

Studies on the growth and mortality of school prawns

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Note: This electronic version of the report contains an amendment for an error in the report printed in June 2010. The original report stated incorrectly that there were no differences in growth between stocks. The correct result is that male growth differed between stocks but female growth did not. The conclusion that a single growth function for each sex could be used to represent growth is therefore incorrect. The changes that have been made were on the following pages: page v 2nd, page 14 3rd paragraph, page 18 4th paragraph, page 28 Abstract, page 33 last paragraph, and page 35 3rd paragraph

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NON-TECHNICAL SUMMARY

2001/029	Studies of the growth and mortality of the school prawn
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OBJECTIVES:

- (1) To estimate values for parameters describing growth of school prawns.
- (2) To estimate values for instantaneous fishing mortality for school prawns.

NON TECHNICAL SUMMARY:

OUTCOMES ACHIEVED

This project has contributed to the ecological sustainable management of the school prawn populations of the east coast of Australia by providing greatly improved information on the growth of the species and the first estimates of rates of natural and fishing mortality. These outcomes were achieved through replicated fishery independent surveys and tag-recapture studies. The information from this project will update parameter estimates in population models which in turn will through stock assessments be transferred into reliable determinations about the optimal harvest strategies for the school prawn populations.

Information about growth and mortality are important in the management of resources because these provide us with an understanding about the productivity of the target population. Estimates are used to assess the impact of fishing upon the target population and the effectiveness of various scenarios in achieving the management objective which is usually the sustainable harvest of resources. The school prawn, *Metapenaeus macleayi*, is one of three target penaeid species of commercial and recreational importance in estuaries of NSW. It contributes around 64% by weight and 46% by value to prawn production in NSW and is harvested by three commercial fisheries; namely the ocean trawl (8% by weight of commercial landings), estuary prawn trawl (64 %) and the estuary general fishery (28%). Because all stocks could not be studied, we adopted the approach of choosing those that were expected to include the greatest variability about growth and mortality parameter estimates. Growth was investigated by doing monthly fishery independent surveys on the Clarence and Hunter Rivers. Monthly length frequencies were separated into groups of prawns of similar age and these data were then fitted to the Schnute growth models. Female prawn growth was best fitted by a special case of the Schnute model which is equivalent to the von Bertalanffy growth function (VBGF; $L_{\infty} = 36.6$ and 40.2 CL mm and $\kappa = 0.005$ and 0.005 day^{-1} , for Clarence and Hunter, respectively), whilst male growth was best fitted by a four parameter Schnute curve ($L_{\infty} = 21.3$ and 33.5 CL mm and $\kappa = 0.025$ and 0.009 day^{-1} , for Clarence and Hunter, respectively). Male school prawns grew to smaller maximum lengths and had faster rates of growth than females and lived for less than two years. While female growth data fitted the VBGF, much of

the observed growth was linear and female prawns never reached the maximum lengths predicted by the growth model, probably because of high rates of mortality. Male growth differed between stocks but female growth did not.

Total mortality is the sum of the components of losses due to harvesting (fishing mortality) and natural mortality where the latter includes losses not only from natural causes such as disease and predation but also losses due to movements of animals out of the fished area. Natural mortality was estimated using meta-analyses that use known associations between natural mortality (dependent variable), longevity and life history parameters for taxonomic groups of species to predict natural mortality of species where only longevity and life history parameters are known. Natural mortality was greater in males than females and was greater in the more northern Clarence stock (0.002 to 0.007 and 0.006 to 0.025 for females and males, respectively) than in the Hunter stock (0.001 to 0.005 and 0.004 to 0.016).

Fishing mortality is the product of fishing effort and the catchability coefficient (the proportion of the stock taken by one unit of fishing effort). A total of 21,096 school prawns were tagged and released in replicated tag-recapture experiments on the Clarence River and Wallis Lake to estimate the catchability coefficient, whilst the records from the Clarence River and Wallis Lake Fishermen's Cooperatives and a daily log book were used to calculate fishing effort. We addressed the assumptions of tag-recapture experiments by randomly dispersing tagged prawns throughout the school prawn population and by doing experiments in the laboratory and in the field to quantify the impacts of tagging and non-reporting of captured tagged prawns. It was estimated that between 50 and 60% of prawns survived the tagging process and that between 100 and 80% of the captured tagged prawns were reported. Numbers of tagged prawns released were adjusted for these effects. Fishing mortality was estimated by fitting the tag-recapture and fishing effort data together with numbers of tagged prawns released and a range of natural mortality values to a population model and using minimum likelihood optimisation to solve for the catchability coefficient. Estimates for the catchability coefficient and therefore fishing mortality varied between years and the values of input parameters. Daily values ranged between 0.00008 and 0.00137 for the Clarence stock and, 0.00008 and 0.00147 for the Wallis stock. Fishing mortality values ranged from 0.0014 to 0.0358 (per day) and 0.0008 to 0.009 for the Clarence and Wallis stocks respectively. The catchability coefficient was estimated with little precision but values for this parameter, natural and fishing mortality were within the ranges of those documented for other penaeid fisheries around the world. There was evidence to suggest that it and therefore fishing mortality increased greatly at times of high river discharge. Exploitation ratios (ratio of fishing mortality to total mortality) again varied with values ranging between 13.3% and 94%, and 8.4% and 87% for the Clarence and Wallis stocks, respectively, but were generally greater than 40% for both stocks.

This study has provided the first estimates of growth and mortality that can be used in population models to assess the impact of scenarios presented by fisheries managers as options for the sustainable exploitation of the valuable school prawn resource. The study incorporated wide variability in growth and mortality by choosing stocks that were near the northern and southern bounds of the main commercial fisheries for school prawns and that were harvested using a broad range of fishing methods. Population models for the school prawn populations need to be updated in light of the results of this study to give information about sustainable levels of exploitation for school prawn resources.

KEYWORDS: growth, mortality, school prawn, length frequency analyses, tag-recapture, New South Wales

1. BACKGROUND

The prawn resources of New South Wales (NSW) are the most economically valuable seafood resource managed solely by the NSW State Government, worth on average between 2003-04 and 2007-08 (inclusive) \$AUS 18 million per annum at the point of first sale. School prawns (*Metapenaeus macleayi*), eastern king prawns (*Melicertus plebejus*) and royal red prawns (*Haliporoides sibogae*) make up the bulk of the catch. The former two species are the target species of commercial and recreational fishers operating in estuaries and of commercial fishers in ocean waters. Royal red prawns are the main target species of commercial fishers in the deepwater fishery off the edge of the Continental Shelf of NSW. School prawns contributed on average 46% by weight to this prawn production over the period 2003-04 to 2007-08 (I&I NSW FINS database).

Not only do the prawn resources of NSW support a significant commercial industry but together with eastern king prawns, school prawns support a substantial recreational fishery in NSW estuaries. For instance, a study of recreational fishing for prawns in four NSW estuaries estimated the recreational catch to be 30% of the landings by commercial fishers from the same estuary (Reid and Montgomery 2005).

School prawns are distributed in estuaries and ocean waters out to depths of around 55 m along the east coast of Australia from Corner Inlet (Vic) to Tin Can Bay (Qld). The resource is now fished by recreational and commercial fishers in estuarine waters and by commercial fishers in oceanic waters across this geographic range. Many methods are used by recreational and commercial fishers in NSW estuaries to catch school prawns, but only trawling is used in ocean waters (for a description of gears see Broadhurst 2008). Because this species does not move far from the estuary from which it emigrates, the NSW government manages the main school prawn populations as unit stocks.

The NSW government and commercial and recreational fishers want to know with reasonable confidence what size at first capture will optimise sustainable yield from the school prawn resource. One management option being considered for the school prawn resource is to introduce a “pseudo-size limit” in the form of a maximum count of prawns to the half kg. Ives *et al.* (2009) have developed a population model that incorporates parameters for environmental factors, recruitment, growth and mortality which can be used to determine with high levels of precision optimal sizes at first capture. What is needed as inputs to the model are more precise estimates of growth parameters and estimates of rates of mortality.

School prawns have been studied to a significant extent in the past, but none of these studies were dedicated to the population dynamics of this species (Ruello 1971 1973a,b 1977, Glaister (1977, 1978a,b). Rather, previous studies concentrated on the distribution and abundance or movements of school prawns and those few studies that addressed the question of declining catches, attributed patterns in catch to the level of river discharge or rainfall (e.g., Ruello 1973b, Glaister 1978a).

There have been few published papers on growth models and rates of mortality either for school prawns or for a metapenaeid species. Ruello (1971) and Glaister (1977) attempted to quantify the growth of school prawns using tagging techniques but sample sizes of recaptures were small and were not representative of the size range of the species. This small amount of tagging information on growth was used by Montgomery (2000) to estimate values for growth parameters. However, the level of precision around these estimates was low, and better estimates are required for the management of the species. Notwithstanding, results from population modelling using these data show that school prawns are currently being caught at sizes that are far smaller than those that would optimise biological “yield per recruit” under an F0.1 fishing policy (Montgomery 2000). But

there can be little confidence in the predictions of the models as they currently stand because the confidence ranges about the estimates of optimum sizes of first capture are so large. This is a direct effect of the wide confidence range in estimates of growth and mortality derived from the data of Ruello (1971) and Glaister (1977). Ives *et al.* (2009) developed a size-based metapopulation model for the school prawn population of the Clarence River that had as its objective to assess the impact of climate change upon the school prawn stock. The model incorporated both biological information from the study of Glaister (1977) and environmental parameters (water temperature and river discharge) and showed that two of the main drivers of catch were the relationship between stock and recruitment and the level of river discharge. More precise estimates of growth and mortality than can be derived from the studies of Glaister and Ruello are needed to improve the confidence about predictions from the yield per recruit and size structured modelling.

The harvesting of small eastern king and school prawns has long been an issue raised at meetings of the Ocean Prawn Trawl Management Advisory Committee. A Juvenile Prawn Summit was held by NSW Fisheries in June 2000 to discuss the issue of catching small prawns. It was attended by representatives from all Management Advisory Committees covering all catching sectors, the NSW Seafood Industry Council, Master Fish Merchants Association, National Conservation Council and Ocean Watch. All agreed that there was a need to harvest the school prawn resource in a way that was fair to all stakeholders. For this reason it was also agreed that research to study the dynamics of school prawn populations was urgently needed.

1.1. The fishery for school prawns in New South Wales

School prawns are a target species of three fisheries in New South Wales; namely the estuary general, estuary prawn trawl and ocean trawl fisheries. A diverse range of gears are used across these fisheries and the fisheries are all managed by a suite of input controls that include limits on gear dimensions, numbers of operators, area and time of operation and minimum and maximum legal mesh openings (Anon 2003a). The estuary general fishery targets school prawns in around 60 of the 130 coastal estuaries of NSW with average annual reported landings between 2003-04 and 2007-08 (inclusively) of 182 tonnes, worth approximately AUD 1.4 million per annum. Several types of gear are used (for descriptions see Broadhurst 2008) and times of operation vary between estuaries. The estuary prawn trawl fishery is restricted to three estuaries in NSW; namely, the Clarence, Hunter and Hawkesbury Rivers and uses otter trawl nets of 11 m total headline length, towed as either single or double rig combinations. Times of operation are restricted and vary between estuaries (Anon 2003b). Average annual reported landings are approximately 406 tonnes, worth AUD 2.9 million per annum. The ocean trawl fishery operates year around (Anon 2007) but targets school prawns primarily between January and June when the species emigrates from estuaries. Otter trawl nets of varying headline lengths are towed in triple, double or quadruple configurations. School prawns are caught by ocean trawl fleets from Shoalhaven Heads (34 °S) to Tweed Heads (28°S). Annual landings average approximately 52 tonnes and are worth AUD 349 thousand per annum.

2. NEED

Considering the prominence of the NSW prawn resources, it is important that managers be equipped with the information necessary to manage the school prawn resource in a sustainable way that provides equity for all stakeholders. Despite its prominence as one of the two most important contributors to the prawn production in NSW, little is known about the population dynamics of this species.

The data upon which population modelling of the species has been based is imprecise. Estimates of growth and mortality with acceptable levels of precision are needed so that population models can be used with confidence to predict the outcomes of scenarios aimed at optimising the use of the school prawn resource. Out of a list of ten topics needing research, attendees at the Juvenile Prawn Summit in June 2000 assigned the highest priority for research to the study of the growth and mortality of school prawns

3. OBJECTIVES

- (1) To estimate values for parameters describing growth of school prawns.
- (2) To estimate values for instantaneous fishing mortality for school prawns.

4. METHODS

4.1. Estimating parameters for growth models

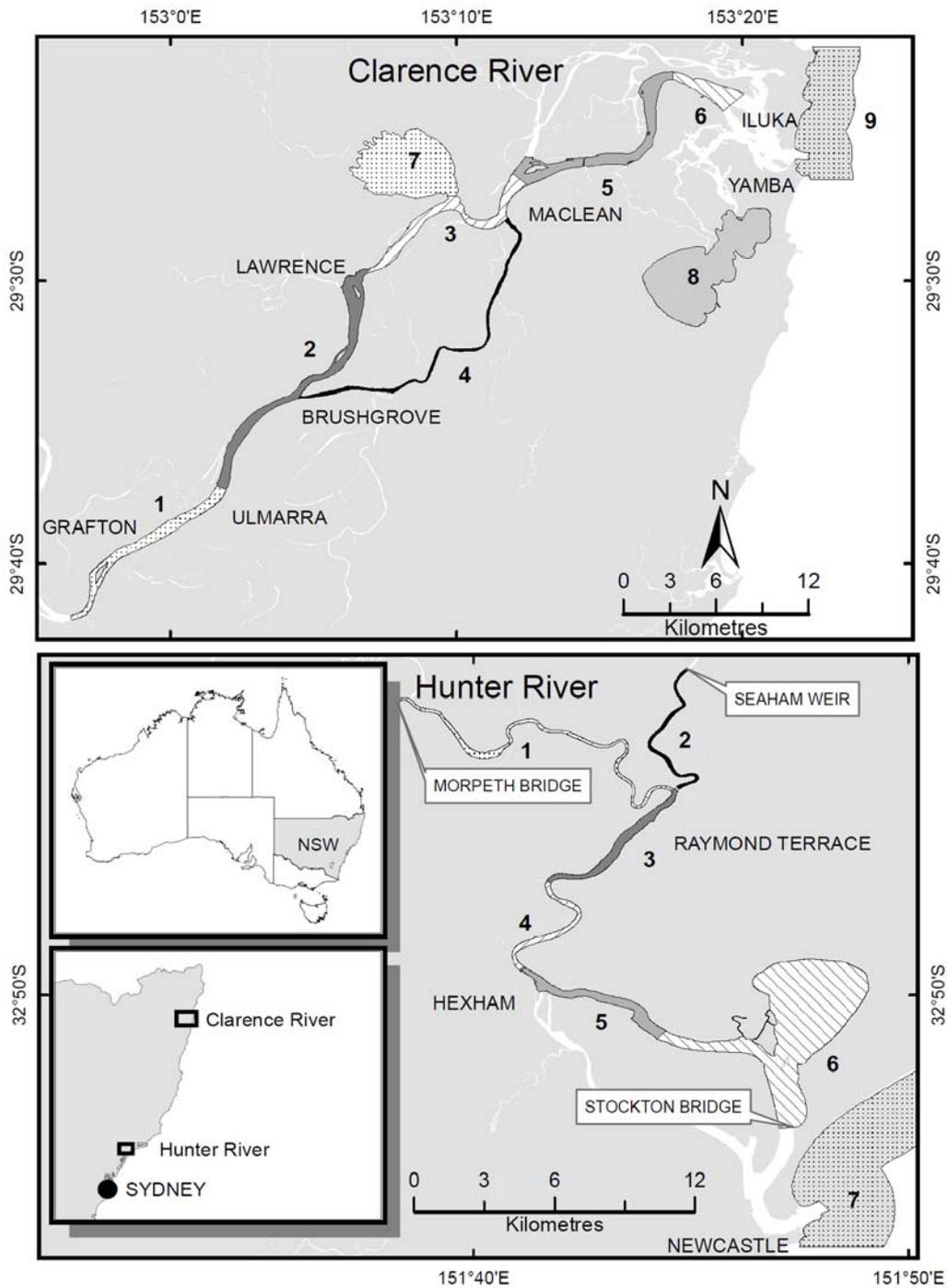


Figure 1. Location of the Clarence and Hunter stocks of school prawns and the zones used in random stratified surveys. Numerals and shading are used to distinguish the zones.

The stocks of school prawns in the Clarence and Hunter Rivers were used to study growth and estimate natural mortality, so that growth parameters were estimated for stocks distanced by a wide spatial range. The stock in the Clarence River (Clarence stock) is exploited by estuary general, estuary prawn trawl and ocean trawl fisheries. It is the most important producer of school prawns in NSW, landing on average between 2003-04 and 2007-08 (inclusive) 52% of the state's total landings of this species by weight each year (I&I NSW FINS database). The stock of school prawns in the Hunter River (Hunter stock) is amongst the southern most stocks that sustain both an estuarine and ocean fishery and accounts for around 5% of school prawn production in NSW per annum.

The Clarence and Hunter Rivers were divided into zones of approximately the same surface area (Fig. 1). In ocean waters, surveys were limited to grounds within 1.5 nm of the shoreline that were fished by the local commercial fishing fleet. Commercial fishing vessels were chartered in each estuary to do the surveys. Each chartered vessel used the standard design of trawl net used in commercial operations in the particular estuary but with a codend of small, square mesh. Surveys were done in the week after full moon in each lunar month for two years. Surveys in estuarine waters consisted of five minute trawls done at each of two shallow and two deep grounds within each zone, whilst in ocean waters three 20 min trawls were done. At the end of each trawl the net was brought on board, and the catch sorted. The catch of prawns was weighed (nearest 10 g) and if too large then a random proportional sample was retained for processing in the laboratory, and the remainder of the prawns were released. In the laboratory each sample of prawns was separated into gender. The length of each individual was measured to the nearest mm as the straight line distance between the base of the eye orbit and the centre of the posterior margin of the carapace (orbital carapace length, CL), using dial callipers.

The measurements were collated into length distributions for each survey and modal analyses were applied to the length distributions to separate these into monthly age-groups (cohorts) (Figure 2 in Appendix 3). Mean lengths for each cohort and sampling time were fitted to the Schnute (1981) growth model.

4.2. Estimating rates of mortality

4.2.1. Tagging procedure

The study area was limited to estuarine waters where the bulk of the school prawn catch is taken. Attempts to include ocean waters in experiments were unsuccessful because of the sporadic nature of the fishery in these waters and the longevity of the tagged prawns. The stocks of school prawns in the Clarence River and Wallis Lake were used to study fishing mortality so that fishing mortality was estimated across a broad range of fishing gears and a wide spatial scale. We chose the estuary general fishery on Wallis Lake rather than the fishery on the Hunter River to study fishing mortality in a southern stock because the fishery on Wallis Lake included a wider range of gears than used on the Hunter River. The stock of school prawns in Wallis Lake (Wallis stock) is amongst the southern most stocks that sustains both an estuarine and ocean fishery and accounts for around 5% of school prawn production in NSW per annum.

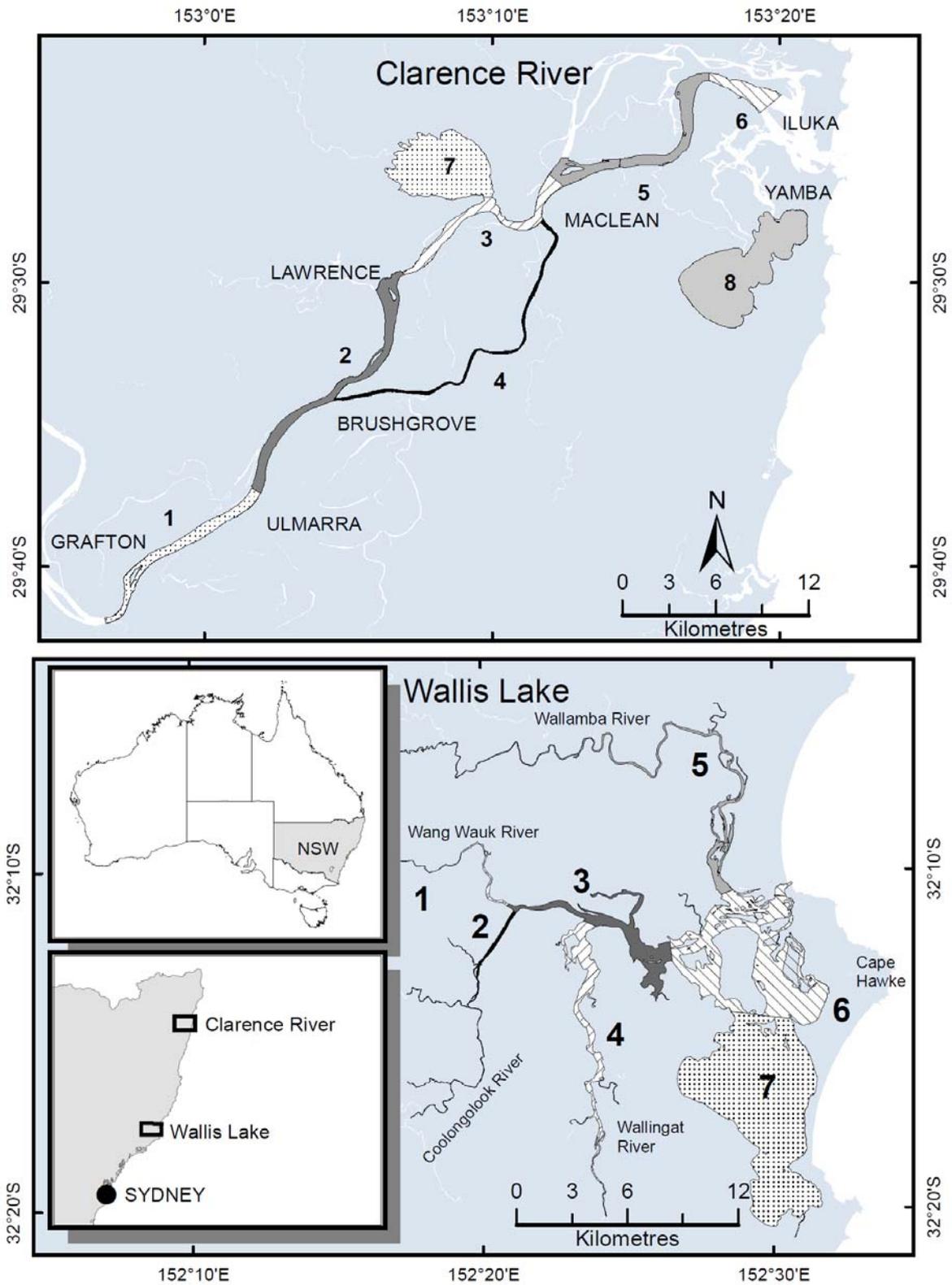


Figure 2. Location of the two school prawn stocks used in tag-recapture studies to estimate rates of fishing mortality. Numerals and shading are used to show the stratification of each estuary into zones.

