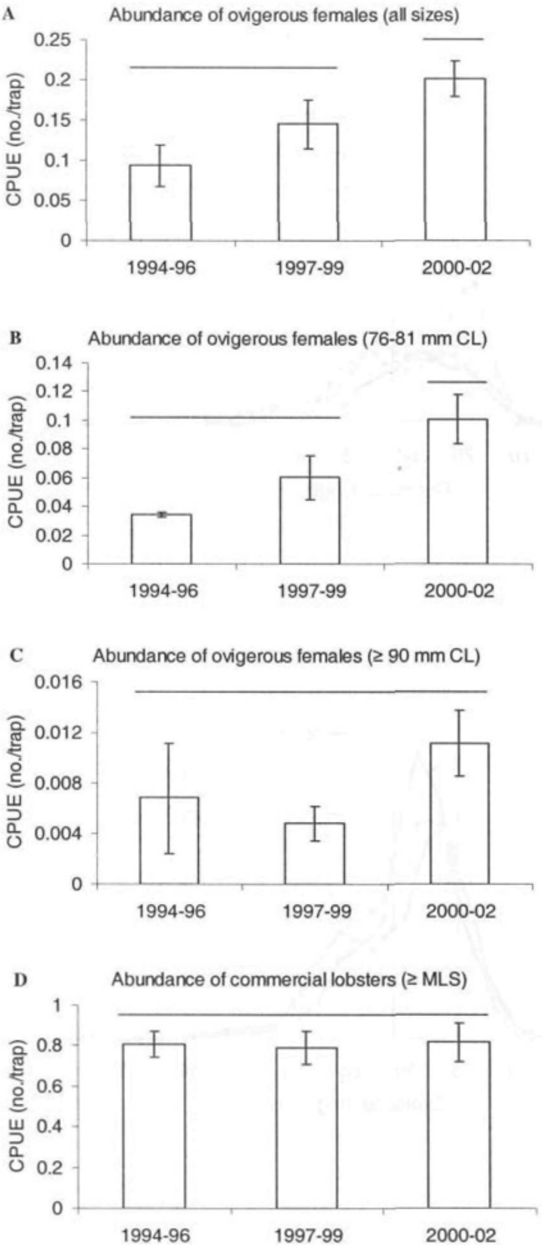


**Fig. 5** Comparison of mean catch-per-unit-effort (CPUE) of ovigerous females in the southern part of the Magdalen Islands, Quebec, Canada for three different 3-year periods: 1994–96, before the increase in minimum legal size (MLS); 1997–99 at the beginning of the increase in MLS; and 2000–02 by the end of the MLS increase programme, and for three categories: **A**, females of all sizes; **B**, females 76–81 mm carapace length (CL); **C**, females 90 mm CL; and **D**, the mean CPUE of commercial lobsters ( MLS) during the three periods. Periods showing no significant differences in mean CPUE ($P > 0.05$) share a common line.

$P = 0.0007$, d.f. = 2). Ovigerous females from these newly protected size classes were significantly more abundant in the recent 3-year period (2000–02) than before the beginning of the increase in MLS (the 1994–96 period), or during the period corresponding to the first years of increase in MLS (1997–99) (Fig. 5B). CPUE of ovigerous females in this size category increased from 0.034 per trap in the 1994–96 period to 0.10 per trap for the 2000–02 period, which corresponds to a 3-fold increase.

The largest ovigerous females (≥90 mm CL) decreased in abundance during the 1997–99 period compared with the 1994–96 period (Fig. 5C). The abundance increased in the 2000–02 period relative to the 1997–99 period to levels comparable to those observed in 1994–97. Differences between periods were, however, not significant ($F = 3.11$, $P = 0.1184$, d.f. = 2).

The changes in the abundance of ovigerous females were observed during a period where lobster recruitment was fairly stable. Mean CPUE of commercial lobsters (≥MLS) did not differ significantly among the three periods ($F = 0.04$, $P = 0.9598$, d.f. = 2) (Fig. 5D).

The increase in the number of ovigerous females of 76–81 mm CL between the 1994–96 and 2000–02

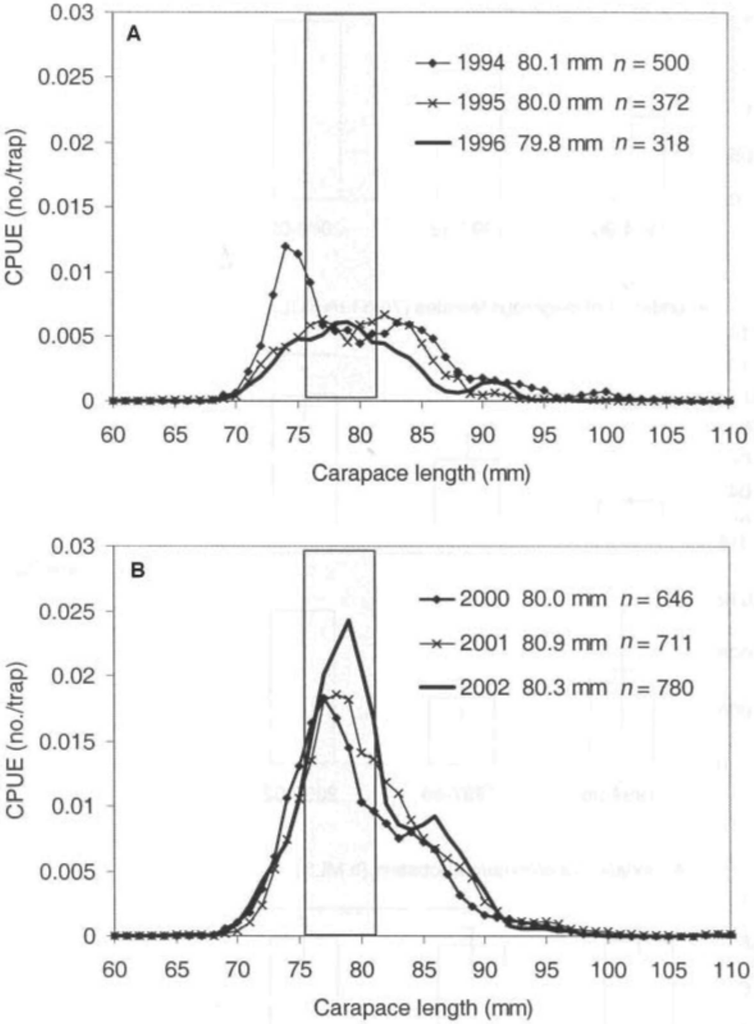


**Fig. 6** Size-frequency distributions of ovigerous females in number per trap for the southern part of the Magdalen Islands, Quebec, Canada during **A**, the 1994–96 period and **B**, the 2000–02 period. Shaded area represents the range of the newly protected size classes following the increase in minimum legal size (MLS). Mean size and number of ovigerous females sampled are indicated.

periods is visible from the size-frequency distributions presented in Fig. 6. Mean size of ovigerous females varied little over the years. Values recorded in the 1994–96 period ranged from 79.8 to 80.1 mm CL and from 80.0 to 80.9 mm CL during the 2000–02 period. However, a shift of the mode can be seen, especially in the 2000–02 period, increasing at the same pace as the increase in MLS, from 77 mm CL in 2000 to 78 mm CL in 2001 and to 79 mm CL in 2002. In addition, in the most recent years, especially in 2002, a second mode at c. 86 mm CL became apparent.

### *Index of egg production*

Cumulative egg production as a function of size is presented for the 1994–96 (Fig. 7A) and for the 2000–02 periods (Fig. 7B). The mean egg production index calculated for 1994, 1995, and 1996 was 755 eggs. The egg production index calculated for 2000, 2001, and 2002 indicates a 2-fold increase (1.9–2.4) over the 1994–96 period. For both periods, 50% of egg production came from females that were below 80 or 81 mm CL, which are considered to be primiparous females. The proportion of egg production from multiparous females (≥90 mm CL)

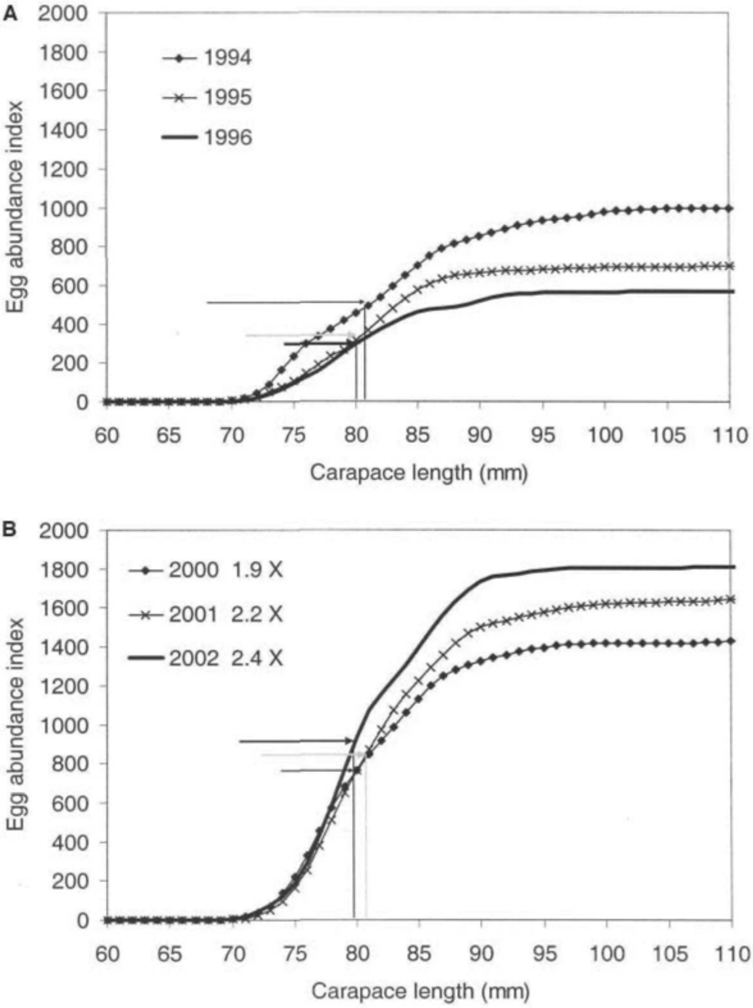


**Fig. 7** Cumulative frequency distribution of egg production of ovigerous females of the southern part of the Magdalen Islands, Quebec, Canada as a function of size for **A**, the 1994–96 period, before the minimum legal size (MLS) increase and **B**, the 2000–02 period, corresponding to the latest increases in MLS. Arrows indicate for each year, the size at which 50% of total egg production is obtained. Numbers in B indicate the increase relative to the mean index of egg production calculated for the 1994–96 period.

varied from 6% to 14% in the 1994–96 period and from 4% to 9% in the 2000–02 period. Relative contribution of multiparous females to egg production was lower in recent years.

## DISCUSSION

The MLS was increased gradually from 1997 to 2003 in the Magdalen Islands, at a pace of 1 mm each year. For various reasons, but mostly for effectiveness and ease of enforcement, industry, science, and fishing communities favoured the increase in MLS as a means of achieving the goal of doubling EPR. This tool was chosen in preference to decreasing fishing effort by several different ways as suggested by Gendron & Brêthes (2002), introducing a maximum legal size, and "v-notching" females (Gendron & Gagnon 2001).

The model used for the calculation of EPR allowed for the inclusion of uncertainty, providing an objective assessment of the reliability of the EPR estimates. The translation of uncertainty into probabilistic statements of reaching a goal provided managers with a direct illustration of the risks associated with their decisions. Risk analysis has not yet been broadly applied to American lobster. This was the first attempt in Canada and for the moment, the level of management risk acceptable to managers was not formally determined. In the Magdalen Islands, the level of MLS increase was set to avoid a risk greater than 50% of not reaching the goal. The model does not incorporate uncertainties associated with the response of lobster populations to the implementation of the new conservation measures. The model assumes that there is no compensatory effect and that implementing new management measures does not alter any aspect of the lobster's biology. If compensatory mechanisms exist in lobster populations, EPR values may be different from those calculated here.

Detecting changes in wild lobster populations resulting from MLS increase that can be attributed to changes in management measures represents a challenge. Often, they are difficult to isolate from natural changes in the population, or from changes caused by shifts in fishing patterns, especially when population surveys are fishery-dependent. Nevertheless, the changes that have been observed in the size structure of the overall population and the increase in abundance of ovigerous females of the lobster population of southern Magdalen Islands are assumed to be the result of the increase in MLS, even though no control exists (e.g., adjacent areas where management measures remained constant) to verify this assumption. Ease of detection in this instance may be a result of several factors: (1) the increase in MLS was important (6 mm CL); (2) the increase was constant and sustained over a significant period of time, giving the opportunity to see gradual changes as they occurred; (3) the increase in MLS from 76 mm CL to 82 mm CL corresponds to a size range where the slope of the female maturity ogive is the steepest; (4) the increase in MLS occurred in a period when lobster recruitment was apparently constant; (5) the size at sexual maturity did not change over the study period (Gendron 2003); (6) the sampling protocol was standardised and remained the same over the whole study period; and (7) the fishing practices and fishing gears did not change over most of the study period. This last point may have been crucial to success since population monitoring was based on trap-caught animals during the commercial fishery. Similar changes observed in the lobster population from the northern part of the Magdalen Islands (Gendron & Savard 2003a) and in the Gaspé (Gendron & Savard 2003b), following increases in MLS of similar magnitudes, further support the contention that changes in the lobster population described herein are management-based.

Except for the first year, these small increases in MLS had no perceptible impact on landings and were easily accepted by fishers. A review of the catch composition of the 1996 landings data had shown that lobster measuring between 76 and 77 mm CL accounted for only 4% of the catch (Gendron & Savard 2000). In addition, losses in landings in the first year of the increase in size were assumed to be offset the following year because some of the lobsters saved the first year would become available to the fishery the next year at a larger size. Growth data show that lobster in this size range moult each year and increase in size by 15%, which corresponds to an increase in weight up to 45% (Dubé 1985). It was also assumed that gains in weight would compensate for losses in numbers by natural mortality. Given these assumptions, the increase in MLS would have permitted increased yield-per-recruit and therefore reduced a problem of growth overfishing.

In this particular situation, the goal of doubling EPR proved also to have some conservation benefits for lobster populations by reducing fishing pressure on immature animals. In the Magdalen Islands, at least in its southern part, the increase in MLS provided the opportunity to set the legal size above the size at sexual maturity. In this part of the Islands, size at sexual maturity is reached c. 79 mm CL (Dubé & Grondin 1985; Gendron 2003). Based on existing female maturity ogives, at a MLS of 76 mm CL, females had less than 30% probability of reaching sexual maturity before entering the fishery. The probability has increased up to 80% with the current MLS of 83 mm CL.

One of the issues that has not been taken into account in this study and in most work dealing with EPR is the question of egg quality. Studies by Attard & Hudon (1987) showed that larger females produce bigger eggs with a greater caloric content than those of smaller females. More detailed studies by Plante et al. (2001) and Ouellet & Plante (2004) in the Magdalen Islands on maternal effects on eggs and larvae suggest that the reproductive status of the female (primiparous versus multiparous) could be more important than size. Eggs and hatching larvae (stage I) from the larger, presumably multiparous females were significantly larger than those from smaller females, mostly primiparous. Female size explained very little of the variance in mean larval size at hatching, when the entire size range of reproductive females was considered. Additional observations also suggest that larger larvae could grow more efficiently. Other work by James-Pirri et al. (1998) showed that larger, heavier larvae grow more rapidly and settle at larger sizes. All of these characteristics may indicate a better potential for survival. These observations point to the fact that conservation measures should aim to ensure that some multiparous females contribute to egg production. In this study, females were considered as multiparous at sizes ≥90 mm CL. Their numbers and their relative contribution to egg production did not increase significantly following MLS increase. Increase in MLS reduces fishing pressure on immature lobsters and favours the contribution of primiparous lobsters to egg production. When fishing mortality is high, as it still is in the Magdalen Islands lobster populations, the chances of seeing multiparous females remain low. However, a second mode of ovigerous females at c. 86 mm CL has appeared in recent years, and it could possibly include multiparous females. Additional work is necessary to better detect female reproductive status and determine more precisely the size at which females have a high probability of becoming multiparous. In this way, monitoring of multiparous females in the wild population would be facilitated and assessed more precisely.

The increase in MLS appears to have been successful in many aspects as shown above. However, as already pointed out by Fogarty & Gendron (2004), because this measure has not been accompanied by a reduction in fishing intensity, some undesirable effects may eventually occur. For example, since ovigerous females are protected from the fishery, the greater protection afforded to females compared with males may result in an asymmetry in fishing mortality between males and females. As a result, the sex ratio could become biased in favour of females and the number of large males could be further reduced. The impact of these changes is not known and research is now under way on the American lobster's mating system to determine whether this species is potentially vulnerable to sperm limitation as observed in rock lobster (*Jasus edwardsii*) and spiny lobster (*Panulirus argus*) (MacDiarmid & Butler IV 1999). Gosselin et al. (2003) showed that similarly sized females accumulated more ejaculate when mated with large males compared with small males. Examination of the seminal receptacle content of females from the Magdalen Islands, where the lobster population is heavily fished, suggested that they were mating mainly with small males. These preliminary observations warrant further studies to determine whether sperm may actually be limiting to females, as well as close monitoring of size of males and size-specific sex ratios in the population. To date, the overall sex ratio in the Magdalen Islands lobster populations appears to be balanced.

The benefits of doubling EPR for lobster conservation were questioned at the time this goal was adopted, preferably to a limit reference point expressed relatively to a virgin population (e.g., 5% or 10% EPR of a virgin stock). It was recognised that conservation benefits would not be equal among lobster populations and most probably would be smaller in areas that needed them the most. Benefits would depend on the initial level of EPR of individual populations. In areas where EPR was very low, simulations showed that doubling EPR could be reached easily with slight changes in management measures, providing minimal additional conservation benefits. It was therefore suggested that doubling EPR be considered only as an interim rather than a final goal. The idea of setting a limit to lobster EPR has not been totally discarded in Canada. This could be done in the context of implementing a precautionary approach to lobster management. As was recently pointed out by Fogarty & Gendron (2004), progress in our understanding of the mechanisms—either density-dependent or independent—affecting stock abundance, and the recognition of possible shifts in the production regimes, will help better define the different possible states of the stock-recruit relationship. This will contribute to setting EPR limits that are sufficiently robust to ensure conservation over a range of environmental and ecological conditions.

Considerations expressed above point to the necessity of developing a multi-dimensional approach to lobster conservation by including alternative reference points that are based on demographic or other features of lobster populations. A unidimensional approach to lobster conservation, such as the one centered on the model-based EPR reference, might prove insufficient to account for all facets of lobster life history that are important for long-term sustainability of lobster populations.

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# Modelling the effects of Marine Protected Areas (MPAs) on the southern rock lobster (*Jasus edwardsii*) fishery of Victoria, Australia

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**Abstract** Since 2002, 5.3% of the Victorian coastal waters have been declared as Marine Protected Areas (MPAs). These are aimed at safeguarding important marine habitats and species, significant natural features, and areas of cultural heritage and aesthetic value. However, MPAs impact the fishery for southern rock lobster (*Jasus edwardsii*), as total allowable catches (TACs) were previously set to allow the biomass to recover to pre-specified target levels. The model on which assessments and risk analyses are based is extended to include the impact of MPAs. The MPAs and the area open to fishing are modelled as subpopulations with different levels of mortality and consequently different density and population size-structure. A range for the probability of a lobster moving from a MPA to the fished area from 0 to 15% is considered, based on the results of tagging studies. The reduction of biomass available to the commercial fishery because of the introduction of MPAs is estimated to be 8% and 16% (Western and Eastern Zones) respectively. The results of a risk assessment show that if the current TACs are maintained, the time to increase the biomass available to the commercial fishery by 50% would be delayed 5–9 years in the Western Zone and 1–4 years in the Eastern Zone because of the impact of displaced effort. In contrast, spawning biomass in the Eastern Zone is currently below the agreed limit reference point, and the introduction of MPAs would enhance the rate of recovery, although only marginally initially, faster than the absence of the MPAs.

**Keywords** spiny lobster; rock lobster; Marine Protected Area; Marine Reserve; modelling; reference points; risk assessment

## INTRODUCTION

Southern rock lobster (*Jasus edwardsii*) is found from south-western Western Australia to southern New South Wales, and in the waters around Tasmania and New Zealand. The catch of southern rock lobster off Victoria (currently 510 t annually; landed value AU$18 million) represents 10% of that off south-eastern Australia. Most of this catch is exported to Japan, China-Taiwan, and the United States. The fishing season in Victoria runs from November to August, with an annual closed season for females from 1 June to 15 November, and for males between 1 September and 15 November.

The stock structure of southern rock lobsters, particularly the dynamics of recruitment, is currently unknown and the fisheries in each Australian state are managed under the assumption that separate stocks are found in each state. The fishery in Victoria is managed as two zones (Fig. 1): the Western Zone (west of Apollo Bay to the South Australian border) and the Eastern Zone (east of Apollo Bay to the New South Wales border). Most of the catch (85%) is taken from the Western Zone. Quota management was introduced into the fishery at the start of the

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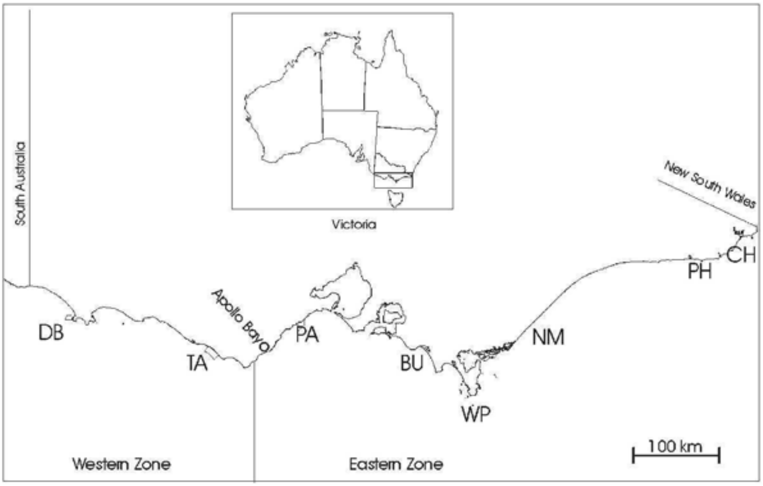


**Fig. 1** Map of Victoria, Australia showing the rock lobster (*Jasus edwardsii*) fishery Management Zones and the locations of the eight Marine Protected Areas referred to in this paper. (DB, Discovery Bay; TA, Twelve Apostles; PA, Point Addis; BU, Bunurong; WP, Wilson's Prommentry; NM, Ninety Mile Beach; PH, Point Hicks; CH, Cape Howe.)

2001–02 fishing season (referred to hereafter by the first year of the season) with the objective of allowing recovery of biomass. At that time, the available biomass (the biomass of lobsters that is available to the commercial fishery—larger than the minimum legal size, and in the area available open to fishing) was estimated to be 25% and 17% (Western and Eastern Zones respectively) of the available biomass in 1951, the first year for which information on catch and effort is available (Hobday & Smith 2001). Total allowable catches (TACs) of 450 and 60 t were set for the Western and Eastern Zones respectively. These TACs were based on the results of a risk analysis that compared a variety of alternative harvest regimes (Hobday & Punt 2001).

A management plan for the Victorian rock lobster fishery was introduced in 2003 which specified that 20% and 40% of the spawning and available biomasses at the start of 1951 were to be limit and target reference points for the fishery (Department of Primary Industries 2003). These particular reference points were agreed to by a group consisting of scientists, managers, and industry, and reflect objectives related to conservation (spawning biomass) and yield (available biomass). The spawning biomass reference points refer to the entire spawning biomass (within the area open to fishing and in the Marine Protected Areas (MPAs)) whereas the available biomass reference points refer to the biomass in the open area only.

Thirteen MPAs and 11 marine sanctuaries covering 54 000 ha or 5.3% of Victoria's marine waters are being established. The Eastern Zone MPAs were introduced in November 2002 and the Western Zone MPAs were introduced in April 2004. The MPAs are aimed at safeguarding important marine habitats and species, significant natural features, areas of cultural heritage and aesthetic value and do not have an explicit fisheries objective (Environment Conservation Council 2000). Only the eight largest MPAs are considered explicitly in this paper because the remaining five are sufficiently small to be inconsequential in terms of their effect on the rock lobster population and fishery. The eight MPAs comprise areas of rocky reef to a substantial extent, and consequently conflict with traditional fishing practices, particularly for rock lobster and abalone.

Several studies (e.g., Polacheck 1990; Sladek Nowlis & Roberts 1998; Apostolaki et al. 2002) have argued that higher yields can be achieved through the imposition of MPAs than through control of fishing effort and catch. Instances in which this could occur include, for example, when the MPA reduces growth overfishing by protecting juveniles (Guénette et al. 1998). However, the bulk of these studies have assumed that fishing mortality is currently not controlled, managers have perfect information about stock size and the biological parameters of the population, and future management is based on setting a target level of fishing mortality.

In contrast, modelling work in Tasmania has suggested that the introduction of a large MPA may be detrimental without a reduction in catch of at least that displaced by the MPA (Haddon et al. 2003).

Stock assessments of the populations of southern rock lobster off Victoria were based on fitting a sex- and size-structured population model to data on catches, catch-rates, and catch length-frequency (Hobday & Punt 2001). The establishment of MPAs in Victoria occurred just after the introduction of

TACs, and no reduction in TAC occurred to compensate for the reduction in the area open to fishing.

This paper describes an approach to stock assessment that includes MPAs, and then examines the effect of MPAs on rebuilding to the target reference points for the fishery (available biomass in the each Zone and spawning biomass in the Eastern Zone) for the current levels of TAC.

## METHODS

### Data sources

*Commercial and recreational fishery data*

The annual catches (by weight) of lobsters and effort (pot lifts) were obtained from commercial fisher returns between 1951 and the end of the 2002 fishing season. Catch (by number) data are available from the 1978 fishing season. The only data on the catch of lobsters off Victoria by recreational divers are based on the results of a dive-shop survey conducted during the 1993 season, which estimated the catch by SCUBA divers to be 10% of the commercial catch in the Western Zone and 2% of that in the Eastern Zone (Hobday & Smith 1997). The annual recreational catch for both zones in all other years is estimated as the product of the annual commercial catch and the ratio of the SCUBA catch to the commercial catch for 1993. Length-frequency distributions by sex were obtained from the commercial catches by catch sampling and from research observer programmes (Hobday & Smith 1997). Length-frequency data are available from catch sampling programmes during 1962–66 and 1995–2002 for the Eastern Zone and during 1960–66, 1972, 1973, and 1993–2002 for the Western Zone. Research observer data are available for both zones from 1994 and were collected by both research staff and commercial fishers, and contain biological measurements and position information.

*Estimating lobster catches within MPAs*

Estimates of the biomass of lobsters within each MPA before they were declared (expressed as a proportion of that in the entire Management Zone) were obtained under the assumption that catches in an area are a proxy for the biomass in that area. The rationale for this assumption is that catch rates within and outside MPAs were examined and found to be similar, thus indicating that the biomass was distributed evenly across the areas fished. The challenge was to be able to determine the catches within each MPA, given the differences between the scale at which fishery data are reported and the scale of the MPAs. Commercial catch and effort data are reported by 10′ sections of longitude and depth. However, the MPAs did not align with the data reporting scheme so the catches by 10′ section had to be allocated to each MPA. Two methods were applied depending on data availability: (1) for areas where sufficient research observer and tagging data were available, the catch within and outside each MPA was apportioned according to the proportion of observations in each area; and (2) for areas with little or no research or tag data, relative areas were calculated using a GIS and the catch distributed accordingly.

The latter method assumes a uniform distribution of the catch or biomass, which is not generally so, but, because the main MPAs are generally within significant lobster habitat, the research observer data method was applicable to the larger MPAs.

*Movement*

Movement rates of lobsters were investigated for each of the MPAs using tag-recapture data collected as part of a wider research programme; a total of 30 368 lobsters were tagged throughout the State during the 9-year period 1994–2003 (recapture rate 14%). Of these, 597 tags have been released or recaptured within the boundaries of the MPAs before their establishment (as defined by the position data in each tag record). Only those recaptures that were at liberty for a minimum of 20 days were used for the analyses of this paper. The numbers of lobsters moving into, out of, or remaining within the MPA were determined and movement rates established.

### Population modelling

*Population dynamics model*

Basic stock assessment model

The number of animals of sex $s$ in size-class $l$ at the start of year $t$ +1, $N^s_{t+1,l}$, is defined according the equation:

$$N^s_{t+1,l} = \sum_{l'} X^s_{l',l} N^s_{t,l'} e^{-M} \{1 - S^s_{t,l'} F_t\} + R^s_{t,l} \tag{1}$$

where $X^s{}_{l',l}$ is the fraction of animals of sex $s$ in size-class $l'$ that grow into size-class $l$ at the end of the year, $M$ is the instantaneous rate of natural mortality (assumed to be independent of size, sex, and time), $S^s_{t,l}$ is the selectivity of the gear on animals in size-class $l$ during year $t$ (selectivity is time-dependent to allow for changes over time in minimum size limits), $F_t$ is the exploitation rate on fully-selected (i.e., $S^s_{t,l} \rightarrow 1$) animals during year $t$, and $R^s_{t,l}$ is the recruitment of animals of sex $s$ to size-class $l$ at the end of year $t$.

Males and females differ in the number of size-classes and the width of each size-class because of differences in, for example, growth and minimum size limits. Specifically, each size-class is 10 mm for males and the model considers carapace lengths (CL) from 80 to 200 mm (all animals 190 mm and larger are pooled in the 190–200 mm size-class) whereas each size-class is 5 mm for females, and the model considers CL from 80 to 165 mm (all animals 160 mm and larger are pooled in the 160–165 mm size-class). Recruitment is assumed to occur to the first size-class (males: 80–90 mm; females 80–85 mm) and the sex-ratio at recruitment is assumed to be 1:1.

The fully-selected exploitation rate for year $t$ is computed from the catch (commercial and recreational; illegal catches are unquantified and ignored) for that year, assuming that the catch is taken in the middle of the year, and that selectivity for commercial and recreational fishers is the same, i.e.:

$$F_t = \frac{C_t^{\mathrm{comm}} + C_t^{\mathrm{rec}}}{\sum_l \sum_s S^s_{t,l} W^s_l N^s_{t,l}\, e^{-M/2}} \qquad (2)$$

where $C_t^{\mathrm{comm}}$ is the commercial catch during year $t$, $C_t^{\mathrm{rec}}$ is the recreational catch during year $t$, and $W^s_l$ is the weight of an animal of sex $s$ in size-class $l$.

The first year considered in the model is 1951. The 1951 size-structure is determined by assuming that the population was in equilibrium with an estimated exploitation rate ($F_{\mathrm{init}}$) at the start of 1946 and then projecting the population forward with stochastic recruitment and an exploitation rate of $F_{\mathrm{init}}$ from 1946 to 1951.

The model has many parameters. However, those related to growth, natural mortality, and selectivity are determined from auxiliary analyses (see Hobday & Punt (2001) for details). The remaining parameters of the model (the mean recruitment over the assessment period ($\bar{R}$) the logarithms of the annual deviations in recruitment about the mean recruitment ($\ln(R_y/\bar{R})$, and $F_{\mathrm{init}}$)) are determined by fitting it to data on catch-rates, the length-frequency of the commercial catch, and estimates of the annual catches in numbers (Punt & Kennedy 1997; Hobday & Punt 2001).

The results from the assessment are random draws from a Bayesian posterior distribution. The prior distributions for $F_{\mathrm{init}}$ and $\bar{R}$ are chosen to be uninformative whereas the prior distribution for $\ln(R_y/\bar{R})$ is normal with mean 0 and standard deviation 0.6 (Hobday & Punt 2001; Table 1). The Markov Chain Monte Carlo method (MCMC; Hastings 1970; Gelman et al. 1995; Punt & Hilborn 1997) based on a single chain of 1 000 000 cycles is used to generate the random samples from the posterior. A variety of diagnostic statistics are applied to ensure that the MCMC algorithm has converged adequately to the posterior distribution. MPAs off Victoria were imposed only in 2002 so they have no impact on the period included in the assessment (1951–2002), i.e., the assessment is conducted under the assumption that the population is distributed randomly within each zone or (more likely) that exploitation is uniform over the range of the population. The Bayesian posterior distribution underestimates the true extent of uncertainty because no account is taken of the uncertainty resulting from growth, natural mortality, and selectivity.

### Extensions to allow for MPAs

The assumption that exploitation is uniform over the range of the population will be violated to some extent in the past, particularly during the early years

**Table 1** Parameters of the model and their prior distributions. Parameter values fixed using auxiliary information are denoted as "fixed".

| Parameter | Description | Prior distribution |
|---|---|---|
| $\ln(R_y/\bar{R})$ | Logarithm of the annual recruitment divided by mean recruitment | $N(0;0.6^2)$ |
| $\ln\bar{R}$ | Mean recruitment | $U(-,)$ |
| $F_{\mathrm{init}}$ | Exploitation rate during 1946–50 | $U(0,1)$ |
| $M$ | Natural mortality | Fixed |
| $S^s_{t,l}$ | Commercial selectivity as a function of sex and length | Fixed |
| $W^s_l$ | Weight as a function of sex and length | Fixed |

of the fishery, and the imposition of MPAs will lead to large areas in which the exploitation rate is effectively zero.

The model outlined above can be extended to take account of a situation in which there is a "fished area" and several MPAs. Although allowance is made in the model for multiple MPAs to allow questions related to the timing of the imposition of MPAs to be examined, the analyses in this paper are based upon all the MPAs being introduced at the same time within each Management Zone (2002—Western Zone; 2004—Eastern Zone). The fraction of the recruitment to the fished area and to each of the MPAs is assumed to be proportional to the "size" of the area concerned. It is also necessary to allow for movement of post-recruit animals (assumed to occur at the start of the year before growth and mortality). The analyses of the paper only evaluate scenarios in which movement occurs from the MPAs into the fished area (i.e., the MPAs are a source of adults). This is consistent with results from tagging studies in the MPAs showing a net migration out of the MPAs (see Results). Given these assumptions, Equation 1 becomes:

$$N_{t+1,l}^{s,A} = \sum_{l'} X_{l',l}^{s} \left( \sum_{A'} Z^{A',A} N_{t,l'}^{s,A'} \right) e^{-M} \{1 - S_{t,l'}^{s} F_t^{A}\} + \lambda^A R_{t,l}^{s} \qquad (3)$$

where $N_{t,l}^{s,A}$ is the number of animals of sex $s$ in size-class $l$ at the start of year $t$ in area $A$ (fished area $A$=1; MPAs $A$>1), $Z^{A',A}$ is the fraction of the animals in area $A'$ that move to area $A$ at the start of the year (assumed to be independent of size, sex, and time), and $\lambda^A$ is the "size" of area $A$ relative to the size of the entire management zone. As noted above, $\lambda^A$ has been assumed to be equal to the fraction of total catch taken from area $A$ (over 1998–2000) within the management zone being modelled in the absence of empirical information about the source-sink dynamics of rock lobsters off Victoria.

### Projecting forward

The implications of different management arrangements (catch limits for the commercial fishery, minimum size limits, and MPAs) are evaluated by the changes in the available biomass in the fished area and the total spawning biomass (MPAs and the area open to fishing) over the 10-year period 2002–12. The recreational catches for the projection period are based on a recreational exploitation rate of 2% and 10% of the average of the exploitation rates in the Eastern and Western Zones respectively (Hobday & Smith 1997). The projections involve selecting 100 sets of parameter values from the posterior distribution (to account for uncertainty about the model parameters), computing the size structure of the population at the start of 1951, and projecting forward for the specified management arrangements.

The model does not incorporate a relationship between the number of eggs released and recruitment in future years because the processes leading to settlement are poorly known, the scale of larval dispersal is conjectural (Booth & Phillips 1994), and several cohorts may contribute to a single recruitment event. Therefore, consistent with previous assessments of the rock lobster populations off Tasmania and Victoria (Punt & Kennedy 1997; Hobday & Punt 2001) recruitment to a management zone is assumed to be independent of the egg production in the management zone and is hence selected randomly from the past recruitments. There is evidence that recent recruitment has been lower than in the past (particularly for the Eastern Zone) so future recruitment is determined by randomly sampling from the estimates of recruitments for 1992–2002, which mimics the possible effects of a stock-recruitment relationship. If such a relationship does exist, increased levels of egg production may lead to increased recruitment, but this possibility is ignored in the approach used to generate future recruitment, so the benefits of allowing the egg production to increase may be underestimated.

### Scenarios considered

All of the projections of the model are based on TACs of 450 and 60 t respectively in the Western and Eastern Zones (i.e., consistent with reality, there is no reduction in TAC when the MPAs are introduced). The minimum size limits for the projections were set to their current values (105 mm and 110 mm CL for females and males respectively). Projections were conducted for a range of movement rates from the MPAs into the fished areas (0, 1, 5, 10, and 15% for the Western Zone and 0, 5, 8, 10, and 15% for the Eastern Zone), as well as for no MPAs. The various scenarios were compared for the amount of spawning and available biomass after 5 years relative to their limit and target levels.

## RESULTS

### Commercial catches within MPA

The total catch from within the MPAs was estimated at 8.2% of the Victorian TAC, with 32.4 t (7.2% of the TAC) from the Western Zone and 9.36 t (15.6%

of the TAC) from the Eastern Zone. The estimates were rounded up to 8% (Western Zone) and 16% (Eastern Zone) for modelling and risk analyses.

### Movement

A total of 746 tagged lobsters were recovered in or moved from the proposed MPAs before their introduction. Of the 149 lobsters recovered in the Eastern Zone, 123 were tagged in the Point Addis MPA (Fig. 1). Most (78%) of these lobsters stayed within the MPA, 16.3% moved outside the MPA boundary, and 5.7% moved into the MPA, resulting in a net movement of 10.6% out of the MPA (Table 2). Using data from the tag recaptures in all Eastern Zone MPAs, a net movement of 7.4% out of the reserve was observed (Table 2).

A total of 597 lobsters were tagged or recaptured in two of the proposed Western Zone MPAs (Discovery Bay and Twelve Apostles; Table 2). Movement differs between these two MPAs, with a net movement of 0.9% into the Discovery Bay MPA and a net movement of 5.2% out of the Twelve Apostles MPA (Table 2). As a result, the overall net movement rate for the Western Zone MPAs was 0.7% out of the reserves (Table 2). The properties of these two MPAs differ, with the Discovery Bay MPA being half the size of the Twelve Apostles MPA (Table 2) and situated on a headland, which is much closer to the continental shelf break. The influence of upwelling in the Discovery Bay area provides nutrients (Lewis 1981) and so contributes to very productive lobster grounds containing a smaller size range of lobsters. For this reason the Twelve Apostles MPA is more representative of the Western Zone fishery in terms of lobster abundance, size-structure, and distance from the shelf break. A movement rate of 5% out of the Western Zone MPAs is considered more realistic than total movement estimated in these MPAs from the tagging data (Table 2).

### Modelling

Projections for all scenarios in the Western Zone were above the available biomass limit reference point with the target reference point exceeded in 2008 with no MPAs and 2011 with an 8% MPA with 15% movement (Fig. 2). For the Eastern Zone, the limit reference point was exceeded in 2002 without MPAs and delayed 1 year when a 16% MPA was introduced (Fig. 3). The target reference point was not reached in any of the scenarios but approached when MPAs were not included (Fig. 3).

The available biomass in the Western Zone rose to an arbitrary level of 50% greater than that at the start of the 2000 fishing season after 5 years. It took between 7 and 11 years with an MPA of 8% to achieve this level of increase depending on the rate of movement out of the MPA. The available biomass in the Eastern Zone took 3 years to increase by 50% without MPAs, and 5–8 years when there was an MPA of 16% of the available biomass.

There was a >99% probability that the available and spawning biomasses in the Western Zone exceeded their limit levels after 5 years for all scenarios (Table 3). After 5 years, all Western Zone projections were above the target spawning biomass reference point. The available biomass target reference point was exceeded with probability 43%

**Table 2** Areas of the Marine Protected Areas (MPAs) considered in the modelling; number of lobsters tagged and released or recaptured within the proposed MPAs; and movement rates for each MPA.

| Zone | MPA | Area (ha) | No. tagged in MPA | Moving out of MPA (%) | Moving into MPA (%) | Remaining in MPA (%) | Nett movement out of MPA (%) |
|---|---|---|---|---|---|---|---|
| Eastern | Bunurong | 2100 | 2 | | | 100 | |
| | Cape Howe | 4050 | 4 | 25.0 | 75.0 | | –50.0 |
| | Ninety Mile Beach | 2750 | 4 | 25.0 | | 75.0 | |
| | Point Addis | 4600 | 123 | 16.3 | 5.7 | 78.0 | 10.6 |
| | Point Hicks | 4000 | 7 | | 14.3 | 85.7 | |
| | Wilson's Prom | 15550 | 9 | | | 100 | |
| Total | | | 149 | 14.8 | 7.4 | 77.9 | 7.4 |
| Western | Discovery Bay | 2770 | 442 | 1.8 | 2.7 | 95.5 | –0.9 |
| | Twelve Apostles | 7500 | 155 | 12.9 | 7.7 | 79.4 | 5.2 |
| Total | | | 597 | 4.7 | 4.0 | 91.3 | 0.7 |

**Fig. 2** Medians of the posterior distributions of future available biomass for the Western Zone compared to limit and target reference points (solid and dashed horizontal lines respectively). Results are shown for no Marine Protected Area (MPA) and for instances with an MPA of 8% and movement rates out of the MPA of 0, 1, 5, 10, and 15%. Total allowable catch (TAC) for all future years is 450 t.

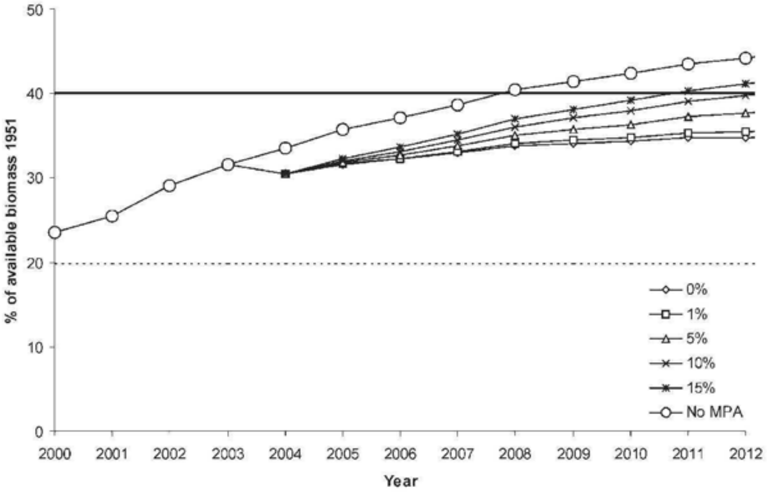
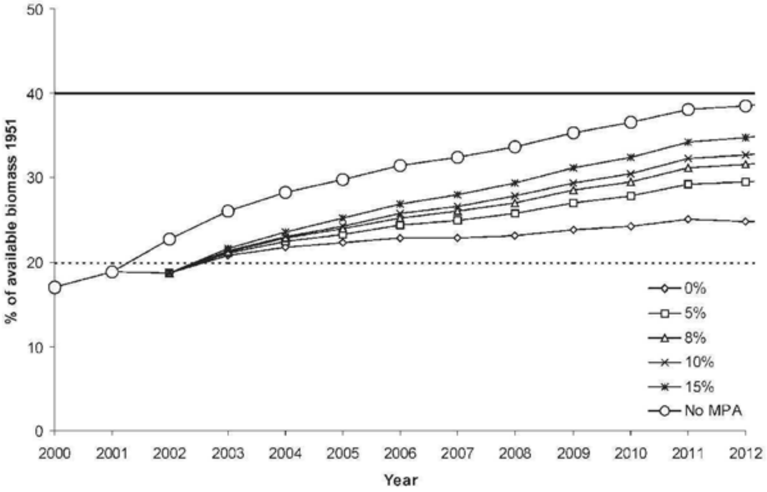


**Fig. 3** Medians of the posterior distributions of future available biomass for the Eastern Zone compared to limit and target reference points (solid and dashed horizontal lines respectively). Results are shown for no Marine Protected Area (MPA) and for instances with an MPA of 16% and movement rates out of the MPA of 0, 5, 8, 10, and 15%. Total allowable catch (TAC) for all future years is 60 t.



without an MPA, and with a probability between 14% and 22% with an MPA, depending on the rate of movement (Table 3). The Eastern Zone available biomass limit reference point was exceeded after 5 years with a probability between 76% and 100%, and the spawning biomass with a probability of 100% (Table 3). Target reference points were not exceeded to a substantial extent after 5 years for any of the scenarios for the Eastern Zone (Table 3).

The available biomass in the Western Zone is currently estimated to be 25% of that in 1951. Without MPAs, and given the current TAC, the available biomass is predicted to recover to the target reference point of 40% of the 1951 available biomass with 50% probability in 6 years (Fig. 4, dashed line). With an 8% MPA and a movement rate out of the MPA of 5%, the target reference point is not reached with 50% probability before 2012 (Fig. 4, solid lines). The available biomass in the Eastern Zone has been below the limit reference point of 20% of the 1951 available biomass since the early 1990s but had recovered to this level in 2002 before the introduction of the MPAs (Fig. 5). However, with the subsequent introduction of a 16% MPA in 2002 and a continued take of 60 t per annum, the available biomass dropped to 16% of the 1951 level. Consequently a further 3 years were needed for the limit reference point to be exceeded with a greater than

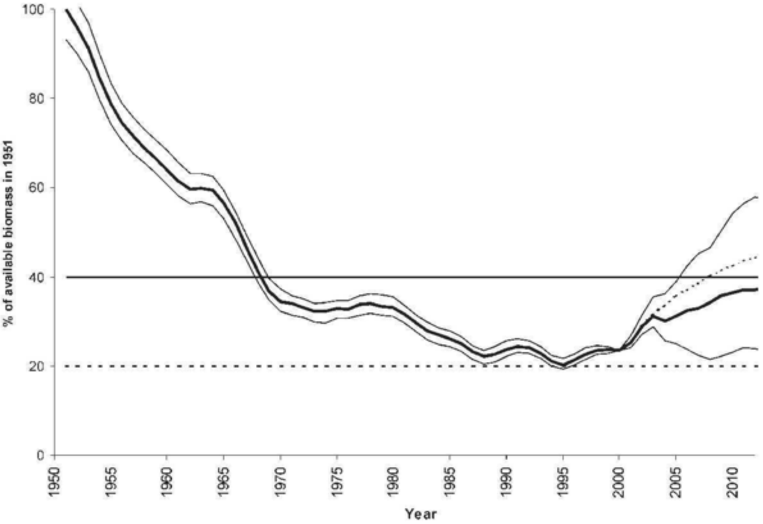


**Fig. 4** Available biomass in the Western Zone relative to the 1951 level, indicating the target (solid horizontal line) and limit (dotted horizontal line) reference points. Solid lines indicate the median and 95% intervals for the time-trajectory of available biomass for an 8% Marine Protected Area (MPA) and a 5% movement rate out of the MPA, whereas the dashed line indicates the median trajectory of available biomass if no MPAs.

**Table 3** Percentage of projections which were above the spawning and available biomass reference points after five years, by zone. (MPA, Marine Protected Area.)

| | | | Movement rate out of MPA | | | | |
|---|---|---|---|---|---|---|---|
| Zone | Reference point | No. MPA | 0% | 1% | 5% | 10% | 15% |
| West | Available biomass limit (20% of available biomass in 1951) | 100 | 99 | 99 | 100 | 100 | 100 |
| | Available biomass target (40% of available biomass in 1951) | 43 | 14 | 14 | 15 | 19 | 22 |
| | Spawning biomass limit (20% of available biomass in 1951) | 100 | 100 | 100 | 100 | 100 | 100 |
| | Spawning biomass target (40% of available biomass in 1951) | 100 | 100 | 100 | 100 | 100 | 100 |
| East | Available biomass limit (20% of available biomass in 1951) | 100 | 76 | 87 | 91 | 94 | 97 |
| | Available biomass target (40% of available biomass in 1951) | 19 | 2 | 3 | 3 | 5 | 6 |
| | Spawning biomass limit (20% of available biomass in 1951) | 100 | 100 | 100 | 100 | 100 | 100 |
| | Spawning biomass target (40% of available biomass in 1951) | 11 | 11 | 11 | 11 | 11 | 11 |

80% probability. The differences between the results for the no MPA scenario and those with MPAs arise because the available biomass in 2001 is estimated to be just below the 20% reference point and this biomass increased to just above this level by 2002. In contrast, the time for the available biomass in the area open to fishing to recover to the 20% reference point was delayed because the MPA reduced the available biomass in the area open to fishing by 16% when it was imposed in 2002.

