Patterns in the distribution and abundance of female eastern king prawns, *Melicertus plebejus* (Hess, 1865), capable of spawning and reproductive potential in waters off eastern Australia

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Abstract

Linear mixed models were used to test the null hypothesis that there were no differences between seasons and locations in the reproductive potential of female eastern king prawns, *Melicertus plebejus* along the east coast of Australia. Three samples were collected in each season between autumn 1991 and winter 1992 (inclusive). Females capable of spawning were found at all locations but proportions were greater in lower than higher latitudes. Females capable of spawning were not found at the southern (highest latitude) most location in all seasons. There was a significant interaction in reproductive potential between seasons and locations suggesting that patterns among seasons differed between locations and vice versa. Reproductive potential was greatest amongst the northern (lower latitudes) most locations and was greatest in autumn at these locations. Seasonal patterns were less pronounced further south (higher latitudes). The length composition of females in catches differed between locations with more larger prawns found in samples from northern locations. The challenge that remains is to quantify the oceanic sources of larvae that contribute to recruitment in each nursery area and the estuarine sources of juveniles that contribute adults back to the effective spawning stock. Maintaining the effective spawning stock and important nursery areas are crucial to the sustainability of this resource.

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1. Introduction

Knowledge of the distribution and abundance of spawning individuals in a population and the reproductive potential of the spawning population is important to the sustainable management of wildlife resources. Reproductive potential is expressed through a population fecundity index which relates the relative abundance of spawners in individual size classes to the fecundity of the particular sized animals (e.g. Crocos, 1987). This, together with information on larval dispersal and movements of juveniles is needed to clearly define the spawning stock that contributes recruits to the fishable population and to understand the relationship between levels of spawning and recruitment (e.g. Cobb and Caddy, 1989; A. Garcia, 1996; S. Garcia, 1996).

It was once thought that penaeid stocks could not be recruitment overfished (e.g. Neal, 1975), however, studies by Penn et al. (1995) and A. Garcia (1996), S. Garcia (1996) demonstrated that recruitment in penaeid fisheries can be affected by the level of fishing effort directed at the spawning stock. It therefore becomes important to have some understanding of the temporal and spatial distribution of the spawning stock so that fisheries managers can, if necessary, conserve this part of the population to maintain a sustainable resource.

The eastern king prawn, *Melicertus plebejus*, is endemic to waters of eastern Australia and is a target species of commercial and recreational fisheries. It is distributed along the east coast of Australia from 21°S to 41°S (Fig. 1). The life cycle of the eastern king prawn is typical of many commercial penaeids, hav-
Fig. 1. Map showing the locations sampled. The inserted map shows the distribution of *M. plebejus* and in relation to this where the study was done. In the figure QLD, NSW, VIC and TAS are the Australian states of Queensland, New South Wales, Victoria and Tasmania, respectively.

ing both an estuarine and oceanic phase (Young and Carpenter, 1977; Young, 1978; Coles and Greenwood, 1983; Dall et al., 1990). Eastern king prawns are unusual among members of the family, **Penaeidae** because they move long distances in a unidirectional pattern from higher (more southern) to lower (more northern) latitudes (Ruello, 1975a; Montgomery, 1990). Ruello (1975a) claimed that this was a spawning migration but had little evidence to support this hypothesis.

Early studies using macroscopic observations of ovaries and plankton tows to sample larval prawns suggested that eastern king prawns spawned in ocean waters between January and June (Dakin, 1938; Racek, 1959). In contrast, Glaister (1983) suggested that eastern king prawns spawned in northern New South Wales (NSW) year round. These studies though did not associate the macroscopic observations with egg development. A more recent study of the reproductive biology of eastern king prawns in southeast Queensland (Qld) waters found that ovarian development increased around the first and last quarters within a single lunar cycle (Courtney et al., 1996) and that whilst spawning occurred throughout the year, it was only the egg production in winter that contributed larvae to the local fishery (Courtney, 1997). The smallest size at which 50% of females were mature was determined to be 42 mm carapace length (CL; Courtney et al., 1995).