The Clarence River and Wallis Lake were divided into grids of approximately the same surface area (Fig. 2). A five minute trawl was done using a chartered commercial fishing vessel at each of two randomised sites within each grid and prawns in the catch were tagged by research staff. Prawns were tagged with streamer tags through the articular membrane between the first and second tail segments. Tagged prawns were placed into collapsible canisters (Emiliani 1971; \approx 100 prawns per canister), and released back on the bottom in the same area from which they had been caught. A subset (100 prawns) of the tagged prawns were measured (carapace length CL) to the nearest mm below and their gender determined.

We relied upon commercial fishers to return captured tagged prawns. Media exposure, extensive liason and a reward system of caps, T-shirts and lottery tickets were used to promote the return of tagged prawns. Research staff were at the sites of landing (Clarence River and Wallis Lake Fishermens Cooperatives) at the time when most of the prawns were weighed-in to collect tagged prawns and pay rewards.

4.2.2. *Effects of tagging*

The assumptions behind a tag-recapture experiment are that (i) the tagged animals become randomly mixed amongst the non tagged population, (ii) the fate of each tagged animal is independent of that of the other tagged animals, (iii) there is no loss of tags, (iv) survival rates of tagged animals are not influenced by tagging, (v) all captured tagged animals are reported and (vi) there is only negligible recruitment to the catchable population (Ricker 1975 and Pollock *et al.* 1991). Whilst (ii) was assumed, we addressed assumption (i) by randomly distributing the tagged prawns throughout the estuary and ocean waters and tested (iii) to (v) through experiments in the laboratory and in the field.

We tested the hypothesis that tagging affects the survival and, or growth of school prawns in experiments done at the I & I NSW, Cronulla Fisheries Research Centre, Sydney, and the National Marine Science Centre, Coffs Harbour, using prawns from the Hawkesbury River and Clarence River populations, respectively. Details of the methods used in these experiments can be found in the published manuscript in Appendix 4. In addition, on-site experiments were done to test the hypothesis that estimates of tag mortality (including tag loss) derived from experiments in the laboratory were the same under field conditions (Appendix 5). The proportion of captured tagged prawns reported (assumption v) was quantified through two experiments at the Clarence River, whilst it was assumed that there was 100% reporting in the Wallis Lake fishery (Appendix 5)

4.2.3. *Data analyses*

Rates of daily natural mortality were calculated using meta-analyses which uses associations between natural mortality and longevity and life history parameters for taxonomic groups of species to predict natural mortality of species where only longevity and life history parameters are known. Fishing mortality was calculated from the equation:

$$R_t = (N_{t+1} - N_t) \frac{F_t}{F_t + M_t} \quad (1)$$

Where R_t is the predicted number of recaptures in period t, F_t is fishing mortality, M_t is natural mortality, N_t is the numbers of tagged prawns surviving to time t,

$$N_{t+1} = N_t e^{-(F_t + M_t)} \quad \text{and} \quad (2)$$

$$F_t = qf_tS, \quad (3)$$

Fishing mortality is assumed to be the product of fishing effort (f_t), the catchability coefficient (q) and the selectivity (S) of the fishing gear. Selectivity was assumed to be 1 because all tagged prawns were longer than the length range over which selection in the trawl net occurred (Broadhurst *et al.* 2004). The only unit of fishing effort available to us was the 'fisher day'. It was collected from voluntary log books completed by fishers and the records of Fishermen's Cooperatives.

The agreement between the observed and predicted numbers of recaptures (R_t) was optimized by solving equation 1 for the catchability coefficient (q) using the Solver™ add-in in Excel™ (which uses numerical differentiation to implement efficient downhill optimisation).

5. RESULTS

5.1. Estimating parameters for growth models

Figure 2 in Appendix 3 shows the separation of each length distribution into cohorts and the time-ordered sequence of cohorts in each stock. When the mean lengths of each cohort are plotted through time it is evident that the growth of prawns in a cohort approximates a straight line, until lengths of around 20 mm CL are achieved, after which the slope of the line declines (Figure 3 in Appendix 3). This change in slope often corresponded to when the cohort occurred in ocean waters, and was less evident for male data.

The best fit for female data from each stock was Case 5 in the Schnute model which was equivalent to the von Bertalanffy growth function (VBGF) whilst for males the best fits were Cases 1 and 2 for the Clarence and Hunter stocks, respectively (Table 1).

Notwithstanding this, there were no differences in the curves between Cases 1 and 2 for male data from the Hunter and as a consequence it is recommended for reasons of simplicity that Case 1 be adopted as the most appropriate fit for the male data for both stocks (Table 1). Male growth differed between stocks but female growth did not (Fig. 3).

Table 1. Estimates of growth parameters for the five cases of the Schnute model fitted to mean length at age data for school prawns from the Clarence (CR) and Hunter (HR) stocks. The first order CIs about each parameter (CI), residual sums of square (RSS), and the number of cohorts contributing to the calculation (n) are shown. $n = 121$ and 91 for Clarence River and, 132 and 105 for Hunter River females (F) and males (M), respectively.

	Case	L_{∞} (CI)	κ (CI)	γ (CI)	RSS
CRF	5	36.6 (43.4 – 34.0)	0.005 (0.006 – 0.004)	1	298.56
CRM	1	21.3 (22.6 – 20.4)	0.025 (0.033 – 0.020)	-1.349 (-0.646 – -2.286)	116.20
HRF	5	40.2 (45.4 – 36.9)	0.004 (0.005 – 0.004)	1	320.44
HRM	1	33.5 (37.6 – 29.7)	0.009 (0.012 – 0.006)	0.145 (0.011 – -0.668)	185.34

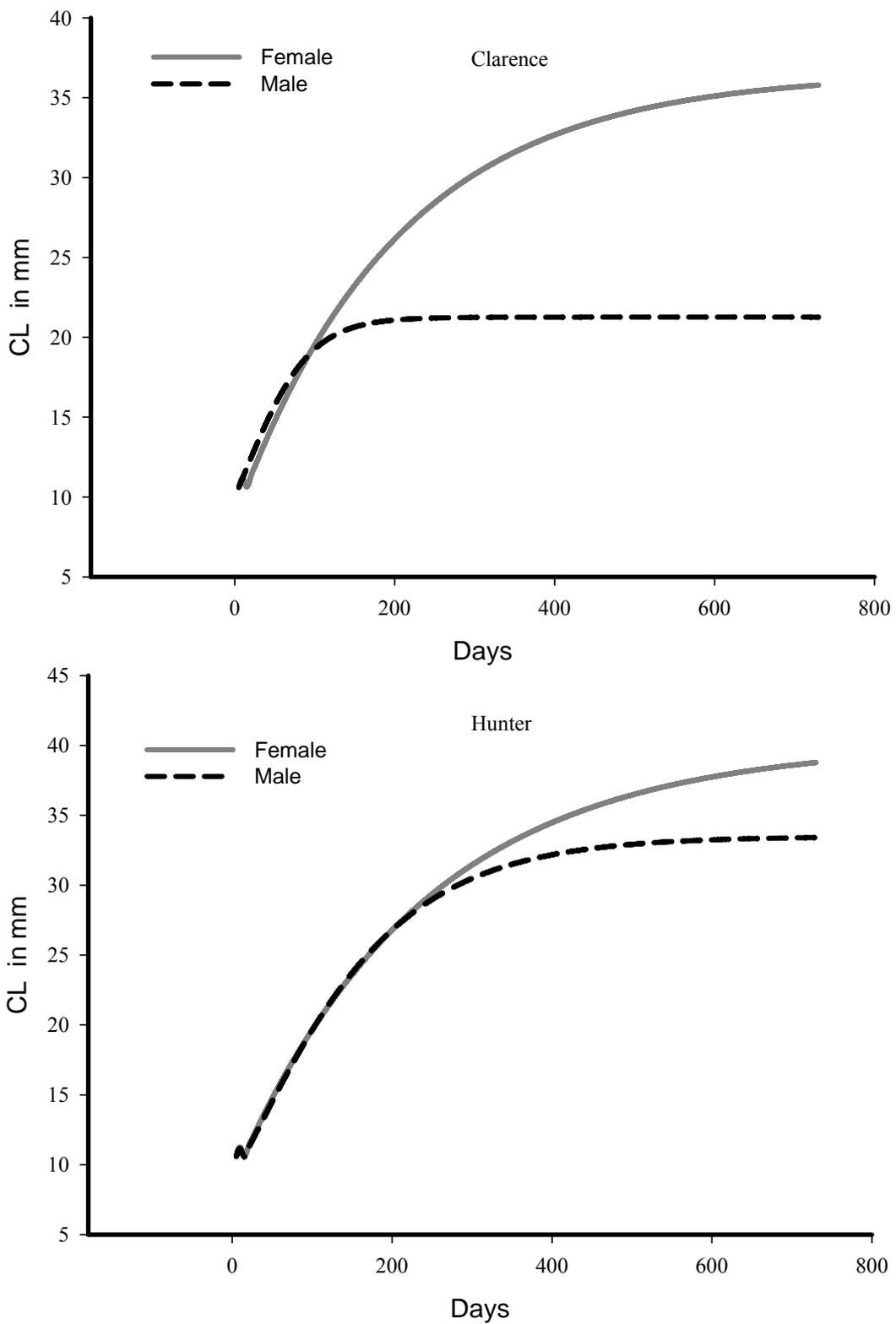


Figure 3. Predicted growth curves for a school prawn of 5 mm CL initial length in the Clarence and Hunter stocks.

5.2. Estimating rates of mortality

Staining and tagging affected the survival of prawns, particularly during the first two weeks of each experiment, but there was no difference in survival (50 – 60%) between these two treatments. The growth of the prawns was not affected by the staining or tagging processes and the size or gender of the prawn did not affect survival (Appendix 4). Results from the field based experiments supported those from the experiments done in the laboratory with survival rates between 60 and 70% (Appendices 4 and 5). Estimates of the proportion of captured tagged prawns reported ranged between 100 and 80% (Appendix 5).

Table 2. Summary of numbers of tagged school prawns released (before being adjusted for the effects of tagging – see text) in each stock, the numbers recaptured from each release and the mean (CL in mm), standard error, and size range (CL in mm) tagged for each release.

	No Released	No Recaptured	Mean CL	SE	Size Range	
					Min	Max
Clarence Stock						
Feb'05	3,100	65	15.9	0.04	12.2	22.1
April'05	5,150	33	16.9	0.04	13.0	23.1
Jan'06	1,921	155	19.4	0.05	16.2	25.5
Mar'06	2,548	178	20.4	0.3	14.3	23.5
Wallis Stock						
Oct'04	2,084	143	16.5	0.08	12.8	22.1
Nov'04	3045	69	16.3	0.08	12.2	23.4
Dec'05	1198	110	19.9	0.08	15.8	24.8
Jan'06	2050	172	20.0	0.09	15.9	25.7

A total of 21,096 tagged school prawns were released across all experiments and 431 and 494 tagged prawns were reported recaptured from the Clarence River and Wallis Lake releases respectively (Table 2). Estimates of natural mortality from meta-analyses ranged from 0.002 to 0.007 and 0.005 to 0.025 for females and males in the Clarence stock and from 0.001 to 0.005 and 0.004 to 0.016 for females and males in the Hunter River (Table 2 in Appendix 5). Values for the catchability coefficient varied between years and the input values of numbers released and natural mortality used to derive it. Ranges in catchability coefficient were similar between the Clarence and Wallis stocks, but estimates of fishing mortality were greater for the Clarence stock because of greater fishing effort (Table 3). The catchability coefficient and therefore fishing mortality were not estimated with much precision probably because there was great variability in the number of tagged prawns captured each day. Exploitation ratios were between 13.3% and 94%, and 8.4% and 87% for the Clarence and Wallis stocks, respectively. Values for fishing mortality and exploitation ratios were greater in 2005-06 than in 2004-05 because catchability coefficient values were greater.

Table 3. Ranges of daily estimates of the catchability coefficient (q), fishing mortality (F) and exploitation ratio (E) for the Clarence River (CR) and Wallis Lake (WL) school prawn stocks.

	Year	q		F		E	
		Lower	Upper	Lower	Upper	Lower	Upper
CL	2004-05	8.93E-05	5.02E-04	1.38E-03	5.12E-03	13.1	71.6
CL	2005-06	7.17E-04	1.37E-03	9.81E-03	3.58E-02	52.7	94.3
WL	2004-05	7.77E-05	5.04E-04	8.63E-04	4.78E-03	8.4	78.1
WL	2005-06	9.37E-04	1.47E-03	5.49E-03	8.95E-03	38.2	88.2

Past studies on school prawns had shown high correlations between catch and river discharge (Ruello 1973b, Glaister 1978a). Therefore, in an attempt to explain the high variability about estimates, the catchability coefficient was plotted against river discharge in the Clarence River and rainfall from Wallis Lake (river discharge data were not available) for those months in which tag-recapture experiments were done to ascertain whether any association existed. There was a significant correlation between river discharge and the catchability coefficient for the Clarence stock but not between rainfall and the catchability coefficient for the Wallis stock (Figure 3 in Appendix 5).

6. DISCUSSION

This study has greatly improved our knowledge on the patterns of growth in school prawns and has provided the first estimates of rates of natural and fishing mortality for this species. Few studies in the past 20 years have estimated rates of mortality in prawn stocks, and we could find no other studies in the literature that had used the Schnute (1981) growth model to explore growth in a penaeid species, despite its wide acceptance in the literature about fish growth. Also, we used a novel approach to model growth by fitting mean length at age (cohort) data to the Schnute model (1981).

The technique of length distribution analyses to study growth in penaeid populations has been used in several past studies (e.g., Baelde 1994, Yamada *et al.* 2007) and was the only option available to study growth in school prawns. Data from tag-recapture experiments were not useful because tagged prawns did not survive long enough to provide information about growth and attempts to use biochemical assay techniques to age prawns were unsuccessful because there were insufficient quantities of lipofuscin in the prawns to use for aging purposes (Krusic Golub pers. Com.).

Growth was linear for much of the prawn's life probably because the prawns only mature toward the end of their life when they move from estuarine to ocean waters. All energies in juvenile prawns are allocated toward growth, but once the prawns mature some energy is diverted to reproduction; hence growth slows (Dall *et al.* 1990). Notwithstanding this linear growth, curvilinear models fitted the data on mean lengths best but no single case of the Schnute model provided an optimum fit to all data sets. In the majority of cases the Schnute model predicted longer maximum lengths than were observed in samples probably because school prawns did not survive long enough to grow to the maximum size. This high mortality means that there were few prawns longer than sizes at maturity (when growth has slowed) in samples to influence the curvature during the model fitting process.

Comparing our results with those published in the peer reviewed literature for other prawn species suggests that school prawns are amongst the smallest of the metapenaeid species and are smaller than their main con-specific in NSW waters, the eastern king prawn. Whilst no formal comparisons in growth between genders could be done because different curves fitted males and females best, the general pattern whereby females grow to a longer length than males but at a slower rate (Dall *et al.* 1990) is consistent with the results in our study.

Many studies remark on the difficulty in estimating natural mortality (e.g., Xiao and McShane 2000). Estimates of natural mortality and the catchability coefficient in our study like in many other studies on short-lived species (Cobb and Caddy 1989, Wang and Ellis 2004) were correlated. Consequently an alternative approach was taken to estimate natural mortality by using a range of meta-analyses, and examining the sensitivity of the catchability coefficient to a range of natural mortality values.

Estimates of natural mortality were with one exception, within the range of those published for other penaeids (Table 6 in Appendix 5). The differences in natural mortality between genders is consistent with the pattern that animals with faster growth rates reach smaller mean maximum sizes and have higher natural mortalities (Quinn and Deriso 1999). Male school prawns have the higher rates of natural mortality and growth and, attain smaller maximum sizes than females. Also, the spatial pattern in natural mortality values fits the general pattern that stocks from cooler waters (Hunter River) have lower rates of natural mortality than stocks in warmer waters (Clarence River) (Quinn and Deriso 1999, Pauly 1980).

We addressed the assumptions underpinning a tag-recapture study by firstly designing our experiments so that tagged prawns were scattered throughout the prawn stock in proportion to the relative numbers of prawns in the wild. Secondly, we quantified tag mortality (including tag loss) and the proportion of tagged prawns reported and adjusted the numbers of tagged prawns released accordingly. Also, by having staff at the main site of landing in each estuary and by offering financially attractive rewards for the return of captured tagged prawns, reporting of captured tagged prawns was maximised. Our experiments did not include ocean waters which may have underestimated fishing mortality on the stock. But considering the sporadic nature of the ocean fishery and that this component generally only lands a small proportion of the total landings of school prawns, this effect is thought to have been minimal.

The imprecision about estimates of the catchability coefficient and fishing mortality probably reflects changes in the behaviour of school prawns and in response to this, changes in the behaviour of the fishing fleet. Most tagged prawns were caught in the first few days of commercial fishing after release, after which there were several days in some instances between captures. It may be that the catchability of school prawns changes throughout a week as fishing may disturb and disperse the uncaught prawns.

The range of catchability coefficient values was similar between stocks even though the main fishing gear used varied between the stocks. The Clarence stock is exploited predominantly by the method of trawling whereas the Wallis stock is predominantly exploited by the method of hauling (for a description of these gears see Broadhurst 2008). This result suggests that given the appropriate fishing gear is used for the fishing ground, catchability does not change much between active forms of fishing gear.

The differences in values for the catchability coefficient between years and the range in values within years for each stock may in part be due to differences in river discharge. Experiments on the Clarence stock were done in what were considered 'dry' (2004-05) and 'wet' (2005-06) years, whilst at Wallis Lake there were also months of high rainfall when experiments were done. Catches of school prawns are greater during times of high river discharge (Ruello 1973b, Glaister 1978a, Ives *et al.* 2009) and our results showed a correlation between this and the catchability coefficient for the Clarence stock. The higher catchability is most likely caused by the prawn's behaviour to be more active and to aggregate more in turbid water (Penn 1984) which occurs at times of high river discharge.

Values for the catchability coefficient for both stocks and those for fishing mortality for the Clarence stock were within the ranges reported for other prawn species. Fishing mortality values for the Wallis stock were generally lower than reported for other prawn fisheries. Levels of exploitation (ratio of fishing mortality to total mortality) were mostly amongst the highest reported for other prawn species. Levels of catchability for the Clarence stock in 2005-06 (when river discharge was high), were around the values that Ives *et al.* (2009) predicted may adversely impact the Clarence school prawn population. Fortunately, being animals that live for less than two years, the school prawn population appears to have the capacity to recover from excessive levels of fishing more quickly than for longer lived species where more than one year class of spawners is affected.

School prawns are a small fast growing prawn species that are being exploited at levels comparable to that in fisheries for other prawn species. The species fits the general biological pattern for a fast growing animal, having a small maximum size and great rate of natural mortality. There are indications however that the catchability coefficient can reach levels where populations may be adversely affected by current levels of fishing effort. The main time when this occurs is when river discharge levels are high. Management and industry need to address potential deleterious impacts from high exploitation during such periods. This study has provided the first estimates of growth

and mortality that can be used with confidence in population models to assess the impact of scenarios presented by fisheries managers as options for the sustainable exploitation of the valuable school prawn resource.

7. BENEFITS

Most of the benefits from this project flow to the school prawn the commercial and recreational fisheries of New South Wales. There are also fisheries for school prawns in north-east Victoria and south-east Queensland that will benefit from the results of this project. These fisheries are all managed by the relevant state governments. The public of Australia benefit indirectly by having information crucial to the sustainable management of these prawn resources available for stock assessments to test the impact of alternative management scenarios.

8. FURTHER DEVELOPMENT

Since the spawner-recruit relationship may have a driving role in the dynamics of the school prawn populations, it would be beneficial to investigate the reproductive biology of this species and the spatial and temporal distribution of the spawning populations. Monitoring processes need to be put in place to collect information on the relative abundance of the spawning stock and of recruits to the fishery to determine if recruitment is affected by high levels of exploitation during times of high river discharge. Manipulative experiments would also need to be done to investigate the effects of flood waters on the survival of school prawns.

9. PLANNED OUTCOMES

The planned outcomes from this project were reliable estimates of growth parameters and rates of mortality that could be used in population models to assess the stocks of school prawns. A size-based metapopulation model for the Clarence River school prawn populations has been developed by Ives *et al.* 2009 and the results from this study will be up dated input values for that model. This will provide managers with a tool to test management scenarios aimed at sustainable harvesting of the school prawn resources. The results of this project are the basis of three manuscripts either submitted for publication in international peer reviewed journals or nearing completion for submission.

10. CONCLUSIONS

This study has provided the first estimates of mortality for school prawns and has improved upon the estimates of parameters for growth. The study incorporated broad variability in growth and mortality by choosing stocks near the northern and southern bounds of the main commercial fisheries for school prawns and are harvested by a wide range of fishing methods.

Growth differs between genders with males growing to a smaller asymptotic length than females. The growth model predicted longer asymptotic lengths for females than the longest prawns found in samples, probably because there were few age groups in the population older than that at which growth slows.

The range of estimates of natural mortality covered that generally reported for penaeid stocks but the upper limit was amongst the highest reported. Females had higher rates of natural mortality than males and natural mortality was less in the southern than northern stock. Catchability was shown to vary and was likely to be associated to the level of river discharge.

Exploitation ratios in some experiments approached the highest values reported for a penaeid species. Being a less than two year stock, recovery from over-exploitation may be quick in school prawn populations, so that times of low catches are assumed to have been caused by environmental perturbations rather than high fishing mortality (Penn 1984). It is unknown whether overfishing has occurred on any of the stocks of school prawns in NSW, but considering the risk of catchability increasing during times of high river discharge, information on the abundances of spawners and recruits to the fishery should be collected as part of the general monitoring of the resource. This study has provided up to date estimates of parameters for growth and the first estimates for rates of mortality which can be used to up date inputs into models such as that of Ives *et al.* (2009) to assess the school prawn stocks. One scenario that should be tested is to determine the level of risk of overfishing school prawn stocks during times of high river discharge. Such information may then be used by fishery managers to develop precautionary measures for these times.