Spawning biomass in the Western Zone is estimated to be currently 60% of the 1951 level (i.e., well above the 40% target) and is predicted to continue to rise. In contrast, the spawning biomass in the Eastern Zone has been below 20% of the 1951 level since 1993 and had increased to 19% of this level before the introduction of the MPAs. In contrast to the time-trajectories of available biomass in the area open to fishing, the impact of an MPA is to enhance the rate at which spawning biomass

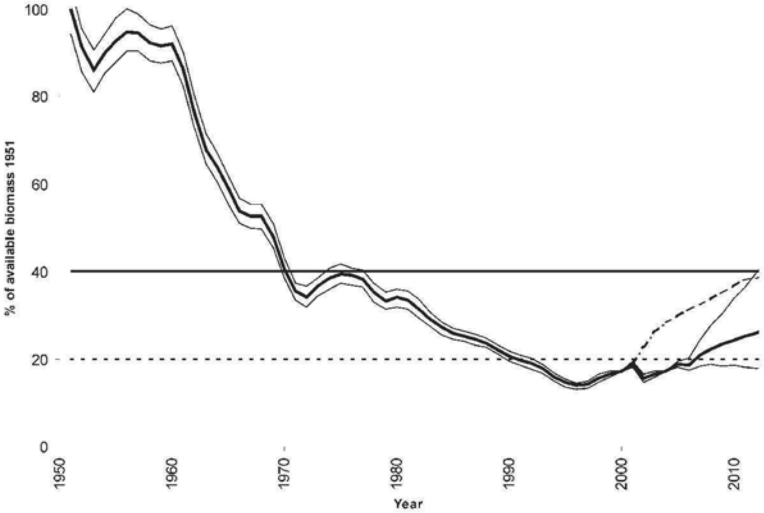


**Fig. 5** Available biomass in the Eastern Zone relative to the 1951 level, indicating the target (solid horizontal line) and limit (dotted horizontal line) reference points. Solid lines indicate the median and 95% intervals for the time-trajectory of available biomass for a 16% Marine Protected Area (MPA) and a 5% movement rate out of the MPA, whereas the dashed line indicates the median trajectory of available biomass if there are no MPAs.

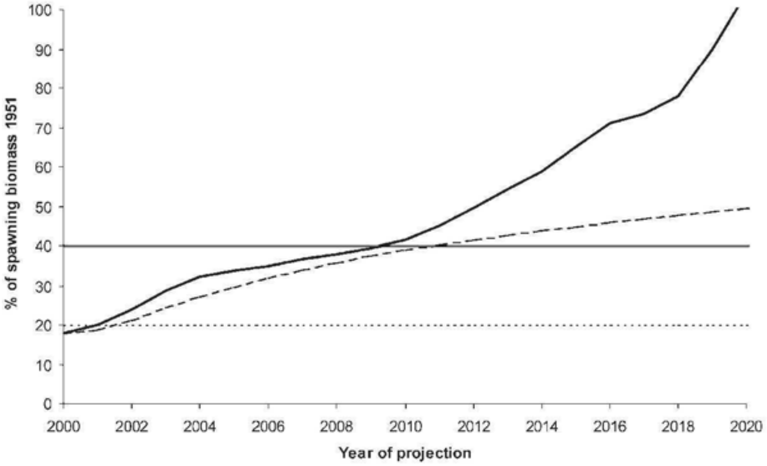


**Fig. 6** Time-trajectories of spawning biomass (posterior medians) in the Eastern Zone relative to the 1951 spawning biomass, indicating the target (solid horizontal line) and limit (dotted horizontal line) reference points. Bold line indicates the results of projections with a 16% Marine Protected Area (MPA) with 5% movement out of the MPA and the dashed line indicates the results of projections without an MPA.

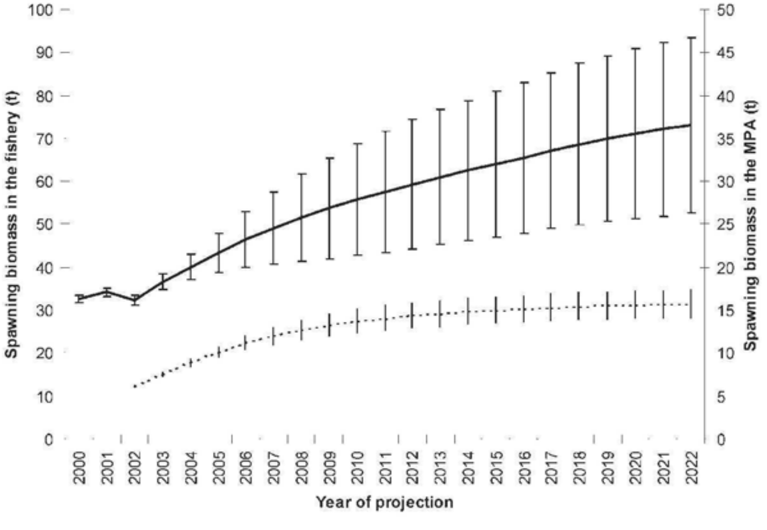


**Fig. 7** Time-trajectories of spawning biomass in the Eastern Zone (posterior means ± one posterior standard deviation) for a 16% Marine Protected Area (MPA) and a movement rate out of the MPA of 5%. Results are shown for the area open to fishing (solid line) and the MPA (dotted line).

increases (Fig. 6). This occurs because the MPA provides more protection for the larger animals than is possible in the area open to fishing (Fig. 7).

## DISCUSSION

### Movement

The rate of movement across the reserve boundary is a key factor when examining the effects of MPAs on existing fisheries. The introduction of MPAs in Tasmania and New Zealand has shown that the mean size and density of lobsters within an MPA increases over time (Edgar & Barrett 1997; Kelly et al. 2000; Davidson et al. 2002). This paper has shown that the biomass in the MPA will continue to build if there is no transfer of biomass from the higher densities within an MPA to the adjacent fishery. In addition, it has shown that most movements recorded are less than that needed to exit an MPA but that even small percentages of lobsters leaving an MPA can compensate to some extent for displaced fishing effort and increased fishing mortality in the adjacent fishery.

Tagging studies for other *J. edwardsii* populations have led to results regarding movement that are similar to those reported here. In New Zealand, long distance (at least 5 km) alongshore migrations by late juveniles against the net coastal flow appear to play a part in larval recruitment (Booth 1997). Similar movements, which may be also related to larval recruitment, have been observed with deepwater rock lobster (*Palinuris gilchristi*) off the coast of South Africa with 25% of tagged lobsters moving more than 20 km (Groeneveld & Branch 2002). A low frequency of movements of over 100 km by *J. edwardsii* has been observed in Victoria, particularly between Queenscliff and Apollo Bay in the Eastern Zone. Many of these lobsters would have moved through the Pt. Addis MPA and travelled alongshore towards the continental shelf adjacent to King Island to the south-west. Studies at the Leigh Marine Reserve in New Zealand have shown a 20% movement rate across the reserve boundary in both directions with a proportion of the reserve population moving out and becoming susceptible to the commercial fishery (Kelly & MacDiarmid 2003).

### Modelling

Haddon et al. (2003) found that the introduction of MPAs to a hypothetical lobster population with rate of movement of 1% from the MPA could cause a stock collapse, depending on the state of depletion in the fishery before their introduction. The results of this study are much less extreme than those found by Haddon et al. (2003), primarily because the TACs used for the calculations have been chosen to allow recovery of biomass, but indicate that increased mortality in an area open to fishing can more than compensate for the impact of protecting lobsters from fishing in reserves.

Equation 3 provides a basis for evaluating the consequences of imposing an MPA given relatively limited information (essentially only the size of the MPA relative to the fished area and the rate of movement from the MPA to the fished area) because it makes several (implicit) assumptions. Some of these assumptions (e.g., that the probability of an animal moving from an MPA to the fished area is independent of size and sex) could, in principle at least, be tested experimentally. However, some of these assumptions are, and will remain, virtually impossible to test empirically. Nevertheless, it is possible to speculate on their qualitative implications.

The model ignores density-dependence in several biological parameters (specifically growth, settlement, and movement). Lower growth rates and lower settlement rates should be expected at high biomass levels as shown empirically for several fish species (Trippel 1995; Helser & Brodziak 1998). These two factors would reduce the rate at which biomass accumulates in the MPA but not effect the status of the resource outside the MPA. The consequences of these factors would therefore be to further reduce the benefits of a system of MPAs in accelerating resource recovery. These factors would also complicate the use of MPAs as areas to determine biological parameters by experimentation because it would not be clear whether values for biological parameters determined from experiments within the MPA could be applied to the fished area.

Density-dependence in movement would lead to higher rates of movement from the MPA as biomass accumulated in the MPA. In the context of Fig. 2 and 3, this would tend to increase the rate at which the available biomass in the open area recovers. The analyses of this paper assume that there is no relationship between egg production and future settlement. The model implicitly assumes that density-dependence does not operate at the egg production stage. Were this to be so, the benefits of having an MPA would be reduced further (Botsford et al. 2003).

The paper has focused on the future implications of imposing an MPA. However, the imposition of an MPA also has implications for stock assessment. In principle, having MPAs could allow experiments to be conducted to estimate key biological parameters. For example, Sladek Nowlis & Roberts (1998) argue that MPAs may offer the potential to generate more accurate estimates of natural mortality because the confounding impact of fishing mortality is eliminated. However, the utility of such experiments depends on whether these quantities are density-dependent. An often overlooked impact of an MPA is that it further violates the homogeneity assumption underlying stock assessments. The quantitative impact of this has not been examined for size-structured models yet, although Punt & Methot (2004) show that inadequate accounting for an MPA when conducting assessments can lead to estimates of management-related quantities that are substantially biased.

### Management implications

The imposition of MPAs in Victoria's coastal zone is predicted to have consequences for conservation of spawning biomass and the size of the biomass available to the fishery. MPAs should enhance the rate of recovery of the spawning biomass in the more depleted Eastern Zone. However, given that MPAs lead to a loss of fishable area (and hence available biomass) to the industry, the imposition of MPAs (and no reduction to TACs) will delay the recovery of the available biomass in the area open to fishing. Nevertheless, with catches at the current levels, the available and spawning biomasses should still rebuild and none of the reference points set in place to manage the fishery are likely to be threatened. In principle, the delays in the recovery of available biomass associated with the imposition of MPAs could have been compensated for by reducing the TAC in each zone by an amount which would depend on the migration rate, if any, of lobsters out of the MPAs. This course of action was, however, not implemented given that reductions in catch of about 15% occurred when quotas were introduced.

## ACKNOWLEDGMENTS

We thank Rhonda Flint and David Reilly from the Department of Primary Industries Queenscliff for their work in tagging and fishery data collection. This work would not have been possible without the support of the Victorian lobster fishers both in providing data and debating the issues at stock assessment workshops. The comments by Paul Breen and one anonymous reviewer on a draft of the paper are gratefully acknowledged.

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# Evolution of operational management procedures for the South African West Coast rock lobster (*Jasus lalandii*) fishery

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**Abstract** The commercial fishery for *Jasus lalandii*, the South Africa West Coast rock lobster, began in the late 1800s and at its peak in the early 1950s yielded an annual catch of 18 000 t. Although this annual catch has dropped to only some 2000 t over recent years, the fishery remains South Africa's third most valuable for landed value. The primary reason for the low total allowable catch (TAC) over these recent years has been a marked drop in somatic growth rate that occurred at the end of the 1980s, for reasons that remain unexplained. A key problem in formulating TAC recommendations with longer-term objectives in mind, has been uncertainties about likely future trends, particularly in somatic growth and recruitment. To address this problem, an "operational management procedure" (OMP) was adopted in 1997 and has twice been re-evaluated and modified (in 2000 and 2003) in the light of further data and changing perceptions of resource dynamics. The history of this process is reviewed, concentrating on the most recent modification. In particular, a summary is given of the process by which the merits of alternative management procedures were evaluated over a range of important uncertainties about the dynamics of the resource. This summary includes a discussion of the key trade-offs between resource rebuilding, future TAC trends and TAC variability, and the eventual choice that was made. The paper concludes by listing a number of lessons learnt concerning best practice for OMP development as this process evolved.

**Keywords** rock lobster; *Jasus lalandii*; management procedure; uncertainty; trade-off

## INTRODUCTION

The West Coast rock lobster *Jasus lalandii* (H. Milne-Edwards) (a panulirid spiny lobster), is found in commercially exploitable densities from 25°S in Namibia to just east of Cape Point in South Africa (see Fig. 1). The commercial fishery for *J. lalandii* began in the late 1800s, and at its peak in the early 1950s yielded an annual catch of 18 000 t (Fig. 2). A review of the historical development of the fishery is given in Pollock (1986). Although the annual commercial catch has dropped to only some 2000 t over recent years, the fishery remains South Africa's third most valuable for landed value (currently worth c. US$40 million, Neville Brink, Oceana Ltd pers. comm.). The primary reason for the low total allowable catch (TAC) over these recent years has been a marked drop in somatic growth rate that occurred at the end of the 1980s (Fig. 3) (Melville-Smith et al. 1995), for reasons that remain unexplained (Mayfield et al. 2000; Hazell et al. 2001).

Early in the fishery hoopnets predominated but, over time, traps have become the primary gear. A number of management measures have been put in place over the history of the fishery. A minimum size limit was introduced in 1933 (89 mm carapace length (CL)), which protected a large proportion of the slower growing female component of the population, and a tail-mass production quota was imposed in 1946. Catches declined however over the 1950s to the 1970s, most likely because of over-fishing, particularly in the more northern areas. In 1979 the tail-mass production quota was replaced by a whole lobster quota. Management by means of TACs, subdivided for individual fishing areas and allocated

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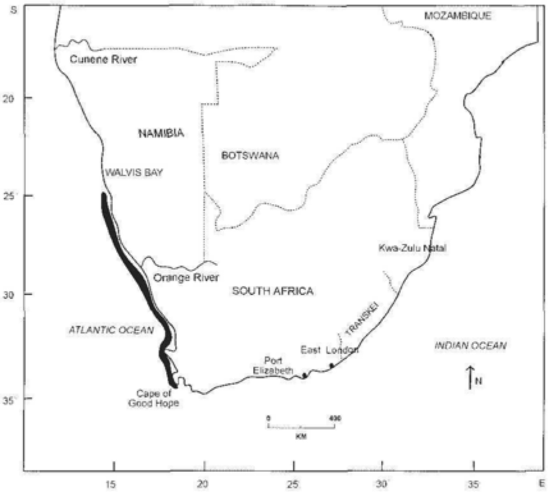


**Fig. 1** Map showing the area of commercially exploitable densities of *Jasus lalandii*.

to individual operators, was introduced in the early 1980s. Other management controls applied include protection of berried females or soft-shelled lobsters, a closed winter season, and a daily bag limit for recreational fishers (Cockcroft & Payne 1999).

During the mid 1980s, scientists considered the resource to have stabilised and be capable of providing annual sustainable harvests in the 3500–4000 t range. However, in 1989 the somatic growth rate suddenly dropped (Fig. 3), resulting in decreased recruitment into the fishable portion of the population. Zero and even negative growth (shrinkage) at moulting were recorded under field conditions (Cockcroft & Goosen 1995). The lower somatic growth rate persisted, and clearly had a large effect on the productivity of the resource which required a management response. Catch rates of legal sized lobsters were poor because a large proportion of the lobsters caught were below the minimum size limit

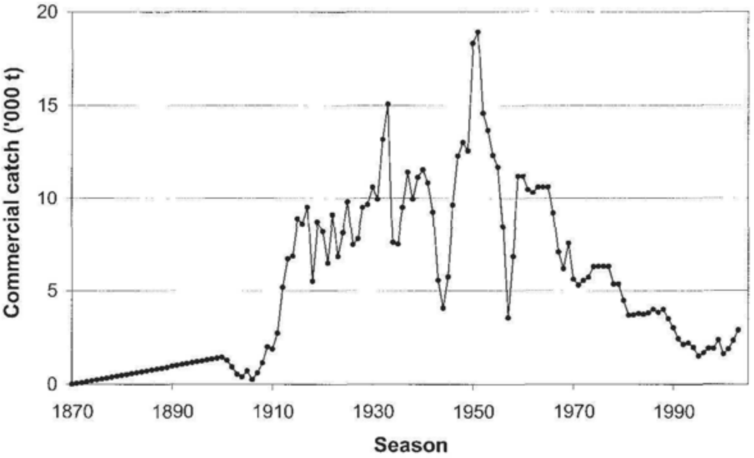


**Fig. 2** Historic commercial catch history.

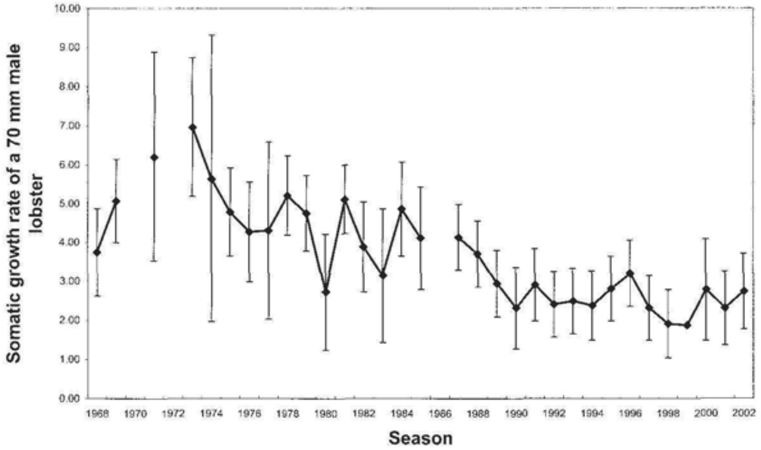


**Fig. 3** Somatic growth of a 70 mm male West Coast rock lobster *Jasus lalandii* (Brandão et al. in press). Error bars show the 95% confidence intervals relative to the 1999 value which was incorporated in the intercept for the general linear model (GLM) analysis applied.

of 89 mm, and had to be returned to the sea. Early in the 1991 season, a temporary reduction of the minimum size from 89 mm to 75 mm CL was announced for scientific reasons as well as a relief measure to the industry. In 1992, the minimum size was initially set at 80 mm CL, but then reduced back to 75 mm CL in 1993 for economic reasons. This reduction aimed to improve catch rates as well as assist the industry in supplying the foreign market with smaller sized lobsters. Scientific arguments for reducing the minimum size included: (1) a reduction in discard mortality would result; (2) models showed that an agreed target for egg production could still be achieved with a size reduction; and (3) harvesting males >89 mm had resulted in the fishery being based on an unproductive "tip-of-the-iceberg", with a large pool of potentially harvestable lobsters below this size limit. During this period TACs were reduced from 3790 t in 1990 to 2400 t in 1992, and even further to 1500 t in 1995.

At this time the management process involved the development of recommendations by a working group of scientists, which were relayed to an advisory group (the then Sea Fisheries Advisory Committee, SFAC) appointed by the responsible minister, for transmission in turn to the minister for decision. The scientific working group was appointed by the research director of the marine section of government's Department of Environment Affairs and Tourism, and comprised government, university, and industry consultant scientists. Their advice was based on projections of resource assessments under different future levels of catch. However, increasing difficulty was experienced in reaching consensus, particularly because projection results and advice depended heavily on assumptions concerning whether and how rapidly somatic growth might recover to its pre 1990 levels, and on an appropriate target for recovery of the stock.

To try to resolve this difficulty, government made the decision to move to an Operational Management Procedure (or OMP) approach. The aim was to pre-specify how future scientific TAC recommendations would be calculated, given monitoring data that focused on catch-per-unit-effort (CPUE) derived from industry catches, a fisheries-independent monitoring survey (FIMS) (Dept. Statistics, University of Cape Town 2003), and annual assessments of somatic growth rate. (In South Africa, the prefix "Operational" is used to emphasise that a specific and immediately applicable formula, e.g., for a TAC, is specified, rather than a general concept only.)

Management procedures (MPs) have also been developed and implemented for the New Zealand rock lobster fishery (Starr et al. 1997; Bentley et al. 2003a,b). The first such MP was implemented in 1997 for the two most southern New Zealand sub-stocks, which were estimated to be fairly depleted (to c. 1/3 $B_{\mathrm{MSY}}$) (Starr et al. 1997). The aim of this MP was to rebuild those sub-stocks to $B_{\mathrm{MSY}}$ level. The MP was based on comparisons between observed and model-predicted CPUE. Bentley et al. (2003a) reports how a new MP was implemented for these two sub-stocks in 2002. This MP was designed with a different target recovery level, based on CPUE and the history of the fishery, rather than a biomass-rebuild target estimated from stock assessment. Both Starr et al. (2003) and Bentley et al. (2003a) discuss the two main sources of uncertainty for these sub-stocks: the levels of migration between the two sub-stocks and of recruitment in each one. Candidate MPs were tested for a range of assumptions about these two processes.

Bentley et al. (2003b) describes the development of a MP for New Zealand rock lobster stocks that are not over-exploited and estimated to be above legislated minimum biomass levels. Bentley et al. (2003a,b) discuss how representatives from the commercial, recreational, customary, and conservation sectors were involved in agreeing on management objectives and associated performance indicators for these fisheries. Trade-offs among these objectives were clearly an important issue, and Bentley et al. (2003b) concludes that the ultimate choice of a MP will depend on the relative weight given to different objectives.

## OMP DEVELOPMENT

An OMP comprises pre-specified monitoring data, together with a formula to be used to convert these to a TAC recommendation. A key aspect of the approach is computer simulation testing to check that the formula is adequately robust in the face of uncertainty about the dynamics of the resource (Butterworth & Punt 1999; Cooke 1999).

In the mid 1990s, this approach was already in use for South Africa's two most valuable fisheries (the primarily demersal trawl fishery for hake, *Merlucius* spp., and the purse seine fishery for sardine, *Sardinops sagax*, and anchovy, *Engraulis capensis*; Geromont et al. 1999). A particular motivation for choosing to use the OMP approach for the West Coast rock lobster was its feedback-control nature,

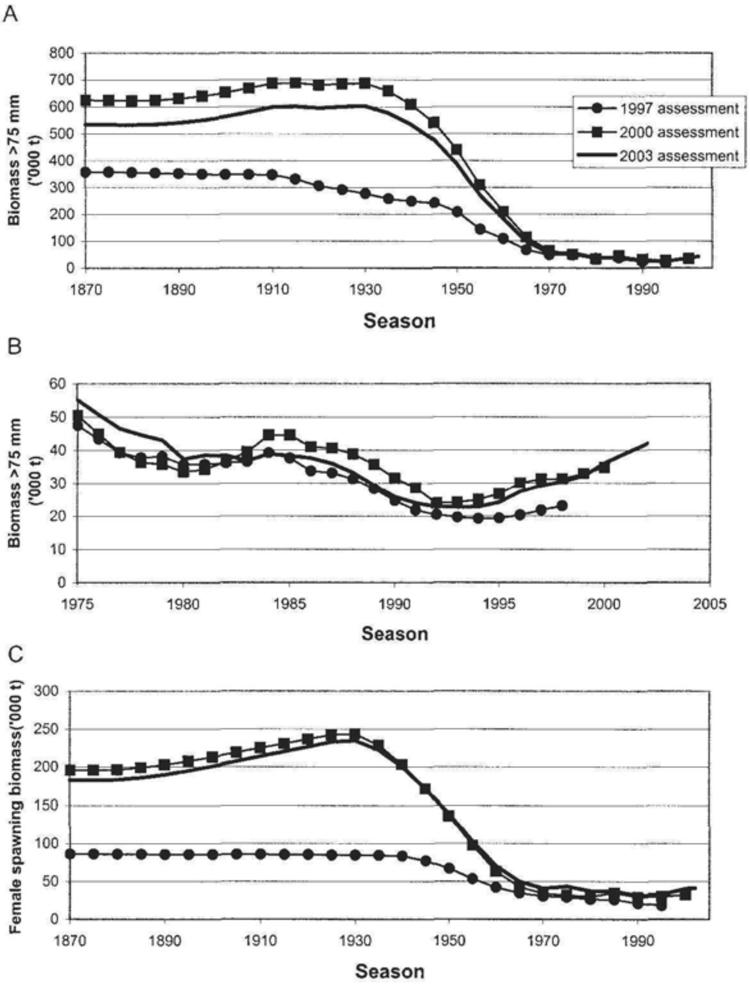


**Fig. 4** Biomass trajectories as estimated by the best assessments of the resource at the time of the 1997, 2000, and 2003 Operational Management Procedure developments. **A**, $B_{75}$ (biomass of both sexes for carapace length >75 mm; **B**, an enlargement for recent years of the upper panel; and **C**, female spawning biomass. (The 2003 results shown are for the RC1 Reference Case.)

i.e., as future information (data) become available, the OMP is able to self-correct for the consequences of having to base previous management decisions on unavoidably inexact assessments. Given uncertainty as to what the future somatic growth rate might be, the formula to be adopted needed to react adequately in adjusting future TACs so that resource-recovery objectives were not unduly compromised.

### 1997 operational management procedure

The first OMP for the resource was implemented in 1997, with the intention that it be applied for a period of three years. The underlying assessment model used for the West Coast rock lobster was (and currently still is) a size-structured model that takes annual variations in somatic growth, recruitment, and survivorship into account (Johnston 1998). A size-structured approach was necessitated because there had been several changes in minimum legal CL, as well as changes in somatic growth over time. Figure 4 shows the best assessment of the resource provided by this approach at that time, and the two subsequent revisions of the assessment in 2000 and 2003. This model, and variations thereof reflecting ranges of uncertainties, were used as the basis for simulation testing of candidate OMPs. These "operating models" represent the "truth" for the model simulations. The operating model generates "data", which the candidate OMP in turn uses to provide scientific TAC recommendations, whose implications are evaluated by projecting the operating model forward in time under these catches.

Before the development of the 1997 OMP, the SFAC was approached to provide some initial feedback about management objectives. They chose to: (1) endorse a resource re-building strategy (given that current biomass was indicated to be at a very low proportion relative to that for the pristine stock—see Fig. 4); (2) suggest that rebuilding targets of between 20% and 50% above the 1996 level for exploitable biomass ($B_{75}$—the biomass of lobsters with a CL >75 mm) over a 10-year period should be investigated; and (3) propose that the 1997 TAC level (which at that time applied only to the commercial component of the fishery, as distinct from the recreational component of a few hundred tonnes annually) should be set at between 10% and 20% above the 1996 level of 1700 t.

In response, scientists developed a number of alternate candidate OMPs (12 in all) which covered the ranges suggested above for management objectives. The objectives for each of the 12 in turn were achieved for the best assessment of the resource projected deterministically under baseline assumptions; the most important of these assumptions were that future recruitment would be maintained at the average level of the previous two decades and that somatic growth would continue to follow a first order auto-regressive time series as estimated from the 1975–95 data. The OMPs used three sources of input data (commercial CPUE, a FIMS index of abundance, and somatic growth rate). The rationale underlying the OMP was that if these inputs showed an increasing trend the TAC would be increased, whereas if a downward trend was observed, the TAC would be decreased. (Appendix 1 provides the formula for the OMP ultimately implemented.) The OMP thus had an implicit feedback structure, i.e., an ability to self-correct. The OMP also contained a maximum inter-annual TAC reduction constraint (15%) and "exceptional circumstances" were defined under which the OMP-generated TAC would be modified if necessary to offset the consequences of an unexpectedly "bad" (such as very poor recruitment or somatic growth) or "good" event.

Model simulations for each OMP candidate were run stochastically (i.e., taking account of future process error in the form of recruitment variability and observation error between abundance and somatic growth indices and their corresponding actual underlying trends), and a wide range of robustness tests were examined. Robustness tests involve changes to one or more of the assumptions or parameter values of the baseline operating model, which maintain compatability between model and data and reflect alternative plausible representations of the real underlying situation. The 1997 OMP showed particularly good robustness in meeting recovery targets in the face of uncertainties relating to the future somatic growth rate. Robustness was less satisfactory for situations where future recruitment (and hence resource productivity) was appreciably lower or higher than the baseline assumption. The final 1997 OMP recommended by the SFAC to the minister was the least conservative of the 12 candidate OMPs, and aimed for a 20% biomass ($B_{75}$) recovery over the 1996–2006 period with a 20% increase in the 1997 TAC over the 1996 level. This OMP was used by the scientific working group to recommend TACs, which were all subsequently duly implemented, over the 1997–99 period.

## 2000 operational management procedure

After the implementation of the 1997 OMP for a period of three years, the underlying size-structured model of the resource was refined and updated given the new data available, and the OMP simulation testing process repeated. Given the longer time-series of CPUE and FIMS data, the new OMP changed from an empirical to a population model basis (see Appendix 1) with a view towards making greater use of the available data and thereby perhaps reducing (unnecessary) variability in TAC outputs. The revised best assessment of the resource estimated current exploitable biomass ($B_{75}$) to be some 50% larger in absolute terms (though not relative to pristine) than it had been three years earlier (see Fig. 4). This result contributed to decision makers selecting an OMP with a lesser target rebuilding level of 14% from 1996 to 2006 (compared with the 20% of the 1997 OMP) and a 6% increase in the 2000 TAC compared with the 1999 level. (By this time, given other legislative changes, the TAC comprised the sum of commercial and recreational components, rather than the commercial component only.)

## Current operational management procedure

The current (2003) OMP for the West Coast rock lobster fishery is similar to the 2000 OMP, although the process undertaken to choose between alternative candidates differed in some important respects. First, at the start of this OMP development phase, two alternate best or "reference case" (RC) assessment models for the resource were proposed. Although both these assessments were based on the size-structured model, RC1 placed no constraint on the recruitment estimates, whereas RC2 forced the recruitment estimates to lie on or not far below the

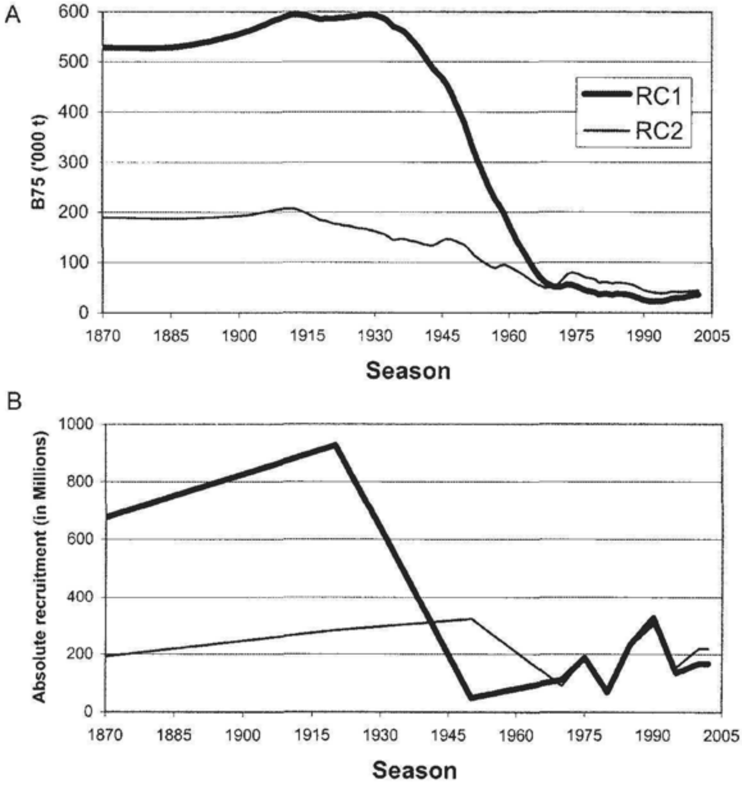


**Fig. 5** Comparison between 2003 reference case assessments RC1 and RC2 estimated trends for **A**, $B_{75}$ (biomass above 75 mm carapace length) and **B**, absolute recruitment.

replacement line. These two models resulted in very different perceptions of the current status of the resource and hence the need for, and extent of, rebuilding required. Essentially the RC1 model was similar to the preceding assessments in that it estimated current biomass levels to be low relative to pristine (see Fig. 4). The alternate model, RC2, estimated current biomass levels to be considerably higher not only in absolute terms, but especially relative to pristine (see Fig. 5). The two assessments yielded very similar results over the period after 1970 for which resource-related data (other than annual catches) are available, but differed in their estimates of abundance and recruitment before that time. RC2 is associated with a very low selectivity for larger female lobsters, i.e., it implies that a relatively large component of the female lobsters must be "cryptic", or unavailable to the fishery, the plausibility of which was questioned by the scientific working group.

Besides the two alternate assessments (RC1 and RC2), considerable uncertainty remained (as in 1997 and 2000), about likely future somatic growth rate and recruitment levels. The working group was able to agree on three scenarios as reflective of the possible ranges for each of these factors, as listed in Table 1. For each reference case assessment there were thus nine representative models to project the resource. In 1997 and 2000, the tuning of OMP candidates to achieve target recovery levels had been based on a single such "baseline" model, even though robustness of performance for alternative models was checked. Objections were raised to this approach in the working group because of the key role then played by the choice of the baseline model, which had typically been selected towards the conservative end of the spectrum on previous occasions. To instead integrate performance over the range of models considered plausible, taking account of their relative plausibilities, weights were agreed for each set of scenarios under consideration (2 assessments × 3 future somatic growth scenarios × 3 future recruitment scenarios). A 0.80:0.20 weighting was assigned to the RC1:RC2 models, and the weights agreed for the other factors are shown in the final column of Table 1; the weight for a specific trial then followed by multiplying together the weights for each of the three factors. When developing weighted ("integrated") combinations of the distributions of a performance statistic across such trials, the RC1 and RC2 results were kept separate because their combination would have led to difficulties in interpretation (e.g., because some rebuilding was desirable if RC1 reflected the true status of the resource, whereas some reduction in abundance was acceptable if RC2 applied). However, because of the much greater weight accorded to RC1, only results under this assessment are presented here.

The formulation of the final candidates for the current OMP is described fully in Appendix 2. It is similar to that of OMP 2000 in that a population model is fitted to the three sets of input data, although it also includes further features to allow refinement of the shape of the anticipated TAC trajectory, as well as time-dependence in the parameter constraining inter-annual TAC changes. This last feature was introduced in response to industry requests for options to allow the possibility of larger changes in TAC in the short term. Furthermore, at industry's request, investigations were restricted to candidate OMPs which placed an upper bound of 10% on the extent to which the TAC could change (up or down) from one year to the next. Results of a final set of six OMP candidates were presented to the working group for consideration. The OMP candidates differed in the extent of resource recovery and the shape of the TAC trajectory anticipated, and the parameters governing the level of likely inter-annual TAC changes. Table 2 specifies the differences in these performance features between the six candidates.

Comparative "integrated" results for each OMP were reported for a range of summary performance statistics, the most important of which were: (1) $B(13/03)$—the biomass above 75 mm CL at the start of 2013 compared with that at the start of 2003; (2) $C_{\text{ave}}(10)$—the average expected catch over the following 10-year period; (3) $V(10)$—the average inter-annual catch variation (expressed as a percentage) over the following 10-year period; (4) $FE(12/03)$—the fishing effort in 2012 relative to that in 2003; and (5) TAC($y$)—the TAC (commercial plus recreational) in year $y$. TAC and biomass (above 75 mm CL) trajectories were also reported (see Fig. 6).

The three factors discussed above (assessment, future somatic growth, and future recruitment levels) were not the only ones subject to uncertainty. Trials were also conducted to investigate robustness of performance to aspects such as alternate levels of natural survivorship and of discard mortality, and

**Table 1** Three representative scenarios for each of future somatic growth rate and future recruitment considered by the rock lobster scientific working group in 2003, with the associated "relative plausibility" weights accorded to each.

| | Option | Weighting |
|---|---|---|
| Future somatic growth rate | Low (1989–2001 average) | 0.50 |
| | Increase to 1968–2001 average over the next 10 years | 0.35 |
| | Increase to 1968–2001 average over the next 3 years | 0.15 |
| Future recruitment | Lowest value over 1975–95 period | 0.10 |
| | Average value over 1975–90 period | 0.60 |
| | Highest value over the 1975–95 period | 0.30 |

**Table 2** Essential features of the six candidates considered for the 2003 Operational Management Procedure by the working group. (TAC, total allowable catch; $B_{75}$, biomass above 75 mm; RC1, reference case 1; CAND1, operational procedure candidate 1 etc.)

| | Median final $B_{75}$ level after 10 years under RC1: $B(13/03)$ | | |
|---|---|---|---|
| | Relatively large increase (27–30%) | Relatively small increase (15–17%) | Almost no increase (3%) |
| Parameter ($w_y$) constraining extent of inter-annual TAC change is modified over time | CAND1 | CAND2 | CAND3 |
| Parameter ($w_y$) constraining extent of inter-annual TAC change is constant over time | CAND4 | CAND5 | CAND6 |

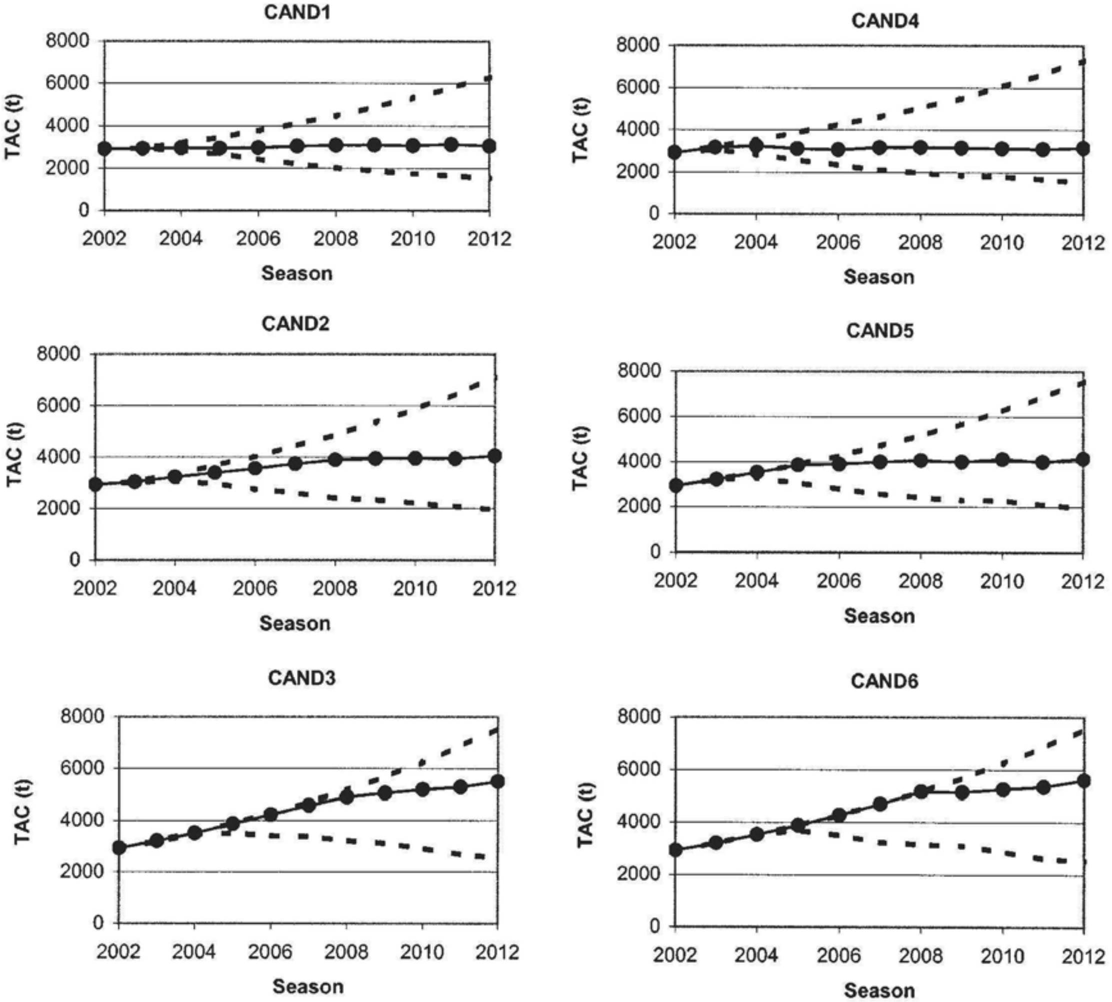
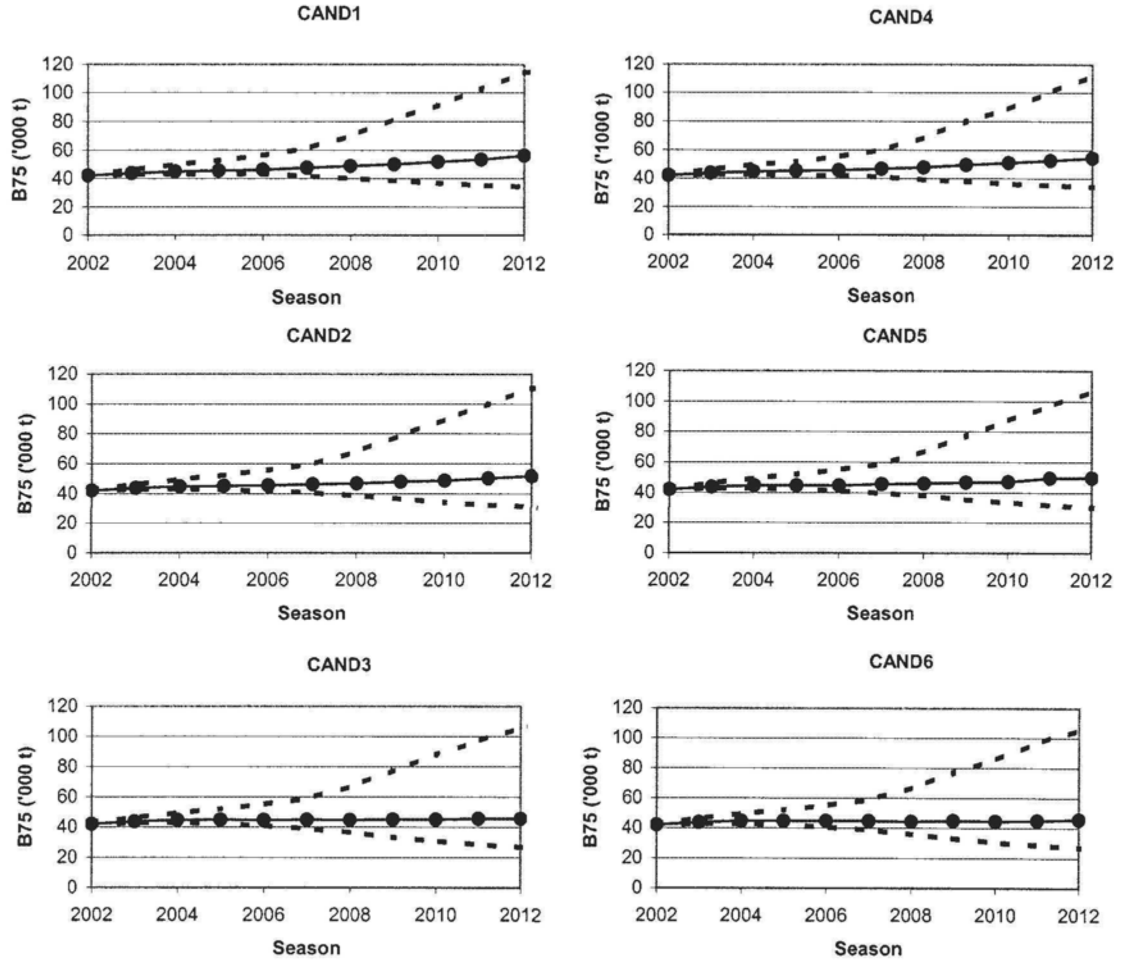


**Fig. 6** **A**, Integrated TAC trajectory envelopes (medians and 80% probability intervals) for RC1 scenarios for each of the six operational management procedure (OMP) candidates considered in 2003. **B**, (*opposite page*) Integrated $B_{75}$ trajectory envelopes (medians and 80% probability intervals) for RC1 scenarios for each of the six OMP candidates considered in 2003.

future "walkouts". (Walkouts refer to the phenomenon of mass strandings, which result from the lobsters moving into very shallow regions near the shore because of the occurrence of low oxygenated water (Cockroft 2002).) However, performance statistics showed much greater sensitivity to the first three factors. Thus, although in principle other factors could also have had plausibility weights accorded to different scenarios and been included in the integration process, this additional (and computationally onerous) complexity was not pursued—instead it was deemed sufficient to check that performance statistics did not change too radically under such further scenarios.

## Choice of final OMP

Discussion of this choice took place in the context that the 2006 recovery targets set under the previous OMPs had already been achieved by 2003 (see Fig. 4). The integrated results (see Fig. 6 and 7) were examined closely by the working group. (It is evident from these plots that the trials conducted considered only future uncertainties, using best estimates of current resource status rather than taking account of estimation imprecision. Because of the large quantity of data available to the assessment, likelihood profile estimates of this imprecision suggest that it is



relatively small. Undoubtedly such estimates are negatively biased through their neglect of positive correlation amongst data which the likelihood formulation treats as independent. The extent of this bias is difficult to quantify. Nevertheless, the uncertainties related to future somatic growth and recruitment are so much larger than the likelihood-based assessment of estimate imprecision that it was considered safe to ignore the last factor in computations.)

Trade-offs between resource recovery ($B$(13/03)) and future catch levels (e.g., $C_{\mathrm{ave}}(10)$) were a particular focus. Clearly the greater the resource recovery, the lower the catch levels over that period. Candidates 3 and 6 were dismissed immediately as not providing sufficient biomass recovery. Although many of the working group were concerned with the greater catch variability associated with candidates 4 and 5 (note for example the TAC(2005) panel in Fig. 7), the industry representatives were willing to accept this risk, in the hope that the future productivity of the resource would prove greater than expected. Candidates 4 and 5 were designed to allow for a faster response in the TAC to future changes in recruitment and somatic growth. Further desirable features seen in candidate 5 were not only the projected increase in TAC (for the distribution median, see Fig. 6A), but also the anticipated increase in fishing effort (see FE(12/03) in Fig. 7). In an economy where unemployment is a problem, options projecting a decrease in effort and hence unemployment over time are undesirable.

On this occasion, the working group recommended candidate 5 as the preferred OMP. This was adopted by the responsible minister, and this candidate OMP was then used to determine the TAC for the 2003/04 season.