Rothlisberg et al. (1995) used information about the larval biology of eastern king prawns and oceanography to suggest that the effective spawning population for this species off southeast Qld occurred in waters nearer than 10 km from the shoreline and that most larvae in deeper water probably did not contribute to any coastal nursery grounds along the east coast of Australia. They claimed that the role of the northerly migration of eastern king prawns in reproduction was overemphasised. However, Courtney (1997) found only low numbers of ripe females (i.e., those with cortical crypts in their oocytes) within 4 km of the coast or in depths less than about 28 m.

Hence, if the hypothesis of Rothlisberg et al. (1995) is correct then only a small proportion of the eastern king prawn egg production contributes recruits to the population. Despite all this information about the reproductive biology of eastern king prawns there is little information about the latitudinal distribution of the spawning stock.

This paper provides information to fill this knowledge gap by testing the hypothesis that the reproductive potential of the eastern king prawn population changes with latitude and season. The results from this study will provide fisheries managers with the knowledge to direct harvest strategies aimed at conserving spawning stock to areas of the fishery where the strategies will be most effective. Females contributing to the spawning stock have been defined as those with ovaries in the vitellogenic or more advanced (ripe) stages of development (Courtney et al., 1995) and are referred to in this paper as ‘females capable of spawning’. Oocytes remain in the vitellogenic stage for probably 2–3 weeks in what is considered a “holding” stage until conditions are suitable for spawning, then the oocytes develop through the more advanced stages of development in rapid (2–4 days) succession (Courtney, 1997).
1.1. Population structure and fishery

A commercial fishery targeting this species has been in operation for over 50 years (Ruello, 1975b) and extends from Swain Reefs (21° S) south to the Gippsland Lakes (38° S). It operates year around in latitudes lower than 32° S but in latitudes higher than this, there are very few vessels and prawn trawling is done mainly over the summer and autumn months (Montgomery, 1990). In excess of 80% of the catch of eastern king prawns is taken from latitudes lower than 32° S (Fig. 1). A recreational fishery targets the species in estuaries from Noosa Heads (26° S) to George Bay (41° S). Observations during fishery dependent studies by Montgomery (1990) and Reid and Montgomery (2005) and fishery independent studies by Graham et al. (1993a, b) did not find mature eastern king prawns in latitudes higher than 32° S.

Currently the eastern king prawn resource is not managed as a unit stock but rather as separate units based on state government (New South Wales and Queensland) jurisdictions. If spawning is concentrated in one area off the east coast of Australia, then it will be important for the management of eastern king prawn stock to ensure that a sufficient number of spawners are conserved to maintain egg production at a level that will sustain the population. Similarly, it will be important to manage fishing pressure on those nursery areas that supply recruits to the spawning stock.

2. Materials and methods

2.1. Experimental design

Data were collected between autumn 1991 to winter 1992 inclusive, from eight regions [Swain Reefs (21° S), Lady Elliot Island (24° S), Mooloolaba (26° S), Moreton Bay (27° S), Bellinga (28° S), Clarence (29° S), Cooffs Harbour (30° S) and Port Stephens (32° S)]. This sampling area encompassed the region where females of sizes capable of spawning were known to occur. The seasons were autumn (March–May inclusive, 1991 and 1992), winter (June–August, 1991 and 1992), spring (September–November, 1991 only) and summer (December–February, 1991 only).

2.2. Collection and preparation of samples

Samples of female prawns were randomly collected each month from the catches of commercial fishing vessels throughout the fishery and transported back to the laboratory. The carapace length (CL) of each female was measured to the nearest 0.1 mm and then rounded down to the nearest millimetre. A section of ovary was dissected from the first abdominal segment from each female prawn. Pilot work had shown that there were no differences in the distribution of oocyte stages between different areas of the ovary along the body of the prawn (Montgomery et al., unpublished data). The ovarian tissue was fixed in a solution of 10% formaldehyde, 5% acetic acid, 1% calcium chloride and 84% seawater, and then stored in 70% alcohol. Tissue sections were then blocked in paraffin wax, cut to a thickness of 6 μm, and stained with haematoxylin and eosin for microscopic examination and staging.

