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Reproductive Biology and Spawning Periodicity of Endeavour Shrimps *Metapenaeus endeavouri* (Schmitt, 1926) and *Metapenaeus ensis* (de Haan, 1850) from a Central Queensland (Australia) Fishery

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Abstract

Metapenaeus endeavouri and *M. ensis* from coastal trawl fishing grounds off central Queensland, Australia, have marked seasonal reproductive cycles. Female *M. endeavouri* grew to a larger size than female *M. ensis* and occurred over a wider range of sites and depths. Although *M. ensis* was geographically restricted in distribution to only the shallowest sites it was highly abundant. Mating activity in these open thelycum species, indicated by the presence or absence of a spermatophore, was relatively low and highly seasonal compared with closed thelycum shrimps. Seasonal variation in spermatophore insemination can be used as an independent technique to study spawning periodicity in open thelycum shrimps. Data strongly suggest an inshore movement of *M. endeavouri* to mature and spawn. This differs from most concepts of *Penaeus* species life cycles, but is consistent with the estuarine significance in the life cycle of *Metapenaeus* species. Monthly population fecundity indices suggest summer spawning for both species, which contrasts with the winter spawning of other shrimps from the same multispecies fishery.

Introduction

Seven species from the genera *Penaeus* and *Metapenaeus* are taken in trawl fisheries off the central Queensland (18°S-21°S) coast of Australia. This mixed-shrimp fishery was described by Robertson and Dredge (1986) and can be partitioned into three components on

the basis of species composition, diurnal and seasonal timing, and spatial distribution. One component is an offshore and near-reef winter night-time fishery for *Penaeus longistylus* and *P. latisulcatus*. *Metapenaeus endeavouri* is taken as a minor component in the fishery, and three smaller species from the genera *Trachypenaeus* and *Metapenaeopsis* are taken as marketable bycatch. The second component of the fishery is an autumn-winter night fishery for *Penaeus esculentus* and *P. semisulcatus* together with *Metapenaeus endeavouri* and *M. ensis*. This fishery takes place in shallow coastal waters, typically no more than 15 km from the shore. The third component is an autumn day-time fishery for *Penaeus merguianus* in the same shallow coastal waters and is characterized by marked changes in annual landings. *Metapenaeus endeavouri* and *M. ensis* are taken as a minor component in this fishery.

Metapenaeus endeavouri is endemic to Australia and distributed along the northern half of the continent's coast. It is often trawled with *M. ensis* and is not differentiated from this species by fishermen (Grey et al. 1983). *Metapenaeus ensis* is also distributed along Australia's northern coastline but also occurs in the Pacific (Choy 1983) and Indian Oceans, through Indonesian waters and the South China Sea (Holthuis 1980) to Japan. Of the 17 commercially important shrimps from Australian waters Dall (1985) has classified both species as "of major commercial importance."

Somers et al. (1987) described *M. endeavouri* as the second most commercially important species in Torres Strait, contributing 44% of the commercial shrimp catch. Coles et al. (1985) also noted that *M. endeavouri* was frequently one of the two most abundant species on the northeastern coast of Queensland. Despite the economic value of *M. endeavouri* and *M. ensis*, the biology of neither species has been reported adequately. This has probably been due to the slightly smaller size and lower commercial value of *Metapenaeus* species than of *Penaeus* species which have received the bulk of marine shrimp research funding. Some aspects of juvenile habitat requirements and timing of the life cycles have been investigated by Staples et al. (1985) and Coles and Lee Long (1985) but generally there is a lack of published literature pertaining to these species. The present study describes, for the first time, the reproductive biology and spawning periodicity of *Metapenaeus endeavouri* and *M. ensis*.

Materials and Methods

Sampling

In the central Queensland area the Great Barrier Reef Lagoon (GBRL) shelves from the shore to an average depth of 45 m. The inter-reef areas are characterized by slightly greater depths of 50-60 m (Fig. 1). Maxwell (1973) identified an inshore zone of the GBRL

