Relative abundances of spanner crabs and the development of a population model for managing the NSW spanner crab fishery

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OBJECTIVES:

(1) Provide fishery-independent estimates of the relative abundances of spanner crabs in NSW;
(2) Use the estimates obtained in (1) with similar estimates obtained in 1988-89 to analyse trends in relative abundances;
(3) Incorporate the information collected in (2) with existing data on the biology and fishery of spanner crabs to develop a population model for this fishery; and
(4) Use the model developed in (3) to provide appropriate advice to fisheries managers and industry on various input and output controls including the TACC.

KEYWORDS:

Spanner crabs, fishery-independent survey, biomass dynamics model, TACC.

NON-TECHNICAL SUMMARY:

In 1988-89, a multifactorial, stratified, randomized survey was done in the spanner crab (*Ranina ranina*) fishing grounds off the coast of New South Wales, Australia to determine fluctuations in relative distributions and abundances across a variety of spatial and temporal scales. This survey was repeated in 1997-98 to provide a new assessment of this stock and to provide fishery-independent data to develop a population model and TACC for the fishery.

The results from these surveys showed the marked sexual dimorphism of this species with males generally attaining larger sizes than females and a sex ratio that was slightly biased towards females. These results, in combination with the 93 mm minimum size limit, meant that: (i) 71-

73% of the population was undersize; (ii) male crabs comprised most of the portion of the population that was targeted by fishers; and (iii) approx. 96% of females were protected. These results imply that this fishery should be in a relatively sound position, ensuring long-term viability through the maintenance of a large spawning population.

Comparing catch rates from the two surveys revealed large variabilities in abundances across several of the spatial and temporal scales investigated. A consistent result was that catches of crabs (especially females) decreased during October and December each year in both repeats of the survey, co-inciding with the spawning period. In one location (Tallows Beach), however, such decreases did not occur, possibly indicating this site as the focus of a spawning migration at this time.

There were some results from the surveys that provide some evidence of the impact of fishing activity, including a significant 6% decrease in the relative abundances of all crabs over the 11 year period of the study, a 11% decline in the numbers of small male crabs (<93mm C.L.) and a 55% decline.

The fishery was modelled from 1984 to 1998 using an observation-error biomass dynamic model conditioned on catch and fitted to the survey results using non-linear optimisation. Confidence intervals for the parameter estimates were determined using bootstrap methods. The results suggested that the median exploitable biomass (with 10% and 90% quantiles) of the NSW stock had been reduced from 1,500 (760, 5,800) tonnes in April 1984 to 940 (400, 4,000) tonnes by December 1998. A risk analysis was completed to predict the effects of various harvest strategies on reference points of the fishery. This analysis indicated that an annual TACC of 290t should not cause any further reduction in the exploitable biomass of the NSW stock (with ≥ 90% confidence). A TACC of 300 t was recommended to the Spanner Crab Management Advisory Sub-Committee in 1999.

A preliminary analysis of the combined NSW and Queensland fisheries was also completed under the unlikely assumption that the data from the NSW survey also reflected relative abundances throughout Queensland. This indicated that a combined harvest of 2,300 tonnes will cause the exploitable biomass in five years to be similar to that now (with ≥ 50% confidence).

We conclude that the continued use of the fishery-independent survey described in this report will provide a powerful tool to monitor fluctuations in the population after changes in management - thus providing new information and, consequently, modified recommendations to management like adjustments to the TACC. Further, we also recommend that the geographic range of the survey be expanded to include the Queensland fishing grounds so that modelling and management of this fishery can incorporate the entire east coast stock.

1. BACKGROUND

The spanner crab (*Ranina ranina*) fishery of NSW is a relatively new fishery that has experienced significant exploitation since its beginning in the early 1980's. In recent years, the development of a live export market for this species led to increases in price and a consequent increase in fishing effort. A draft management plan for this fishery was prepared some time ago using information from industry and an earlier research project (FIRTA project no. 86/63) but its implementation was delayed so that it could incorporate changes required under the new NSW Fisheries Act. A review of the implementation of the new Act highlighted the spanner crab fishery as a candidate to become a share-managed fishery based on a combination of input and output controls, including a Total Allowable Commercial Catch (TACC). In addition, concerns about over-exploitation of spanner crabs around this time led to restricted entry to the commercial fishery. To ensure that the pending management plan for this fishery was developed with the best scientific information available, we needed to: (i) assess the current status of the stock by providing an objective estimate of exploitation and (ii) develop a population model with a view to recommending a TACC.

To provide information for setting and reviewing a TACC and other management strategies, ideally one would construct a population model based on as much information about the animal and its fishery as possible. Unfortunately, it is difficult to rely solely on fishery-dependent estimates of catch and effort due to inaccuracies in the data collected by fishers. This is particularly true of new fisheries where fishers are expected to show an increase in efficiency as the fishery develops. A better way to assess TACCs is to use fishery-independent estimates of the population in a model that incorporates such estimates with catch-effort data and other information. Fortunately, we already had a great deal of information about the biology of spanner crabs in NSW and its fishery as a result of the earlier project (see Kennelly, 1989; 1992; Kennelly and Craig, 1989; Kennelly et al., 1990; Kennelly and Watkins, 1994). Some of this information is in the form of an extensive catch-effort database on the fishery, growth and movement data from a large-scale tagging project, fecundity estimates and estimates of the mortality of discards. Most importantly, however, the earlier work provided good fishery-independent estimates of the relative abundances of spanner crabs during 1988 and 1989 when a stratified, randomized survey was done (for details see Kennelly, 1992). In 1996, we applied to FRDC to fund a repeat of this 2 year survey to provide independent estimates of the status of the stock in 1997-98 and to use this information to develop a population model for this fishery from which we could recommend an appropriate TACC. It was noted in that application that the existence of the earlier "baseline" dataset was rare for the fisheries of NSW and provided an ideal opportunity to establish a TACC-based fishery on a very solid foundation.

Spanner crabs are large marine brachyuran decapods found throughout the Indo-Pacific region (Barnard 1950). They are found in coastal waters in depths of 10 to 70 m on sandy substrata in which they bury (Skinner and Hill 1987). Populations of spanner crabs are exploited commercially using baited traps made of tangle-nets suspended over flat frames. Fisheries have developed in Hawaii, Japan, the Philippines, the Seychelles with by far the largest fishery occurring along the east coast of Australia. Despite a growing literature concerning the biology and fishery of this species (Brown, 1986, Brown et al., 1999, Fielding and Haley 1976, Tahil 1983, Skinner and Hill 1986, 1987, Kennelly 1989, 1992, Kennelly and Craig 1989, Kennelly et al. 1990. Kennelly and Watkins, 1994, Sumpton et al., 1995), several basic aspects of its biology and ecology remain unknown. Of particular importance to resource management, there have been few surveys of changes in the species' relative abundances throughout its fishing grounds. In the work described in this report, we used standardized baited traps in two repeats of a multi-factorial, stratified, randomized survey to estimate changes in relative abundances of spanner crabs across a broad spectrum of spatial and temporal scales, encompassing over a decade of time and the main geographical range of the fishery in NSW.

2. NEED

The possible management of the NSW spanner crab fishery as a TACC-based fishery meant that NSW Fisheries would need to provide recommendations for the setting and/or adjusting of a TACC and other input and output controls. The availability of the data gathered from the survey done in the late 1980's provided a baseline which, together with the repeat of the survey completed in this current project, provided the information necessary to build (at a relatively low cost) a simple population model for this fishery. Such a model allows us to provide fisheries managers and industry with advice on TACCs and other management initiatives and so permits the management of this fishery on a scientifically rigorous and cost-effective basis.

3. OBJECTIVES

The specific objectives of this study were:

(1) Provide fishery-independent estimates of the relative abundances of spanner crabs in NSW;
(2) Use the estimates obtained in (1) with similar estimates obtained in 1988-89 to analyse trends in relative abundances;
(3) Incorporate the information collected in (2) with existing data on the biology and fishery of spanner crabs to develop a population model for this fishery; and
(4) Use the model developed in (3) to provide appropriate advice to fisheries managers and industry on various input and output controls including the TACC.

4. METHODS

This project involved: (i) a repeat (in 1997-98) of the stratified randomized survey that was first done in 1988-89; (ii) modelling the fishery using the survey data and catch statistics; and (iii) an analysis of previously collected tag-recapture data to determine rates of growth.

4.1. Survey

This study was done off the north coast of NSW, Australia (Fig. 1). To obtain estimates of relative abundances, we used modifications of commercial fishing methods deployed from chartered commercial fishing vessels (6 m twin-hull boats). Traps were square frames 1.2 x 1.2 m and made of mild steel with 85 mm, 4-ply net doubly hung over each frame with a standard 230 mm fall in the net. This type of trap was found to catch the maximum number and widest size-range of spanner crabs (Kennelly and Craig 1989). One bait (fish-skeleton) was placed in the middle of each trap (the type of fish used was found to be unimportant - Kennelly and Craig 1989). Replicate traps were set out 60 m apart along trot-lines placed cross-current on the substratum in the area or depth to be sampled (60 m is the distance at which neighbouring traps are known to be independent - Kennelly and Craig 1989). These sets of traps were left for a minimum soak-time of 60 mins during which all susceptible crabs in the vicinity were attracted to the bait odour and became entangled on the net (Kennelly 1989). When traps were hauled, crabs were disentangled, counted, measured (posterior edge of the eye-orbit to the posterior edge of the carapace), sexed and returned to the sea.

The survey design involved sampling 5 traps from each of 3 replicate, randomly-located sets at each of 3 depths (22, 40 and 58 m) at 5 locations throughout the main NSW fishing grounds (total of 225 traps). Three sets of 5 traps were found to be the optimal levels of replication for a given depth and location from cost-benefit analyses of a pilot survey (Kennelly 1989) which took account of (i) different variances among replicate traps and replicate sets of traps and (ii) the limited time available to sample a given location and depth at sea. The 5 locations sampled were offshore from Kingscliff, Pottsville, Tallows Beach, Sand Point and Riordan's Shoal and the depths were selected to encompass the range of depths fished by the commercial fleet (see Fig. 1). This survey was done every 2 months for 2 consecutive years in 1988-89 and again in 1997-98.

For each trap, we determined the total number of crabs caught, the numbers of males and females, the number of crabs that were >93 mm (those above the marketable size-limit) and the number of undersize crabs (<93 mm). Each of these 5 sets of data was tested for homogeneity of variances (Cochran's test) and analysed in the relevant 6-factor analysis of variance (ANOVA) which examined all spatial and temporal scales covered during both repeats of the survey. That is, 2 complete repeats (in 1988-89 and 1997-98) of 2 years of 6 bi-monthly periods sampled at each of 5 locations (spaced 16 to 31 kms apart), 3 depths (from 22 to 58 m), 3 sets (set 0.5 to 1 km apart) and 5 traps (set 60 m apart). Student-Newman-Keuls multiple comparisons (SNK-tests) were used to isolate differences among means for significant high-order interactions.

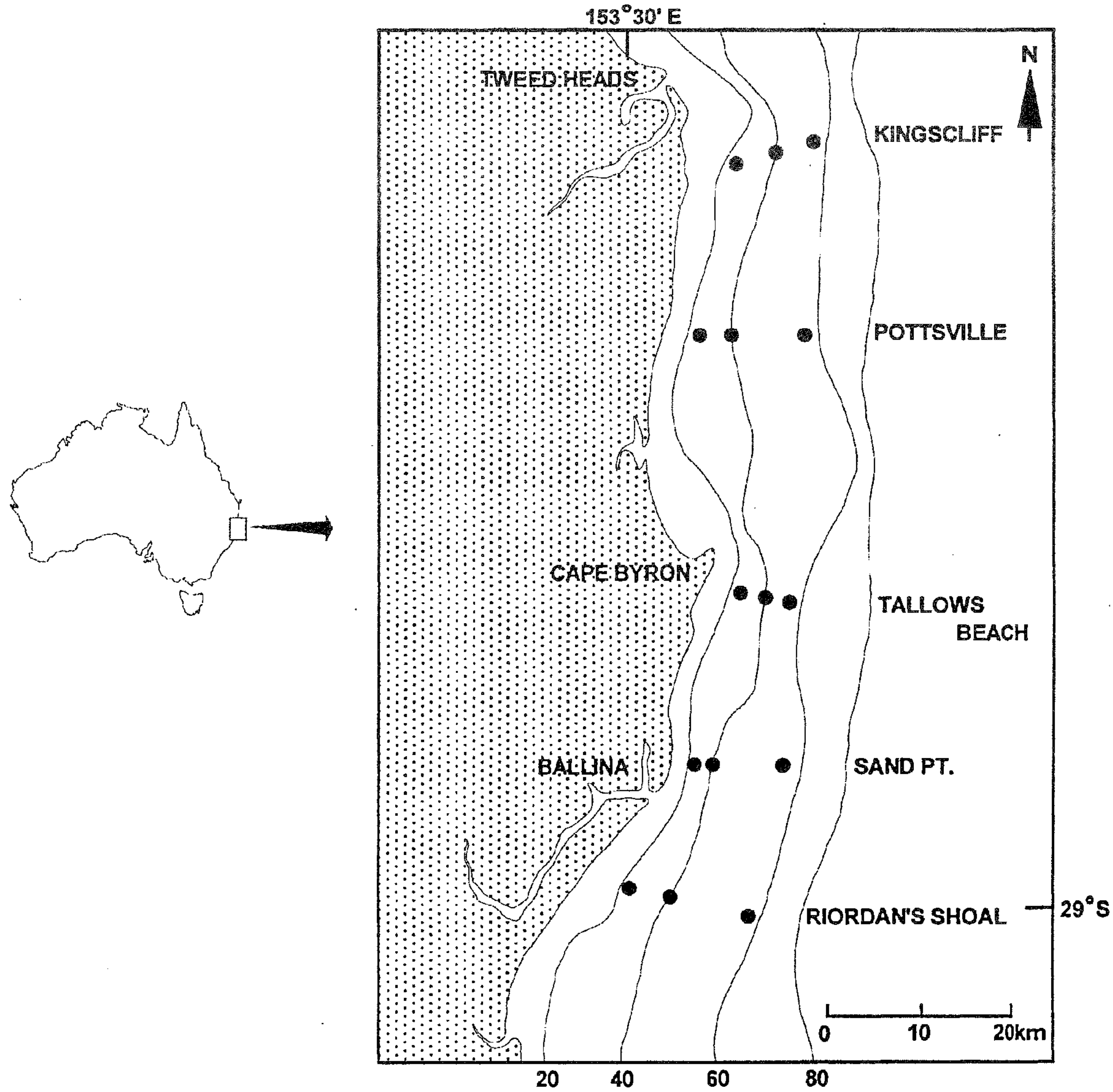

Figure 1. Map showing the 5 locations and 3 depths which were sampled in the survey. Depth contours are in metres.

4.2. Population modelling

A biomass dynamic model was used to represent the NSW spanner crab fishery. These types of models are the simplest representations of stock dynamics and deliberately confound individual growth and recruitment within the single growth parameter *r*. Certain data were available that could suggest a length-structured model as the best strategy to represent this stock (e.g. the crab lengths presented in this study and growth data from Chen and Kennelly, 1999's tagging study). However, the attraction towards these complex models (that are more realistic to the biologist's eye) must be balanced by an appreciation of their appetite for information. For example, little is known about stock-recruitment relationships and the length-structure of recruits into the population. Such patterns would have to be assumed in developing a length-structured model. Complex models may appear to make more use of available biological data but often require just as many, or more, assumptions as simpler models. Population modelling should be an incremental process: i.e. start simply and then build more complex models as demand dictates. We believe that the first iteration of an assessment model should put parsimony above biological detail and this was the strategy followed here. Ludwig and Walters (1985) wrote the seminal paper that illustrated the fallacy of assuming that more complex models always give better results. These authors showed that age-structured models are not necessarily the most appropriate methods for estimating optimal effort (also see Schnute and Richards, 1995 and Burnham and Anderson, 1998).

Estimating a sustainable rate of harvest for a species involves three distinct components: (a) the underlying data; (b) a dynamic model of the system; and (c) a risk analysis of alternative harvesting strategies.

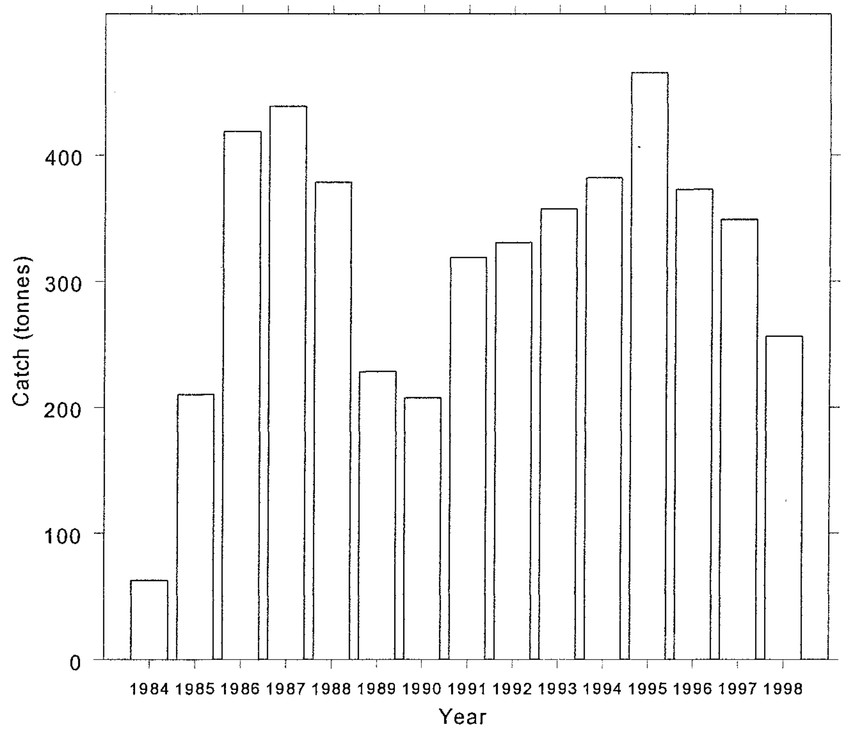

Figure 2. Time series of the NSW commercial spanner crab catches from 1984 to 1998 (calendar years).