2.3. Microscopic examination

Ovarian tissue sections were viewed under 100× magnification using monocular microscopes and the oocyte developmental stage determined by using the criteria of Courtney et al. (1995). An overall stage of development was assigned based upon the oocyte development stage which occupied more than 50% of the field of view under the microscope.

2.4. Length distributions

Data on the length of individuals in samples were grouped by 1 mm class intervals, expressed as the proportion of the total number in the sample, weighted by the relative abundance of the month when the sample was taken and compiled into annual distributions.

The Kolmogorov–Smirnov Two-Sample Test (Siegel and Castellan, 1988) was used to compare the shapes of the annual length distributions. The probability for each pairwise comparison among the eight locations was adjusted using the Bonferroni inequality so that the significance level of the overall test was approximately 5% (Miller, 1966).

2.5. Catch data

Commercial fishers are required by law to provide on statu- torily forms details about their fishing operations, including information on catch and fishing effort. This information was used to standardise catch per unit effort (cpue; kg of prawns caught per standard vessel month); relative improvements in vessel fishing power were included from O’Neill and Leigh (2006).

The catch data were also used to weight the reproductive potential data to the number of female prawns in the commercial catch at the times of sampling. Numbers of female prawns were calculated by using the sex-ratio by weight in samples to determine the weight of the female catch and then converting this weight to numbers by using the average weight of the female prawns in samples.

2.6. Proportions of females capable of spawning and reproductive potential

Numbers of females in each mm CL size class capable of spawning were expressed as a proportion of the total number of females in the sample. The mean (S.E.) proportions of females capable of spawning were calculated across samples for each season and then plotted.

Proportions of females capable of spawning in each mm CL size class were multiplied by the relationship between fecundity and prawn length given in Courtney (1997) and then weighted by the number of female prawns in the catch at the different sampling times and Locations. This provided an index of repro-
productive potential for replicate sampling times within seasons and by location.

2.7. Statistical analyses

A linear mixed model (LMM) was applied using the method of residual maximum likelihood (REML; GenStat, 2007; Montgomery, 1997) and following the approach of O’Neill and Leigh (2007) to ascertain differences in the reproductive potential between seasons and locations. The response variable was reproductive potential. The model had the fixed terms of fishing effort (log days), season, location and the random term of individual vessel. Definition of the model was as follows:

$$ C = X\alpha + Z\gamma + \epsilon $$

(1)

where $C$ is the vector for reproductive potential on the natural logarithm scale; $\alpha$ the vector of fixed terms including the model intercept, linear covariate for standardising different log days of fishing effort between vessels and factor parameters measuring the interaction between seasons and locations, matrix-multiplied by data $X$; $\gamma$ the vector of random vessel terms with design matrix $Z$ indicating which monthly catches belong to each vessel; and $\epsilon$ is the normally distributed error term. Fishing power differences between vessels were standardised through the linear covariate for log fishing effort (log days), the random vessel terms and vessel improvements were offset for minor changes in technologies between 1991 and 1992 ($\approx 3.5\%$; O’Neill and Leigh, 2006).

$$ \log C = \log catch_{wt} - \log fishpower_{offset} $$

$$ + (\log mat + \log ratio + \log fec) $$

(2)

where catch (in number) is the monthly catch for the individual vessel, fishpower is that for the vessel taken from O’Neill and Leigh (2006), mat the proportion of females capable of spawning by mm CL size class, ratio the proportion of females in the catch and fec is the average number of eggs carried by a female by each mm CL size class.