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12. APPENDICES

Appendix 1: Intellectual Property

Chapters of this report will be published in scientific journals. These works should be cited in the context of the published paper rather than this report. No specific commercial value was derived in terms of patents or copyrights.

Appendix 2: Staff

Staff who worked on this project using funds from NSW I&I:

Dr C. Gray
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Appendix 3: Montgomery, S.S., Walsh, C.T., Haddon, M., Kesby, C.L. and Johnson, D.D. (submitted). Use of length data and the Schnute model to describe growth in the school prawn, *Metapenaeus macleayi*, in waters off New South Wales, Australia. Marine and Freshwater Research.

USE OF LENGTH DATA AND THE SCHNUTE MODEL TO DESCRIBE GROWTH IN THE SCHOOL PRAWN
METAPENAEUS MACLEAYI IN WATERS OFF NEW SOUTH WALES, AUSTRALIA

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Running Head Application of Schnute Growth Model to *Metapenaeus macleayi*

ABSTRACT

This paper demonstrates how growth data from length distribution analyses can be used with the Schnute model to describe growth and provides the first published information on the growth of the school prawn, *Metapenaeus macleayi*. Two years of monthly fishery independent surveys were done on the Clarence and Hunter river stocks of school prawns to collect length distribution data. Case 5 within the Schnute model, the special case representing the von Bertalanffy growth function, provided the best fit to data for females ($L_{\infty} = 36.6$ and 40.2 CL mm and $\kappa = 0.004$ and 0.005 day⁻¹, for Clarence and Hunter, respectively) whilst Case 1 of the Schnute model gave the best overall fit to data for males ($L_{\infty} = 21.3$ and 33.5 CL mm and $\kappa = 0.025$ and 0.009 day⁻¹, for Clarence and Hunter, respectively). Apart from Clarence males, individuals did not reach the predicted mean maximum lengths. Growth differed between genders within each stock. There were no differences in female growth between stocks but males from the Hunter (lower latitude) grew to a longer mean maximum length but at a slower rate than those from the Clarence (higher latitude). These results will contribute to the management of the school prawn stocks as input data to yield per recruit and length-based population modelling.

INTRODUCTION

Information about the growth pattern of individuals is important in stock assessments because it can provide knowledge about the age-structure of individuals in the stock, and can provide insights into mortality and productivity. Techniques for collecting information about growth from fish resources are well documented (Campana 2001), but the task is more complex in difficult to age taxa, such as Crustacea, which have no retained hard parts upon which to base age determinations. Rather, crustacean growth is through step-wise moulting, whereby the exoskeleton (including all hard parts) is shed to be replaced by a new, hydraulically expanded shell (Hartnoll 1982). Age determination studies on such invertebrates have had to concentrate on techniques that do not use hard parts including (i) tag-recapture studies (Buckworth 1992; Glaister *et al.* 1987), (ii) modal analysis of length distribution data (for a review see Pauly and Morgan 1987), (iii) assays of the concentration of the biochemical waste product lipofuscin (Sheehy *et al.* 1998), and (iv) raising animals under laboratory conditions.

Age determination data are fitted to growth functions which are then used in age-structured population models (e.g., Dichmont *et al.* 2003; Gordon *et al.* 1995), and more recently in size-structured models, to ascertain the response of the population being studied to various management scenarios. (e.g., Ives *et al.*; 2009; Punt *et al.* 2009). Mathematical functions most often represent growth as a continuous process, although this is not the case for crustaceans because of the moulting process. Size-structured models allow a form of discontinuous growth to be represented by combining within a size-transition matrix a mathematical function expressing growth with a probability distribution ascertaining what proportion of animals are expected to grow from one size class into the next within the time represented by the transition matrix probabilities (Punt *et al.* 2009). Ives *et al.* (2009) developed a variation to the general suite of size-structured models by grouping prawns into size categories and genders and applying a separate growth function to each category.

Several mathematical functions have been developed to describe growth (for a review see Quinn and Deriso 1999), the most commonly used of which has been the von Bertalanffy growth function (VBGF). Many studies have found that the VBGF has biological validity because it has predicted mean asymptotic lengths that were similar to the maximum sizes observed in nature, although this does not necessarily have to be the case (Knight 1968). Also, the VBGF possesses a parameter that describes the rate at which this maximum length is attained. However, whether the VBGF is the most appropriate growth model for all occasions has been questioned, usually for reasons of

discontinuity of growth and the importance of incorporating individual variability in growth (Knight 1968; Sainsbury 1979; Schnute 1981). Attempts to address these weaknesses led to the development of several alternative growth functions such as the Richards (Richards 1959), Gompertz (cited Haddon 2001) or the Schnute (1981) models. The Schnute model is very general and incorporates the VBGF, the Gompertz, the Richards, and the Logistic curves as special cases (see Quinn and Deriso 1999). Alternatively, a two-phase VBGF has been fitted separately to the different life phases of particular stocks (e.g., Hearn and Polacheck 2003).

In their review of the biology of penaeids, Dall *et al.* (1990) noted that growth in these species approximated a continuum because the inter-moult period was usually relatively short (days or weeks) and so the stepped growth was smoothed out over the longer life span of the species. They noted that prawn growth conformed to a sigmoidal pattern although most studies had concentrated upon prawn growth after the first point of inflection. While individuals are juvenile their growth rates approach a constant value so size at age increases approximately linearly, but growth rates decline as the animals become older and mature. As a result Dall *et al.* (1990) recommended that overall a curvilinear model should be used. They provided many examples where the curvilinear VBGF has been used successfully to model prawn growth, but there have been few published studies on the growth of wild penaeid populations since their review and none could be found that investigated alternative models to the VBGF for fitting penaeid growth data. This paper uses length distribution data for the school prawn, *Metapenaeus macleayi* to demonstrate how the Schnute (1981) growth model can be used to model invertebrate growth when no direct information about length at age is available.

The school prawn, *Metapenaeus macleayi*, is endemic to the waters off the east coast of Australia, distributed in estuaries and ocean waters out to depths of around 55 m between Corner Inlet (38 °S) and Tin Can Bay (25 °S). The species is one of three found in these waters that have both commercial and recreational importance and support average annual landings worth around AUD 8 million per annum. School prawns have been extensively studied in the past (Ruello 1971, 1973a,b, 1977; Glaister 1977, 1978a,b), but none of these publications studied the growth of individuals in the populations in any useful detail. Dissertations by Ruello (1971) and Glaister (1977) attempted to quantify growth using data from tag-recapture studies, however, numbers of recaptures were small and were not representative of the size range of the species, and so these studies were only able to generate uncertain estimates of growth parameters. This paper presents the first representative growth curves for the species.

MATERIALS and METHODS

Study area

Fishery independent surveys were done on the school prawn stocks of the Clarence and Hunter River regions (Fig. 1). Each region consisted of an estuarine and an ocean component. The two regions were chosen because of their importance as school prawn producing regions. On average between 2003-04 and 2007-08 the Clarence River stock accounted for 52% (by weight) of annual reported landings of school prawns in New South Wales (NSW) and is part of the northern most major stock in NSW (Ruello 1977). In contrast, the Hunter River is one of the southern most stocks that sustains both an estuarine and ocean fishery and accounts for 5% of school prawn production.

Procedure

The estuary in each region was divided into zones of approximately the same surface area. In ocean waters, surveys were limited to grounds within 1.5 nm of the shoreline that were fished by the local commercial fishing fleet. Commercial fishing vessels were chartered in each estuary to conduct the

surveys. Each chartered vessel used the standard design of trawl net used in commercial operations in the particular estuary but with a modified codend of small, square mesh. This codend was made entirely from 12-mm knotless polyamide mesh hung on the bar (i.e., square-shaped mesh with stretched-mesh opening of ~ 12 mm and bar length of ~ 6 mm) and measured 1.2 m in circumference (242 bars) and 1.4 m in length (270 bars to the drawstring).

In the Clarence River, the vessel towed two 11 m '4 set Florida flyer' nets. While both nets were towed to stabilise the fishing operation, only the gear on the starboard side of the vessel, was used for sampling. In the Hunter River the vessel towed a single 5.5 m, 4 seam saandi-kan trawl. Surveys in ocean waters off both regions used standard trawl gear (3 x 11 m Florida flyer nets). The small mesh codend was not used in ocean waters because of the volume of biomass that would be caught and because it was assumed that the commercial fishing gear (with codends of 29 mm square mesh and 40 mm diamond mesh for vessels chartered at the Clarence and Hunter Rivers, respectively) caught all length classes of prawns (in representative proportions) present on ocean prawn trawl grounds. This was assumed because the 50% selection point (8.6 mm CL) of trawl gear being used by the commercial fishing fleet (Broadhurst *et al.* 2004) was shorter than the lengths of prawns caught on ocean grounds.

The starting zone for each survey was determined by taking into consideration tidal and weather conditions. Considering that the surveys were to collect information on growth, the commercial fisher in each case was asked to choose areas within a zone where catch would be maximised and therefore be most likely to be representative of the sizes of prawns in the zone at the time of sampling.

Starting in December 2005, surveys were done in the week after the full moon in each lunar month for two years. Surveys in estuarine waters consisted of five minute trawls done at each of two shallow and two deep grounds within each zone, whilst in ocean waters three 20 min trawls were done. At the end of each trawl the net was brought on board, opened on the 'sorting tray' and the catch separated into specific bins of circulating seawater for school prawns and 'other animals'. Once sorting was completed the 'other animals' were released immediately over the side of the vessel to maximise survival. The catch of prawns was weighed (nearest 10 g) and if greater than 100 prawns then random proportional samples were retained for processing in the laboratory, and the remainder of the prawns were released. The proportion of the sample retained depended upon the size range of prawns in the catch. The target was to measure the lengths of at least 100 prawns of each gender.

In the laboratory each sample of prawns was separated into gender. The length of each individual was measured to the nearest mm as the straight line distance between the base of the eye orbit and the centre of the posterior margin of the carapace (orbital carapace length), using dial callipers. The weight of each gender in the sample was measured to the nearest 0.1 g. These data were entered into a relational Microsoft Access™ database where these could be linked to information about the time, place and weight of the catch of the trawl from which the sample originated. Data for subsamples were rescaled to the number of individuals in the total catch of the survey trawl.

Modal progression analyses

Size frequency distributions of the weighted data for each trawl were constructed using 1 mm size class groupings. For each region, data were pooled across depth and zones to give a single size distribution for each gender and survey period. Ocean and estuarine components were kept separate during modal analyses because the fishing gears were larger and had different sized cod-ends and, trawl times were different. Modal analyses were applied only to length distributions where there were 30 or more prawns of each gender measured.

The length distribution of most cohorts (modal groups) of school prawns were adequately described using the Normal Probability Density Function. Separate modes were fitted to the length distribution data for each gender from each survey period using procedures implemented in Microsoft Excel™ (modified from Haddon, 2001; see Eq. 1; e.g., Fig. 2). Each mode, m , was described using a separate normal distribution whose parameters were the mean size, μ_m , the standard deviation, σ_m , and the count of individuals making up the mode, N_m . There were a maximum of ten modal groups fitted to any single sampling time (j). For each modal group, m , the expected frequencies, $\hat{f}[L_i]$, for each of the 1 mm carapace length classes, L_i , were obtained by subtracting the cumulative normal probability for the bottom of the length class ($BotL_i$) from the cumulative normal probability for the top of the class ($TopL_i$), and multiplying this by the expected frequency of individuals N_m within the specific mode m . The overall expected frequency for each length class, L_i , was then obtained by summing across all n fitted modes:

$$\hat{f}[L_i] = \sum_{m=1}^n N_m \times \left(\int_{-\infty}^{TopL_i} \frac{1}{\sigma_m \sqrt{2\pi}} e^{-\frac{(L_i - \mu_m)^2}{2\sigma_m^2}} - \int_{-\infty}^{BotL_i} \frac{1}{\sigma_m \sqrt{2\pi}} e^{-\frac{(L_i - \mu_m)^2}{2\sigma_m^2}} \right) \quad (1)$$

For each sample date and each mode, initial guesses were made for the various parameters from a visual inspection of the data. Modes were identified using three criteria: (i) simple visual inspection of the length distributions, (ii) comparisons with the assumed modal structure in earlier or later samples, and (iii) prior knowledge of the seasonality of recruitment events. Prawns recruited to grounds in the Clarence River over 10 months of the year and so a maximum of 10 modes were permitted to be identified in a single month's length distribution.

Given the initial parameter guesses, the agreement between the observed and expected frequencies was optimized using the Solver™ add-in in Excel™ (which uses numerical differentiation to implement efficient downhill optimization). Multinomial likelihoods were log-transformed (2) and maximized (Haddon 2001):

$$LL(f | \mu_{1:n}, \sigma_{1:n}, N_{1:n}) = \sum_{i=1}^c f(L_i) Ln \left(\frac{\hat{f}(L_i)}{\sum \hat{f}[L_i]} \right) - \sum_{m=1}^n (N_m - \hat{N}_m)^2 \quad (2)$$

where μ_m , σ_m , and N_m are the means, standard deviations, and proportional count frequency of the 1 to n modes

$f(L_i)$ is the observed frequency of length class L_i ,

$\hat{f}(L_i)$ is the expected frequency of length class L_i .

A penalty function was included with the multinomial log-likelihood to force the predicted number of observations (\hat{N}) making up the length distribution to equal the number of observations (N). The penalty function always reduced to an inconsequential quantity that did not significantly contribute to the final log-likelihood.

The Akaike Information Criterion (AIC) value was calculated using the approach of Haddon (2001; $AIC = 2LL + 2p$, where LL is the negative log-likelihood and p is the number of parameters) for each set of cohorts fitted to the length distribution. In cases where it was unclear whether the number of modes had been selected appropriately, the smallest AIC value was used to determine whether the statistical fit was improved by adding a new mode.

Generation of growth curves

Once all cohorts had been identified, the length distributions showing the separated cohort components were plotted in time-ordered sequence for each gender. This permitted a visual comparison through time and between areas. It was possible to generate alternative hypotheses concerning the exact modal progression. Where uncertainty about a modal progression existed all options were analysed.

Given a particular modal progression, the mean length and standard deviation parameters from each mode relating to a particular date were identified and used as the data for fitting a standard growth curve. Where samples from the ocean component provided extra information about the modal progression of a cohort once it had entered ocean waters, these modal values were included in the data to be fitted. Once the modal progression had been determined the mean lengths for each cohort were plotted through time to depict the suggested growth patterns.

Data for each gender were fitted to the growth model of Schnute (1981), using all five cases of the model and for circumstances where no direct information about length at age were available (Quinn and Deriso 1999). The VBGF, Gompertz, Richards and Logistic growth functions are special cases of the Schnute model depending upon the values of κ and γ .

Case 1, where $\kappa \neq 0$ and $\gamma \neq 0$

$$Y_{2j} = \left[Y_{1j}^\gamma e^{-\kappa \Delta t_j} + \varepsilon^\gamma (1 - e^{-\kappa \Delta t_j}) \right]^{1/\gamma} \quad (3)$$

Case 2, where $\kappa \neq 0$ and $\gamma = 0$

$$Y_{2j} = \exp \left[\ln(Y_{1j}) e^{-\kappa \Delta t_j} + \ln(\varepsilon)(1 - e^{-\kappa \Delta t_j}) \right] \quad (4)$$

Case 3, where $\kappa = 0$ and $\gamma \neq 0$

$$Y_{2j} = \left(Y_{1j}^\gamma + \varepsilon^\gamma \Delta t_j \right)^{1/\gamma} \quad (5)$$

Case 4, where $\kappa = 0$ and $\gamma = 0$

$$Y_{2j} = Y_{1j} \varepsilon^{\Delta t_j} \quad (6)$$

Case 5, where $\kappa \neq 0$ and $\gamma = 1$

$$Y_{2j} = \left[Y_{1j} e^{-\kappa \Delta t_j} + \varepsilon (1 - e^{-\kappa \Delta t_j}) \right] \quad (7)$$

Where Y_1 and Y_2 are mean lengths for the same cohort at sampling times t_j and t_{j+1} , κ is a growth parameter with units in this study of days⁻¹, γ is related to the point of inflection in the 'S'-shaped growth curve, Δt_j is elapsed time between t_j and t_{j+1} , Y_1 and Y_2 and ε in Cases 1, 2 and 5 is an asymptotic maximum length equivalent to the VBGF L_∞ .

The best fit of the model to each set of data was determined by (i) the Akaike weights that provided a proportional index of the best fit and (ii) the similarities to what had been observed in nature. The 'Akaike weight' ω_k was calculated as:

$$\omega_k = (\exp(-0.5\Delta_k)) / \left(\sum_{k=1}^5 \exp(-0.5\Delta_k) \right) \quad (8)$$

Where k is Schnute cases 1 – 5, and $\square_k = AIC_k - AIC_{\min}$

Models were bootstrapped 1000 times to estimate first-order corrected 95% CIs about each parameter (Haddon 2001). The hypotheses that growth varied between genders and between regions was tested by comparing the ranges of the CIs and by using the likelihood ratio test of Kimura (1980).

RESULTS

Modal progression analyses

Figure 2 shows the separation of each length distribution into cohorts and the time-ordered sequence of cohorts in each stock. When the mean lengths of each cohort are plotted through time it is evident that the growth of prawns in a cohort approximates a straight line, until lengths of around 20 mm CL are achieved, after which the slope of the line declines (Figs. 3 and 4). This change in slope often corresponded to when the cohort moved to or occurred in ocean waters, and was less evident for male data.

Generation of growth curves

Akaike weightings indicated that Case 5 provided the best fit for female data from each stock (Tables 1 and 2). This is the special case of the Schnute model which is equivalent to the VBGF when γ is fixed to a value of 1. Fits of the data for both genders to Case 3 gave unrealistic parameter values, very high Residual Sums of Squares (RSS) and the residuals were heteroscedastic, all indicating a poor fit. For these reasons results from fitting Case 3 are not presented. Residuals for Case 4 were also heteroscedastic. While Case 5 provided the optimum fit to female data from the Hunter, the CIs for both L_{∞} and κ overlapped between Cases 1 and 5 and those for γ in Case 1 (the parameter fixed at 1 in Case 5) ranged over 1, indicating that there was no real difference between these two curves.

Male data from the Clarence stock was best fitted by Case 1 whilst those from the Hunter stock were best fitted by Case 2. In each Case the Akaike weights provided a strong indication that these were the best fits to the data. Notwithstanding this, there were no differences in the curves between Cases 1 and 2 for male data from the Hunter. Confidence intervals overlapped and values for γ in Case 1 ranged over 0, the fixed value for γ in Case 2. The CIs for each parameter in Cases 1 and 2 for male data from the Clarence stock did not overlap suggesting that curves were different from each other within this region.

The CIs for Cases 5 and 2 (the best fit for these data) predicted mean maximum lengths (L_{∞}) for females and Hunter males, respectively, that were longer than the longest lengths observed in samples from each stock (Fig. 5). Those for Clarence males fitted to Case 1 included the longest lengths observed in samples.

First order CIs for each parameter in the respective Cases of best fit did not overlap suggesting that growth was different between sexes. Kimura's (1980) likelihood ratio test indicated that curves for females did not differ between stocks (Pooled RSS = 625.96, $\chi^2 = 2.83$, $df = 3$ $P > 0.05$). Because there were no differences in parameters between Cases 1 and 2 for Hunter males, Kimura's Test was used to compare Case 1 curves for males between regions and there were differences (Pooled RSS = 298.06, $\chi^2 = 15.27$, $df = 5$ $P < 0.05$).

DISCUSSION

This paper has demonstrated how growth data from length distribution analyses can be used in the Schnute model to describe growth. It is one of only a few to report on the growth of a penaeid species in the wild since the review of the biology of penaeids by Dall *et al.* (1990) and we could find no other studies in the literature that had used the Schnute (1981) growth model to describe growth in a penaeid species, despite its wide acceptance in the literature on fish growth (e.g., Katsanevakis 2006). All other studies of penaeids have directly fitted a VBGF rather than selecting between alternative curves. We studied growth over the major proportion of the school prawn's life cycle by representatively sampling prawns from early juvenile to late adult life stages. Growth varied between genders, but appears not to vary between stocks.

The technique of length distribution analyses to study growth in penaeid populations has been used in several past studies (e.g., Baelde 1994; Yamada *et al.* 2007) and was the only viable option available to study growth in school prawns. Size distribution analyses rely upon being able to identify groups of individuals from the same recruitment event. This approach has the disadvantage that the size distributions for older cohorts tend to coalesce into one another as the animal's growth rate slows and growth between individuals becomes more varied. Also, if recruitment to the stock occurs over a long time period, then it can become impossible to identify the recruiting cohort from other cohorts in the stock. We used a slightly modified approach from Haddon (2001) to separate length frequencies into cohorts rather than that of the more popular programs (for a review see Pauly and Morgan 1987) because we were able to determine by maximum likelihood the best fit for each individual cohort to each length distribution. The fine detail present in the prawn length frequency samples required the flexibility of a customized analysis.

In estuarine waters school prawns remain juveniles and growth rates are relatively constant leading to approximately linear growth as all energies are being allocated to somatic growth (Dall *et al.* 1990). Once in ocean waters prawns mature, so some energy is diverted to reproduction and hence somatic growth slows. Macroscopic examination of ovaries by Glaister (1977) and Ruello (1971) suggested that female prawns did not mature until at least mean lengths of 22 mm CL and 23 mm CL in the Clarence and Hunter stocks, respectively. On this basis therefore we would expect the growth of school prawns to slow at around 22 mm CL and as a result the straight line growth of a cohort would start to curve. Such a pattern was observed in those cohorts where large prawns were represented (Figs. 3 and 4). But prawns of these lengths and longer were only available for a few months of each year. Cohorts where growth has been traced through to the adult stages represented less than 50% of the cohorts in the analyses. This has affected the fitting of growth models for the older ages and appears to have been most influential when fitting female data sets, leading to predicted maximum mean lengths that were longer than observed in samples.

We used a novel approach by fitting mean length at time data to the Schnute model (1981) modified by Baker *et al.* (1991) for mark-recapture data where you have the known lengths L_1 and L_2 of an individual at two different times t_1 and t_2 , respectively. In this study we used the cohort as the individual and the estimates of mean length $L_{1,n}$ for the same cohort from independent sampling periods $t_{1,n}$. No single case of the Schnute model provided an optimum fit to all data sets. It is possible that the dearth of large, mature prawns in samples influenced this outcome. But the Akaike weights gave clear indications about which case provided the best fit for all but data from the female Hunter stock.