4.2.1. The underlying data

Two sources of data were used in this analysis: the commercial catch history of the NSW spanner crab fishery; and the fishery-independent surveys done in 1988-89 and 1997-98.

Commercial catch statistics were obtained from the NSW Fisheries Form 49 and LCATCH databases which contain information on landings and effort as reported by all commercial fishers in NSW each month. Total catches were aggregated into bimonthly periods (January-February, March-April, etc.) from July-August, 1984 (when the fishery began in NSW) to November-December, 1998, giving a total of 87 records. Bimonthly aggregates were used to be consistent with the time periods used in the independent surveys. The commercial catch history of spanner crabs in NSW is presented in Figs. 2 and 3, and is also tabulated in Appendix 1.

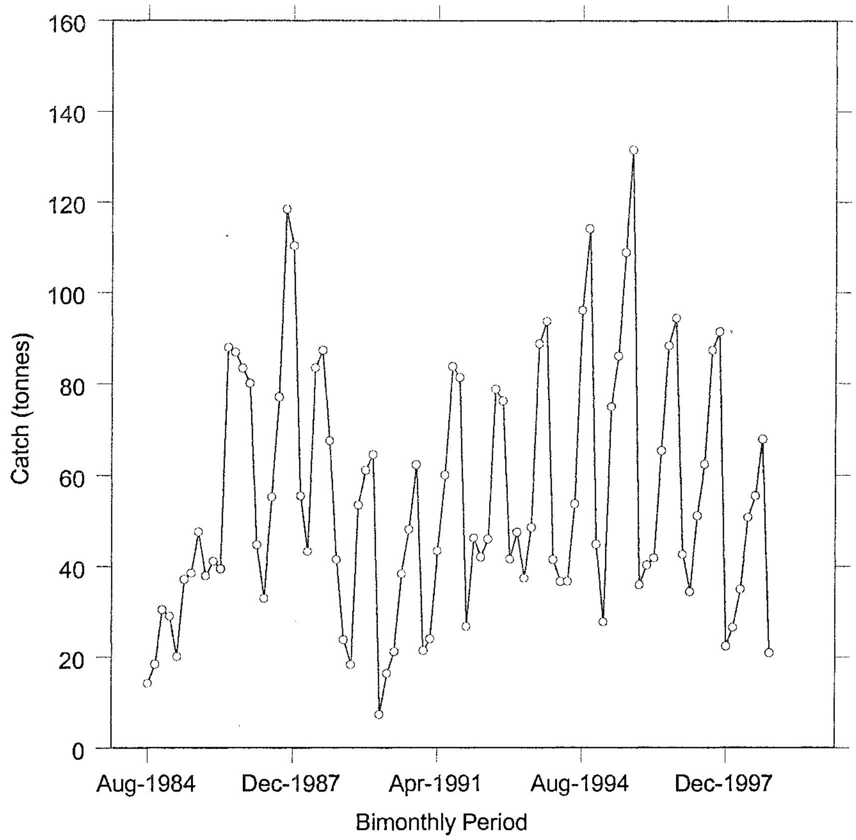

Figure 3. Time series of the NSW commercial spanner crab catches summed by bimonthly period (Jan-Feb, Mar-Apr, May-Jun, Jul-Aug, Sep-Oct, Nov-Dec).

Fishery-independent estimates of abundance were available from the 2 repeats of the survey. The average catch rates of legally sized crabs for each time period were calculated and are presented in Fig. 4. These indices of relative abundance were used to calibrate the model (which generated estimated catch rates) to the observed catch rates.

4.2.2. Model of the System Dynamics

The model implemented was a simple modification of an observation error biomass dynamic model (Hilborn and Walters 1992; Hilborn and Mangel 1997) with two extensions: (i) the timestep of the model was bimonthly (January-February, March-April, May-June, July-August, September-October, November-December) instead of the usual annual timestep; and (ii) a periodic catchability function was used to relate exploitable biomass to estimated catch rates. The indices of abundance used to calibrate the model were the fishery-independent catch rates (of legal-sized crabs per trap-lift).

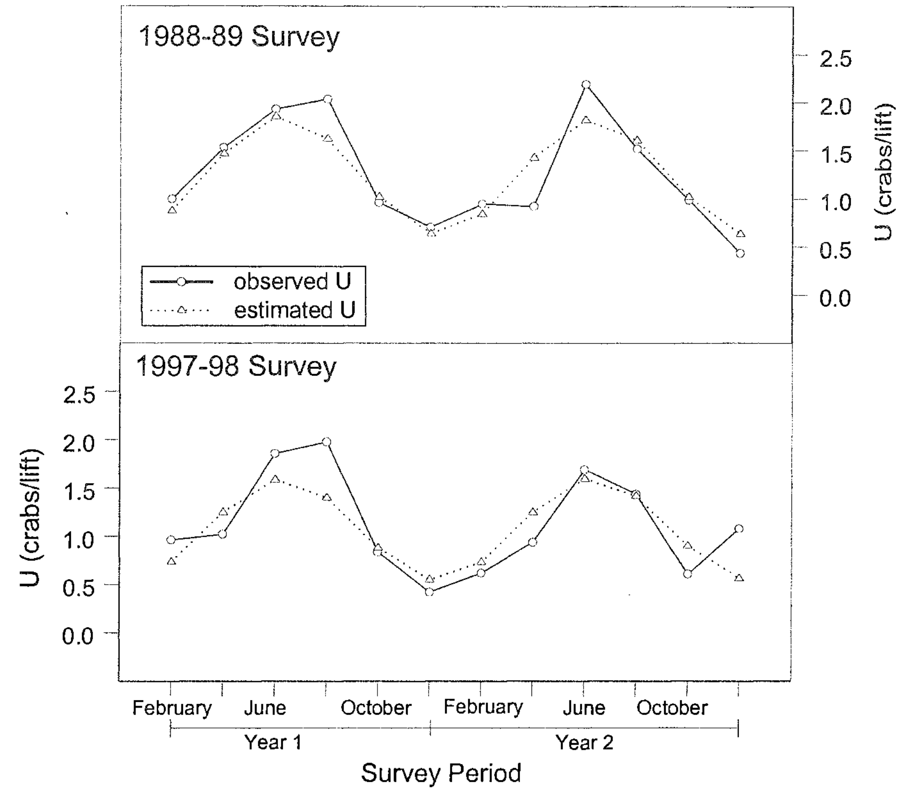

Figure 4. Comparison of the observed and estimated catch rates (U_{obs} and U_{est} measured in crabs/lift) for the two NSW spanner crabs surveys. Surveys were completed every two months (February, March, June, August, October and December) in 1988, 1989, 1997 and 1998.

The exploitable biomass at timestep *t+1* was related to the exploitable biomass at time *t* with:

$$B_{t+1} = B_t + r \cdot B_t \cdot \left(1 - \frac{B_t}{B_0}\right) - C_t$$

Where B_t represents the exploitable biomass (hereafter just the biomass) at the end of time t, B_0 the initial unexploited biomass, r the bimonthly growth rate of the biomass, and C_t the catch in tonnes during time period t.

The estimated survey catch rate during t (U_t^{est}) is related to the biomass at the end of time t with:

$$U_t^{est} = \left[q_0 + q_1 \cdot \cos\left(\frac{2\pi \cdot t}{6} + q_2\right)\right] \cdot B_t$$

In this equation q_0, q_1 and q_2 are the mean, deviation amplitude and phase shift of the periodic catchability function respectively. This simple cyclic function has a period of 6 time steps in a single year, reflecting the observable annual cycle in catch rates (see Fig. 4).

It was assumed that the distribution of errors around the observations was lognormal. Hence the following equation was used to measure the sum-of-squared (*ssq*) residuals between the estimated and observed catch rate.

$$ssq = \sum_{t=1988-Feb}^{1989-Dec}\left[\ln(U_t^{obs}) - \ln(U_t^{est})\right]^2 + \sum_{t=1997-Feb}^{1998-Dec}\left[\ln(U_t^{obs}) - \ln(U_t^{est})\right]^2$$

The model was calibrated to the observed catch rates by estimating the parameters r, B_0, q_0, q_1 and q_2 using non-linear optimisation – i.e. estimating the values of these parameters that minimise the sums-of-squares above. The Hooke-Jeeves optimisation algorithm (Kaupe, 1963) was used for this purpose with a step-size parameter value of 0.8.

Variation around the parameter estimates was simulated using a simple residual bootstrap method. Log deviations of the best model fit were stored in vector ***e***, where:

$$e_i = \ln(U_i^{obs}) - \ln(U_i^{est})$$

The index i ranged from February, 1988 to December, 1998 and re-sampling was done on the pooled sets of residuals and not on the first and second survey datasets independently. The e_i were uniformly re-sampled with replacement to generate a new time series of catch rates using:

$$U_t^{obs*} = U_t^{est} \cdot \exp(e_i)$$

Where U_t^{est} is the estimated catch rate of the best-fitting time series. These resampled time series were re-generated 1000 times and the model re-fitted. Resultant frequency distributions of the optimal parameter values were used to estimate the confidence intervals for each estimated parameter.

4.2.3. *Risk Analysis of Alternative Harvest Strategies*

Risk analysis of alternative harvest strategies provided an estimate of the impact of various TACCs on defined reference points for the fishery (see Table 4 for the reference points used). This analysis was a simple extension to the re-sampling scheme described above to estimate the variability of the parameter estimates. For each fitted parameter set (1001 in total, including the original fitted parameter values), the biomass simulation was extended for an additional 60 time periods (or 10 years). During that extension, a simulated catch of one sixth of the total allowable catch was removed from the exploitable biomass at each bimonthly step. After each simulation was complete, the reference points were re-calculated. The model simulated TACC values from 0t to 500t per year in steps of 25t, providing an informative response surface of the reference points (and their variability) over a range of harvest policies.

4.3. Tag-recapture data

Estimating the growth of individual spanner crabs is valuable in estimating stock productivity and completing yield-per-recruit analyses. We therefore decided to examine the tag-recapture data obtained during the previous project. All details from this work, including estimates of rates of growth, are provided in the attached paper (Chen and Kennelly, 1999). In summary, we found that size-increments per moult tended to increase with the pre-moult sizes, indicating that larger crabs grew more in a moult than smaller crabs. However, small crabs moulted more often than large crabs. The growth curve developed in this work provided reasonably slow rates of growth but was not applicable to crabs less than 66 to 69 mm CL.

We outlined above why we did not use this information about individual growth in the population model. Should it appear that a second, and more costly, population model of spanner crabs be required then a fully length-structured model will be prepared. At present such an investment is not justified.

5. RESULTS

5.1. Survey

The sizes of crabs caught during the repeats of the survey showed the well-known sexual dimorphism of spanner crabs, with males generally attaining larger sizes than females (Fig. 5). Of all crabs caught, 44.9% and 48.5% were male in 1988-89 and 1997-98 respectively (see also Table 2), indicating a slight bias towards females in the sex ratio of this population. Most of the crabs caught during the 2 repeats (71.6% and 73%, respectively) were smaller than the legal minimum size with 96.3% and 96.2% of females undersize, respectively. In general, the size-structures of the populations measured during the 2 repeats appeared to be similar (Fig. 5), although Kolmogorov-Smirnov tests revealed statistically significant differences between them. Fig. 5 shows that, for males, such differences were caused by 10.97% more smaller crabs (<93mm) and 55.21% less larger crabs (>108mm) being caught in 1997-98 than in 1988-89. For females, there was more of a general increase in size between the surveys.

Table 1 summarizes the 6-factor ANOVAS of the five sets of data examined from the surveys. For all variables, there were highly significant 2- and 3-factor interactions involving period, location and depth, indicating that abundances of all categories of spanner crabs differed depending on the particular location, depth and period in question. There were few significant interactions involving repeat and year indicating that abundances of all categories of spanner crabs were consistent in different years and within each repeat of the survey, despite the above fluctuations among locations, depths and periods. An exception was the significant difference in the repeat x location interaction for the total number of crabs, males, legal-sized and undersize crabs, which indicates that the changes in abundances of these variables between repeats of the survey depended on the particular location in question. These patterns are seen in more detail in Figs. 6, 7, 9 and 10 below.

The apparent temporal stability in abundances of spanner crabs at the largest time scales examined (repeats of the survey and years) was consistent for all variables examined except for a significant difference ($p<0.05$) for the total number of crabs between each repeat of the survey. This main effect quantifies increases or decreases in abundances of this species between 1988-89 and 1997-98 (the longest time-scale examined) and indicates that the 6.14% decrease detected in the total number of crabs between repeats (Table 2) was a statistically significant decline. In addition to this decrease, Table 2 also showed decreases in the numbers of females (12.27%), legal sized (10.86%) and undersize crabs (4.26%), although the ANOVA results (Table 1) indicated that these were not statistically significant.

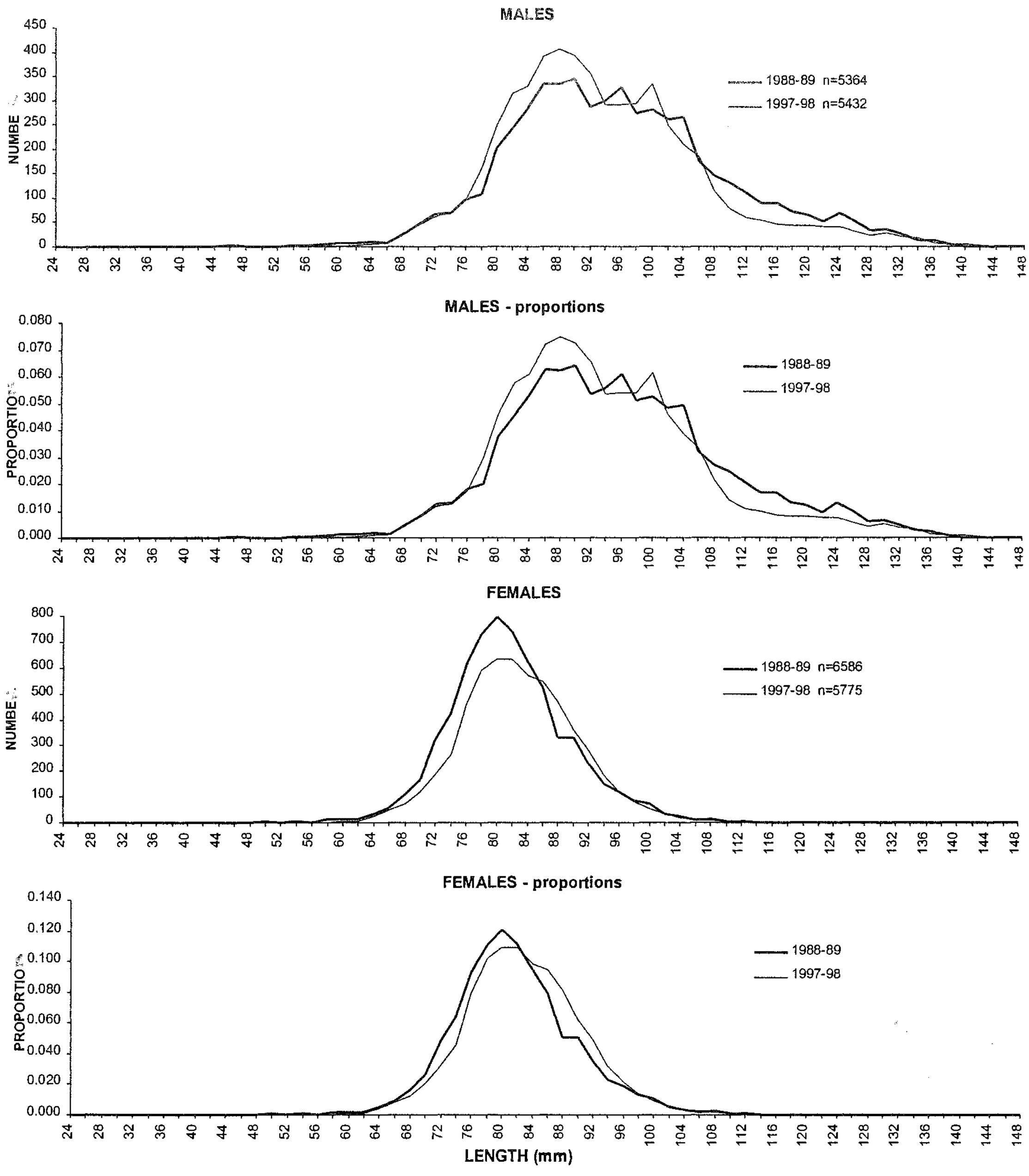

Figure 5. Size-frequencies of male and female spanner crabs sampled during both repeats of the survey.

Table 1. Summaries of the 6 factor analyses of variance for the 5 sets of data. *** denotes sig. p<0.001, **sig. p<0.01, *sig. p<0.05, ns non-significant.