Fig. 2. Length distributions of female $M$. plebejus in samples from each location. The mean ($\bar{x}$), standard deviation (S.D.) and sample size ($n$) are shown. Note the differences in scales on the vertical axes between graphs.
The importance of individual terms in the linear model was assessed using Wald statistics. The Wald statistic was calculated by dropping individual fixed terms from the model. They have asymptotic chi-squared distributions with degrees of freedom equal to those of the fixed model terms (GenStat, 2007). Parameter estimates determined from the analysis were used to predict the reproductive potential by location and season. The statistical software package GenStat (2007) was used for the analysis providing asymptotic standard errors for all estimates. Analysis of residuals, and the importance of having multiplicative errors, supported the use of the normal residual distribution on the log scale.

3. Results

3.1. Length distributions

The shape of the length distributions varied between locations (Kolmogorov-Smirnov Test, $D_{m,n}$ values ranged between 0.88 and 0.17; 28 comparisons, $p < 0.002$; Fig. 2). There were proportionally more prawns in the larger length groups, particularly those longer than 50 mm CL, at locations in the lower latitudes than in the higher latitudes.

3.2. Temporal and spatial patterns in proportion of females capable of spawning

The ovarian developmental stage was determined from histological observations for each of a total of 7265 female eastern king prawns. Data for Moreton Bay were only available for 1 year. There were no differences in the proportion of females capable of spawning in samples between seasons within a Location but, there were differences between locations (Fig. 3). With the exception of Moreton Bay, the proportion of females capable of spawning was less at the higher latitude locations of Clarence, Coffs Harbour and Ports Stephens than at Ballina, Mooloolaba, Lady Elliot Island and Swain reefs. It is also noteworthy that females capable of spawning were only in samples from off Port Stephens during winter and spring in 1991 and in autumn and winter in 1992.

### Table 1

Wald statistics from the linear mixed model of the reproductive potential (fecundity index) of the female Melicertus plebejus population (number of data = 3131)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Reproductive potential</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
</tr>
<tr>
<td>Sequentially adding terms</td>
<td></td>
</tr>
<tr>
<td>Log days = D</td>
<td>1</td>
</tr>
<tr>
<td>Season = S</td>
<td>3</td>
</tr>
<tr>
<td>Location = L</td>
<td>7</td>
</tr>
<tr>
<td>S × L</td>
<td>20</td>
</tr>
<tr>
<td>Residual variance (S.E.)</td>
<td>0.681 (0.0187)</td>
</tr>
<tr>
<td>Variance of random vessel term</td>
<td>0.3592 (0.0373)</td>
</tr>
<tr>
<td>Sequentially dropping terms:</td>
<td></td>
</tr>
<tr>
<td>S × L</td>
<td>20</td>
</tr>
<tr>
<td>Log day</td>
<td>1</td>
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3.3. Temporal and spatial patterns in reproductive potential

Data for replicate seasons were combined in the LLM model because initial runs of the model found no differences within seasons between years ($\chi^2 = 0.82$, df = 1, $p > 0.05$). Table 1 lists the LLM model statistics for each of the variables. There was a significant interaction between seasons and locations suggesting that different seasonal patterns occurred at different locations and different spatial (locations) patterns occurred between seasons. This is apparent from Figs. 3 and 4. Wald statistics indicated that whilst log days contributed most to the significance of the model, seasons and locations were still highly significant through the interaction term.

Fig. 4 shows the predicted values (with 95% confidence intervals) from the LLM model for reproductive potential. Overall, the highest values occurred in samples from Locations in the lower latitudes (north) and the lowest values were from the higher latitudes (south). Values were significantly higher for samples from Swain Reefs, Lady Elliot Island and Ballina, than those from Locations further south (higher latitudes). Also, values for samples from Clarence and Coffs were always higher than those for Port Stephens. Reproductive potential was signif-
icantly higher in autumn at the Swain Reefs and Ballina than in other seasons. Reproductive potential at Mooloolaba was highest in autumn and spring, while winter was higher than summer.