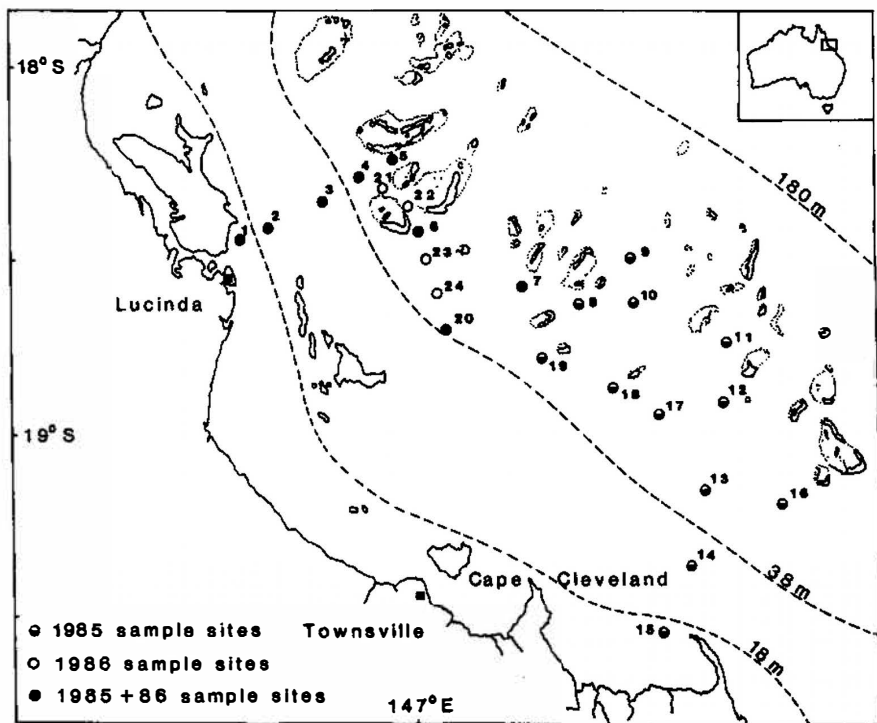


Fig. 1. Map of the central Queensland coast with depth contours and positions of the stations sampled each lunar month from January 1985 to December 1986.

characterized by terrigenous sediments with relatively high silt and mud fractions. A monthly sampling regime, described in Courtney and Dredge (1988) was established to sample penaeid shrimp across the GBRL from the inner zone to the inter-reef areas. The sampling program commenced in January 1985 and continued for 24 consecutive lunar months. Twenty stations, ranging in depths from 17 m to 65 m, between 18°S and 20°S in Barrier Reef waters were sampled in 1985. In the following year 12 of the original stations were abandoned and four others were established (Fig. 1). Sampling was

carried out at night over a period of 4-5 nights coinciding with the new moon each month. Samples taken in May 1985 were delayed for eight days due to adverse weather conditions.

Thirty-minute (bottom time) trawls with two trawl nets (50.0 mm and 37.0 mm mesh) were undertaken at each station. Depth, bottom temperature and salinity were recorded from each station and all *Penaeus* and *Metapenaeus* species were sorted to species, sexed and measured on board. All female shrimp were snap frozen on board for later analysis of reproductive condition. In the laboratory, a maximum of 40 females from each station, representing about half of all females trawled, were examined. Data recorded for each female included carapace length (CL) and total wet weight. The thelycum was examined to ascertain whether a spermatophore had been deposited and the ovary of every second female was dissected out and weighed on an electronic balance.

Each female shrimp examined had a histological section of its ovary prepared. Ovarian tissue from the first abdominal segment was either cut directly from the dissected ovary or taken by a transverse section through the undissected shrimp. The tissue was preserved in 4% (v/v) formalin. Hematoxylin and eosin were used to stain the tissue which was sectioned in paraffin at a thickness of 6 μm . Developmental staging of the ovary was determined by a combination of criteria describing primary development (Tuma 1967) and absorption and rematuration (Yano 1984).

Female Maturation and Migration

Depths associated with each ovary maturation stage were compared. Similarly, the depths associated with different size classes of females were also compared. No significant difference between depths (Null hypothesis: H_0) would indicate that the shrimps did not migrate to different depth zones (i.e., seaward migration) as they matured. Analysis of variance was used to determine if there was a significant difference between depths for the various ovary stages and size classes.

Population Fecundity Index (PFI)

Monthly population fecundity indices were estimated for both species. The indices incorporated not only the abundance of adult

female shrimps each month but also the relative proportions of different size classes of females, since egg production was influenced by the size of shrimps as well as abundance. Egg production from different size classes of females was estimated from the relationship between ovary weight and carapace length in vitellogenic females and this relationship was also incorporated in the index formula. The regression of ovary weight on carapace length for these early mature (stage 3) and ripe (stage 4) females was calculated as

$$\text{Ovary weight} = a \cdot \text{CL}^b$$

where a and b are constants.