Source	df	Total no. of crabs		Males		Females		Legal		Undersize	
		F		F		F		F		F	
Repeat	1	28.83	*	0.01	ns	1.26	ns	2.07	ns	1.99	ns
Year	2	0.00	ns	0.43	ns	0.15	ns	0.18	ns	0.02	ns
Period	20	66.10	***	30.37	***	71.06	***	27.29	***	63.37	***
Location	4	130.33	***	57.97	***	91.51	***	26.57	***	101.83	***
Repeat x Location	4	10.45	**	13.15	**	1.83	ns	5.47	*	6.22	*
Year x Location	8	0.18	ns	0.39	ns	0.22	ns	0.60	ns	0.23	ns
Period x Location	80	27.71	***	15.85	***	31.79	***	7.94	***	30.15	***
Depth	2	13.86	*	11.10	*	11.26	*	22.25	**	10.23	*
Repeat x Depth	2	0.82	ns	1.32	ns	0.25	ns	0.36	ns	1.00	ns
Year x Depth	4	0.97	ns	1.35	ns	0.77	ns	1.03	ns	0.91	ns
Period x Depth	40	11.62	***	9.14	***	8.53	***	7.29	***	9.72	***
Location x Depth	8	8.90	***	3.14	*	9.67	***	1.13	ns	11.97	***
Repeat x Location x Depth	8	1.45	ns	2.02	ns	0.93	ns	0.95	ns	1.97	ns
Year x Location x Depth	16	0.76	ns	1.11	ns	0.70	ns	1.26	ns	0.71	ns
Period x Location x Depth	160	7.47	***	7.79	***	5.83	***	5.85	***	6.65	***
Set	720	2.42	***	1.75	***	2.71	***	1.47	***	2.31	***
Residual	4236										
Total	5315										

Table 2. Mean (SE) catch rate of the total number of crabs, males, females, legal and undersize crabs during the 2 surveys. Also given is the percentage change between the 1988-89 and 1997-98 repeats for each variable.

	Mean catch rate (crabs per trap)		% of the sampled population	% change between surveys
Total no. of crabs				
1988-89	4.49	(0.12)		-6.14
1997-98	4.22	(0.12)		
Males				
1988-89	2.02	(0.06)	44.9	1.34
1997-98	2.04	(0.06)	48.5	
Females				
1988-89	2.48	(0.09)	55.1	-12.27
1997-98	2.17	(0.08)	51.5	
Legal				
1988-89	1.28	(0.04)	28.4	-10.88
1997-98	1.14	(0.04)	27.0	
Undersize				
1988-89	3.22	(0.10)	71.6	-4.26
1997-98	3.08	(0.10)	73.0	

Figs. 6 - 10 are graphs of the means from the 2 repeats of the survey for each location, depth and period for the 5 variables. Not surprisingly, SNK-tests of the 360 means compared for each variable revealed few consistent differences. Despite this, several trends are apparent in these figures.

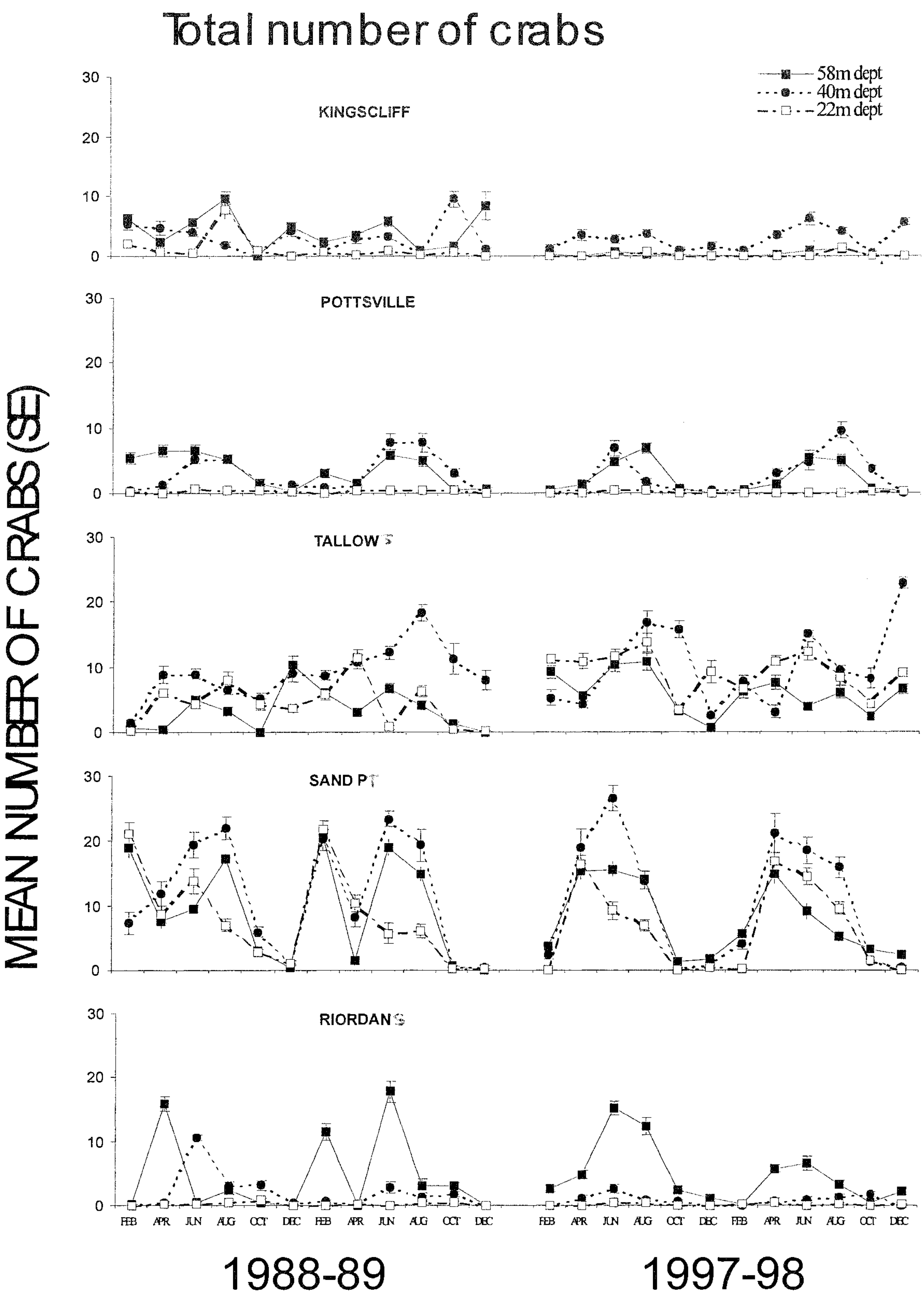

Figure 6. Fluctuations in the mean catch rate (± SE) of spanner crabs during both repeats of the survey at each location and depth (n = 15).

Firstly, more spanner crabs were caught off Sand Point than any other location, with Tallows Beach recording the next largest abundances and, at certain times, large numbers of crabs were caught in the deep site off Riordan's Shoal (Fig. 6). There were small numbers of crabs caught in the shallow depth off Kingscliff, Pottsville and Riordan's Shoal. In general there were much smaller numbers of crabs recorded in October and December each year compared to other times at most locations except Tallows Beach. Patterns between repeats of the survey were similar, although it appeared that during the 1997-98 survey, less crabs were caught in the deepest site off Kingscliff.

Fig. 7 shows that the relative abundances of male crabs were greatest off Sand Point at most times except October and December each year. Abundances were also large in the mid-depth site off Tallows Beach at most times. There were large numbers of males recorded at certain times off Kingscliff, Pottsville and Riordan's Shoal in the deep and middle depths in 1988-89, but few males were caught in the deep site off Kingscliff in 1997-98.

Fig. 8 shows that the relative abundances of female crabs were consistently small off Kingscliff and Pottsville during both surveys. Larger numbers occurred at the deep site off Riordan's Shoal at certain times. Tallows Beach had large numbers of females in the shallow and middle depth at certain times but by far the largest numbers of females occurred off Sand Point in most depths at most times except in October and December each year. This decline in abundances of females in October and December was also seen for the few females caught off Pottsville, Riordan's Shoal and Tallows Beach.

Fig. 9 shows that the relative abundances of legal-sized crabs were greatest off Sand Point and Tallows Beach in all depths at most times except in October and December each year off Sand Point. Such a decline at these times was not evident off Tallows Beach. Numbers of legal crabs fell slightly in 1997-98 off Sand Point but increased a little off Tallows Beach. Large catches occurred off Kingscliff in the middle and deep sites during the 1988-89 survey but fell sharply in the deep site during the second survey. Consistent catches of males were recorded off Pottsville throughout both surveys in the deep and middle depths except in October and December each year. Riordan's Shoal recorded large catches of males at certain times in the middle and deep sites but these were reduced in 1997-98. Because a large proportion of legal-sized crabs were male (see Fig. 5), many of the trends in their abundances were similar to those seen above for male crabs (Fig. 7).

Fig. 10 shows that fewer undersize crabs were caught off Kingscliff during 1997-98. The small number of undersize crabs occurring off Pottsville in deep and middle depths was consistent during the 2 surveys with the lack of crabs in October and December apparent. Large numbers of undersize crabs were recorded in all depths off Sand Point during all periods except October - December each year. Large numbers were also caught off Riordan's Shoal in deep water at certain times (again with low numbers in October and December) and off Tallows Beach at all times, particularly in the middle and shallow depths. Because a large proportion of undersized crabs were female (see Fig. 5), trends in their abundances were similar to those seen above for female crabs (Fig. 8).

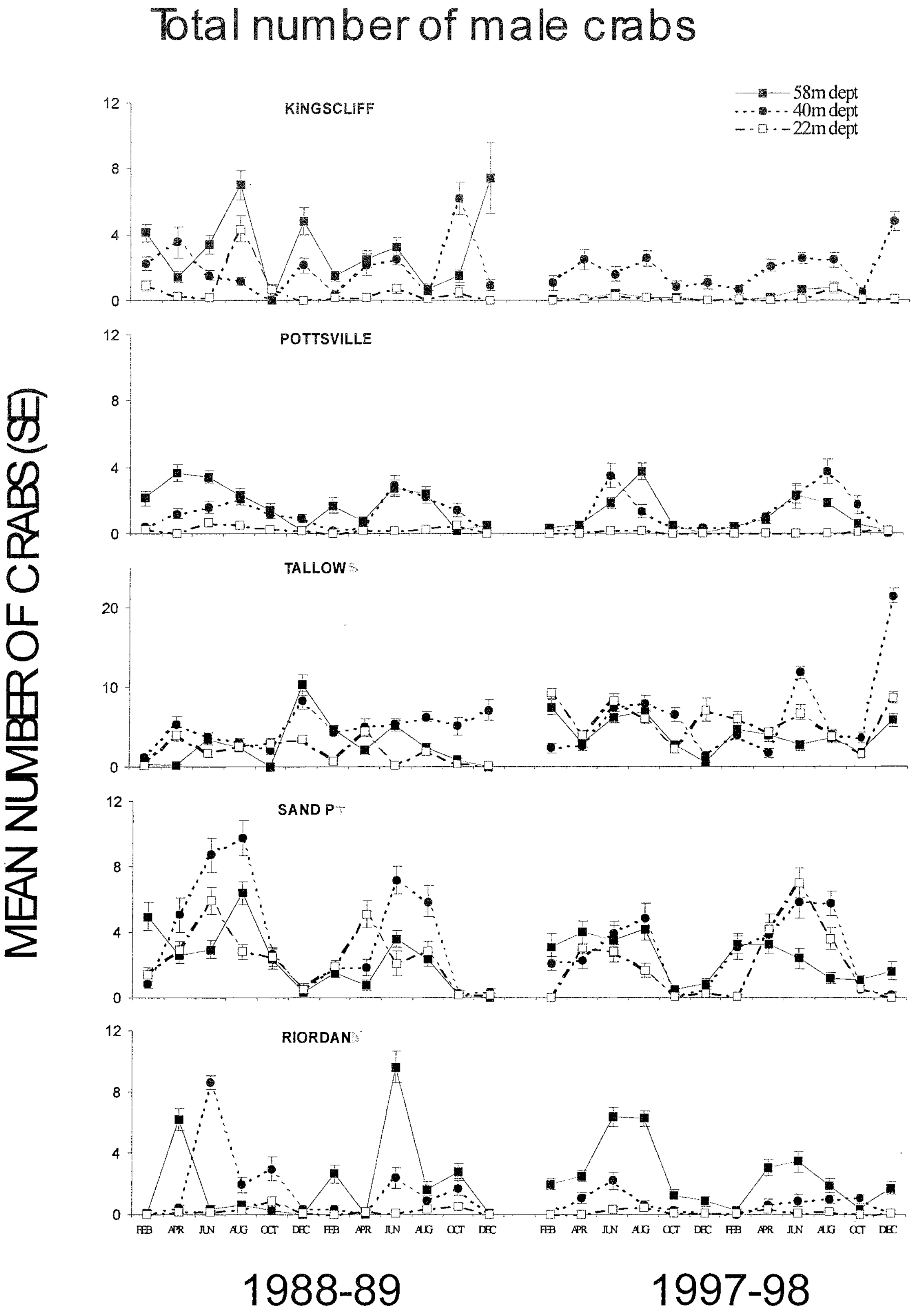

Figure 7. Fluctuations in the mean catch rate (± SE) of male spanner crabs during both repeats of the survey at each location and depth (n = 15).

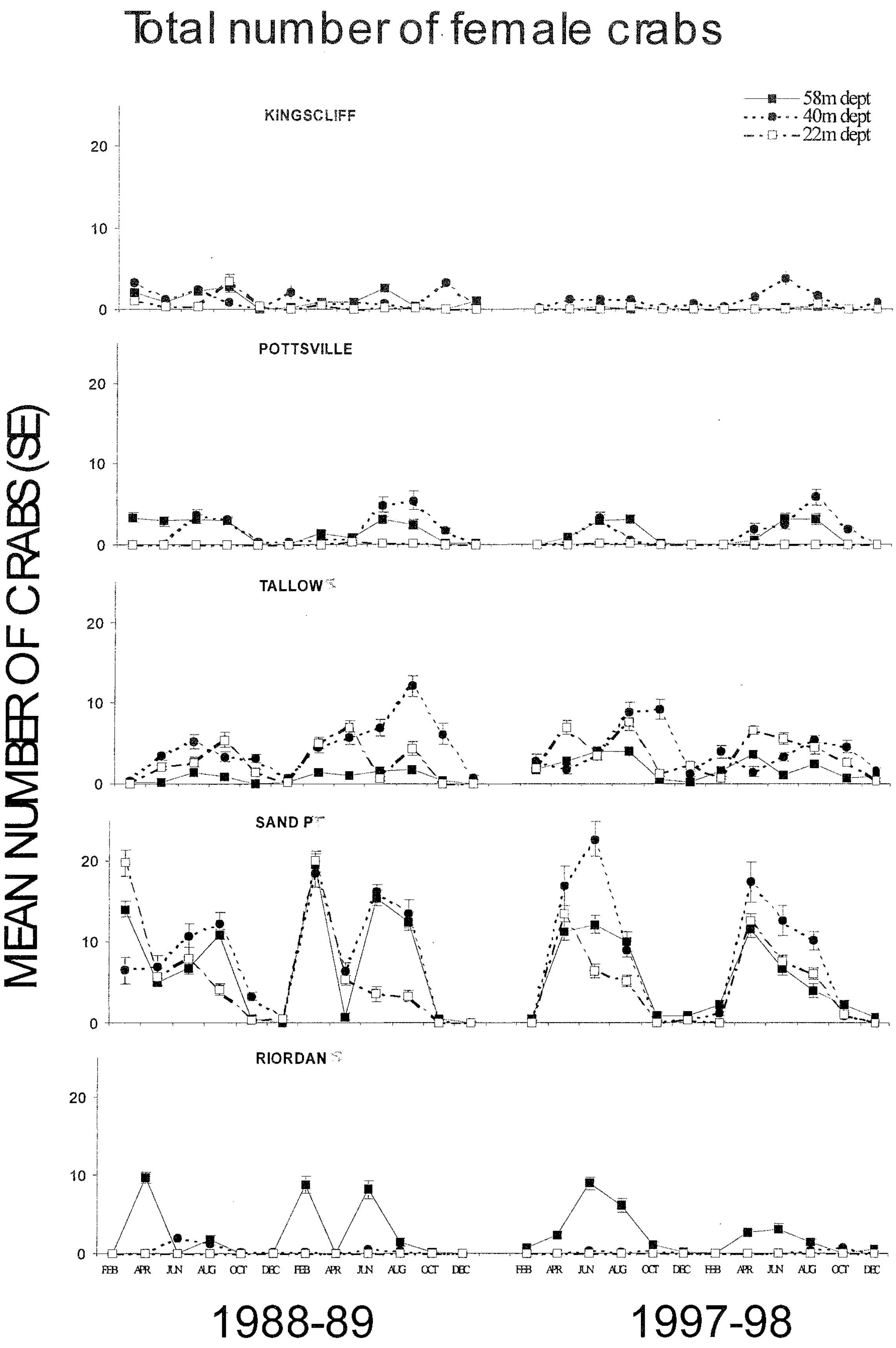

Figure 8. Fluctuations in the mean catch rate ($\pm$ SE) of female spanner crabs during both repeats of the survey at each location and depth (n = 15).

