6. REPRODUCTIVE BIOLOGY OF *PENAEUS ESCULENTUS* HASWELL, 1879 AND *METAPENAEUS ENDEAVOURI* (SCHMITT, 1926) IN TORRES STRAIT

J.A. Keating, R.A. Watson and D.J. Sterling

6.1 Introduction

In the past, management of the Torres Strait Prawn Fishery has relied on the reproductive biology and larval and juvenile abundance information on *Penaeus esculentus*, brown tiger prawn, from the Northern Prawn Fishery and the Queensland East Coast Prawn Fishery. Seasonal trawling closures in Torres Strait are adjusted to coincide with the main seasonal closure in these areas (Section 1). *Metapenaeus endeavouri*, endeavour prawn is often taken in association with *P. esculentus* (Grey et al. 1983). Although *M. endeavouri* is a major contributor to the commercial prawn landings of Torres Strait, very little information on its reproductive biology is available compared with *P. esculentus*. As the commercial catch of the Torres Strait Prawn Fishery increases (Section 2), knowledge of the reproductive biology of the penaeid prawns present in Torres Strait is required for management purposes.

The reproductive biology of *P. esculentus* has been investigated in the Gulf of Carpentaria (Northern Prawn Fishery) (Buckworth 1985; Robertson et al. 1985; Crocos 1987b), Exmouth Gulf (Western Australia) (Penn and Caputi 1986) and the Low Isles (Queensland East Coast Fishery) (O'Connor 1979). Somers et al. (1987), investigated the reproductive activity of *P. esculentus* and *M. endeavouri* in Torres Strait. Interpretation of this study was restricted due to the three-monthly interval between sampling periods (Courtney and Dredge 1988).

To enable documentation of the reproductive patterns and spawning seasons for the commercial prawn species in Torres Strait, an egg production index or a PFI (Population Fecundity Index) has been estimated. Population fecundity is the sum of the fecundities of all the females in a population (Bagenal 1973) and can be expressed in terms of an index of population fecundity (PFI) which is the number of eggs produced or potentially produced by a population. This measure has been used in combination with estimates of spawning frequency to document spawning seasons (Penn 1980). Past calculations of a PFI for penaeid species (Penn 1980; Crocos and Kerr 1983; Crocos 1987a and 1987b; Courtney and Dredge 1988) have incorporated the proportion of female spawners in the population, their length distribution and the relationship between an individual female's fecundity with its carapace length.

The PFI calculated in this study does not incorporate the proportion of female spawners in the population but uses the number of female prawns with mature ovaries per square metre of seabed swept by trawl nets as estimated from our surveys. This method is equivalent to the methods used in other reproduction studies on *P. esculentus* (O'Connor 1979; Buckworth 1985; Robertson et al. 1985), except these studies identified spawning peaks from the proportion of females with mature ovaries in a population (Crocos 1987a).

To assess the true reproductive potential of a female prawn, the probability that it will be inseminated and therefore have fertile eggs must be determined. Crocos and Kerr (1983), Crocos (1987a and 1987b) and Courtney and Dredge (1988) studied the proportion of inseminated female penaeids but did not, however, incorporate this information into their egg production index or PFI. In this study, probability of insemination of ripe females has been incorporated into the PFI calculations.

The aim of this report is to investigate the reproduction dynamics of both species to facilitate study of spawning seasonality and spawning areas for future management of the Torres Strait Fishery.
6.2 Materials and Methods

6.2.1 Sampling methods

The Torres Strait Prawn Fishery was divided into two areas for analysis: (1) west of Warrior Reef (West), an area not fished for prawns since 1981, and (2) east of Warrior Reef (East), the current fishing grounds (Section 5 - Figure 1).