The proportion of females preparing to spawn (i.e., those with early mature (stage 3) and ripe (stage 4) ovaries) each month also influenced the population's fecundity, and therefore this proportion was also incorporated into the index. Population fecundity indices were calculated as follows:

$$\text{PFI} = np \sum_{\text{fm}}^{\text{ms}} (a\text{CL}^b)$$

where "n" represents a standardized abundance of adult females. Because both species were taken at a limited number of stations, "n" was standardized by using only those stations from which a particular species was consistently sampled over the two years; "p" represents the proportion of mature (stages 3 and 4) adult females; and "s" represents the proportion of adult females in size classes between first maturing (fm) and maximum size (ms) encountered in the sample.

Results

Over the two years 36,511 shrimp were sampled, with endeavour shrimps contributing 28%. A total of 2,989 *M. endeavouri* and 7,397 *M. ensis* were taken. The sex ratio (males:females) differed significantly (*M. endeavouri* $X^2 = 64.9$ $P < 0.001$; *M. ensis* $X^2 = 94.6$ $P < 0.001$) within monthly samples, with females outnumbering males by more than 2 to 1 in some months in both species. There was no

consistent pattern in the observed variation of sex ratios between months and years. For both years the sex ratio did not differ significantly from a 1:1 ratio when the total number of males and females were pooled over the two-year period.

Minimum and maximum size of females trawled was 14.0 mm and 47.0 mm CL for *M. endeavouri*. Female *M. endeavouri* were consistently larger than those of *M. ensis* whose minimum and maximum sizes were 11 mm and 41 mm CL. Linear regressions fitted to the relationship between log CL and log total body weight for females of the two species were highly significant ($P < 0.0010$) and expressed as

$$\log \text{ Total weight} = 2.5113 \log \text{ CL} - 2.364$$

(*M. endeavouri*, $n = 505$, $r = 0.97$)

$$\log \text{ Total weight} = 2.6443 \log \text{ CL} - 2.696$$

(*M. ensis*, $n = 622$, $r = 0.98$)

Mating Activity

Of the 1,441 female *M. endeavouri* trawled, 613 were examined for reproductive status and only 48 (7.8%) showed signs of spermatophore insemination. The smallest female inseminated was 26.2 mm CL (Fig. 2a), indicating the minimum mating size for females. Similar results were found for *M. ensis*, with only 57 (7.9%) of the 723 females examined showing signs of mating. The smallest of these was 20.5 mm CL (Fig. 2b), suggesting that *M. ensis* begins mating at a much smaller size, and probably younger age, than *M. endeavouri*. For any particular size class the proportion inseminated was rarely over 20% for either species (Fig. 2a and b).

Females of both species that were large enough to mate showed a marked seasonality in the proportion inseminated (Fig. 3). Very few females of either species, particularly in *M. ensis*, were found with spermatophores during the winter (May to September). In both species the frequency of females with spermatophores increased from September to a peak in summer (December to February).

Ovary Development

The smallest female *M. endeavouri* which had commenced yolk production (stage 3 (vitellogenesis), Tuma 1967), as revealed by

ovarian tissue sections, was 25.6 mm CL. Seven (1.1%) of the 613 females had ova with the peripheral bodies (stage 4, Tuma 1967) indicative of the ripe condition. These ranged in size from 32.4 mm CL to 38.0 mm CL. The smallest *M. ensis* producing yolk was 24.2 mm CL, but surprisingly, none of the 723 females examined over the two years was classed as ripe. Generally, adult female *M. ensis* were in a low state of maturation. Over the two-year period 30% of all female adult *M. endeavouri* were classed histologically as early mature or ripe (stages 3 and 4, Tuma 1967) while less than 7% of all female *M. ensis* fell into the same classification.

Ovary weight varied greatly with size of postvitellogenic females. Crocos and Kerr (1983) have shown that the molting and reproductive cycles of *P. merguiensis* were not independent of each other and part of the variation in ovary weight is likely to be explained by the molt stage of the individual. Coefficients for the relationship between ovary weight and carapace length for early mature (stage 3) and ripe (stage 4) females were calculated resulting in the following regressions:

$$\text{Ovary weight (g)} = 1.0122 \times 10^{-4} \text{ CL}^{2.7715}$$

(*M. endeavouri*, n = 105, r = 0.70)

$$\text{Ovary weight (g)} = 2.6533 \times 10^{-6} \text{ CL}^{3.6525}$$

(*M. ensis*, n = 28, r = 0.80)

These expressions were incorporated in the population fecundity indices (PFI).