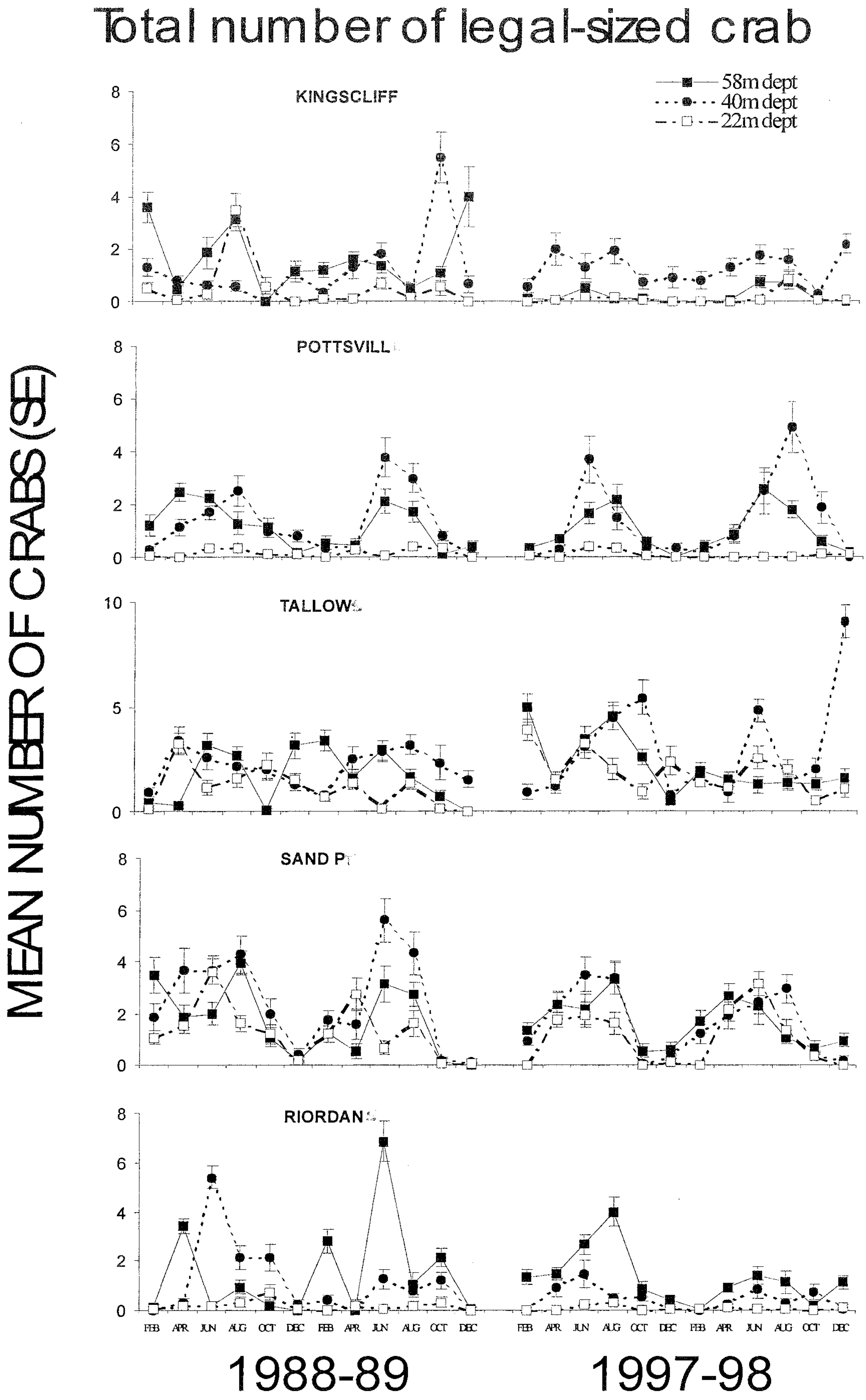

Figure 9. Fluctuations in the mean catch rate (± SE) of legal-sized spanner crabs during both repeats of the survey at each location and depth (n = 15).

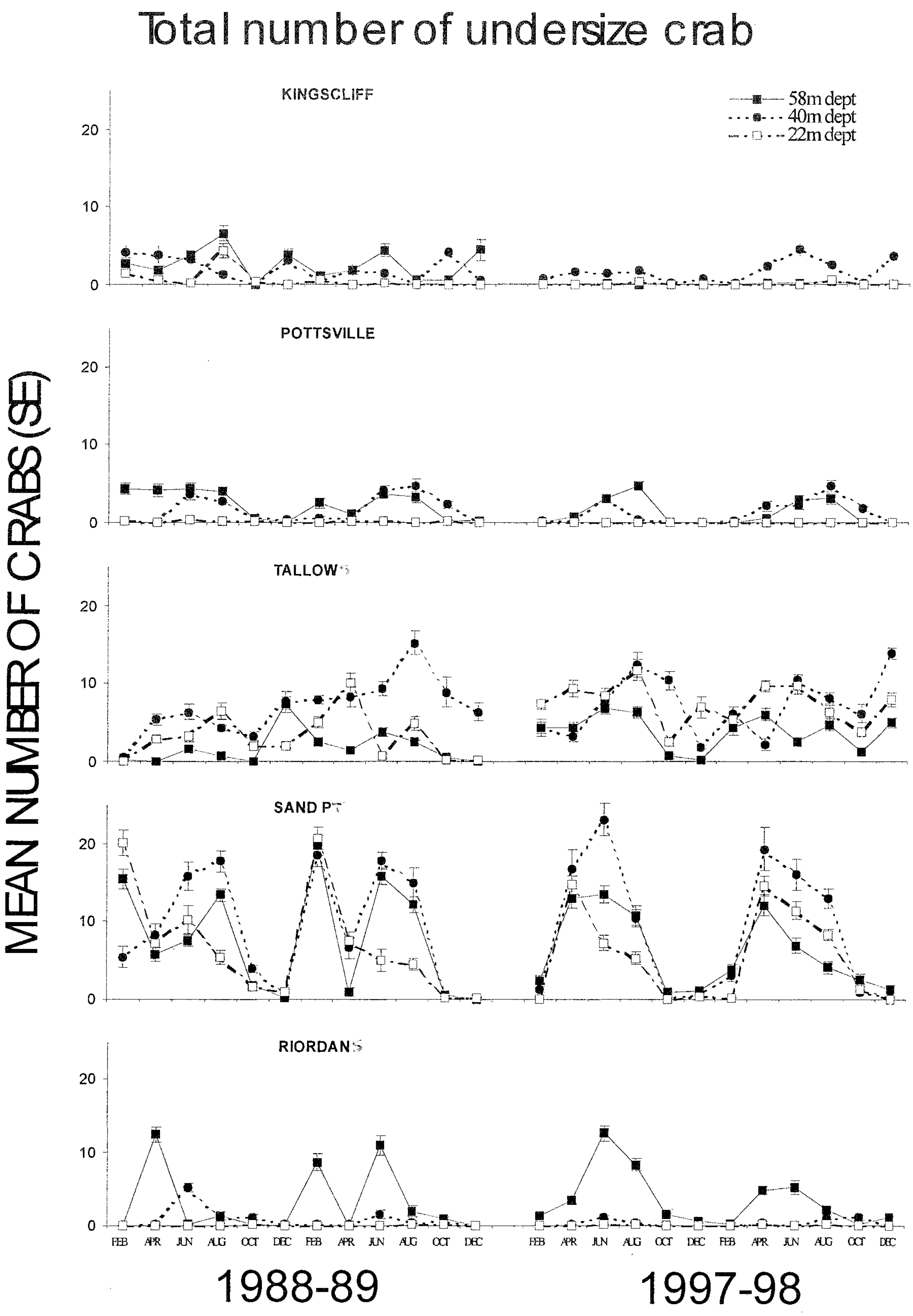

Figure 10. Fluctuations in the mean catch rate (± SE) of undersize spanner crabs during both repeats of the survey at each location and depth (n = 15).

5.2. Population modelling

5.2.1. Testing

The initial analysis tested the optimisation algorithm. Observed catch rates were generated from the model with a defined error structure. The model was then fitted to this simulated data to ensure that the optimisation algorithm could faithfully find optimal parameter values with a known solution. Using a lognormal observation error with a co-efficient of variation (CV) of 5%, the model had no difficulty finding the generated parameter values. Beyond a CV of 10%, however, the optimisation algorithm started to show undesirable dependencies on the initial starting points and convergence to the bounds of parameter domains. We were satisfied that our computer programs were working correctly but acknowledge that this model cannot deal with datasets where the signal to noise ratio is low.

5.2.2. Estimated Parameters

The model was calibrated to the observed catch rates and Table 3 shows the initial values used for the search algorithm and the boundaries imposed on the parameter search space. Fig. 4 illustrates the extent to which the model regenerated the observed patterns. Our assumption that the temporal variation in catch rates had a period of one year was confirmed. The optimisation processes estimated parameter values that matched the displacement, phase and amplitude of the sinusoidal catchability function - with the pattern particularly well-matched for catch rates from the second repeat of the survey. Fig. 11 is a quantile-quantile plot of the log deviations. These points would be expected to fall in a straight line if the assumptions about the distribution of errors were correct. Estimated parameter values are presented in Table 5. Table 5 also includes the values of reference points *msy* and B_{now} as these are independent of future harvest strategies (see also Table 4).

Table 3. Summary of the estimated parameters. Table includes the initial starting point for the non-linear optimisation and the upper and lower bounds for each fitted parameter.

Parameter	Initial Value	Minimum Value	Maximum Value
q_0	0.001	0.00	0.1
q_1	0.005	0.00	1.0
q_2	1.57	0.00	3.14
B_0	1000	10	50000
r	0.1	0.001	2.0

Table 4. Description of the reference points used to evaluate the impact of total allowable commercial catches on the NSW spanner crab fishery.

Symbol	Description
msy	Annual "Maximum sustainable yield" which was calculated using $\frac{6 \cdot r \cdot B_0}{4}$. The multiplier 6 makes an approximate adjustment from a bimonthly *msy* to an annual *msy*.
B_{f5}	Estimated exploitable biomass in five years (or 30 time periods) from the most recent available catch records. In this case December 2003.
B_{f10}	Estimated exploitable biomass in ten years (or 60 time periods) from the most recent available catch records. In this case December 2008.
B_{f5}:B_0	Ratio of the estimated exploitable biomass in five years to the estimated virgin exploitable biomass.
B_{f5}:B_{now}	Ratio of the estimated exploitable biomass in five years to the estimated present (as at December 1998) exploitable biomass.
$P_{collapse}$	The proportion (or probability) of exploitable stock collapse. Calculated by counting the proportion of simulations where $B_{f5}:B_0 \leq 1\%$

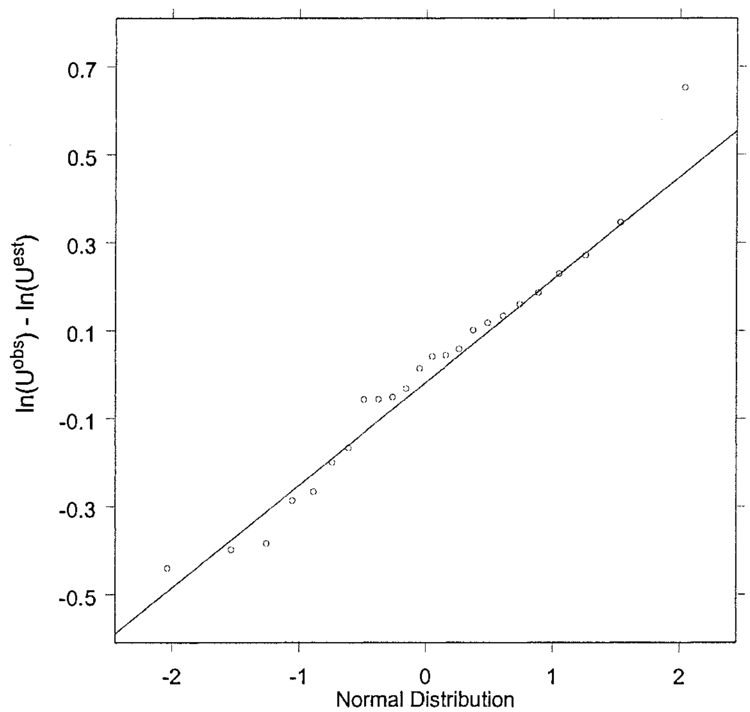

Figure 11. Quantile-quantile plot of the estimation errors (differences between the log of observed and log of estimated catch rates) from the model fit. The assumption that the error structure of the model is lognormal is supported by this figure.

Table 5. Summary of the estimated parameter values and associated uncertainties. The table also includes a similar summary of the reference points that are independent on the total allowable commercial catch (*msy* and B_{now}).

Parameter	Estimate	5% quantile	10% quantile	25% quantile	50% quantile	75% quantile	90% quantile	95% quantile
q_0	0.000 4	0.000 2	0.000 3	0.000 5	0.001 2	0.002 2	0.003 0	0.003 6
q_1	0.000 2	0.000 1	0.000 1	0.000 2	0.000 6	0.001 0	0.001 4	0.001 7
q_2	0.88	0.66	0.71	0.79	0.90	1.00	1.09	1.15
B_0	3 841	659	765	1 000	1 540	3 242	5 795	7 772
r	0.07	0.03	0.04	0.08	0.16	0.25	0.33	0.39
B_{now}	2 674	354	416	549	937	2 148	4 070	5 483
msy	391	297	324	347	365	387	451	530

Table 5 also presents initial estimates of the bimonthly growth rate and the exploitable biomass at the beginning of the fishery. A bimonthly growth rate of 0.07 corresponds approximately to an annual growth rate of the biomass of 0.42, which would imply that the exploitable biomass doubles every two to three years. The initial biomass estimate of the stock is 3,841 tonnes. These figures are not unreasonable given the harvesting of between 300 and 400 tonnes per year (or about 10% of the estimated unexploited biomass).

An apparent problem arises because the r, q_0 and the B_0 are extremely correlated in this model (discussed in more detail below). After extensive exploration with initial starting values and two different optimisation procedures, we were satisfied that the parameter estimates calculated above represented the best fit of the model to the data. Note, however, that the key reference points for fisheries managers such as *msy* and ratios of biomass estimates have much less dependence on the actual values of r, q_0 and B_0.

5.2.3. *Variation in Parameters*

Using the scheme outlined in the Methods section, we calculated the quantiles of estimated parameter values from the generated datasets. Two simple modifications to the procedure were required before this could be completed. First, if the model could not be fitted to a generated dataset because of convergence failure or convergence to a boundary, another dataset was generated and the fitting algorithm re-applied. Failure to fit the model to a generated dataset was a common phenomenon with the acceptance rate only 71.3%. After 1,000 "acceptable" estimates were obtained, the results were graphically evaluated but about 20% of these solutions still had unusable results. These were essentially unrealistic combinations of very high r, B_0 and q_0 resulting in uninterpretable estimates of the parameter values (e.g. many parameter estimates had the *msy* estimated to be around 2,000t). These stray parameter estimates occurred often enough to distort the frequency distributions so, to avoid this, we applied an additional filter to the estimates derived from the re-sampled data. These filters only accepted sets of parameters where: $r \leq 0.75$, $B_0 \leq 10{,}000$t and $msy \leq 2{,}000$ t (removing 133 records). Whilst setting these limits was unfortunate, not using them would have led to many distorted parameter estimates being included in the analysis.

Fig. 12 is a scatter-plot matrix that graphically summarises the results from the work that estimated variabilities and Table 5 presents the quantiles for the parameter estimates from this analysis. The expected correlation between *q0* and *q1* (*q0*,*q1*) was present as were inverse correlations between (*q0*,*B0*), (*q1*,*B0*) and (*B0*,*r*). No parameters were correlated with the phase parameter *q2*. Fig. 12 also includes schematic frequency histograms of the parameter values. All distributions were unimodel and therefore interpretable quantiles could be calculated (Table 5).

5.2.4. Risk Analysis

The objective of the risk analysis is to determine, with uncertainty, the impacts of various harvest policies on key reference points. Initial results are presented as the reference point median as a function of TACC. The risk analysis used the same filtering process for the removal of questionable parameter estimates as was applied above.

Figs. 13, 14 and 15 illustrate the median value of the reference point distributions for various TACC. Fig. 13 illustrates median B_{f5}:B_0 and B_{f5}:B_{now} versus the TACC and indicates that the exploitable biomass would be retained at its current level (about 60% of B_0) with a harvest rate of 350t per year. Fig. 14 illustrates median biomass estimates as a function of TACC - note that (i) B_0 and B_{now} are independent of the TACC (as expected) and (ii) forecast biomass estimates are much more sensitive to changes in harvest rates beyond 350t. It is important to recall that these interpretations are median responses and actual outcomes have a 50:50 chance of being higher or lower than these values. Fig. 15 illustrates the probability of collapse in the exploitable biomass as a function of TACC and implies that a risk-averse TACC would set the harvest rates to no higher than 300t.

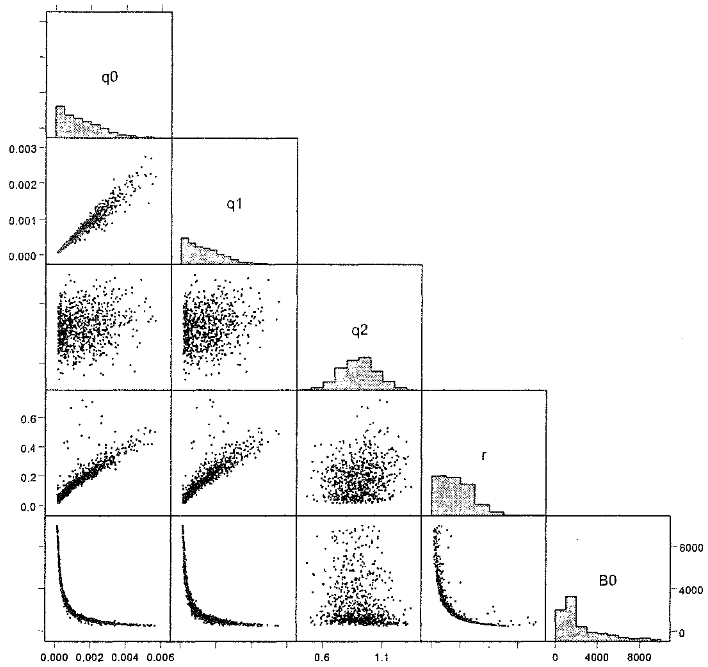

Figure 12. Scatterplot matrix illustrating parameter correlation and frequency distributions of the estimated parameters from the re-sampled datasets (after filtering). Subplots on the diagonal are frequency histograms of the annotated row or column variable. Off-diagonal subplots are scatterplots of the row variable versus column variable. Axis tick-marks indicate the scales of the annotated column or row variable. Strong inverse correlations between (q_0,B_0), (q_1,B_0) and (r,B_0) are evident.