Monthly sampling of sites and processing and examination of samples were completed as described in Section 5. For the purpose of this study, the insemination status of female *M. endeavouri* and maturity of male *P. esculentus* and *M. endeavouri* were recorded. Insemination of female *M. endeavouri* was determined by the presence of a spermatophore attached to the thelycum. Male *P. esculentus* and *M. endeavouri* are considered mature when the first pair of pleoninc endopodites fuse to form a petasma, the organ used to transfer spermatophores to the female during copulation (Tuma 1967). Ovary stages III and IV (Tuma 1967) were used to designate female prawns with mature ovaries.

Lengths of prawns referred to are carapace lengths (CL), and were measured in millimetres (mm).

6.2.2 Size at maturity

Size at maturity curves for *P. esculentus* and *M. endeavouri* were obtained from 24 monthly surveys from January 1986 to December 1987. As spawning is assumed to be asynchronous (Crocos 1985), the probability that all females in a particular length class are ripe is quite low, except in the larger length classes where fewer prawns are present. Therefore, we defined size at maturity as the carapace length that has a probability of maturity equal to 0.5 of the probability curve’s upper asymptote.

Analysis of variance (ANOVA) was used to test differences between years with relation to the proportion of ripe females. As the difference between the two years was not significant for *P. esculentus* (*p > 0.1*) and *M. endeavouri* (*p > 0.1*), the 24 months of data were combined for each species, and the proportion of ripe females for each carapace length from each area was calculated.

The relationship between female carapace length and the probability of the prawn being a ripe female from the East or being a ripe female from the West for both species was modelled using the logistic equation:

\[ y = \frac{x_1}{1 + e^{(x_2 (CL - x_3))}} \]  
\( y \) is the proportion of ripe females  
\( x_1 \) is the upper asymptote  
\( x_2 \) is the gradient of the slope  
\( CL \) is the carapace length in mm  
\( x_3 \) is the value of CL where the curve reaches 0.5 of the upper asymptote (size at maturity)

The three parameters for the model were obtained by nonlinear regression and were estimated with standard errors and regression coefficients. Length classes represented by only five or fewer prawns were not included in the model as samples of this size were not considered representative of the length class.

This model was also used to determine size at maturity for male *M. endeavouri*. It is assumed that when maturity is reached, all males will remain mature. For this reason parameter \( x_1 \) was fixed at 1.0 which is the expected upper asymptote for this case and parameter \( y \) is the proportion of mature males.

6.2.3 *Penaeus esculentus*

**Calculation of PFI.** The PFI was determined as:

\[ PFI = \frac{1}{\sum n \times E \times i} \]  
\( PFI \) is the PFI  
\( n \) is the number of fish  
\( E \) is the biomass  
\( i \) is the index of catchability
where:

- \( r \) is the carapace length of the smallest recruit
- \( I \) is the greatest carapace length

for:

- \( n \) the number of females with mature ovaries per metre of swept area,
- \( E \) the number of eggs per ripe female
- \( i \) the proportion of inseminated females at that carapace length

Information from previous published studies on egg production indices for *P. esculentus* was required to enable calculation of several parameters before a true PFI could be determined. It was assumed that these derived parameters would be identical for all populations of *P. esculentus*.

The number of ripe eggs per female \( (E) \) was calculated using Crocos's (1987b) linear relationship between carapace length and total ovary egg count for *P. esculentus* in the Gulf of Carpentaria.

\[
E = 22,573 \times CL - 529.29 \tag{equation 3}
\]

where:

- \( E \) is the number of eggs in the ovary
- \( CL \) is the carapace length (mm)

Further, a logistic relationship between female carapace length and the proportion of females inseminated was derived from information on *P. esculentus* in Crocos (1987b).

\[
i = \frac{0.7701}{1 + e^{-(0.6 \times (CL - 29.566))}} \tag{equation 4}
\]

where:

- \( i \) is the proportion of females inseminated
- \( CL \) is the carapace length (mm)

This gave an asymptote of 0.77 at a carapace length of 37 mm.