Differences in reproductive potential between seasons were less pronounced at Clarence, Coffs Harbour and Port Stephens than at locations in the lower latitudes further north. Values from Clarence (except for summer) and Coffs were not significantly different from the summer values from Moreton Bay and Mooloolaba.

4. Discussion

This study showed the latitudinal pattern in reproductive potential of female eastern king prawns along the east coast of Australia. Results showed that overall reproductive potential was greater in the lower than higher latitudes and that whilst egg production occurred year-round, it was greatest in autumn, particularly in the lower latitudes.

Use of catch per unit effort data as an index of relative abundance relies upon an assumption of constant catchability (for a review on the use of catch per unit effort data see Quinn and Deriso, 1999). However, many factors may affect catchability including fishing vessel characteristics (e.g. size, types of fishing equipment) and environmental factors (water temperature and lunar phase). By using a general linear model approach we were able to examine patterns in the reproductive potential of the population in light of any effects that catchability may have had upon the index of spawner abundance (catch per unit effort data) used in this study.

The linear mixed model we used included both fixed and random model terms. Fixed terms were used for analysing fishing effort, Season and Location variables. Random terms treat an attribute as a random selection from an overall population. Random terms covered individual vessels in the trawl fleet. Mixed models measure multiple sources of variation in the data, thus providing estimates of variance components associated with random terms in the model. Mixed models have the advantage that the significance of the fixed terms can be assessed considering more than one source of error, improving the accuracy of significance tests. The non-constant nature of catchability is reflected by the fishing effort variate log days accounting for much of the variability in the LLM model. Despite this, analyses showed that the variables of location and season were still highly significant.

Whilst our results showed female eastern king prawns capable of spawning in waters off NSW year around, Montgomery et al. (2007) found no females with oocytes in the cortical specialisation stage in these waters in winter. The most likely reason for this inconsistency is that in our study we included the vitellogenic stage in our definition of a female capable of spawning, following the suggestion of Courtney (1997) to minimise the risk of spawners going undetected. The vitellogenic stage appears to be a ‘holding stage’ in eastern king prawns whereby oocytes remain at this stage for possibly long periods of time until conditions are favourable for spawning whence there is a swift development (through 96 h) of the oocytes through the ripe stages to spawning (Courtney et al., 1995; Courtney, 1997).

Hence, whilst females capable of spawning occur (and therefore reproductive potential exists) in NSW waters during winter, spawning does not take place. Dakin (1938) and Racek (1959) also suggested that there was no spawning over winter in NSW waters. Our results support those of Courtney et al. (1996) that eastern king prawns spawn year around in waters off Qld and are consistent with patterns in larval immigration to estuaries in these waters (Young and Carpenter, 1977; Coles and Greenwood, 1983).

Garcia (1985) concluded that year around spawning with peaks in autumn and spring was the most common in penaeids, but that this periodicity may be reduced in species in higher latitudes (see also a review by Dall et al., 1990). For example, Penn (1980) found that P. latusulcatus on the west coast of Australia spawned year around in the lower latitudes but only during the warmer months in the higher latitudes. With the exception of the data from Port Stephens, a similar pattern seems apparent for eastern king prawns. The species spawns year around in the lower latitudes from Ballina and further north with greatest reproductive potential in autumn, but in higher latitudes south of that point the seasonality of reproductive potential is not as pronounced. At Port Stephens, females capable of spawning were not found over the summer season which is in contrast to the general pattern described by Garcia (1985). Perhaps waters off the higher latitudes in NSW, particularly those south of Port Stephens, are too cool most of the time for spawning to take place. Under laboratory conditions Preston (1985) found that eastern king prawn hatching success and larval survival was poor in water temperatures of ≤15°C and that maximum success occurred at the temperature and salinity at which spawning took place. Similarly Kelemeec and Smith (1984) found poor incidences of fertilisation in eastern king prawns held in water temperatures of ≥15°C for prolonged periods. Bottom water temperatures off NSW in winter range from 13 to 18°C and from 13 to 15°C south of 33°C (Ridgway et al., 2002) and so may be too cool for successful spawnings. Alternatively, most females capable of spawning may have moved from the higher latitudes of NSW into warmer waters off Qld.