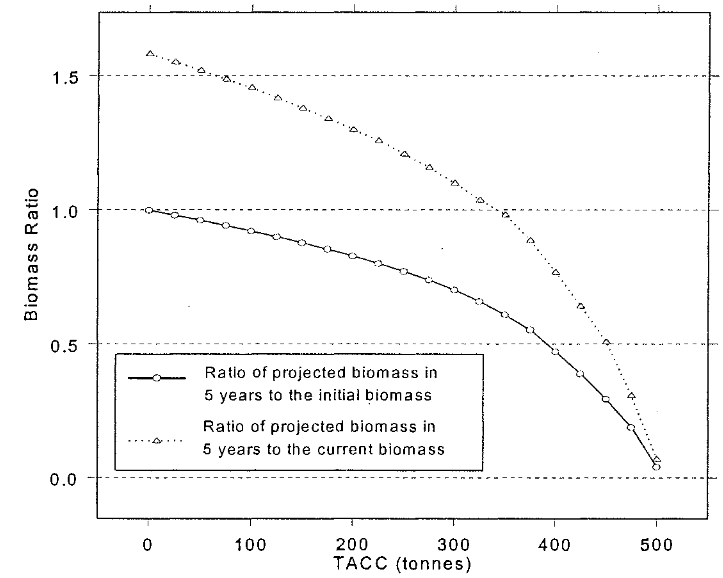

Figure 13. Plot of the median values of the ratios of biomass estimates for various total allowable commercial catches (TACC). The lower line indicates how the ratio of the biomass in 5 years time to the initial biomass changes over a range of harvest rates. The upper line gives that same ratio with respect to current (December 1998 biomass). A TACC of about 340 tonnes would maintain the current exploitable biomass with only 50% confidence.

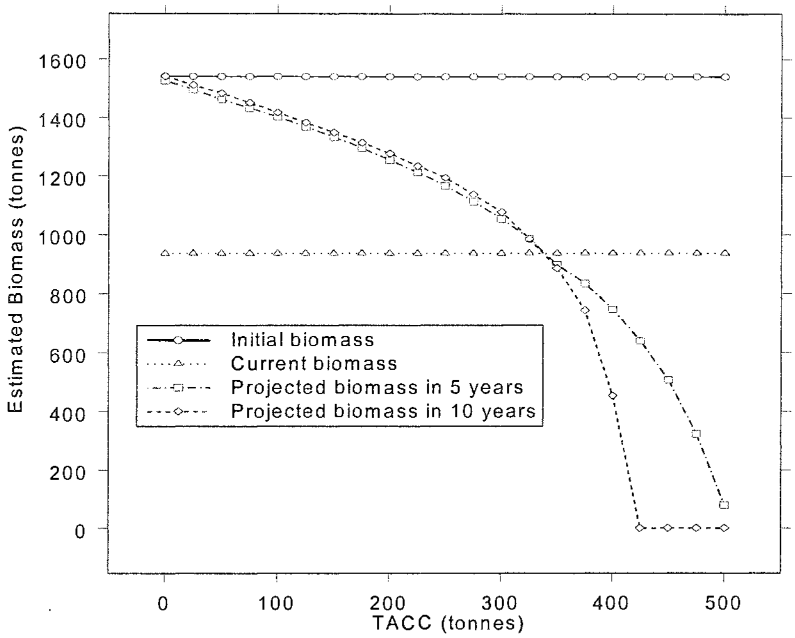

Figure 14. Plot of the median values of the biomass estimates for various total allowable commercial catches (TACC). The initial and current biomass estimates are independent of future TACC (as expected). There are rapid decreases in the projected biomass estimates once the TACC exceeds 350 tonnes.

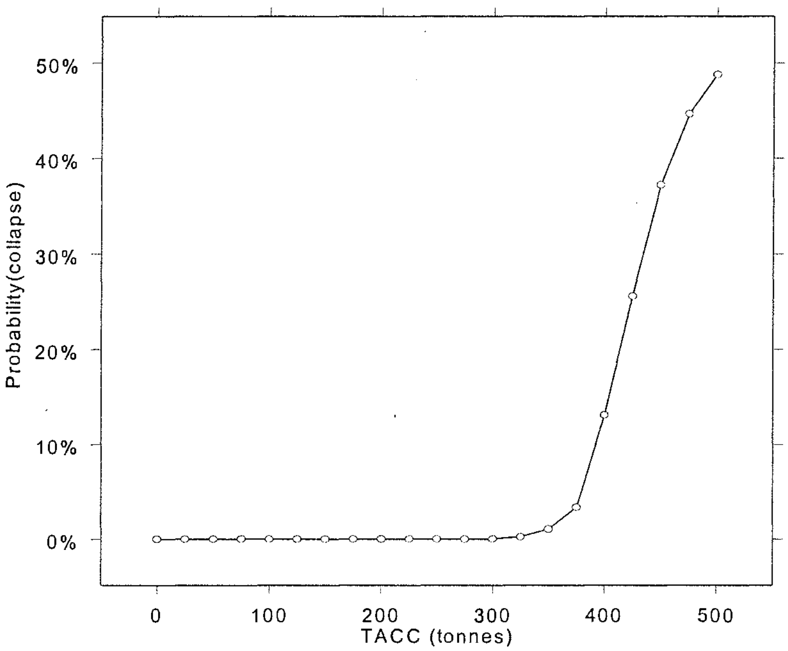

Figure 15. Plot illustrating the probability of collapse in the exploitable biomass as a function of TACC. Note that the spawning biomass is essentially not vulnerable in this fishery and there is no suggestion that the spawning stock will collapse. Risks to the exploitable stock become evident at a harvest rate of around 380 tonnes/year.

Because the reference point B_{f5}:B_{now} provides an easily interpretable measure of the exploitable biomass without being confounded by the correlation between r and B_0, we will only present uncertainties associated with harvest forecasts in terms of this reference point. Fig. 16 is a contour plot that illustrates the relationship between the TACC and the uncertainty of this reference point. The contour height is B_{f5}:B_{now}, so that when the contour is 1.0, the biomass is maintained at the current level. For higher contours, the exploitable stock recovers and for smaller values, it declines. One interpretation of Fig. 16 is as follows: should one want to be at least 70% sure that the exploitable biomass will remain constant over 5 years, find the 30% confidence interval marker on the x-axis, trace vertically until reaching the contour marked 1.0 (constant) and then trace left to the appropriate TACC. In this case about 330t or less should be harvested (this example is annotated on the plot). The contour lines diverge widely for very high and low levels of confidence because the tails of the frequency distribution are long.

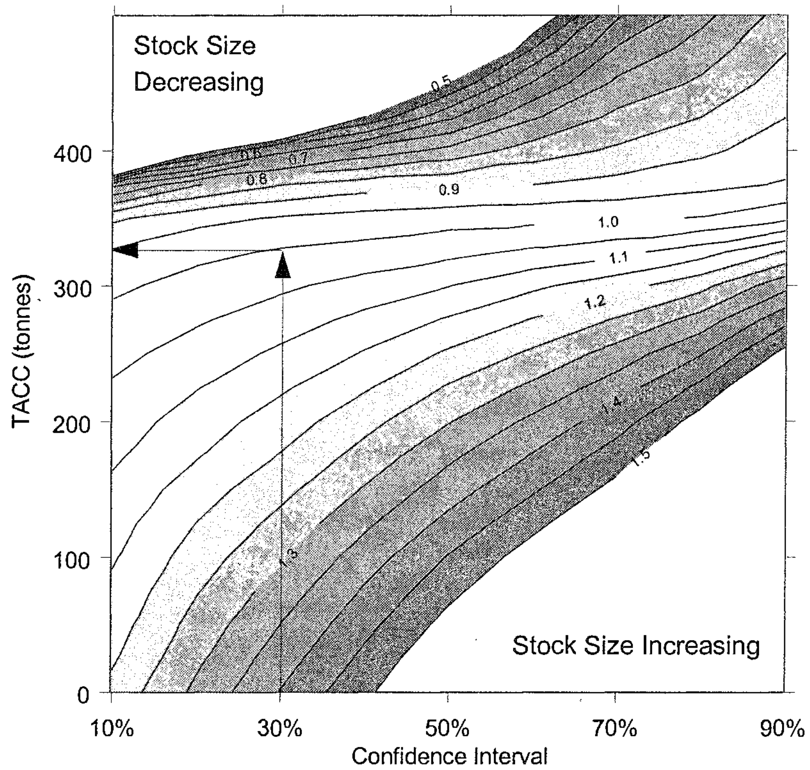

Figure 16. A contour plot of the ratio of the projected biomass in 5 years to the estimate of the current biomass as a function of TACC and projection uncertainty. The contour marked 1.00 indicates the TACC and confidence relationship where no change in the exploitable biomass will occur over the next 5 years. The lower right area indicates the region where the exploitable stock is likely to recover and the upper left where the exploitable biomass will decline. If you require 70% confidence that the exploitable stock size will remain the same over five years, move vertically from the 30% tick-mark on the horizontal axis to the contour marked 1.00 and then left to find the appropriate TACC (about 330 tonnes). Greater confidence in the outcome would require harvesting a lesser biomass of crabs.

5.2.5. Incorporation of catch data from Queensland

An additional analysis was completed for the entire east-coast spanner crab fishery by including available catch data from Queensland (where the majority of spanner crabs are caught in Australia). This extension had to make the unlikely assumption that the surveyed catch rates in NSW were also indices of abundance for the Queensland stocks. Whilst this assumption is probably unfounded, this analysis is a reasonable approximate estimate of the sustainable harvest capacity of the entire spanner crab resource.

Catch statistics from the Queensland fishery were formatted in an identical fashion to those from NSW. The catch data used in this combined (NSW plus Queensland) analysis are presented in Appendix 1. Unfortunately data were unavailable before 1988 but Brown (pers. comm.) suggested that the growth in catches up to the 1988 harvest was relatively uniform. Queensland catches from August 1984 (the earliest NSW record) to December, 1987 were therefore estimated by proportional scaling of the 1988 bimonthly pattern back to an assumed zero catch in 1983. Despite this approximation, estimates of sustainable harvest should not be greatly affected by small errors in the catches estimated from the beginning of the fishery.

The analysis was completed using the same procedure as used for the NSW data with two exceptions: (i) the additional filtering of results removed parameter estimates where $r \geq 1.0$, $B_0 \geq$ 50,000 and $msy \geq 10{,}000$; and (ii) the risk analysis was modified to evaluate the impacts of harvesting between 0 and 5,000t per year. Figs. 17, 18, 19 and 20 have an identical format and interpretation as Figs. 13, 14, 15 and 16 respectively, except that the results apply to the entire east coast fishery - not just the NSW fraction.

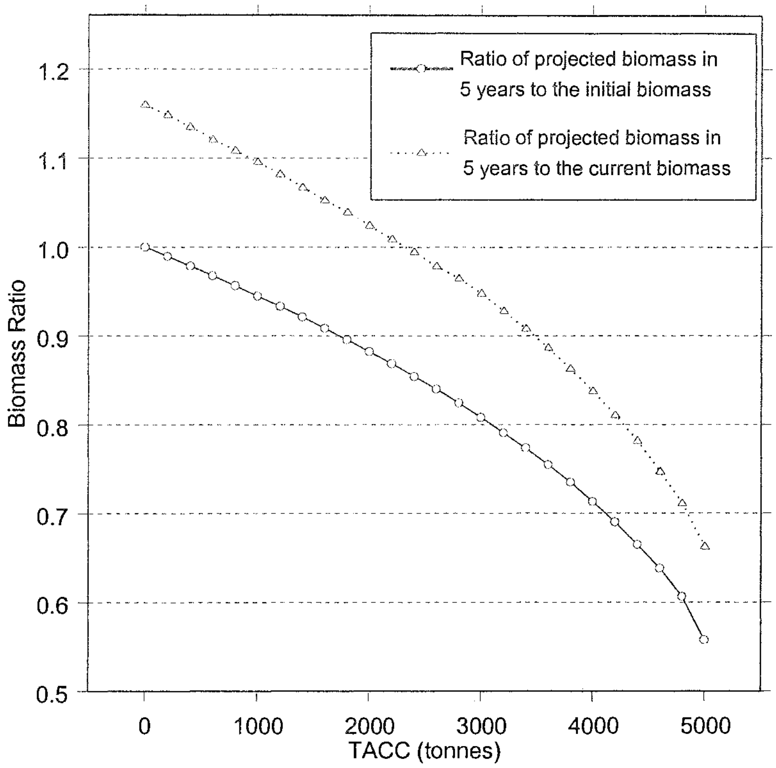

Figure 17. Plot of the median values of the ratios of biomass estimates for various total allowable commercial catches (TACC) for the combined NSW and Queensland fishery. The lower line indicates how the ratio of the biomass in 5 years time to the initial biomass changes over a range of harvest rates. The upper line gives that same ratio with respect to current (December 1998 biomass). A TACC of about 2200 tonnes would maintain the current median exploitable biomass. This model will generate less reliable results for the entire fishery than those suggested for the NSW fishery.

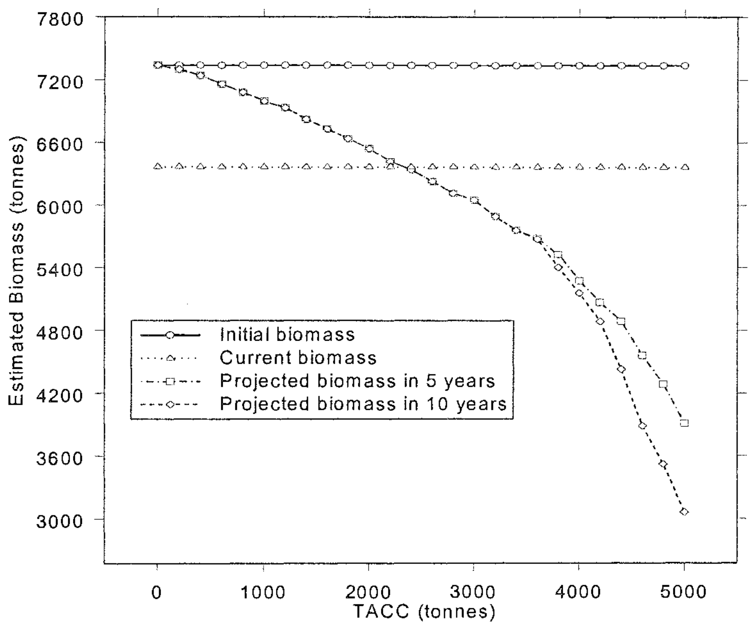

Figure 18. Plot of the median values of the biomass estimates for various total allowable commercial catches (TACC) for the combined NSW and Queensland fishery. The initial and current biomass estimates are independent of TACC (as expected). This model will generate less reliable results for the entire fishery than those suggested for the NSW fishery.

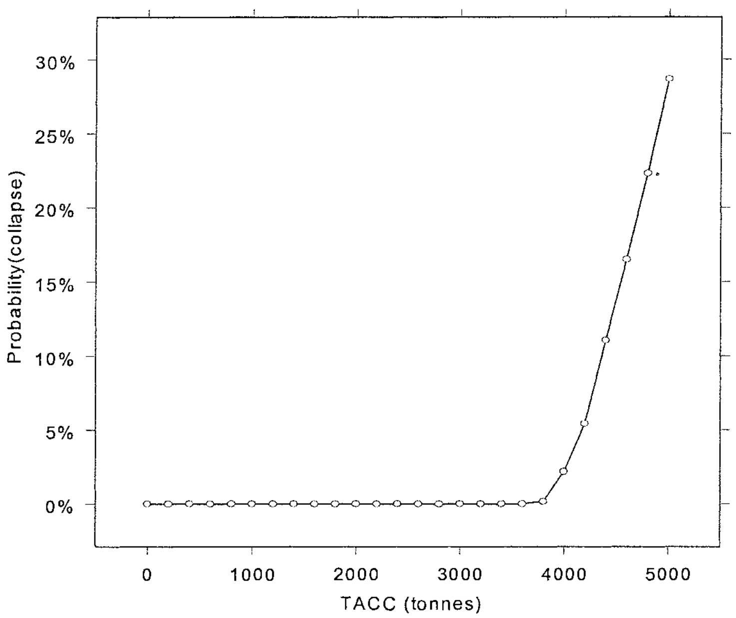

Figure 19. Plot illustrating the probability of collapse in the exploitable biomass as a function of TACC for the combined NSW and Queensland fishery. Note that the spawning biomass is essentially not vulnerable in this fishery and there is no suggestion that the spawning stock will collapse. Risks to the exploitable stock become evident at a harvest rate of around 3 800 tonnes/year. This model will generate less reliable results for the entire fishery than those suggested for the NSW fishery.