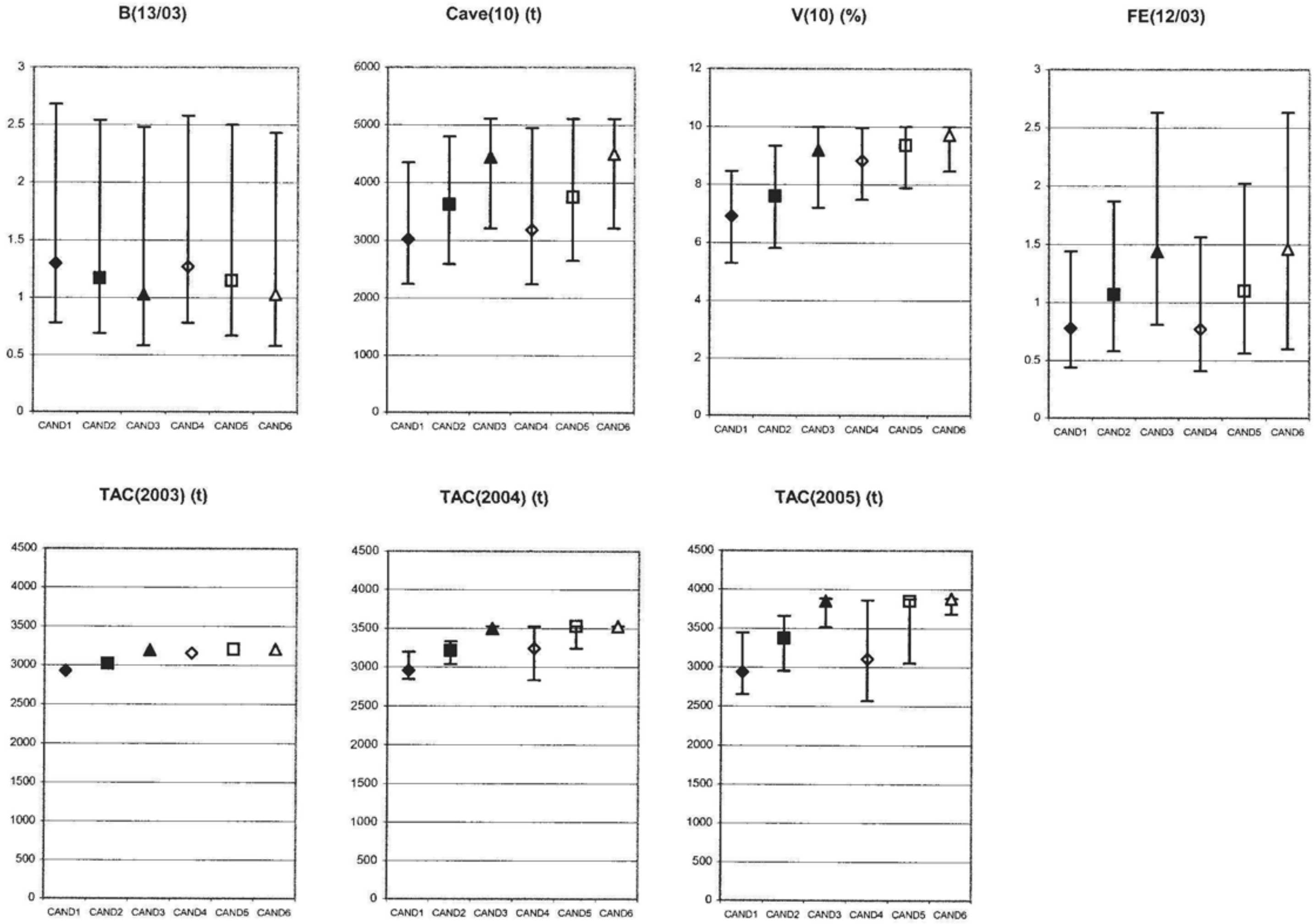


**Fig. 7** Performance comparison plots for the six Operational Management Procedure candidates considered in 2003 under assessments for RC1. Each panel represents a particular performance statistic, in which the median (shown by a symbol) and the 80% probability interval (shown by the bar) are compared for the candidates. Catch statistics are in t, and inter-annual catch variability V is percentage.

## DISCUSSION

The first two OMPs developed for the resource (1997 and 2000) were specifically designed to respond quickly to future changes in somatic growth rate. The lobsters had experienced a period of particularly low somatic growth since the late 1980s, and the industry was anxious to be able to benefit as soon as possible (from increased TACs) if and when the somatic growth rates improved. At this stage, the general linear models (GLMs) applied to the somatic growth data suggested that the annual somatic growth rate could be estimated with a fairly high degree of precision. In 2003 however, the GLM model was improved and extended to a mixed linear or "random effects" GLM which allowed for interactions between years and locations to be taken into account even though data were not available for every combination of these factors. This improved approach (Brandão et al. in press) revealed that the annual somatic growth estimates were much less precisely estimated than had previously been thought (the present estimated errors are shown in Fig. 3). Following this development, it was decided by the working group (and endorsed by the industry) that the 2003 OMP should down-weight the responsiveness of the OMP to the somatic growth rate data.

The 2003 OMP was also developed to contain a set of rules (also tested in the computer simulations) to be implemented if a situation arises in the future where a particular input datum value is unavailable. Essentially, if a particular index is missing in any year, the previous year's index is used. The implementation of the OMP 2000 had been caught short on this account, when in 2000 the somatic growth data were not collected from several of the key sampling areas, thus preventing the calculation of a comparable 2000 somatic growth input data value.

The development of the two alternate assessment models, RC1 and RC2, during the 2003 OMP development highlighted the problems of estimating past recruitment trends for the resource when it is treated as a single stock. These different assessments imply appreciably different extents of depletion of the resource below pre-exploitation levels, and accordingly confound discussions over the degree of resource recovery that is appropriate as a target for management. It is possible that the RC1 results, which suggest recruitment was well below replacement levels for much of the earlier part of the 20th century, are an artefact of treating the resource as a single homogenous stock in circumstances where there is clear evidence of sequential depletion from north to south along the west coast. Historical catches were originally largest in the north, unlike the current situation where most of the catch is taken in the vicinity of the Cape of Good Hope (Fig. 1). In consideration of analyses to date, the tacit assumption has generally been made that RC1 assessment type results, which suggest a heavily depleted resource, are quite plausible as they are consistent with the expected consequences of serial depletion. This, however, needs to be checked more carefully. Future work will thus concentrate on developing spatially disaggregated assessments of the resource, with the possibility of these leading to a movement away from single stock management towards the development of separate OMPs for perhaps three separate areas.

The 1997 OMP contained "exceptional circumstances" rules defining circumstances under which the OMP-generated TAC could be modified. These rules covered very optimistic as well as very pessimistic scenarios. Including such an "opt-out" in the OMP at this initial stage of OMP implementation appeared to alleviate fears, particularly amongst industry, that if the then current assessments were shown in the future to be substantially in error, the OMP-generated TAC could be superseded, i.e., they would not be locked into recommendations from a formula with a flawed basis. With time, confidence grew in the reliability of the operating model and the whole OMP approach in general, and it was not felt necessary to include such "exceptional circumstances" provisions explicitly for the following two OMPs. Nevertheless, the understanding has always been that the OMP-generated TAC would be reconsidered if future data or research indicated the resource behaviour to be outside the range of possibilities considered in the robustness trials of the OMP.

The West Coast rock lobster is a particularly slow-growing lobster. This impacts the trade-off between recovery and current catch levels. The slow somatic growth results in a low surplus yield:biomass ratio. This in turn demands a large sacrifice in catch to obtain resource recovery. Unsurprisingly, the nature of this trade-off led to strong opposition from industry interests to setting high recovery targets.

### Lessons learnt

One of the most successful aspects of moving towards management using an OMP approach has been the substantial reduction in the time spent annually in haggling over TAC recommendations. Although the scientific processes of developing each of the three OMPs summarised here have not been without difficulties and extensive debate, when it came to implementing agreed TAC formulae, only minor questions related to input data have arisen, and the resultant TAC recommendations have, without exception although sometimes with some debate, been implemented without change by decision makers. The pre-specified TAC calculation rules have also resulted in an increase in transparency and improved understanding by all parties, and have allowed the focus of research to move towards other important management issues such as area-disaggregated assessments.

Other important lessons learnt have included: (1) "Bribery"—in one form or another, the TAC (or its possible range) in the first year of implementation of an OMP or OMP revision has served as an important axis in the suite of candidates considered; "sweetening the pill" proved a useful bargaining chip in acquiring industry consensus to buy into continued future application of the TAC formula in question, whose feedback nature then provided greater longer-term guarantees of continued sustainable usage and safeguarding of the resource. (2) Missing data—whatever assurances of certainty of future availability of resource monitoring data may be given at the time an OMP is developed, provision needs to be made in the TAC formula for defaults if this does not happen. (3) OMP complexity—that the assessment model within the 2003 OMP is somewhat complex has not been an issue; over time, stakeholders have come to greater acceptance that it is not the details of the OMP itself that matter, but rather the anticipated performance to be expected, as illustrated (for example) in Fig. 6 and 7. (4) TAC changes—placing bounds on the extent to which the TAC can change from one year to the next is important to stakeholders, and assists in achieving consensus on their acceptance of an OMP. (5) Recovery targets—given a biomass recovery target, considerable scientific debate can arise concerning under which of a number candidate Reference Case operating models this target is to be achieved (i.e., the OMP process provides no escape from the issue of "which is the 'best' resource assessment?"). It proved easier to gain acceptance of the approach adopted for the 2003 OMP of a Reference Case of "integrating" over some key uncertainty axes through a scenario weighting system than the earlier approach of selecting a single scenario. (6) Presentation of results—OMP testing provides a plethora of tabulations and plots. These have to be ruthlessly culled for final presentation of options to decision makers. The integrative approach set out in (5) above, assists in this.

## ACKNOWLEDGMENTS

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(*Appendices overleaf*)

**Appendix 1** Summary of operational management procedure (OMP) total allowable catch (TAC) formulae for the 1997 and 2000 OMPs.

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### 1997 OMP

An empirical approach was implemented for calculating the TAC each year as follows:

$$TAC_t^* = \left(\frac{CPUE_{t-1,t-2,t-3}}{CPUE_{93,94,95}}\right)^{0.5}\left(\frac{FIMS_{t-1,t-2,t-3}}{FIMS_{92,93,94,95}}\right)^{0.5}\frac{Y^Q_{ARMA97}}{Q} \tag{A1.1}$$

where $Y^Q_{ARMA97}$ is the sustainable yield (assuming future recruitment to be the average of the recent past level) at the target biomass recovery level $QB_{1996}$, for the expected baseline (ARMA'97) somatic growth scenario (an AR(1) time series model fitted to the 1975–95 somatic growth data), where for this OMP the target biomass increase Q is 1.2 (reflecting a 20% increase); $CPUE_{t-1,t-2,t-3}$ and $FIMS_{t-1,t-2,t-3}$ are the average CPUE and FIMS values respectively for seasons *t*-1, *t*-2 and *t*-3; $CPUE_{93,94,95}$ is the average CPUE over the 1993–95 period; and $FIMS_{92,93,94,95}$ is the average FIMS index over the 1992–95 period.

The algorithm in Equation A1.1 needed to take into account that the somatic growth rate in the future might well deviate from the baseline ARMA'97 prediction. Equation A1.1 was thus modified as follows:

$$TAC_t^{**} = TAC_t^* \frac{Y_g^Q}{Y^Q_{ARMA97}} \tag{A1.2}$$

where $Y_g^Q$ is the sustainable yield at the target biomass level, calculated for growth *g*, and is calculated as the arithmetic average over seasons *t*-1, *t*-2 and *t*-3. Given this adjustment, eventual attainment of the target biomass recovery level $QB_{1996}$ is achieved whatever somatic growth scenario eventuates.

To allow flexibility in targets for the TAC in the short term, the algorithm was modified to include a number of tuning parameters: *w*, *h*, and *k*. The final TAC setting algorithm was thus:

$$TAC_t = \max\left\{\begin{matrix} wTAC_{t-1} + (1-w)TAC_t^{**}\left[1-h(t-1997)^\gamma\right]k \\ 0.85TAC_{t-1} \end{matrix}\right\} \tag{A1.3}$$

Note: *w* is the weight given to the previous year's TAC and was set at 0.5; *h* is a parameter which can be tuned to produce a given biomass target (e.g., $1.2B_{1996}$) at the end of the 10-year period (2006); *k* is the parameter tuned to produce a specified expected 1997 TAC value; and $\gamma$ is a parameter which determines the "shape" of the TAC trajectory. A value of 0.5 was found to lead to smooth and usually monotonic trends.

Furthermore, a maximum inter-annual TAC reduction constraint of 15% was imposed. The values of *k* and *h* for the selected 1997 OMP were 1.0066 and 0.9 respectively.

### 2000 OMP

The underlying approach was to fit a simple population model to available CPUE, FIMS, and somatic growth data to provide a basis to compute a catch that would see a target biomass achieved by the end of the 2000–06 period. The simple population model was identical to that used for the 2003 OMP and is described in Appendix 2. The only difference here is that the population model was fitted by minimising a sum-of-squares function involving CPUE and FIMS data, and that the trap and hoopnet catchability coefficients were estimable parameters. The penalty function for the "*a*" parameter (see Equation A2.2 below) was as follows:

$P = 1–e^{-(a-3500)^2/2\sigma_a^2}$ for $a < 3500$
$P = 0$ for 3500 $a$ 5000
$P = 1–e^{-(a-5000)^2/2\sigma_a^2}$ for $a > 5000$
where $\sigma_a = 1000$

The population model was projected forwards to 2006, under the following catch strategy:

$$C_t^* = C_1 e^{\delta(t-2005)}$$

with $C_1$ being selected (using a bisection method) to achieve the biomass target level, and $\delta$ selected to achieve a certain TAC(2000) value. The final TAC formula was as follows, and included a 15% maximum inter-annual TAC reduction constraint:

$$TAC_t = \max\begin{pmatrix} wTAC_{t-1} + (1-w)C_t^* \\ 0.85TAC_{t-1} \end{pmatrix} \tag{A1.4}$$

where $w = 0.7$.

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**Appendix 2** Current 2003 operational management procedure (OMP) for the South African West Coast rock lobster fishery.

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The underlying approach of this OMP is to fit a simple population model to available catch-per-unit-effort (CPUE), FIMS, and somatic growth data to provide a basis to compute a catch that will see a target biomass achieved by the end of the period under consideration (i.e., the start of the 2013 season) for the RC1 assessment model, coupled with the assumptions of continued low somatic growth and future recruitment at its average level over 1975–90.

A simple surplus production population model is used for this procedure to model the dynamics from 1992 to 2013:

$$B_{t+1}^p = B_t^p + G_t - (C_t + P_t) \tag{A2.1}$$

where $B_t^p$ is the population model biomass in season $t$; $G_t$ is the annual "growth" of resource in season $t$; $C_t$ is the annual commercial + recreational catch in season $t$; $P_t$ is the annual estimate of poaching for season $t$ (poaching is also taken into account in the underlying operating models); and $B_{1992}^p$ is a parameter estimated in fitting this model to data.

In the population model, the annual "growth" of the resource, $G_t$, is set to be:

$$G_t = a(\beta_t + b) \tag{A2.2}$$

The value of $b$ is set externally by regressing against $\beta$ the equilibrium sustainable yield for the model's estimate of the biomass in 2002 for different values of $\beta$ (this relationship is near linear). This was done for both RC1 and RC2. The intercept of these regressions with the horizontal axis ($\beta$) was averaged over RC1 and RC2, and yielded a value of $b = -9.332$. Using a value derived from the underlying operating model in the OMP may seem to be providing the OMP more information on resource dynamics than is appropriate; remember, however, that though this gives the OMP an advantage in trials under the Reference Case operating model, it is also *dis*advantaged in robustness trials for which this assumed value for $b$ will be incorrect.

The annual somatic growth rate parameter $\beta_t$ is the GLM estimated somatic growth of a male rock lobster as extrapolated to 1 mm CL. For any season $Y$ in the future ($Y$  2003): $\beta_t$ is known for 1992  $t$  $Y-1$, and $\beta_t$ is set equal to the average of the values for the three preceding seasons for the balance of the projection period (for which $\beta_t$ would not be known in practice in season $Y$), i.e.,

$$\left(\sum_{t=Y-3}^{Y-1} \beta_t\right)/3 \text{ for } Y \quad t \quad 2013.$$

Each season (from $y = 2003$), as new data become available, the population model (see Equation (A2.1)) is fitted by minimising the following negative log-likelihood:

$$-\ln\ L = \sum_{T=1993}^{t-1}\left\{\ln\sigma_{cpue} + \frac{1}{2\sigma_{cpue}^2}(\ln\ CPUE_T - \ln\ q_{cpue} - \ln\ B_T^P)^2\right\} + \sum_{T=1992}^{t-1}\left\{\ln\sigma_{FIMS} + \frac{1}{2\sigma_{FIMS}^2}(\ln\ FIMS_T - \ln\ q_{FIMS} - \ln\ B_T^P)^2\right\} + Q \tag{A2.3}$$

where $CPUE_T$ is the trap CPUE for season $T$; $FIMS_T$ is the FIMS CPUE for season $T$; $q_{CPUE}$ is the trap catchability coefficient; and $q_{FIMS}$ is the FIMS catchability coefficient. The parameters of the likelihood $L$ estimated in the fitting process are $B_{1992}^p$ and $a$ (closed form expressions provide $\sigma_{cpue}$ and $\sigma_{FIMS}$).

A penalty function ($Q$) is added to the negative log-likelihood function (see Equation A2.3 above) for the "$a$" parameter of the $G_t$ relationship (see Equation A2.2) used. The penalty function is as follows:

$$Q = \frac{(a - 4000)^2}{2\sigma_a^2}$$

where $\sigma_a = 1000$.

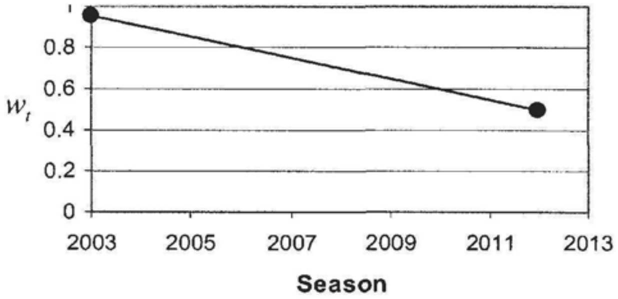
This penalty function was introduced to provide an appropriate trade-off between too little impact of the data upon $a$ (which leads to an inability to show adequate reaction to a changed somatic growth rate), and too much impact (which causes TAC variability that is too large).

### OMP formula

The final TAC-setting formula is as follows:

$$TAC_t = w_t TAC_{t-1} + (1 - w_t)\alpha\left(1 + \lambda(\beta_t^m - \overline{\beta}^m)\right)\frac{\hat{B}_t^p}{\hat{B}_t^p}\left[\left(\frac{CPUE_{t-3,t-2,t-1}}{CPUE_{93,94,95}}\right)^{0.25}\left(\frac{FIMS_{t-3,t-2,t-1}}{FIMS_{92,93,94,95}}\right)^{0.75}\right]^p$$

where $\alpha$, $\gamma$, and $p$ are three control parameters, and $w_t$ changes as follows:



The vertical axis intercept ($w_t$ for 2003) is a tuning parameter and termed $W$, and $w_{2012} = 0.5$. Here values of $W = 0.95$ and 0.50 (i.e., constant $w_t$ over time) were considered for CAND1-3 and CAND4-6 respectively.

Note that the $W = 0.5$ candidates allow the TAC to increase (or decrease) at a faster level relative to the corresponding $W = 0.95$ candidates.

Allowing the $w$ value to vary with time in this way created further control over how much the TAC is allowed to change in the short term compared with the 2002 TAC (of 2915 MT).

For all six candidate OMPs, the following control parameter values were fixed externally: $\lambda = 1$ and $P = 2$. Note that the reason for introducing the $p$ factor and the term in the formula involving CPUE and FIMS was to attempt to render the OMPs more responsive (in TAC terms) to circumstances of either high or low future recruitment, which become manifest in the monitoring data only towards the end of the projection period. The rationale for the CPUE:FIMS weighting power of 0.25:0.75 was to secure a better reaction to changes in abundance index trends that would arise from changes in recruitment strength. The FIMS index reflects the biomass of lobster 60 mm and larger, whereas the CPUE reflects the biomass of lobster only 75 mm and larger.

### Tuning of the six OMP candidates

The above OMP candidates were tuned as follows: CAND1 and CAND4—$\alpha$ selected so that the deterministically estimated $B(13/03) = 1.10$ ($\alpha = 580$ and 650 respectively); CAND2 and CAND5—$\alpha$ selected so that the deterministically estimated $B(13/03) = 1.00$ ($\alpha = 890$ and 920 respectively); and CAND3 and CAND6—$\alpha$ selected so that the deterministically estimated deterministic $B(13/03) = 0.85$ ($\alpha = 1520$ and 1505 respectively). These tunings were conducted for the scenario of low future somatic growth and average future recruitment (see Table 1). Deterministic projections were used (i.e., no account was taken of future process error in the form of recruitment variability and observation error between abundance and somatic growth indices and their underlying trends) to speed the tuning process.

### Restrictions on inter-annual TAC variability

Candidates 1–6 were tested under a restriction of a maximum inter-annual TAC change of 10% (up and down).

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# Characterisation of the recreational fishery for southern rock lobster, *Jasus edwardsii*, in Tasmania, Australia: implications for management

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**Abstract** Southern rock lobster (*Jasus edwardsii*) support significant commercial and recreational fisheries in Tasmania, Australia. Since the mid 1990s the number of persons holding recreational lobster licences increased by over 80%, with c. 15 500 persons licensed in 2002/03. Assessment of the recreational fishery has been undertaken periodically since 1996 using a telephone-diary survey method. The fishery was concentrated off the south-east and east coasts of Tasmania and characterised by strong seasonality in catch and effort, which peaked markedly early in the fishing year (November–January). Although pots were the most popular fishing method, daily catch rates by divers were more than double those for pots. Divers selectively harvested larger lobsters than those taken by pots and more frequently attained the daily bag limit of 5 lobsters. The estimated recreational harvest increased significantly since 1996/97 and in 2002/03 effectively reached a management trigger level of 10% of the total allowable commercial catch, flagging a review of recreational management arrangements.

**Keywords** southern rock lobster; *Jasus edwardsii*; recreational lobster fishery; recreational fishing survey; recreational-commercial fishery interactions

## INTRODUCTION

Southern rock lobster (*Jasus edwardsii* (Hutton)) provide the basis for a major commercial fishery as well as being a highly prized catch for recreational fishers in Tasmania, Australia. The species is harvested commercially by pots whereas recreational fishers are permitted to use a variety of methods, including pots, ring or hoop nets, and dive collection. Recreational licences (first introduced in the late 1970s) are required to harvest rock lobster. The licences are method-based and before the mid 1990s comprised rock lobster pot and general dive licences, the latter permitted dive collection of rock lobster, abalone, and scallops. The licensing system was revised in 1995 and the general dive licence was split into rock lobster, abalone, and scallop dive licences. In 1998, a lobster ring net licence was also introduced, effectively closing a loophole in the legal take of rock lobster. Pot fishers are permitted to use one pot, ring net fishers up to four rings, and divers can use artificial breathing apparatus (scuba and surface air supply or hookah). Licences are issued annually, with the fishing year extending from November to the end of the following August. Recreational fishers may, therefore, hold up to three categories of rock lobster licence in any given fishing year. In addition to licensing and closed seasons, minimum size limits and a ban on the taking of females in berry apply to both recreational and commercial sectors. Recreational fishers are also subject to a daily bag of 5 lobsters and a possession limit of 10 lobsters.

Since the introduction of the present licensing system, the number of persons holding at least one recreational lobster licence has increased steadily from c. 8500 to 15 500 in 2002/03, representing an overall increase of more than 80% since 1995. Increases occurred in each of the licence categories,

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with c. 12 300 pot, 6600 dive, and 3200 ring net licences issued during 2002/03. Set against this trend was the introduction in 1998 of quota management in the commercial fishery, with objectives to reduce catches to sustainable levels and allow for rebuilding of legal-sized biomass (Ford 2001). The total allowable commercial catch (TACC) was initially set at 1502 t, representing an effective reduction in catches which had averaged over 1700 t per annum for the preceding decade. The TACC was increased to 1523 t in 2002.

The size of the recreational harvest has been identified as a management performance indicator for the Tasmanian rock lobster fishery. Specifically, if the recreational harvest exceeded 10% of the TACC in a year, recreational management arrangements would be reviewed (Anon. 1997). The recreational catch also represents an input into the stock assessment model developed to assess stock status and undertake risk assessments under different management scenarios (Punt & Kennedy 1997; Gardner et al. 2002).

There have been few previous attempts to assess the size of the recreational lobster harvest in Tasmania. A household survey of home food production for the year ending April 1992, established that c. 57 t of rock lobster was "home produced" in Tasmania (ABS 1994), equivalent to 3% of the commercial catch at the time. More recently, a telephone survey of licensed fishers produced a harvest estimate of c. 111 000 lobsters for the 1995/96 fishing year, c. 5% of the commercial harvest by numbers (Lyle & Smith 1998).

In this paper we present the results of a series of surveys conducted since 1996 which were designed to provide robust and detailed assessments of the recreational lobster fishery, with the capability to disaggregate catch and effort data regionally, temporally, and by fishing method.

## MATERIALS AND METHODS

### Survey design

Recreational (lobster) fishers were surveyed during the 1996/97, 1997/98, 2000/01, and 2002/03 fishing seasons using a telephone-diary method (Lyle et al. 2002). Potential respondents for each survey were selected at random from the recreational licence database. Although the methodology remained consistent during the four surveys, there were differences in sample selection and survey duration between the first two and the last two seasons. The first two were conducted as part of more general surveys of recreational fishers, only a portion of whom possessed rock lobster licences (Lyle 2000). These surveys were also confined to Tasmanian residents (who comprised 98% of all rock lobster licence-holders in both seasons) and only encompassed a portion of each season (Table 1). Licence databases were grouped into nine strata according to the previous fishing activity level of the licence-holder (days fished in the previous 12 months was recorded as part of the licence application) and the mix of recreational licences held. For the purposes of the current analyses, the data sets were post-stratified to include only those licence-holders in the sample and population who held rock lobster licences. In contrast, the latter two surveys included both resident and non-resident licence-holders and surveyed fishers during the entire season (Table 1). Moreover, in 2000/01 a simple random sample was selected whereas in the latter the population was stratified based on whether or not fishers at least held a lobster dive licence (two strata), with a greater sample take from the "diver" stratum. This strategy was designed to increase the precision of dive estimates, recognising that there were roughly half as many dive licences issued compared with pot licences.

### Telephone-diary survey method

Respondents were contacted initially by telephone in October/November, before the commencement of the fishing year, for a screening interview to assess eligibility to participate in the diary survey. Eligibility was based on the respondent's intention to renew their lobster licence(s) in the coming season, with all eligible respondents invited to participate in the follow-up diary survey. Sampling was conducted without replacement, i.e., licence-holders who did not have a telephone listing or could not be contacted were not replaced.

Diary respondents were issued with "memory jogger" diaries (*sensu* Lyle et al. 2002) and encouraged to record key information for all lobster fishing activities undertaken. Respondents were contacted regularly by telephone throughout the diary period by survey interviewers who recorded details of any fishing activity since the last contact. The frequency of the contact was tailored to the needs and behaviour (level of fishing activity) of individual respondents such that detailed information was routinely collected shortly after each fishing event, reducing potential recall bias problems for any

**Table 1** Details of recreational fishing season, survey period, and sampling of lobster licence-holders in Tasmania, Australia.

| Fishing year: | 1996/97 | 1997/98 | 2000/01 | 2002/03 |
|---|---|---|---|---|
| Season start | 18 Nov 1996 | 22 Nov 1997 | 11 Nov 2000 | 2 Nov 2002 |
| Season end | 31 Aug 1997 | 31 Aug 1998 | 31 Aug 2001 | 31 Aug 2003 |
| Diary survey period | 1 Dec 1996–30 Apr 1997 | 22 Nov 1997–30 Apr 1998 | 11 Nov 2000–31 Aug 2001 | 2 Nov 2002–31 Aug 2003 |
| Sample selection | Systematic random (post-stratified to include only rock lobster licences) | Systematic random (post-stratified to include only rock lobster licences) | Random | Random stratified |
| Sample population | Licensed Tasmanian residents | Licensed Tasmanian residents | All licence-holders | All licence-holders |

non-diarised data. By maintaining regular telephone contact, interviewers were also able to immediately clarify any misunderstandings or inconsistencies at the time of the interview, thereby ensuring overall data quality and completeness. As a general rule, respondents were contacted at least once a month if no fishing trips were planned or more frequently during periods of activity.

Data collected for each fishing activity or event included date(s), fishing region, method, duration, numbers of lobster kept (harvested) and released or discarded. Pots were generally fished overnight; in a small number of instances pots were not checked for several days, usually because of the inability to retrieve the pots due to unfavourable weather conditions. For the purposes of calculating effort, overnight sets were considered to represent a single pot-day of effort. In addition, regardless of how many times pots or ring nets were checked, or number of dives undertaken on a given day, daily method-based totals (catch and effort) were used in analyses.

### Data analyses

Although initial sample selection was based on the previous year's licence database, licence details for the survey year were used for data expansion. That is, the licensing status (licences held and date of issue) for all diarists was established and expansion factors calculated as the size of the licensed population divided by the number of licensed diarists. Not all diarists renewed licences and in instances where stratification was used in initial sample selection, a very small proportion of diarists, by virtue of licences held in the survey period, changed strata for the purposes of data analysis. As initial sample selection was random these effects were not assumed to have introduced systematic biases.

The progressive increase in the number of licence-holders during the year meant that the sample size (i.e., number of licensed diarists) and total number of licensed fishers changed within the diary enumeration period. For instance, in the years surveyed, 51–60% of licences were issued by the end of November, 79–83% by the end of December, and 91–92% by the end of January. To account for this dynamic, the number of fishers registered on the licence database and the number of diarists licensed at the end of each month provided the basis for calculating expansion factors that were applied to fishing activity that took place in the particular month. Any fishing activity reported by diarists whilst unlicensed (either before renewing a licence or by diarists who did not renew licences) was excluded from the analyses. Such unlicensed fishing represented c. 4% of all reported fishing events.

Since the distributions of effort (days fished) and catch were highly skewed, standard statistical methods that assume normality were not appropriate for calculating confidence intervals. Therefore, the "bootstrap" method was used to estimate confidence limits, determined using the percentile method (Haddon 2001). Where appropriate, stratification was maintained for these analyses and 5000 simulations were conducted.

Calculation of standard errors for population proportions (proportion of licence holders who fished or caught no rock lobster) was based on Pollock et al. (1994).

### Size composition

Size composition information for recreationally caught lobsters was collected during 2002/03 from on-site surveys and information provided by volunteer fishers. Method, fishing location, sex, and carapace length (mm) were recorded. Average weights were determined by converting lengths into weights using the following relationships:

$W = 0.000285L^{3.114}$ males

$W = 0.000271L^{3.135}$ females

where $W$ is body weight (g), and $L$ is carapace length (mm) (Punt & Kennedy 1997). A two-way analysis of variance, using Type III sum-of-squares, was used to test carapace length against sex, method, and sex × method, and contingency table analysis was used to compare sex ratio against method.

### Commercial fishery data

Commercial catch and effort data were obtained from compulsory catch returns in which data were reported on a daily basis by depth and by ½ degree fishing blocks. Catches were reported in terms of numbers and weights. To compare commercial and recreational fisheries, commercial catch data were summarised (numbers and weight) for periods corresponding to the surveys and according to the reporting regions used in the surveys. Where commercial fishing blocks were bisected by recreational boundaries, catches within such blocks were apportioned equally between the two appropriate recreational regions. Since the quota year (March–February) differed to the fishing year (November–August) these comparisons were subject to variability arising from when commercial fishers chose to take their catch within each quota year.

## RESULTS

### Response rates

When sample loss (no telephone listings) was discounted, screening survey response rates ranged between 90% and 96% (mean 93%), with non-contacts accounting for 3–9% and refusals less than 1% of the sample in each of the four surveys. Of those respondents who indicated that they expected to renew their licences and actually did so (eligible respondents), 90–95% fully responded to the diary surveys (Table 2). Non-response to the diary arose from initial refusal to participate and dropouts during the diary period, the latter occurred almost exclusively because of loss of contact (typically telephone disconnection). No adjustments have been made for non-response because of the very high response rates and only data for fully responding diarists (whether they fished or not) have been used in analyses.

### Catch and effort

During 2000/01, 86.5 ± 1.9% (± SE) of licence-holders fished for lobster compared with 88.4 ± 1.7% for the 2002/03 fishing year. Inclusive of those who did not fish, 24.6 ± 2.4% and 25.0 ± 2.2% of licensed fishers harvested no lobster during 2000/01 and 2002/03, respectively.

Estimates of catch (harvest), effort and catch rate by fishing year, and by method are presented in Fig.

**Table 2** Number of license-holders surveyed and diary response rates by fishing year.

| Fishing year: | 1996/97 | 1997/98 | 2000/01 | 2002/03 |
|---|---|---|---|---|
| Eligible respondents (screening survey) | 362 | 400 | 343 | 442 |
| Accept diary | 351 | 387 | 332 | 409 |
| Full diary response | 333 | 359 | 325 | 400 |
| Response rate (%) | 92.0 | 89.8 | 94.7 | 90.5 |

1. Despite the similarity in effort levels for 1996/97 and 1997/98, lower catch rates for the primary fishing methods (pot and dive) in 1997/98 resulted in a 22% reduction in estimated catch compared with 1996/97. It is noteworthy that although confidence intervals for catch overlapped between years, catch estimates for November 1996 were not available, implying that inter-seasonal differences would have been greater (and possibly significant).

Total catch estimates for 2000/01 and 2002/03 represented substantial increases over the earlier years, largely attributed to increased effort across all methods (Fig. 1). The 27% increase in harvest between 2000/01 and 2002/03 was due primarily to the combined effects of increased pot effort and higher pot catch rates, with dive catches comparable between years.

Overall, pots were the most frequently used method, deployed on 80–83% of the total days fished for lobster and accounting for 62–66% of the total catch in each of the years surveyed apart from 2000/01, when they produced 55% of the total catch (Fig. 1). Although dive effort accounted for just 18–21% of the total days fished, higher daily catch rates (2.1–2.6 lobster compared with 0.9–1.2 lobster for pots) meant that the dive catch was proportionately greater, at between 32% and 44% of the total. Although ring net usage was undoubtedly underestimated in the first two surveys, conducted before the introduction of ring net licences, subsequent surveys confirmed that the method was of minor significance (Fig. 1). Annual catch rates for ring nets varied widely between years (1.1–2.5 lobster/day), possibly influenced by small sample sizes.

Catch rates for all methods were highest in 1996/97 but were inconsistent in how they varied thereafter, with lowest dive catch rates recorded in 1997/98 and lowest pot and ring net catch rates in 2000/01 (Fig. 1).

## Temporal and spatial patterns in catch and effort

The surveys revealed strong seasonality in the fishery, with three distinct phases of activity; high levels of catch and effort between November and January, intermediate levels between February and April, and low levels for the remainder of the fishing year (Fig. 2). In 2000/01 and 2002/03, the November to January period alone accounted for over 70% of the total catch and effort whereas the final four months contributed just 5%. This implies that the 1997/98 survey would have accounted for the vast majority of that year's catch and effort and that inter-annual differences between 1996/97 and 1997/98 were underestimated (because of the unavailability of information for November 1996).

Five fishing regions were defined for the 1996/97, 1997/98, and 2000/01 surveys and eight regions, corresponding to "areas" used in the rock lobster stock assessment (Punt & Kennedy 1997), for the 2002/03 survey (Fig. 3). Regionally, the relative distribution of catches has remained consistent over time with catches concentrated off the south-east (SE or Area 1) and east (E or Areas 2–3) coasts (Fig. 3). The combined catch from these regions accounted for 67–75% of the total (numbers) in each of the years surveyed. North coast (NE and NW or Areas 4–5) catches represented c. 14% of the total whereas a further 12–18% of the total was taken from the west coast (W or Areas 6–8).

Spatial structuring of the fishery based on method was also evident. The majority of the combined south-east and east coast harvest was taken by pots (62–79% depending on fishing year), with dive collection of secondary importance (21–38%). By contrast, dive collection consistently dominated north coast catches (64–86%) with pots accounting for the bulk of the remainder (14–35%). Pots were the main capture method (48–60%) off the west coast, followed by dive collection (20–46%) and, contrary to elsewhere, ring net catches were of some significance (6–24%).

## Daily catch by method

Catch distributions differed markedly by fishing method (Fig. 4). The combined data set indicated that overall, 47% of pot-days (range of 45–50% depending on fishing year) yielded no retained catch and 27% produced only 1 lobster. The bag limit of 5 rock lobster was rarely attained or exceeded (<3% of pot-days). By contrast, success rates for divers were substantially higher, with 24% of the total dive effort (range of 17–28%) resulting in no retained catch and, significantly, the bag limit was achieved (or exceeded) on almost 25% of all diver-days (Fig. 4). Dive method also proved to be an important factor. Divers using hookah achieved the greatest success rates, taking the bag limit in over 35% of dive-days compared with 17% for scuba and 11% for snorkel methods (Fig. 4). Mean annual catch rates ranged between 2.8 and 3.3 lobster/day for hookah compared with 1.6–2.8 for scuba and 1.0–2.2 for snorkel. Catch distributions for ring nets tended to be intermediate between pots and diving, with nil catches reported on 39% and the bag limit reached on 20% of the days fished with rings (Fig. 4).

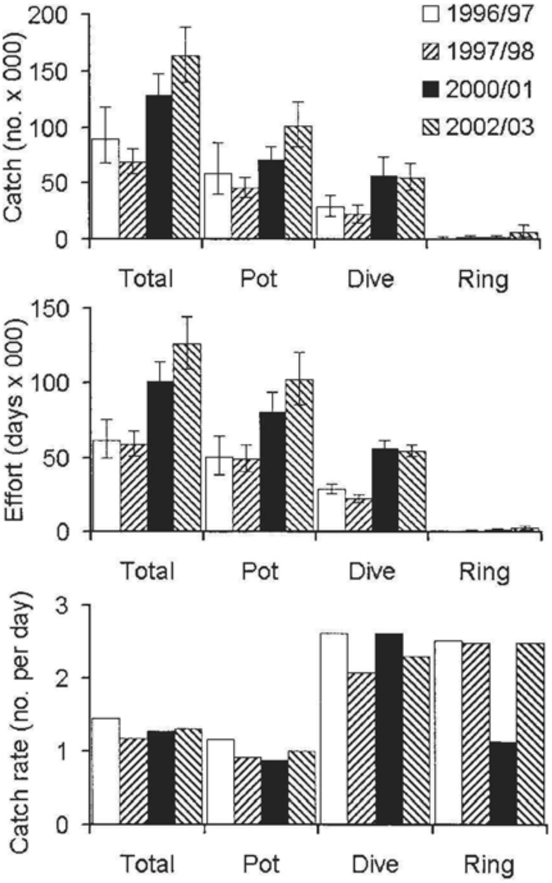


**Fig. 1** Estimated recreational catch (number harvested), effort (days fished), and catch rate (number per day) by method and by fishing year for lobster in Tasmania, Australia. Error bars represent 95% confidence interval.

### Size composition

Lengths of 491 dive and 251 pot-caught lobster taken from the south-east and east coasts of Tasmania were available (Fig. 5). Analysis of variance demonstrated significant method (*F* = 59.6; d.f. = 1; $P < 0.001$), and sex (*F* = 22.2; d.f. = 1; $P < 0.001$) effects, and a significant sex × method interaction (*F* = 9.3; d.f. = 1; *P* = 0.002). Dive-caught lobster were significantly larger than pot-caught lobster, averaging 124 mm and 114 mm respectively, with males larger than females. The estimated average weight for dive-caught lobster was 1006 g, 33% greater than that for pot-caught lobster (757 g). Contingency table analysis of sex ratio by method produced a highly significant result ($\chi^2 = 36.4$; $P < 0.001$), with male to female ratios of 0.66:1 and 1.71:1 for pot and dive methods respectively.

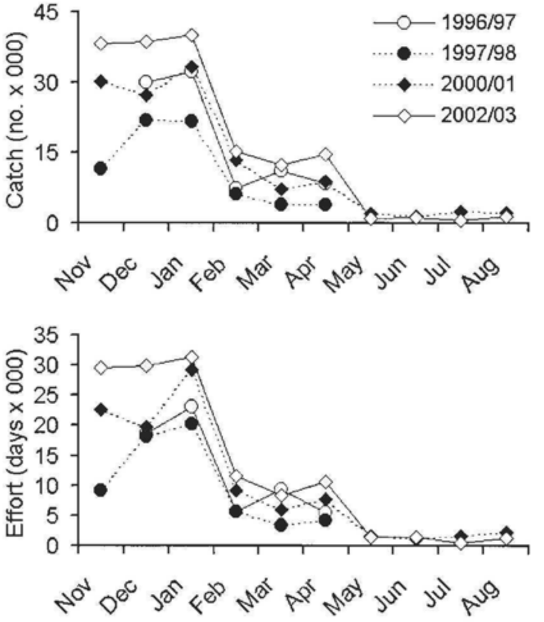


**Fig. 2** Estimated recreational catch (number harvested) and effort (days fished) by fishing year and month for lobster in Tasmania, Australia.

### Comparison with commercial catch

Relative to the commercial catch (numbers), the recreational harvest increased from c. 5% in 1996/97 to 12.5% in 2002/03 (Fig. 6). The sharp increase in the recreational proportion between 2000/01 and 2002/03 was partly the result of increased recreational catch but also a reduction in commercial landings during the 2002/03 fishing year (noting that the TACC for the 2002 quota year was in fact caught).

The weight of the 2002/03 recreational harvest was approximated by applying mean lobster weights (by method) determined from size composition data to catches for Areas 1–3 and 8. In the absence of size information for the other areas, mean lobster weights based on commercial catch returns were used, with an adjustment factor of 1.33 for dive-caught lobster. Lobsters caught by ring nets were assumed to have the same mean weight as pot-caught individuals. On this basis the 2002/03 recreational harvest was estimated as 148.5 t, equivalent to 13% of the commercial catch taken during the fishing year (Fig. 5). However, relative to the 2002 quota year catch

**Fig. 3** Maps of Tasmania, Australia showing regions or areas used for data reporting and recreational catch estimates (thousands of lobster) by region or area and fishing year. (SE, south-east; E, east; NE, north-east; NW, north-west; W, west; 1, Area 1; 2, Area 2; 3, Area 3; 4, Area 4; 5, Area 5; 6, Area 6; 7, Area 7; 8, Area 8.)

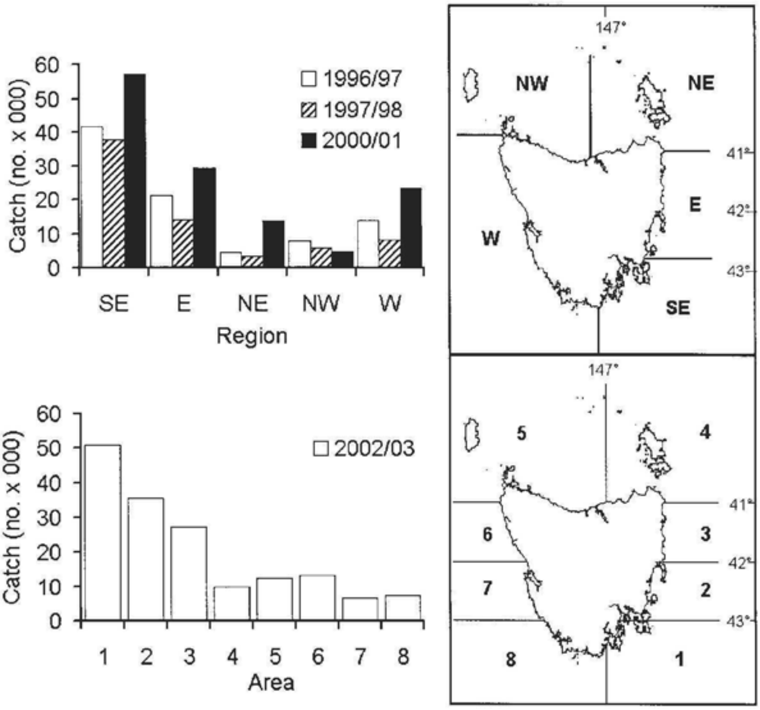
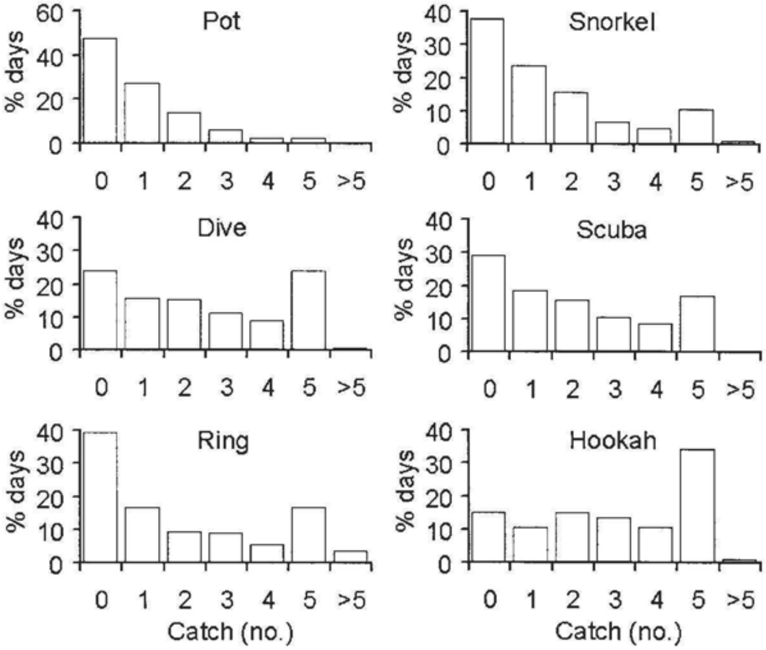


**Fig. 4** Relative distribution of recreational catches (numbers harvested per day) by fishing method for lobster in Tasmania, Australia. Data have been combined across years.



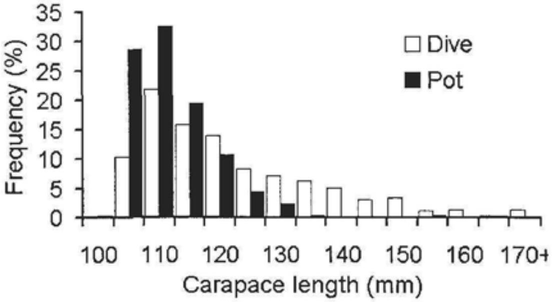


**Fig. 5** Relative length-frequency distributions by 5 mm size class for recreationally caught lobster taken by dive and pot fishing methods in Tasmania, Australia.

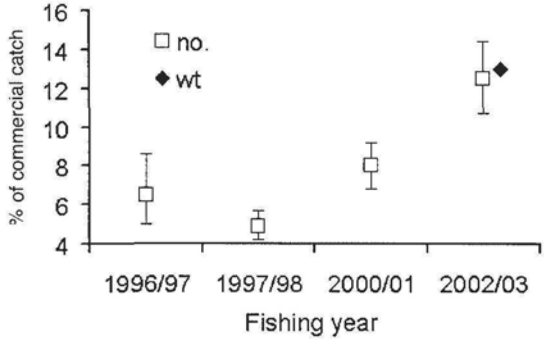


**Fig. 6** Tasmanian recreational lobster catch as a percentage of the commercial catch taken during periods corresponding to the recreational surveys, based on numbers (no.) and weight (wt). Error bars represent 95% confidence interval based on recreational harvest estimates.

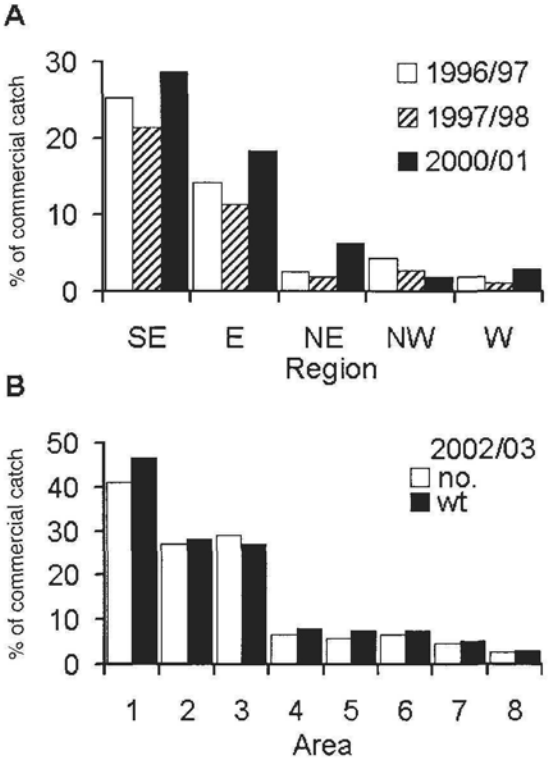


**Fig. 7** Tasmanian recreational lobster catch as a percentage of the commercial catch by fishing region or area (refer Fig. 3): **A**, catches based on numbers for the 1996/97, 1997/98, and 2000/01 fishing years; and **B**, catches based on numbers (no.) and weight (wt) for 2002/03.

(effectively the 2002 TACC) the recreational catch was equivalent to 9.8% of commercial landings.

In south-east Tasmania (SE or Area 1), the recreational catch relative to the commercial catch (numbers) increased from 25% to 41% between 1996/97 and 2002/03 (Fig. 7). East coast (E or Areas 2–3) catches almost doubled in relative importance over this period, to c. 30% in 2002/03. By contrast, north (NE and NW or Areas 4–5) and west (W or Areas 6–8) coasts catches remained relatively stable, equivalent to less than 7% of the total commercial catch in each of the years surveyed.