### 6.2.4 Metapenaeus endeavouri

**Calculation of PFI.** Parameter values for equation 2 are obtained from the examination of field collected material.

To determine egg numbers, females at ovary stage IV were dissected and the ovary weighed and preserved in 10% buffered formalin. The ovary was represented by two subsamples, sectioned from the first abdominal segment of each prawn, as development is considered constant in all sections of the ovary (Penn 1980; Crocos and Kerr 1983).

The first sample was dehydrated, embedded in paraffin, sectioned at 4 \( \mu m \), and stained with Haematoxylin and Eosin. Microscopic staging was used to differentiate between the third and fourth stages of ovarian development (Tuma 1967). The presence of cortical specialization in the ripe oocyte of stage IV ovaries indicated spawning would occur within 7 to 9 days (Anderson *et al.* 1985). If the first subsample indicated an ovary at stage IV, then a second ovarian subsample was weighed and carefully teased apart in water which allowed the eggs to be easily counted. The number of eggs per ovary was then calculated using simple proportions. Only stage IV ovaries were used for calculations involving egg number \( (E) \) (equations 2 and 3), as they most reliably indicate individual spawning activity (Crocos and Kerr 1983).

### 6.2.5 Assumptions in calculating PFI.

The methods used to calculate a PFI assume that the duration of ripe ovary stages III and IV is shorter than one month (the period of sampling frequency), the duration of development of ovary stages III and IV remains constant for the population, spawning is asynchronous, and catchability is constant (Penn 1980).
Crocos (1985) investigated spawning periodicity and duration of ovary stages of *P. esculentus* in order to refine population reproduction models. He observed that female *P. esculentus* at ovary stage III will develop to stage IV between monthly sampling times but is dependant on the moult period, and found no evidence of synchrony of spawning over the lunar month. Multiple spawnings were not included for estimation of the PFI and all female prawns were assumed to only spawn once within a single moult interval (Crocos 1985). Catchability of prawns can be affected by temperature (Hill 1985) or by behavioural processes such as moulting, feeding or spawning.

### 6.3 Results and Discussion

#### 6.3.1 *Penaeus esculentus*

**Size at maturity.** Estimated parameters (Table 1), from the model (equation 1) gave a logistic relationship between carapace length and the proportion of ripe female *P. esculentus* (Figure 1). The curves are essentially the same for both areas except that the size at maturity curve for the East is shifted more to the left than that of the West (Figure 1).

**Table 1.** Estimated parameters for logistic equation 1 obtained by using nonlinear regression for size at maturity of female *P. esculentus*.

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<td></td>
<td>Estimate</td>
<td>SE</td>
<td>r²</td>
<td>Estimate</td>
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<tr>
<td>x₁</td>
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<tr>
<td>x₃</td>
<td>35.90</td>
<td>0.73</td>
<td>0.93</td>
<td>31.52</td>
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The smallest ripe female caught in the East measured 19 mm CL compared with 23 mm CL in the West. The size at maturity of females (from equation 1), measured 32 mm CL for the East and 36 mm CL for the West (Figure 1).

The average proportion of ripe females in the East and in the West was significantly different (t = 1.771, d.f = 52, p < 0.10) (Student t-test). At any given carapace length, the probability of a prawn having a developing or ripe ovary was higher in the East than the West, although size at maturity of a female prawn in the West was larger than in the East. Further studies on the proportion of ripe females have found considerable within year seasonal variations. This has an effect on the relationship between the proportion of ripe females and female prawn size. Results could be biased, depending on relative numbers caught in different months. Investigations by the Torres Strait Prawn Project are continuing into the effect of season on proportion of ripe females.