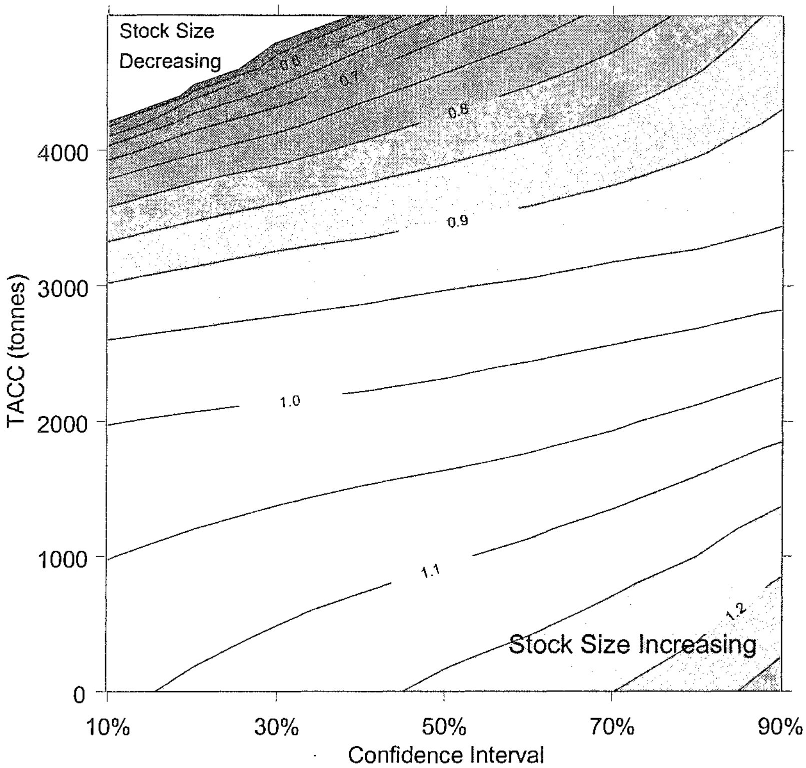

Figure 20. A contour plot of the ratio of the projected biomass in 5 years to the estimate of the current biomass as a function of TACC (for the combined NSW and Queensland fishery) and projection uncertainty. The contour marked 1.00 indicates the TACC and confidence relationship where no change in the exploitable biomass will occur over the next 5 years. The lower right area indicates the region where the exploitable stock is likely to recover and the upper left where the exploitable biomass will decline. This model will generate less reliable results for the entire fishery than those suggested for the NSW fishery.

After fitting the model to the data, it indicated B_0 to have a median value (with 10% and 90% quantiles)] of 7,300 (3,600, 24,500) tonnes and the median of the current biomass to be 6,400 (3,100, 24,000) tonnes. As for the NSW analysis, estimated values for r and B_0 were confounded. The r value estimated was 0.49 (0.14, 0.87). Large values of r are unrealistic.

Fig. 17 suggests that a combined harvest of 2,300 tonnes will cause the median exploitable biomass in five years to be similar to that now. Fig. 20 allows interpretation of these results with different amounts of confidence. For example, should combined harvests for NSW and Queensland be 3,200 t then there is a 90% chance that the biomass will decrease by 5%, or a 10% chance that the exploitable biomass will decrease by 15%.

5.2.6. Comparing estimates of biomass reduction derived from the survey and the model

To determine how our estimates of changes in exploitable biomass from the biomass dynamic model compared to estimates of such changes derived empirically from the survey, we compared the ratios of exploitable biomasses between the repeats of the survey. Length frequencies from the two repeats were converted to total crab weights assuming a length-weight relationship of:

$$weight = 1.98 \times 10^{-4} \cdot length^{3.13}$$

Where the resultant *weight* (in g) can be calculated from a crab of *length* mm. The same relationship was used for male and female crabs. This equation was applied to the mean of each length class presented in Figure 5. The weight of crabs within each length class was then estimated by multiplying the number of crabs in each class by the mean weight of crabs in that class. Weights of length classes at or above the legal size (93 mm) were then summed to obtain the weight of exploitable crabs in each of the two surveys. For the first repeat of the survey (1988-1989) the weight was 1,402 kg and for the second (1997-1998), the weight was 1,203 kg. The ratio of these weights (second/first) is 85.8%.

A comparable biomass ratio from the model was calculated by taking the mean of estimated exploitable biomass for all bimonthly periods in 1988-1989 (first) and 1997-1998 (second) for each of the 867 acceptable simulations. The biomass ratio (second/first) was calculated for all simulations resulting in a median value of 86.2% with the interval (76.7%, 96.4%) representing the 10% and 90% quantiles.

This analysis verifies that the estimated change in exploitable biomass from the model is comparable to the empirical estimates from the survey. Given that the model was calibrated using the survey data such a close correspondence is not surprising.

6. DISCUSSION

6.1. Survey

One of the most basic aspects of any population is its sex-ratio and the 1997-98 repeat of the fishery independent survey confirmed the 1988-89 result showing a slight bias towards females. In contrast, other studies have reported this species' sex ratio as dominated by males (Fielding and Haley 1976, Brown 1986, Skinner and Hill 1986) and a number of factors may account for this difference: (i) high rates of exploitation of the larger, targeted, male crabs may have reduced their numbers (Fielding and Haley 1976, and see below); (ii) because females respond quicker to food stimuli, they may be more caught more easily in baited traps (Skinner and Hill 1987); (iii) the traps used in the present study were designed to catch a wider size-range of crabs than traps used in previous studies (Kennelly and Craig 1989); and/or (iv) this merely may reflect a natural phenomenon as deviations from a 1:1 sex ratio are not unusual for marine crustaceans (Wenner 1972).

Another characteristic of spanner crabs is their marked sexual dimorphism with males being generally larger than females (Fig. 5; see also Fielding and Haley, 1976, Tahil, 1983, Brown, 1986, Kennelly, 1992). In the present study, male crabs comprised the majority of the targeted portion of the population and most females were protected by the legal minimum size limit of 93mm (Fig. 5). Further, 72% and 73% of the available population were undersize in the two repeats of the survey, respectively, and 96% of females were undersize. Given (i) the protection of these large numbers of females by the minimum size-limit, (ii) the sexual maturity of males at a small size (approx. 60 mm - Fielding and Haley, 1976), (iii) their promiscuity in mating (Onizuka, 1972; Skinner and Hill, 1987), (iv) their acceptance of spermatophores so that most females are impregnated during the spawning period (Brown 1986, Skinner and Hill 1987), and (v) their high fecundity (100,000 - 200,000 eggs per female - Fielding and Haley 1976, Brown 1986, Kennelly and Watkins 1994), the population of, and therefore the fishery for, spanner crabs should be in a sound position, ensuring long-term viability through the maintenance of a large spawning population. Whilst some of the results comparing the relative abundances of crabs from the two repeats of the survey do not negate this conclusion, there were results that indicated some cause for concern for these fisheries.

The large variabilities evident from highly significant interaction terms among locations, depths and periods in the ANOVAS (Table 1) indicated that, in general, the relative abundances of these crabs depends on the particular location, depth and period that one considers. There were, however, certain consistencies in abundances of spanner crabs detected in these surveys, such as the result that abundances within years and repeats of the survey were quite similar. There was a consistent annual decline in relative abundances of most variables (and particularly females) in October and December each year at most locations (see Figs. 6 to 10), coinciding with the spawning period of spanner crabs - females are ovigerous from October to January (Tahil, 1983, Brown, 1986, Skinner and Hill, 1987). Perhaps during this time of the year, spanner crabs (especially females) are less susceptible to capture, probably due to reduced feeding and/or some migratory behaviour at this time. This confirms Skinner and Hill's (1986) results of declines in commercial catches (particularly females) during the spawning period, and reduced rates of emergence of ovigerous females in aquaria at this time.

Another pattern to emerge from the surveys was that more male and female crabs occurred off Sand Point than off other locations (Figs. 6, 7 and 8). This aggregation was evident at all times of the year except during the above-mentioned spawning period, perhaps due to spawning migrations at this time. In terms of the long-term management of this fishery, the existence of such an aggregation of crabs suggests this location's potential as a reservoir of spawning stock and the possibility that similar pockets occur elsewhere along the coast.

Another pattern to emerge from these surveys was that small numbers of both sexes were detected in shallow depths off Kingscliff, Pottsville and Riordan's Shoal (Figs. 6, 7 and 8). This would be of particular interest to the commercial fishery as it suggests that shallow areas in these places may be less productive than deeper sites. Further, the consistent appearance of male and legal-sized crabs off Tallows Beach at most times highlights the potential for this location as a regular supplier of marketable crabs (Figs. 7 and 9). The fact that male crabs were present in the deep and mid-depths off Tallows Beach in October and December each year (when they were found to be scarce off other locations - see Fig. 7) may be evidence that these places were the destinations of the spawning migration eluded to above.

Whilst the above trends in abundances of spanner crabs provide useful insights into these populations, there were several results that indicated some significant decreases in the populations of spanner crabs over the 11 year period of these two surveys. Firstly, the size-frequencies of the crabs sampled during the 2 repeats (and the associated Kolmogorov-Smirnov tests of these data) indicated a significant decrease of approx. 55% in the abundances of large crabs (>108mm CL) from the first to the second repeat (see Fig. 5).

This conclusion is also indicated by a statistically significant decrease of approx. 6% in the relative abundances of all crabs between repeats of the survey and similar trends for decreases for abundances of females, legal and undersize crabs (Tables 1 and 2). Whilst such a decrease in the population over an 11 year period is not indicative of a collapsed stock, it does indicate that this population should be carefully monitored to determine the level of this decline. It also suggests that additional management restrictions on this fishery may be required to limit any further decline (particularly for those observed for the numbers of large crabs). These restrictions could include output controls such as TACCs or supplementary input controls.

6.2. Population modelling

The modelling approach implemented for this project is parsimonious - the biomass dynamic model was the simplest representation of the productivity of the stock. Time scales of the analysis reflected the data available and the medium term (up to 10 years) management timeframe.

Results from the analysis of the NSW fishery are more reliable than the results for the NSW and Queensland fisheries combined - the latter was completed for the general result only. We do not condone the use of this result for the management of the Queensland spanner crab fishery because the survey catch rates are not an index of abundance of the entire stock. Results from the model are presented in Figs. 16 (NSW) and 20 (NSW and Queensland) which indicate the likely response of the exploitable stock biomass over the next 5 years given a range of imposed catches. Uncertainties of these forecasts are also represented in these figures. In NSW, retention of the exploitable biomass at the current level for the next 5 years (about 60% of the initial biomass) would involve a maximum harvest rate of 290 t. This result should be true 90% or more of the time. If the Spanner Crab Management Advisory Sub-Committee was willing to accept higher levels of risk in achieving this objective, or if a lower ratio of the current exploitable biomasses was considered acceptable, the catches could be higher.

From Fig. 2 it is evident that the actual historical harvest is quite variable but our model projections have been calculated assuming that the future TACC is fixed. Imposing variability in projected TACC will increase the variability of the projected stock biomass. It would be sensible to observe the pattern of catch variability under an output-controlled management regime before modelling this process. If the catch is capped at the TACC, stock projections from this model will be conservative.

It is tempting to add additional parameters to our model to represent recruitment from Queensland and the protected NSW spawning stock. In which case our model might then look something like:

$$B_{t+1} = B_t + r \cdot B_t \cdot \left(1 - \frac{B_t}{B_0}\right) - C_t + I_t$$

The immigration term I_t could be a constant or a variable time series. Unfortunately, however, we have no information that would allow the meaningful estimation of this parameter or time series so such an inclusion would just lead to more parameters that would be confounded with r and B_0. This would not be a helpful addition to the analysis.

The NSW stock is, to some unquantifiable degree, dependent upon the health of the Queensland stock and, should there be a failure in recruitment from Queensland, the NSW exploitable stock may be impacted. We are not in a position of knowing how large such an impact will be until it actually occurs.

We are unsure if the NSW spanner crab fishery is represented by a small biomass of rapidly growing animals or a large, slow-growing biomass. Confounding of growth and initial biomass is a common problem in biomass dynamic modelling (Hilborn and Walters, 1992) when there is little contrast in abundances and fishing effort. This problem is exacerbated in this model due to the relatively short time series of abundance information. Given that the important reference points such as biomass ratios do not completely depend on the actual biomass values, however, we see no need to be overly concerned about this uncertainty. Readers should interpret the estimated values of r and B_0 with a degree of scepticism: they are patterns of numbers, not hard and fast estimates of NSW spanner crab production and initial biomass.

Decision makers should note that this modelling exercise could not capture important components of system uncertainty (e.g. we are unable to predict recruitment failure). Other scientific and management processes need to be in place to detect such failures and take appropriate decisions.

Monitoring of the fishery with systematic fishery independent surveys would provide a robust method to ensure that large changes in stock size do not go undetected.

Finally we re-iterate our former warning about interpreting the results from the model involving Queensland and NSW data. The data to which this model is fitted are indices of abundance of spanner crabs in NSW waters alone. It would be unwise to use the above results to determine the appropriate harvest rate for the Queensland fishery.

7. BENEFITS

The development of a population model based on a repeat of the stratified survey has allowed improved recommendations to management concerning the spanner crab fishery in NSW. We anticipate, therefore, that if the recommendations put forward in this report are implemented (i.e. a TACC for this fishery of approx. 300t), all commercial and recreational fisheries that target spanner crabs should benefit from this work by arresting the apparent declines in relative abundances of spanner crabs (particularly those larger than 108mm CL). If the results are implemented as management changes, the benefits from this research should, in the long-term, be evident as increased export earnings from the spanner crab fishery, improved prices for the commercial sector, improved economic benefits for fishers endorsed to catch spanner crabs, improved recreational fishing for the species and improved economies for the townships of northern NSW and southern Queensland.

Another benefit from this particular project is that we now have a tool (involving a repeatable, stratified, randomized , fishery-independent survey) that, when combined with a relatively simple population model, provides a mechanism by which fisheries managers can assess and manage this fishery so that it remains sustainable in the long-term.

8. FURTHER DEVELOPMENT

This study has shown that the repeated use of a stratified, randomized baited trap survey, replicated throughout appropriate spatial and temporal scales, will provide quantitative information on the relative abundances and distributions of various components of populations of spanner crabs. These estimates were shown to be valuable in identifying potential problems in this fishery and in developing management strategies to solve them. We conclude that the continued use of such a survey would be a powerful tool to monitor fluctuations in the population after changes in management - thus providing new information and, consequently, modified recommendations to management like adjustments to the TACC.

In addition to the continued monitoring of the NSW fishery using this survey, we also recommend that the geographic range of the survey be expanded to include the Queensland fishing grounds. By including estimates of relative abundances of spanner crabs throughout the whole east coast, modelling and management of this fishery will be able to be done on the entire stock. Once such a coast-wide survey is in operation, it may be prudent to consider further modelling work that examines the utility of a length-based model to describe the entire east coast spanner crab fishery.

9. CONCLUSION

Under the heading of "Performance Indicators" in the original application for this project, we said that "this research should be deemed successful if, at the end of the allotted two and a half years, we have: (i) determined the relevant relative abundance estimates for spanner crabs in NSW after repeating the abundance survey; (ii) incorporated all relevant sets of data into a population model for the fishery; and (iii) provided the relevant fisheries managers and industry representatives with advice on various input and output controls including the TACC."

Clearly all these indicators have been met in this project with the result that we recommend that the management and research for spanner crabs in NSW proceeds as a TACC-based fishery monitored by continued repeats of the 2 year fishery-independent survey, regular catch monitoring and the use of a simple biomass dynamics population model to recommend appropriate adjustments to management strategies.

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11. APPENDICES

Appendix 1 – Table of Catch Statistics Used for Population Modelling
P.T.O.

Appendix 2 - Intellectual Property
There are no issues concerning intellectual property associated with the work done in this project.

Appendix 3 - Staff
Dr Steve Kennelly (Principal Research Scientist) - Principal Investigator
Dr James Scandol (Resource Assessment Modeller)
Dr Yong Chen (Fisheries Modeller)
Max Beatson (Fisheries Technician)
Jack Lavis (Commercial Fisherman)
John Spedding (Commercial Fisherman)

We also would like to acknowledge the assistance that Dr Ian Brown and the Queensland Dept. of Primary Industries gave us in providing the data on catches of spanner crabs in Queensland.

Appendix 4 - Publication from this project
Chen, Y., Kennelly, S.J. (1999). Growth of spanner crabs, *Ranina ranina*, off the east coast of Australia.. Mar. Freshwater Res., 50: 319-325.