## DISCUSSION

A variety of methods have been applied to assess and monitor recreational lobster fisheries throughout the world, including direct observation of changes in abundance (Davis 1977; Eggleston & Dahlgren 2001), creel surveys (Davis & Dodrill 1989), mail surveys (Melville-Smith & Anderton 2000; Muller et al. 2000), telephone surveys (Cockcroft & Mackenzie 1997; Lyle & Smith 1998), diary surveys (Bradford & George 2002), and telephone-diary surveys (McGlennon 1999; Venema et al. 2003). On-site methods such as direct observation and creel surveys tend to be limited in spatial and temporal scale and thus off-site methods have been more commonly applied in large-scale studies. Off-site methods, however, may suffer from several sources of non-sample error, including non-response and recall biases, that compromise data reliability (Pollock et al. 1994). In respect to these biases, the telephone-diary method as applied here and elsewhere (McGlennon 1999; Lyle 2000; Venema et al. 2003) consistently resulted in very high response rates (>90%), and potential problems arising from recall bias were addressed through the combined use of the diary and frequent telephone contact. As such, recall periods for non-diarised information were limited to a maximum of about one month. Cockcroft & Mackenzie (1997) used a multi-stage telephone survey to address recall bias, with a series of samples of licence-holders taken throughout the fishing season and respondents required only to recall their lobster fishing activity for the two weeks before the interview. Typically, however, telephone (or mail) surveys rely on information recalled over much longer periods (Lyle & Smith 1998; Melville-Smith & Anderton 2000). Further concerns relating to off-site methods arise from self-reporting of information and include exaggeration of catches (prestige bias) (Pollock et al. 1994). These biases are harder to assess, but by developing rapport between the respondent and interviewer in the telephone-diary method, the respondent was brought into the survey process in terms of understanding objectives and recognising the need for reporting accuracy. We consider, therefore, that the telephone-diary method represented a robust survey approach, providing detailed and reliable information about fishing activities.

Recreational licence numbers in Tasmania have increased steadily since 1995, with high licence usage rates (>86%). The main drivers for this trend are unclear. In Western Australia, recreational lobster licence numbers are generally responsive to changes in rock lobster abundance and in fact future catch predictions (based on puerulus settlement indices) are used in the promotion of recreational licence sales (Melville-Smith et al. 2001). Although legal-sized lobster biomass has generally increased in Tasmania since the mid 1990s (Gardner et al. 2002), the overall increase in licence numbers has also been underpinned by substantial turnover in fishers. In most years more than one third of licence holders did not hold a licence in the previous year. A more formal examination of licensing dynamics, including an evaluation of fisher motivations and attitudes in relation to rock lobster, may prove informative in predicting future developments in the Tasmanian fishery.

Increased licence numbers have resulted in the marked expansion of catch and effort, with the recreational harvest almost doubling since 1996/97. Regionally, the fishery was concentrated in the relatively sheltered waters off the south-east and east coasts of Tasmania, adjacent to major population and holiday centres. Limited areas of productive (for rock lobster) inshore coastal reef and generally exposed waters off the north coast, and restricted access points and exposed waters off the west coast have meant that these regions attracted comparatively low levels of recreational fishing pressure for lobster.

Recreational fishing activity was highly seasonal, being most intense immediately following the opening of the season in November and over the summer period, with peaks in effort during January and highest catches recorded in December and January. This pattern reflected the timing of the summer holidays (more days available to fish and favourable weather conditions) and increased lobster availability (reserve accumulation phase of moult cycle). The sharp fall in catch and effort in February was a consistent feature of the fishery, as were slight increases in effort attributable to fishing over the Easter holiday period (March 1997 and April in the other years). Activity levels remained low during the final four months of the fishing year, corresponding to closure of the fishery to the taking of female lobsters at the end of April and the onset of cooler and unsettled weather. High catches early in the season appear typical of other lobster fisheries where there are discrete fishing seasons, for example Western Australia (Melville-Smith & Anderton 2000), South Australia (McGlennon 1999; Venema et al. 2003), South Africa (Cockcroft & Mackenzie 1997), and Florida (Muller et al. 2000).

Pots were the main method used by recreational fishers in Tasmania, with 1.8–2.0 times more pot than dive licences issued each year and over four times more days fished using pots than dive collection. Ring nets, although an important method off the west coast, were of minor significance in terms of overall catch and effort. Pots also represent the most commonly used capture method for southern rock lobster in South Australia (Venema et al. 2003) and western rock lobster (*Panulirus cygnus*) in Western Australia, though there has been a shift towards increased participation by divers in recent years in the Western Australian fishery (Melville-Smith & Anderton 2000). Melville-Smith & Anderton (2000) noted that divers consistently reported higher daily catch rates (1.5–2.4 lobster) than potters (1.0–1.5 lobster) in the western rock lobster fishery. Recreational catch rates in the Tasmanian fishery were generally comparable to those for Western Australia and, in terms of pots, were also similar to those for southern rock lobster in the southern zone of the South Australian fishery (0.9 lobster/pot-lift) (Venema et al. 2003).

Consideration of fishing method highlighted factors that have implications for management and impacts on the lobster populations. First, daily catch rates for divers were 2.2–3.0 times higher than those for pot fishers, and thus the contribution by dive collection to the catch was proportionally greater than implied by effort levels. Second, artificial breathing apparatus (hookah and scuba) conferred a clear advantage over free-diving for lobster. Highest success (at least one lobster) and catch rates were achieved by divers using hookah, presumably because the gear enabled divers to access confined spaces more readily (lobsters can only be taken using gloved hand in Tasmania) and bottom time was less constrained than for the alternative dive methods. There was some evidence to support the latter; hookah dives were on average longer in duration (between 1.6 and 1.9 h depending on fishing year) than those reported by scuba divers (1.1–1.6 h). Third, by actively targeting individual lobsters, divers selectively harvested larger lobsters (and proportionally more males) than those taken by passive capture methods (pots). High-grading of catches, presumably in response to bag limits, is a common practice amongst divers and may further contribute to the observed size differences. In addition, there is potential for handling damage (e.g., broken antennae and limbs) as a result of attempted capture or removal from dens before divers can assess size, sex, or condition. The implications of such damage on subsequent growth, reproduction, and survival are generally unknown.

Bag limits represent the primary strategy to constrain recreational catches in Tasmania. In practice, being restricted to a single pot, pot fishers rarely attained the bag limit and thus this management measure had little direct impact on the overall pot catch. By contrast, bag limits had an obvious impact on dive catches, with about one quarter of all dive effort resulting in the capture of at least five lobster. Any measures to reduce bag limits would, therefore, have very different impacts on pot and dive catches.

Relative to the commercial catch, the recreational lobster harvest in Tasmania had more than doubled since the late 1990s to over 12%, reflecting the combined effects of increased recreational catch and the introduction of catch limits (quota) on the commercial sector. In Western Australia and South Australia, recreational lobster catches have been in the order of 4–5% of commercial production (Melville-Smith & Anderton 2000; Venema et al. 2003). In South Africa, recreational catches of *Jasus lalandii* exceeded 20% (Cockcroft & Mackenzie 1997) and in Florida *Panulirus argus* catches have exceeded 30% (Muller et al. 2000) of commercial landings in recent years. Statewide comparisons, however, can underestimate regional impacts. This was particularly evident off south-east Tasmania, where in 2002/03 the recreational catch exceeded 40% of the commercial take. By contrast, recreational catches were comparatively small (<7% of the commercial catch) off the north and west coasts. Furthermore, because of depth limitations on diving and practicalities of hauling pots and ring nets, the recreational fishery operates primarily in shallow waters, at depths of less than c. 20 m. On the other hand, commercial fishers operate over wider areas, including deeper offshore reefs, and catch returns confirmed that typically only about one third of the catch was taken from depths of less than 20 m. Thus where the sectors overlap, the recreational proportion of the catch was higher than implied by comparisons based on total commercial catch. For instance, the 2002/03 recreational harvest equalled 35% of the commercial catch from shallow-water, whereas off the south-east coast the recreational catch exceeded the commercial catch by 34% based on numbers and 48% based on weight.

In reviewing management arrangements for recreational lobster fisheries worldwide, Melville-Smith et al. (2000) noted that management has tended to focus primarily on issues of sustainability in the commercial fishery. However, with trends towards increased participation and harvest of lobsters in recreational fisheries (e.g., Cockcroft & Mackenzie 1997; Melville-Smith & Anderton 2000; Muller et al. 2000; Venema et al. 2003; present study) there is growing recognition of the significance of the recreational sector and the need for it to be accounted for in stock assessments, ecological impacts of fishing, and resource sharing and access. In South Australia resource sharing has been defined in a de facto fashion, with the recreational catch capped at 4.5% of the total (recreational plus commercial) catch. If this level is exceeded the government will enter the open market to lease quota or pots from the commercial sector to offset the estimated recreational over-catch (Venema et al. 2003). Although such issues have yet to be addressed explicitly in Tasmania, the size of the recreational catch relative to the TACC has been identified as a management performance indicator (Anon. 1997). The recreational catch estimate for 2002/03 effectively reached the management trigger level of 10% and, as a consequence, a review of recreational management arrangements has been initiated. Notwithstanding such issues, the regional importance of the recreational lobster fishery highlights the need for ongoing assessment to monitor future developments and to quantify impacts on stocks. The telephone-diary survey method represents a viable and efficacious approach to provide such information.

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# Comparison of catches on two types of collector of recently settled stages of the spiny lobster (*Panulirus argus*), Florida, United States

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**Abstract** This study compared catches of *Panulirus argus* pueruli and very young juveniles between Hunt and Sandwich collectors at Long and Big Munson Keys, Florida, United States. Catch comparisons were made over the peak puerulus settlement period between February and July 2002, using six Sandwich and six Hunt collectors at each site. The collectors were set out in arrays and the relative positions of the two collector types were reversed each month after they had been checked and the catch removed. A total of 3470 pueruli and juveniles were collected; 2011 and 1459 by Sandwich and Hunt collectors, respectively. Sandwich collectors caught an average of 5.43 more pueruli and juveniles per check than Hunt collectors, with this difference being significant for catches of clear pueruli (P1s), pigmented pueruli (P3s), and juvenile stages (J1s and J2s) ($P < 0.05$), but not for catches of semi-pigmented pueruli (P2s). The catches made by both collector types were highly dependant on the month of collection and site of the collectors ($P < 0.01$). Catches were generally not influenced by the location of the collector in the array ($P = 0.50$), but corner collectors caught significantly fewer P1s, P2s, P3s, and J1s and J2s than all other collectors ($P < 0.01$). Conditioning time influenced the total catch ($P < 0.01$) but was not significant for all individual P1s, P2s, P3s, and J1s and J2s stages of development. Overall, the time taken for collectors to condition in Florida was less than the Sandwich collectors used for *P. cygnus* in Western Australia.

**Keywords** *Panulirus argus*; juvenile; pueruli; spiny lobster; Sandwich; Hunt; collectors; Florida

## INTRODUCTION

The life cycle of spiny lobsters (*Panulirus argus*) is complex and includes a long oceanic larval phase varying in length between species. Spiny lobsters hatch as planktonic phyllosoma larvae (c. 1–2 mm long) and develop through a series of moults, increasing in size. After developing in offshore

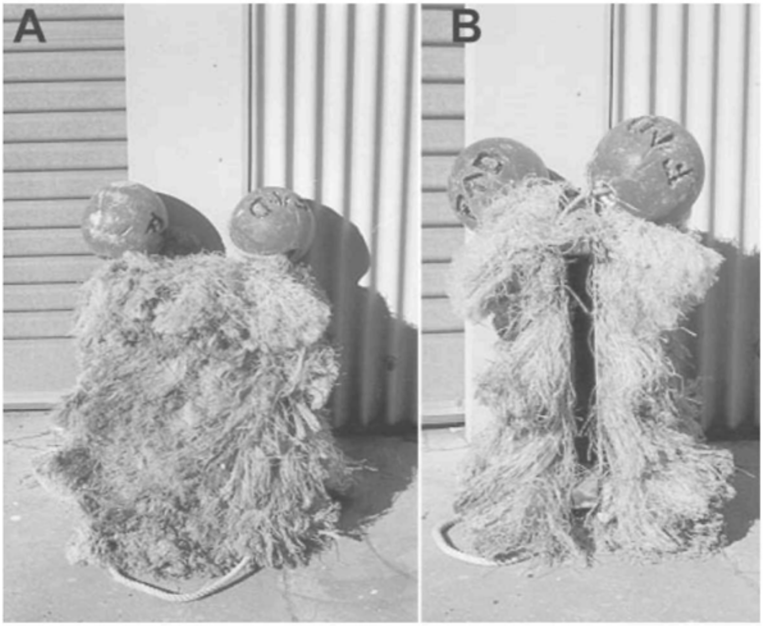

**Fig. 1** **A**, Front view and **B**, side view of Sandwich collectors used to catch *Panulirus cygnus* pueruli in Western Australia.

**Fig. 2** Hunt collector designed to catch pueruli and juveniles of *Panulirus argus* in Florida, United States.

waters, phyllosoma return towards the continental shelf where the final stage larvae metamorphose into the puerulus, a non-feeding stage (c. 30 mm long), which then swims towards the coast. When the puerulus settles, it moults after a few days to weeks into a benthic juvenile stage.

Various designs of collectors have been used with considerable success to capture the puerulus stage of spiny lobsters (see review by Phillips & Booth 1994). In Western Australia, a new collector type, based on the collector developed by Montgomery & Craig (1997), called the Sandwich collector (Fig. 1) has recently been introduced as a more robust version of the Phillips collector, and has been shown to be highly effective in catching the pueruli of *P. cygnus* (Phillips 1972; Phillips et al. 2001; Rossbach et al. 2001).

The Hogs-hair collector was designed to catch the pueruli of *P. argus* in Florida (Witham et al. 1968), however, there have been several modified versions of this collector used. The version used in this study was the Hogs-hair collector dubbed Hunt collector by Phillips & Booth (1994) (Fig. 2; see Cox et al. (1997) for a complete description).

These collectors, the Phillips and Hunt, and their variations, have been used in the United States, Mexico, Australia, Japan, and many Caribbean countries in attempts to measure the levels of puerulus settlement and/or to understand larval recruitment levels (Phillips & Booth 1994).

The main objective of this study was to compare the effectiveness of Sandwich and Hunt collectors in catching *P. argus* pueruli at two locations in Florida. Phillips et al. (2001) used Sandwich collectors to collect lobster pueruli of *P. cygnus* in Western Australia. That study revealed that catches of the collectors showed effects of soak time, as well as marginally significant corner and layer effects, carry-over effects, and square-of-time effects (all these terms as defined in Phillips et al. 2001). In the current study, the significance of the same effects was explored for *P. argus* using both Sandwich and

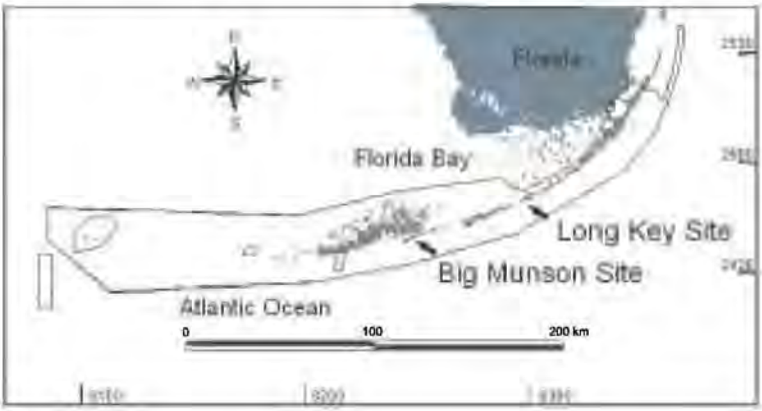

**Fig. 3** Study sites at Long Key and Big Munson Key in Florida, United States. Line around the keys is the boundary of the Florida Keys National Marine Sanctuary.

Hunt collectors. A second objective of this study was to test the ability of the two types of collectors to retain the juvenile settled lobsters.

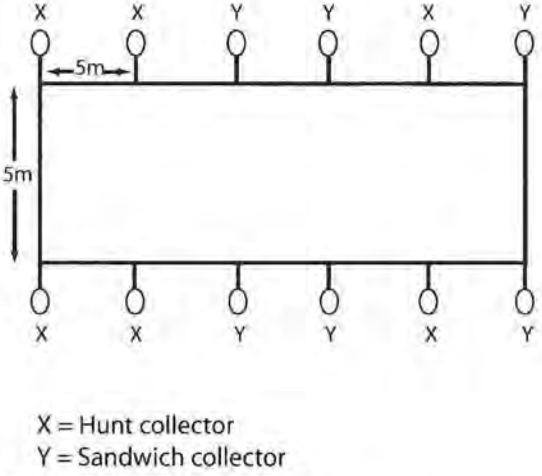

**Fig. 4** Arrays of Hunt and Phillips collectors used to catch pueruli and juveniles of *Panulirus argus* at the two sites in Florida, United States.

## METHODS

### Terminology

To provide conformity with other studies including those of Booth (1979, 2001), pueruli are called P1–P3s in this paper. P1s are pueruli without exoskeletal pigment or with it present only on the distal parts of the second antennae; in P2s the hepatopancreas is visible; P3s have exoskeletal pigmentation in parts of the body other than the second antennae. J1s and J2s are first instar juveniles and second instar juveniles, respectively. J1s were easily distinguished from J2s on the basis of size.

### Study sites

The relative effectiveness of the Sandwich and Hunt collectors was compared using collectors placed in the nearshore surface waters on the Atlantic Ocean side of Long Key (N 24° 37.08′ W 81° 23.66′) and Big Munson Key (N 25° 48.31′ W 81° 50.37′) in the Florida Keys, United States (Fig. 3). Collectors were deployed on permanent mooring eyebolts located in depths of 1.2–3.0 m in January 2002.

### Experimental design

Sandwich and Hunt style collectors were set out in an array, with collectors spaced c. 5 m apart (Fig. 4). Sandwich collectors were "conditioned" by imersion in the ocean for 1 month before deployment at the same site and the same tassels were used for the duration of the experiment. With the Hunt collectors, the Hogs-hair material was replaced after 12 weeks of deployment, in April 2003. Collectors were checked monthly from February through July 2002. The collectors were pulled monthly during the full moon period and all pueruli and juveniles were removed from the collectors before returning the collectors to the sea. After being checked, and the animals removed each month, the collectors were repositioned so that the Hunt and Sandwich collectors occupied reverse positions.

### Statistical analysis

Catches of the collectors were compared by row (offshore versus inshore) and by position (corner versus interior). An analysis of variance with covariate (ANCOVA), general linear model (GLM) and a $t$ test were used to test the significance of each

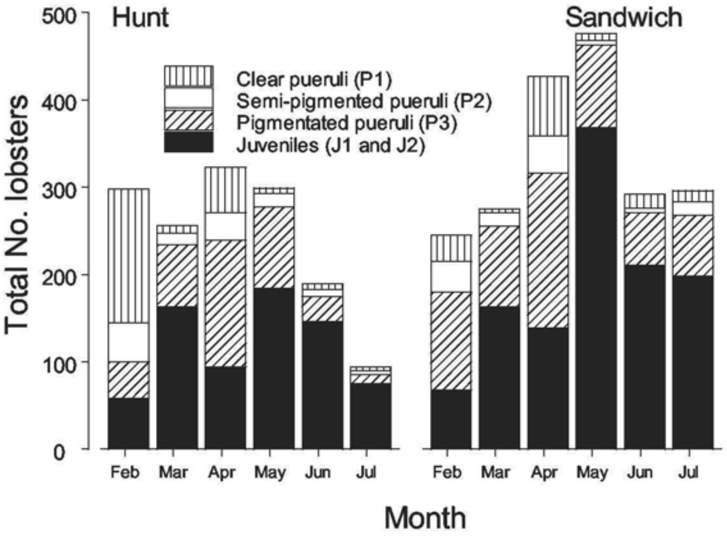

**Fig. 5** Plot of frequency distribution of different development stages of pueruli and juveniles of *Panulirus argus* collected in Florida, United States in February to July 2002 with two different types of collectors.

effect on the catch rate of P1s, P2s, P3s, and J1s and J2s. ANCOVA was used to investigate the effect of each factor on the response variable directly and GLM was used to test the effect of each level in each factor compared with the control. *F* tests and *t* tests were used to test the significance of each factor or level in ANCOVA and GLM results respectively. The response variables used were the total number of pueruli collected and the total number of each P1s, P2s, P3s, and J1s and J2s caught. As a result of four missing observations from lost collectors (three observations) and a lost record of soaking time (four observations), the number of replicates was different within each level of some factors, and therefore Type III sums of squares were used in the ANCOVA and GLM analyses. Type III sums of squares are invariant for the cell frequencies as long as the general form of estimability remains constant, making them useful for an unbalanced model with no missing cells.

The variables were: type of collector (Sandwich, Hunt); site (Long Key, Big Munson Key); location (inshore, offshore); corner (yes, no); and month (February through July). It was considered that the performance of the collector type might vary with time (month). This was called the interaction between the factor variable "type of collector" and the factor variable "month". Because of this interaction the linear or non-linear tendency of time, with number of P1s, P2s, P3s, and J1s and J2s caught, could not be studied. The effect of time (month) was treated as a factor and soaking time (numbers/day) was considered as a covariate. To compare the catching ability of the two types of collectors, *t* tests were applied directly.

## RESULTS

Total numbers of lobsters collected by month are shown in Fig. 5. There were 369 (10.64%) P1s, 238 (6.86%) P2s, 996 (28.70%) P3s, and 1867 (53.80%) J1s and J2s (Table 1). From *t*-test results (Table 1), there were either marginal, or no difference, in the performance of both types of collectors in collecting P1s ($P = 0.10$) and P2s ($P = 1.00$). Sandwich collectors outperformed Hunt collectors in collecting P3s ($P < 0.001$), J1 and J2s ($P < 0.001$), and total pueruli ($P < 0.001$).

The highest catch of lobsters made by Hunt collectors was in April, whereas Sandwich collectors recorded their highest catches in May. Sandwich collectors showed increased catches of P1s–J2s from February to May and then remained at a steady catch rate from June to July. Conversely, the Hunt collectors had steady catches during the first 4 months and then catches decreased from June to July (Fig. 5). The mean and standard deviation of the number of P1s–P3s collected per collector are shown in Table 2.

The results from the ANCOVA and GLM with soak time (i.e., the collector age) as a covariate, have been given for each developmental stage of pueruli and juvenile *P. argus* (Table 3). The coefficient of determination ($R^2$) varied from 0.47 to 0.6 and all the regressions were significant ($P < 0.001$) for the three puerulus and two juvenile stages.

Both site (Long and Big Munson Keys) ($P < 0.01$, GLM and ANCOVA) and the time of sampling (month of year) ($P < 0.01$, ANCOVA) were highly significant for the number of pueruli and juveniles, of all stages, caught by the collectors (Table 3). The mean catch at Long Key was 2.06 (P1s), 1.01 (P2s), 3.81 (P3s), and 1.25 (J1s and J2s) more than the mean catch at Big Munson Key (Table 3).

### P1s

Hunt collectors performed significantly better than Sandwich collectors with on average 9.92 more clear pueruli (P1s) per collector in the catch ($P < 0.01$). There were insignificant ($P = 0.24$) corner effects. There were insignificant ($P = 0.91$) improvements in the catches with soak time ($P < 0.05$). The interaction effect between type of collector and time was significant ($P < 0.01$), indicating that catches of P1s improved over time disproportionately for the two collector types. There was no difference in the catch from offshore compared with the inshore collectors ($P = 0.89$).

### P2s

The effect of collector type was not significant ($P = 0.42$). There were no corner effects ($P = 0.68$) on the catch. The interaction effect of collector type and time was not significant ($P = 0.21$) and neither was there any difference in the catch from collection on the outside or the inside of the array ($P = 0.81$). The effect of soak time was not significant ($P = 0.81$).

### P3s

Sandwich collectors performed significantly better than Hunt collectors, with on average 6.26 ($P = 0.01$) more pueruli per collector in the catch. There were no corner effects ($P = 0.13$) but, as for P1s, the effect of time (month of sampling) was significant ($P < 0.01$). The interaction effect of type of collector and time was marginally significant ($P = 0.06$). There was no difference in the catch from offshore or inshore ($P = 0.91$), or effect owing to soak time ($P = 0.50$).

### J1s and J2s

The effect of collector type was not significant ($P = 0.70$). There were insignificant corner effects ($P = 0.18$). The interaction effect of type of collectors and time was insignificant ($P = 0.14$). There was no difference ($P = 0.35$) in the catch between offshore and inshore collectors. However, there were significant ($P = 0.02$) improvements of on average 0.42 juveniles per collector over the duration of the experiment, with increasing soak time showing that the collectors were more efficient with conditioning.

### Total catches

The mean catch of pueruli and juveniles in Long Key was 4.69 ($P < 0.01$), larger than the mean catch at Big Munson Key (Table 3). Corner collectors caught on average 1.68 ($P = 0.04$) fewer pueruli and juveniles than other positions in the array.

**Table 1** Summary of the total number of pueruli and juveniles (P1, P2, P3, J1 and J2) collected from Sandwich and Hunt collectors.

| Developmental stage | Sandwich | Hunt | *P* value from *t* test |
|---|---|---|---|
| P1 | 139 (6.91%) | 230 (15.76%) | 0.10 |
| P2 | 119 (5.92%) | 119 (8.16%) | 1.00 |
| P3 | 606 (30.13%) | 390 (26.73%) | 0.00 |
| J1 and J2 | 1147 (57.04%) | 720 (49.35%) | 0.00 |
| Total | 2011 (100%) | 1459 (100%) | 0.00 |

**Table 2** Summary of the mean, standard deviation (shown in parentheses) and sample size (*N*) of pueruli and juveniles collected from Sandwich and Hunt collectors at Big Munson and Long Keys, Florida, United States.

| Collector type | Big Munson Key | Long Key |
|---|---|---|
| Sandwich | 22.81 (11.65) $N = 34$ | 33.06 (11.58) $N = 36$ |
| Hunt | 15.31 (7.72) $N = 35$ | 25.22 (11.92) $N = 36$ |

**Table 3** Summary of the estimated coefficient of predictor variables with the response variables at different pueruli and juvenile stages, from the GLM and ANCOVA analysis. Value in parentheses is the *P* value of the *t* test or *F* test.

| Predictor variables | | P1s | P2s | P3s | J1s and J2s | Total |
|---|---|---|---|---|---|---|
| Intercept | | 1.91 (0.22) | 2.67 (0.00) | 7.60 (0.00) | 6.73 (0.01) | 16.05 (0.00) |
| Collector type (control—Sandwich) | | 9.92 (0.00) | 0.58 (0.42) | –6.26 (0.01) | –0.49 (0.70) | –0.86 (0.66) |
| Location (control—inshore) | | –0.08 (0.89) | 0.06 (0.81) | 0.09 (0.91) | 0.43 (0.35) | 0.46 (0.51) |
| Corner (control—no) | | –0.73 (0.24) | 0.12 (0.68) | –1.36 (0.13) | –0.70 (0.18) | –1.68 (0.04) |
| Site (control—Big Pine Key) | | 2.06 (0.00) | 1.01 (0.00) | 3.81 (0.00) | 1.25 (0.01) | 4.69 (0.00) |
| Time (control—Feb) | Mar | –2.69 (0.07) | –2.85 (0.19) | –1.62 (0.02) | 3.39 (0.00) | –1.41(0.31) |
| | Apr | 2.91 (0.06) | 3.95 (0.08) | 0.54 (0.46) | –0.75 (0.18) | 1.79 (0.04) |
| | May | –2.39 (0.21) | –3.86 (0.16) | –2.53 (0.01) | 3.11 (0.00) | 1.36 (0.01) |
| | Jun | –1.53 (0.49) | –6.76 (0.04) | –2.52 (0.01) | –0.16 (0.61) | –2.17 (0.00) |
| | Jul | –2.07 (0.43) | –6.81 (0.07) | –1.60 (0.19) | –0.94 (0.01) | –2.39 (0.00) |
| Time (*F* test from ANCOVA) | | (0.00) | (0.00) | (0.00) | (0.00) | (0.00) |
| Time* collector type (control—Feb and Sandwich) | | (0.00) | (0.21) | (0.06) | (0.14) | (0.11) |
| Soaking time (covariate) | | 0.01 (0.91) | –0.01 (0.81) | 0.10 (0.50) | 0.42 (0.02) | 0.53 (0.07) |
| Coefficient of determination ($R^2$) | | 0.60 | 0.47 | 0.50 | 0.66 | 0.60 |
| Residual standard error | | 3.19 | 1.49 | 4.64 | 16.37 | 8.22 |

The effect of time was significant ($P < 0.001$), with mean catches in April and May 1.79 and 1.36 more and in March, June, and July 1.14, 2.17, and 2.39 less, respectively, than in February. There were no differences in the catch from offshore or inshore layers in the array ($P = 0.51$), but there were marginally significant ($P = 0.07$) improvements in catches with increased soak time.

## DISCUSSION

Settlement on Hunt collectors at Long Key and Big Munson Key during this study, followed the same yearly trend that has been recorded at these sites since 1996, with peak recruitment in February, March, and April, and collectors at Long Key receiving more settlers per year (Cox et al. 1997). Mean monthly catches on Hunt collectors at long-term monitoring sites at Long Key over the test period were 34.5 pueruli and juveniles per collector, and at Big Munson 15.5 pueruli and juveniles per collector (Cox unpubl. data). Hence, the catches by the Hunt collectors at the long-term monitoring site and our test site were very similar over the same time period.

There were differences in catches made by the two collector types. Overall, Sandwich collectors performed on average 38% better than Hunt collectors, with the only exception being catches of P1s, for which Hunt collectors were marginally ($P = 0.10$) better than Sandwich collectors. To some extent the difference in catches may be a result of differences in the overall dimensions of the two collectors. The Hunt collector is smaller than the Sandwich collector, but the effective surface area on which the pueruli settle on each collector is unknown.

Juveniles (J1s and J2s) comprised c. 50% or more of the total number of lobsters taken from the collectors (Fig. 5). This study indicates that Sandwich collectors are able to retain juveniles between months better than Hunt collectors. For example, in Fig. 5 it can be seen that there were good catches of pueruli recorded in April by both collector types, yet in May only the Sandwich collector recorded high catches of juveniles.

The difference in catch between collectors on the seaward and shoreward sides of the arrays was not significant. Phillips et al. (2001) found that in *P. cygnus*, collectors on the seaward side of the array caught significantly more pueruli than collectors on the shoreward side. The lack of difference in the catches in this instance may be because the collectors at Long and Big Munson Keys are in embayments rather than being behind reefs (as in the *P. cygnus* study). This might have diminished the influence of water flow on the choice of collector settled by the pueruli.

In this current experiment, carry-over effects (Cheng 1996; Cheng & Street 1997) could not be studied because the experimental design had only two rows of collectors compared with three rows of collectors in previous comparisons of collectors set out in sampling arrays (Phillips et al. 2001).

The mean soak time of Sandwich collectors was 21 days and the mean soak time of the Hunt collectors was 7.92 days. Soak time was correlated with the catches of J1s and J2s and total pueruli ($P = 0.00$, $0.00 - t$ test, $P = 0.70$, $0.66$ – GLM with $t$ test), but was mostly not significant with (P1s, P2s, and P3s, separately).

This may indicate that conditioning of collectors in the warm tropical Florida waters may be much faster than in the cooler Western Australian waters (Phillips et al. 2001). Optimal conditioning times of Sandwich collectors for *P. cygnus* in Western Australia have not been established, but unlike some other fibre types, catch rates with "Kinnears" fibre are considered to improve after some conditioning (Phillips et al. 2001).

There were on average 1.68 fewer total pueruli caught in the corners of the array compared with other positions ($P < 0.01$; Table 3). This result was similar to that of Phillips et al. (2001), who recorded interior collectors catching significantly more *P. cygnus* pueruli than those on the corners.

This study did not intend to establish a conversion factor for two types of collectors. However, there was a good correlation between month-to-month catches of all stages of pueruli and juveniles made by the two different collector types (Fig. 5), which gives confidence that a reliable conversion factor could be established with a different sampling design. This is likely to be an objective in the near future because Hogs-hair air conditioning material is becoming difficult to access and without it, the long-term puerulus monitoring project carried out by the Florida Fish and Wildlife Conservation Commission would be placed in jeopardy.

Comparisons of the two collector types have allowed us to evaluate more than just their abilities to catch pueruli and retain pueruli and juveniles. Compared to Hunt collectors, Sandwich collectors were found to be heavy to retrieve from the water, larger and therefore requiring a lot of deck space, difficult to spin at an appropriate speed so as to dislodge the post-larvae clinging to the tassels, and more costly and time consuming to construct. This might be important as collectors are frequently lost or damaged as a result of boats running over them, or in storms. However, Sandwich collectors were found not to require quarterly replacement during the experiment as did the Hunt collectors. The frequency of replacement of Sandwich collectors has yet to be determined for the Florida coast. In addition, the method of lifting and handling the Sandwich collectors in Western Australia is to have a small gantry fitted to the vessel, and this and other modifications make the operation more efficient.

## ACKNOWLEDGMENTS

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# Status of the major lobster fisheries in India

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**Abstract** Commercial exploitation of lobsters from the Indian seas began in the 1950s. Annual landings have been declining from a peak of 4075 t in 1985 to 1364 t in 2002. Major fisheries were located on the north-west, south-west, and south-east coasts. Among the 12 species recorded, only four species of spiny lobsters (three littoral and one deep sea) and one species of slipper lobster are commercially important. At Kayalpattinam and Tharuvaikulam, on the south-east coast, lobster landings sharply declined for the gill-net fishery. Of the two species that contributed to the fishery, *Panulirus ornatus* and *Panulirus homarus*, the latter has been more affected owing to high vulnerability to fishing activities. Catch composition analysis of the trammel-net fishery showed that 35% of the landings consisted of *P. homarus* in the size range of 23–50 mm carapace length. On the north-west coast, the spiny lobster *Panulirus polyphagus* and the slipper lobster *Thenus orientalis* are incidentally caught in trawl nets. However, the fishery for *T. orientalis* in the waters off Mumbai lasted only up to 1994. Large-scale exploitation of spawning females, which formed 60% of the total catch, might have been detrimental to the recruitment process resulting in rapid decline and total collapse of the fishery. Abundance of *P. polyphagus* reached its maximum during September, constituting 23% of the average annual landing during 1988–2002. A high exploitation ratio (>0.7) indicated over-fishing of the stock. Repeated spawning and high annual egg production are probably responsible for sustaining the stock, despite over-exploitation. Major problems confronting the resource management of the multi-gear and multi-species lobster fisheries in India are discussed. An operational project, involving fisher community, has been taken up for creating awareness of the need for sustainable exploitation of the resource. Regulatory measures, such as closure of the fishery during the peak of the breeding season, ban on trammel-net, mandatory release of egg-bearing lobsters, and establishment of lobster sanctuaries are suggested to the State Governments for implementation.

**Keywords** lobster fishery; stock assessment; over-exploitation; management

## INTRODUCTION

Lobsters are one of the most valuable and highly priced crustaceans in India, as well as an important export commodity. Though widely distributed along the entire coast, major fisheries are located on the north-west, south-west, and south-east coasts (Radhakrishnan & Manisseri 2003). The north-west coast is particularly rich in lobster resources, contributing to nearly three quarters of the total lobster landing in India (Kagwade et al. 1991; Radhakrishnan 1995). Two species, the palinurid spiny lobster *Panulirus polyphagus* (Herbst) and scyllarid *Thenus orientalis* (Lund) predominate in the fishery along the north-west coast (Chhapgar & Deshmukh 1971). At Mumbai and Veraval, in the north-west, lobsters are incidentally caught in trawl nets. Extensive information is available on the reproductive biology and growth of *P. polyphagus*

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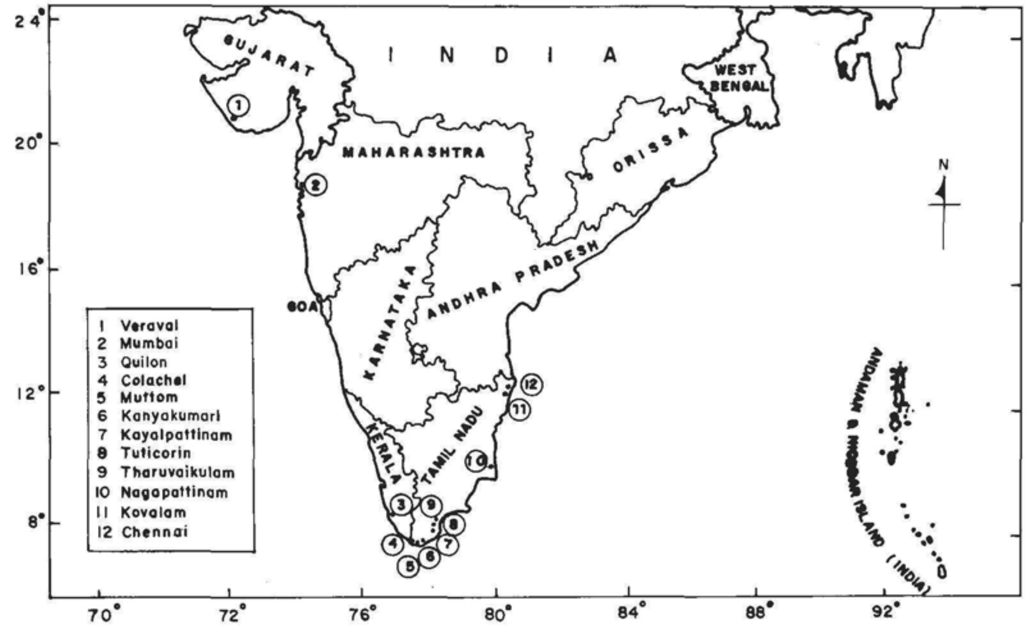

**Fig. 1** Major lobster fishing centres along the Indian coast.

(Kagwade 1987a,b, 1988a,b) and *T. orientalis* (Kabli & Kagwade 1996a,b,c). As a result of the absence of regulatory measures for the fishery in the State of Maharashtra, the sand lobster fishery collapsed by 1994 and there is no sign of its recovery (Deshmukh 2001).

In the south-west, *Panulirus homarus* (Linnaeus) and the deep sea lobster, *Puerulus sewelli* (Ramadan), are the top contributors to the fishery. However, *Panulirus versicolor* Latreille and *Panulirus ornatus* (Fabricius), are also landed in small quantities. Colachel and Muttom are the major fishing grounds, where gill-net, trammel-net, and traps are used for catching lobsters. The fishery and biology of *P. homarus* were studied during the 1950s and 1960s (Miyamoto & Sheriff 1961; Balasubramaniam et al. 1960, 1961; George 1965). Mohammed & George (1968) conducted tagging experiments at Muttom to study the movement and growth of *P. homarus*. Major fishing grounds for the deep sea lobster, *P. sewelli* were located off Quilon in the south-west and off Tuticorin in the south-east coasts, at depths ranging from 150 m to 400 m. The commercial importance of the resource was established through exploratory surveys (John & Kurian 1959; Kurian 1964; Silas 1969).

Along the south-east coast, *P. homarus*, *P. ornatus*, and *T. orientalis* were the major species exploited. *Linuparus somniosus* was reported from the Andaman and Nicobar Islands, but has not been commercially exploited. Kayalpattinam and Tharuvaikulam are important gill-net fishing centres, landing mainly *P. ornatus* and *P. homarus* (Nair et al. 1973; Rajamani & Manickaraja 1991, 1995, 1997a,b). Further north, lobsters are mainly caught off Chennai and nearby fishing villages. *T. orientalis* and small quantities of spiny lobsters are landed as bycatch by trawlers at Chennai.

The present work is an attempt to review the general status of the lobster fishery in India. An assessment of the exploited stock of spiny lobster from Mumbai waters during 1998–2002 has also been carried out, which would enable formulation of a management plan for using the lobster resources on a sustainable basis. The "Minimum Legal Size Law" (promulgated in 2003 by the Ministry of Commerce and Industry, Government of India) prohibiting export of lobsters below a certain size, and an educational programme taken up for creating awareness among fishers of the adverse effects of large-scale exploitation of egg-bearing lobsters and juveniles, are also discussed.

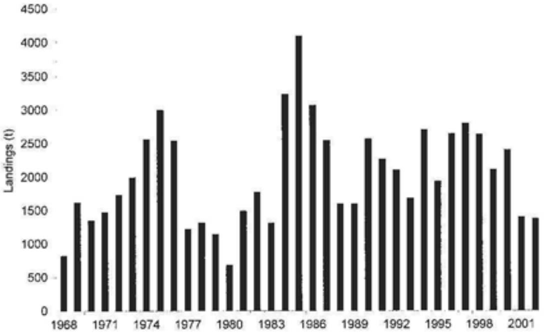

**Fig. 2** Total annual lobster landing (t) in India, during 1968–2002.

## MATERIALS AND METHODS

Data on the total landing of lobsters by mechanised trawlers were collected based on a multistage stratified random sampling design. Month-wise catch, fishing effort, and species composition of lobsters caught by the artisanal fishery were estimated by collecting data from major landing centres (Fig. 1). At the landing centres, sex-wise total length (Mumbai) and carapace length (CL) (other centres) were measured by examining 100 specimens each from random samples, once a week. The stock parameters and exploitation rates of the lobster fishery from Mumbai waters were studied in detail. During 1998–2002, a total of 12 727 specimens, comprising 4974 males and 7753 females, were examined at the two trawl landing centres (Sassoon dock and New Ferry Wharf, in Mumbai) for size, sex, and ovigerous condition of females. For *T. orientalis* total length (TL) was measured from the notch in front of the carapace to the posterior margin of the telson. In spiny lobster, it was from the transverse ridge between the supraorbital horns to the tip of telson. CL was measured from the transverse ridge between the supraorbital horns in front, to the posterior margin of the carapace. The lengths were grouped into 10 mm size classes and sex-wise size frequencies were obtained from each sample. With the help of sex-wise length-weight relationships (Kagwade 1987a; Kabli & Kagwade 1996c), sample weights were calculated for both sexes in the two species mentioned and a factor was obtained to raise the length-frequencies to the day's catch. The same procedure was followed for raising the length-frequencies to the monthly estimated catch after pooling the data for observation days. The monthly length-frequencies were then pooled on an annual basis.

Growth parameters for spiny lobster (Kagwade 1987b) were used to find the exploitation rates during 1998–2002. The natural mortality coefficient was estimated by using Pauly's empirical formula (Pauly 1980) and total mortality coefficient (Z) by length converted catch curve method (Pauly 1984). The exploitation ratio (E) that gave maximum relative yield per recruit ($E_{max}$) and the exploitation ($E_{0.50}$) at which the relative biomass per recruit of the stock was reduced to 50% level, were calculated by using FISAT program (Gayanilo et al. 1996).

## RESULTS

The annual lobster landing increased from 800 t in 1968 to 3000 t in 1975, and attained a peak of 4075 t in 1985 (Fig. 2). Thereafter, the fishery showed a trend of decline, averaging 2200 t for nearly 15 years. The landings further declined to 1389 and 1364 t in 2001 and 2002, respectively. The north-west region contributed 70%, the south-east 16%, and the south-west 14% of the total landing during 1992–2001.

### North-west coast fishery

At Veraval, the annual landing of lobsters decreased from 315 t in 1987 to 102 t in 2000, and then sharply declined to 22 t in 2002 (Fig. 3). During 1987, 189 t of *P. polyphagus* were landed. However, the landing decreased to just 3.9 t during 2002. A similar trend was observed for *T. orientalis* (Fig. 3). The annual mean CL of *P. polyphagus* decreased from 68.5 mm in males and 74.9 mm in females in 1997, to 41.5 mm and 47.9 mm respectively, in 2001. Adults and spawners mainly comprised the trawl catch, whereas gill-net and other traditional gears brought more juveniles. Gill-nets were operated on the shallow reefs, which were inhabited by juveniles and subadults. Peak landing of *P. polyphagus* by trawl nets coincided with the breeding season and the onset of winter in October–December. Maximum landing by gill-nets was during September–October. *T. orientalis* is exploited mostly by multi-day fishing vessels. The mean CL of this species did not show much variation.

Year-wise landing of lobsters at Mumbai during 1978–2002 is shown in Fig. 4. The annual landings increased from 200 t in 1978, reaching a peak of 1040 t in 1986 and thereafter declining to 104 t in 2002. Commercial fishery for *T. orientalis* was initiated in 1978, with a catch of 1.5 t. The landing

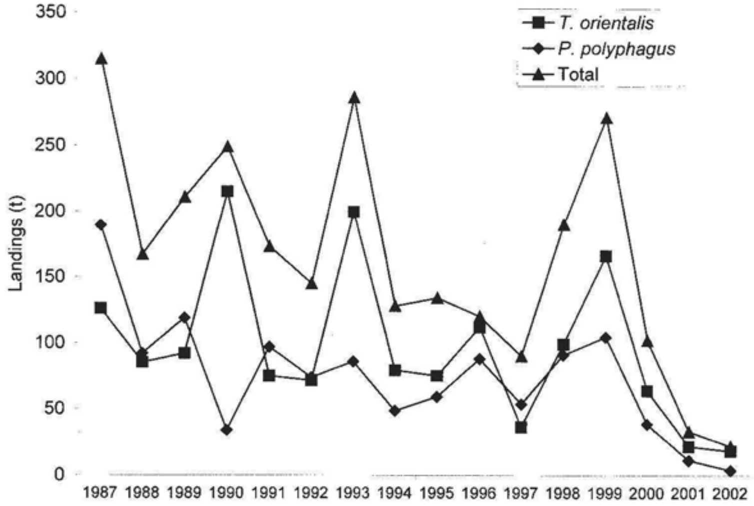

**Fig. 3** Annual landing of lobsters (*Panulirus polyphagus* and *Thenus orientalis*) in trawl fishery at Veraval, India.

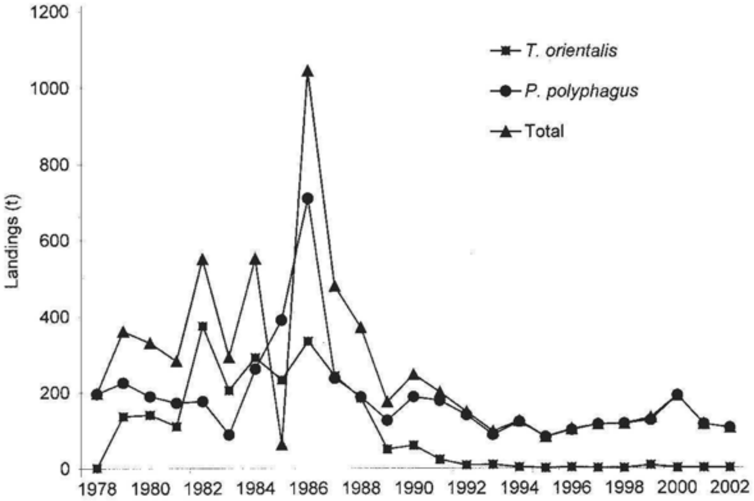

**Fig. 4** Annual landing of lobsters (*Panulirus polyphagus* and *Thenus orientalis*) in trawl fishery at Mumbai, India.

reached a maximum of 375 t in 1982. Subsequently the catch declined to 250 t and reached another peak (334 t) in 1986. Thereafter the catch declined rapidly, landing only 2.2 t in 1994. As a consequence, the fishery collapsed, and the species occurred only in small quantities in the following years.

The spiny lobster *P. polyphagus*, also showed a gradual decline in landing at Mumbai. The average annual landing during 1978–85 was 217.5 t. However, the catch declined from 390 t in 1985 to 104 t in 2002 (Fig. 4). Month-wise percentage of catches during 1998–2002 showed that the maximum abundance of *P. polyphagus* was in September and the minimum in July. The size of both males and females ranged from 75 mm to 385 mm TL, the size between 160 mm and 230 mm forming the mainstay of the fishery. The sex ratio showed dominance of females in all years (1:1.16). Ovigerous females occurred throughout the year (23.8%) with the peak occurrence (56.1%) in September. Recruitment of juveniles, ranging from 70 mm to 120 mm TL, was generally observed during December–February, in shallow nearshore waters. From the length composition of the two sexes of *P. polyphagus*, the total mortality coefficient (Z), natural mortality coefficient (M), exploitation rate (U), and the $E_{max}$ were estimated (Table 1). The Z for the entire 5-year period for males was 1.9 which varied from 2.57 in 1998 to 1.57 in 2001. For females, Z was 1.63 which varied from 1.57 in 1998 to 2.01 in 2000. With the mean seawater temperature at 28°C, M for males and females were 0.53 and 0.60, respectively. The relative yield per recruit (Y/R) analysis indicated that the yield can be maximised when the exploitation ratios are 0.46 and 0.53 for males and females, respectively. However, the present exploitation ratios are 0.65 for males and 0.63 for females, which are much higher. At such exploitation ratios the biomass is reduced to 0.30, which may not sustain future stock.