Apart from the Clarence male data, the Schnute model predicted maximum lengths that were longer than the largest prawns observed during this study and those of Ruello (1971) and Glaister (1978b). The parameter L_∞ of the VBGF does not necessarily have to have biological significance (Knight 1968), however, if representative sampling is done across most of the phases within the species' life cycle then there is an expectation that the growth curve would fit to the longest animals

sampled. The lack of fit for Clarence data for females and Hunter data for both genders either reflects (i) poor sampling of the largest prawns so that there were insufficient data points to influence the curvature of the derived lines or (ii) that school prawns never reach the predicted mean maximum length because of the impact of mortality. The latter is the most likely as distributions of sizes sampled during this study are similar to those of earlier studies by Ruello (1971) and Glaister (1978b), suggesting that sizes of prawns in the stocks have not changed over time and that the largest prawns have been sampled representatively in our study.

The best fits for male data were Cases 1 and 2 for the Clarence and Hunter stocks, respectively. While the Akaike weights strongly indicated these cases as the best fits, there were no significant differences in parameter values between Cases 1 and 2 for male data from the Hunter stock. For this reason and that of having a general form of the growth curve for male data, we recommend that male data be fitted to the Case 1 of the Schnute model. Case 1 is not the simplest model but using Case 2 for both regions would generate a sub-optimal fit to the Clarence males because CI's for the κ parameter do not overlap between Cases 1 and 2 and are therefore different. The fit of the male data from both stocks to those combinations of values within the CI ranges where κ were positive and γ negative for Case 1 were equivalent to a Richards Curve for growth (Quinn and Deriso 1999).

There were differences in growth between genders within each stock, a phenomenon that is common in nature, including amongst Crustacea (see Hartnoll 1982). In his review of crustacean growth, Hartnoll (1982) claimed that for most crustacean species, females tend to grow to a smaller size than males as moult increments shorten and inter-moult periods increase once maturity is reached. Penaeids however, do not conform to this generalisation and females attain longer maximum lengths than males (Dall *et al.* 1990).

Dall *et al.* (1990; Table 6.5) provided a comprehensive list of estimates of the von Bertalanffy κ and L_{∞} values for the various species of penaeids and little information has been published since then. Based upon this information, school prawns with L_{∞} values up to 40.2 CL mm and 32.6 CL mm for females and males respectively, are one of the smaller metapenaeid species. Also, the species is smaller than its con-specific, the eastern king prawn, *Melicertus plebejus*, which grows in NSW to a mean maximum length of 59.5 mm CL and 45.4 mm CL for females and males respectively (Glaister *et al.* 1987). The curves derived from the Schnute model suggest that male school prawns attain maximum lengths in less than two years, which is typical of many penaeids.

This paper gives the first published growth models and information about the variability in growth between school prawn stocks. A conclusion from the review of prawn biology by Dall *et al.* (1990) was that 'better estimates of growth parameters of penaeids were required, especially for species other than the genus *Penaeus*'. This present study provides estimates of growth parameters for a metapenaeid and is one of only a few published since 1990 to describe penaeid growth. It provides an alternative approach to conventional ones by using length distributions to model growth and demonstrates how curves other than the conventional VBGF can be fitted to growth data for a penaeid species. These results will contribute to the management of the school prawn stocks as input data into the current length-based model for these stocks (Ives *et al.* 2009).

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Table 1. Estimates of growth parameters for four of the five cases of the Schnute model fitted to mean length at age data for school prawns from the Clarence population. The first order CIs about each parameter (CI), residual sums of square (RSS), number of cohorts contributing to the calculation (n) and weighted Akaike's Information Criterion (ω_i) are shown. An asterisk (*) identifies the Case of best fit.

Case	L_∞ (CI)	κ (CI)	γ (CI)	RSS	ω_i (%)
Females $n = 121$					
1	33.77 (46.16-29.99)	0.0068 (0.0099-0.0031)	0.7328 (1.1805-0.2941)	296.93	31.0
2	29.22 (31.05-27.94)	0.0119 (0.0130-0.0108)	0	308.43	9.0
4	1.0040 (1.0043-1.0035)	0	0	963.22	0
5	36.55 (43.36-33.96)	0.0049 (0.0057-0.0038)	1	298.56	60.0 *
Males $n = 91$					
1	21.26 (22.57-20.38)	0.0252 (0.0331-0.0195)	-1.3492 (-0.6458—2.2863)	116.20	79.0 *
2	24.40 (26.50—23.35)	0.01332 (0.0147-0.0119)	0	122.25	21.0
4	1.0065 (1.0075-1.0059)	0	0	372.50	0
5	34.21 (51.38-30.55)	0.0048 (0.0060-0.0020)	1	136.86	0

Table 2. Estimates of growth parameters for four of the five cases of the Schnute model fitted to mean length at age data for school prawns from the Hunter population. The first order CIs about each parameter (CI), residual sums of square (RSS), number contributing to the calculation (n) and weighted Akaike's Information Criterion (ω_i) are shown. An asterisk (*) identifies the Case of best fit.

Case	L_∞ (CI)	κ (CI)	γ (CI)	RSS	ω_i (%)
Females $n = 132$					
1	34.68 (41.75-31.87)	0.0070 (0.0101-0.0035)	0.5428 (1.2359-0.0426)	317.20	28.0
2	31.62 (33.01-30.23)	0.0103 (0.0116-0.0093)	0	321.26	33.0
4	1.0040 (1.0047-1.0038)	0	0	780.26	0.0
5	40.16 (45.37-36.85)	0.0043 (0.0052-0.0035)	1	320.44	39.0 *
Males $n= 105$					
1	34.38 (37.59-29.71)	0.0080 (0.0120-0.0061)	0.281 (0.0112 - -0.6682)	159.52	27.0
2	31.77 (33.84-30.37)	0.01 (0.0107-0.0091)	0	160.11	57.0 *
4	1.005 (1.0055-1.0047)	0	0	494.49	0.0
5	56.09 (70.65-46.91)	0.0025 (0.0032-0.0018)	1	163.49	13.0

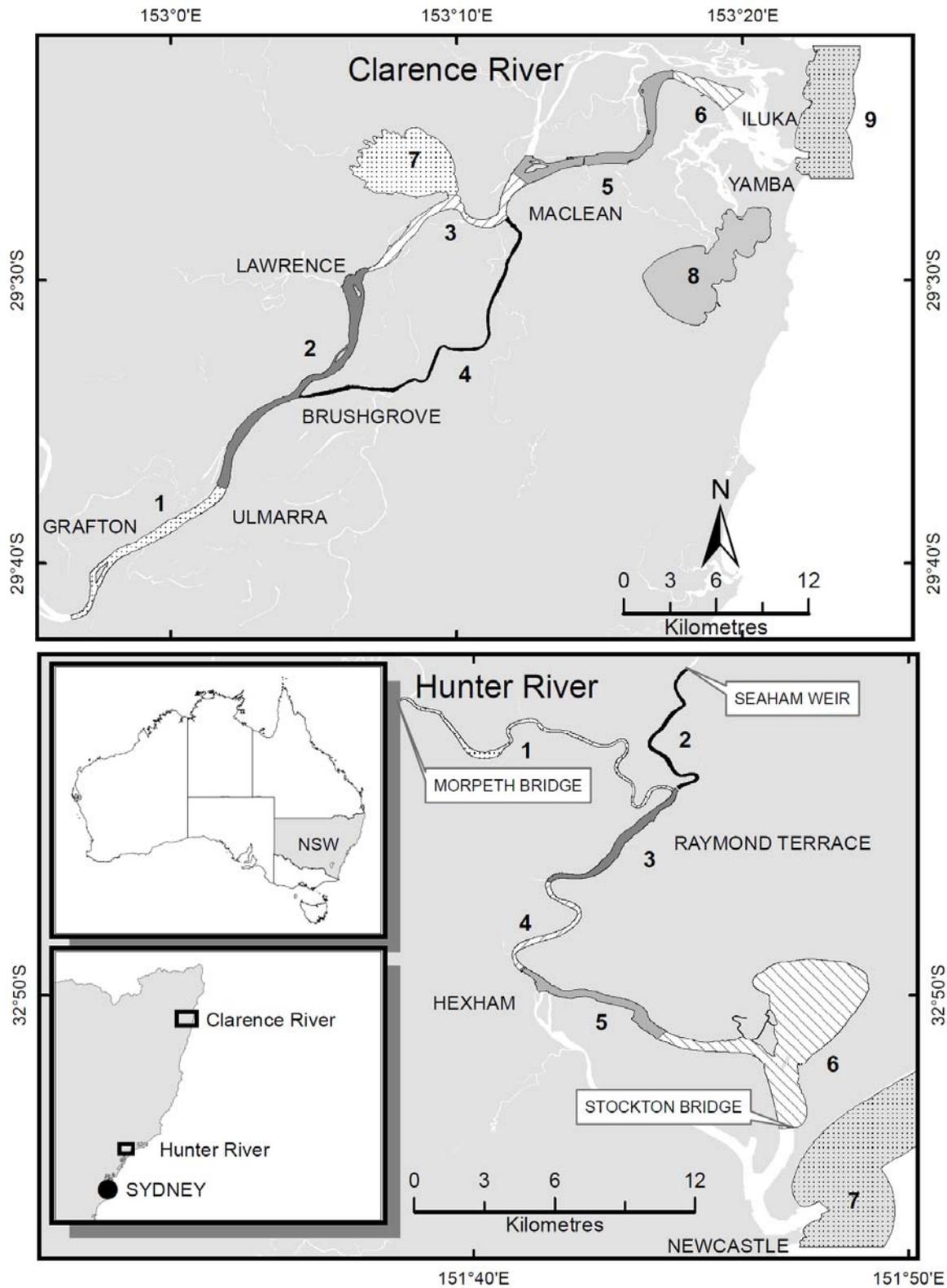


Figure 1. Location of the Clarence and Hunter stocks of school prawns and the zones used in random stratified surveys. Numerals and shading are used to distinguish the zones.

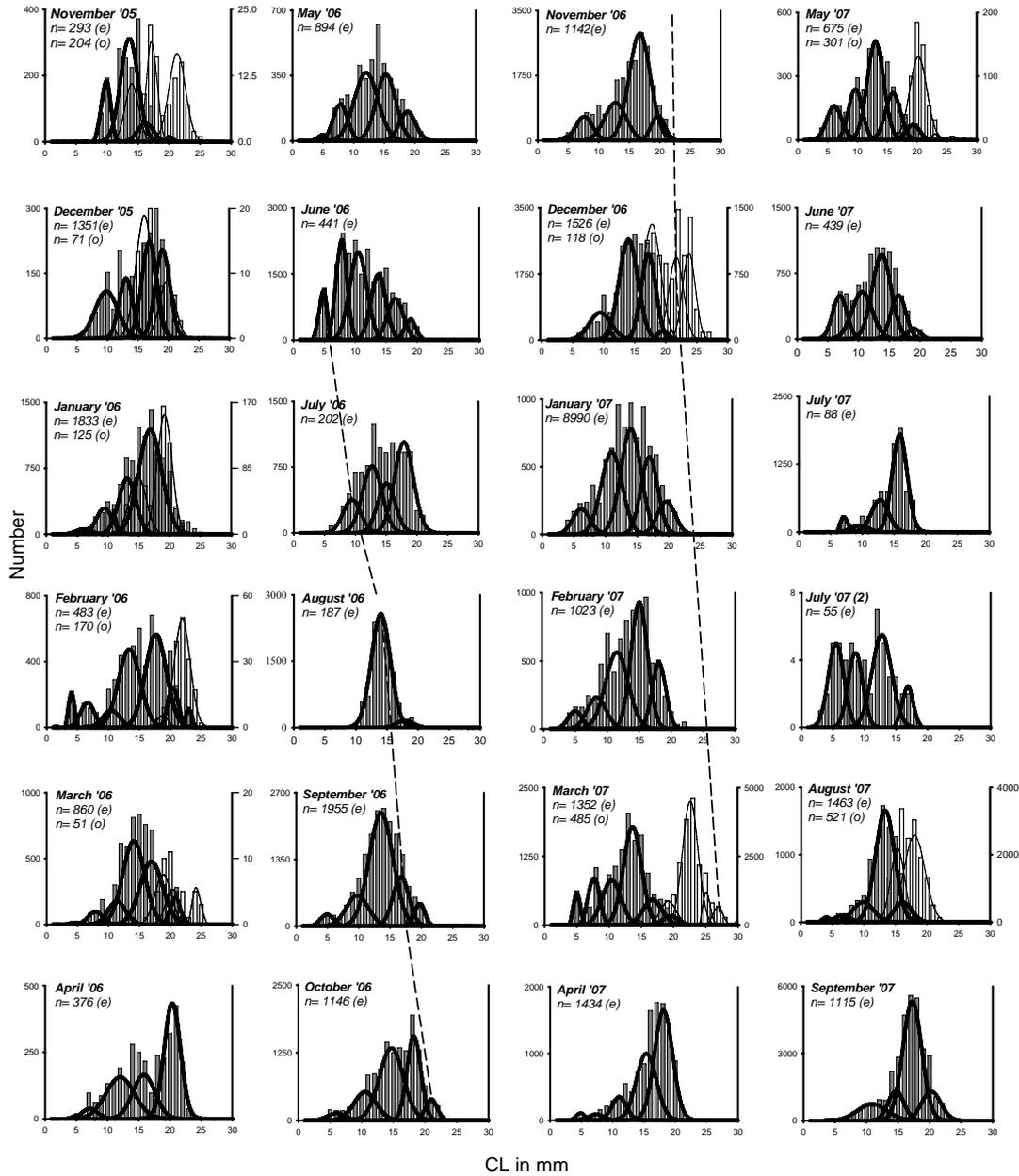


Figure 2a. Length frequency data for female school prawns from the Clarence stock separated into cohort groups (dark bell shaped patterns). Length frequencies from surveys in the estuary are shaded in dark whilst those from ocean surveys are in the light shade. The number of prawns measured from surveys in the estuary (e) and ocean (o) are shown. The dashed line traces the June 2006 cohort through time. Note that surveys were done each lunar month which meant that there were two survey periods in July. Also, survey periods for some ocean length frequencies are hidden from view by that from the estuary.

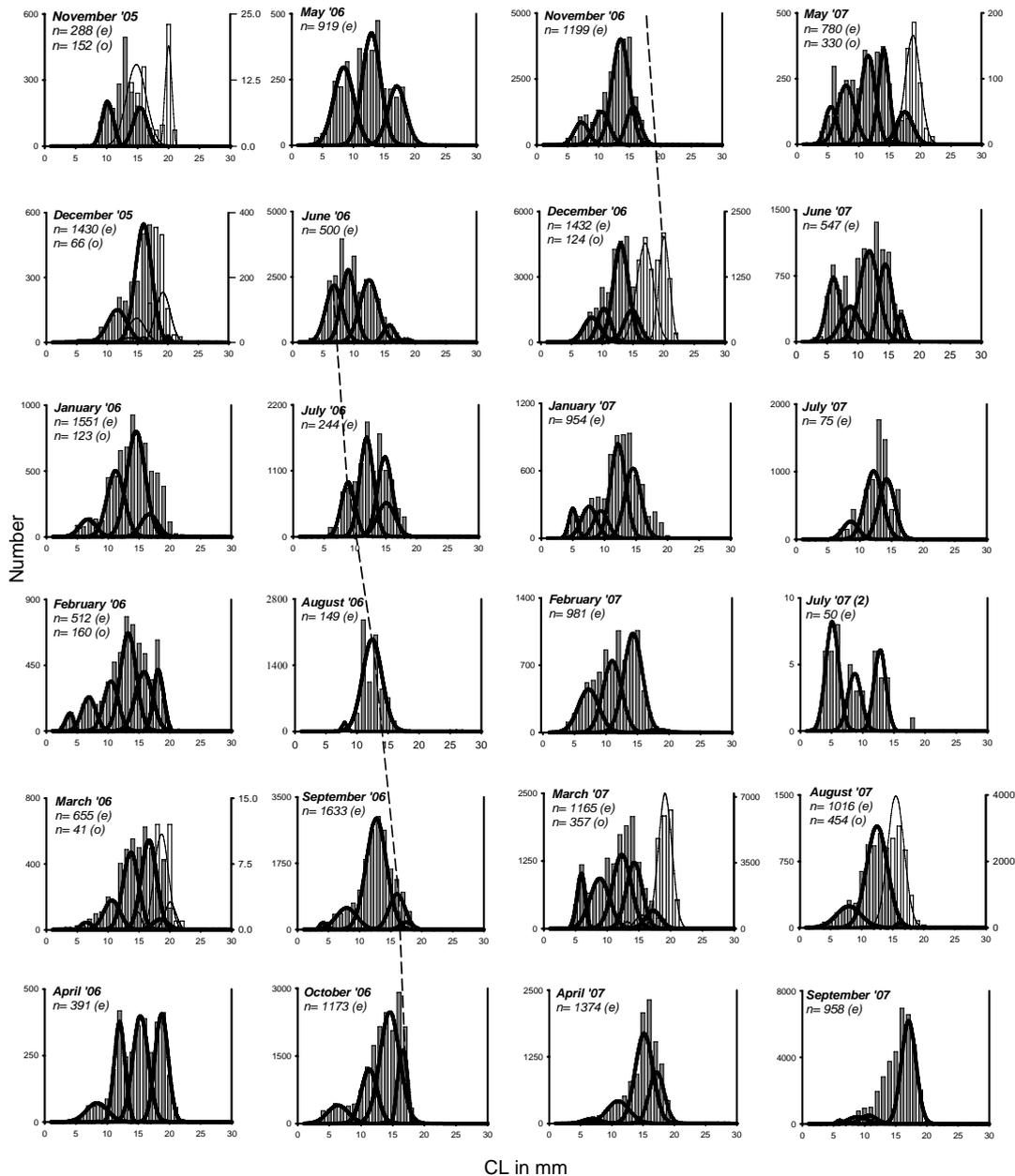


Figure 2b. Length frequency data for male school prawns from the Clarence stock separated into cohort groups (dark bell shaped patterns). Length frequencies from surveys in the estuary are shaded in dark whilst those from ocean surveys are in the light shade. The number of prawns measured from surveys in the estuary (e) and ocean (o) are shown. The dashed line traces the June 2006 cohort through time. Note that surveys were done each lunar month which meant that there were two survey periods in July. Also, survey periods for some ocean length frequencies are hidden from view by that from the estuary.

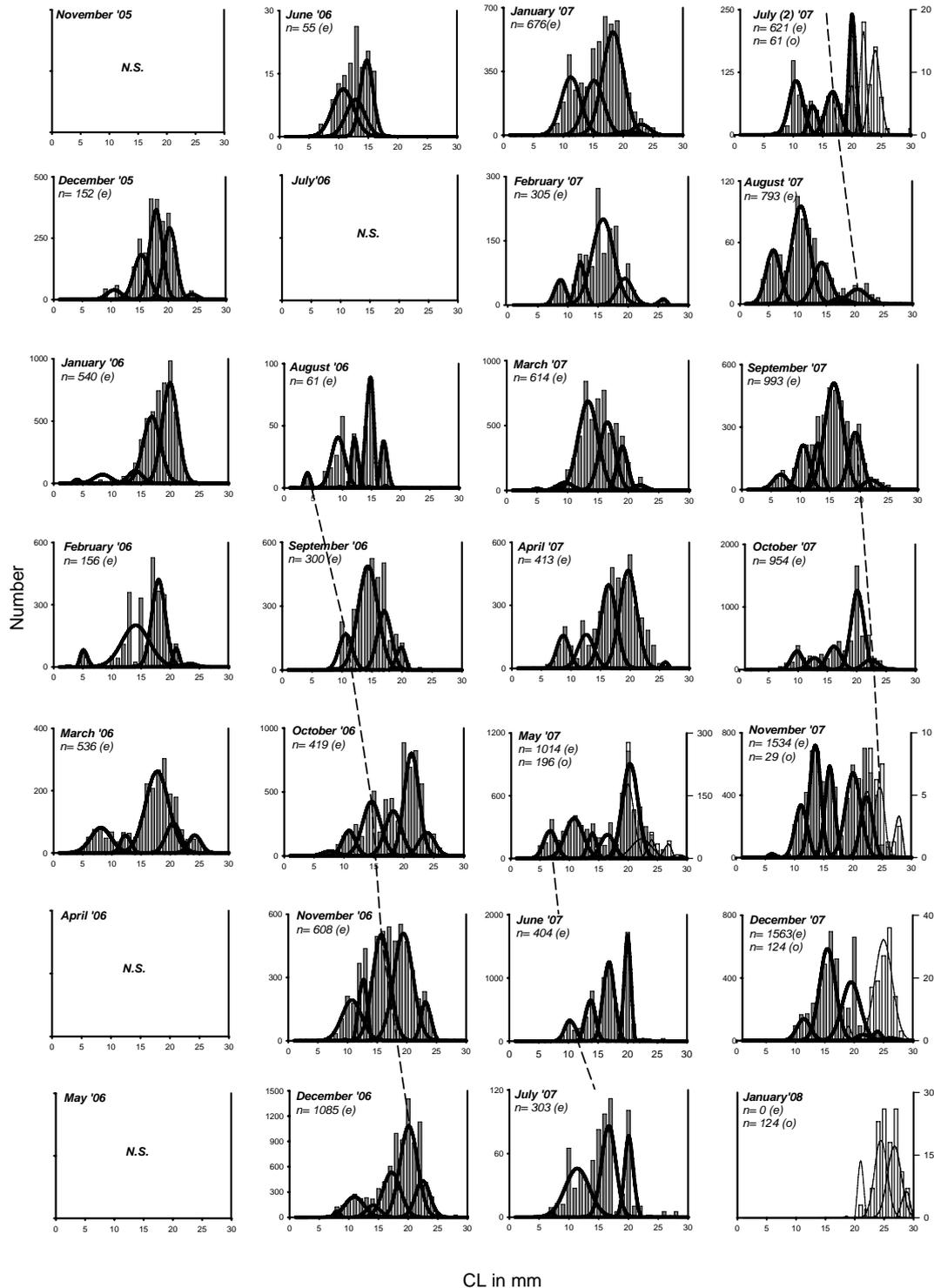


Figure 2c. Length frequency data for female school prawns from the Hunter stock separated into cohort groups (dark bell shaped patterns). Length frequencies from surveys in the estuary are shaded in dark whilst those from ocean surveys are in the light shade. The number of prawns measured from surveys in the estuary (e) and ocean (o) are shown. The dashed lines trace the August 2006 and May 2007 cohorts through time. Note that surveys were done each lunar month which meant that there were two survey periods in July. Also, survey periods for some ocean length frequencies are hidden from view by that from the estuary.