Appendix 1 - Table of Catch Statistics Used for Population Modelling

Calendar Year	Bimonthly Period	NSW Catch (tonnes)	NSW + QLD Catch (tonnes)	Calendar Year	Bimonthly Period	NSW Catch (tonnes)	NSW + QLD Catch (tonnes)
1984	Jul-Aug	14.187	56.263	1992	Jan-Feb	46.197	142.180
1984	Sep-Oct	18.404	105.656	1992	Mar-Apr	41.978	166.339
1984	Nov-Dec	30.375	41.487	1992	May-Jun	45.946	220.936
1985	Jan-Feb	28.933	59.499	1992	Jul-Aug	78.752	337.825
1985	Mar-Apr	20.068	48.942	1992	Sep-Oct	76.201	506.789
1985	May-Jun	37.130	85.819	1992	Nov-Dec	41.554	242.081
1985	Jul-Aug	38.487	87.576	1993	Jan-Feb	47.494	325.143
1985	Sep-Oct	47.508	149.302	1993	Mar-Apr	37.367	263.424
1985	Nov-Dec	37.866	50.830	1993	May-Jun	48.549	316.396
1986	Jan-Feb	41.090	76.022	1993	Jul-Aug	88.663	490.921
1986	Mar-Apr	39.410	72.409	1993	Sep-Oct	93.650	698.363
1986	May-Jun	87.915	143.560	1993	Nov-Dec	41.476	394.854
1986	Jul-Aug	86.842	142.944	1994	Jan-Feb	36.619	387.463
1986	Sep-Oct	83.394	199.730	1994	Mar-Apr	36.669	447.188
1986	Nov-Dec	80.132	94.948	1994	May-Jun	53.630	568.235
1987	Jan-Feb	44.734	84.033	1994	Jul-Aug	96.045	618.931
1987	Mar-Apr	32.920	70.044	1994	Sep-Oct	114.058	1147.891
1987	May-Jun	55.188	117.788	1994	Nov-Dec	44.824	487.502
1987	Jul-Aug	77.097	140.211	1995	Jan-Feb	27.681	401.795
1987	Sep-Oct	118.380	249.258	1995	Mar-Apr	74.966	552.361
1987	Nov-Dec	110.255	126.923	1995	May-Jun	86.009	490.512
1988	Jan-Feb	55.467	99.132	1995	Jul-Aug	108.796	645.866
1988	Mar-Apr	43.314	84.563	1995	Sep-Oct	131.512	950.898
1988	May-Jun	83.464	153.020	1995	Nov-Dec	35.911	250.885
1988	Jul-Aug	87.281	157.408	1996	Jan-Feb	40.253	606.690
1988	Sep-Oct	67.589	213.009	1996	Mar-Apr	41.812	604.308
1988	Nov-Dec	41.464	59.984	1996	May-Jun	65.308	623.312
1989	Jan-Feb	23.776	53.109	1996	Jul-Aug	88.280	630.118
1989	Mar-Apr	18.295	57.729	1996	Sep-Oct	94.291	762.894
1989	May-Jun	53.434	109.686	1996	Nov-Dec	42.623	59.382
1989	Jul-Aug	61.095	187.865	1997	Jan-Feb	34.347	916.682
1989	Sep-Oct	64.510	205.736	1997	Mar-Apr	51.031	374.638
1989	Nov-Dec	7.267	56.461	1997	May-Jun	62.390	530.454
1990	Jan-Feb	16.384	78.096	1997	Jul-Aug	87.241	721.989
1990	Mar-Apr	21.088	63.220	1997	Sep-Oct	91.339	889.548
1990	May-Jun	38.270	113.989	1997	Nov-Dec	22.331	160.279
1990	Jul-Aug	48.049	161.067	1998	Jan-Feb	26.475	493.913
1990	Sep-Oct	62.269	228.774	1998	Mar-Apr	34.906	385.829
1990	Nov-Dec	21.369	83.017	1998	May-Jun	50.751	222.224
1991	Jan-Feb	23.955	103.558	1998	Jul-Aug	55.389	366.836
1991	Mar-Apr	43.362	176.513	1998	Sep-Oct	67.863	642.232
1991	May-Jun	60.014	207.276	1998	Nov-Dec	20.833	205.655
1991	Jul-Aug	83.735	243.191				
1991	Sep-Oct	81.364	272.782				
1991	Nov-Dec	26.655	125.032				

APPENDIX 4

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Growth of spanner crabs, *Ranina ranina*, off the east coast of Australia

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Abstract. Spanner crab, *Ranina ranina*, is the target of an important fishery off the east coast of Australia, yet its rate of growth is unknown. Descriptions of growth rates for spanner crabs, like those for other crustaceans, are difficult because during each moult all hard parts that might be used for ageing are lost, and because, as a result of moulting, the growth process is discontinuous. Tag–recapture data were used to model the relationships between the probability of moulting and the number of days at large and between the size increments per moult and the size at tagging. For crabs in similar size classes, males moulted about twice as often as females and had larger increments in size per moult. The relationship between increment per moult and size at tagging was not strong (small r^2), but statistically significant. Size increments per moult tended to increase with the pre-moult sizes, indicating that larger crabs tended to grow more in a moult than smaller crabs. However, small crabs moulted more often than large crabs. A probabilistic stepwise growth simulation was used to generate a distribution of growth curves that mimics discontinuous growth patterns and samples the variation in the data.

Introduction

One of the most important aspects of the biology and life-history of a species is its growth rate. For wild-caught marine fisheries, estimates of species' growth rates form one of the most basic elements in population models that aim to provide advice for sustainable and optimal management of the fishery. Whereas the determination of growth rates for fin-fishes is relatively straightforward, direct measurements of the growth of crustaceans is difficult because of the replacement of the old exoskeleton by a new one at moulting.

Moulting in crustaceans causes at least two problems when trying to quantify growth: *(i)* all hard parts that might be used for ageing are lost at each moult, and *(ii)* growth is discontinuous, occurring in a step-wise fashion. The first problem may be overcome by tagging a large number of animals with a tag that is retained through moulting, thereby allowing identification upon recapture (Aiken 1980; Hartnoll 1982; Taylor and Hoenig 1991). By measuring the increase in sizes during the period of liberty, a mathematical function can be derived to describe the growth of body sizes with time (e.g. Ricker 1975; Annala and Bycroft 1988; Francis 1988). The additional problem of discontinuous growth has received much less attention. Almost all growth models developed in fisheries assume that fish undergo continuous growth in size and there have been few attempts to model the step-wise growth of crustaceans (but see McCaughran and Powell 1977; Annala and Bycroft 1988).

Spanner crabs *Ranina ranina* are large marine brachyuran decapods found throughout the Indo–Pacific region (Barnard 1950) in coastal waters to 70 m on sandy substrata in which they bury (Skinner and Hill 1987). Populations of *R. ranina* are exploited commercially in Hawaii, Japan, the Philippines, the Seychelles and, more recently, along the east coast of Australia. They are captured in baited traps made of tangle-nets suspended over flat frames (Kennelly and Craig 1989). Despite a growing literature concerning the biology and fisheries of this species (Fielding and Haley 1976; Tahil 1983; Skinner and Hill 1986, 1987; Kennelly 1989, 1992; Kennelly and Craig 1989; Kennelly *et al.* 1990; Kennelly and Watkins 1994), several basic aspects of its biology remain unknown. In particular, and of importance to the stock assessment and management of this species, its growth has not been quantified.

This paper reports a large-scale tagging study, stratified across several spatial and temporal scales throughout the fishery in New South Wales (NSW), Australia. Recaptures from this study permitted an estimation of moult frequency and the size increment per moult. We then applied a probabilistic approach to model the growth of spanner crabs.

Materials and methods

Study site and tagging

This study was done off the north coast of NSW, Australia (Fig. 1). All tagged crabs were caught during a stratified, randomized survey of the relative abundance of spanner crab populations throughout the NSW fishing grounds. Modifications of commercial fishing methods were deployed from chartered commercial vessels (6 m twin-hull boats). Traps were square frames 1.2 × 1.2 m and made of mild steel with 85 mm, 4-ply net doubly hung over each frame with a standard 230 mm fall in the net. This type of trap was found to catch the maximum number and widest size-range of *R. ranina* (Kennelly and Craig 1989). One bait (fish-skeleton) was placed in the middle of each trap and replicate traps were set out along trot-lines placed cross-current on the substratum in the area or depth to be sampled. These sets were left for a minimum soak-time of 60 min, during which all

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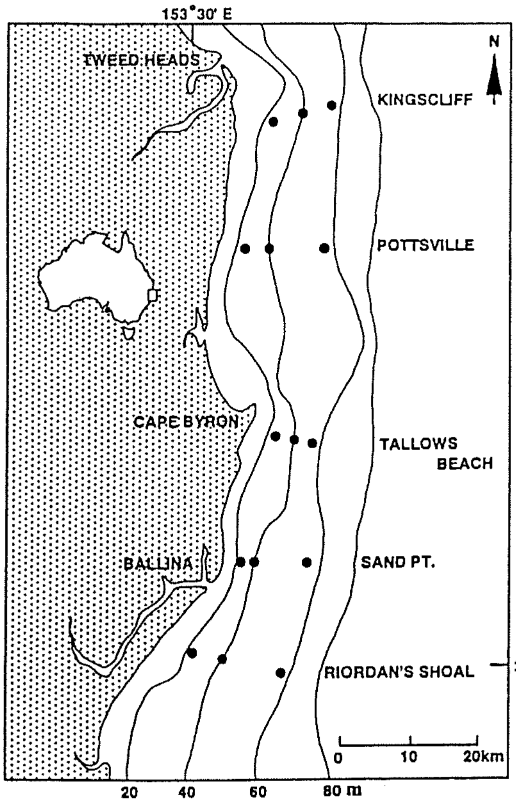

Fig. 1. Locations of tagging sites throughout the main fishing grounds in NSW, Australia.

susceptible crabs in the vicinity were attracted to the bait odour and became entangled on the net (Kennelly 1989). When traps were hauled, crabs were disentangled, sexed, measured (posterior edge of the eye-orbit to the posterior edge of the carapace) and tagged.

Standard t-bar tags were used; they consisted of a vinyl anchor (10 mm length, 1 mm diameter) attached perpendicularly to a shaft (15 mm length, 0.5 mm diameter), which was connected to a sheath (25 mm length, 1.75 mm diameter) containing identification information. The blue sheath contrasted with the orange crabs and so facilitated identification of recaptures by commercial fishers. The tags were inserted into the dorsal ecdysial suture line between the posterior margin of the carapace and the first abdominal segment. To avoid the gut, nerve chord and main artery, tags were inserted into the leg musculature at the right side of the centre of the dorsal surface. Once attached, the end of the tag was gently tugged to ensure proper insertion. After tagging, crabs were placed in a holding tank containing oxygenated seawater onboard the vessel. A specially designed release bin was used to transport crabs back to the bottom. This bin held ~20 crabs and protected them from any potential predators until they reached the bottom where the lid was released and crabs were freed.

The full design of the tagging programme involved setting five replicate traps on each of three replicate, randomly located sets at each of three depths (22, 40 and 58 m – the range of depths fished by the commercial fleet) at five localities throughout the main NSW fishing grounds: offshore from Kingscliff, Pottsville, Tallows Beach, Sand Point and Riordan's Shoal (Fig. 1). This whole procedure was repeated every two months for 12 months (June 1988 to April 1989) during which all crabs caught were tagged and released. In total, 4149 crabs were tagged. Although the recaptured crabs from each release locality/time were too few to allow meaningful estimates of growth rates at the smallest spatial and temporal scales examined, the stratified design of this programme ensured that the estimates calculated below (which were modelled from pooled data) encompassed the largest spatial and temporal variabilities occurring in the spanner crab populations of NSW.

Recaptured animals and details of the date and place of recapture came from commercial spanner crab fishers. An advertising campaign involved posters, media releases, magazine articles and presentations at port meetings to notify all relevant fishers of the study and what to do with recaptured crabs, and offered a cash reward for recaptures. When a recaptured crab was received, it was measured and sexed by us and the data were compared with the release information. In all, 360 crabs were recaptured, with the time at liberty ranging from 18 days to over 5 years.

Data analysis

Large differences in growth were observed between female and male crabs, so all analyses were done separately for each sex. Recaptured crabs were grouped according to multiples of 50 days at large. Thus, day groups 1, 2, ..., n corresponded to 50, 100, ..., 50n days at large. The selection of 50 days as the interval, although rather arbitrary, was to ensure that the number of samples in each day interval was not too small. Because of the consistent moult increments incurred by spanner crabs (see Results, Fig. 4), it was relatively easy to identify crabs that had undergone more than one moult. Only a few crabs were found to moult more than once in this study (Kennelly, unpublished) and, because no estimates existed about their size increments after each moult, they were excluded from further analysis. The proportion of crabs that had moulted once was calculated for each day group. This proportion tended to increase from 0 to 1 with increasing numbers of days at large. The following model was used to describe the relationship between the proportion of moulting and number of days at large:

$$\text{Logit}\ (P_i) = a + bD_i + \varepsilon_i,$$

where P_i is the proportion of crabs that had moulted once in day group i, D_i is the numbers of days at large of day group i, a nd b are two parameters to be estimated, and ε_i is an error term. Thus, the number of days at large at which 50% of crabs had moulted (D_{50}) can be calculated as $-a/b$ (Chen and Paloheimo 1994). The parameters a and b were estimated by using PROC LOGISTIC in SAS (Anon. 1987). Because it is possible for crabs of different sizes to have different relationships between P_i and D_i, crabs were divided into several groups based on their sizes, and the above modelling practice was done separately for each size group. Three size groups were defined for females: ≤80 mm, 81–90 mm, and >90 mm. For males, four size groups were defined: ≤80 mm, 81–90 mm, 91–100 mm and >100 mm. Each of these groups contained a reasonably large number of moulted, recaptured crabs. Differences in the estimated D_{50} were evaluated among different size groups of crabs. Although the size groupings were arbitrary, the results (below) suggest that they were appropriate because differences in the estimated parameters a, b and D_{50} were smaller between neighbouring size classes than between non-neighbouring size classes.

Size increments resulting from moulting in crustaceans are often assumed to be related to the pre-moult size (e.g. Annala and Bycroft 1988). This assumption was evaluated in the present study by using a simple linear regression model to describe the relationship between the size increment per moult and the size at tagging (i.e. pre-moult size). This model can be written as

$$\Delta L_i = a + bL_i + \varepsilon_i,\ i = 1, ..., N \tag{2}$$

where ΔL_i is the size increment resulting from a moult, L_i is the size at tagging, ε_i is an error term, all for the ith crab and N is the number of crabs included in the analysis. The least-squares method was used to estimate the parameters a and b.

Many growth models such as the von Bertalanffy growth function (Chen *et al.* 1992) commonly used in describing fish growth assume implicitly that growth is continuous. The stepwise-growth-curves method (Annala and Bycroft 1988) generates growth curves (i.e. predictions of size at age) that mimic discontinuous patterns of growth. However, it is deterministic and disregards intrinsic variation in the data. Consequently, we applied an approach similar to that of McCaughran and Powell (1977) to construct growth curves. This approach, referred to as probabilistic stepwise growth curves (PSGC), generates a distribution of growth curves that mimic discontinuous patterns of growth. It thus provides parameters such as ranges, prediction intervals and medians. The following estimation procedure was used for the PSGC approach: *(1)* choose a start size L_1; *(2)* choose a start number of days at large D_1 (= 50 days in this study) and calculate the corresponding probability, P_1, of a moult according to Eqn 1; *(3)* select a number q at random from a uniform distribution between 0 and 1, whereby if $q < P_1$ pertains one moult occurred, whereas if $q > P_1$ pertains a moult did not take place and D_1 is increased by 50 days, this being repeated until the value for D results in a moult; *(4)* calculate the probability of size increments for each size class as

$$Q_i = \frac{N_i}{\sum_{i=k_1}^{k_n} N_i}, \quad i = k_1, \ldots, k_n$$

where N_i is the number of crabs with size increment K_i and Q_i is the probability of having the size increment K_i; *(5)* conduct binomial sampling based on L_1 as defined in step (1) and Q_1 as defined in step (4) to decide the size increment ΔL_1; *(6)* calculate the new size after the moult as $L_2 = L_1 + \Delta L_1$; and *(7)* replace L_1 with L_2 in step (1) and repeat steps (2) to (6) until size L reaches L_{max}. By applying the above procedure many times (100 times in this study), a distribution of growth curves was generated. Because the age at start length L_1 was unknown for female and male crabs, the growth curves estimated using the PSGC approach were relative to the age at L_1.

Results

The observed proportion of crabs that moulted once during their liberty between mark and recapture increased with the number of days at large within each defined size class for both females (Fig. 2) and males (Fig. 3). This relationship was well described by Eqn (1), with high r^2 values and low standard errors associated with the estimated model parameters (Table 1). The estimated values of parameter D_{50} increased with size class for both female and male crabs (Table 1), indicating that moulting occurred more frequently for small crabs than for large crabs. For crabs smaller than 90 mm, the D_{50} of females was about twice that of males (Table 1), suggesting that male crabs moulted about twice as frequently as females. There was a significant increase in D_{50} when male crabs reached 100 mm and females reached 90 mm.

Size increments per moult tended to increase with the premoult size (Fig. 4). For females, the size increments per moult tended to be greater than 6 mm for the majority of crabs >80 mm, and less than 6 mm for the majority of crabs ≤80 mm. For males, size increments per moult were more likely to be 11 mm for crabs ≤80 mm, 13 mm for crabs of 81–100 mm, and 14 mm for crabs >100 mm (Fig. 4). Size increments per moult for females were about half of those for males. Regression analyses indicated that the relationships between size increments and pre-moult sizes were significant for both females ($P < 0.043$) and males ($P < 0.001$). However, pre-moult size accounted for only 15% and 11% of variances in post-moult size increments for female and male crabs, respectively. The estimated least-squares regression equations were

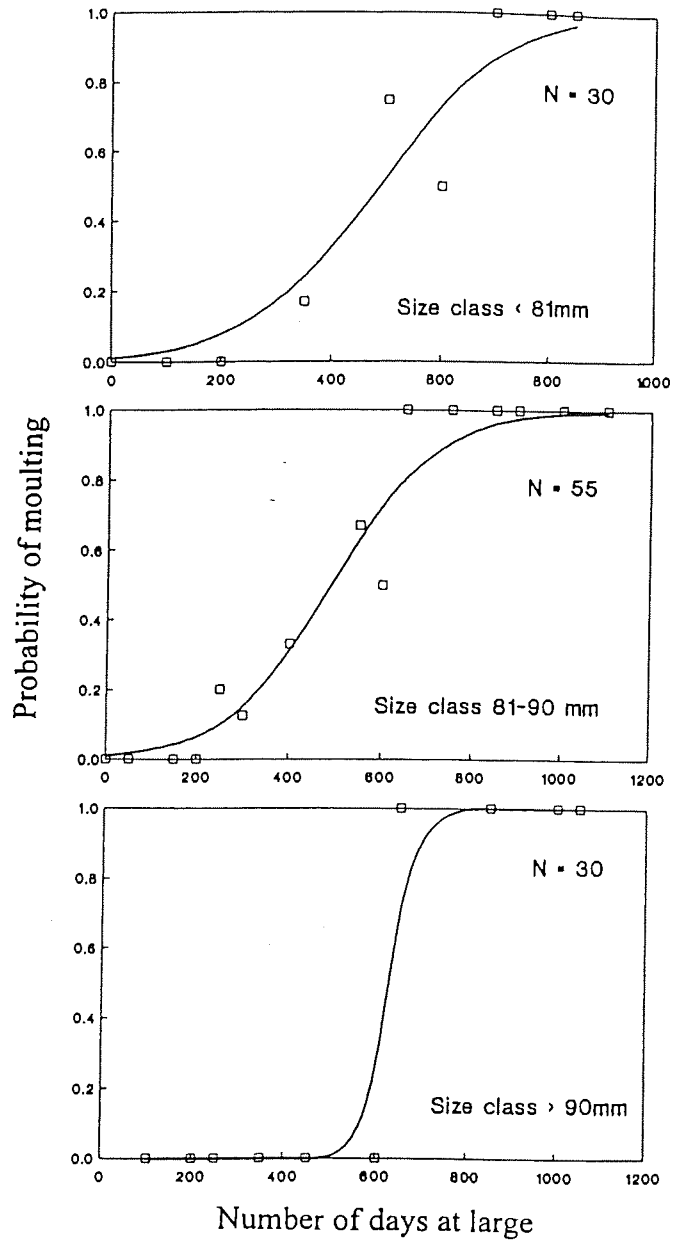

Fig. 2. Probability of moulting for female spanner crabs of different size classes in relation to the number of days at large: □, observed value; curve, predicted value.