### South-west coast fishery

On the south-west coast, spiny lobster fishing began at subsistence level and gradually transformed into a commercially important fishery. Colachel and Muttom were the two important landing centres where traditional traps made of palmyrah frond were used. Fishers used to dive in the evening and place the baited traps near the mouth of large crevices. Traps were lifted the next morning. Later, gill-nets and trammel-nets were introduced and now traps are used at a few centres. Annual landings gradually decreased from a peak of 301 t in 1966 to 7.6 t in 1996, with only 4 t recorded in 2002. About 92% of the catch comprised *P. homarus*, the remainder being *P. ornatus* and *Panulirus versicolor*. The fishery was seasonal, extending from October to May with maximum landing during November–January. The fishing season coincided with the peak breeding season and 40% of the females caught during this period were egg-bearing. The size of *P. homarus* in the catches ranged from 91 mm to 280 mm TL.

In 1999, fishers ventured into deeper waters (150–400 m) off Quilon ("Quilon Bank") along the south-west coast. The deep-sea lobster *P. sewelli* was landed by trawlers as a bycatch along with deep-sea shrimps. The average annual landing of the species from the Quilon Bank during 1999–2002 was 340 t. The fishery was seasonal, commencing by September–October and extending until February–March. The total landing of *P. sewelli* during 1999–2000 was 574 t, with a peak monthly landing of 180 t in December. The landing decreased to 297 t and 236 t during the years 2000–01 and 2001–02, respectively. Maximum monthly landing was recorded in December (110 t) during 2000–01 and March (49 t) during 2001–02. The size (TL) of *P. sewelli* ranged from 76–80 mm to 186–190 mm in males and from 71–75 mm to 201–205 mm in females. Occurrence of smaller size classes during December–January indicated entry of young ones into the fishery during these months. Maximum numbers of immature lobsters were recorded in January. Sexes were more-or-less equally distributed, with females comprising 47% of the catch during 2000–01 and 56% during 2001–02.

### South-east coast fishery

The south-east coast lobster fishery region encompasses Kanyakumari in the south to Chennai in the north. Gill-net is the major gear operated in the southern region as against the trawl nets used widely in the northern region with *T. orientalis* dominating the trawl fishery. In the gill-net fishery at Kayalpattinam, lobster catches increased from 42.2 t (with a catch rate of 6.5 kg/unit) in 1993, to the peak catch of 50.6 t (with a catch rate of 5.5 kg/unit) in 1994 (Fig. 5). However, the fishery declined to 4.4 t (with a catch rate of 1.1 kg/unit) in 2002. A change in the relative abundance of *P. ornatus* and *P. homarus* was also observed. *P. homarus* formed 72.3% of the total catch during 1978–89 whereas *P. ornatus* dominated the fishery (60.6%) during 1993–2002. The modal length of male *P. homarus* occurring in the fishery decreased from 245 mm TL during 1978 to 145 mm TL during 2002. The modal length of females also decreased from 195 mm TL to 165 mm TL during this period. Meanwhile, the modal length of both

**Table 1** Stock parameters of males and females of *Panulirus polyphagus* in Mumbai, India. (Z, total mortality coefficient; F, Fishing mortality; E, exploitation ratio.)

| Parameter | Sex | 1998 | 1999 | 2000 | 2001 | 2002 |
|---|---|---|---|---|---|---|
| Z | Males | 2.57 | 1.96 | 2.01 | 1.57 | 2.71 |
| | Females | 1.57 | 1.87 | 2.04 | 1.66 | 1.76 |
| F | Males | 2.02 | 1.43 | 1.48 | 1.04 | 2.18 |
| | Females | 0.97 | 1.27 | 1.44 | 1.06 | 1.16 |
| E | Males | 0.79 | 0.73 | 0.74 | 0.66 | 0.80 |
| | Females | 0.62 | 0.68 | 0.71 | 0.64 | 0.66 |

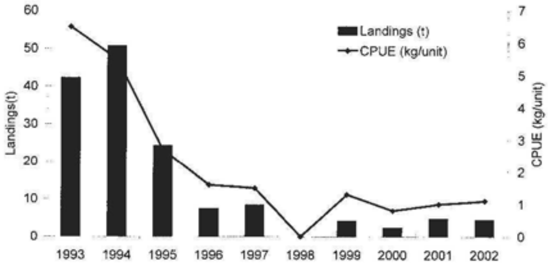

**Fig. 5** Annual landing and catch per unit effort (CPUE) of spiny lobsters (*Panulirus homarus* and *P. ornatus*) in the gill-net fishery at Kayalpattinam, India.

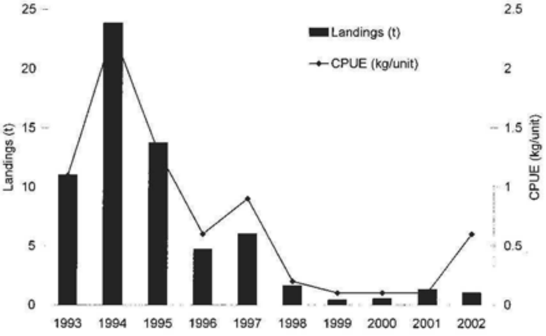

**Fig. 6** Annual landing and catch per unit effort (CPUE) of spiny lobsters (*Panulirus homarus* and *P. ornatus*) in the gill-net fishery at Tharuvaikulam, India.

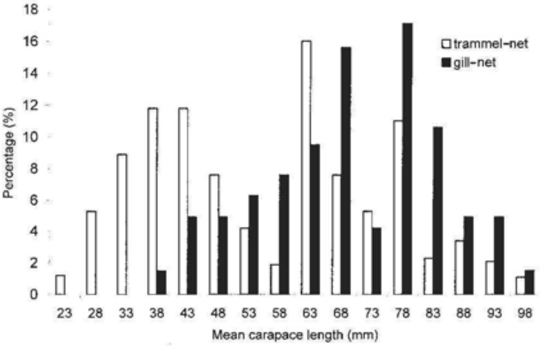

**Fig. 7** Length-frequency distribution of *Panulirus homarus* in the trammel-net and gill-net fishery at Kovalam, India.

males and females of *P. ornatus* showed an increase from 175 mm to 195 mm TL. At Tharuvaikulam, another gill-net landing centre, the landings decreased gradually from 11 t (with a catch rate of 1.1 kg/unit) in 1993, to 1.1 t (with a catch rate of 0.6 kg/unit) in 2002 (Fig. 6). Though lobsters were landed throughout the year, the peak seasons were October–December and April–May. During the entire period of study, ovigerous females of *P. ornatus* were not encountered in the inshore gill-net fishery. However, large males and berried females of *P. ornatus* were landed in small quantities at Nagapattinam by gill-nets operated in deeper waters.

In a previous study conducted at Kovalam, near Chennai, during 1986–88, the catch composition of lobsters from the gill-net fishery and trammel-net fishery was examined. The size of *P. homarus* in the trammel-net fishery ranged from 23 mm to 100 mm CL with nearly 35% in the range of 23–50 mm CL. In comparison, size of lobsters caught in gill-nets ranged from 38 mm to 100 mm CL with a majority in the range of 55–80 mm CL. Studies showed that 50% of *P. homarus* caught in trammel-nets were below 55 mm CL, the size at first maturity, whereas only 25% were below the size at first maturity in the gill-net catches (Fig. 7).

## Awareness programme for lobster conservation

A project on community participation in lobster resource management was initiated in the fishing village of Kadiyapattinam (near Kanyakumari) (Fig. 1), in November 2002. It is increasingly understood that lobster management is not possible just through an isolated promulgation of a law. Involvement of fishers in the management of the resources, on which they depend for their livelihood, could be an alternative strategy. Five meetings, involving fishers, traders, exporters, and fisheries officials were held to discuss the need for development of strategies for sustainable exploitation of the lobster resources. Fisher meetings were organised at Kadiyapattinam near Kanyakumari, Veraval in Gujarat, and Mumbai in Maharashtra to convey the message of responsible fishing to the community. Lobster conservation leaflets, stickers, and wall posters were distributed in lobster fishing villages. Two hundred egg-bearing lobsters purchased from fishers were "V" marked on the uropods and released, to educate the fishers on the need for protection of lobsters carrying eggs. On two occasions, fishers released the marked lobsters voluntarily. They were shown the advantage of using wire traps with escape vents and are slowly being convinced that, in the long term, such responsible fishing methods will benefit them economically. Rallies were also held at three fishing villages in Gujarat to convey the message of conservation.

## DISCUSSION

Though not big in volume, lobster is an important crustacean resource from the Indian seas. Commercial exploitation of the lobster fishery in India began in the early 1950s. However, reliable data on the landings are available only from 1968. The fishery experienced rapid growth in 10 years, landing 3000 t in 1975. Though the fishery suffered a setback for nearly 5 years afterwards, it attained the peak landing of 4075 t in 1985. The sharp fall in the landings in 2001 and 2002, however, was an indication of the growing instability of most of the lobster stocks on both the east and west coasts of India.

In the north-west, lobsters are incidentally caught in trawl nets, except for a small quantity landed by gill-nets at Veraval. In Mumbai, the slipper lobster *T. orientalis* disappeared from the fishery by 1994 (Deshmukh 2001). Heavy reduction in the biomass of the species from overexploitation resulted in the collapse of the fishery. Unlike most of the tropical species, *T. orientalis* showed a single well-defined breeding period from October to January. The sex ratio was disproportionate with females outnumbering males, particularly during the breeding period. It is also a slow-growing species with relatively low fecundity (Kabli & Kagwade 1996a). Exploitation of the spawning females which formed 60% of the total landing might have been detrimental to the recruitment process, resulting in rapid decline of the fishery in the waters off Mumbai. This is a classic example of recruitment overfishing which is not precluded by the growth overfishing.

The ovigerous females of *P. polyphagus* occurred throughout the year, the month-wise abundance showing peaks in August–September. Thus, unlike *T. orientalis*, the species breeds throughout the year. However, Kagwade (1988a) reported two major spawning peaks, in January and September. In the present study, no such peak was observed in January. The size at 50% maturity of females is 205 mm TL weighing 218 g (Kagwade 1988a), and the annual production of eggs is as high as 143 000 and 4.72 million in specimens of 180 mm and 353 mm TL, respectively (Kagwade 1988b). With the assumption that natural mortality remained constant during the period, the maximum yield of *P. polyphagus* could have been obtained at the exploitation ratio ($E_{max}$) of only 0.46 for males and 0.53 for females. However, it was as high as 0.66–0.80 for males and 0.62–0.71 for females. It is important to note that at such exploitation ratios, the biomass of the stock is reduced to less than 50%, which clearly indicates overfishing of the stock. This situation, therefore, calls for immediate management action to save the stock from collapse. Action should be taken to conserve the spawning stock during September–October and the juveniles during December–January when they abound in the shallow coastal waters.

In Kanyakumari district, on the south-west coast, the fishery for *P. homarus* flourished during 1964–73. Increase in effort, introduction of gill-nets for fishing, and exploitation of egg-bearing lobsters during the peak breeding season have been the major factors responsible for reduction in landings. George (1965, 1973) observed that the peak breeding season for *P. homarus* coincided with the active fishing season and suggested a minimum legal size of 130 mm or 140 mm TL for the species exploited from the south-west coast. *P. homarus* is an inshore species with restricted movements (Mohamed & George 1968) and is therefore highly vulnerable to fishing. Trammel nets bring in large quantities of juveniles and subadults, which otherwise would sustain the fishery. Based on the current landing data and biological information on the mean size of *P. homarus*, it could be deduced that the stock has been overexploited. A similar situation prevails in the gill-net fishery at Kayalpattinam and Tharuvaikulam. Reduction in the landing and modal size of *P. homarus* is indicative of growth overfishing and requires immediate remedial measures to protect the juvenile population and breeding females. *P. ornatus* landed by gill-nets from the inshore fishing grounds along the south-east coast comprise juveniles and subadults. Adults are caught incidentally in trawl nets. Exploitation of the juvenile population from the inshore nursery areas may have an adverse impact on the fishery in the long term. Kagwade et al. (1991) did not notice a single berried specimen of the species either in the gill-net or in the trawl fishery. The possibility of *P. ornatus* migrating through the Palk Strait to a deeper breeding ground near the northern Sri Lankan coast cannot be ruled out. Similiar migratory behaviour of spawning females of *P. ornatus* through the Torres Strait in northern Australia has been reported (Skewes 1994). Migration to deeper areas keeps the breeding population away, probably giving a natural protection from large-scale exploitation. Fishers from Nagapattinam, who fish in deeper waters, land adult lobsters and berried females from this ground, though in small quantities. Subramanian (2004) studied the fishery for *T. orientalis* in the trawl fishery along the Chennai coast during 1982–99. The average annual catch of 10 t during 1982–85 increased to 60 t (0.14 kg/h) in 1993 and 115 t (0.23 kg/h) in 1994. However, a declining trend was recorded in the following years with only 8 t (0.01 kg/h) in 1999. Maximum landing was in October. The mean sizes of *T. orientalis* landed were 153.6 mm and 156.9 mm TL for males and females respectively. The females attained maturity at 105.5 mm TL. Maximum spawning activity was observed during January–March and June–July with peak recruitment around October and January.

## Management

Unlike many other countries, the trawl fishery for lobsters in India does not constitute an exclusively targeted fishery. Therefore, optimising the trawlers for lobsters alone is not an option. Neither is observing a closed season for *P. polyphagus* along the Maharashtra coast during the peak breeding season (September–October) as fishing by mechanised boats in the State is already banned during the monsoon (10 June–15 August). Therefore, one of the management options left is to return egg-bearing females back to sea, at least during August–October so that the spawning stock is protected. Recruitment of juvenile lobsters (40–160 g) generally takes place during December–February. These undersized lobsters do not fetch good prices and therefore could also be returned to sea. *P. polyphagus* is a hardy species which remains alive for 1–2 h after it is brought on board by trawl net. Hence, releasing back the undersized and berried lobsters would ensure future recruitment process. As *T. orientalis* occurs only in small numbers along the coast of Maharashtra, total conservation of the remaining residual population by returning the lobsters caught and a legal ban on landing of the species are the only options which can be followed in future.

**Table 2** Minimum legal size for export of lobsters from India (Notification No. 16 (RE 2003)/2002–07 dated 17 July 2003, Ministry of Commerce and Industry, Government of India).

| Species | Live/chilled/ frozen (g) | Whole cooked (g) | Tail (g) |
|---|---|---|---|
| *Panulirus polyphagus* | 300 | 250 | 90 |
| *P. homarus* | 200 | 170 | 50 |
| *P. ornatus* | 500 | 425 | 150 |
| *Thenus orientalis* | 150 | – | 45 |

The drastic decline of the fishery along the coast of Gujarat is also of serious concern and demands similar management measures. Intensive exploitation of juvenile *P. polyphagus* from the inshore reef area by gill-net at Veraval in Gujarat should be banned, if the fishery is to be sustained.

On the south-west coast, closure of the fishery for *P. homarus* during the peak breeding month of November may protect the spawning stock. A ban on operation of trammel-nets on the entire south-west and south-east coasts may prevent exploitation of juveniles which comprise nearly 35% of the catch. Although the spawning stock of *P. ornatus* in deeper waters may not be in danger of being overfished along the south-east coast, the gill-net fishery for juveniles may be detrimental to the stock, as indicated by the decline in the catch and catch rate during the last decade.

The spiny lobster fishery in India is an open-access one and any restriction imposed is likely to be resisted by fishers. Co-operation among fishers, scientists, and government agencies is important for implementing sustainable management programmes. Apart from legal implementation of fishing regulations, education and creation of awareness among fishers on the negative impact of fishing and marketing egg-bearing lobsters and juveniles, may bring a subtle change in their mindset. The educational programme initiated in 2002 is making slow progress in inculcating a sense of responsible fishing and trade. However, fishers are realising that the lobster fishery on which they depend for their livelihood is gradually becoming depleted, and implementation of regulatory measures would benefit them in the long run. Village-level meetings, distribution of educative posters, stickers and pamphlets, video film shows, V notching and releasing of egg-bearing lobsters, and distribution of lobster traps as a less destructive fishing method, are some of the activities implemented under this programme. Enforcement of the minimum legal size, for export of four commercially important species of lobsters in the country (Table 2), is a positive step from the Ministry of Commerce and Industry, Government of India. Implementation of the minimum legal size for fishing, closure of spiny lobster fishery during the peak spawning season in the southern region, and a ban on trammel-nets are the regulatory measures recommended for implementation by the State Governments. As lobster fishing is a socio-economic activity involving fishers and traders, any regulatory measure implemented should also consider socio-economic aspects.

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# Long-term trends in the recreational lobster fishery of Florida, United States: landings, effort, and implications for management

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**Abstract** In Florida, United States, the Caribbean spiny lobster, *Panulirus argus*, supports an important commercial fishery and also perhaps the most intensive recreational fishery of any lobster species, with sales of recreational lobster fishing permits exceeding 100 000 annually. For the past decade, we have used mail surveys of recreational lobster license holders to estimate spatially explicit landings and fishing effort when recreational fishers are most active—during the state's "Special Two-Day Sport Season", which takes place just before the opening of the commercial season, and during the first month of the regular recreational season, which coincides with the commercial season. From 1993 through 2002, fishing effort during the Special Two-Day Sport Season has ranged from 60 000 to 112 000 person-days, and landings have ranged from c. 112 to 255 t. Both fishing effort and landings have varied without trend. Fishing effort during the regular season over the same period has ranged from 261 000 to 514 000 person-days, and landings have ranged from 434 to 825 t. Fishing effort has shown a marginally statistically significant decreasing trend, the result of a progressive decrease in effort since 1999. The largest proportion of both fishing effort and landings was concentrated along the south-east coast. Despite the recent decrease in landings, the proportion of total landings made by the recreational fishery has increased. From 1993 through 1998, the fishery was responsible for c. 30% of commercial landings; by 2001, that percentage increased to nearly 40%. Such a shift in landings away from the commercial trap fishery toward the recreational fishery was recognised as a potential but unintended effect of the ongoing management plan of restricting effort in the commercial trap fishery. Our 2001 surveys revealed that recreational lobster fishers spent more on a person-day basis than the general visitor to the Florida Keys did, but less than those visitors using the region's coral reefs. Consequently, managers must establish management strategies that allow the coexistence of this resource's user groups and also incorporate the social and environmental concerns of nonuser groups.

**Keywords** Caribbean spiny lobster; *Panulirus argus*; recreational fishery; mail survey

## INTRODUCTION

The Caribbean spiny lobster, *Panulirus argus* Latreille, 1804, has been harvested in commercial quantities in Florida, United States, for more than 100 years. For the past several decades, it has consistently been the state's first or second most valuable fishery, with an annual ex-vessel value of c. US$30 million (Muller et al. 1997). About 90% of the state's landings occur along Florida's extreme south-eastern coast, especially along the Florida Keys archipelago. The warm, shallow waters of the Florida Keys are also conducive to a popular recreational fishery for the species.

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Before 1991, this recreational fishery was completely open access, managed only through a spawning season closure, a personal daily bag limit, and gear restrictions. Effort by the recreational fishery was unknown, and the only estimate of landings by this fishing sector was accomplished using a Delphi exercise (Linstone & Turroff 1975) that estimated them to be equal to c. 10% of commercial landings (Zuboy 1980). In 1991, Florida instituted a recreational spiny lobster license, purchased as an additional endorsement to the state's saltwater fishing license (required by all fishers more than 16 years old except Florida residents more than 65 years old). The additional permit allowed the state's fishery scientists to identify potential recreational lobster fishers and estimate their lobster fishing effort and landings.

In 1991, using a mail survey of persons purchasing a lobster permit, we estimated that 50 000 people fished for lobsters during the opening month of the lobster fishing season and landed c. 957 t of lobsters, or 22% of the state's total lobster landings (Hunt 1994). The results of this survey underscored the importance of collecting detailed information about this fishing sector to manage the Florida *P. argus* fishery effectively. Therefore, we have continued to conduct annual mail surveys to estimate and evaluate trends in statewide and regional lobster landings, fisher participation, and fishing effort, and to provide a means to evaluate this user group's perceptions and opinions about the fishery.

The primary recreational lobster fishing season coincides with the commercial season and extends from 6 August through 31 March. Commercial trap fishers are allowed to place lobster traps in the water five days before the opening of their season to allow them to soak. In 1975, the state's fishery managers instituted the "Special Two-Day Sport Season" that is held during the last week of July to compensate recreational fishers for this concession to the commercial fishery and to reduce user conflicts on the opening day of the regular lobster fishing season. During the Special Two-Day Sport Season, recreational fishers are permitted 6 lobsters per person per day in the Florida Keys and 12 lobsters per person per day in other areas of the state. The bag limit during the regular lobster fishing season is 6 lobster per person per day, or 24 per boat per day, whichever is greater. Recreational fishers are not permitted to capture lobsters with traps. Diving (breath-hold, SCUBA, or hookah) and "bully nets", which are used by fishers from boats to ensnare lobsters in shallow water, are the only allowable fishing methods. Divers are not permitted to use any device to capture lobsters that could puncture a lobster's exoskeleton.

Each year, we conduct two separate mail surveys of recreational lobster license holders. One survey includes a questionnaire that queries license holders about their lobster fishing activities during the Special Two-Day Season, and the other surveys a separate group of license holders about their lobster fishing activities from the opening day of the regular season through the Labor Day holiday (the first Monday in September). We restrict the regular season survey to this period because our experience indicated that the majority of fishing effort occurred during the first month of the season, and fishers would have more difficulty accurately recalling their fishing activities many months later. We did, however, conduct one end-of-season mail survey at the conclusion of the 1994 season to obtain an estimate of fishing effort and landings during the remainder of the lobster fishing season. Additionally, from 1993 through 1996 our annual mail surveys asked fishers about their intentions to fish for lobsters after our survey period.

Here, we present an overview of the recreational *P. argus* fishery in Florida. We present statewide and regional trends in landings and fishing effort from 1993 though 2002 during the Special Two-Day Sport Season and the first month of the regular lobster fishing season. We also present the results from the mail survey conducted at the conclusion of the 1994 season and a socio-economic profile of the fishery that was collected during the 2001 season's mail survey. Finally, we discuss the management issues that the state's fisheries managers are currently facing associated with the *P. argus* fishery in Florida.

## MATERIALS AND METHODS

### Mail surveys

Recipients of our mail surveys were randomly selected from the state's saltwater fishing license database of individuals who purchased a lobster permit that was valid during our survey period. To ensure that this selection process did not over- or under-sample any geographic region, these selections were stratified based upon license sales in each of 10 residence areas defined by postal codes (Fig. 1). The number of lobster license holders we attempted to survey each season has ranged from 4000 to 5000, with an exception in 2001. That year's survey included a detailed socio-economic component, which necessitated a much more detailed

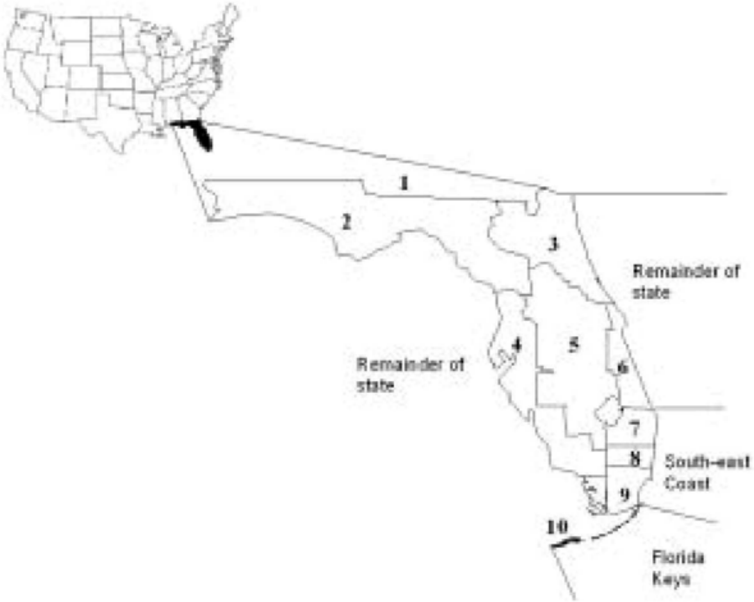

**Fig. 1** Map of Florida, United States. Areas denoted by numerals are the 10 residence areas defined by postal codes. Relative sales of recreational lobster license in each region were used to stratify the random selections of mail survey recipients. "1" refers to all areas in the United States outside of Florida. Areas referred to as "Florida Keys" and "south-east coast" are zones from which we report regional lobster landings and fishing effort. All lobster landings and fishing effort outside of these two zones are referred to as "remainder of state".

questionnaire than those mailed during other years. In anticipation of a decreased response rate resulting from the additional length, we attempted to survey 10 000 license holders.

The general methodology of our mail survey followed the "Total Design Method" (Dillman 1978). Surveys were mailed to the license holders chosen to receive a questionnaire about the Special Two-Day Sport Season 1 week after the end of that season, and those chosen to receive a regular-season questionnaire were mailed their surveys 1 week after Labor Day. A personally addressed, signed cover letter and a postage-paid return envelope accompanied each questionnaire (see Sharp et al. 2004). We guaranteed anonymity to each survey respondent. One week after the initial mailings, each addressee was mailed a "thank you/ reminder" postcard. Survey recipients who had not returned their questionnaires after having them for c. 7 weeks were sent a reminder letter and a replacement questionnaire. To provide an incentive for recipients to return their completed questionnaires, we offered each recipient the option of receiving a brief summary of the results of the survey.

### Landings and fishing effort models

Landings and fishing effort were derived from the questionnaires for a particular survey by estimating the number of fishers participating in a particular season, the time (in days) they fished for lobster, and their lobster catch rate (lobsters per day). We used a sampled randomisation technique (Monte Carlo) to calculate these basic parameters (Sokal & Rohlf 1981). This method entailed generating 1000 independent bootstrap samples. Samples were weighted by geographic residence areas (Fig. 1) based on the proportion of the total number of surveys mailed to each area. We have found that lobster catch rates of recreational fishers can vary considerably between those areas, as do the recreational fishers' response rates (Bertelsen & Hunt 1991). This weighting factor ensures that one area is not over-sampled relative to the others. Equations 1–6 below describe the detailed calculations used to estimate landings and fishing effort (person-days) during the Special Two-Day Sport Season for each of the 1000 bootstrapped samples.

For each residence area, we calculated the number of licensed lobster fishers that fished for lobster during the survey period. The percentage of those that fished for lobster during the survey period was then multiplied by the number of lobster licenses sold that year to persons that lived in each of our defined residence areas to determine the total number of licensed fishers residing in each of those areas that fished for lobster:

$$\mathrm{LF_r} = \left(\sum \mathrm{L_r} \times \mathrm{P_r}\right) \tag{1}$$

where LF = number of licensed fishers; L = number of lobster licenses estimated to be valid during the survey period; $P$ = proportion of survey respondents that fished for lobster during the survey period; and r = residence region.

We determined in which of three fishing zones those persons fished for lobster (Fig. 1) by estimating the number of licensed fishers in each zone on the first and second day of the season using Equation 2. This equation yielded the number of fishers in each zone from each residence area on each day. The total number of fishers in each zone was then determined by summing the number of persons from all the residence areas that fished in a particular zone:

$$LF_{zd} = \left( LF_r \times \frac{\sum n_{rzd}}{\sum n_r} \right) \qquad (2)$$

where LF = number of licensed lobster fishers; n = survey respondents that fished for lobster; r = residence area; z = fishing zone; d = day of the season.

We determined the number of fishing parties (NG) in each fishing zone on each day using Equation 3. We estimated this by dividing the number of licensed fishers (LF) in that zone by the mean licensed group size. If we included non-licensed lobster fishers (i.e., those younger than 16 and Florida residents older than 65), this calculation would underestimate the total number of fishing groups in each fishing zone. Therefore, the non-licensed fishers (NL) were subtracted from the total fishing party size (GZ). The number of groups fishing in each fishing zone was equal to the number of licensed fishers that fished in a given zone ($LF_j$), divided by the average licensed group size:

$$NG_{zd} = \frac{LF_{zd}}{\left( \frac{\sum GZ_{zd}}{n_{zd}} - \frac{\sum NL_{zd}}{n_{zd}} \right)} \qquad (3)$$

where NG = number of lobster fishing parties; GZ = number of persons in the fishing party (includes both licensed and non-licensed persons); NL = number of non-licensed fishers in the party; and n = number of observations.

We calculated lobster landings separately for the first and second day of the season in each zone using Equation 4. This was equal to the mean number of lobsters caught per fishing party (GC), multiplied by the number of fishing parties (NG) found in Equation 3. Landings for each day in each fishing zone were then summed to estimate total landings:

$$L_{zd} = GC_{zd} \times NG_{zd} \qquad (4)$$

where L = lobster landings (number of lobsters).

We calculated the number of person-days in each fishing zone on each day using:

$$PD_z = \sum D_{zd} \times GZ_{zd} \qquad (5)$$

where PD = number of person-days; D = number of days spent lobster fishing.

Estimating fishing effort and landings for the regular season involved most of the same steps described above. However, because the survey period extends about 1 month, survey recipients were asked about their average daily lobster landings and fishing party size. Therefore, Equations 1 through 3 were based upon the respondents' average daily fishing activities. To estimate landings during the regular season, we first calculated the average number of days the respondents fished in each fishing zone ($D_z$). Then, for each fishing zone, we multiplied that value by the average fishing-party catch rate (GC) and the number of fishing parties (NG) (Equation 6):

$$L_z = GC_z \times NG_z \times D_z \qquad (6)$$

We then converted our estimated landings, which are in numbers of lobsters, into an estimate of weight using the equation of Matthews et al. (2003):

$$LWT_j = 0.001989 \times CL^{2.80327}$$

where LWT = lobster landings (g); and CL = mean carapace length of lobsters landed by the commercial fishery during the survey period.

We evaluated temporal trends in license sales, the number of people who used their licenses, lobster landings, fishing effort, and catch per unit effort by using the non-parametric Mann-Kendall sign test and Sen's estimator of slope (Gilbert 1987). When evaluating trends in lobster landings and person-days that were generated by the sampled randomisation procedure, we used the mean value for those variables produced by the procedure.

### Socio-economic models

To estimate the socio-economic impact of recreational lobster fishing on the Florida Keys fishing region, the mail surveys of recreational lobster license holders during 2001 included a section asking each recipient to detail the expenditures associated with his or her lobster fishing activities. Using this information, we estimated total expenditures of survey respondents fishing for lobsters in the Florida Keys during the survey period by multiplying the mean expenditures per person-day of these respondents by the total estimated number of person-days of lobster fishing in the region.

## RESULTS

### Survey response rates

Effective survey response rates (the number of completed survey questionnaires returned to us out of the total number mailed, excluding surveys that did not reach the intended recipient because of an incorrect address) remained c. 60% each fishing season from 1993 through 1997 (Table 1). In 1998, we added questions to the survey to obtain fishers' opinions about the fishery and some that were designed to examine fisher demographics in more detail than earlier surveys. Since the two surveys were lengthened, the combined return rates have ranged from 45% to 52%, the exception being in 2001, when the survey also included a socio-economic component that resulted in a multi-page questionnaire. The combined return rate from both surveys that season was 43%.

### Trends in license sales

Annual sales of recreational lobster fishing licenses showed an increasing trend from 1992 through 2002 (Z = 2.18, *P* = 0.29; Mann-Kendall sign test; Sen's slope = 2779) (Fig. 2A). Sales increased steadily from 1992 through 2000, with the largest number of licenses sold being 139 553 in 1997. However, license sales decreased in successive years after 2000.

The number of license holders who used their licenses during the Special Two-Day Sport Season from 1993 through 2002, however, has not shown the same trend (Z = –0.18, *P* = 0.858; Mann-Kendall sign test; Sen's slope = –109); instead, it has fluctuated without trend from c. 32 500 (1995) to c. 57 000 persons (1999) (Fig. 2B). The number of license holders who used their licenses during the first month of the regular season ranged from

**Table 1** Number of questionnaires mailed to recreational lobster license holders, the number of completed questionnaires returned to the Florida Fish & Wildlife Conservation Commission, United States and the effective return rate. Effective return rate is the percentage of returned questionnaires out of the total, once undeliverable questionnaires were removed.

| | No. of questionnaires | | | |
|---|---|---|---|---|
| Season | Mailed | Returned | Undeliverable questionnaires | Effective response rate (%) |
| **Special Two-Day Sport Season** | | | | |
| 1993 | 2491 | 1302 | 410 | 63 |
| 1994 | 2283 | 1184 | 402 | 63 |
| 1995 | 1996 | 983 | 327 | 59 |
| 1996 | 1998 | 962 | 377 | 59 |
| 1997 | 1981 | 984 | 311 | 59 |
| 1998 | 2076 | 1074 | 127 | 55 |
| 1999 | 1884 | 844 | 174 | 49 |
| 2000 | 2002 | 948 | 177 | 52 |
| 2001 | 4809 | 1974 | 466 | 45 |
| 2002 | 2500 | 1082 | 249 | 48 |
| **Regular season** | | | | |
| 1993 | 2497 | 1189 | 459 | 58 |
| 1994 | 2295 | 1137 | 400 | 63 |
| 1995 | 1686 | 860 | 236 | 59 |
| 1996 | 1999 | 930 | 357 | 57 |
| 1997 | 2006 | 954 | 325 | 57 |
| 1998 | 1967 | 910 | 110 | 49 |
| 1999 | 2031 | 839 | 189 | 46 |
| 2000 | 2002 | 820 | 225 | 46 |
| 2001 | 5181 | 1883 | 523 | 40 |
| 2002 | 2500 | 972 | 287 | 44 |

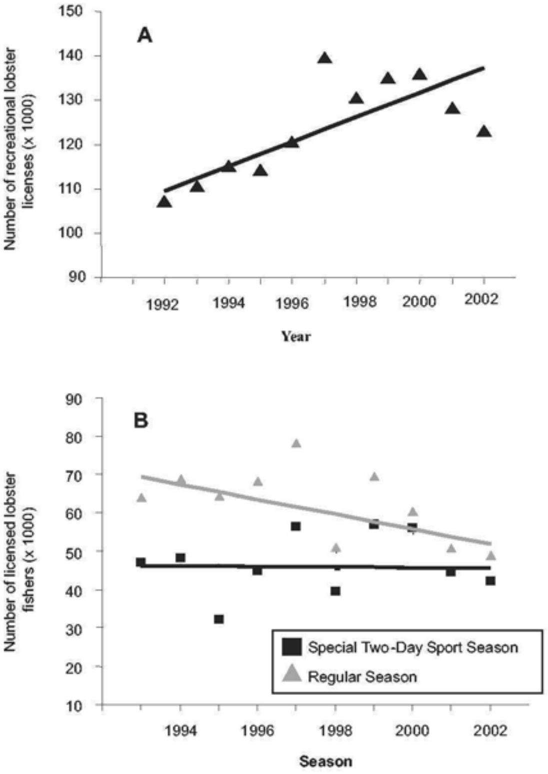

**Fig. 2** **A**, Number of annual recreational lobster licenses sold, 1992–2002; and **B**, estimated number of recreational lobster license holders that used their licenses during the Special Two-Day Sport Season and during the first month of the regular lobster fishing season, 1993–2002. Solid line denotes Sen's estimate of slope.

c. 49 000 (2002) to c. 78 000 (1997) but has decreased progressively each year since 1999, though a significant trend was not apparent (Z = –1.61, $P = 0.107$; Mann-Kendall sign test; Sen's slope = –1954).

## Fishing effort and landings

### *Special Two-day Sport Season*

Fishing effort during the Special Two-Day Sport Season from the 1993 through the 2002 fishing seasons, expressed in terms of person-days, has generally mirrored the interannual variation in the number of lobster fishers who used their licenses and has not shown any detectable trends (Table 2). We estimate that fishing effort statewide has ranged from c. 60 000 to 112 000 person-days (Fig. 3). Fishing effort was concentrated in the Florida Keys, where effort has ranged from 39 000 to 79 000 and accounted for 64% or more of the statewide fishing effort estimate each season. Most of the remaining fishing effort occurred along the south-east coast of the state, where effort ranged from 16 000 to 36 000 person-days. Fishing effort throughout the remaining areas of the state ranged from c. 2000 to 10 000 person-days.

Annual landings during the Special Season have not shown any distinct temporal trends (Table 2) but have fluctuated more than 2-fold throughout the period, ranging from 112 to 255 t (Fig. 4). The largest proportion of landings occurred in the Florida Keys and have ranged from 73 to 179 t, or c. 60% to 70% of the annual statewide total. Landings along the

**Table 2** Results of nonparametric trend analysis on regional fishing effort and lobster landings during the Special Two-Day Sport Season from 1993 through 2002.

| | Mann-Kendall sign test | | Sen's slope estimator | | |
|---|---|---|---|---|---|
| | | | | Confidence intervals | |
| | z | *P* | Slope | Upper | Lower |
| **Person-days** | | | | | |
| Statewide | 0.00 | 1.000 | – 529.7 | 4514.1 | – 9899.7 |
| Florida Keys | 0.54 | 0.592 | 657.3 | 3669.2 | –3775.6 |
| South-east coast | 0.00 | 1.000 | –192.3 | 1387.5 | –3107.9 |
| Remainder of state | –0.54 | 0.592 | –122.0 | 364.6 | –970.5 |
| **Lobster landings** | | | | | |
| Statewide | 0.18 | 0.858 | 3.8 | 15.8 | – 13.3 |
| Florida Keys | 0.18 | 0.858 | 10.0 | 61.4 | – 41.3 |
| South-east coast | 0.00 | 1.000 | –1.7 | 18.0 | –26.6 |
| Remainder of state | 0.54 | 0.592 | 0.25 | 5.1 | –3.1 |

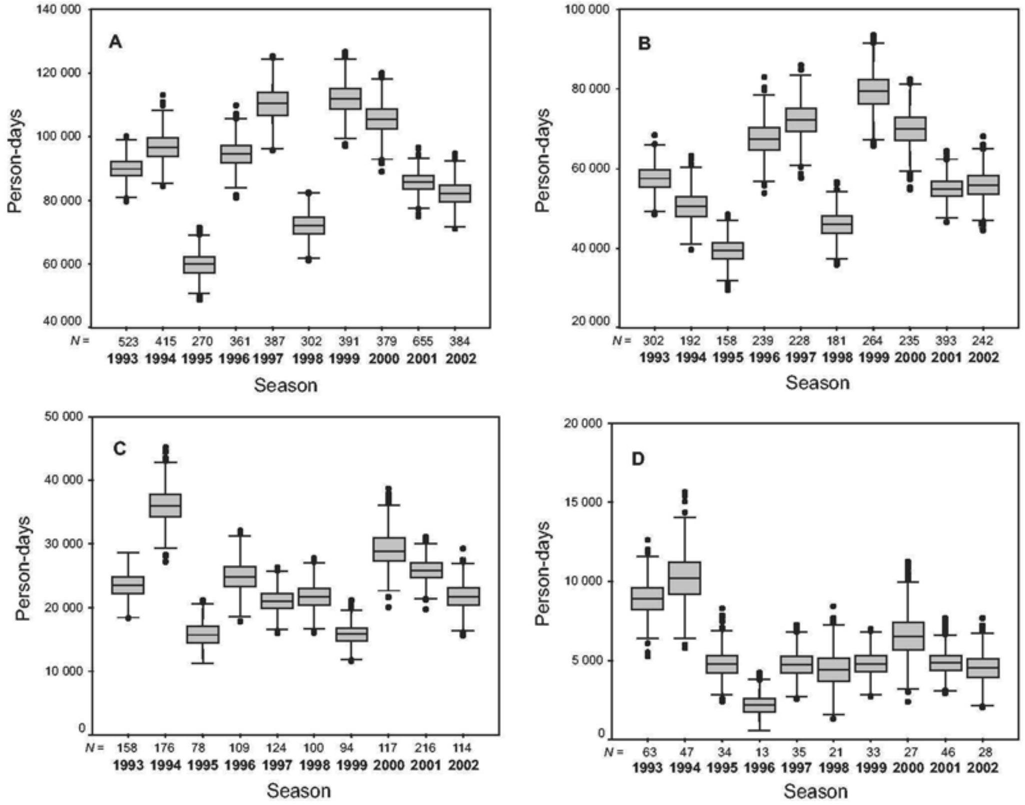

**Fig. 3** Boxplots depicting the results of a Monte Carlo simulation estimating fishing effort during the Special Two-Day Sport Season: **A**, statewide; **B**, in the Florida Keys region, United States; **C**, south-east coast; and **D**, in the remaining areas of the state based upon mail survey returns, 1993–2002. Sample sizes listed along the horizontal axis represent the number of survey recipients, from the total number of questionnaires we received, that fished for lobsters.

south-east coast during the Special Season ranged from 31 to 68 t, and those throughout the remainder of the state ranged from 2 to 13 t.

### *Regular season*

We estimate that statewide fishing effort during our regular season survey period (i.e., 1993–2002) ranged from c. 261 000 to 514 000 person-days (Fig. 5). Regional fishing effort was proportionally similar to that of the Special Two-Day Sport Season. Fishing effort in the Florida Keys over the same period ranged from 168 000 to 366 000 person-days. Most of the remaining fishing effort occurred along the south-east coast of Florida, where effort ranged from 62 000 to 150 000 person-days. Effort in the rest of the state ranged from 25 000 to 66 000 person-days.

A marginally significant decreasing trend was detected in statewide fishing effort during the period, and a similar significant trend was detected in the Florida Keys (Table 3). A statistically significant trend was not detected in fishing effort in the south-east coast region; however, fishing effort there has also progressively decreased (Fig. 5). This decrease in fishing effort shows the same general pattern as that observed in the number of license holders who used their licenses during our survey period, which also decreased progressively after the 1999 season (see Fig. 2B). However, the decrease in person-days in the Florida Keys was clearly not solely the result of fewer license holders using their licenses. Among survey respondents who did fish for lobsters in the Florida Keys, the mean number of days spent fishing also decreased progressively after the 1999 season. Although the number of days spent fishing had been relatively stable through 1999, this recent decrease resulted in a significant negative trend (Z = –2.71,

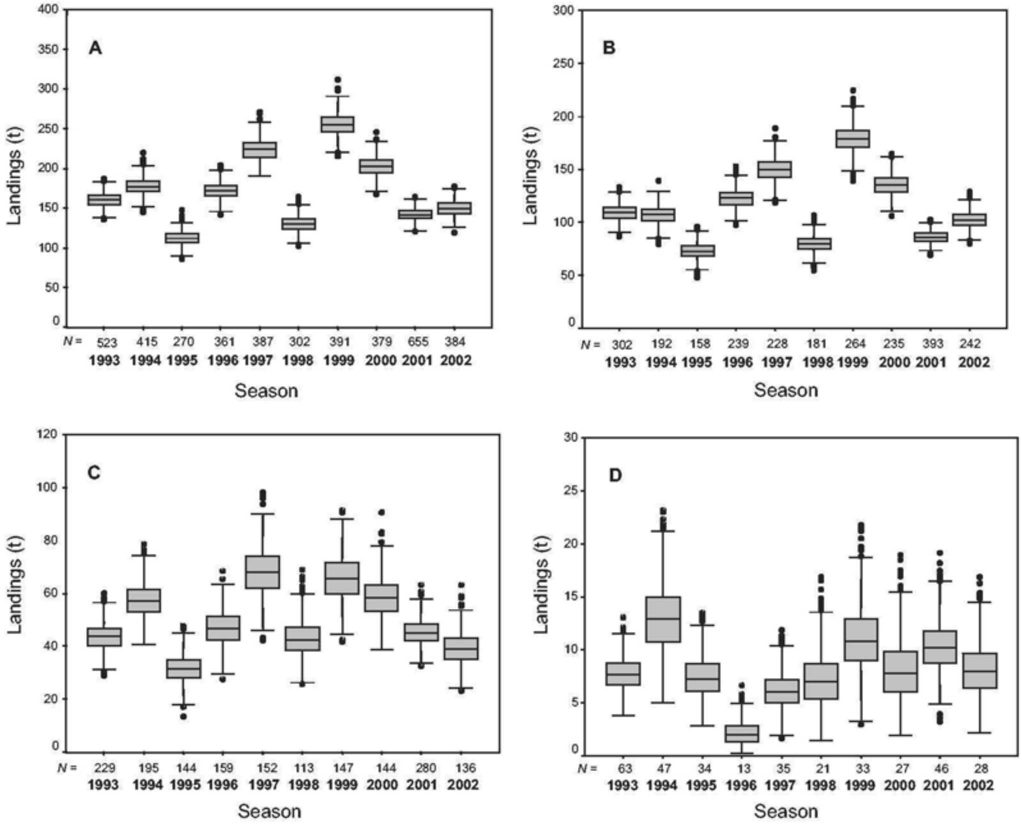

**Fig. 4** Boxplots depicting the results of a Monte Carlo simulation estimating lobster landing during the Special Two-Day Sport Season: **A**, statewide; **B**, in the Florida Keys region, United States; **C**, the south-east coast; and **D**, in the remaining areas of the state based upon mail survey returns, 1993–2002. Sample sizes listed along the horizontal axis represent the number of survey recipients, from the total number of questionnaires we received, that fished for lobsters.

$P = 0.007$; Mann-Kendall sign test; Sen's slope = –0.093) (Fig. 6).

A significant decreasing trend in the number of person-days of lobster fishing was also detected in the areas outside the Florida Keys and south-east coast region (Table 3). However, the trend was different than that observed in the latter two regions. The number of person-days decreased noticeably from the 1995 to the 1996 season but has remained generally stable over subsequent seasons.

Statewide landings during the regular season survey period ranged from 434 to 825 t (Fig. 7). The largest proportion of landings occurred in the Florida Keys and ranged from 301 to 573 t. As with the Special Season, landings in that region accounted for 60 to 70% of the annual statewide total ($\bar{x}$ ± 1 SE = 66 ( 1.2%). Landings in the south-east coast ranged from 301 to 201 t, and landings in the remainder of the state ranged from 29 to 76 t.

The decrease in fishing effort, both in terms of person-days and the number of days spent lobster fishing during our regular season survey period, has not yet resulted in a detectable trend in landings statewide or either in the Florida Keys and south-east coast regions. Yet, we note that landings in the Florida Keys have decreased progressively since the 1999 season, and those of the two most recently completed seasons represent two of the three lowest landings estimates since 1993.

A highly significant decreasing trend was detected in lobster landings in areas outside the Florida Keys and south-east coast regions (Table 3; Fig. 7D) that generally followed the trend in fishing effort. Landings were generally similar from 1993

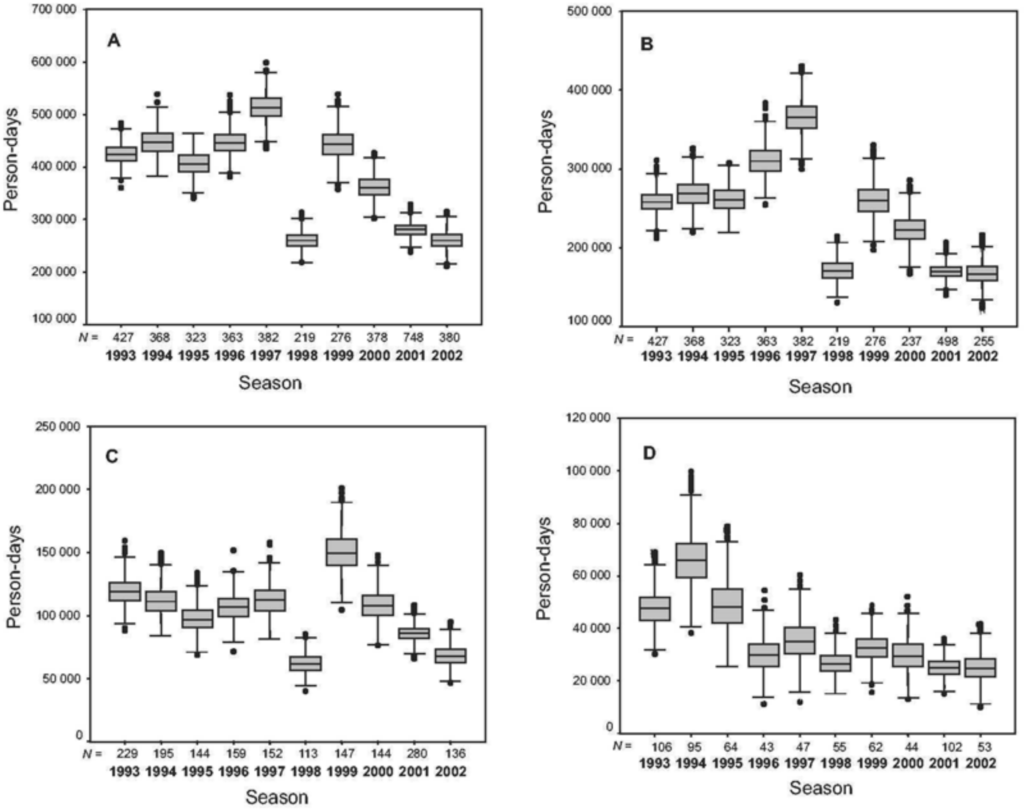

**Fig. 5** Boxplots depicting the results of a Monte Carlo simulation estimating fishing effort during the regular lobster fishing season; **A**, statewide; **B**, in the Florida Keys region, United States; **C**, the south-east coast; and **D**, in the remaining areas of the state based upon mail survey returns, 1993–2002. Sample sizes listed along the horizontal axis represent the number of survey recipients, from the total number of questionnaires we received, that fished for lobsters.