Monthly mean ovary weights were calculated for both species from the dissected and weighed ovaries (Fig. 4a and b). Poor handling and storage of *M. ensis*, which is a small species, caused the cephalothorax to partly detach from the abdomen in some monthly samples. Consequently, ovaries were not dissected out of this species during those months (Fig. 4b). Seasonal variability in mean ovary weight for *M. ensis* was marked. Ovary weights were lowest between June and August (winter) and increased from August in both years to peaks in March 1985 and February 1986.

Seasonal changes in ovary weight followed a similar pattern to changes in the histology. The proportion of mature female *M. ensis* never exceeded 40% in any month (Fig. 4b) and was typically lower than that of *M. endeavouri*. During the winter months from May to August the proportion of mature *M. ensis* was always less than 20%

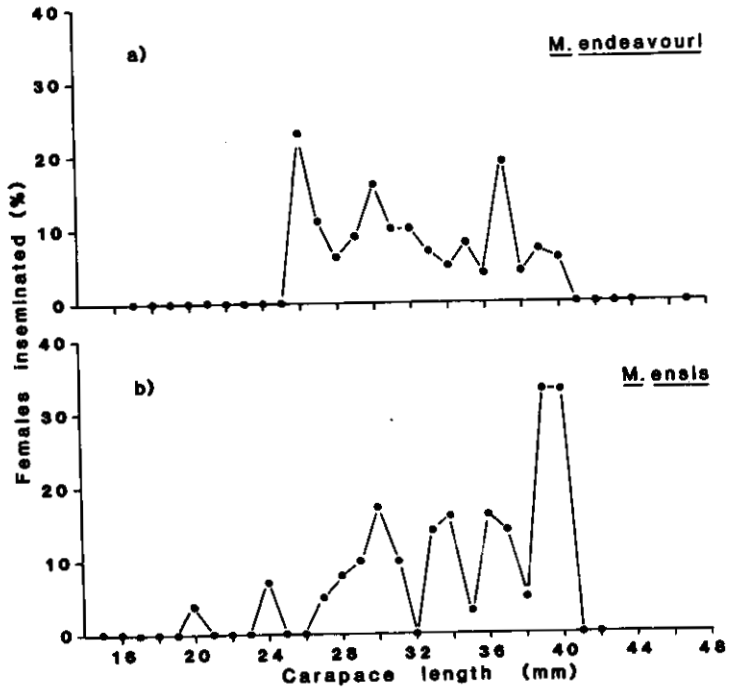


Fig. 2. The percentage of females inseminated in different size classes for a) *Metapenaeus endeavouri* and b) *Metapenaeus ensis*.

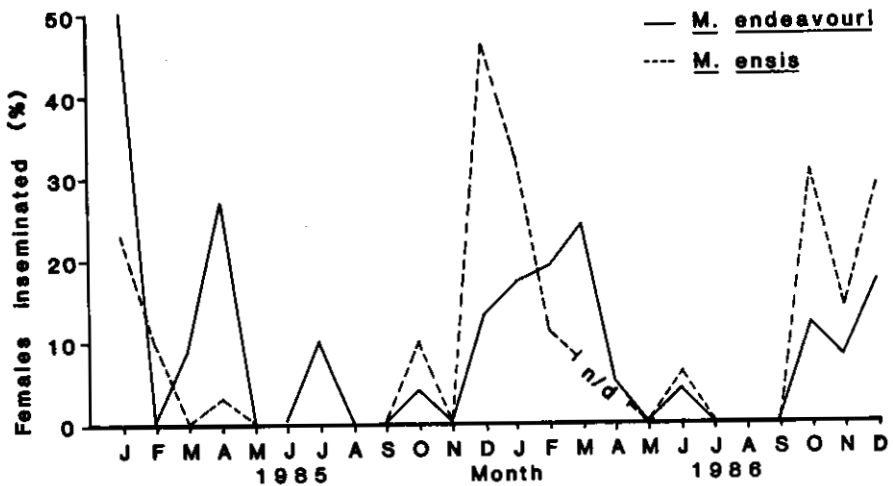


Fig. 3. The proportion of females inseminated each month over a period of two years for *Metapenaeus endeavouri* and *Metapenaeus ensis*.