Although reproductive potential is highest in the lower latitudes off Ballina and further north, the importance of the spawning stock in the higher latitudes further south cannot be underestimated. If the suggestion of Rothlisberg et al. (1995) that only spawners near shore contribute to local recruitment is correct, then females capable of spawning in NSW (albeit in lower abundances) become extremely important to the recruitment of larvae to NSW estuaries and to the fisheries in these estuaries. However, most of the coastal estuaries in NSW and some areas in Qld do not have an eastern king prawn spawning stock in adjacent, offshore waters, but are nursery grounds to eastern king prawn larvae in sufficient abundances to support significant commercial fisheries. So where do recruits to these estuaries and coastal areas come from?

Montgomery (1990) hypothesised that eastern king prawn larvae were transported from the lower latitudes to the estuaries in higher latitudes by the East Australian Current (EAC) (see Cresswell, 2001 for a review). On its run from 18°S to higher lat-
itudes the current frequently crosses onto the Continental Shelf and moves close inshore (Marchesiello and Middleton, 2000). This onshore movement coupled with favourable winds possibly creates the opportunity for larval entrapped in the EAC to migrate into the nursery areas of estuaries far away from where the larve hatched.

The latitudinal patterns in size distributions of eastern king prawns observed in this study are consistent with the conclusion from tagging studies by Ruello (1975a) and Montgomery (1990) that individuals of this species move from higher (more southern) latitudes to lower (more northern) latitudes. Most of the prawns observed at Port Stephens were smaller than the size at maturity (42 mm CL), whilst samples from Ballina and locations in lower (more northern) latitudes contained mostly prawns larger than this size. Consistent with this was the observation that the proportions of females capable of spawning found at this location were small.

Rothlisberg et al. (1995) claimed that the importance of this migration to the spawning dynamics of eastern king prawns was over emphasised. There is no information available about the relative contribution of recruits from different areas to the eastern king prawn spawning stock. It may be that the larve in estuaries of southeast Australia contribute little back to the spawning stock, however, these support commercial and recreational fisheries in these estuaries and because of this remain important.

An alternative explanation for the patterns in sizes observed in this study could be that there are differences in rates of growth and sizes of maturity between areas. This is unlikely however because there does not appear to be any spatial pattern in size distributions of prawns emigrating from different estuaries along the east coast of Australia that would suggest different rates of growth between estuaries at different latitudes (e.g. Montgomery, 1990). Also, observations made during fishery independent surveys of eastern king prawn stocks (Graham et al., 1993a,b; Graham and Wood, 1997) and catch monitoring programmes (NSW Department of Primary Industries, unpublished data) along the coast of NSW found only immature prawns in latitudes higher (i.e., south of) than around 32°S.

This study has demonstrated that the reproductive potential of eastern king prawns is greater in lower than higher latitudes. The real challenge that remains is to quantify the oceanic sources of larvae that contribute to recruitment in each nursery area and the estuarine sources of juveniles that contribute adults to the spawning stock areas. Some information about the latter was presented by Montgomery (1990) and indicated that patterns in sources of recruitment to the spawning stock vary between months and years. Before this research on recruitment can be done, however, we need to better understand the relation between the hydrodynamics off the east coast of Australia, the temporal pattern of immigration by eastern king prawn larvae to estuaries and the migration of juveniles into spawning areas. This understanding together with findings from the present study would assist fishery managers with harvest strategies to protect nursery habitat across the population so that the spawning stock and important nursery areas are conserved for the sustainability of the resource.

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