**Table 3** Results of non-parametric trend analysis on regional fishing effort and lobster landings during the Regular season survey period from 1993 through 2002.

| | Mann-Kendall sign test | | Sen's slope estimator | | |
|---|---|---|---|---|---|
| | z | *P* | Slope | Upper | Lower |
| **Person-days** | | | | | |
| Statewide | –1.79 | 0.074 | –20 927.1 | 2995.8 | –47 927.2 |
| Florida Keys | –1.79 | 0.074 | –12 727.8 | 339.0 | –29 063.9 |
| South-east coast | –1.25 | 0.211 | –4154.6 | 2204.7 | –11 514.1 |
| Remainder of state | –2.68 | 0.007 | –2829.0 | –1015.5 | –5872.44 |
| **Lobster landings** | | | | | |
| Statewide | –1.07 | 0.283 | –26.9 | 23.0 | –56.6 |
| Florida Keys | –1.07 | 0.283 | –24.7 | 15.1 | –51.6 |
| South-east coast | –0.72 | 0.474 | –5.8 | 8.6 | –17.6 |
| Remainder of state | –2.50 | 0.012 | –4.8 | –1.3 | –6.6 |

through 1997, and after a noticeable decrease in 1998 from earlier seasons, they remained similar through the remaining seasons. This marked difference in landings in this region coincided with a change in our survey questionnaire for the regular season in the way recipients indicated their lobster landings on a regional basis. Questionnaires before 1998 asked respondents to provide only one value for their daily lobster catch, even though many respondents fished in different regions of the state during the month, and the daily catch in these different areas was potentially very different. This likely caused a slight overestimate of landings in this region, because many of those respondents fished for lobsters in the Florida Keys and then in areas of the state where lobsters are much less abundant. From 1998 onward, the questionnaire was modified to allow respondents to provide their daily landings for each of our defined

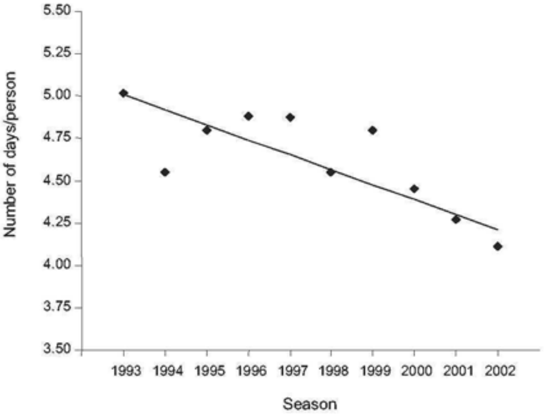

**Fig. 6** Mean number of days spent lobster fishing by mail survey respondents that fished for lobster during the regular season in the Florida Keys, United States 1993–2002.

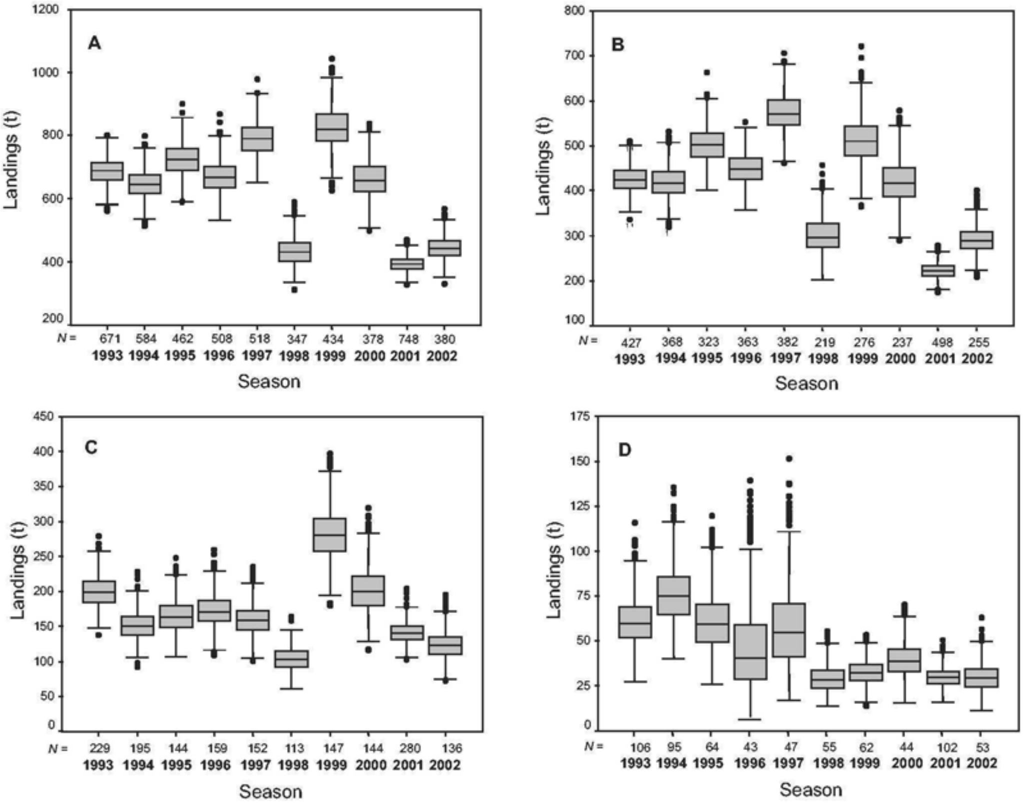

**Fig. 7** Boxplots depicting the results of a Monte Carlo simulation estimating lobster landings during the regular lobster fishing season: **A**, statewide; **B**, in the Florida Keys region, united States; **C**, the south-east coast; and **D**, in the remaining areas of the state based upon mail survey returns, 1993–2002. Sample sizes listed along the horizontal axis represent the number of survey recipients, from the total number of questionnaires we received, that fished for lobsters.

fishing areas of the state (Fig. 1). We believe this change increased the accuracy and precision of our landings estimates. Though this bias was likely small, our landings estimates for the state outside of the Florida Keys and the south-east coast were based upon many fewer responses, and this bias, coupled with the small sample size, caused the detectable change in our landings estimates in the region.

### Recreational fisher demographics

During each season of our survey period, a relatively consistent proportion of survey respondents indicated they fished for lobster during the Special Two-Day Sport Season only, the regular season, or both. An average (±1SE) of 17% (±1.4) of respondents fished during the Special Season only, an average of 45% (±1.2) fished only during our regular season survey period, and an average of 39% (±0.9) fished during both periods.

Although the largest proportion of the recreational fishing effort occurs in the Florida Keys, most of that effort is the result of fishers travelling from other areas. During the course of our survey period, residents of the Florida Keys accounted for only c. 7–11% of the recreational lobster licenses sold annually. Non-residents of the Florida Keys have consistently accounted for c. 80% of the proportion of mail survey respondents that fished for lobster in the Florida Keys during both the Two-Day Special Sport Season and the regular season, and more than 60% of those respondents travelled further than 250 km to reach the Florida Keys. In comparison, 88% of survey respondents who fished along the south-east coast region during the Special Two-Day Sport Season lived in that area, and 80% of residents that resided in our south-east coast region fish for lobster in that region during our regular season survey period.

### Economic impact of the fishery on the Florida Keys

We estimate that lobster fishers visiting the Florida Keys spent US$129.41 per person-day during the Special Two-Day Sport Season and US$122.35 per person-day during our regular season mail survey period. Residents of the Florida Keys spent US$33.99 during the Special Two-Day Sport Season and US$42.83 during the regular season.

In all, we estimated that c. US$24 million was spent on recreational lobster fishing in the Florida Keys during the 2001 mail survey period. Of that total, c. $18 million (74%) was spent during the regular season and c. $6.3 million (26%) was spent during the Special Two-Day Sport Season. Fishers who resided outside the Florida Keys accounted for c. $22 million (92%) of the total monies spent on recreational lobster fishing in the Florida Keys.

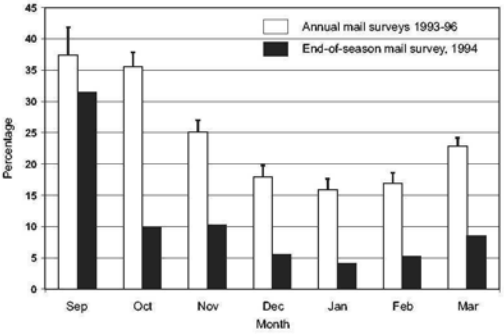

**Fig. 8** Mean (±1SD) percentage of mail survey respondents that indicated they intended to fish after the Labor Day holiday, 1993–96, and the percentage of the 1994 end-of-season survey respondents that indicated they actually fished for lobster.

### Post Labor Day fishing effort and landings

To obtain a coarse estimate of lobster fishing effort after the Labor Day holiday, our surveys from 1993 through 1996 included questions that asked respondents about which month they intended to fish for lobsters after the survey period. Nearly 60% of respondents of our regular season survey had fished for lobsters before Labor Day, but only 37% of respondents to both surveys indicated they intended to do so during the remainder of September, and that percentage progressively decreased during the subsequent months (Fig. 8). However, our end-of-season survey that was conducted after the conclusion of the 1994 lobster fishing season indicated that lobster fishing effort during those months was even lower than that indicated by respondents of the former surveys. Only 13% of those survey recipients indicated that they actually fished for lobsters after Labor Day, and no more than 10% of those respondents fished for lobster in any single month during the survey period (Fig. 8). From that same survey, we estimated that statewide there were only c. 50 673 (±1SD = 9163) person-days of lobster fishing during that period and that 67 (± SD = 17) t of lobsters were landed. Because of the small number of surveys from which these estimates were derived ($n$ = 52), we did not attempt to estimate regional

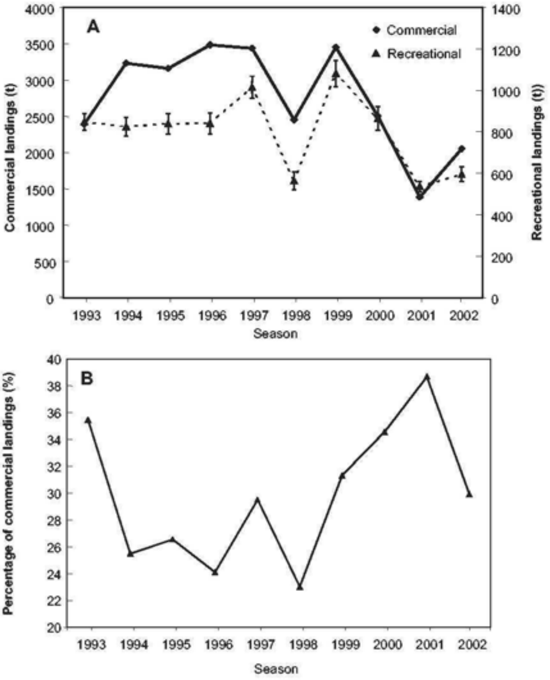

**Fig. 9** Comparison of: **A**, total commercial and estimated recreational landings during the Special Two-Day Sport Season and the regular season through Labor Day; and **B**, those recreational landings expressed as a proportion of commercial landings, 1993–2002.

landings. Comparing this estimate with estimates from the Special Two-Day Season and regular season during 1994 indicated that less than 7% of lobster landings that season occurred after Labor Day.

### Comparison of estimated recreational landings to commercial landings

The estimated combined landings from the Special Two-Day Sport Season and the regular lobster fishing season were highly correlated with the total commercial landings (Pearson's Correlation Coefficient = 0.805; $P = 0.05$) (Fig. 9A). Expressed as a percentage of total commercial landings, our recreational landings estimates have varied from 23% to 39% of commercial landings, but the percentage has been higher from 1999 through 2003 than in the five previous years (Fig. 9B).

## DISCUSSION

The Florida recreational spiny lobster fishery is perhaps the most intensive recreational lobster fishery on the globe. Within a 5-week-long period beginning with the state's Special Two-Day Sport Season held during the last week of July and continuing through the first week of September, the fishery over the past decade has landed, on average, c. 800 t of lobsters, an amount equal to c. 30% of the commercial fishery's total annual landings. Removal rates of legal-sized lobsters by recreational fishers at some locations in the Florida Keys during the Special Season have been estimated to be c. 90% (Eggleston et al. 2003). By comparison, Western Australia's recreational fishery for *Panulirus cygnus* has been estimated to land c. 626 t, but over a 7-month-long period, and this amount is equal to only c. 5% of commercial fishery landings (Melville-Smith & Anderton 2000). Other recreational lobster fisheries have reported landings no greater than 500 t, and most of those report landings far lower (reviewed by Melville-Smith et al. 2000). The only other recreational fishery for *P. argus* of which we are aware for which recreational landings have been estimated is located in Bermuda. Annual landings there have been estimated at 3.5 t (Melville-Smith et al. 2000). *P. argus* is undoubtedly landed throughout its range for personal consumption, with the possible exception of areas where such landings are expressly forbidden (e.g., Brazil and Mexico) (Melville-Smith et al. 2000). However, with the exception of the Bahamas, such landings are likely to be negligible.

The progressive increase in the sales of Florida's recreational spiny lobster license since its inception in the early 1990s suggests that there is the potential for increased expansion of the fishery. Yet, increased license sales did not result in increased fishing effort over the same period. Rather, fishing effort and landings during the Special Two-Day Sport Season varied without a discernable trend, and fishing effort during the regular season has actually decreased during recent seasons. The increase in license sales is likely the result of increased sales of Florida's saltwater fishing license (Florida Fish & Wildlife Conservation Commission unpubl. data), which is necessary to fish recreationally for all finfish species in the state's marine waters (Florida Statute 360, Chapter 68). The recreational spiny lobster license is a relatively inexpensive endorsement to this license. Therefore, we believe it likely that many of those purchasing a saltwater fishing license simply include the lobster license with their purchase without having definite plans to fish for lobster.

Fishers' perceptions about annual lobster abundance to a certain extent influence license sales, and hence fishing effort. Annual landings by the commercial fishery decreased precipitously from 1999 to 2001, when landings were the lowest in more than 30 years, and during 2002 remained well below the long-term landings average experienced by the fishery over the past several decades, indicating a clear decline in lobster abundance. We note that license sales, after a nearly decade-long progressive increase, decreased noticeably following the 2000 season, the first of what were generally considered to be disappointing seasons, and continued the following season. The lower lobster abundance in these recent seasons also apparently influenced the fishing effort of those recreational fishers that did fish for lobster in the Florida Keys during the regular season, as the number of days spent fishing by survey respondents also decreased during those seasons.

Of considerable concern to Florida's fishery managers during these recent seasons has been a shift in landings allocations away from commercial fishers and toward the recreational lobster fishing sector, whose landings had equaled less than 30% of commercial landings throughout the 1990s, but increased rapidly from 1999 to 2001, when it reached nearly 40%. This sudden shift, coming at a time when the resource was exceedingly limited, sparked heightened user conflicts between the two fishing sectors and threatened to undermine the ongoing effort-reduction plan that had governed management of the commercial sector throughout much of the 1990s (see Hunt 1994 for a description of that plan). Though the proportion of lobster landings by the recreational fishery decreased during 2002, the state's fishery managers decided to reduce the daily bag limit of recreational lobster fishers to ensure no further shifts in the proportion of landings was accrued by recreational fishers. Beginning in 2003, recreational lobster fishers were limited to 6 lobsters per person per day only.

In addition to dealing with such inevitable user conflicts between recreational and commercial fishers, the state's fishery managers have also had to address socially based conflicts associated with the recreational fishery. The Special Two-Day Sport Season has been exceedingly unpopular with many of the residents of the Florida Keys, who have continually expressed their dismay to fisheries managers over the crowding caused by the numbers of vacationers who travel to the region for the week. Their concerns were primarily caused by what they perceived to be widespread deleterious impacts to marine resources and noncompliance with daily bag limits by fishers brought about by the season's derby-like atmosphere. In 1992, the state's fisheries managers attempted to redirect fishing effort away from the Florida Keys during this season through a series of rule changes, including moving the season from its traditional weekend to the mid-week and doubling the daily lobster bag limit in all areas of the state except in the Florida Keys. However, those strategies had no measurable long-term effects on regional fishing effort. Because the Florida Keys is the premier vacation spot in Florida and the Special Two-Day Sport Season is held at the height of the summer vacation season, it was perhaps inevitable that such controls on fishing effort would have little effect. The distance many licensed lobster fishers travel to reach the Florida Keys underscores the popularity of this region as a vacation destination. Moreover, the Florida Keys is the only area of the state where lobsters are abundant in shallow water (<3 m) and consequently the only area where relatively inexperienced divers can actively participate in lobster fishing.

In the years since those major regulatory changes, there has continued to be political pressure from the local populace to either discontinue the Special Two-Day Sport Season or implement a limited-entry system that would curtail the number of people allowed to participate in the season in the Florida Keys. However, the state's fisheries managers were concerned that discontinuing the season would shift some portion of the fishing effort associated with those fishers who fish only during the Special Season, which we estimate to be nearly 20% of the licensed fishers who fish for lobster annually, to the regular season, thereby increasing recreational effort when commercial fishers are also active. Moreover, because many of the issues associated with the Two-Day Season have been primarily social, the state's fishery managers have been reluctant to implement any further regulatory changes to this season.

Florida's lobster fishery managers must consider the benefit provided by the recreational fishery to the economy of the Florida Keys. The socio-economic component of our 2001 mail survey provides the first quantitative evaluation of the economic value of this or, to our knowledge, any recreational spiny lobster fishery. The Florida Keys region is a tourism-based economy, and our survey clearly outlined the effect that visiting recreational lobster fishers, who accounted for more than 90% of the total monies spent on lobster fishing during our survey period, have upon the region. By way of comparison, those lobster fishers spent c. 25% more per person-day than did general visitors to the Florida Keys during 2000–01 (Leeworthy & Wiley 2002). However, non-consumptive uses of the area's marine resources are perhaps more beneficial to the region's economy. Non-residents of the Florida Keys who visited the region to dive the coral reefs—perhaps the region's most valuable marine attraction—but not to fish for lobsters, spent more on a person-day basis than did recreational lobster fishers (Johns et al. 2003). Consequently, when assessing the economic benefits of the lobster fishery for the region, managers must also consider that benefit in light of environmental impacts that lobster fishing—resulting not only from recreational diving and but also from commercial trap gear—has upon the region's marine resources.

Our mail surveys remain the sole method by which the recreational fishery can be monitored in a comprehensive manner, and we believe them to be an effective tool by which we can monitor long-term trends in this fishing sector. Our response rates have ranged from 45% to 60% over our survey period, which is at the high-end of the range typically achieved with mail surveys of interest groups (Davis 1995 as cited in Melville-Smith & Anderton 2000). Higher rates, however, have been achieved in other mail surveys: Guillory (1998) reported a 79.4% response rate from blue crab fishers in Louisiana, United States. We note that our response rates did decrease when we increased the length of the questionnaires in order to gain more detailed information from survey recipients. Consequently, we are considering including a cash incentive in our future surveys via a lottery, similar to that described by Melville-Smith & Anderton (2000).

We do acknowledge, however, that potential biases exist in using mail surveys to gather data from recreational fishers. Foremost amongst these biases are the uncertainties associated with nonrespondents, who potentially may have very different fishing experiences than do those who respond to a survey (see Cowx 1991). We have conducted one telephone survey following one of our mail surveys and detected no differences between the nonrespondents' answers to specific questions we use to estimate landings or fishing effort and the answers we received from mail survey respondents (Florida Fish & Wildlife Conservation Commission unpubl. data). Though it would be desirable to conduct such follow-up surveys on a regular basis, they are labour-intensive, and we have not repeated this effort.

Another potential bias of mail surveys can result from the faulty memory of those surveyed or from an individual's penchant to exaggerate their catch out of pride. We evaluated this bias by conducting on-site creel surveys of recreational lobster fishers during our 2001 mail survey period (Florida Fish & Wildlife Conservation Commission unpubl. data). Lobster fishers were interviewed at boat docks and ramps immediately upon returning from their fishing trip for pertinent catch and effort information that could be compared with similar information from mail survey respondents. In many instances, port agents also directly examined the catch of those they interviewed. The agents also collected other information, such as fishing experience, to ensure that no differences in fisher demographics existed between those interviewed and survey respondents that could confound direct comparisons of the catch and effort data. Preliminary results indicate no differences in the catch data collected from the creel survey and those collected through mail surveys.

Until very recently the commercial spiny lobster fishery has garnered virtually all the attention of Florida's fishery managers. However, our annual surveys of recreational lobster fishers over the past decade have clearly indicated that the recreational spiny lobster fishery must also be considered so as to manage this valuable stock effectively. Yet, managers also face challenges beyond those of establishing strategies that allow the coexistence of this resource's user groups. They must ensure that such strategies incorporate the social and environmental concerns of nonuser groups as well. This challenge will undoubtedly be formidable. Florida's lobster fishery is concentrated in one of the state's premier tourist destinations, the Florida Keys, whose attraction lies primarily in its marine ecosystem and associated recreational activities. Consequently, managers will require a diverse array of information to formulate such a comprehensive strategy. Our annual mail surveys will continue to provide not only fishery-based information but also information that incorporates recreational fishers' motivations and opinions regarding fishery resources and associated social and environmental issues.

## AKNOWLEDGMENTS

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# Impact of lunar cycle and swell on the daily catch rate of western rock lobster (*Panulirus cygnus*) using time series modelling

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**Abstract** The western rock lobster fishery is one of the most valuable single-species fisheries in Australia, valued at AU$300 million per year. The impact of environmental factors such as lunar cycle and swell on the daily catch rate of the western rock lobster (*Panulirus cynus*) is of particular interest in the stock assessment and management of the fishery. The variation in daily catch rates was examined for two periods (migrating period November–January, non-migrating period February–June), at different depths in three management zones for three categories of lobster (undersize, legal size, and setose). Regression and transfer function models for relationships between catch rates and environmental data were considered and compared. The lunar cycle has a significant impact on the daily catch rates with c. 30% lower catch rate during the full moon and c. 20% higher catches near the new moon. This impact occurs mainly during the non-migrating period both in deep water (40–100 m) and shallow water (<40 m). The swell on the day before fishing was also shown to be significantly related to the catch rate with an increase of c. 10–15% for an increase in swell from light to moderate or moderate to high. These environmental factors can be used to standardise catch rates to provide an improved abundance index for stock assessment. Also, management closures are being considered for 3–5 days over the low catch rate, full moon period to reduce fishing costs and lower fishing effort.

**Keywords** daily catch rates; western rock lobster; lunar cycle; swell; time series

## INTRODUCTION

The fishery for western rock lobster (*Panulirus cygnus*) is Australia's most valuable single-species fishery with an annual catch of c. 11 000 t worth c. AU$300 million per annum. The western rock lobster distribution extends from the south-west coast of Western Australia to the north-west cape (Fig. 1). The fishing area is divided into three zones.

Limited research has been undertaken on the environmental factors which have an impact on lobster catch rates. Morgan (1974, 1977) studied the relationship between three conditions (i.e., water temperature, water salinity, and moulting activity) and monthly catches of western rock lobsters at Rat Island in the Abrolhos Is. Morgan found that water temperature and salinity had a positive correlation with catchability whereas the percentage of lobsters in a premoult condition had a negative correlation with the catchability coefficient. Caputi & Brown (1986) examined factors affecting juvenile abundance to obtain a standardised index of abundance. They found that juvenile catch rates decreased slightly during the full moon. Roberts (2000) examined the impact of lunar cycle on the legal-sized lobsters and showed a negative impact during the full moon period.

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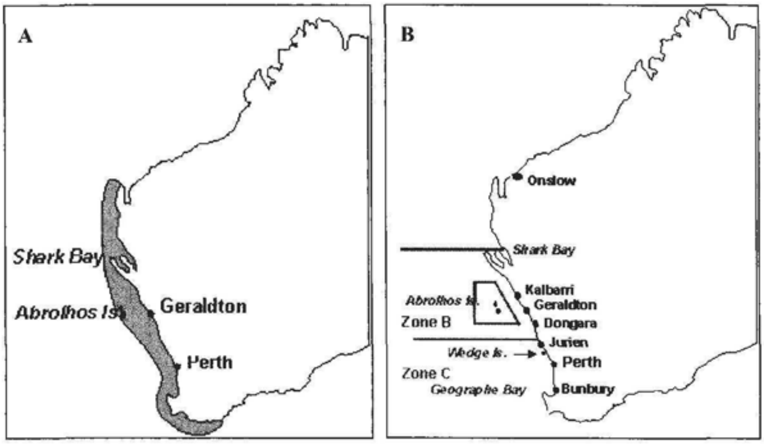

**Fig. 1** **A**, Distribution and **B**, three fishing zones of the western rock lobster (*Panulirus cygnus*) fishery: the offshore Abrolhos Is. (known as Zone A) and the north and south coastal zones (known as Zones B and C, respectively).

Kanciruk (1980) reviewed the impact of lunar cycle on other spiny lobster species and indicated that the activity and catch rates of *P. japonicus* and *P. argus* were affected by the lunar cycle. Yamakawa et al. (1994) showed that water temperature, lunar cycle and intensity of ocean waves affected the catch rates of *P. japonicus*.

Considerable research has been undertaken on the environmental impact on prawn populations. Courtney et al. (1996) showed an interaction between the catch rates, lunar phase, and sex ratio among adult eastern king prawns, *Penaeus plebejus*, in relatively deep (160 m) coastal waters off south-eastern Queensland. Females dominate catches, but males dominate peaked catches during the three days before and after the full moon when the sex ratio is 1:1. Information on the lunar effect of catch rates from the prawn fisheries in Shark Bay and Exmouth Gulf have been used to introduce 3–5 day closure near the period of the full moon to improve the economic performance of the fisheries and also reduce fishing effort (Penn et al. 1989).

Catch rates from fisheries are used in stock assessment as an index of abundance. Understanding the environmental factors affecting catch rates provides a way of standardising these catch rates to provide a more reliable abundance index and hence an improved stock assessment and a more effective management of stocks.

Every year, from November to January, some pale-coloured and recently moulted juvenile rock lobsters (known as "whites") migrate to deep water. During their migration, these lobsters are vulnerable to fishing and large catches are taken. The fishing for the rest of the year (February to June) is on non-migrating lobsters, known as "reds", because of their darker colouring. Rock lobsters reach the legal size for fishing at c. 4–5 years and generally reach their adult stage between 5 and 7 years. Mature female lobsters (known as "setose" females) that have setae or long fine hairs on their pleopods, are required to be returned to the sea by fishers. Breeding female lobsters (known as spawners) carry the eggs underneath their tails. As the behaviour of lobsters alters during the different life history changes, the impact of the environmental factors may vary.

This research focused on the impact of two environmental conditions (lunar cycle and swell) on the western rock lobster's daily catch rates as there is evidence from previous localised studies of such impacts. The cyclic pattern of the catch rates, after removing the trend (i.e., the change in the mean level over the daily catch rate data), was investigated in the three lobster categories (undersize, legal size, and setose) and the fishing season was divided into two periods (whites and reds). The research was carried out in all three fishing zones and at different water depths. Models were fitted to the relationships between the environmental factors and the daily catch rates to determine the correction factors that could be used to obtain more reliable abundance indices in the stock assessment of the western rock lobster.

## METHODS

### Research database

The daily catch rates (kg or number per pot lift) were derived from voluntary daily logbooks collected from fishers. These logbooks were completed by c. 35–40% of the fleet of c. 600 vessels. Seven fishing seasons from 1992/1993 to 1998/1999 were examined. Data sets are composed of catches (kg) of legal-size lobsters and number of pot lifts, catches (numbers) of undersize and setose lobsters at five different depths in 10 fathom increments to facilitate data collection by fishers (0–18, 18–36, 36–54, 54–72, and >72 m) in the three major fishing zones. There are two types of pots used in the fishery, the batten and beehive pot. Both have 3 or 4 escape gaps fitted that significantly reduce the catch of undersize lobsters.

A fishing season in Abrolhos Is. is shorter than that in Zones B and C and starts on 15 March (instead of 15 November in the other two zones). The fishery closes on 30 June. Each fishing season in Zones B and C was separated into two parts. The first part, November–January, coincides with peak catch rates for migrating whites (Fig. 2). During the second part, February–June, catches of non-migrating reds predominate. The catch rates are generally based on 24-h soak time and soak times greater than this were rejected.

For legal-sized lobsters, catch rates were combined into two groups: (1) depths of 0–36 m (shallow water); and (2) depths of >36 m (deep water). Moreover, most undersized lobsters are in depths of 0–18 m, whereas most mature (setose and spawner) lobsters have their major habitat at a depth of 36–54 m. Thus this research focuses on these two depths for each specific category of lobster.

There were some problems with missing data in the daily catch rates, especially those for setose lobsters. Consequently, only the catch rates of setose lobsters for the seasons 1992/1993, 1995/1996, 1996/1997 in Zone C, and the season 1993/1994 in Zone A, were studied because there were fewer missing values in these series. The selected data of setose lobsters were used after the missing values were estimated by the software package, STAMP (Structural Time Series Analyser, Modeller, and Predictor is a computer software package with two programs. One is a special version of the system for time series facilities for the management of the data sets. The other one performs the estimation and testing of structural time series models). Likewise, gaps of missing values appeared in some catch rate data of legal sized and undersized lobsters, but most of these missing values could also be estimated by STAMP. However, STAMP could not be used with missing data with big gaps in values for some of the catch rates, so such data were not analysed.

The lunar cycle was recorded in four phases of the moon, i.e., new moon, first quarter, full moon, and last quarter. The swell data came from voluntary daily logbooks and was recorded on an ordinal scale (0 = no swell, 1 = low, 2 = moderate, 3 = high). An average daily swell was recorded from all fishers

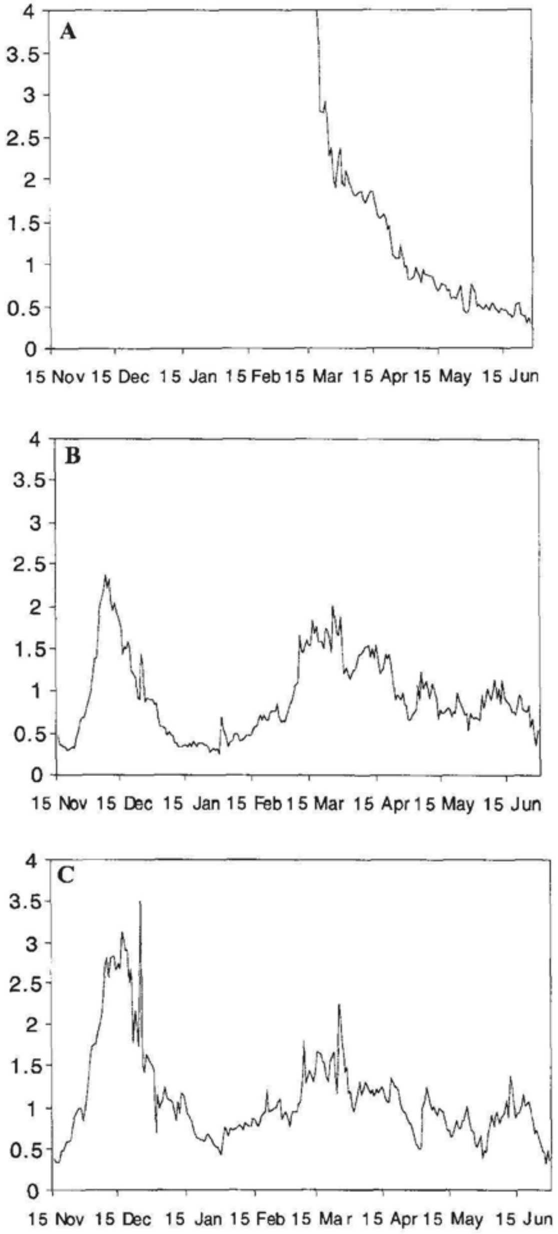

**Fig. 2** Time series plots of catch rates of legal-sized lobsters (*Panulirus cygnus*) in shallow water for the fishing season 1998/99 in Zones A, B, and C. The plot of Zone A is shorter than those of Zones B and C because of the shorter fishing season.

providing information on that day. STAMP was used to estimate any missing values.

### Statistical analysis

This study used a number of mathematical methods such as moving averages, cross correlations, classical decomposition, Holt-Winters method, ARIMA models, multiple regression models, and transfer function models.

*Moving averages and centred moving averages*

Moving averages and centred moving averages were used to smooth data or eliminate seasonal effects and irregular fluctuations (residuals or random noise components) from observed series. To examine the influence of the lunar cycle and swell on the daily catch rate of lobsters, the trend in the daily catch rate data was removed by using centred moving averages. The number of observations used for each moving average was 30 because there appeared to be a cycle of c. 30 days in the data. The time series for the original catch rates was considered to be multiplicative as catch rates generally have a skewed distribution. Hence the detrended catch rates can be calculated as follows:

Detrended catch rates = Original catch rates/Centred moving averages

*Cross correlations*

Cross correlations represent the degree of linear relationship between two time series at various time lags (Vandaele 1983). In this study, cross correlations were used to investigate the relationship between daily catch rates and the environmental factors (lunar phase, swell). Chatfield (1996) indicated a problem in the estimation of cross correlations when the sequential values of the time series are autocorrelated, and the variances in the data correspond to the autocorrelation functions of the two observed series. For the cross correlation function, purely random series or white noise processes after fitting Box-Jenkins models to both estimated time series were considered, to identify if there was correlation between the original time series.

*Classical decomposition*

Classical decomposition was used to identify each component (trend, cyclical effects, seasonality, and irregular fluctuations) in a time series for individual study or to show a clearer image of the data (Hanke & Reitsch 1998). The multiplicative decomposition model is defined as:

$$X_t = T_t \times C_t \times S_t \times I_t$$

where at time $t$, $T_t$ is the trend component, $C_t$ is the cyclical component, $S_t$ is the seasonal component, and $I_t$ is the irregular (error or random noise) component.

To obtain each component in this research, centred moving averages were first used to remove seasonality and irregular fluctuations. Then the original data were divided by the trend-cyclical component to get the seasonal-irregular component ($S_t I_t$). The seasonal indices were derived from the seasonal-irregular component by finding the medians of the values that were located $s$ positions away from each other ($s$ is the seasonal length). Deseasonalised data were obtained by dividing the original data with the seasonal component.

*Holt-Winters method*

The Holt-Winters method or Winters' method is an exponential smoothing technique used for smoothing data when both trend and seasonal variations are present. It separates a time series into three components which are local level, trend, and seasonal. Newbold & Bos (1990) have given the following Holt-Winters model for when the seasonality is multiplicative:

$$L_t = \alpha\,(X_t / S_{t-s}) + (1-\alpha)(L_{t-1} + T_{t-1}) \qquad 0 < \alpha < 1$$

$$T_t = \beta\,(L_t - L_{t-1}) + (1-\beta)\,T_{t-1} \qquad 0 < \beta < 1$$

$$S_t = \gamma\,(X_t / L_t) + (1-\gamma)\,S_{t-s} \qquad 0 < \gamma < 1$$

where $X_t$ is an observation on a time series; $L_t$, $T_t$, and $S_t$ are the current level, trend and seasonal index; $\alpha$, $\beta$, and $\gamma$ are smoothing parameters of level, trend and seasonal; $s$ is the seasonal length.

This method can also be applied to cyclic data such as a lunar cycle. Although the lunar cycle seems to appear every 29.5 days, the cyclic length of $s = 30$ can be applied. The Holt-Winters method was used in this research to validate the use of the classical decomposition to obtain suitable lunar indices for detrended catch rates. Unlike the classical decomposition method, the Holt-Winters method allows users to estimate the seasonal or cyclic indices by using the original catch rate series, which vary with time.

*Transfer function models*

The transfer function model (TFM) combines the characteristics of an ARIMA model and a multiple regression model. It allows for interdependence of the variables at different time lags. It is a dynamic system, which provides a model involving an independent variable or an input series ($X_t$), a dependent variable or an output series ($Y_t$), and a disturbance term ($N_t$). By means of the transfer function structure, the independent variable in current and past time periods has an impact on the dependent variable in the current time period. Box & Jenkins (1976), Makridakis et al. (1983), and Newbold & Bos (1990) describe transfer function models in more detail.

Assuming the input and output time series $X_t$ and $Y_t$ are stationary, the general form of the linear TFM with one input variable at different time lags can be defined as follows:

$$Y_t = \alpha + \nu(B) X_t + N_t$$

where $\alpha$ is a fixed parameter.

$$\nu(B) = \nu_0 + \nu_1 B + \nu_2 B^2 + \nu_3 B^3 + \dots$$

$\nu_0, \nu_1, \nu_2, \dots$ are impulse response weights or $\nu$-weights.

$$\omega(B) = \omega_0 - \omega_1 B - \omega_2 B^2 - \dots - \omega_s B^s$$

$$\delta(B) = 1 - \delta_1 B - \delta_2 B^2 - \dots - \delta_r B^r$$

$$X_{t-b} = B^b X_t$$

$$N_t = \frac{\theta(B)}{\phi(B)} a_t$$

$a_t$ is a random noise value.

$$\theta(B) = 1 - \theta_1 B - \theta_2 B^2 - \dots - \theta_q B^q$$

$$\phi(B) = 1 - \phi_1 B - \phi_2 B^2 - \dots - \phi_p B^p$$

$\{\nu_i \mid i = 1, 2, \dots\}$, $\{\omega_j \mid j = 1, 2, \dots, s\}$, $\{\delta_k \mid k = 1, 2, \dots, r\}$,

$\{\theta_l \mid l = 1, 2, \dots, q\}$, and $\{\phi_m \mid m = 1, 2, \dots, p\}$ are fixed parameters.

$r, s, p, q$, and $b$ are constants.

To demonstrate the influence of the swell on the catch rates, transfer function models were used after considering all relationships found from other statistical methods mentioned earlier.

## RESULTS

A small number of outliers were identified and removed from the catch rates as they were considered erroneous. This is probably because only a few boats fished on these days (such as Christmas Day). These data points were significantly higher than other points around them. In addition, they were higher than other observations at the same time for different seasons. Therefore, these observations were treated as missing values and estimated by the STAMP software package.

The plots of the daily catch rate data in Zones A, B, and C for 1998/99 were typical of the trends shown in the daily catch rates of legal-sized rock lobsters during a season (Fig. 2). The catch rates in Zone A were highest at the beginning of the season and declined until the end of the season. The daily catch rates in Zones B and C have fairly similar characteristics where catch rates in both zones increased at the beginning of the season and declined to a minimum point towards the end of January. They then started increasing again in February with a peak in March, declining for the remainder of the season. This pattern is related to the periods of whites and reds where a moult occurs in November and February with large numbers of rock lobster becoming legal size.

### Lunar phase

A 30-day centred moving average was used to remove the trend from the time series. The detrended data of the catch rates showed a cyclical pattern in the series compared to the moon phase (Fig. 3).

Although minima of the catch rate data in Zone A coincided with the full moon they did not show as clear a cyclical pattern as data from Zones B and C. The detrended series in Zones B and C illustrated clearer and stronger cycles with minimum values near the full moon phase. However, it was observed that the cyclical pattern was unclear, especially from the beginning of the season to the end of February, for every category and for the end of the season for legal-sized lobsters in deep water and for setose lobsters (Fig. 4). The cycle was more pronounced in the period of reds (February–June) than in that of migratory whites. The cyclical pattern in the detrended series of the legal-sized lobsters in shallow water seemed to be the strongest pattern compared with those in deep water and the other categories.

Classical decomposition and Holt-Winters methods were used to estimate the cyclic indices of the daily catch rates. These values were measured in the form of medians. Median values were used to obtain a set of 30-day cyclic indices. Unlike cyclic indices calculated by classical decomposition, each set of 30-day indices derived from the Holt-Winters method varied slightly over the length of the season. However, 30-day median cyclic indices were chosen from those calculated by the Holt-Winters method for every data set to compare the results from both techniques and confirm the accuracy of the outcomes from the decomposition method. The plots of 30-day cyclic indices estimated by both methods were compared with the four moon phases for every season

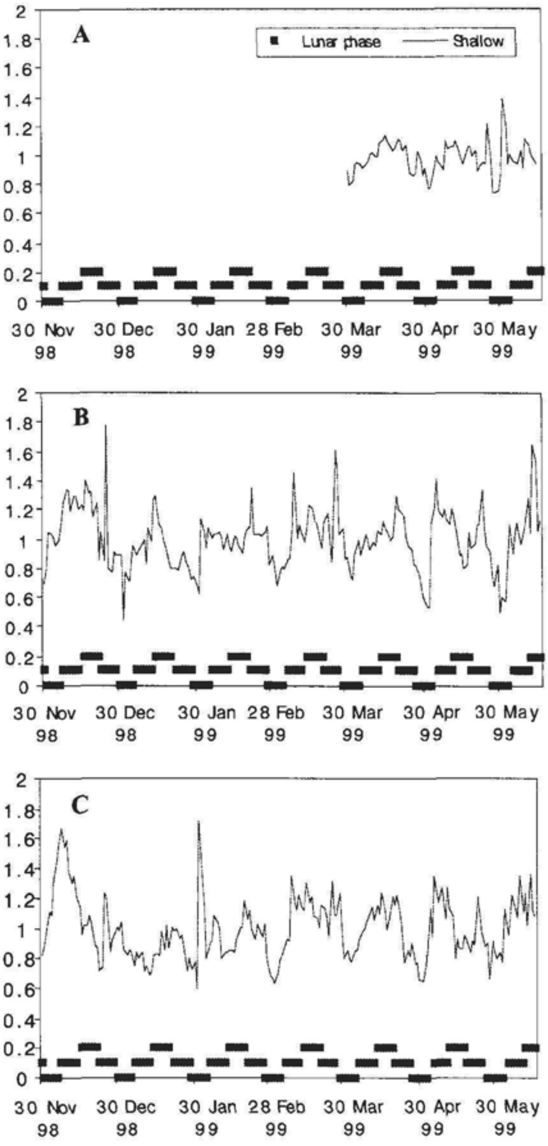

**Fig. 3** Time series plots of the detrended catch rates for legal-sized lobsters (*Panulirus cygnus*) in shallow water during the season 1998/99 in Zones **A**, **B**, and **C** against the four moon phases. The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

and every zone. The graphs indicated a 30-day cycle with minima during the full moon period (Fig. 5).

In general, the cyclical pattern had its minimum during the full moon period with the approximate index of 0.7 for catch rates of legal sized lobsters in both shallow and deep water and for catch rates of undersized lobsters. The cycle in catch rates of legal-sized lobsters in shallow water seemed to show the strongest pattern. The same pattern does not appear for some of the fishing seasons for undersized lobsters in Zone A. For setose lobsters, the pattern occurs in the catch rates of Zone C, but it does not appear in the data set for the season 1993/94 in Zone A, which is the only data set of setose lobsters used for Zone A.

The cyclic indices for the catch rates were calculated for two different periods, the whites and reds. The catch rates during the reds stage in both Zones B and C illustrate strong cyclical patterns that have minima during the full moon and maxima near the new moon period (Fig 6). The evidence of a cyclical pattern for the whites stage is not as strong although some of the plots have minima during the full moon period. The main reason is probably the different behavioural characteristics of the lobsters during the two periods.

To investigate the general behaviour of the cyclic indices for the catch rates of the western rock lobster over all years, the mean values of the 30-day indices for each category of lobsters and each zone (including means of the indices for the catch rates during the periods of whites and reds) were computed.

The cycle in general had low values during the full moon period, increasing values during the last quarter period, high values during the new moon period, and decreasing values during the first quarter period. In addition, most averages of the indices for the whole period over the season of legal-sized lobsters in both shallow and deep water, especially in Zones B and C, reached their maximum values at the end of the last quarter period or at the beginning of the new moon period (Fig. 7). The average values of both decomposition and Holt-Winters methods were quite similar for the 30-day indices of legal-sized lobsters in shallow water and slightly different for those in deep water. The averages of the indices for the period of reds had the same pattern as those for the whole season, whereas those for the period of whites were more variable but still maintained the general configuration.

The averages for undersized lobsters showed the maxima falling towards the late period of the new moon phase or the early period of the first quarter phase (Fig. 8). Thus, the catch rate of undersized lobsters was significantly higher than the average trend during that time. The values for undersized

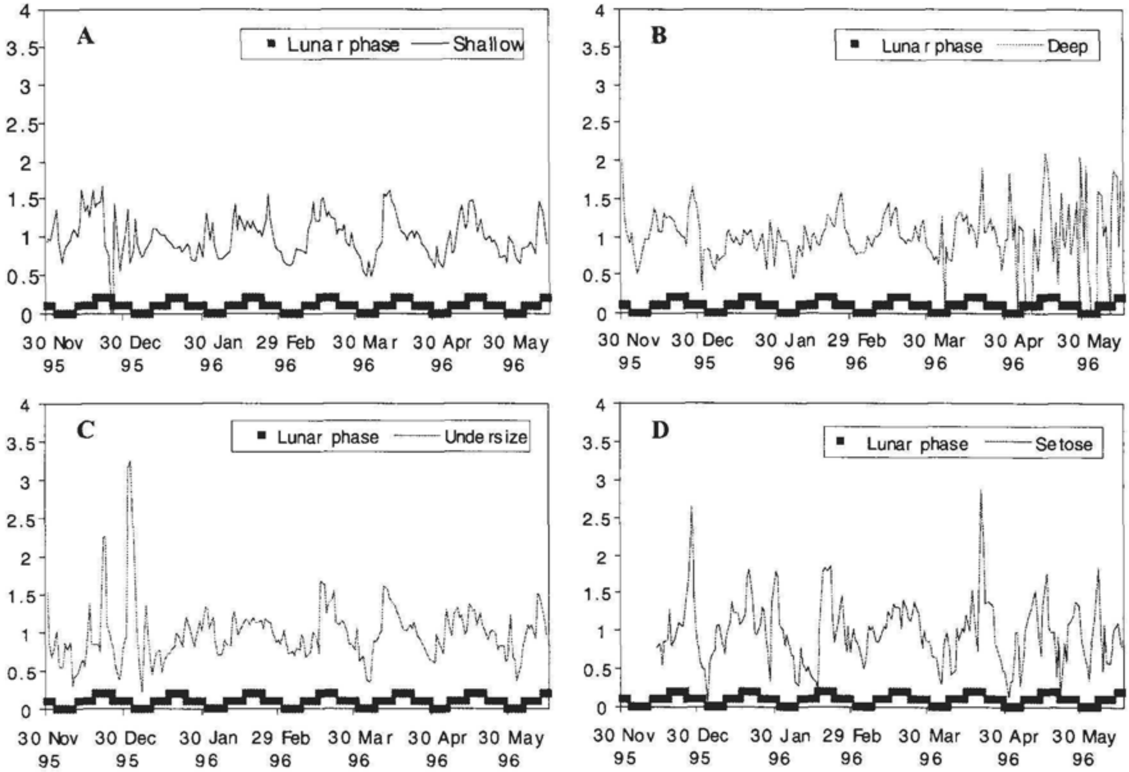

**Fig. 4** Time series plots of the detrended catch rates for legal-sized in: **A**, shallow; **B**, deep water; **C**, undersized; and **D**, setose lobsters (*Panulirus cygnus*) during the season 1995/96 in Zone C against the four moon phases (the detrended data for the setose lobsters at the start of the season are not obtainable because of missing data). The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

lobsters during the whites phase were more varied than those during the other two periods. However, the main configurations of these average values for all periods were similar. The pattern where the minimum occurs during the full moon period also appeared for setose lobsters in Zone C.

### Swell

The influence of the swell on the catch rates after removing both trend and cyclic components (adjusted catch rates) was investigated using cross correlations. The relationships of the catch rates in each zone and each category for the whole season with swell have been examined (Srisurichan 2001).