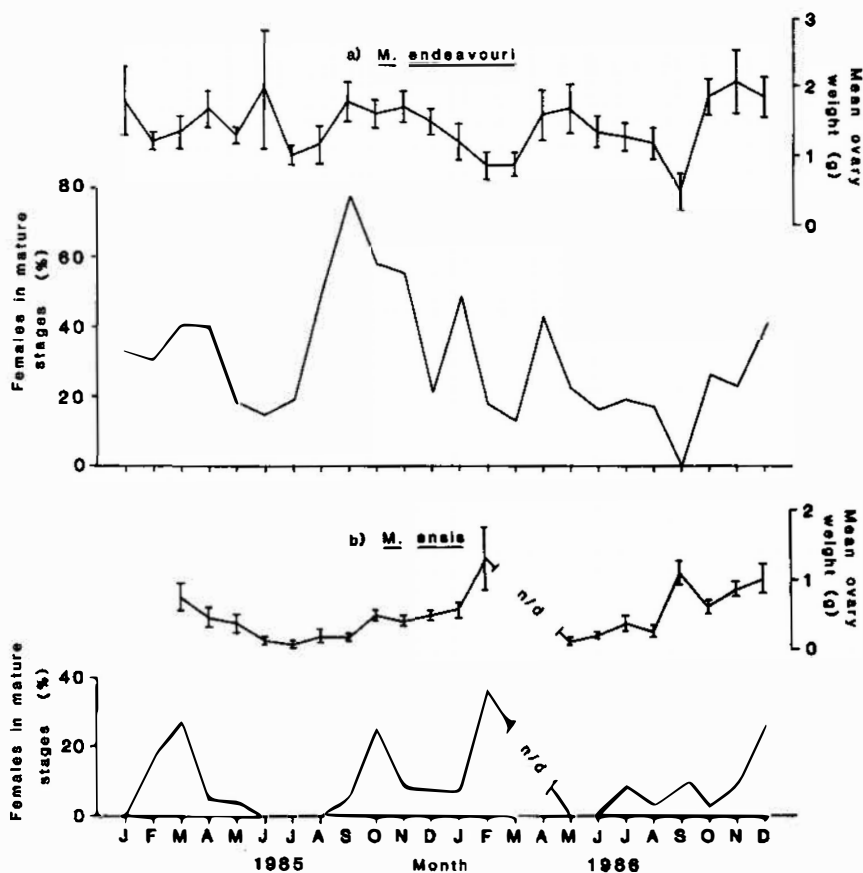


Fig. 4. Mean ovary weight and the proportion of early mature (stage 3) and ripe (stage 4) females each month for a) *Metapenaeus endeavouri* and b) *Metapenaeus ensis*. Vertical bars represent one standard error either side of the mean weight.

and frequently zero. Seasonal variability in the maturation of *M. endeavouri* (Fig. 4a) was less apparent than for *M. ensis*. Some trends were apparent, however. The proportion of mature females was low during winter, from May through to July for both years and relatively high in early summer, October and November each year. An anomalous feature of the data was evident in September 1985 and 1986 for *M. endeavouri*. In September 1985, both the proportion of mature female *M. endeavouri* and the mean ovary weight were at or near maximum values for the year, while in September 1986 both were near their annual minimum.

Metapenaeus endeavouri was distributed over a broad geographic range within the study area, but generally absent from the shallowest (station 1, depth 17 m) and deepest (stations 9-12, depth > 50 m) stations. Female *M. endeavouri* of different ovary developmental stages were associated with significantly different ($P < 0.001$) mean depths (Table 1) indicating that specific depths were preferred during maturation. Interestingly, immature shrimps tended to occur in greater depths than the more mature animals. Results from this analysis suggest that *M. endeavouri* move into shallower depths to mature and spawn. This result was supported by analysis of size classes and depth of all female *M. endeavouri* trawled over the two year sampling program (Table 2). Again depths differed significantly ($P < 0.001$) between size classes of females.

Table 1. The mean depths for different stages of ovary development in female *Metapenaeus endeavouri* from central Queensland.

Ovary stage	Mean depth (m)	(S.D.)	No. shrimp
1 Immature	40.7	(12.0)	139
2 Developing	34.3	(12.6)	101
3 + 4 Mature and Ripe	31.4	(11.4)	132

Table 2. The mean depths for adult (all shrimp > 25 mm CL trawled over the two-year program) female *Metapenaeus endeavouri* of different size classes.