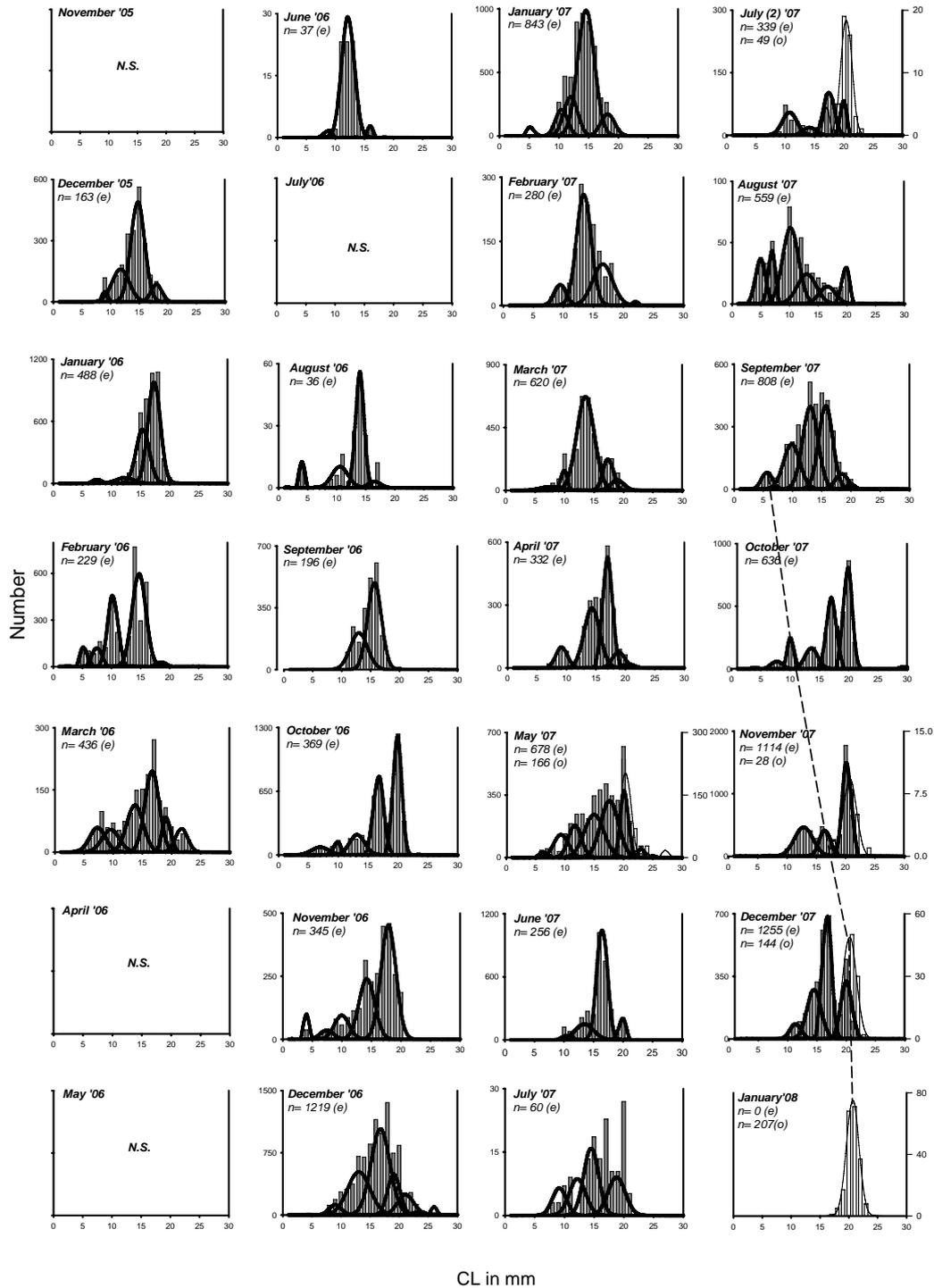


Figure 2d. Length frequency data for male school prawns from the Hunter stock separated into cohort groups (dark bell shaped patterns). Length frequencies from surveys in the estuary are shaded in dark whilst those from ocean surveys are in the light shade. The number of prawns measured from surveys in the estuary (e) and ocean (o) are shown. The dashed line traces the September 2007 cohort through time. Note that surveys were done each lunar month which meant that there were two survey periods in July. Also, survey periods for some ocean length frequencies are hidden from view by that from the estuary.

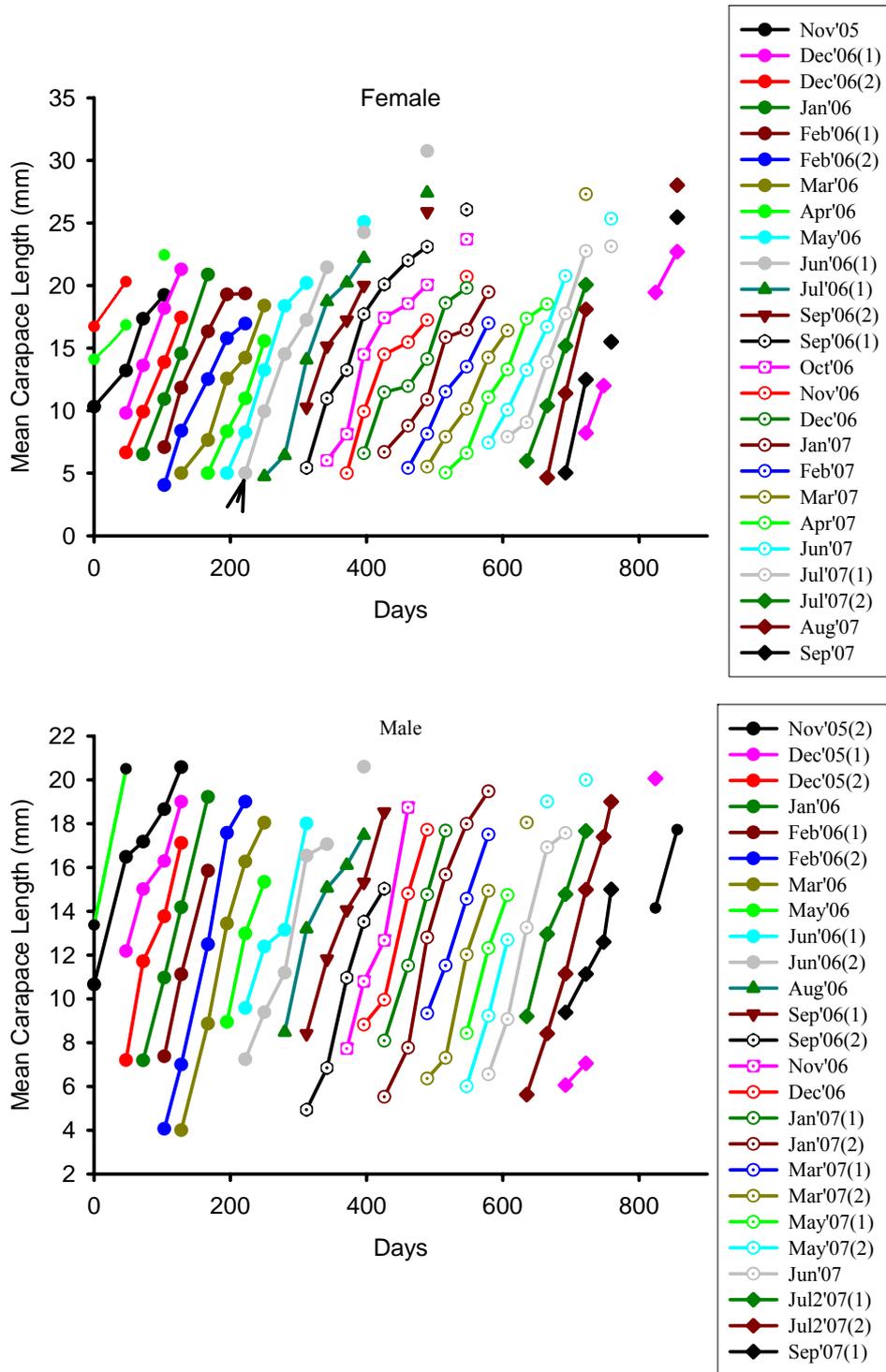


Figure 3. Patterns in mean lengths of each cohort at each sampling period (Days since beginning of surveys) for female and male school prawns in the Clarence stock. The legend shows the first time a cohort occurred in samples. When more than one survey occurred in a month, the month is preceded by a numeral (e.g., Jul_2'07) to identify the sampling period. When more than one cohort first appeared in samples within the same survey month, the cohorts are identified by the numerals in parentheses (e.g., Jul_2'07(2)). The arrow in the female graph shows the cohort traced through time in Figure 2.

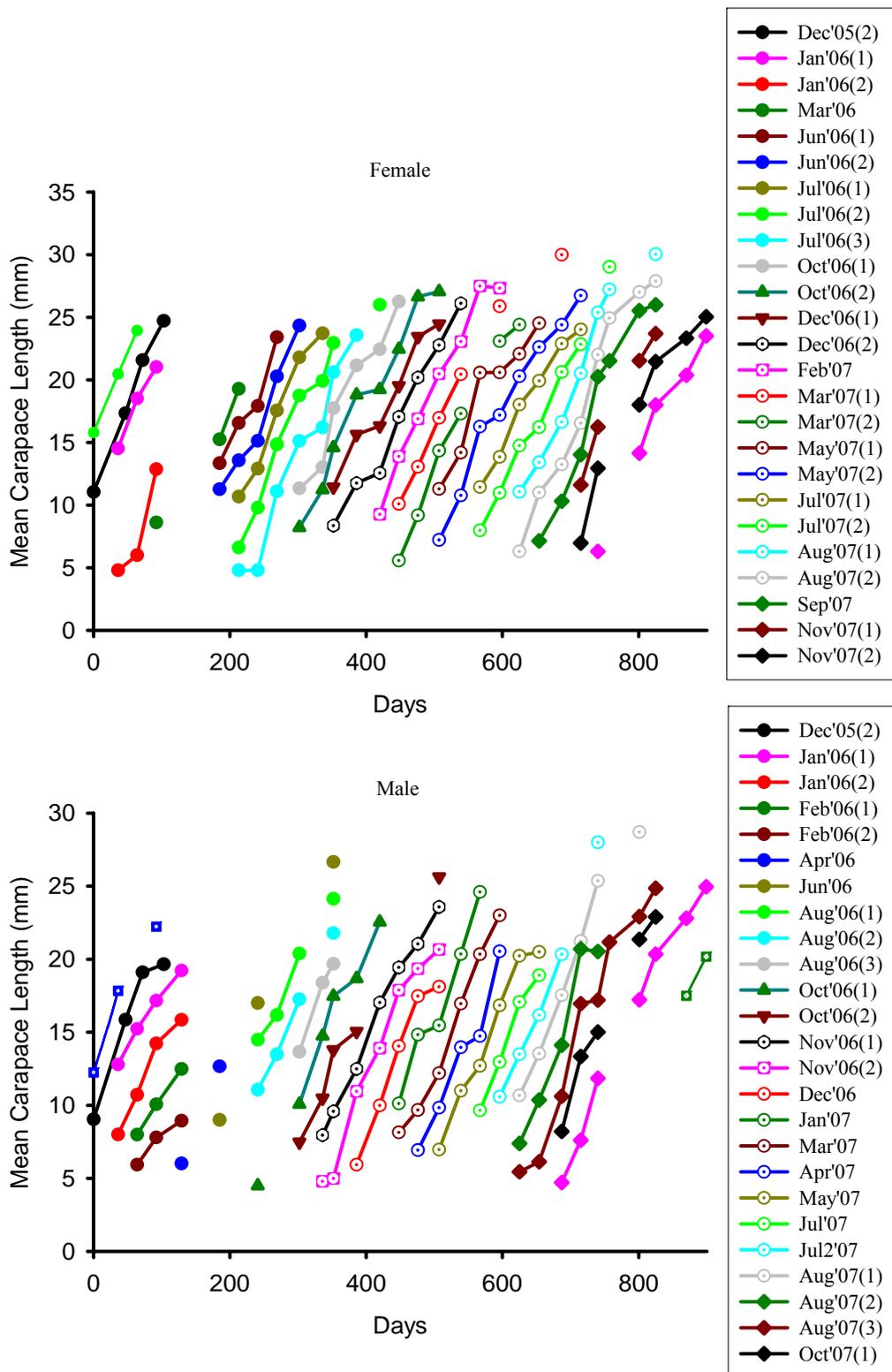


Figure 4. Patterns in mean lengths of each cohort at each sampling period (Days since beginning of surveys) for female and male school prawns in the Hunter stock. The legend shows the first time a cohort occurred in samples. When more than one survey occurred in a month, the month is preceded by a numeral (e.g., Jul_2'07) to identify the sampling period. When more than one cohort first appeared in samples within the same survey month, the cohorts are identified by the numerals in parentheses (e.g., Jul_2'07(2)).

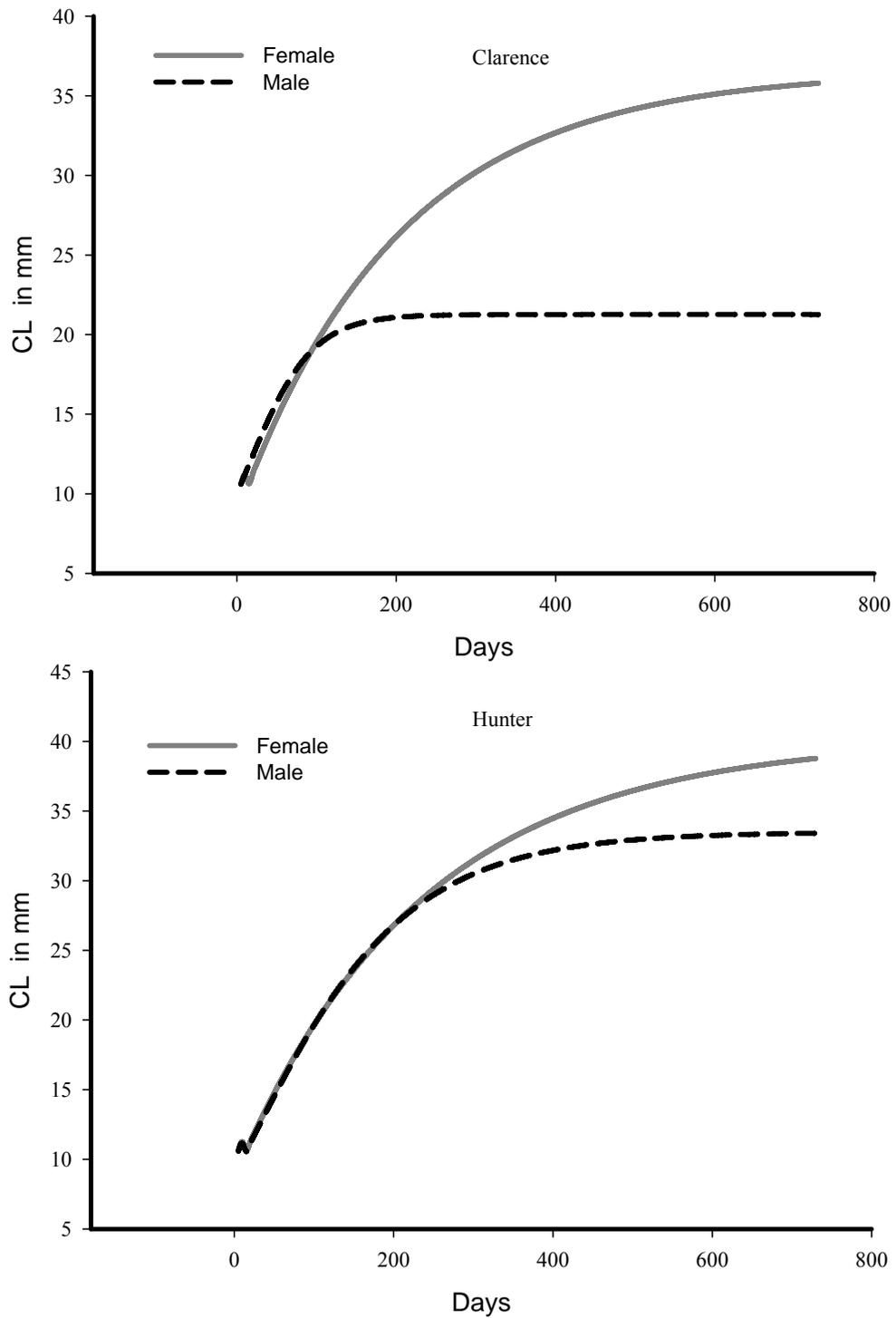


Figure 5. Predicted growth curves for a school prawn of 5 mm CL initial length in the Clarence and Hunter stocks.

Appendix 4: Walsh, C.T., Montgomery, S.S., Reid, D.D., and McLeod, J.R. (2007). Effects of staining and streamer tags on survival and growth of juvenile school prawns, *Metapenaeus macleayi*, under laboratory conditions. Asian Fisheries Science 20, 369 – 382.

Introduction

The tagging or marking of prawns are widely used techniques for identifying animals for demographic studies and have been used for many years to examine dispersal, rates of growth and mortality, as well as numbers of individuals in wild populations (Penn 1976; Xiao and McShane 2000; Loneragan et al. 2002). Mark-recapture studies that identify individual animals offer the greatest potential for accurately estimating population parameters provided the individual marks or tags are retained and any detrimental effects of the marking process are quantified (Burnham et al. 1987). The effect that tagging has on an individual, either from tag-induced mortality (including tag loss) and/or differences in growth needs to be quantified when analysing tag-recapture data, otherwise estimates of mortality and even rates of recruitment to the fishable stock can be grossly underestimated. Likewise, tagging studies that are used to estimate growth parameters need to account for the effects of tagging on growth of the tagged individual.

There have been various types of marks used to study penaeid prawns (Farmer 1981; Penn 1976). As with all crustaceans, the marking of prawns is difficult due to the process of ecdysis that leads to the periodic shedding of the exoskeleton. Earlier tagging methods for prawns included intramuscular dyes or pigments (stains), internal tags, as well as the commonly known Petersen and Atkins type tags (Lucas et al. 1972; Glaister 1978). Although the method of staining prawns has its restrictions in tracking individual growth and movement, it has been useful as a marking technique in population studies. This procedure is considered less intrusive than physical tags making it more feasible for marking the smallest of juveniles (Costello 1959; Racek 1959; Kilma 1965). However past studies have shown that stain induced mortality and visibility of the stain vary greatly within and between prawn species (Dawson 1957; Costello 1964).

The various types of external tags used to study penaeid prawns have been discussed by Kilma (1981) and Penn (1981). The streamer tag has been increasingly used since it was developed by Marullo et al. (1976) because it is easy to apply, does not appear to affect the normal behaviour of prawns and causes low mortality (Hill and Wassenberg 1985; Montgomery and Gray 1991). High tag-related mortalities in penaeids have been mainly due to the inexperience of the tagger, the poor condition of the prawn and/or the stage of the prawn's moult cycle when the tagging was

done, and the artificial environment in which the test animals were kept (Howe and Hoyt 1982; Benzie et al. 1995).

Recent studies on the effects of tagging penaeids have suggested that tag-induced mortality from streamer tags is size-dependent and as a consequence the range of prawn sizes that can be tagged may be limited (Penn 1976; Hill and Wassenberg 1985; Benzie et al. 1995). Likewise conclusions about the effect of tagging upon growth have varied between studies. Some laboratory and field studies have concluded that tagging does not affect growth in penaeids (Primavera and Caballero 1992; Montgomery et al. 1995). In contrast Menz and Blake (1980) stated that tagged *Penaeus vannamei* grew more slowly than unmarked individuals.

The school prawn *Metapenaeus macleayi* (Haswell) is one of a number of prawns caught along the east coast of Australia. It plays an extremely important role in marine and tidal ecosystems and forms the basis of an important commercial fishery in New South Wales, Australia (Glaister 1978). To date there has been limited information available on growth and mortality rates either of school prawns or of any metapenaeid species that lives in temperate waters. Ruello (1977) and Glaister (1978) determined tag-induced mortality in school prawns using Atkins type tags. However only small prawns (mean ≤ 20 mm CL) were examined over a short time period (five days) when moulting did not occur. Tagging trials using streamer tags have been done on other Australian penaeids (Montgomery and Gray 1991; Benzie et al. 1995; Wassenberg and Kerr 1990) but not on *M. macleayi*.

In the present paper we investigated the effect of tagging and staining on *M. macleayi* in the laboratory and whether tag or prawn size affected survival. This information was used to select a tag type for future studies on wild school prawns. The null hypothesis tested was that survival and/or growth of juvenile *M. macleayi* were unaffected by tagging (stain or streamer tag) or size of the tagged individual.

Methods

Equipment used

The hypothesis was tested on school prawns from the Hawkesbury River NSW, Australia. Two experiments were done at the aquarium facilities at the Cronulla Fisheries Research Centre of Excellence between No-

vember 2003 and April 2004 using three 4000L fibreglass holding tanks and 30 smaller fibreglass tanks (160L). All small tanks had a sand substratum (mean depth, 50-80mm), were supplied with flow through seawater (at ambient temperature, approx. 18-24°C), aerated using air-stone diffusers and equipped with outflow pipes designed to maintain 300 mm water levels. The tanks were evenly distributed on opposite sides of an enclosed room with a regulated 12:12 h photoperiod.

Collection and handling of prawns

Prawns were captured using a commercial prawn trawl vessel equipped with a standard prawn trawl net with a codend mesh size of 30 mm. Nets were towed for 10 minutes and then the captured prawns were placed into holding tanks supplied with oxygen. These holding tanks were transported to the aquarium facilities and prawns were placed into the large holding tanks. Prawns were allowed to acclimatise in these tanks for at least 7 days, during which they were fed a diet of commercial prawn pellets (Primo starter 3, 40% protein).