In shallow water of Zone A, the swell does not seem to have any significant effect on the catch rates of legal-sized lobsters at any lags in the cross correlations of the adjusted catch rates with the swell. In deep water, most of the cross correlation functions show the significant values at lag –1 with the correlations varying from 0.28 to 0.47. A few cross correlation functions show the significant values at lag 0 or lag –2. Thus, the swell on the day before fishing appears to have a significant effect on the catch rates.

There was no consistent result for undersize lobsters in Zone A. The cross correlations have the significant values at different lag numbers for different fishing seasons. However, the interesting outcome is that almost all of the significant values occurring in the cross correlation functions were negative. The cross correlations for setose lobsters in Zone A were calculated only from the season 1993/94 because of missing values in the catch rate data. However, the cross correlation functions of the adjusted catch rates with swell for the fishing season

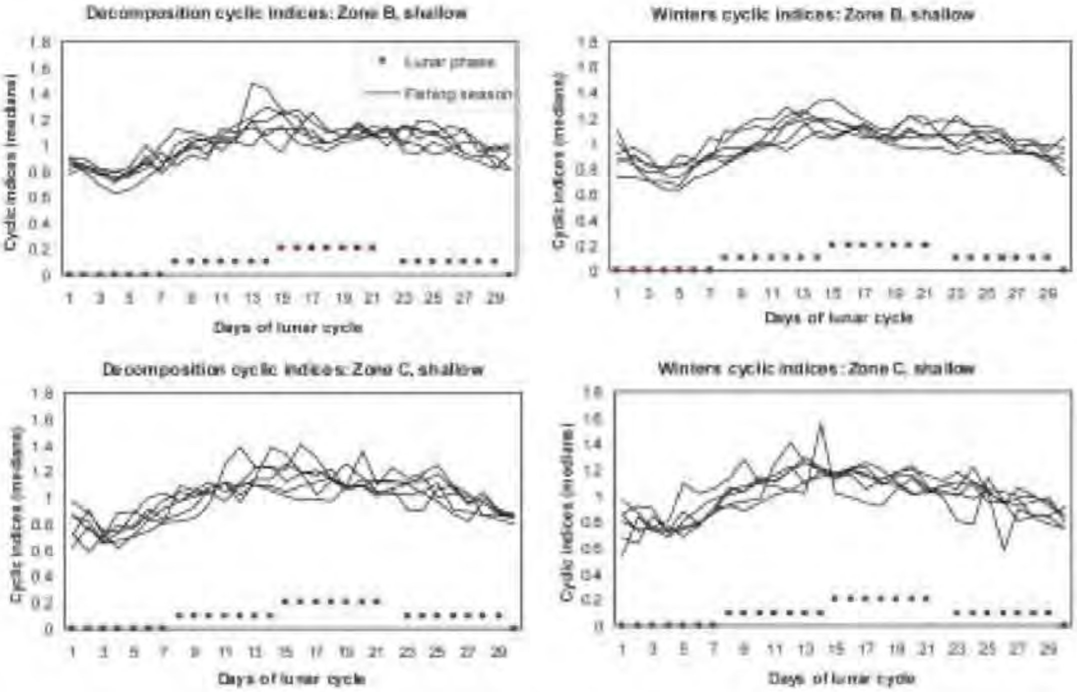

**Fig. 5** Time series plots of 30-day cyclic indices derived from the decomposition and Holt-Winters methods compared with the lunar cycle for legal-sized lobsters caught in Zone B and C in shallow water of every fishing season (1992/93 to 1998/99) considered for these two zones. The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

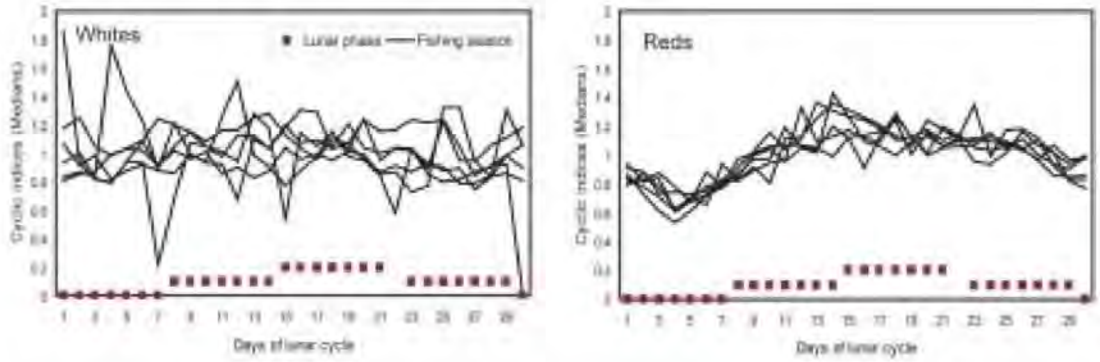

**Fig. 6** Time series plots of 30-day cyclic indices derived from the decomposition method comparing the lunar cycle for legal-sized lobsters in shallow water for the whites and reds period in Zone B of every fishing season available (1993/94 to 1998/99). The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

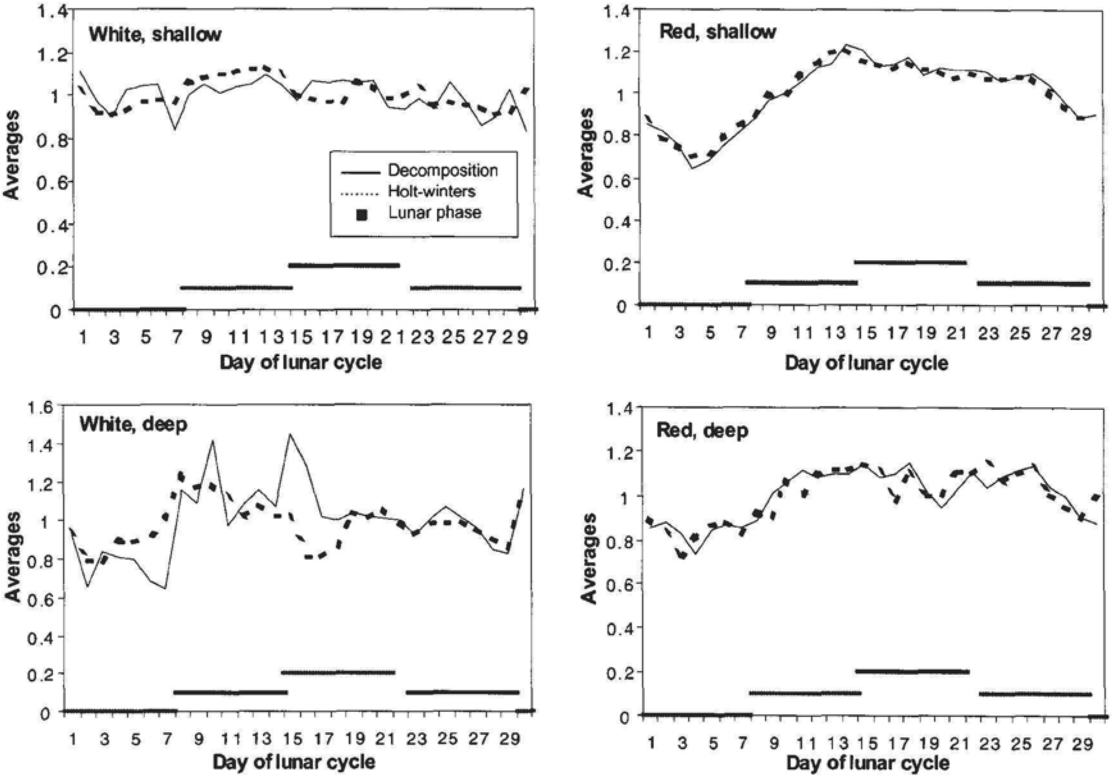

**Fig. 7** Averages of 30-day cyclic indices for catch rates of legal-sized lobsters (*Panulirus cygnus*) in both shallow and deep water and for the whites and reds period. The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

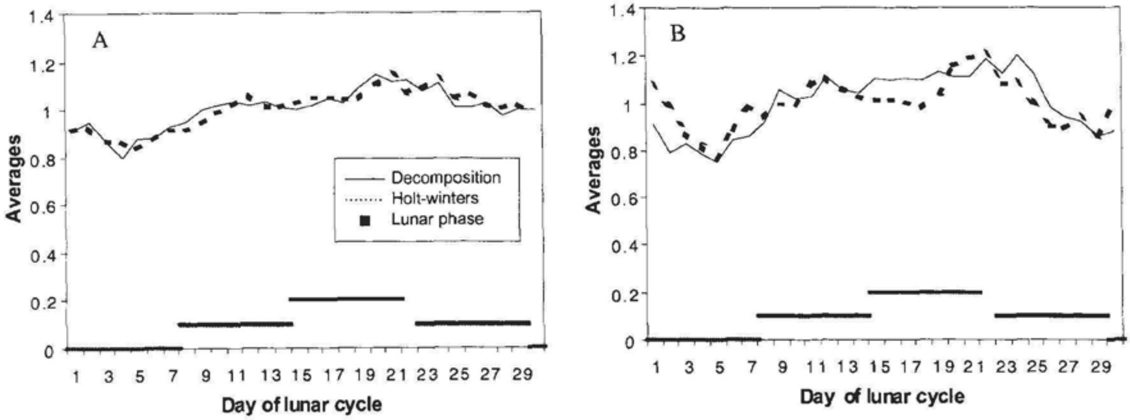

**Fig. 8** Averages of 30-day cyclic indices for catch rates of undersized lobsters (*Panulirus cygnus*) in: **A**, Zone B; and **B**, Zone C. The lowest horizontal line stands for the 7 days near the full moon whilst the next three lines correspondingly represent the periods of the last quarter phase, new moon phase, and first quarter phase.

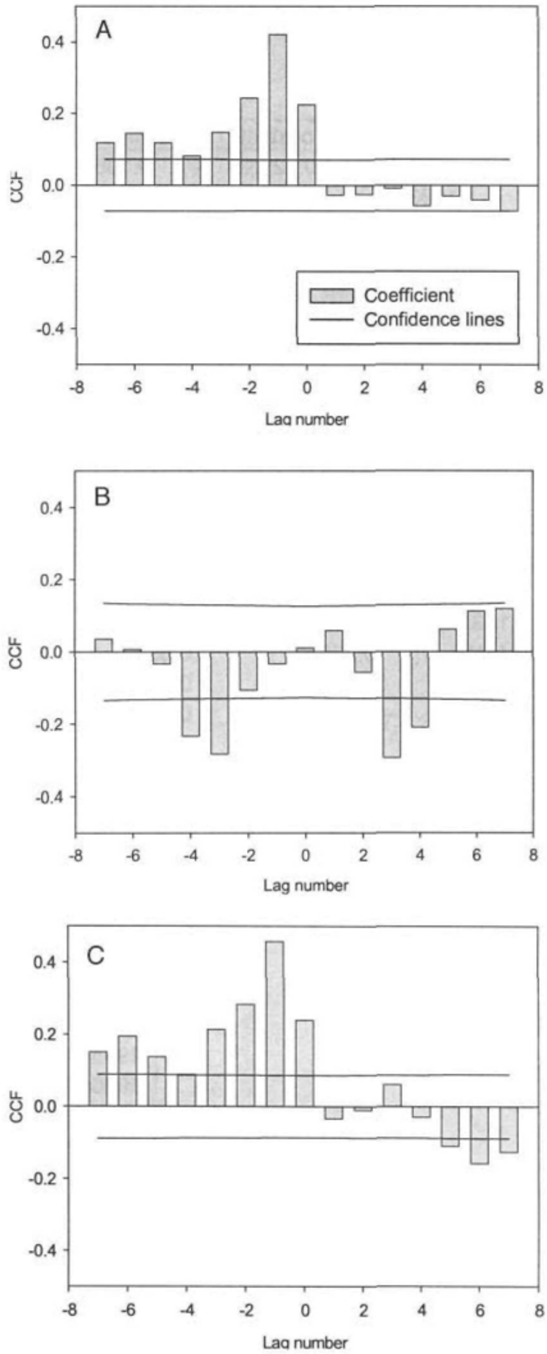

**Fig. 9** Cross correlations of the adjusted catch rates of legal-sized lobsters in shallow water with the swell in Zone C for: **A**, the whole season 1993/94; **B**, the periods of whites; and **C**, the period of reds.

do not show any significant impact for swell on catch rates.

In shallow water of Zone B, the swell appeared to have a significant effect on the catch rates of legal-sized lobsters the day before and possibly two days before the catch. All the cross correlations for the data showed a significant value at lag –1 varying from 0.16 to 0.41. Some of the cross correlations also had significant values at lag –2 or lag 0.

In deep water in Zone B, half the cross correlation functions considered had significant values at lag –1 whereas at least one of these correlation functions had a significant value at lag –2 or lag 0. The range of cross correlation values for lag –1 was located between 0.20 and 0.31. Thus, the swell possibly had a significant effect on the catch rates the day before the catch. Moreover, the impact of the swell on catch rates in shallow water was stronger than that in deep water since the significant values of the cross correlations for the legal-sized lobsters in shallow water were higher.

Although some of the cross correlations for undersize lobsters in Zone B in different fishing seasons were significant at lag 0 with the negative values, the cross correlation functions for this lobster category in Zone B did not illustrate any clear evidence for the impact of the swell on the undersized catch rates.

For the legal-sized lobsters in shallow water in Zone C, the cross correlations of all fishing seasons had the significant values at lag –1 and lag 0 (the correlations range from 0.26 to 0.52 and from 0.16 to 0.38 respectively). However, the correlation values of lag –1 were higher than those of lag 0 for every season. Almost all of the correlations at lag –2 were also significant. Therefore, the swell influenced the catch rates for the previous two days and for the day of the catch (Fig. 9).

In deep water in Zone C, the effect of swell on catch rates was not as clear compared with that of shallow water. However, it seemed that swell influenced the catch rates the day before the catch because most of the examined correlation functions showed the significant values at lag –1. The range of the correlation values was from 0.15 to 0.46.

None of the cross correlations calculated for the three seasons of undersize catch rate data examined had strong significant values in any lags. There was also no consistent significant effect for swell on the setose lobster catch rates for the three seasons examined. The cross correlations of the seasons 1992/93 and 1995/96 had some significant values at some different lags whereas those of 1996/97 did not show any significant values at all.

The relationship between catch rates and swell for whites and reds showed that significant values of the cross correlations during the period of reds were higher than those during the whites in Zones B and C (Fig. 9). The cross correlations for period of whites in all fishing seasons did not have strong significant values at any specific lags for any categories.

The problem of estimating cross correlation functions, resulting from the possible autocorrelations occurring within each of the time series, was examined by taking into account the autocorrelations of each series using ARIMA models. These cross correlation functions supported the earlier results given for catch rates and swell for deep water data in Zone A, and for both shallow and deep data in Zones B and C which correlated at lag –1. Moreover, the cross correlations of the purely random series for undersized catch rates and swell in Zone B illustrated that swell probably has a negative impact on the undersized catch rates on the day of the catch (the cross correlation coefficients were significant at lag 0).

The swell had an impact on the catch rates of legal-sized lobsters. The swell on the day before the catch had a positively significant correlation on the catch rates of the deep series in Zone A and the shallow and deep series in Zones B and C. The

**Table 1** Regression models with the response variable $Y_t$ (adjusted cate rate at day $t$), and the explanatory variables $X_{t-1}$ (swell on date $t$–1) for legal-sized data or $X_t$ for undersized data in Zone B and $Y_{t-1}$. (–, no variables for that model are significant; NS, the variable is not significant for the model.)

| Zone | Depth | Season | Constant | Coefficient* | Coefficient† | $R$-square |
|---|---|---|---|---|---|---|
| A | Deep | 1992/93 | –0.122NS | 0.105NS | 0.454 | 27.2 |
| | | 1993/94 | –0.150 | 0.112 | –0.013NS | 7.3 |
| | | 1995/96 | –0.133 | 0.108 | 0.054NS | 22.7 |
| | | 1996/97 | –0.144 | 0.101 | 0.345 | 21.1 |
| | | 1997/98 | –0.031NS | 0.037NS | 0.348 | 13.2 |
| | | 1998/99 | – | – | – | – |
| B | Shallow | 1993/94 | –0.092 | 0.081 | 0.433 | 25.3 |
| | | 1994/95 | –0.104 | 0.103 | 0.533 | 43.2 |
| | | 1995/96 | –0.067 | 0.068 | 0.546 | 37.3 |
| | | 1996/97 | –0.143 | 0.139 | 0.508 | 43.3 |
| | | 1997/98 | –0.050NS | 0.047 | 0.576 | 36.1 |
| | | 1998/99 | –0.087 | 0.090 | 0.643 | 50.0 |
| | Deep | 1993/94 | –0.286 | 0.265 | 0.327 | 20.0 |
| | | 1994/95 | –0.045NS | 0.047NS | 0.523 | 28.0 |
| | | 1995/96 | –0.156 | 0.156 | 0.281 | 11.8 |
| | | 1996/97 | –0.133 | 0.121 | 0.391 | 17.7 |
| | | 1997/98 | –0.014NS | 0.009NS | 0.590 | 34.4 |
| | | 1998/99 | –0.133NS | 0.142 | 0.302 | 12.9 |
| | Undersize | 1993/94 | 0.018NS | –0.017NS | 0.464 | 21.6 |
| | | 1994/95 | 0.060 | –0.060 | 0.301 | 13.5 |
| | | 1995/96 | 0.025NS | –0.025NS | 0.433 | 19.6 |
| | | 1996/97 | 0.016NS | –0.020NS | 0.423 | 18.6 |
| | | 1997/98 | 0.061 | –0.060 | 0.397 | 21.0 |
| C | Shallow | 1992/93 | –0.077 | 0.102 | 0.415 | 25.1 |
| | | 1993/94 | –0.118 | 0.124 | 0.275 | 25.4 |
| | | 1995/96 | –0.098 | 0.113 | 0.446 | 31.3 |
| | | 1996/97 | –0.147 | 0.162 | 0.366 | 35.3 |
| | | 1997/98 | –0.087 | 0.095 | 0.511 | 41.8 |
| | | 1998/99 | –0.132 | 0.161 | 0.274 | 33.9 |
| | Deep | 1992/93 | –0.128 | 0.162 | 0.535 | 34.7 |
| | | 1995/96 | – | – | – | – |
| | | 1996/97 | –0.105 | 0.111 | 0.244 | 8.9 |
| | | 1997/98 | –0.117 | 0.123 | 0.499 | 28.8 |
| | | 1998/99 | –0.263 | 0.327 | 0.135NS | 23.1 |

*Coefficient values of $X_{t-1}$ for legal-sized rock lobsters or the coefficient values of $X_t$ for undersized data in Zone B.
†Coefficient values of $Y_{t-1}$.

reason for this positive correlation may be that the swell disturbed the bottom and increased the availability of food and also provided greater protection of increased turbidity. Thus, legal-sized lobsters were more active and hence more easily caught when the swell occurred. The swell also had a greater impact during the reds season, as this is the period when the lobsters are sedentary. During the migration whites phase, many lobsters were already active, moving from shallow water to deep water, so there was no clear evidence of increased benefit of the swell on their activity level. However, the swell also appeared to have a negative correlation on the catch rates of undersized lobsters in Zone B on the day of the catch. This point needs to be examined further but may be related to the ability of undersized lobsters to move out of the pots more readily, using the escape gaps.

### Swell-regression models

The relationship between adjusted catch rates, $Y_t$, and swell for each series was examined using linear regression models with a combination of three explanatory variables, $X_t$, $X_{t-1}$, and $X_{t-2}$, which were the swell on the day of fishing and the swell on the day and two days before fishing. The effects of the swell on the day of fishing and two days before the catch for legal-sized lobsters and those for one day and two days before the catch for undersized data in Zone B did not have consistent and strong effects on

**Table 2** Transfer function models for all considered data sets of the effect of swell on adjusted catch rates. None of the variables for the data set of the season 1998/99 in Zone A are significant. (–, no variables for that model are significant; NS, the variable is not significant for the model.)

| Zone | Depth | Season | Constant | V0 | V1 | V2 | THETA1 | THETA2 | PHI1 | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| A | Deep | 1992/93 | –0.156NS | | 0.139 | | –0.777 | | | 41.5 |
| | | 1993/94 | –0.087 | | 0.064 | | | 0.528 | | 26.2 |
| | | 1995/96 | –0.146 | | 0.117 | | | | | 22.7 |
| | | 1996/97 | –0.185 | | 0.124 | | –0.339 | | | 18.9 |
| | | 1997/98 | 0.028NS | | | | –0.628 | | | 27.5 |
| | | 1998/99 | – | – | – | – | – | – | – | – |
| B | Shallow | 1993/94 | –0.111 | | | 0.093 | 0.409 | | 0.742 | 27.0 |
| | | 1994/95 | –0.163 | | 0.155 | | | | 0.565 | 45.5 |
| | | 1995/96 | –0.123 | | 0.114 | | 0.281 | | 0.764 | 43.2 |
| | | 1996/97 | –0.209 | –0.070 | 0.200 | 0.066 | | | 0.579 | 48.9 |
| | | 1997/98 | –0.101 | | 0.094 | | | | 0.597 | 37.4 |
| | | 1998/99 | –0.128 | | 0.131 | | | | 0.686 | 51.9 |
| | Deep | 1993/94 | –0.342 | | 0.313 | | | | 0.328 | 19.6 |
| | | 1994/95 | –0.164NS | | 0.159 | | | | 0.551 | 29.7 |
| | | 1995/96 | –0.238 | | | 0.228 | | | 0.256 | 14.3 |
| | | 1996/97 | –0.188 | | 0.162 | | | | 0.380 | 18.3 |
| | | 1997/98 | –0.021NS | | | | | | 0.576 | 36.4 |
| | | 1998/99 | –0.207 | | 0.217 | | –0.294 | – 0.253 | | 16.4 |
| | Undersize | 1993/94 | 0.086NS | –0.079 | | | | | 0.490 | 22.7 |
| | | 1994/95 | 0.103 | –0.102 | | | | | 0.361 | 15.8 |
| | | 1995/96 | 0.000NS | | | | | | 0.430 | 19.5 |
| | | 1996/97 | –0.008NS | –0.125 | 0.121 | | | | 0.422 | 26.5 |
| | | 1997/98 | 0.109 | –0.107 | | | | | 0.433 | 23.7 |
| C | Shallow | 1992/93 | –0.100 | | 0.144 | | | | 0.379 | 27.5 |
| | | 1993/94 | –0.157 | | 0.160 | | | | 0.317 | 28.3 |
| | | 1995/96 | –0.162 | | 0.180 | | | | 0.493 | 36.3 |
| | | 1996/97 | –0.199 | | 0.211 | | | | 0.406 | 39.6 |
| | | 1997/98 | –0.113 | | 0.180 | –0.062 | | | 0.609 | 52.4 |
| | | 1998/99 | –0.180 | | 0.214 | | 0.539 | | 0.819 | 42.4 |
| | Deep | 1992/93 | –0.158NS | | | 0.215 | | | 0.521 | 34.5 |
| | | 1995/96 | –0.142 | | 0.163 | | –0.193 | – 0.335 | | 9.3 |
| | | 1996/97 | –0.161 | | 0.154 | | 0.462 | | 0.627 | 14.1 |
| | | 1997/98 | –0.180 | | 0.180 | | | | 0.517 | 29.9 |
| | | 1998/99 | –0.295 | | 0.360 | | | | 0.225 | 25.9 |

catch rates. Consequently, these variables can be excluded from the models. The variable $X_{t-1}$ therefore becomes the only independent variable considered for the regression models of the legal-sized data, and the variable $X_t$ is the only explanatory variable considered for the models of the undersized data in Zone B.

All models showed the same pattern with negative constants and positive coefficients for the variable $X_{t-1}$ in the models for the legal-sized data and with positive constants and negative coefficients for the variable $X_t$ in the models for the undersized data in Zone B. Moreover, these models correspond to the results of the cross correlation functions given before. The $R^2$ values for most of the models were quite low, ranging from 3% to 27%. The residuals from the regression models indicated that almost all the error terms for these models were autocorrelated. Thus the fitted regression models in this stage may not be the most appropriate models for the data.

From the preliminary analysis using ARIMA models, it was quite clear that most of the data sets can be explained by the AR(1) process (Srisurichan 2001). Thus, including the first autoregressive term ($Y_{t-1}$), i.e., the past values of the adjusted catch rates $Y_t$, as an explanatory variable in each model, would probably improve the model's goodness-of-fit. Fitted models with the response variable $Y_t$, and the explanatory variables $X_{t-1}$ and $Y_{t-1}$, for each data set considered for modelling showed that the new $R^2$ values now ranged from 7% to 50% (Table 1). The autocorrelation functions of the residuals showed that the new fitted models were more appropriate than the models without the variable $Y_{t-1}$. Almost all of the autocorrelation functions illustrated that the residuals for each model were compatible with a white noise process.

### Swell-transfer function models

Transfer function models were also used to model the relationships between the adjusted catch rates and the swell. From previous results of the cross correlation functions, the swell at lag –1 and lag 0 seems to have most effect on the catch rates of legal-sized lobsters and on those of undersized lobsters in Zone B respectively. In addition, the swell at lag –2 had an impact on the catch rates for some data sets. Therefore, only three impulse response weights (transfer function weights or $\nu$-weights) have been considered for each linear transfer function model. In addition, an AR(1) process was first approximated for representing the disturbance term since there was no existing seasonality.

The appropriate transfer function models for all data sets considered for modelling were calculated (Table 2). Overall, the fitted transfer function models indicated that the swell on the day before the catch has a significant effect on the catch rates of legal-sized lobsters in Zones A (only in deep water), B, and C. In addition, the catch rates of undersized lobsters in Zone B had the opposite relationship with the swell at the day of the catch. The past values of the catch rates with one day lag seem to be the most important factor for the change of the catch rates in Zones B and C. Unlike the results for Zones B and C, the most significant variable for the catch rates in Zone A appeared to be the irregularity in the catch rates.

## DISCUSSION AND CONCLUSION

### Lunar phase

This study showed that lunar cycle had an impact on the daily catch rates for legal-sized and undersized lobsters. The results also illustrate that lunar cycle had an influence on the setose catch rates in Zone C, but there is no evidence for such an effect on the catch rates in the other two zones. In addition, the cycles of the legal-sized lobsters in shallow water appeared to show the clearest patterns for all three zones compared with those of the legal-sized lobsters in deep water, undersized lobsters, and setose lobsters.

The results for Zone A (Abrolhos Is.) do not show as clear a pattern as those in Zones B and C. Although most of the minimum values from the cycles in Zone A for legal-sized and undersized lobsters appeared during the full moon phase, the cyclical pattern was not strong. The results from Zones B and C gave clearer and stronger cycles with the minima near the full moon. The results for the period of whites and those for the period of reds displayed different cyclical patterns. There were no clear patterns related to moon phases for the migrating phase (whites) even though some cycles had the minimum values during the full moon phase. During the migrating period the lobsters may move during the day and thus their activity was not influenced as much by light. On the other hand, the cycles during reds showed a strong cyclical pattern with the minima during the full moon period.

This study supported the results from other research that has indicated an impact on lunar cycle on rock lobster catch for *P. cygnus* (Morgan 1974), *P. japonicus* (Yamakawa et al. 1994), *P. argus* (Sutcliffe 1956), and *P. guttatus* (Evans & Lockwood 1994). All these studies demonstrated increased activity and/or increased catch rates near the new moon compared with the full moon.

Information about the varying catch rates with moon phase can be used in the management of the rock lobster fishery by consideration of closures of c. 3–5 days during the low catch rate periods near the full moon. These moon closures are currently being considered for the April–June period which is generally a lower catching period because of declining abundance and lower water temperatures. This would result in a saving of up to 10% of the daily operational expenses of bait, fuel, and crew payments with minimal loss of catch. This approach has been successfully used in the Shark Bay and Exmouth Gulf prawn fisheries in Western Australia where king prawns have a strong lunar periodicity with low catch rates during full moon periods (Penn et al. 1989).

## Swell

The cross correlation functions between the adjusted catch rates and the swell showed significant correlation of the swell with the legal-sized catch rates. Most of the results for the shallow data sets in Zones B and C and deep data sets in Zones A, B, and

**Table 3** $R^2$ values for all models fitted to the relationships between the adjusted catch rates ($Y_t$) and the swell ($X_t$, $X_{t-1}$, $X_{t-2}$) and log catch rate ($Y_{t-1}$).

| | | | Regression* | | Regression† | | Transfer function | |
|---|---|---|---|---|---|---|---|---|
| Zone | Depth | Season | $R^2$ | MSE | $R^2$ | MSE | $R^2$ | MSE |
| A | Deep | 1992/93 | 9.2 | 0.108 | 27.2 | 0.087 | 41.5 | 0.067 |
| | | 1993/94 | 7.3 | 0.064 | 7.3 | 0.065 | 26.2 | 0.050 |
| | | 1995/96 | 22.5 | 0.015 | 22.7 | 0.015 | 22.7 | 0.014 |
| | | 1996/97 | 9.1 | 0.064 | 21.1 | 0.056 | 18.9 | 0.055 |
| | | 1997/98 | – | – | 13.2 | 0.044 | 27.5 | 0.035 |
| | | 1998/99 | – | – | – | – | – | – |
| B | Shallow | 1993/94 | 5.7 | 0.045 | 25.3 | 0.036 | 27.0 | 0.034 |
| | | 1994/95 | 16.3 | 0.034 | 43.2 | 0.023 | 45.5 | 0.022 |
| | | 1995/96 | 7.5 | 0.029 | 37.3 | 0.020 | 43.2 | 0.017 |
| | | 1996/97 | 17.9 | 0.041 | 43.3 | 0.028 | 48.9 | 0.025 |
| | | 1997/98 | 2.7 | 0.040 | 36.1 | 0.026 | 37.4 | 0.025 |
| | | 1998/99 | 9.2 | 0.036 | 50.0 | 0.020 | 51.9 | 0.019 |
| | Deep | 1993/94 | 9.7 | 0.286 | 20.0 | 0.255 | 19.6 | 0.252 |
| | | 1994/95 | – | – | 28.0 | 0.180 | 29.7 | 0.173 |
| | | 1995/96 | 4.2 | 0.239 | 11.8 | 0.221 | 14.3 | 0.212 |
| | | 1996/97 | – | – | 17.7 | 0.238 | 18.3 | 0.232 |
| | | 1997/98 | – | – | 34.4 | 0.111 | 36.4 | 0.106 |
| | | 1998/99 | 4.1 | 0.253 | 12.9 | 0.231 | 16.4 | 0.218 |
| | Undersize | 1993/94 | – | – | 21.6 | 0.050 | 22.7 | 0.049 |
| | | 1994/95 | 4.7 | 0.031 | 13.5 | 0.029 | 15.8 | 0.027 |
| | | 1995/96 | – | – | 19.6 | 0.040 | 19.5 | 0.039 |
| | | 1996/97 | – | – | 18.6 | 0.036 | 26.5 | 0.032 |
| | | 1997/98 | 5.8 | 0.035 | 21.0 | 0.029 | 23.7 | 0.028 |
| C | Shallow | 1992/93 | 7.0 | 0.045 | 25.1 | 0.036 | 27.5 | 0.035 |
| | | 1993/94 | 18.2 | 0.025 | 25.4 | 0.023 | 28.3 | 0.021 |
| | | 1995/96 | 13.0 | 0.042 | 31.3 | 0.033 | 36.3 | 0.030 |
| | | 1996/97 | 22.9 | 0.039 | 35.3 | 0.033 | 39.6 | 0.030 |
| | | 1997/98 | 17.4 | 0.027 | 41.8 | 0.019 | 52.4 | 0.015 |
| | | 1998/99 | 27.5 | 0.023 | 33.9 | 0.021 | 42.4 | 0.018 |
| | Deep | 1992/93 | 6.1 | 0.204 | 34.7 | 0.143 | 34.5 | 0.141 |
| | | 1995/96 | – | – | – | – | 9.3 | 0.108 |
| | | 1996/97 | 3.1 | 0.133 | 8.9 | 0.126 | 14.1 | 0.117 |
| | | 1997/98 | 2.7 | 0.160 | 28.8 | 0.117 | 29.9 | 0.114 |
| | | 1998/99 | 21.5 | 0.102 | 23.1 | 0.100 | 25.9 | 0.095 |

*Regression models with the explanatory variables $X_t$, $X_{t-1}$, and $X_{t-2}$.

†Regression models with the explanatory variables $X_{t-1}$ and $Y_{t-1}$.

C have positively significant cross correlations at lag –1. Thus, on the day before the catch, there is evidence that the swell has an effect on legal-sized catch rates for shallow water in Zones B and C and on legal-sized catch rates for deep water in all three zones. The positive impact of the swell on the legal-sized catch rates might be because legal-sized lobsters are more active and catchable when the swell disturbs the bottom and increases food availability as well as providing greater protection.

The significant cross correlations for the shallow data sets for the western rock lobster fishery were c. 60% higher than those for the deep-water data sets. This indicated that the impact of the swell on the catch rates in shallow water was stronger than that on the catch rates in deep water. On the other hand, the cross correlation functions of the adjusted catch rates with the swell did not indicate any clear evidence of a relationship between the catch rates and the swell in any other categories such as undersized and setose lobsters. Cross correlation functions for the period of reds were also significant at lag –1. However, there were few significantly strong cross correlations between catch rates of whites and swell at any lags.

To ensure that the overall correlation was not the result of correlation within each data set, the cross correlation functions between the residuals of the catch rates and the residuals of the swell after removing the AR or MA trend from both series were calculated. The outcomes of this confirmed the results of the cross correlation functions of adjusted catch rates with swell. Furthermore, most of the cross correlation functions between the purely random series for the undersized data sets and the purely random series for the swell in zone B displayed negatively significant values at lag 0. As a result, swell should have an influence on the catch rates of undersized lobsters in Zone B at the day of the catch. One of the reasons for the negative effect of the swell on the undersized catch rates might be the habitat of undersized lobsters. Undersized lobsters were usually in highest abundance in the inshore reefs. When the swell occurs, fishers would tend not to fish close to these areas. Therefore, the catch rates of undersized lobsters in Zone B may decrease. Escape gaps in pots also enable undersize lobsters to escape in periods of stronger swell.

Regression models used to fit the relationships between the adjusted catch rates and the swell showed that only the explanatory variable $X_{t-1}$ had a strong effect on the response variable $Y_t$ for the legal-sized data sets. This is probably because the variables $X_t$, $X_{t-1}$, and $X_{t-2}$ are correlated, so some problems of singularity of the variables may occur. However, the regression models given at this state were not really appropriate for the data since the residuals from the fitted models were autocorrelated. Therefore, more suitable models were required for explaining the relationship between the adjusted catch rates and the swell.

Since the preliminary analysis indicated that most of the adjusted catch rates for each data set could be fitted by the AR(1) process, the past values of the adjusted catch rates at lag –1 or $Y_{t-1}$ should be included as an explanatory variable to improve the models. Only the explanatory variable $X_{t-1}$ remained in the models for legal-sized catch rates whereas only the explanatory variable $X_t$ remained in the models for undersized catch rates in Zone B. Therefore, the new regression models for the legal-sized data sets were models with the response variable $Y_t$ and the two explanatory variables $X_{t-1}$ and $Y_{t-1}$. In addition, the response variable $Y_t$ and the two explanatory variables $X_t$ and $Y_{t-1}$ could be used to create new regression models for undersized data sets in Zone B.

The transfer function models demonstrated that the swell at the day before the catch had a positive impact on the legal-sized catch rates in Zone A (in deep water only), and Zones B and C. In addition, the swell at the day of the catch had a negative influence on undersized catch rates in Zone B. As a result, the catch rates on the day before appeared to be the most important explanatory variable in the variation of the current catch rates in Zones B and C although this was not so for Zone A.

All of the fitted models showed similar relationships between catch rates and swell. The models indicate that the legal-sized catch rates have a positive relationship with the swell on the day before the catch, and the undersized catch rates in Zone B have a negative relationship with the swell on the day of the catch. The transfer function models appear to be the most appropriate models for the data sets used in this study. The statistical values such as $R^2$ and MSE confirm this.

Overall, the $R^2$ values for the transfer function models were higher than those for the regression models in both instances: (1) regression models with the predictor variables $X_t$, $X_{t-1}$, and $X_{t-2}$; (2) regression models with the predictor variables $X_{t-1}$ and $Y_{t-1}$ for legal sized data or those with the predictor variables $X_t$ and $Y_{t-1}$ for undersized data in Zone B. The MSE values for the transfer function models were slightly lower than those for the regression models (Table 3). In addition, the transfer function models were no more complicated than the regression models with the predictor variables $X_{t-1}$ and $Y_{t-1}$ for legal-sized data or with the predictor variables $X_t$ and $Y_{t-1}$ for undersized data in Zone B.

The positive impact of strong swell conditions on catch rates of the Japanese spiny lobster, *P. japonicus*, gillnet fishery was also noted by Yamakawa et al. (1994). They hypothesised that the change in catchability that was observed for changes in water temperature and lunar cycle as well as swell conditions was probably a result of the changes in the level of activity of the lobsters because of environmental factors.

In conclusion, these results will enhance the management of the western rock lobster fishery by providing a better understanding of some environmental variables affecting catch rates at different times and different locations. The moon phases and the swell may need to be taken in consideration when standardising catch rates to provide an improved abundance index for stock assessment, and hence result in a more effective management of this important fishery.

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# Marine protected areas in Australia: towards a coordinated rock lobster industry position

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**Abstract** Plans by government to accelerate the establishment of a national representative system of marine protected areas (NRSMPAs) in Australia have caused increasing disquiet within the fishing industry. Rock lobster fishers have raised concerns regarding plans to establish large "multiple-use" MPAs that may or may not contain a substantial no-take component in the continental shelf waters adjacent to the coast. Key industry concerns including the potential impacts on present and future harvest rates are examined. The industry response to government MPA policy in each of the major jurisdictions is outlined. An industry position developed at the National Rock Lobster Congress in Perth, Western Australia (September 2003) is put forward. The position advocates the need for an adjustment scheme to account for displaced effort, the need for government commitment to the development of management plans that include the long-term monitoring of all MPAs, and the need for a thorough risk assessment process to be conducted before the establishment of an MPA. The issues raised in this paper should be relevant to the establishment of MPAs in an international context.

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## INTRODUCTION

Over the last decade the global interest in the establishment of marine protected areas (MPAs) has intensified. In Australia, at both federal and state levels, governments are committed to the establishment of a national representative system of marine protected areas (NRSMPAs) via a number of binding and non-binding agreements. These include the Intergovernmental Agreement on the Environment 1992 (National Oceans Office 2002) and Australia's Oceans Policy 1998 (Commonwealth of Australia 1998). The Guidelines for Establishing the National Representative System of Marine Protected Areas developed by the Australian and New Zealand Environment and Conservation Council (ANZECC 1998) provide a framework for the creation of MPAs to be included in the national representative system. The NRSMPA programme has three primary goals, the conservation of biodiversity, the maintenance of ecological processes and systems, and to contribute to the long-term ecological viability of estuarine and marine ecosystems (ANZECC 1998). With the exception of some small sanctuary zones, for example four small rock lobster sanctuaries in South Australia, MPAs are not explicitly established to compliment other fisheries management tools.

The legislative responsibility for the establishment of MPAs is shared between the Commonwealth, State, and Territory governments. The Commonwealth has responsibility for the establishment of MPAs from the edge of State and Northern Territory waters, generally 3 n mile from the low water mark out to the edge of the exclusive economic zone (EEZ), 200 n mile from the coast (Commonwealth of Australia 2003a). Likewise the responsibility for fisheries management is shared between the Commonwealth, State, and Territory governments. The instrument used to delineate the management responsibilities of the respective tiers of government is the Offshore Constitutional Settlement (OCS). As with MPAs generally, the Commonwealth is responsible for the management of fisheries outside 3 n mile. Exceptions occur where the State/Territory and Commonwealth agree to manage a particular fishery in accordance with either State/Territory and Commonwealth law to account for traditional fishing practices and management arrangements (NOO 2002). Under the OCS arrangements the management of rock lobster fisheries in Australia is predominately the responsibility of the State governments. The only lobster fishery managed by the Commonwealth is the Torres Strait lobster fishery.

The fishing industry has become increasingly concerned with the planned additions to the NRSMPAs, which may include large no-take zones in the continental shelf waters adjacent to the Australian coast. Industry participants in Australia's rock lobster fisheries have expressed the belief that the creation of large no-take MPAs may threaten the sustainability of rock lobster fisheries unless the potential impacts of displaced fishing effort is explicitly addressed (Australian Southern Rock Lobster Industry 2003; RPDC 2003).

The following developments have raised the level of concern within the fishing industry. The release of: (1) the Draft South-east Regional Marine Plan, Implementing Australia's Oceans Policy in the South East Marine Region which proposes "further development of a comprehensive, adequate and representative system of marine protected areas" (NOO 2003); (2) two state MPA strategies in Tasmania (MMIC 2001) and South Australia (Government of South Australia 2002); (3) a "user's guide" designed to assist stakeholder participation in the identification and selection of suitable areas for inclusion in the NRSMPAs in the south-east marine region (Commonwealth of Australia 2003a). Included in the users guide are broad areas of interest in which it is proposed the new MPAs will be established; (4) the creation of 13 marine national parks and 11 marine sanctuaries in Victoria; and (5) the creation and proposed creation of new MPAs in New South Wales and Western Australia.

The intent of this paper is to outline the major concerns of the rock lobster fishing industry with the establishment of the NRSMPAs. In addition, the industry response to government MPA policy in each of the major jurisdictions is briefly discussed. Finally, a consolidated industry position proposed at the 3rd National Rock Lobster Congress held in Fremantle in September 2003 is put forward.

## DISCUSSION

For rock lobster fisheries, as with other wild fisheries, there are five key questions that are posed when any new proposal to establish an MPA or a system of MPAs is announced. (1) Where will the MPA, or system of MPAs be placed? (2) How many MPAs will be established? (3) How big will they be? Specifically how big are the no-take areas that exclude rock lobster fishing (International Union for the Conservation of Nature (IUCN) categories I to V)? (4) How difficult will it be to change the boundaries including zoning (IUCN categories) of the MPA? (5) What are the potential effects on harvest rates?

In addition to the key questions outlined above, Baedle et al. (2001) found that Commonwealth and State governments had failed to address the full implications of MPA establishment for the management of Australia's fisheries. Baedle et al. (2001) assert that fishers have little confidence in MPAs because of the possible loss of access to fishing grounds, perceptions of poor planning and consultation, a lack of government commitment to long-term monitoring and enforcement, and continued "mixed and confusing messages on whether or not MPAs achieve their objectives". Fishing industry perceptions of MPAs are reinforced by a review conducted by Ward et al. (2001) that concluded that the purported fisheries benefits from MPAs remain mostly theoretical and are not backed by empirical research.

The location, number, and size of reserves are questions that are interlinked. Different approaches to these questions across different jurisdictions cause considerable angst amongst industry participants. The MPA strategies developed in South Australia and Tasmania have reaffirmed the commitment of the two state governments to the NRSMPAs (MMIC 2001; Government of South Australia 2002). The strategies propose that an MPA be established in each bioregion as identified by the Interim Marine and Coastal Regionalisation Australia (IMCRA) Technical Group (IMCRA Technical Group 1998). There are eight bioregions identified for both South Australia and Tasmania. Although there are no specific targets for the size of proposed MPAs mentioned in either strategy, both strategies state that the system of MPAs should be comprehensive, adequate, and representative (CAR). Edgar & Barrett (1999) suggest that in a Tasmanian context the no-take portion of an MPA should extend at least 10 n mile along the coast.

The South Australian and Tasmanian strategies adopt a "multiple-use" approach to MPA planning with core no-take areas embedded within larger MPAs. This approach has also been adopted in Western Australia, New South Wales, and by the Commonwealth (CALM 2003: Types of marine conservation reserves—http://www.calm.wa.gov.au/national_parks/marine/types.html—accessed 5 Feb 2004; Commonwealth of Australia 2003a; NSW Marine Parks Authority 2003a). In contrast, the 13 marine national parks and 11 marine sanctuaries currently being established in Victoria are all no-take MPAs where rock lobster fishing is prohibited.

Industry requires certainty from the process established to develop MPA proposals. The need for stakeholder input into the development process is widely recognised (RPDC 2002; Commonwealth of Australia 2003a; NSW Marine Parks Authority 2003a). One of the most prominent concerns expressed by fishers is there is no certainty about the proportion of any MPA that will be designated no-take, and that governments may increase the no-take component on an MPA at some time in the future without adequate consultation (Baedle et al. 2001).

The potential impacts of MPA establishment on harvest rates of lobster will be influenced by four main factors. First, possible benefits to the fishery from "spillover" and increased larval production. Second, potential for spatial differences in the biological characteristics of the stock. Third, potential changes to fisher behaviour in response to the establishment of MPAs. Fourth, the response of fisheries managers to the establishment of MPAs.

All species of lobster targeted by commercial fishers in Australia exhibit a high degree of site fidelity for at least part of their life history (Phillips 1983; Skewes et al. 1997; Montgomery 1998; Melville-Smith & Cheng 2002; Gardner et al. 2003). Three of the four commercial species *Panulirus cygnus* (western rock lobster), *Panulirus ornatus* (tropical rock lobster), and *Jasus verrauxi* (eastern rock lobster) do display along-shore or on-shore/off-shore movement associated with reproductive behaviour (Phillips 1983; Skewes et al. 1997; Montgomery 1998). Movement of *Jasus edwardsii* (southern rock lobster), specifically migratory behaviour, is not as pronounced (Gardner et al. 2003; McGarvey 2003).

Preliminary modelling of Tasmanian rock lobster fishery to evaluate the likely effects of large no-take MPAs in Tasmania, assuming limited migration, raises two questions that must be examined when considering a proposal to establish an MPA from a fisheries management perspective. Will an increase in egg production/biomass inside an MPA lead to a corresponding increase in egg production/biomass across a total allowable catch (TAC) managed fishery? And, will the establishment of an MPA result in increased fishing pressure in areas outside the MPA, and thus negate any benefit from the MPA (Gardner et al. 2000)? These are crucial questions given the spatial heterogeneity between regions in relation to growth, size at maturity, and catch rates (Punt & Kennedy 1997). Importantly, the model assumes that there will be no reduction in the TAC for the fishery. Assessing the potential benefits from an increased distribution of propagules from within marine reserves is problematic. For most lobster species the lack of knowledge of "source-sink" dynamics coupled with the complex life history characteristics of rock lobster larvae adds considerable complexity to the task of determining which areas of a fishery are important for egg production (Bruce et al. 2002).

Wilen et al. (2002) state that nearly all analyses of marine reserves, including the potential benefits that may accrue from their establishment ignores the response of fishers to area closures. Driven by economic imperatives, in the absence of increased control on harvesting activity outside reserves, it is predicted that fishers will attempt to maintain catch rates at previous levels, and that the creation of a reserve in itself will influence effort decisions made by fishers (Smith & Wilen 2003).

Management plans for Australia's rock lobster fisheries all contain objectives that emphasise the need for the sustainable management of the resource both at the species and ecosystems level (DPIF 1997; Zacharin 1997a,b; Donohue 2000; Fisheries Management (Lobster Share Management Plan) Regulation 2000: http://www.fisheries.nsw.gov.au/com/lob/lobster_homepage.htm—accessed 1 Feb 2004; DPI 2003). Key objectives listed in the majority of the management plans include maintaining or increasing legal size biomass and establishing a performance indicator for a minimum level of egg production. Logically, if the stated objectives of the management plans are to be realised, given the uncertainty surrounding the benefits to rock lobster fisheries flowing from reserve creation, the issue of displaced fishing effort and its effect on sustainable harvest rates must be addressed. In lobster fisheries managed by output controls, a reduction of the TAC must be considered. For fisheries managed by input controls, a reduction in the amount of gear to be used, or the length of season, or a combination of both may be required.

## Industry response to the establishment of a NRSMPA across jurisdictions

The industry response to the development of state MPAs has been varied. Hodge (2001) estimated the catch forgone by the creation of MPAs in Victoria to the rock lobster industry would be 71 t out of a fishery with a statewide TAC of 510 t. Further, industry expressed dissatisfaction with the consultation process, the lack of a socio-economic analysis of the potential impacts on the commercial fishery, and government claims that compensation was not payable as the proposed MPAs would benefit fish stocks. Industry lobbied intensively to have the "no compensation" provisions removed from the proposed legislation, claiming that the government position that MPAs would benefit fish stocks has no scientific basis. Finally, the Victorian government legislated that compensation would be payable on a case by case basis (Hodge 2001).