Although prawns to the West are unfishable and those to the East are fished with size-selective gear, the difference in the minimum size of female *P. esculentus* with developing ovaries between the areas was not anticipated as they were assumed to be a homogenous population. The migration of prawns from the West to the East (Section 7) was expected to allow interbreeding and eliminate any biological differences that fishing might select for. Precocious females may have migrated from the West to the East causing a difference in the size at maturity. Fishing pressure may also contribute to the phenomenon by causing females to mature earlier, but more studies are required. External cues such as increased photoperiod or water temperature are thought to stimulate ovary development (Penn 1980). When these cues occur, the prawns that respond to such stimuli are at different stages of development in the East and the West because they have originated from different spawning periods (Section 5). Females from the West may be larger on average than those from the East because they are older, and mature at a larger size.
Figure 1. Logistic relationship between probability of ripe females (ovary stages III and IV) and carapace length in the East and the West for female *P. esculentus*, indicating size at maturity.

In an earlier study of *P. esculentus* in Torres Strait, Somers *et al.* (1987) found the smallest mature females was 25 mm CL and the size at maturity was 31 mm CL. These values correspond approximately with those of the present study where sampling strategy permitted finer resolution.

Because few immature male *P. esculentus* were caught in survey trawls, the size at maturity of male *P. esculentus* could not be determined. In the present study the smallest male prawn carapace length with a joined petasma was 11 mm CL in the West and 12 mm CL in the East. Most male *P. esculentus* were mature by 21 mm CL in the West and 23 mm CL in the East. A very small number of males were still immature at 36 mm CL, perhaps attributable to bopyrid parasites which stunt sexual development (Reinhard 1956), or to the effects of on board handling. It is likely that most males mature before leaving the seagrass beds, but do not necessarily have the capacity at that time to inseminate females successfully.

Tuma (1967) found small, sexually mature male *P. merguiensis* in nursery areas, but these were seldom found in the company of inseminated females. Burkenroad (1934) reported that the small spermatophores found in juvenile male *P. setiferus*, were never found attached to females. It is also possible that our sampling was not in areas which could harbour immature male *P. esculentus*.

**Population fecundity index.** Relationships between female abundance, size, insemination and number of eggs (Figure 2), indicate the potential level of reproduction. The distribution of female abundance relative to egg production occurred because there were relatively few large females producing large numbers of eggs.
Inseminated ripe females
Ripe females
Females

Eggs

Number of prawns ha\(^{-1}\)

Eggs \(\times 10^5\) ha\(^{-1}\)

Carapace length (mm)

Figure 2. Relationship between numbers of females, ripe females (ovary stages III and IV), inseminated ripe females, eggs produced by inseminated ripe females and carapace length for \(P.\) esculentus from January 1986 to December 1987.

In order to study the relationship between spawning time, spawning areas and PFI, a monthly PFI was calculated for the East and West (Fig. 3). Monthly estimates of a PFI for \(P.\) esculentus for Torres Strait ranged from 5-103 in the East and from 2-90 in the West (Figure 3). These monthly values were used to identify peaks of spawning (Section 5).

Crocos (1985) found no evidence for lunar synchrony of spawning for \(P.\) esculentus in Moreton Bay. Other cues, external or environmental, may cause seasonal spawning peaks at particular times of the year (Figure 3). Water temperature change has been correlated with peaks in PFI for \(P.\) esculentus in Torres Strait (Section 5). This change in absolute water temperature may result in decreasing or increasing intermoult periods, catchability and egg production.

**Insemination.** Insemination of female \(P.\) breviceps species reportedly occurs at the time of molting. A spermatophore is deposited on the thelycum and enclosed by the hardening shell (Penn 1976 and 1980). Penn (1976 and 1980) observed that it was necessary for spawning and insemination to occur within the same intermoult period because the spermatophore was lost during the moult. Crocos (1987b) found that 60 to 80% of female \(P.\) esculentus in the Gulf of Carpentaria > 32 mm CL were inseminated while only 22% at 28 mm CL were inseminated. If insemination rates are not incorporated into PFI calculations, and all ripe females are assumed to be inseminated, the number of fertilized eggs will be overestimated, particularly for females under 32 mm CL with developing ovaries. There were many ripe female prawns > 25 mm CL and < 32 mm CL (Figure 2). Insemination of these prawns commenced at approximately 27 mm CL and the insemination rate at this size was quite low. The low insemination and egg production rates of smaller prawns meant that they contributed relatively little to PFI values. The model in this study takes these parameters into account for calculation of a PFI.