Treatments used

School prawns were grouped into two size classes (11-20 and 21-30 mm CL). Two sizes of streamer tags (small 12P, 43 mm long by 2 mm wide and large 4S, 63mm long by 3 mm wide both with a central notch) manufactured by Hallprint Pty Ltd were used. All tags were inserted through the articular membrane between the first and second abdominal segments of the prawns with needles of 0.7 mm diameter. Stained prawns were injected with a 0.2mls (0.5 % solution) of fast green FCF (Di Colours, Australia – benzyldiethyldiamino, hydroxytriphenyl – carbinol trisulphonic acid anyhydride: manufacturer HCA Australia), dissolved in distilled water (Ruello 1977). The solution was injected through the articular membrane between the fourth and fifth abdominal segment with a 0.5ml, 29-gauge needle. As the stain was not found to be visible for a sufficient time in the first experiment (see results) the treatment was not examined in the subsequent experiment.

Experimental procedure

School prawns were randomly assigned one of the treatments in each particular experiment (Table 1). Each individual prawn was measured (to the nearest 0.1 mm) between the base of the orbit of the eye and the centre of the posterior margin of the carapace (carapace length, CL). The gender of the prawn was determined by the presence of a thelycum (fe-

males) or petasma (males). The experiments ran for 70 days with each tank being monitored every 24 h for dead prawns, loose tags and exuviae. At the same time, water temperature and salinity were recorded from three randomly selected tanks. Dead prawns were replaced with prawns from reserve stocks in the larger stock tanks and were identified by removing part of their right uropod. These prawns remained identifiable throughout the experiment and maintained similar densities of prawns in each tank. Every two weeks two replicates of each treatment were randomly selected and the surviving prawns counted. The surviving prawns were then placed back into their respective treatment tank along with restocked prawns to maintain appropriate densities and were not processed again until the end of the experiment. Dead prawns and exuviae collected throughout the experiment and all prawns at the end of their selected time period were inspected for evidence of a tag wound and had their gender determined. Where applicable, the tag number of the prawn was also recorded.

Table 1. Experimental design for estimating tagging mortality on Hawkesbury River school prawns

Experiment	Size of prawn	Treatment	Replicates	No. per tank
1	Small*	Small tag	10	20
		Stain	10	20
		Control	10	20
2	Large ⁺	Small tag	10	15
		Large tag	10	15
		Control	10	15

* Prawns between 11 and 20mm carapace length

+ Prawns between 21 and 30mm carapace length

Analysis of data

Mortality was expressed as the proportion of treated prawns released that had died or shed their tag (stain) at the end of each time interval (14, 28, 42, 56 and 70 days). The null hypothesis was tested for data from each experiment using a two-factor analysis of variance (ANOVA). Student-Newman-Keuls (SNK) multiple comparisons were used to detect patterns in mean rates of mortality between treatments. To estimate rates of mortality a double exponential model of the form:

$$y = y_0 + a e^{bx} + c e^{dx}$$

was fitted to mean weekly mortality data of tagged and untagged prawns in each of the two experiments, with y being the cumulative proportion of

prawns which died in period x . The double exponential (or exponential mixture), which is the sum of a fast decaying term and a slower decaying term was fitted using a reparametrisation of the form:

$$y = y_0 + a b^x + c d^x$$

using the MLP software (Version 3.08, Numerical Algorithms Group, Oxford UK). This provided stable starting values for the five parameters in refitting the double exponential model using Sigmaplot (Version 8.02, SPSS Inc., Chicago, IL).

The distributions of lengths of prawns at the start and those of prawns that survived to the end of the experiment were compared using the Kolmogorov-Smirnov test to investigate the effects of tagging and staining on the growth of school prawns. To investigate any size-related survivability associated with the tagging of school prawns a Kolmogorov-Smirnov test was used to compare the initial carapace length of all prawns with the initial carapace length of prawns that survived to the end of the experiment. Chi-squared contingency tables were also done to compare sex ratios between school prawns recorded at the beginning of the experiment and those that survived to the end of the experiment. For all tests, analyses were done using both Statistica (Version 6, Tulsa, OK) and SPlus (Version 6.1, Insightful, Seattle, WA) with a P value of <0.01 considered significant (Zar 1974).

Results

Stain or tag loss and mortality

When the prawns in experiment 1 were injected with the fast green FCF solution, the stain immediately accumulated in all parts of the body including the head. By day 14 the stain was visible only in the gills and by day 70 all but one prawn was still showing evidence of stain. Streamer tags remained intact and legible throughout each experiment. There was no observed difference in burying or moulting behaviour between control, stained and tagged prawns. The only visible damage from the streamer tag was at the point of entry of the tag where a small black scar occurred, but this scar was lost at the first moult.

At the end of each experiment 98% and 97% of the treatment, control and restocked prawns were accounted for in experiments 1 and 2 re-

spectively. The most likely scenarios for the unaccountable were either that the prawns had escaped from the tanks, or that other prawns within the tanks had eaten them. Only one (small) and four (two small, two large) dislodged tags were found in experiments 1 and 2, respectively.

Deaths of untagged (control) prawns represent the mortality that can be attributed to factors other than tagging (e.g. handling and tank environment). Therefore, the differences in proportional mortality between untagged and the treated prawns provided an estimate of actual tag or stain induced mortality (Adjusted mortality, Table 2). Results from the two-factor ANOVA showed that the proportion of prawns that had died or shed their tags (stain) in each experiment differed significantly amongst treatments (Table 2). Mean mortality of untagged prawns (controls) was significantly less than stained or tagged prawns (ANOVA, $P < 0.01$) in both experiments. There were no significant differences in mean mortality between stained prawns or prawns with small tags (Experiment 1) nor between large and small tags (Experiment 2) (Table 2).

Table 2. Analysis of variance of proportional mortality of school prawns (small and large) during the two experiments

Analyses of variance					
Exp.	Source	df	MS	F	p
1	Hawkesbury (small)				
	Treatment	2	7066	58.88	<0.01*
	Time	4	162	1.35	0.30
	Treatment x Time	8	196	1.63	0.20
2	Hawkesbury (large)				
	Treatment	2	0.43	8.76	<0.01*
	Time	4	0.06	1.22	0.34
	Treatment x Time	8	0.01	0.12	0.99
Student-Newman-Keuls tests					
1	Small tag (0.68) (0.53) = Stain (0.64) (0.49) < Control (0.15)				
2	Small tag (0.75) (0.40) = Large tag (0.85) (0.50) < Control (0.35)				

Variances were homogeneous (Cochrans test, $p > 0.01$). (=) in Student-Newman-Keuls tests denotes no significant differences between two means.

*denotes significant difference. Proportion in bold indicates adjusted mortality.

Trends in mortality amongst tagged and stained prawns were similar in the two experiments with rates of mortality being the highest during the first 2 weeks of the experiment for all treatments, particularly the first three to four days. Figures 1a and b show fitted lines to the mean weekly cumulative mortalities in both tagged (small tag) and untagged prawns for the entire duration of each experiment. Tagged animals in both experiments showed similar patterns of mortality over the 10 week study period,

with a rapid increase in mortality in the initial two weeks and a levelling off from week 4. Parameter estimates and fit statistics for tagged and untagged prawns derived from the double exponential model are shown in table 3 for each experiment.

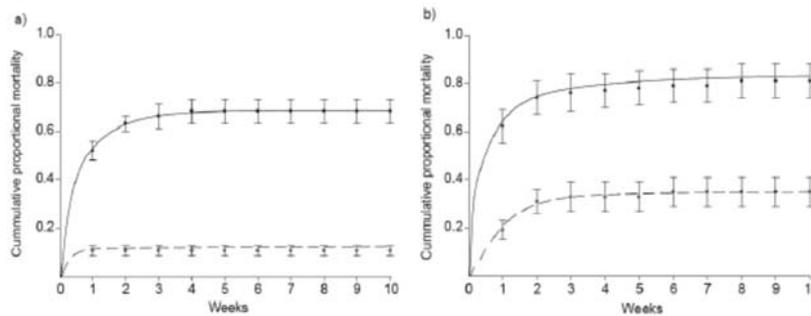


Fig. 1. Mean ± S.E. cumulative proportion of school prawns tagged with small streamer tags (●) or untagged (○) that died during experiments a) 1 and b) 2. The fit of the double exponential model is shown.

Table 3. Parameter estimates, standard errors and adjusted r squared values of mortality among prawns that were tagged (small tag) and untagged in Experiments 1 and 2

Exp	Tagged			Untagged		
		Coefficient	Std. Error		Coefficient	Std. Error
1	a	-37.37	3.58	a	-14.79	1.29
	b	-0.63	0.13	b	-0.53	0.06
	c	-39.75	4.21	c	-58.53	4832.12
	d	-0.14	0.01	d	0	0.02
	y0	68.2	0.14	y0	70.57	4832.38
		R ² = 0.99			R ² = 0.91	
2	a	-47.7	2.9	a	-42.59	2.55
	b	-0.23	0.02	b	-0.16	0.01
	c	-13.56	2.79	c	-57.75	35778.1
	d	-0.04	0.013	d	0	0.17
	y0	83.69	0.69	y0	91.66	35780.92
		R ² = 0.99			R ² = 0.97	

Moulting and growth

Daily patterns in the frequency of moulting were similar among all treatments within both experiments (Kolmogorov-Smirnov tests; p>0.1) although it was impossible to distinguish between exuviae from tagged and restocked prawns. The frequency of moulting of prawns initially peaked

within two weeks of the beginning of each experiment followed by several small irregular moulting events.

Mean lengths of prawns before and at the end of the each experiment did not differ significantly among treatments. Nor were there significant differences among treatments in the distributions of lengths of prawns at the beginning of each experiment or for those that survived to the end of each experiment (Table 4; Kolmogorov-Smirnov tests, $P > 0.1$).

Table 4. Mean (\pm S.D.) carapace length of treated prawns at the beginning of each experiment and those that survived to the end of each experiment. P value for all distribution comparisons among treatments

Exp.	Treatment	Start of experiment mean (\pm S.E.)	KS p-value*	End of Experiment mean (\pm S.D.)	KS p-value*
1	Control	16.88 (± 0.10)		17.81 (± 0.19)	
	Small tag	16.73 (± 0.11)		17.84 (± 0.20)	
	Stain	16.79 (± 0.12)	$p > 0.1$	18.10 (± 0.19)	$p > 0.1$
2	Control	24.28 (± 0.17)		24.58 (± 0.29)	
	Small tag	24.33 (± 0.18)		24.53 (± 0.29)	
	Large tag	24.50 (± 0.17)	$p > 0.1$	24.93 (± 0.25)	$p > 0.1$

Size and sex- related mortality

There were no significant differences in the mean lengths and distributions of initial tagged prawns and the mean lengths and distribution of lengths tagged prawns at release that survived to the end of each experiment (Fig. 2; Kolmogorov-Smirnov tests, $P > 0.05$). This indicated that rates of mortality of tag and stained prawns was not size selective. Also, there were no differences in mortality between genders for prawns with small tags (Chi-squared test, $P = 0.1$ and $P = 0.06$ for experiments 1 and 2 respectively) and large tags (Chi-squared test, $P = 0.1$, experiment 2).

Discussion

This study showed that tagging and staining significantly affected the survival (by up to 50%) of school prawns however there was no difference in mortality between sizes of tags used. It also showed that growth of

school prawns appeared to be unaffected by the tagging or staining process, and that mortality of tagged prawns was not size or gender dependent.

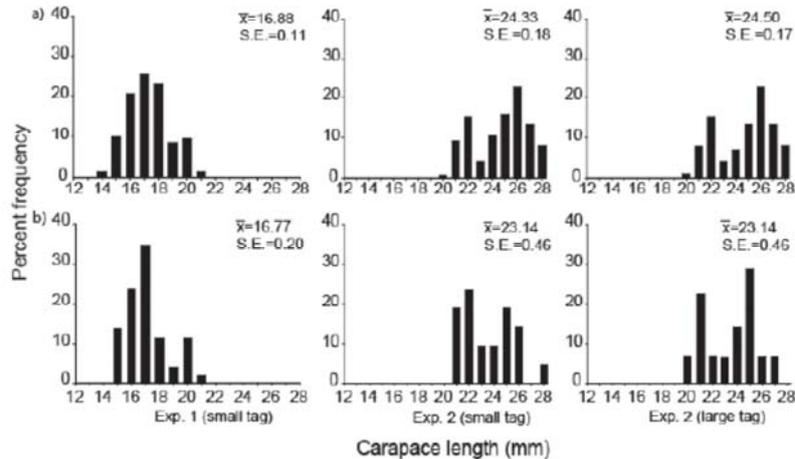


Fig. 2. Distributions of all small and large tagged school prawn carapace lengths at (a) the start of each experiment and (b) the distribution of initial school prawn carapace lengths of tagged small prawns that survived to the end of each experiment

Whilst there were no differences in rates of mortality between stained and tagged prawns, the stain was only evident in the head and gill area of the treated prawns for the first week of experiments and there was high variability in the visibility of the stain. Costello (1959) and Farmer (1981) found that there was minimal mortality in prawns that had been immersed in stain but the stain was only visible for a few days. Therefore, it appears that the initial trauma due to catching together with the stress associated with handling and the injection of the stain may play a significant role in the survival of stained prawns. The use of an injected stain as a marker in school prawns (11-20mm carapace length) may prove reliable for short-term fishery independent studies where individual information is not required. However in longer-term studies where the stain needs to be easily detected by untrained personnel such as commercial fishers and members of the general public, staining is unlikely to be a viable option.

Only seven dislodged streamer tags out of the 500 originally stocked tagged prawns were found throughout the three experiments. There was no evidence of treated prawns surviving to the end of the experiment without their tags intact. Therefore, either the prawns died with the tag

attached and were eaten leaving the tag behind, or they lost their tag and then were eaten. Tag shedding has often been associated with experiments to quantify the survival of tagged prawns (Benzie et al. 1995; Montgomery et al. 1995). Authors attributed the incidences of dislodged tags to the moulting behaviour of prawns, a problem also faced by other tagging experiments on crustaceans (Prentice and Rensel 1977). In our study prawns consistently moulted and streamer tag loss was considered negligible. The tags used have a central notch in which the body of the prawn sits, to reduce the risk of tag loss (Marullo et al. 1976).

In regards to behaviour, prawns with both small and large streamer tags were observed to swim, bury and moult normally. These treated prawns also appeared to have no trouble in shedding their moult with complete exuviae found across all tanks in each experiment. In similar studies on tiger prawns, Hill and Wassenberg (1985) found there to be no significant difference in the time and method it takes for streamer tagged and untagged prawns to complete ecdysis. In this study for both experiments the main frequency of moulting was within weeks one and two followed by a series of several smaller events. There were no significant differences in the frequency of moulting among treated and control (untagged) prawns for the two experiments.

Overall survival rates in school prawns as a direct result of tagging with streamer tags were lower compared to those recorded for other penaeid species (Primavera and Caballero 1992; Hill and Wassenberg 1985; Montgomery et al. 1995). Mortality rates for both tagged and stained prawns in both experiments were greatest over the first two weeks, suggesting that the high mortality in this smaller penaeid species maybe attributable to the initial effects of handling and more importantly the application of the actual tag or stain. This becomes evident as rates slowed after the first 2-4 weeks to a point where mortality was comparable to those of the untagged prawns (control) in each experiment. Estimates of rates of tag-induced mortality for other penaeids have been derived using an exponential decay model (Lucas et al. 1972; Montgomery et al. 1995). In this study a double exponential model accounted for data within the range of standard errors for replicate groups about each mean (Figs. 1a & b). The resulting high adjusted r squared values (>0.90) for tagged and untagged prawns in both experiments (Table 3) indicates that this exponential 'mixture' model is suitable for describing tag-induced mortality in school prawns.

The result in Experiment 1 that tagging or staining does not appear to affect growth is supported by other studies (Farmer 1981; Hill and Was-

senberg 1985; Montgomery et al. 1995). However the non-significant increase in growth for all treatments from Experiment 2 may have been the result of a higher stocking density (total weight of prawns per m²) than Experiment 1. High stocking densities have been shown to increase mortality and inhibit growth in both untagged and tagged/marked individuals (Maguire and Leedow 1983; Jewett 1986) and therefore appear to have confounded any treatment effects on growth in this particular experiment. Within the size range of prawns studied our results demonstrated that the mortality associated with tagging was not size-dependent. This is in contrast to other studies that report that the survival rate of prawns tagged with streamer tags significantly decreased in prawns of a carapace length less than 20mm (Hill and Wassenberg 1985; Wassenberg and Kerr 1990). This study also showed that mortality associated with tagging and staining was not dependent upon the sex of the prawn.

We have shown that school prawns can be tagged with streamer tags but that rates of survival are low. The low rates of survival can be countered in experiments done in the wild if large numbers of prawns can be tagged. However any extrapolation of estimates of mortality from laboratory experiments should be verified with experiments in the field. Streamer tags are easy to apply, are readily identified in the catches of commercial and recreational fishers with the added benefit of an individual identity. In contrast the staining of prawns has no less impact upon mortality than streamer tags but the stain is difficult to detect in prawns after one week. We conclude that streamer tags are the most suitable method for use in mark-recapture population studies for juvenile school prawns.

Acknowledgements

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Appendix 5: Montgomery, S.S., Walsh, C.T. and Barchia, (in prep) Estimating rates of mortality in school prawn populations of eastern Australia.

ESTIMATING RATES OF MORTALITY IN SCHOOL PRAWN POPULATIONS OF EASTERN AUSTRALIA

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ABSTRACT

The school prawn, *Metapenaeus macleayi*, is one of two species that predominate in the landings of penaeids off New South Wales, Australia. This study presents the first estimates of fishing mortality (that due to harvesting) and natural mortality (e.g., disease, movement from the fishing area) for this species. Replicated tag-recapture experiments were done on two stocks (Clarence and Wallis Lake) to estimate rates of fishing mortality whilst rates of natural mortality were estimated from meta-analyses. Experiments were done across spatial and temporal scales to consider variability between stocks and variability between fisheries targeting this resource. Rates of fishing mortality were derived by fitting tag-recapture data in a population model across a range of natural mortality values (0.002 – 0.01 per day). Rates of survival of tagged prawns were corrected for tag mortality and non-reporting of tags. Estimates of fishing mortality in year one of experiments (1.38E-05 – 4.78E-03 per day) and natural mortality were comparable to those reported for other penaeid fisheries world wide but fishing mortality (6.0E-03 – 1.56E-01 per day) increased in the second year of experiments. Estimates of natural mortality and fishing mortality were greater for the Clarence than Wallis Lake stocks. Differences in natural mortality were attributed to differences in growth whilst those for fishing mortality were most likely due to the catchability of the trawl fishery on the Clarence stock being greater than that of the variety of gears other than a trawl net used on the Wallis Lake stock. The increase in fishing mortality in the second year of experiments was associated to increased river discharge that increased prawn activity in more turbid waters which led to increased catchability. It is unknown whether recruitment to the populations was affected by the rise in fishing mortality at these times. Consequently, it is recommended that a precautionary approach be taken to exploiting these populations during times of high river discharge.

INTRODUCTION

Estimates of rates of mortality are important to stock assessments and to the effective management of fish resources. Total mortality (Z) has two components; namely, losses to the population caused by harvesting (fishing mortality, F) and losses from natural causes (natural mortality, M). Fishing mortality is the product of the amount of fishing effort (f) exerted on a stock per unit of time and the proportion of the stock caught by one unit of this effort, known as the catchability coefficient (q) (Quinn and Deriso 1999). Hence, total mortality can be expressed algebraically as:

$$Z = M + qf \quad (1)$$

Fishing mortality is regulated normally through fishing effort to maintain sustainable stocks. Natural mortality is used in association with growth to measure the productivity of a population. Usually it is most difficult to estimate because it is rarely observed directly and is confounded by levels of recruitment, an animal's age, patterns of movement of the target animals and can be correlated to fishing effort (Quinn and Dersio 1999).

Reviews about the methods available to estimate rates of mortality have been published by Vetter (1988), Caddy (1996) and Quinn and Deriso (1999). Estimating rates of mortality in crustaceans is made more difficult than in vertebrate and cartilaginous fishes because crustaceans do not have hard parts upon which to base age determinations and classic catch curve or virtual population analyses. Rather, studies estimate rates of mortality by using the approaches of catch per unit effort (CPUE) analyses (Xu *et al.* 1995, Wang 1999), length frequency analyses (Wang and Ellis 2004, Wang and Liu 2006), tag (or mark)-recapture experiments (e.g., Lucas *et al.* 1979, Die *et al.* 2002, Xia and McShane 2000) and life-history analyses (Mohammed *et al.* 1996). Mortality is estimated from CPUE, length frequency analyses and tag-recapture experiments by quantifying the change either in the relative abundance of individuals or numbers of tagged individuals over time. Life history analyses associate life-history parameters of many closely related species to environmental parameters (e.g., water temperature) in predictive relationships that have natural mortality as the dependent variable (e.g., Pauly 1980). These studies, referred to as meta-analyses, have shown that animals from the same taxonomic groups and with similar life histories have similar rates of natural mortality (e.g., Pauly 1980, Zang and Megrey 2006).

Tag-recapture is one of the most common methods used to estimate fishing and natural mortality in penaeid populations (e.g., Die *et al.* 2002, Xiao and McShane 2000, Lucas *et al.* 1979). The assumptions behind a tag-recapture experiment are that (i) the tagged animals become randomly mixed amongst the non tagged population, (ii) the fate of each tagged animal is independent of that of the other tagged animals, (iii) there is no loss of tags, (iv) survival rates of tagged animals are not influenced by tagging, (v) all captured tagged animals are reported and (vi) there is only negligible recruitment to the catchable population (Ricker 1975 and Pollock *et al.* 1991). In this study assumption (i) is addressed through experimental design, whilst assumptions (iii) and (iv) were tested by Walsh *et al.* (2007) as a precursor to designing the research reported in this paper. Assumption (v) is tested as part of the research reported in this paper but (ii) and (vi) are assumed.