Female: $\Delta L_i = 0.77 + 0.067\,L_i$, df = 28, $r^2 = 0.15$

Male: $\Delta L_i = 5.05 + 0.084\,L_i$, df = 91, $r^2 = 0.11$.

The positive slopes in both regression equations suggested that a large crab tended to have a larger size increment per moult than did a smaller crab (Fig. 5). However, it should be noted that although the slopes are larger than 0 their values are small for both females and males. This, together with small r^2, may suggest that more studies are needed to confirm the positive relationships between size increments and premoult sizes.

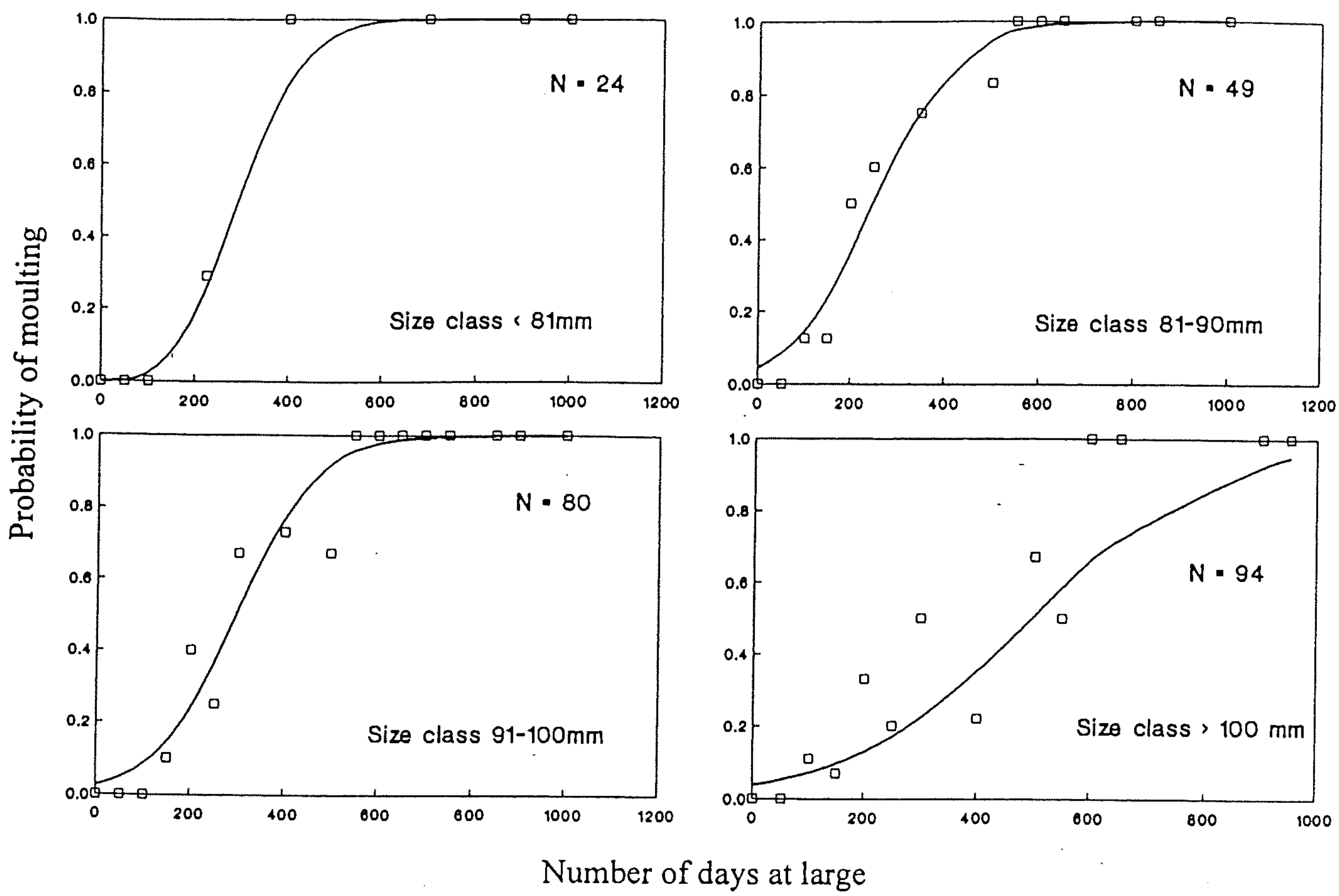

Fig. 3. Probability of moulting for male spanner crabs of different size classes in relation to the number of days at large: □, observed value; curve, predicted value.

Table 1. Parameter estimates in modelling the relationship between the proportion of crabs moulted and number of days at large using a logistic function defined in Eqn (1)

Sex	Size class	Parameter estimate			
		a	b	D_{50}	N
Female	≤81 mm	−5.67	0.0116	489	30
	81–90 mm	−5.27	0.0108	488	55
	>90 mm	−1109.2	1.775	625	30
Male	≤81 mm	−46.32	0.2018	230	24
	81–90 mm	−2.97	0.0120	248	49
	91–100 mm	−4.07	0.0137	297	80
	>100 mm	−3.20	0.0065	492	94

Results from 100 simulation runs using the PSGC approach are presented in Fig. 6. Variation in size at age tended to be smaller for younger crabs and increased with age, particularly for males. There were six distinct patches in size at age for females. Patches could only be seen for males younger than about 4 years (Fig. 6). This difference in patchy patterns between females and males may have resulted from smaller variations in size increments per moult for females than for males (Fig. 5). Males appeared to reach their maximum asymptotic size (L_{max}) at ~140 mm, whereas in females L_{max} may be >110 mm. In the majority of the 100 simulation runs, both females and males increased their sizes from L_1 to near L_{max} within 10 years (Fig. 6).

Mean, median, lower 5 and upper 5 percentiles of size at relative age estimated from the 100 simulation runs using the PSGC approach are presented in Fig. 7. In only a few runs (<3) did male crabs reach a relative age of 12 years because of their slow growth rate, and this resulted in the small variation in size at relative age for crabs older than relative age 12 (Fig. 7).

Discussion

The time period between two moults was approximated by the time period between tagging and recapture for crabs that moulted once while at liberty. Like most growth studies of crustaceans using tagging data, this approximation assumes that crabs had just completed moults before tagging and recapture. In this study, this assumption may introduce some errors in modelling the relationship between the number of days at large and the proportion of crabs that had

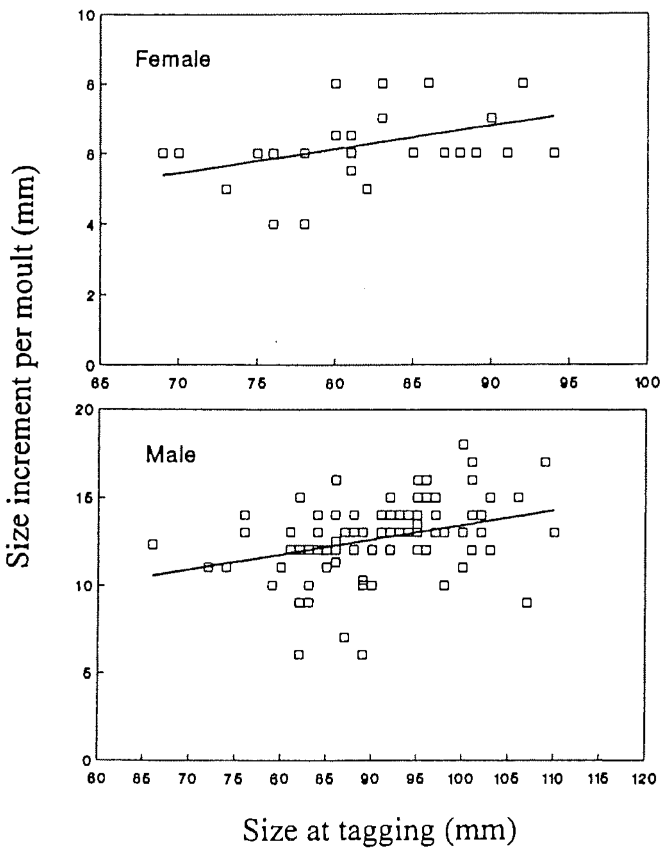

Fig. 4. Frequency of size increment per moult for spanner crabs of different size classes.

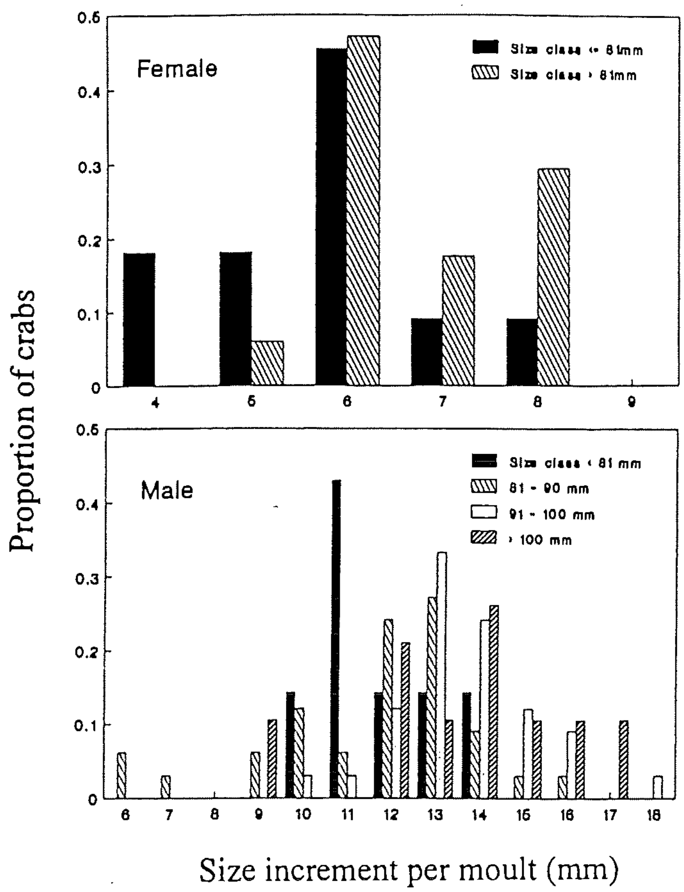

Fig. 5. Relationship between size increment per moult and pre-moult size.

moulted. However, the number of days at large was grouped as day classes with an interval of 50 days and we assume that such a large interval should reduce the errors. The estimates of D_{50} were shown to be very robust to errors in the data (e.g. Chen and Paloheimo 1994), thus errors associated with the D_{50} estimates are likely to be small, and should not affect the estimation of growth curves using the PSGC approaches.

Slopes of the regression equations between post-moult size increments and pre-moult sizes were significantly larger than zero, suggesting that larger spanner crabs tend to have larger size increments per moult than smaller crabs. However, large crabs tend to moult less frequently; it is, in fact, apparent from the growth curves generated by using the PSGC approach that the growth rate decreased with increased sizes.

Despite the significant relationships between size increments and pre-moult sizes, pre-moult size accounted for only 15% and 11% of variances in post-moult size increments for female and male crabs, respectively. This may suggest that there are other factors, in addition to pre- moult size, that may significantly affect size increments. These factors may include biotic and abiotic environmental variables such as food supply and temperature (Annala and Bycroft 1988). Further studies are needed to identify the effects of such variables.

Males <100 mm tended to moult twice as frequently as females and also yielded much greater size increments. Thus, one can conclude that male spanner crabs along the NSW coast grow much faster than females. This result is of significance to the management of this fishery, which involves a minimum size limit of 93 mm. This size limit effectively excludes the majority of females in the population from exploitation, and the fact that males grow much faster than females is an obvious advantage for the sustainable exploitation of this male-dominated fishery. The corollary is that, in protecting the much slower growing females, the size limit should be enhancing the fecundity of the population and subsequent stock sizes.

The growth curves generated in this study show that male spanner crabs reach legal size (93 mm) from 66 mm in <2 years whereas females take ~4 years to reach legal size from 69 mm. Because there are no data for the growth of spanner crabs smaller than these sizes, these growth rates are relative to the smallest sizes observed for females and males in this study. Only by including growth information for smaller crabs (ideally from newly settled juveniles through to 60 or 70 mm), will it be possible to provide a growth model based on true age.

In a study that attempted to consider discontinuous growth, Annala and Bycroft (1988) proposed an approach that uses the moult frequency and size increment per moult as input data to generate growth curves for New Zealand rock

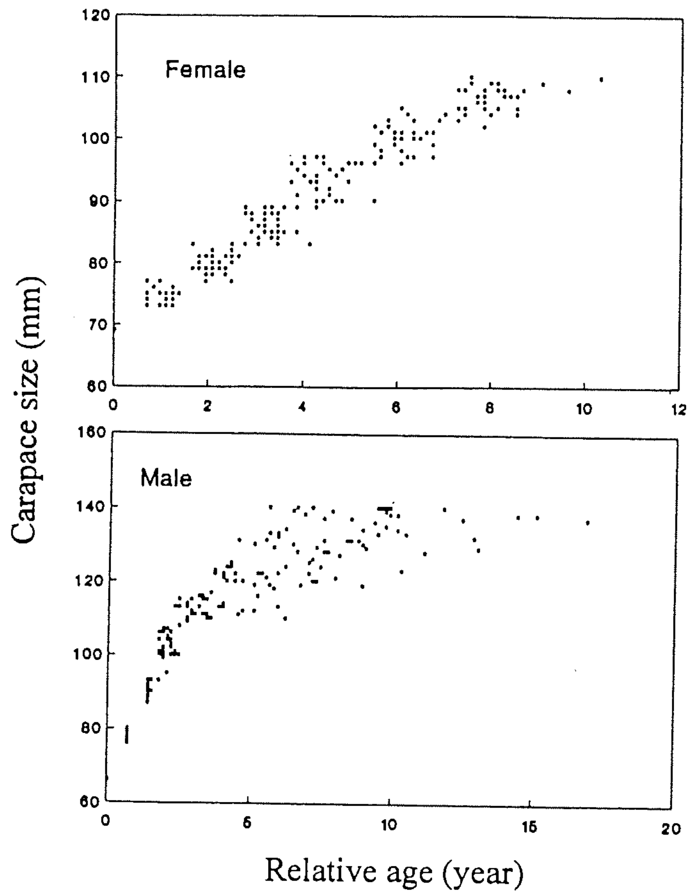

Fig. 6. Scatterplot of size at relative age generated from 100 simulation runs using the probabilistic stepwise growth simulation approach.

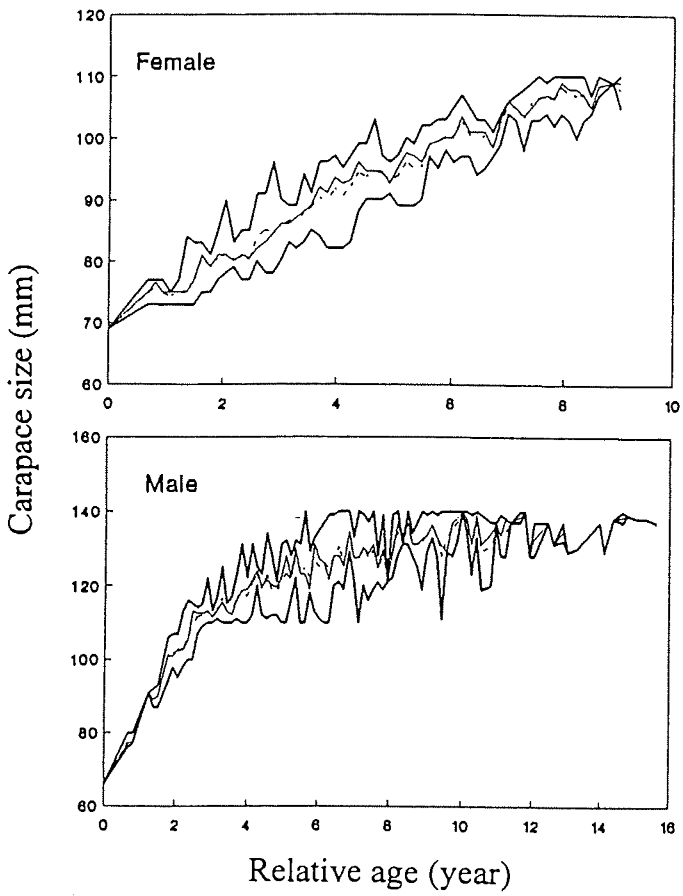

Fig. 7. Mean (dashed line), median (central thin line), and lower and upper 5th percentiles (outer thick lines) of carapace size at (relative) age resulting from 100 simulation runs using the probabilistic stepwise growth simulation approach.

lobster *Jasus edwardsii*. However, this approach is deterministic and disregards the variation intrinsic to the observed data. The PSGC approach used in the present study provides probabilistic projections of the stepwise growth. The distributions of simulated growth trajectories are assembled by allowing sample crabs to grow in accord with size-specific moult frequencies and size increments per moult. When large numbers of growth curves are simulated, estimates of ranges, prediction intervals, medians and means may be obtained that reflect the variation in growth rates implicit in the raw data. Because the PSGC approach allows estimates of uncertainty for estimated growth curves that reflects true variation in the raw data, we recommend its application for estimating growth in crustaceans using tag–recapture data.

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