The probable cause of low insemination rates of ripe female \(P.\) esculentus < 32 mm CL was undeveloped thelyca. Although we observed all females to have an externally developed thelycum, it is probably not functional until the thelycal plates reach a particular size (Tuma 1967). Tuma (1967) found that although female \(P.\) merguiensis have a structurally complete thelycum at 24 mm CL, insemination rates were low at carapace lengths < 30 mm. He assumed that insemination was dependant on the size of the thelycum.
Spawning seasonality. Monthly PFI values indicated that spawning occurred throughout the year in Torres Strait (Figure 3). Periods of spawning activity were observed in July-August and October-November, 1986 and January, July and October in 1987 in the West. In the East, spawning activity was observed from January-March and August-September in 1986 and January-February and May-June, 1987. The October-November spawning period contributed the most eggs in the West and the January-March spawning period contributed the most eggs in the East in 1986.

These results extend the findings of Somers et al. (1987). They found that although the abundance of ripe females was highest in March, abundance was relatively low in other cruises in Torres Strait. Catch rates of small prawns however were consistent over their three-monthly sampling schedule, indicating the inherent potential for year round reproduction. This limited sampling regime of Somers et al. (1987) could have missed other spawning periods, identified by our monthly sampling.

Other studies on *P. esculentus* (reviewed in Crocos 1987b), have reported a constant and protracted period of egg production for the species with moderate peaks occurring in spring and autumn, with a July-October spawning contributing most to recruitment in the Gulf of Carpentaria. These studies considered only the proportion of ripe females present and egg production level was based on the success of subsequent recruits. The proportion of ripe females does not necessarily indicate egg production correctly unless parameters of abundance and size are incorporated (Crocos 1987b). Based on seasonal PFI (Figure 3), egg production during January-March would appear to contribute equally or greater to the population of *P. esculentus* in Torres Strait than does any of the other spawning periods. As peaks of PFI can precede recruitment, this index has great potential for management.

Physiological changes as a result of varying environmental factors may account for the protracted level of ripe females and the seasonal variations in egg production. The physical oceanography of Torres Strait (Section 1) may also account for the differences of these parameters in Torres Strait compared with the studies from the Gulf of Carpentaria and east coast of Queensland. A decrease in water temperature can cause a physiological effect such as a reduction in metabolic rate and therefore catchability (Fuss and Ogren 1966; Penn 1976 and 1980). Hill (1985) also found emergence and therefore catchability to be a function...
of water temperature for *P. esculentus*. During colder months, catch rates of *P. esculentus* are reduced due to low water temperatures (White 1973). During the periods of low water temperatures, the metabolic rate of ripe females does not reduce because of egg production, and the catchability of these prawns may be increased as they forage for additional food (Penn 1976 and 1980). This increased catchability promotes unexpectedly high levels of ripe females in catches, and gives rise to inflated levels of egg production that are not indicative of the total female population (Penn 1980). Fuss and Ogren (1966) investigated prawn behaviour of *P. duorarum* and correlated cold water temperatures with extended activity and a decrease in the number of active prawns, while more prawns were active in warm water temperatures over a shorter period of time. Thus the proportion of ripe females may be overestimated from June-August, a time of low water temperatures (Section 5 - Fig. 3c), when activity is increased causing increased catchability and distorting estimations of peak spawning periods. The use of both ripe and early ripe stages may also overestimate spawning activity if large sized ripe females are present and their intermoult period exceeds the monthly sampling frequency (Crocos 1985). Food foraging may account for the continuing catch of ripe females during colder months but further studies on *P. esculentus* behaviour are required to establish this fact.