The school prawn, *Metapenaeus macleayi*, is endemic to the waters off the east coast of Australia and is found in estuaries and in ocean waters out to depths of around 55 m between Corner Inlet (38 °S) and Tin Can Bay (25 °S). The species is one of five commercially important species found in these waters supporting average annual landings worth around AUD 8 million per annum and is fished by recreational and commercial fishers. School prawns have been studied extensively by Ruello (1971 1973a,b 1977) and Glaister (1977, 1978a,b), but none of these were dedicated to the dynamics of the populations. Ruello (1977) suggested that there were seven major stocks of school prawns along the east coast of Australia; namely Noosa (26°S), Clarence (29 °S), Manning (31 °S),

Hunter (32 °S), Hawkesbury (33 °S), Shoalhaven (34 °S) and Batemans Bay (35 °S). Ives *et al.* (2009) used best estimates of parameters for growth from Glaister (1997) and mortality (from that published for other penaeid species) in a size-based meta-population model to examine the impact of climate change upon the school prawn stock of the Clarence River. Results showed that the catchability coefficient, stock-recruitment process and river discharge were the main drivers in the dynamics of the Clarence River school prawn population.

The life history of the school prawn is typical of a penaeid (Garcia and Le Reste 1981) where juveniles inhabit estuarine waters before moving to ocean waters where they mature and spawn. Once in ocean waters the species do not disperse beyond a 70 km radius from the estuary from which they emigrated (Ruello 1977). The species lives for around 18 months (see Appendix 3) and spawns between January and June (Ruello 1971, Glaister 1977). Despite the extensive research there are no estimates of rates of mortality for school prawns. Information presented in this paper fills that knowledge gap.

The commercial fishery for school prawns in New South Wales

School prawns are a target species of three fisheries in New South Wales; namely the estuary general, estuary prawn trawl and ocean trawl fisheries. A diverse range of gears are used across these fisheries and the fisheries are all managed by a suite of input controls that include limits on gear dimensions, numbers of operators, area and time of operation and minimum and maximum legal mesh openings (Anon 2003a). The estuary general fishery targets school prawns in around 60 of the 130 coastal estuaries of NSW with average annual reported landings of 182 tonnes, worth approximately AUD 1.4 million per annum. Several gear types (seine, stow, and haul nets are used; for descriptions see Broadhurst *et al.* 2005) and times of operation vary between estuaries. The estuary prawn trawl fishery is restricted to three estuaries in NSW; namely, the Clarence, Hunter and Hawkesbury Rivers and it uses otter trawl nets of 11 m headline length, towed as either single or double rig combinations. Again its times of operation are restricted and vary between estuaries (Anon 2003b). Average annual reported landings are approximately 406 tonnes, worth AUD 2.9 million per annum. The ocean trawl fishery operates year around (Anon 2007) but targets school prawns primarily between January and June when the species emigrates from estuaries. Otter trawl nets of varying headline lengths are towed in triple, double or quadruple configurations. School prawns are caught by ocean trawl fleets from Shoalhaven Heads (34 °S) to Tweed Heads (28°S). Annual landings average approximately 52 tonnes and are worth AUD 349 thousand per annum.

MATERIALS AND METHODS

Study area

The study area was limited to estuarine waters where the bulk of the school prawn catch is taken. Attempts to include ocean waters in experiments were unsuccessful because of the sporadic nature of the fishery in these waters and the longevity of the tagged prawns. The Clarence River and Wallis Lake were selected as study sites because the former is the main producer of school prawns and the latter is a representative estuary general fishery for school prawns. By using both these estuaries, the study considered all methods used to catch school prawns, except the ocean trawl fishery. The Clarence River accounted on average for 52% of the state's school prawn landings between 2003-04 and 2007-08 (inclusively). The commercial fisheries targeting school prawns in this region are the estuary general (set pocket net September-May), estuary prawn trawl (December-May) and ocean trawl (February–May). Trawling predominates in the estuary once the season opens. A recreational fishery for prawns also operates over November to April, inclusive.

Wallis Lake accounted on average for 5 % of the state's landings of school prawns between 2003-04 and 2007-08 (inclusively). There is an estuary general fishery (set-pocket, seine and haul nets; September-April) and recreational fishery (November-April) operating in this estuary, and an ocean trawl fishery (February-April) in surrounding ocean waters.

Tagging procedure

Replicated tagging experiments were done in each of two years in both the Clarence River and Wallis Lake (Table 1). Each estuary was divided into grids of approximately the same surface area (Fig.1). Commercial fishers were chartered to use their vessels and gear to catch the prawns for tagging by research staff onboard. A five minute trawl was done at each of two randomised sites identified by fishers as places where prawns would be caught within each grid.

After each trawl, school prawns were tagged and released before another trawl was commenced. School prawns for tagging were placed in 220 L tanks of aerated seawater. Seawater in the tanks was exchanged approximately every 30 min, and ice was placed in the water to keep the water at an acceptable temperature.

School prawns were scooped from the 220 L tanks into 5L containers of seawater for tagging. Prawns were tagged with streamer tags (12P-T573) manufactured by HallPrint Pty Ltd. Tags were yellow and had the legend NSW DPI and a unique serial number printed in black. These were inserted through the articular membrane between the first and second segments and in a position that avoided nervous and digestive tissue. Tagged prawns were then placed back into 220 L tanks of aerated seawater ready for release. When all prawns had been tagged, tanks were checked for dead or damaged tagged prawns and then prawns to be released were placed into collapsible cannisters (Emiliani 1971; \approx 100 prawns per canister), and released back onto the same ground from which they were caught. Cannisters were left on the bottom for approximately 30 min (Montgomery *et al.* 1995) before being retrieved.

A subset (100 prawns) of the tagged prawns were measured (carapace length CL) to the nearest mm below and their gender determined, to provide information about the gender ratio and length distribution of school prawns tagged.

Recovery of tagged prawns

We relied upon commercial fishers to return captured tagged prawns. Media exposure, extensive liason and a reward system were used to promote the return of tagged prawns. The bulk of the commercial catches of seafood in NSW are marketed through a centralised system of fishermen's cooperatives. This system of marketing provided us with the opportunity to inspect just about the entire commercial catch of prawns from the Clarence River and Wallis Lake fisheries. Research staff were at the Clarence River and Wallis Lake Fishermens Cooperatives at the time when most of the fishers returned with their days prawn catch. They liaised with fishers, collected captured tagged prawns and paid rewards.

Effects of tagging

On-site experiments were done to test the hypothesis that estimates of tag mortality derived by Walsh *et al.* (2007, Appendix 4) from laboratory experiments were the same as for tagged prawns kept at the study area.

The experiments were done in 12 tubes which were suspended in a tidal, saltwater creek at the Clarence River. Tubes were made of plastic 5 mm mesh and were 260 mm in diameter and 1200 mm in height. In the experiment were the treatments tagged or untagged (control) and there were 6

replicate tubes for each treatment type with 6 prawns of a treatment placed in each tube (a total of 72 prawns).

During tagging operations prawns were randomly selected from the five minute trawl catches over the course of a day for use in the experiment. At the end of the day's tagging, the chosen prawns were assigned a treatment (tagged or untagged). Prawns selected were tagged following the procedures outlined above. All prawns were measured (CL), had their gender determined and were then assigned to a tube containing either tagged or untagged prawns. Each tube was inspected daily for dead prawns and exuviae. Dead prawns were measured and had their gender determined and any tags were removed. Experiments were terminated after five days for logistic reasons. The null hypothesis that there was no difference in the rate of mortality between tagged and untagged prawns was tested using one-way ANOVA.

Estimation of the proportion captured tagged prawns reported

Two experiments were done on the Clarence River fishery to estimate rates of reporting. A selected fisher whose 'silence' could be trusted was engaged to 'seed' 10 tagged prawns into the landings of school prawns at the Clarence River Fishermen's Cooperative over the course of a week. This rate of seeding was assumed to approximate the incidence of tagged prawns in catches. Tagged prawns were seeded unnoticed into various stations during the 'weigh in' process at the Cooperative. Similar experiments were not done at Wallis Lake because it was assumed that reporting of captured tagged prawns would be at least as high at Wallis as at the Clarence River. There were fewer fishers and closer cooperation between fishers at Wallis Lake than at the Clarence River and the fisher chartered to catch the school prawns for tagging was extremely vigilant in searching for captured tagged prawns not only in his own catch but also in the catches of all other fishers. This plus the presence of the research staff at the cooperative at the main time of weighing in catches gave us confidence that approximately all captured tagged prawns were detected.

Fishing effort

The best unit of fishing effort available for use in this study was the 'fisher day'. It does not differentiate between the different types of fishing gear the fisher uses to catch prawns in any 24 hour period. Information about fishing effort was collected from the records of the Fishermen's Cooperatives and voluntary log books completed by fishers. Both these sources of information were validated through interviews by research staff with fishers as they landed their catch for the day.

Estimation of natural mortality

In this study estimates of natural mortality and catchability derived from the models of Chapman (1961) and Lucas (1975) were negatively correlated (r values as high as 0.998) and were not suitable for calculating both natural mortality and the catchability coefficient. Rather, rates of daily natural mortality were calculated using different meta-analysis methods.

Estimation of the catchability coefficient and fishing mortality

The approach of Die *et al.* (2002) to fit tag recapture data to a predictive population model was adopted to estimate fishing mortality. Natural mortality was fixed to the lower, median and upper values across genders for each stock. To estimate fishing mortality for the fishery in Wallis Lake, it was assumed that estimates of natural mortality for the Hunter stock were representative of the prawns in Wallis Lake. The upper natural mortality value for the Clarence stock was limited to 0.01 per day based on the recommendation of Caddy (1996) that values higher than 5.0 per year (0.014 per day) were unrealistic for short-lived species.

In the model the predicted number of recaptures is assumed to be proportional to the ratio of fishing and natural mortality in period t .

$$R_t = (N_{t+1} - N_t) \frac{F_t}{F_t + M_t} \quad (2)$$

Where F_t is fishing mortality, M_t is natural mortality and N_t is the numbers of tagged prawns having survived to time t , calculated as.

$$N_{t+1} = N_t e^{-(F_t + M_t)} \quad (3)$$

and N_0 is the number of tagged prawns released in an experiment and adjusted for the effects of tagging and reporting of tags (Tables 3 and 4).

Fishing mortality is assumed to be a function of fishing effort f_t , and the catchability coefficient (q) and the selectivity (S) of the fishing gear (Eq. 4). All tagged prawns were assumed to be recruited to the fishery, i.e., there was no selectivity over the size range of prawns tagged because all prawns tagged were longer than the 50% selection point of the commercial trawl gear of 8.6 mm CL (Broadhurst *et al.* 2004).

$$F_t = qf_t S \quad (4)$$

The agreement between the observed and predicted numbers of recaptures was optimized using the Solver™ add-in in Excel™ (which uses numerical differentiation to implement efficient downhill optimization).

The exploitation ratio (E_t) was also calculated as:

$$E_t = \frac{F_t}{F_t + M_t} \quad (5)$$

The log-ratio test (Kimura 1980) was used to test for differences in the fitted model between tagging experiments when the median natural mortality values of 0.007 and 0.005 per day for the Clarence and Wallis stocks were used, respectively. We tabulated from the literature estimates of natural mortality, the catchability coefficient, fishing mortality and exploitation ratio from studies on other penaeids to compare with the estimates of these parameters calculated for the school prawn.

RESULTS

Effects of tagging

Results supported those found from the laboratory experiments. Tagging with streamer tags affected survival in each experiment (ANOVA $F_{1,10}=12.25$, $P,0.005$ and $F_{1,10} = 14.71$ $P<0.003$ for Experiment 1 and Experiment 2 respectively, Fig. 2). The proportion of tagged prawns surviving in Experiment 1 was 45% whilst 83% of untagged prawns survived. This means that 17% of the untagged prawns did not survive for reasons other than those associated with tagging. When the tagged treatment is adjusted for this experimental effect 62% of tagged prawns could be expected to have survived in Experiment 1. The proportion of both untagged and tagged prawns surviving in

Experiment 2 was far less. Only 30% of untagged and 3% of tagged prawns survived. When adjusted for the 70% of prawns that died for reasons other than the tagging process, 73% of tagged prawns could be expected to have survived in Experiment 2.

Estimation of the proportion of captured tagged prawns reported

In the first experiment all tags were detected at the Clarence River Fishermens Cooperative. In the second experiment 8 prawns were detected at the Clarence River Fishermen's Cooperative, one prawn was detected at a seafood processing and sales facility and the other tag was never reported. We assumed from these results that the proportion of captured tagged prawns reported ranged between 100 and 80%.

Estimation of natural mortality

Estimates of natural mortality from meta-analyses ranged from 0.002 to 0.007 and 0.006 to 0.025 for females and males respectively in the Clarence stock (Table 2). Values for the Hunter stock ranged from 0.001 to 0.005 and 0.004 to 0.016 for females and males, respectively. Natural mortality values were within the same range as those published for other penaeids (Table 6).

Estimation of the catchability coefficient and fishing mortality

A total of 21,096 tagged school prawns were released across all experiments and 431 and 494 tagged prawns were reported recaptured from the Clarence River and Wallis Lake releases respectively (Table 1). High Residual Sums of Squares (RSS) values for most experiments suggest that the catchability coefficient (Tables 3 and 4) and therefore fishing mortality have not been estimated with much precision. This probably reflects variability in the numbers of tagged prawns caught between days and the response of the commercial fishing fleet to this change in the catchability of prawns within each experimental period. Experiments with greater numbers of captured tagged prawns tended to have these distributed over a longer time period than experiments with low numbers of recaptures. Variability was greater in the former case because there were more days with no tagged prawns caught. Despite this high variability the log-ratio test detected differences in the model between experiments (Table 5). The only comparison where there was no difference in estimates of the catchability coefficient between models was that between November 2004 and January 2006 experiments at Wallis Lake. Apart from this comparison, estimates of the catchability coefficient were greater for experiments in 2005-06 than in 2004-05.

In an attempt to explain the high variability about estimates, the catchability coefficient was plotted against river discharge in the Clarence River and rainfall (river discharge data were not available) from the Wallis Lake for those months in which experiments were done to ascertain whether any association existed. Past studies on school prawns had shown high correlations between catch and river discharge (Ruello 1973b, Glaister 1978a). High catchability coefficient values in the Clarence stock occurred when river discharge was high but the same association was not evident between rainfall and the catchability coefficient of the Wallis stock (Fig. 3). Values of catchability coefficients equated to daily fishing mortality values between 8.35E-05 and 1.37E-03 for the Clarence stock and 7.77E-05 and 1.95E-02 for the Wallis stock. Exploitation ratios were between 13.3% and 94%, and 8.4% and 87% for the Clarence and Wallis stocks, respectively. Values for fishing mortality and exploitation ratios were higher in 2005-06 because of the higher values for the catchability coefficient in that year.

DISCUSSION

The results presented in this study are the first estimates of natural and fishing mortality reported for the school prawn. Rates of natural mortality and catchability coefficient values were generally consistent with those reported for other penaeids and catchability increased when rates of river discharge were high.

We attempted to address the assumptions underpinning tag-recapture experiments. Stratified random surveys were done to ensure as far as was possible that tagged prawns were released throughout the estuaries in numbers proportional to their abundance in each area in the estuary. The mixing of tagged prawns amongst the untagged was assisted by only tagging prawns on weekend days when there was no commercial fishing, leaving a minimum of 24 hours for tagged prawns to recover from tagging and to disperse. We quantified tag mortality and tag loss by doing experiments in the laboratory (Walsh *et al.* 2007) and in the field. Results from laboratory experiments done prior to designing the tagging experiments indicated that the impact from tagging on school prawns was high (50-60% survival, Walsh *et al.* 2007). The results of Walsh *et al.* (2007) were supported by one of the two experiments done in the field as part of this study whilst the other experiment had a higher survival rate. Tagged prawns survived under laboratory conditions for up to 10 weeks when experiments were terminated, but the low numbers of tagged prawns captured in field experiments and the temporal distribution of the numbers of tagged prawns caught suggests that survival in the wild was not as high as in the laboratory. Consequently, the catchability coefficient may have been overestimate. But we consider that we have allowed for the lower survival in the wild by estimating the catchability coefficient over a wide range of natural mortality values. Further, values for the catchability coefficient in this study were similar to those reported for other penaeid stocks (Table 6). Our experiments did not include ocean waters which may have underestimated fishing mortality on the stock. However, considering the sporadic nature of the ocean fishery and that this component generally only lands a small proportion of the total landings of school prawns, this effect is thought to have been minimal.

Whilst we could not find any estimates of the proportion tags reported for tagging studies on other penaeid species, the range we estimated in this study is within that of, or greater than those estimated for tagging studies on fish species (e.g., Whitlock and McAllister 2009, Bachelet *et al.* 2008, Jiang *et al.* 2007, Polacheck *et al.* 2006). We adopted a precautionary approach when estimating the catchability coefficient by using the range of rates of survival for tagged prawns found from the laboratory experiments together with estimates of reporting to adjust the numbers of tagged prawns released in each experiment.

As there were no differences in growth between the stocks (Montgomery *et al.* in press), we used estimates of natural mortality for the Hunter stock to estimate catchability for the estuary general fishery in nearby Wallis Lake so that our analyses covered a broad range of the fishing gears used in the commercial fisheries to catch school prawns in NSW. Most of the catch however is caught using a trawl or seine net (Broadhurst 2008).

Estimating the catchability coefficient requires an accurate value for fishing effort. Unfortunately the only unit of fishing effort available was the fisher day which is imprecise. It neither considers only the time spent fishing within any 24 hour period nor the different gears a fisher may use within the same 24 hour period to catch prawns. In other words in our analyses the fisher is akin to the unit of fishing gear.

We found like so many other studies that natural mortality was correlated to the catchability coefficient (Cobb and Caddy 1989, Wang and Ellis 2004). Consequently we estimated natural mortality by the independent technique of meta-analyses and examined the sensitivity of the catchability coefficient to the range of natural mortality values so derived. We have no information

about how accurate our estimates of natural mortality were but some confidence is taken from the fact that the estimates derived in this study were with one exception, within the range of those published for other penaeids (Table 5.6). The exception was that the upper value for the Clarence stock exceeded the 0.01 per day maximum annual value that Caddy (1996) proposed short-lived populations such as penaeids could sustain. For this reason we substituted the upper value for the Clarence stock for the maximum recommended by Caddy (1996).

Sums of squared values suggested that we did not estimate the catchability coefficient with much precision. However, values for the catchability coefficient were consistent with those reported for other penaeid species (Table 6) and therefore are probably representative of the boundaries within which the value lies. Estimates differed between experiments suggesting that the catchability coefficient changed temporally. This variability probably reflects changes in the behaviour of school prawns between days and in response to this, changes in behaviour by the fishing fleet (e.g., Hilborn and Walters 1992).

It is well documented that the catchability of penaeids is associated with environmental conditions (e.g., Penn 1984) and in particular river discharge (Ruello 1973b, Glaister 1978a, Ives *et al.* 2009). Whilst there were only four points to fit to the association, there was a high correlation between river discharge from the Clarence River and the catchability coefficient for the Clarence stock. Data representative of river discharge in Wallis Lake was not available and we found no significant correlation between its substitute (rainfall) and the catchability of the Wallis Lake stock. This association in the Clarence stock supports the suggestion of Ives *et al.* (2009) that high catches occur at times of high river discharge because catchability increases. The higher catchability is most likely caused by the prawn's behaviour to be more active and aggregate in turbid water (Penn 1984).

Values for fishing mortality and exploitation ratios are comparable to those reported for other penaeid stocks (Table 6). The exceptions to this are the high values recorded for the Clarence stock from the March 2006 release (Table 3). In his assessment of the impact of fishing upon the banana prawn *Penaeus merguensis*, a species with a very similar life history to the school prawn, Somers (1990) remarked that fishing mortality needed to be constantly greater than 0.65 per month (0.022 per day) to affect the sustainability of the fishery. Lucas *et al.* (1979) found for the same species and fishery that exploitation ratios of 0.78 to 0.86 were sustainable. Apart from the one exception above, estimates of fishing mortality and exploitation ratios calculated in this study for 2005-06 approached the values of Somers (1990) and Lucas *et al.* (1979), respectively. Also, Ives *et al.* (2009) in their modelling of the school prawn population of the Clarence River found that at high levels of river discharge 'catch increased so much that there was some risk that recruitment to the fishery in the subsequent few years would reduce'. The levels of catchability recorded in our study for 2005-06 approach the upper bound used in the modelling by Ives *et al.* (2009). Therefore, catchability can reach these levels that may impact upon the future recruitment to the fishery.

Whilst the value of the catchability coefficient for school prawns has not been estimated with much precision, results from this study provide the first estimates of natural mortality and catchability coefficient for school prawns. Perhaps a more accurate estimate of natural mortality and fishing mortality would have been derived if we had implemented a Brownie *et al.* (1985) type experimental design commonly used in studies on terrestrial fauna and fish species. However this design was considered cost prohibitive for the short lived school prawn because intervals between tagging episodes would have had to have been at least fortnightly. The values for natural mortality and catchability coefficient derived in our study are the first credible input values for these parameters that can be used in population models to assess the status of the school prawn stocks along the NSW coast and provide fisheries managers with knowledge about how school prawn stocks may respond to alternative management scenarios. In particular fisheries managers and

industry may need to discuss options for managing school prawn stocks during times of prolonged periods of high river discharge.

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Table 1. Summary of numbers of tagged school prawns released (before being adjusted for the effects of tagging – see text) in each stock, the numbers recaptured from each release and the mean (CL in mm), standard error, and size range (CL in mm) tagged for each release. ns = no sample was measured.

	No Rel	No Recapt	Mean CL	SE	Size Range	
					Min	Max
Clarence Stock						
Feb'05	3,100	65	15.9	0.04	12.2	22.1
April'05	5,150	33	16.9	0.04	13.0	23.1
Jan'06	1,921	155	19.4	0.05	16.2	25.5
Mar'06	2,548	178	20.4	0.3	14.3	23.5
Wallis Stock						
Oct'04	2,084	143	16.5	0.08	12.8	22.1
Nov'04	3045	69	16.3	0.08	12.2	23.4
Dec'05	1198	110	19.9	0.08	15.8	24.8
Jan'06	2050	172	20.0	0.09	15.9	25.7

Table 2. Estimates of natural mortality (M) (per day) calculated for female (F) and male (M) school prawns of the Clarence and Hunter Rivers stocks using meta-analysis approaches described in the three referenced studies. The values for growth rate κ , and the maximum age of prawns in the in these analyses are shown. The parameter t_0 (days) is assumed.