Smallridge (2002), in a submission on behalf of the Seafood Council (South Australia) Ltd to the draft government strategy (Government of South Australia 2002), stressed that industry needed certainty from the MPA process. For this to be achieved, the submission stated four main points that should be considered: (1) the identification and declaration of MPAs should be undertaken and considered within a holistic marine-planning framework; (2) the MPA planning process must include consultation with all stakeholders, and be "clear, transparent and based on robust science and economics"; (3) there must be compensation for displaced fishing effort. The submission highlighted concerns that environmental sustainability maybe compromised if the effects of displaced fishing effort are not explicitly addressed. The effect of displaced fishing effort would vary from region to region and from fishery to fishery. If compensation was to be made available, the preferred industry option is for a direct measurement of displacement effects, with the removal of agreed amounts of effort/quota at commercial market rates; and (4) adequate funding for the establishment and on-going management of the MPAs must be made available. The industry position outlined in the submission did not support the use of no-take MPAs as a fisheries management tool in South Australia.

The fishing industry in general, and the rock lobster fishery in particular, have been supportive of the process implemented by the government to establish additional MPAs in Western Australia (Leyland 2001; Anon. 2003). An independent statutory authority, the Marine Parks and Reserves Authority oversees the process of establishing and managing MPAs in Western Australia. The Authority has three main functions: (1) to provide advice to the Minister of Environment and Heritage; (2) to develop and submit management plans; and (3) to provide broad policy advice to the advisory committees that assist in the development of individual MPA proposals. The Department of Conservation and Land Management (CALM) is responsible for the management of marine reserves on behalf of the Authority.

Industry successfully argued that the potential negative impacts of MPA creation should be explicitly addressed during the MPA establishment process. Section 14 (g) (i) of the Fisheries Adjustment Schemes Act 1987, Section 4 (d) (i–iii) of the Fisheries Resources Management Act 1994, and the Fisheries and Related Industries Compensation (Marine Reserves) Act 1997 are the relevant pieces of legislation that address the right for compensation if there is displaced fishing effort resulting from the creation of a marine reserve. One key aspect of the MPA establishment process that received strong industry endorsement in Western Australia was that management arrangements for the proposed MPA, including zoning issues, monitoring and research, and community education, are an integral part of the planning process.

New South Wales, as with Western Australia, has established an independent authority to coordinate the establishment of multiple-use MPAs in each of five bioregions (NSW Marine Parks Authority 2003a). The New South Wales lobster fishery is a share-managed fishery with less than 10% of participants fishing exclusively for rock lobster, and the majority of operators holding multiple fishing endorsements (Firkin 2001). The fragmented nature of the fishery, and the absence of an industry body whose primary function is to represent the interests of rock lobster fishers is an impediment to formulating an industry position on MPAs (S. Westley, NSW lobster fisher pers. comm.). Industry participants have expressed concern with the process implemented by government to buy out fishing effort from the Solitary Islands and Jervis Bay MPAs. Although a total of 183 lobsters shares were purchased by the government as part of the buyout (NSW Marine Parks Authority 2003a), industry members state that very few of the shares were purchased from fishers who had traditionally operated in grounds included in the new MPAs (S. Westley, D. Stewart NSW lobster fishers pers. comm.).

The Tasmanian Marine Protected Areas Strategy (MMIC 2001) provides a framework for the identification, selection and creation of new MPAs in Tasmanian waters that will be included in the NRSMPAs. The body charged by the government to conduct the identification and the selection process is the Resource Planning and Development Commission (RPDC). The first reference issued to the Commission by the Minister for Primary Industries Water and Environment was to conduct an inquiry, and to make recommendations to the Minister on the establishment of MPAs within the Twofold Shelf and Davey bioregions (RPDC 2002).

In its submission to the RPDC inquiry the Tasmanian Rock Lobster Fishermen's Association (TRLFA), although not opposed to the establishment of MPAs, raised the following issues. First, although requested to restrict its response to the terms of the present inquiry, the TRLFA stated it was difficult to consider the proposals in isolation. It is the potential cumulative effect of MPA creation that concerned Tasmania's rock lobster fishers, given that the intent of the strategy was to create at least one MPA in each bioregion. If the MPAs include significant no-take areas, industry participants believe that the TAC would have to be adjusted. Second, if there was a need to consider the issue of displaced fishing effort by adjusting the TAC, then compensation should be payable. Third, the TRLFA stated that it supported multiple-use MPAs and with core no-take areas embedded within the larger multiple-use MPAs. The TRLFA submission acknowledged the value of scientific reference areas but stressed the need for adequate funding for long-term monitoring and management. The final major concern raised in the submission was the need for an enforcement and compliance strategy so the integrity of the newly created MPAs could be guaranteed (RPDC 2003).

### Marine protected areas in the south-east marine region

The South-east Regional Marine Plan, still being finalised, is the first of a series of plans that will eventually provide an overarching framework that will guide the development and use of Australia's marine resources based on the following key principles: ecologically sustainable development (ESD), ecosystem-based management (EBM), and integrated oceans management (IOM). The creation of MPAs to add to the NRSMPAs is one of the key intended outcomes of the Commonwealth's marine planning policy (NOO 2003).

The process for the identification and selection of areas suitable for inclusion in the NRSPMAs involves scientific assessment of the biodiversity in areas under consideration, stakeholder consultation, a socio-economic assessment of the potential impacts of MPA declaration, and a consideration of conservation objectives (Commonwealth of Australia 2003b). A "users guide" produced to assist stakeholders identify candidate areas MPAs in the south-east marine region includes 11 broad areas of interest (BAOI) in which it is proposed the MPAs will be established (Commonwealth of Australia 2003a).

Nine of the BAOI (Fig. 1) contain areas where rock lobster fishing occurs. To highlight the potential impact on rock lobster fisheries if any MPAs established in the BAOI include a large no-take component, an assessment of the "worst case" scenario for Tasmania's rock lobster fishery is provided. Six of the BAOI (Apollo, Bass Basin, Zeehan, Tasman Fracture, Huon, and Banks Strait) contain areas managed by Tasmania under OCS arrangements. The average catch (976 000 kg) and estimated value of the catch (AU$36.7 million) taken from waters either wholly or partially contained within the BAOI for 2001–02 is presented in Table 1. Depending on the exact location of the no-take proportion of any MPA established in each BAOI, the potential impact on the Tasmanian rock lobster fishery could be quite significant. For example, if 20% of the combined BAOI are designated no-take then a reduction to the TAC of 193 t may be required.

## TOWARDS A COORDINATED INDUSTRY POSITION

### MPA identification, selection and declaration process

The rock lobster industry, as with all stakeholders, requires a transparent process based on the best available information for the identification, selection, and declaration of MPAs. As outlined in the previous section there are different approaches across the different jurisdictions. Only the process adopted for the establishment of MPAs in Western Australia requires that a management plan be developed as an integral part of the identification and selection process. The Commonwealth process separates the identification and selection process from the declaration and management planning process (Commonwealth of Australia 2003b). In New South Wales, the declaration process for an MPA is completed before

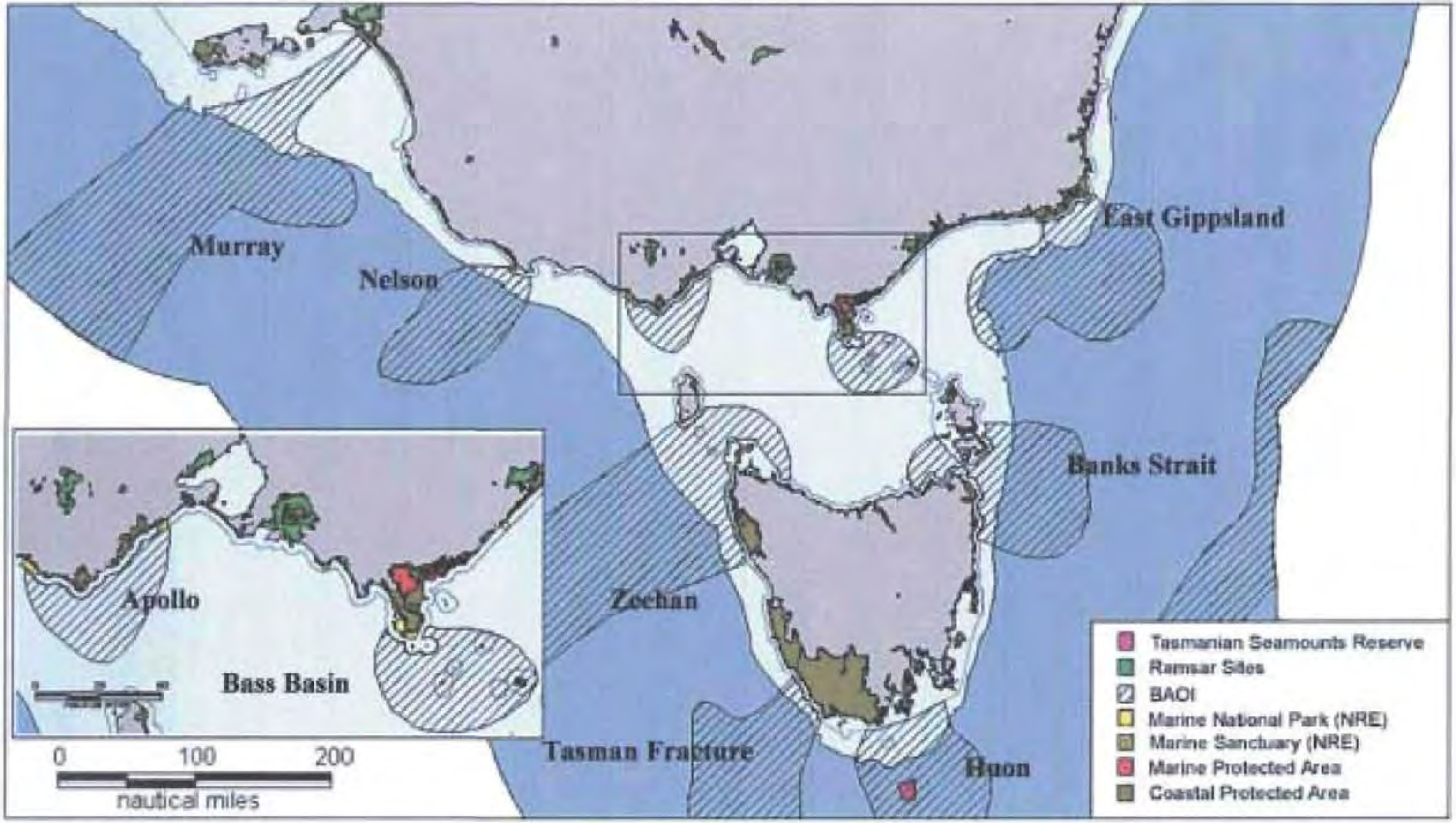

**Fig. 1** Broad areas of interest in the south-east marine region which include rock lobster fishing grounds. (Source: Commonwealth of Australia 2003a.)

management arrangements including zoning issues are finalised after consultation with stakeholders a (NSW Marine Parks Authority 2003b). The lack of an establishment process that fully integrates identification, selection, declaration, and management components with management plans before declaration provides uncertainty for stakeholders. In addition to providing greater certainty for stakeholders, an integrated approach will provide direction and in the long-term prove more cost effective.

As part of the selection process, industry should support the application of the "least costs" principle when faced with a choice between ecologically equivalent candidate areas. Baelde et al. (2001) states that industry would favour the option with least socio-economic and cultural impacts. Extensive habitat mapping which clearly identifies the extent of the different habitat types and ecosystems is required to assist stakeholders to make informed decisions. At the present time there is little published information on the distribution of marine habitats throughout Australia (Barrett et al. 2001). Obtaining information on habitats and ecosystems should be an essential prerequisite of MPA planning.

## Displaced fishing effort

To evaluate the possible negative impacts on rock lobster fisheries associated with the establishment of MPAs, socio-economic and cultural data should be overlaid on the habitat data. For rock lobster fisheries this is an important process as data collected for management purposes is generally fairly coarse. For example, fishers in the Tasmanian rock lobster fishery record catch and effort data as occurring in 30 × 30 n mile statistical blocks (Punt & Kennedy 1997). It would be reasonable to assume the extent of habitat and the concentration of catch and effort will vary from block to block, and some locations within a block will be more important from a fishery perspective than others. To calculate the potential socio-economic impacts on rock lobster fisheries, the development of a methodology based on agreed principles is essential.

**Table 1** Average catch 2001–02 and estimated value of catch using average beach price for financial years 1999–2000, 2000–01, and 2001–02 for the Tasmanian rock lobster fishery in areas included in the south-east marine region broad area of interest (BAOI).

| BAOI | Av. catch 2001–02 (kg) | Value @ AU$38 per kg |
|---|---|---|
| Apollo | 2000 | $76,000 |
| Banks Strait | 321 600 | $12,220,800 |
| Bass Basin | 2130 | $80,940 |
| Huon | 127 880 | $4,859,440 |
| Tasman Fracture | 148 240 | $5,633,120 |
| Zeehan | 365 550 | $13,890,900 |
| Total | 967 400 | $36,761,200 |

All Australian governments have agreed that structural adjustment may be required to address the issue of fishing effort displaced by the declaration of MPAs, although the Commonwealth has only recently acknowledged the need to make provisions for structural adjustment (Australian Government 2004). However, there is a lack of consistency in the approach to compensation across jurisdictions. A consistent approach across jurisdictions in relation to who receives compensation may not be practical because of the disparate management arrangements for the different fisheries, yet details on how any proposed readjustment package will be implemented remain unresolved in most jurisdictions. Industry, in addition to requesting an agreed methodology for the calculation of potential socio-economic impacts, should advocate the need for an agreed methodology for the calculation of any payable compensation that is consistent across jurisdictions.

## Ecological assessment of the impacts of rock lobster fishing

The Guidelines for the Ecologically Sustainable Management of Fisheries developed by the Commonwealth Department of Environment and Heritage (DEH) enunciate the guiding principles for the sustainable management of Australia's fisheries. One of the key objectives of the guidelines is to minimise the impact of fishing operations "on the structure, productivity, function and biological diversity of the ecosystem" (Commonwealth of Australia 2001). These objectives are closely aligned with the rationale for the establishment of the NRSMPAs. The Western Australian (DEH 2002: Assessment of the western rock lobster fishery—http://www.deh.gov.au/coasts/fisheries/assessments/wa/rocklob/report/index.html—accessed 2 Feb 2004), South Australian (DEH 2003: Assessment of the South Australian rock lobster fishery: Assessment of the ecological sustainability of management arrangements for the South Australian rock lobster fishery—http://www.deh.gov.au/coasts/fisheries/assessments/sa/rock-lobster/executive-summary.html—accessed 2 Feb 2004), and Tasmanian (DEH 2001: Assessment of the Tasmanian rock lobster fishery against the *Guidelines for the Ecologically Sustainable Management of Fisheries* for the purposes of Part 13 and Part 13A of the EPBC Act 1999—http://www.deh.gov.au/coasts/fisheries/assessments/tas/rocklob/report/manage.html—accessed 2 Feb 2004) lobster fisheries have been accredited as ecologically sustainable against the benchmarks and assessment criteria contained in the guidelines. The direct physical impacts from setting and hauling rock lobster pots on the benthos are generally considered to be minimal (Casement & Svane 1999). There are, however, considerable gaps in our knowledge of the indirect affects of fishing activities both on target and non-target species (Leadbitter et al. 1999). As a result, an emerging issue for fishers, scientists and managers is the difficulty in distinguishing the consequences of fishing from other environmental and anthropogenic effects (Wahle 1997). The growing recognition that some fishing activities will not be allowed in the multiple-use sections of MPAs (RPDC 2003), coupled with a growing need to demonstrate that fishing operations are sustainable at all levels, should provide the impetus for the Australian rock lobster fishing industry to support the implementation of generic risk assessments for both fisheries management and MPA planning purposes. Ideally the risk assessment process should begin when a reference is given to the relevant body to conduct an inquiry and to make recommendations on the establishment of MPAs within the reference area.

### Scientific reference areas and long-term monitoring

One potential benefit to fisheries from the establishment of MPAs is that it allows a comparison of areas open to fishing with areas closed to fishing and provides information on population structure, species composition and abundance, source/sink dynamics, and the ecosystem impacts of fishing (Edgar & Barrett 1999; Carr 2000). This requires a firm commitment by government to provide adequate funding for long-term monitoring and research. MPAs are expensive to establish and manage (Kriwoken 1996), therefore it is contingent upon all stakeholders to ensure the government meets its obligations in relation to the management of marine reserves.

### Review of management arrangements

Baelde et al. (2001) highlight fishing industry perceptions of lack of certainty in MPA review arrangements, specifically in relation to zoning arrangements. The rock lobster industry advocates the development of a transparent consultation process consistent across jurisdictions, before consideration is given to the reclassification of MPA zones and boundaries. Again the justification for any proposed changes should be based on robust science.

## CONCLUSIONS

This paper has used Australian rock lobster fisheries as an example. The issues raised that are of concern to Australian rock lobster fisheries would equally apply to other fisheries given the worldwide interest and willingness to establish MPAs. Although the implementation process and progress towards establishing additional MPAs to contribute to the NRSMPA differs between jurisdictions there are clear synergies across the different lobster industries. The need for transparency, direct industry involvement in the identification and selection process, and integrated identification, selection, declaration and management process, a properly funded structural adjustment package to account for displaced fishing effort, the need for long-term monitoring of MPAs, and support for risk assessments are themes that appear consistently across the different industry sectors. There will always be the potential for conflict with other users of marine resources. From a commercial fishery perspective, in Australia the process would be improved and the potential for conflict reduced if the industry concerns raised in this paper are addressed.

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# Trap-based indicators of egg production following increases in minimum legal size in *Homarus americanus* fisheries

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**Abstract** Minimum legal size (MLS) is an important conservation measure in trap fisheries for *Homarus americanus*. MLS has increased in several management areas in the Canadian Maritimes since 1987. A key conservation objective has been to increase egg production, with predictions of the effects of MLS increase based on egg-per-recruit models. We evaluated whether expectations of increases in ovigerous females (OF) were realised when MLS was increased. Data were examined from at-sea samples of the commercial trap catch from 11 ports from 1986 to 2003. OF indicators were developed based on the OF catch-per-unit-effort (CPUE) of different sizes, and on the percentage (PCT) of females that were ovigerous. Because there were within-season increases in CPUE and PCT, annual indicators were based on regressions of CPUE on day in the season. There was considerable variability in all the time series of OF annual indicators and any effects of smaller MLS increases could not be detected. Increases in OF indicators were evident in areas that undertook the largest MLS increases (6–6.5 mm CL).

**Keywords** lobster; *Homarus americanus*; minimum legal size; E/R; egg production; indicators

## INTRODUCTION

Minimum legal size (MLS) and the protection of ovigerous females (OF) are key conservation measures for trap fisheries of *Homarus americanus* Milne Edwards in Atlantic Canada. A review of these fisheries suggested that industry adopt measures to increase egg-per-recruit (E/R) (FRCC 1995) and the Canadian Government followed with a target to double E/R. Early E/R models (Campbell 1985; Ennis 1985) and more enhanced versions (Idoine et al. 2001; Gendron & Gagnon 2001), were essential for providing advice to managers and industry on the contributions of different management measures to increased E/R. Since MLS increase was an efficient way to increase E/R and had the added value of increasing yield-per-recruit, this was a key measure adopted for several areas, including several management units in the Canadian Maritimes (Fig. 1, Table 1).

Models can predict the changes in E/R resulting from different management regimes, but models provide no way of evaluating whether predictions were realised. To evaluate the effects of management changes on egg production, empirically based indicators are needed. Such indicators are particularly relevant in invertebrates where age composition and stock-recruitment relationships are poorly understood (Caddy 2003). Indicators are also of interest to the fishing industry, which has an increasing role in the collection of data on stock health, and is generally more comfortable in drawing conclusions from measurable changes in their catch than in model predictions. Model predictions might not be realised if some of the model input parameters were incorrect,

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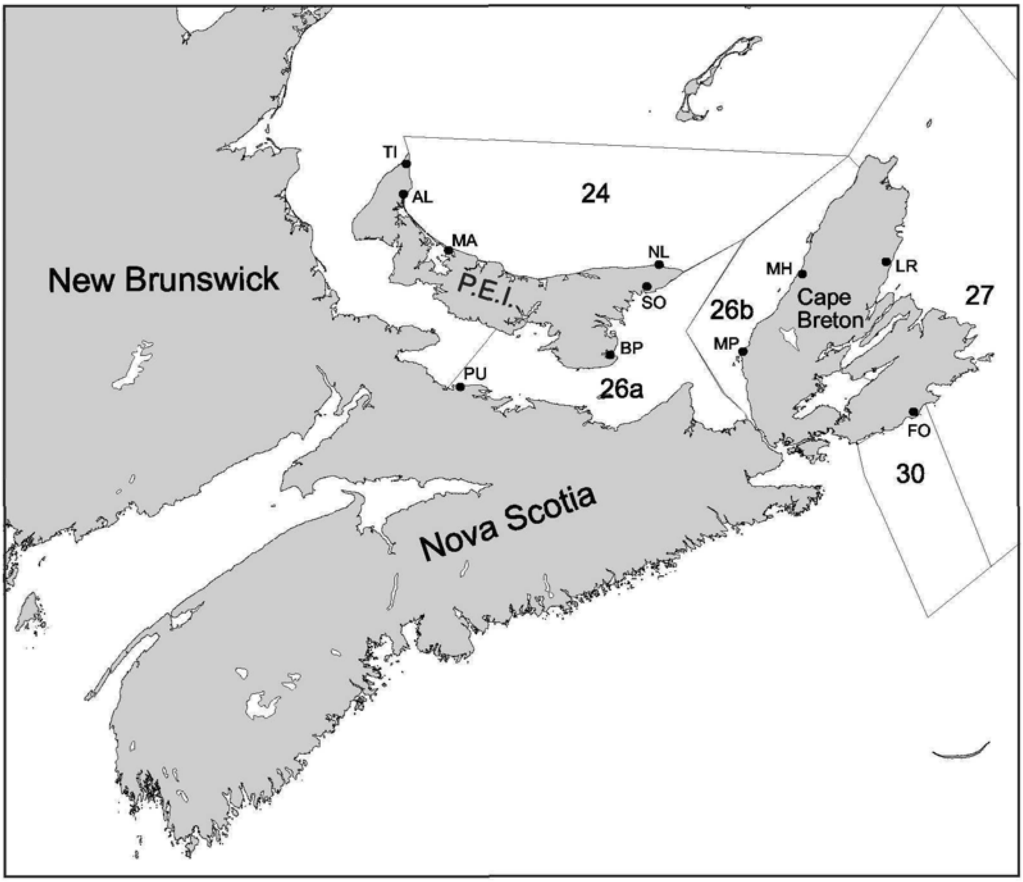

**Fig. 1** Map of the Maritime Provinces, Canada showing Lobster Fishing Areas (LFAs) in bold, and fishing ports where at-sea samples were obtained.

**Table 1** Descriptions of increases in minimum legal size (MLS) (carapace length in mm) by LFA (Lobster Fishing Area) and data available from at-sea samples of the commercial catch from 1986 to 2003. (No. port-year comb. is the number of port-year combinations where there were at least two at-sea samples.)

| LFA | Start MLS | End MLS | Years of increase | Representative fishing ports | No. port-year comb | No. of samples |
|---|---|---|---|---|---|---|
| 26B | 63.5 | 70 | 1987–90 | MH (Margaree Harbour),<br>MP (Murphys Pond) | 19 | 146 |
| 26A | 63.5<br>65.1 | 65.1<br>67.5 | 1991<br>1998–2001 | PU (Pugwash), SO (Souris),<br>BP (Beach Point) | 39 | 166 |
| 24 | 63.5 | 67.5 | 1998–2001 | AL (Alberton), MA (Malpeque),<br>NL (North Lake), TI (Tignish) | 32 | 175 |
| 27 | 70 | 76 | 1998–2002 | LR (Little River) | 8 | 76 |
| 30 | 81 | 82.5 | 1998 | FO (Fourchu) | 8 | 62 |

or if the environment or fishing effort changed and affected lobster survival. Conversely, model predictions might be accurate, but not detectable if the signal-to-noise ratio is low.

MLS for lobster has increased a number of times over the last 50 years, but there are few published evaluations of the effects of these increases. In a review of MLS increases between 1947 and 1963 in eastern Nova Scotia, Wilder (1965) focused on landings and could not find "consistent, convincing evidence that minimum size limits have improved landings significantly". Increased landings might be difficult to detect given variations in recruitment and in fishing effort that are independent of landings. More direct effects of MLS changes should be apparent in lobster size and reproduction. Since the objective of the recent Atlantic Canadian programme was to increase E/R, we focused on indicators of egg production.

In this paper we develop indicators for lobster OF in the Canadian Maritimes. In areas where females can be mature at the MLS, increases in MLS should increase the abundance or proportion of OF within the newly protected size range. After the MLS has been in place for a few years there should also be an increase in the proportion of egg-bearing females that are a molt or more beyond the MLS. This is because they will have experienced less cumulative fishing mortality compared to the situation with a smaller MLS. An increase in the proportion of larger females with eggs assumes that the fishing industry does not target larger animals after the MLS increase. Increases in OF indicators should correspond to increased E/R assuming there is no downward shift in size structure, and to increased egg production with the additional assumption of consistent recruitment.

## METHODS

### MLS increases and data sources

MLS was increased 1.6–6.5 mm carapace length (CL) in a number of Lobster Fishing Areas (LFAs) off Cape Breton and in the Southern Gulf of St Lawrence, Canada from 1987 to 2002 (Table 1, Fig. 1). Throughout these LFAs a portion of females are mature within the size range covered by the MLS increase. The 50% size at maturity ($M_{50\%}$) for lobsters in the Southern Gulf (LFAs 24, 26A, and 26B in the current paper) is 70–72 mm CL (Lanteigne et al. 1998). The $M_{50\%}$ for the area just north of Little River (Ingonish) was estimated at 73 mm in the 1980s; for the Fourchu area the estimate was 78 mm CL (F. Watson & R. Miller unpubl. data). MLS increases of more than 1.6 mm occurred in annual steps over several years. At-sea samples of the commercial catch provided the data for analysis. Each sample consisted of sexing and measuring CL to the nearest mm of all lobsters in commercial traps. The fishing ports with the most consistent sampling for the periods of interest from the mid 1980s through 2003 are listed in Table 1. Between 1986 and 2002 the mean number of traps sampled per trip for the different ports ranged from 97 (SE = 3.2) for Margaree Harbour (MH) to 264 (SE = 22.8) for Beach Point (BP). Each port was sampled twice or more per season, and only years in which samples included the first 3 weeks and last 3 weeks of the 9-week fishing season are included here. The commercial lobster season start dates are fixed: May 1 for LFAs 24, 26A, 26B; May 15 for LFA 27; and May 20 for LFA 30. However, in some years the start of the season may change by a few days because of ice or storms.

### Annual indicators of ovigerous females

We examined four OF indicators with data available from ports from 1986 to 2003 (Table 1). The first two indicators were based on CPUE, calculated as number per 100 trap hauls: CPUE of OF within the newly protected size range (CPUE1), and CPUE of ovigerous females of all other sizes (CPUE2). The next two indicators were based on the percentage (PCT) of females that were ovigerous within the newly protected size range (PCT1) and the percentage of females that were ovigerous for all other female sizes (PCT2). The percentage-based indicators of OF might be expected to be less sensitive to recruitment variation since ovigerous females and non-ovigerous females of a given size usually represent different year classes. Regression techniques were used to develop annual indicators for each port for the period 1986–2003.

### Tests of expected effects of size increase

Once the annual OF indicators were estimated, we regressed the indicators on year in the MLS increase programme. It was hypothesised that with each additional year the OF indicators would increase. In the American lobster, a mature female typically molts and mates one summer, spawns (extrudes eggs to pleopods) the following summer, and carries the eggs on her pleopods until the next summer when they hatch (Waddy et al. 1995). Thus no increase in OF was expected until one year after the initial MLS

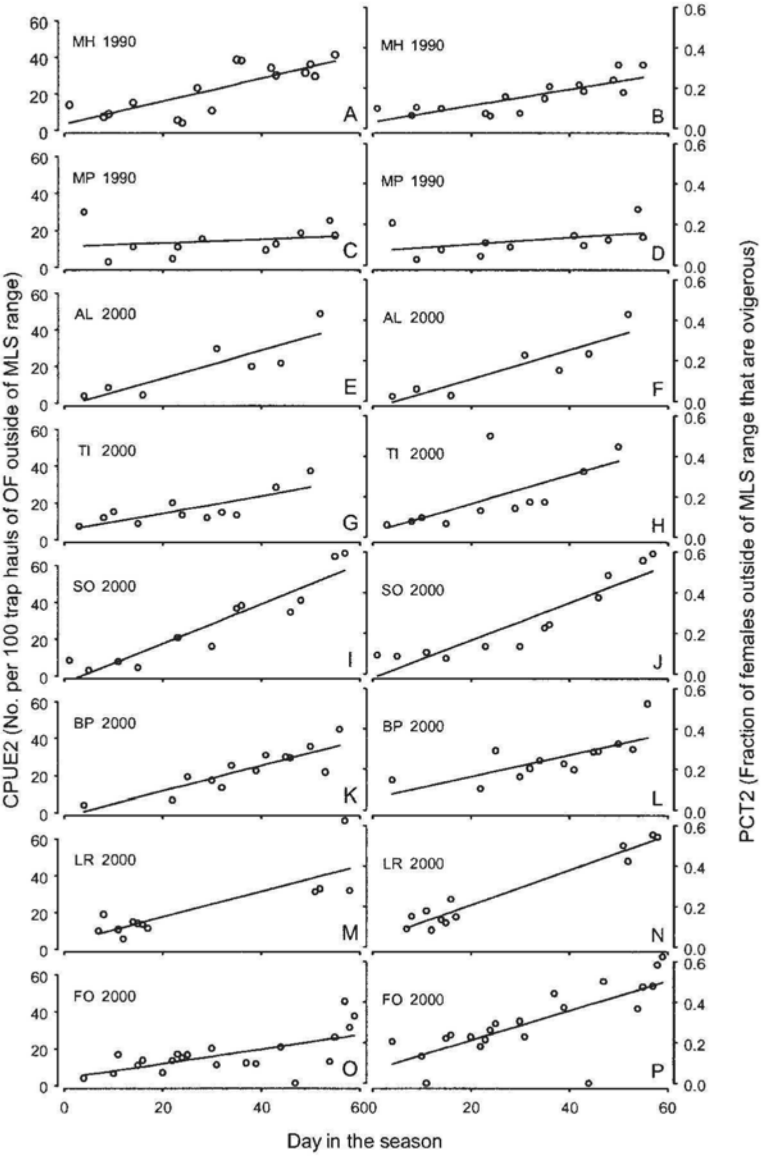

**Fig. 2** Ovigerous female (OF) indicators versus day in the fishing season for representative ports of different Lobster Fishing Areas (LFAs) in 1990 and 2000. Linear regression lines are superimposed. Graphs in left column are CPUE (catch-per-unit-effort) of OF outside the newly protected size range (CPUE2), graphs in right column are percentage of OF outside the newly protected size range (PCT2). Data are from LFA 26B (A-D), LFA 24 (E-H), LFA 26A (I-L), LFA 27 (M,N), and LFA 30 (O,P). Text in each panel is abbreviated port name and year.

increase when the newly protected females would extrude eggs if mature. If no samples were available from the year of the first MLS increase, samples from the previous year were used to estimate the first year value of the OF indicators. The last year used in the regressions was the last year available, or up to 2 years after the last MLS increase. Thus for a 4-year MLS increase programme the maximum number of data points for a given port was 6. Ports were compared based on the timing of MLS increases, location, and data availability.

## RESULTS

### Development of annual indicators

The catch rate of ovigerous females typically increased as the fishing season progressed, but not always (Fig. 2). For the 106 port-year combinations, the percentage of instances where the slope of the regression was positive was 63% (CPUE1), 83% (CPUE2), 69% (PCT1), and 94% (PCT2). Some of these data appeared to have a non-linear component (e.g., Fig. 2J), but a substantial portion of the data

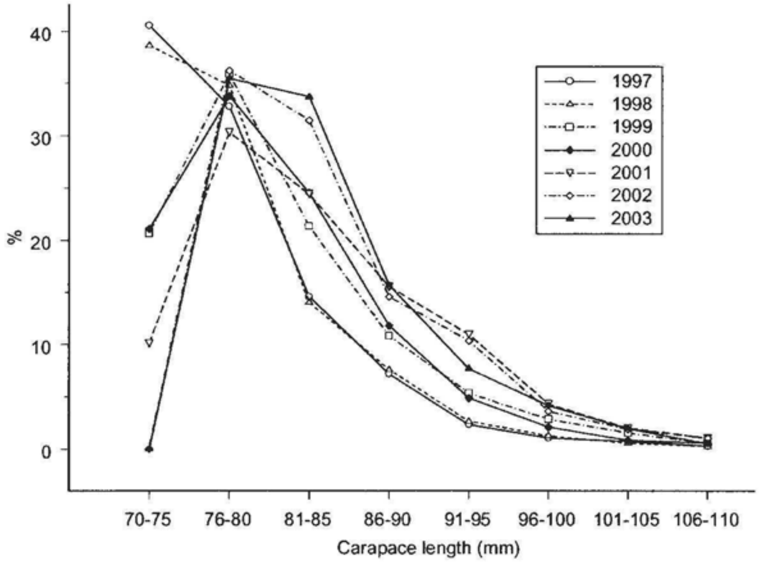

**Fig. 3** Example of change in size structure of females in the landed catch as minimum legal size was increased. Data are from at-sea samples off Little River, Canada where MLS increased from 70 to 76 mm carapace length from 1998 to 2002.

were amenable only to linear regression because of low sample sizes. For the period from 1986 to 2002, almost 60% of the port-year combinations had fewer than five samples, too few for non-linear regressions requiring the estimation of at least three parameters.

Annual estimates for CPUE1, CPUE2, PCT1, and PCT2 were developed for each port-year combination from linear regressions on day in the season. The regression was used to estimate the indicator on day 30, mid-way through the fishing season. Where the regression line was flat, this procedure differed little from taking the mean of the points during the season.

To evaluate any improvement from fitting non-linear versus linear regressions, we examined seven port-year combinations where the number of samples was at least 12 (MH 1990, LR 1994, 2000, NL 1999, SO 2000, BP 2000, and FO 2001). Linear and second degree polynomial models were fit for the dependent variables (CPUE1, CPUE2, PCT1, and PCT2) for each of the seven port-year combinations and the models compared with an *F* test. The linear regressions were significant at 0.05 (and often at 0.0001) in 20/28 instances. Improved fits from the polynomial models resulted in 8 of 28 instances ($P < 0.05$). Where the linear fit was not significant, the polynomial model was also not significant.

### Ovigerous female indicators and increased MLS

As the MLS increased, the size structure of females in the landed catch typically shifted to the right, with the shape of the size-frequency curve not changing over the course of the MLS increase programme (Fig. 3).

The time series of OF indicators available for any one port was variable. The two OF indicators that are related to the MLS size range (CPUE1 and PCT1), show generally similar patterns within any given port (Fig. 4). OF indicators for ports in LFA 26B showed variable increases from 1988 to 1991 during the MLS increase and declines in 1992 or 1994 after MLS increases (Fig. 4A,B). Ports in LFA 26A (small MLS increase in 1991) from 1988 to 1991 had variable trends (Fig. 4C,D,E). OF indicators for LFA 27 (MLS increase of 6 mm 1998–2002) increased erratically from 1997 to 2003 (Fig. 4F), whereas indicators for LFA 30 declined during the same period (Fig. 4G). In LFA 24 there was an increasing trend for OF indicators for some ports during the 1998–2001 MLS increase (Fig. 4H-K). LFA 26A ports had inconsistent trends over the same period (Fig. 4C,D,E).

Regressions of OF indicators on year in the LFA 26B MLS increase programme yielded positive correlation coefficients for LFA 26B ports. For ports in LFA 26A during the same period, correlations were both positive and negative (Table 2). All correlation coefficients between LFA 27 OF indicators and year during the test period were positive, and negative or weakly positive for the same period in LFA 30 (Table 2). Correlation coefficients between OF indicators and year for the period of the MLS

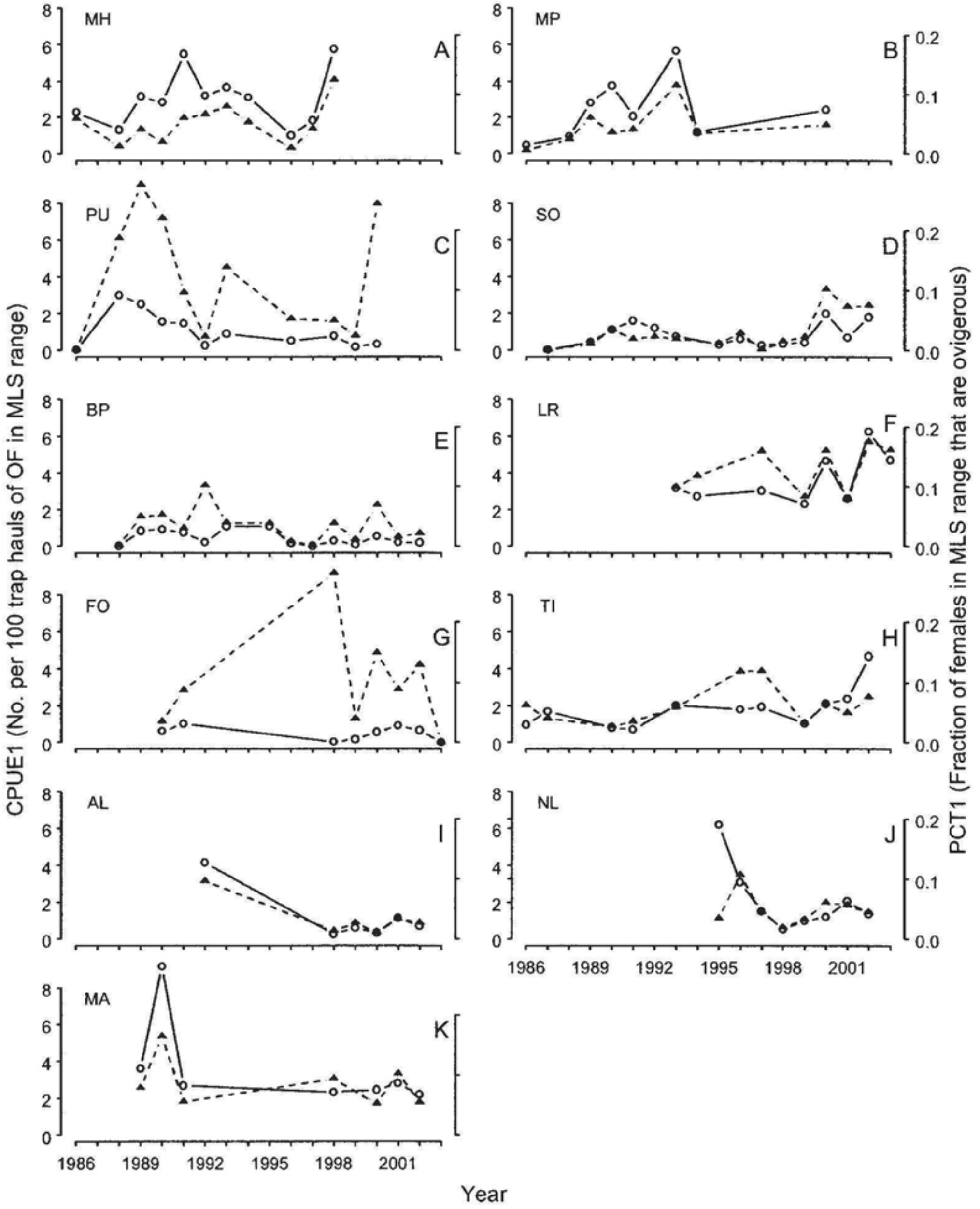

**Fig. 4** Ovigerous female (OF) indicators from 1986 to 2003 for ports representative of different Lobster Fishing Areas (LFAs). CPUE (catch-per-unit-effort) of OF in the newly protected size range (CPUE1) is solid line with open circles, percentage of OF in the newly protected size range (PCT1) is dashed line with solid triangles. Minimum legal size (MLS) was increased by: 6.5 mm (1987–1990) in LFA 26B (A and B); 1.6 mm (1991) and 2.4 mm (1998–2001) in LFA 26A (C, D, and E); 6 mm (1998–2002) in LFA 27 (F); 1.6 mm (1998) in LFA 30 (G); and 4 mm (1998–2002) in LFA 24 (H–K).

increase programmes in LFAs 24 and 26A (1998–2001) were mainly positive but not consistently (13/16 positive for LFA 24, 6/8 positive for LFA 26A).

The power to detect significant effects in the above tests was low because of the low sample number (years) for any given port. To increase statistical power we conducted the same analyses as above but grouped ports by LFA. The grouping with the largest MLS increase (LFA 26B) had the consistently highest correlation coefficients (Table 2). One regression was significant at $P < 0.05$, and two were significant at $P < 0.10$. None of the regressions involving LFA 26A during the same period were significant. For the MLS increase programme of 1998–2002, the correlations involving LFA 26A were positive, whereas there was only one modest positive correlation involving LFA 24.

## DISCUSSION

This study provides support for the hypothesis of an increase in the catch rate (and presumably abundance) and proportion of OF in response to increases in MLS, but only in those management areas that undertook the largest increases in MLS. Before discussing this further, we need to deal with the phenomenon of seasonal increases in OF and methodological implications.

### Annual indicators of ovigerous females

In addition to complicating the task of developing annual OF indicators, the seasonal increase in OF is of interest from the perspective of lobster population biology. The seasonal increase likely results from the interplay of three factors: (1) increased availability of OF because of movements inshore; (2) removals of commercial sized lobsters; and (3) females extruding eggs during the season. The first two factors are likely most important. Increased availability of OF likely results from movements inshore during late spring and summer. This may result in OF becoming more available to lobster traps as they move to areas where fishing intensity is higher. These movements inshore are thought to provide a reproductive advantage by increasing egg maturation rates in warmer near-shore waters (Campbell 1990; Ugarte 1994; Lawton & Lavalli 1995). OF may also become more active foragers as bottom temperatures warm.

Exploitation rates of commercial lobsters in these spring fisheries can range from 20% to upwards of 80% (Comeau & Mallet 2001; Claytor & Allard

**Table 2** Tests of expected effects of minimum legal size (MLS) increase on ovigerous female (OF) indicators. Shown are data specifications and correlation coefficients (*r*) between OF indicators and year during MLS increase programme. (MLS inc., MLS increase in mm; period, years used in regression; CPUE1, catch rate of OF within newly protected range; CPUE2, catch rate of all other OF; PCT1, OF as a percentage of all females in newly protected range; PCT2, as for PCT1 but all other sizes.)

| | | | | | Correlation coefficient (*r*) | | | |
|---|---|---|---|---|---|---|---|---|
| LFA | Port | MLS inc. | Period (yr) | No. pts | CPUE1 | CPUE2 | PCT1 | PCT2 |
| 26B | MH | 6.5 | 1987–92 | 6 | 0.65 | 0.48 | 0.38 | 0.57 |
| | MP | 6.5 | 1987–92 | 5 | 0.70 | 0.68 | 0.63 | 0.58 |
| 26A | PU | 1.6 | 1987–92 | 6 | –0.20 | –0.24 | –0.10 | 0.11 |
| | SO | 1.6 | 1987–92 | 5 | 0.90 | –0.33 | 0.70 | –0.17 |
| | | | | | $P < 0.05$ | | | |
| 27 | LR | 6.0 | 1998–2003 | 6 | 0.64 | 0.62 | 0.26 | 0.68 |
| 30 | FO | 1.6 | 1998–2003 | 6 | 0.25 | –0.11 | –0.65 | –0.49 |
| 24 | TI | 4.0 | 1998–2002 | 5 | 0.79 | 0.78 | 0.34 | 0.58 |
| | AL | 4.0 | 1998–2002 | 5 | 0.64 | 0.27 | 0.55 | 0.21 |
| | NL | 4.0 | 1998–2002 | 5 | 0.78 | 0.69 | 0.69 | 0.55 |
| | MA | 4.0 | 1998–2002 | 4 | 0.08 | –0.86 | –0.38 | –0.78 |
| 26A | SO | 2.4 | 1998–2002 | 5 | 0.65 | 0.45 | 0.72 | 0.38 |
| | BP | 2.4 | 1998–2002 | 5 | –0.08 | 0.33 | –0.20 | 0.33 |
| 26B | All | 6.5 | 1987–92 | 11 | 0.67 | 0.54 | 0.49 | 0.57 |
| | | | | | $P < 0.05$ | $0.05 < P < 0.10$ | | $0.05 < P < 0.10$ |
| 26A | All | 1.6 | 1987–92 | 11 | 0.10 | –0.21 | –0.07 | –0.06 |
| 24 | All | 4.0 | 1998–2002 | 19 | 0.42 | 0.12 | 0.02 | –0.06 |
| | | | | | $0.05 < P < 0.10$ | | | |
| 26A | All | 2.4 | 1998–2002 | 10 | 0.34 | 0.37 | 0.32 | 0.35 |

2003) while OF are protected from harvesting. Over the course of the season, OF as a percentage of total females will increase. In addition, OF may also become more catchable as other components of the population are fished down, increasing OF catch rates. Lastly, some females will extrude new eggs as the season progresses. Most OF in these spring fisheries carry old eggs, extruded in the previous year. The dynamics of the timing of new egg extrusion have not been studied systematically. Data from the LFA with the latest season closure (LFA 30, 20 July) in the year 2000 indicates females with new eggs do not show up until the last week of the season and comprise a small proportion (<12%) even in the last week. The timing and rate of change in seasonal catch rates is likely influenced by environmental conditions such as the seasonal increase in bottom temperature. We need to understand more about the dynamics of seasonal increases in OF catch rates.

In the development of annual OF indicators, linear fits were the only option for much of the data because of low sample sizes. Nevertheless, it appears the linear models provided reasonable fits to the data. Where there were a sufficient number of samples to compare linear and non-linear models, the latter provided a significantly better fit for a little less than one third of the examples. Improved indicators would likely result from larger samples sizes within a few key ports rather than a few samples in many ports.

### Effects of MLS increase

There was no indication that the shape of the size frequency changed as might happen if there was a shift in the sizes targeted by the fishery as a result of MLS increase. This finding is supported by recent exploitation estimates for LFA 27, that indicate no increase in exploitation on sizes one molt above the MLS (Tremblay & Reeves 2004).

All four OF indicators increased with year in the MLS programme in LFAs 26B and 27, where the largest increases in MLS occurred. OF indicators did not increase consistently during the same period at adjacent ports where MLS increases were small. When ports were grouped by LFA, only 26B had consistently positive correlations.

There are a number of possible reasons for not detecting consistent increases in OF indicators in the LFAs, but it appears the MLS increase has to be greater than 5 mm for detection with current sampling methods. Factors that will contribute to the low signal-to-noise ratio include natural variability in the indicators, sampling variability and possible bias, local variation in population size structure, and variability in fishing strategy. Variation in the OF indicators occurred in the absence of MLS changes and is likely related to natural variability in the catchability or availability of this component of the lobster population. The contribution of sampling variability (number and timing of samples in the different ports per year) and bias to variability in the OF indicators is difficult to evaluate. Sampling within any port usually occurred on less than 5 days in a 60 day season, and was unevenly distributed over the years. Possible bias comes from the observation that fishers avoid areas where their traps have a higher proportion of OF. Lastly, local variation in size structure could make increases in OF difficult to detect when grouping data from different fishing ports. Some of the limitations of at-sea samples may be overcome with indicators based on industry collection of data on a daily basis while fishing, which will better delineate within-season trends (e.g., Claytor & Allard 2003).

An increase in OF in response to increased MLS is positive for lobster conservation. With the size structure simply shifting to the right, this corresponds to an increase in E/R and to total egg production given consistent recruitment. Demonstrating increased recruitment from increased egg production is another challenge. Increasing egg numbers can provide the basis for increased recruitment, but larval and juvenile survival must be favorable to translate higher egg numbers into higher numbers of recruits to the fishery. Lastly, MLS increases place more reliance on smaller, newly mature females for a higher percentage of population egg production, and this strategy might have risks (Plante et al. 2001). Consideration should be given to protecting large females where such regulations currently do not exist.

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