### 6.3.2 *Metapenaeus endeavouri*

**Size at maturity.** As with *P. esculentus* differences in the size at maturity for *M. endeavouri* between the unfished West and the fished East were unexpected. The estimated parameters (Table 2) resulted in logistic curves for *M. endeavouri* in both areas (Figure 4), were similar to those derived for *P. esculentus* (Figure 1). The smallest ripe females were found at 13 mm CL in the East and 16 mm CL in the West. The size at maturity was 27 mm CL for the East and 31 mm CL for the West (Figure 4).

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<td>x₃</td>
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The proportion of ripe females < 32 mm CL between the East and the West was significantly different (*t* = 1.748, d.f. = 29, *p* < 0.10) (Student t-test). Above 32 mm CL the difference was not significant (*t* = 0.149, d.f. = 15, *p* > 0.10) (Student t-test). Below 32 mm CL, there was a higher probability of ripe females occurring in the East than in the West whereas above 32 mm CL, the probability was similar. This indicated a seasonal or environmental factor affecting the probability of a female being ripe. Investigations into seasonal effects are still continuing, although considerable seasonal variation does exist.

Somers *et al.* (1987) found the smallest mature female *M. endeavouri* in Torres Strait were 20 mm CL and the size at maturity was 27 mm CL. The results from the present study showed much smaller mature prawns in both the East and West, a similar size at maturity in the East, but a much greater size at maturity in the West.

Size at maturity of male *M. endeavouri* in Torres Strait was 18 mm CL in the West and 17 mm CL in the East. The smallest carapace length with a joined petasma was 11 mm CL in the West and 8 mm CL in the East (Figure 5). Most male *M. endeavouri* were mature by 23 mm CL. The majority of *M. endeavouri*, unlike *P. esculentus*, appear to leave the nursery grounds and move into the fishery before maturation. The minimum carapace length at which a male *M. endeavouri* is able to inseminate is unknown.
Figure 4. Logistic relationship between probability of ripe females (ovary stages III and IV) and carapace length in the East and the West for female *M. endeavouri*, indicating size at maturity.

Figure 5. Logistic relationship between probability of mature males and carapace length in the East and the West for male *M. endeavouri*, indicating size at maturity.
Population fecundity index. Due to insufficient samples, PFI values for *M. endeavouri* have not yet been determined for this report. Data from egg counts of *M. endeavouri* are presently being assessed in order to calculate a relationship between carapace length and the number of eggs per ovary.

Insemination. Unlike the genus *Penaeus*, the metapenaeids are "open thelyca" prawns where insemination occurs during the intermoult period (Potter et al., 1986). As the thelycum is always open, the probability that the spermatophore will be dislodged during handling and during normal behavioural activity is high. This arrangement favours spermatophore deposition immediately before spawning (Potter et al. 1986), so only early ripe and ripe female (stages III and IV) *M. endeavouri* were included in the insemination studies. This provides a more accurate and reliable indication of insemination percentages.

Potter et al. (1986) found that the fertilization times of *M. dalli* was consistent with the presence of mature (stage IV) ovaries. Our study of the spermatophore deposition of *M. endeavouri* and the relationship between the presence of a spermatophore and the maturity of ovaries is still continuing.

Spawning seasonality. As the PFI for *M. endeavouri* has not yet been calculated, spawning seasonality cannot be deduced.

6.4 Conclusions

It appears from this study that determination of a PFI is a useful method for assessing the reproductive potential of a population. Its use in fisheries management for predicting spawning periods, stock recruitment and catches could assist in seasonal and area closures.

In Torres Strait *P. esculentus* are not entirely in reproductive synchrony with the *P. esculentus* populations of the Gulf of Carpentaria and the east coast of Queensland and therefore should be regarded as a separate fishery for closure periods. Additional studies on *M. endeavouri* should be completed by 1990.

6.5 Acknowledgements

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6.6 References