Stock	Gender	Parameters			Hoenig (1983)	Hewitt and Hoenig (2005) Values Of M	Zhang & Megrey (2006)
		T_{max}	κ	t_0			
Clarence	F	700	0.005	21	0.007	0.002	0.005
	M	165	0.025	21	0.025	0.006	0.021
Hunter	F	925	0.004	21	0.005	0.001	0.003
	M	435	0.010	21	0.011	0.004	0.016

Table 3. Daily estimates of the catchability coefficient (q), fishing mortality (F) and exploitation ratio (E) for the Clarence River school prawn stock. Estimations were done for a range of natural mortality values (M) using tag-recapture data where the numbers released (N_r) had been reduced to 50% and 40% survival to allow for tag mortality (including non-reporting of tags) (see text) in the model of Die *et al.* (2002). RSS = Residual Sums of Squares, N_c = number of tagged prawns recaptured.

Date	M = 0.002						M = 0.007				M = 0.01			
	N_r	N_c	q	F	E	RSS	q	F	E	RSS	q	F	E	RSS
Feb'05	1860	65	8.35E-05	1.38E-03	0.409	345.53	8.93E-05	1.48E-03	0.175	332.14	9.13E-05	1.51E-03	0.131	395.16
	930	65	1.73E-04	2.87E-03	0.589	340.38	1.85E-04	3.07E-03	0.305	326.68	1.93E-04	3.20E-03	0.242	318.52
Apr'05	3090	33	2.46E-04	2.51E-03	0.556	45.7	2.48E-04	2.53E-03	0.265	44.37	2.49E-04	2.54E-03	0.203	43.50
	1545	33	4.95E-04	5.05E-03	0.716	45.02	4.99E-04	5.09E-03	0.421	43.70	5.02E-04	5.12E-03	0.339	42.92
Jan'06	1152	155	7.17E-04	1.88E-02	0.904	3396.60	5.29E-04	1.38E-02	0.664	4020.62	5.44E-04	1.42E-02	0.588	3951.55
	576	155	1.26E-03	3.29E-02	0.943	3798.45	1.33E-03	3.47E-02	0.832	3665.37	1.37E-03	3.58E-02	0.781	3586.11
Mar'06	1528	178	3.99E-04	9.81E-03	0.831	10245.65	4.33E-04	1.07E-02	0.603	9947.51	4.54E-04	1.12E-02	0.527	9766.50
	764	178	1.12E-03	2.76E-02	0.933	9465.05	1.23E-03	3.03E-02	0.813	9079.53	1.30E-03	3.19E-02	0.762	8848.29

Table 4. Daily estimates of the catchability coefficient (q), fishing mortality (F) and exploitation ratio (E) for the Wallis Lake school prawn stock. Estimations were done for a range of natural mortality values (M) using tag-recapture data where the numbers released (N_r) had been reduced to 60% and 50% survival to allow for tag mortality (including non-reporting of tags) (see text) in the model of Die *et al.* (2002). RSS = Residual Sums of Squares, N_c = number of tagged prawns recaptured.

Date	M = 0.001						M = 0.005				M = 0.01			
	N_r	N_c	q	F	E	RSS	q	F	E	RSS	q	F	E	RSS
Oct'04	1250	143	3.05E-04	2.89E-03	0.743	2080.14	3.48E-04	3.30E-03	0.398	2022.87	4.07E-04	3.86E-03	0.278	1946.496
	1042	143	3.76E-04	3.57E-03	0.781	2072.34	4.30E-04	4.08E-03	0.449	2013.39	5.04E-04	4.78E-03	0.324	1934.64
Nov'04	1827	69	7.77E-05	8.20E-04	0.451	480.23	8.18E-05	8.63E-04	0.147	480.25	8.68E-05	9.15E-04	0.084	480.53
	1522	69	9.35E-05	9.87E-04	0.497	480.22	9.84E-05	1.04E-03	0.172	480.25	1.04E-04	1.10E-03	0.099	480.55
Dec'05	718	110	6.93E-04	6.0E-03	0.857	1700.93	7.48E-04	6.48E-03	0.594	1672.73	8.24E-04	7.13E-03	0.416	1636.12
	599	110	8.65E-04	7.49E-03	0.882	1690.52	9.37E-04	8.11E-03	0.619	1661.12	1.03E-03	8.95E-03	0.472	1622.95
Jan'06	1681	172	1.06E-03	5.49E-03	0.846	9515.29	1.12E-03	5.80E-03	0.537	9393.81	1.19E-03	6.19E-03	0.382	9250.59
	1401	172	1.3E-03	6.76E-03	0.871	9480.99	1.37E-03	7.14E-03	0.583	9359.14	1.47E-03	7.62E-03	0.432	9216.00

Table 5. Results of log-ratio tests comparing models determined from each tag-recapture experiment to estimate the catchability coefficient (q) on the Clarence (CL) and Wallis Lake (WL) stocks. Natural mortality was assumed to be 0.007 and 0.005 for the Clarence and Wallis stocks, respectively. In the Table are the Dates of each experiment (m,yy where A = April, D = December, F = February, J = January, M = March, N = November and O = October), the suffix n identifying the first and second datasets in each comparison and nt the pooled sample size. The Chi-Square (χ^2) value and level of significance (P) are also shown. Non-significant at $P < 0.05$

Stock	Comparison	Datasets Combined					Datasets Pooled				
		q_1	q_2	n_1	n_2	RSS	n_t	RSS	df	χ^2	P
CL	F'05 v A'05	1.34E-04	4.99E-04	65	33	450.25	98	8925.44	1	139.28	<0.0001
	F'05 v J'06	1.34E-04	1.33E-03	65	155	4071.93	220	5211.33	1	59.28	<0.0001
	F'05 v M'06	1.34E-04	1.23E-03	65	178	9486.09	243	1287.99	1	485.21	<0.0001
	A'05 v J'06	4.99E-04	1.33E-03	33	155	3709.07	188	4805.29	1	48.68	<0.0001
	A'05 v M'06	4.99E-04	1.23E-03	33	178	9123.23	211	8925.44	1	4.63	0.0315
	J'06 v M'06	1.33E-03	1.23E-03	155	178	12744.90	333	23973.48	1	210.40	<0.0001
WL	O'04 v N'04	4.30E-04	9.84E-05	143	69	2515.17	212	2669.15	1	12.59	0.0004
	O'04 v D'05	4.30E-04	9.37E-04	143	110	3827.90	253	7172.32	1	158.86	<0.0001
	O'04 v J'06	4.30E-04	1.37E-03	143	158	11372.53	301	15441.07	1	98.06	<0.0001
	N'04 v D'05	9.84E-04	9.37E-04	69	110	2316.29	179	2579.81	1	19.29	<0.0001
	N'04 v J'06	9.84E-5	1.37E-03	69	158	9860.92	227	9885.67	1	0.569	0.4507
	D'05 v J'06	9.37E-04	9.84E-05	110	158	11173.65	268	17.419.22	1	119.00	<0.0001

Table 6. Daily estimates of the catchability coefficient (q), fishing mortality (F), natural mortality (M), losses other than from fishing (X) and exploitation ratio (E) for penaeid species. The method used by each study to derive parameter estimates are given as catch per unit effort and including both fishery dependent and fishery independent data (CPUE) and tag-recapture studies (Tag). *ng* = a value not given in the publication.

Species	Author	Method	Q	F	M or X	E
<i>M. endeavouri</i>	Ye <i>et al.</i> (2008)	CPUE	0.000176 – 0.000213	<i>ng</i>	<i>ng</i>	<i>ng</i>
<i>P. aztecus</i>	Klima (1964)	Mark	<i>ng</i>	0.009	0.03	0.23
<i>P. duorarum</i>	Kutkuhn (1966)		<i>ng</i>	0.137	0.0786	0.64
<i>P. duorarum</i>	Costello and Allen (1968)	Tag	<i>ng</i>	0.0099 – 0.0198	0.0235 – 0.0312	0.030 – 0.39
<i>P. duorarum</i>	Berry (1969)	Tag	<i>ng</i>	0.013	0.009	0.59
<i>P. duorarum</i>	Klima (1974)	Tag	<i>ng</i>	0.015 – 0.018	0.003 – 0.017	0.47 – 0.86
<i>P. esculentus</i>	Dichmont <i>et al.</i> 2008	CPUE	0.0000592 – 0.0000663	<i>ng</i>	<i>ng</i>	<i>ng</i>
<i>P. indicus</i>	Loneragan <i>et al.</i> (1997)	Tag	0.0006 – 0.0035	<i>ng</i>	0.00041 – 0.00068	<i>ng</i>
<i>P. indicus</i>	Die <i>et al.</i> 2002	Tag	0.00012 – 0.00058	<i>ng</i>	0.00457 – 0.00957	<i>ng</i>
<i>P. latisulcatus</i>	Penn (1976)	Tag	<i>ng</i>	0.002	0.003	0.40
<i>P. merguensis</i>	Lucas <i>et al.</i> (1979)	Tag	<i>ng</i>	<i>ng</i>	0.007	0.78 – 0.86
<i>P. merguensis</i>	Somers and Wang (1997)	Ng	0.00024	<i>ng</i>	<i>ng</i>	<i>ng</i>
<i>P. merguensis</i>	Wang and Haywood (1999)	CPUE	<i>ng</i>	<i>ng</i>	0.0029	<i>ng</i>
<i>P. plebejus (adult)</i>	Lucas (1974)	Tag	<i>ng</i>	0.0031	0.0071	0.30
<i>P. plebejus (juveniles)</i>	Lucas (1974)	Tag	<i>ng</i>	0.0057	0.0031	0.65
<i>P. plebejus</i>	Lucas (1975)	Tag	<i>ng</i>	0.010	0.014	0.42
<i>P. plebejus</i>	Glaister <i>et al.</i> (1990)	Tag	<i>ng</i>	0.0051 – 0.0076	0.016 – 0.08	<i>ng</i>
<i>P. plebejus</i>	Gordon <i>et al.</i> (1995)	Tag	<i>ng</i>	<i>ng</i>	0.0096	<i>ng</i>

Table 6 Cont'd

Species	Author	Method	<i>Q</i>	<i>F</i>	<i>M or X</i>	<i>E</i>
<i>P. semisulcatus</i>	Wang and Die (1996)	CPUE	0.000088	<i>ng</i>	0.0064	<i>ng</i>
<i>P. semisulcatus</i>	Wang (1999)	CPUE	<i>ng</i>	<i>ng</i>	0.004 – 0.009	<i>ng</i>
<i>P. semisulcatus</i>	Xu <i>et al.</i> (1995)	CPUE	<i>ng</i>	<i>ng</i>	0.011	<i>ng</i>
<i>P. semisulcatus</i>	Ye <i>et al.</i> (2008)	CPUE	0.0000621 – 000123	<i>ng</i>	<i>ng</i>	<i>ng</i>
<i>P. setiferus</i>	Klima & Benigno (1965)	Tag	<i>ng</i>	0.009 – 0.027	0.011	<i>ng</i>
<i>H. sibogae</i>	Baelde (1994)	CPUE	<i>ng</i>	0.0333 – 0.1	0.0333 – 0.0667	<i>ng</i>

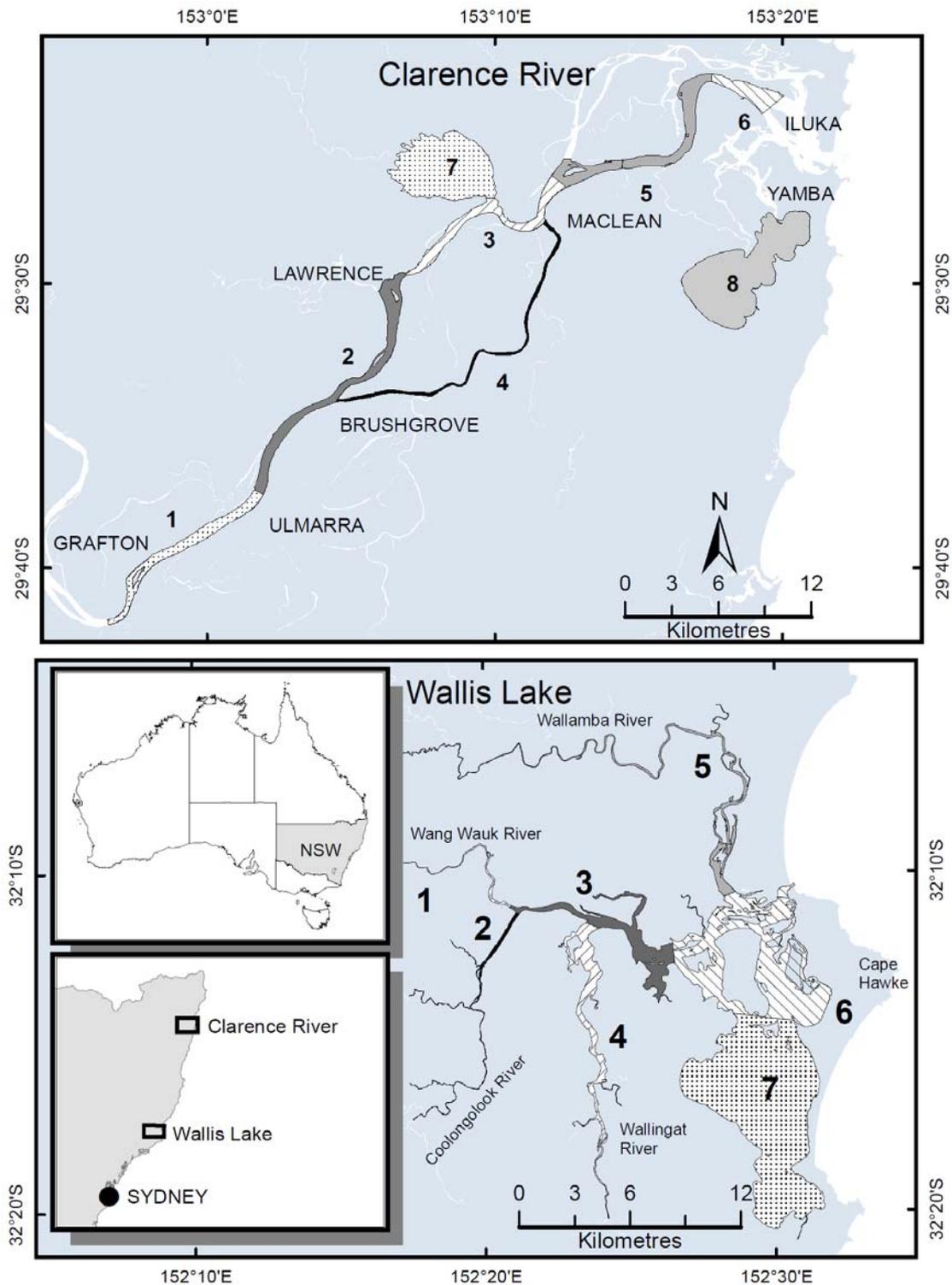


Figure 1. Location of the two school prawn stocks used in tag-recapture studies to estimate rates of fishing mortality. Numerals and shading are used to show the stratification of each estuary into zones.

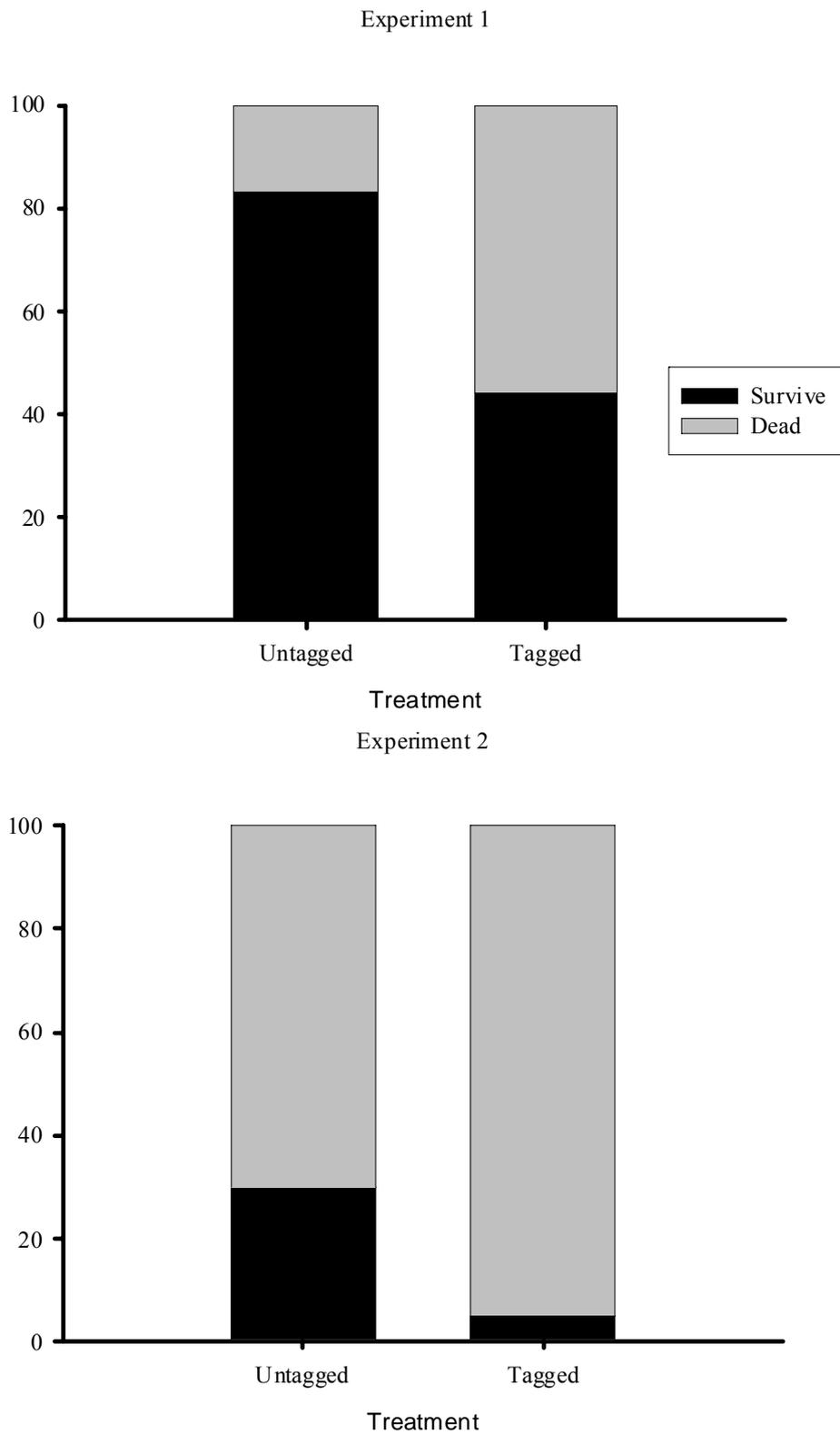


Figure 2. Mean number of tagged and untagged school prawns surviving after 5 days in field-based experiments at the Clarence River; $n = 6$.

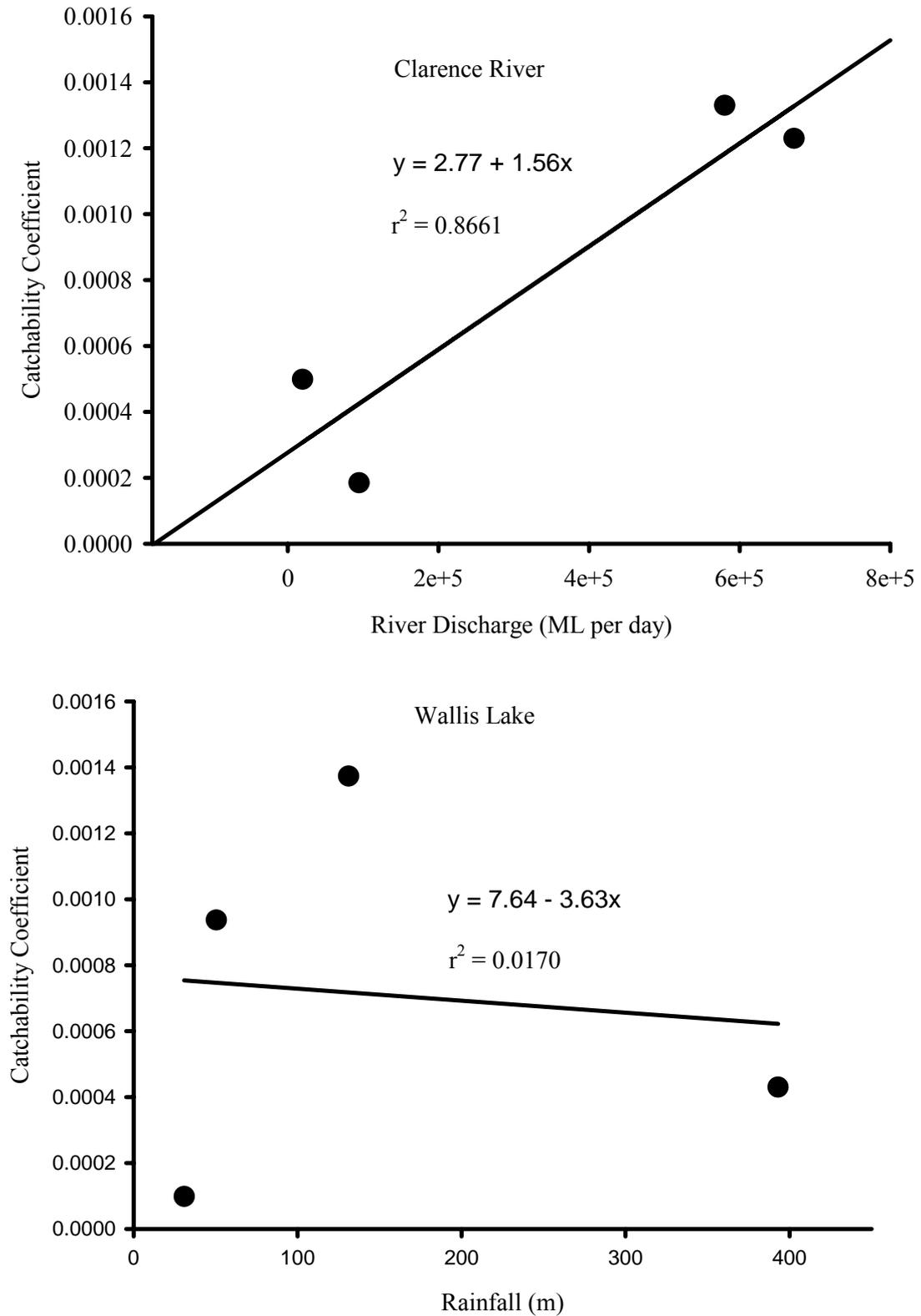


Figure 3. Association between monthly river discharge (Clarence River) and rainfall (Wallis Lake), and the catchability coefficient. The r^2 values for each association are given.

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