CL range (mm)	Mean depth (m)	(S.D.)	No. shrimp
25 - 30	40.0	(11.2)	377
31 - 34	34.6	(11.7)	418
35 - 50	32.4	(11.2)	371

Metapenaeus ensis was much more restricted in its distribution within the study area than *M. endeavouri*. More than 90% of all *M. ensis* were sampled from only one station, the shallowest and most inshore (station 1) with a depth of 17 m (Fig. 1). The remaining individuals were taken at the next two shallowest stations (2 and 15).

There was marked variability in population fecundity in 1985 for *M. endeavouri* (Fig. 5) with peaks occurring in March and September.

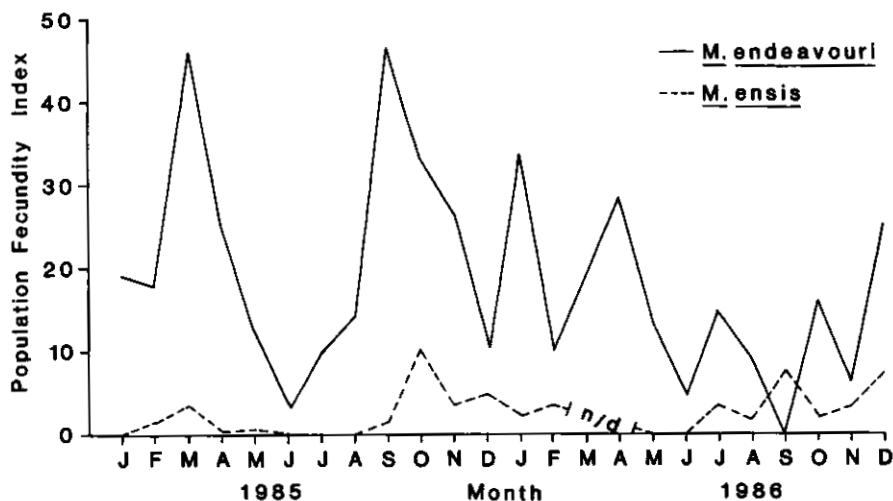


Fig. 5. Monthly population fecundity indices (PFI) for *Metapenaeus endeavouri* and *Metapenaeus ensis* over a two-year period from Queensland's central east coast fishery.

During winter (May to August) the index was consistently low. Seasonal trends in population fecundity were less marked in 1986, although the low winter index values observed in 1985 were repeated. Indices for *M. ensis* were consistently less than those of *M. endeavouri*. This occurred because the PFI formula included a component relating ovary weight and CL which was consistently lower for *M. ensis* than *M. endeavouri*. The index also included the proportion of mature (stages 3 and 4) females and this proportion was always lower for *M. ensis* than for *M. endeavouri*. Hence, as few or no vitellogenic shrimps were found during the winter months (Fig. 4b) the indices were subsequently also low, even though females may have been reasonably abundant. Population fecundity for *M. ensis* peaked in summer, from September to December in both years, with second minor peaks in March 1985 and February 1986.

With the exception of October 1985, when instrument failure prevented measurement, temperatures were recorded at each site between September 1985 and August 1986. Variability between sites was minimal and temperatures reached a minimum of 23.6°C in September 1985 and a maximum of 28.5°C in March 1986. Salinity was always 34 ppt or greater at all sites except for stations 1 and 15 where it dropped to between 19 and 26 ppt in September 1985.

Discussion

Both species studied were open thelycum type shrimps and both consistently had low proportions of inseminated females compared with the closed thelycum species. Maximum proportions of inseminated females never exceeded 50% (Fig. 3) whereas high proportions (60-100%) of females with closed thelycums are inseminated all year-round (Crococ and Kerr 1983; Crococ 1987a, 1987b; Courtney and Dredge 1988). The present results support the conclusions made by Potter et al. (1986) from their study of another open thelycum shrimp, *Metapenaeus dalli*. They concluded that selection pressures favored deposition of spermatophores close to the time of spawning and that mating took place during intermolt for *M. dalli* and not during postmolt, as with closed thelycum shrimp. A consequence of this is that the seasonality associated with insemination in open thelycum shrimps is marked, unlike that for closed thelycum shrimps, and can be used as a simple and independent technique to monitor spawning periods.

Somers et al. (1987) found, by macroscopic examination, that 1% of *M. endeavouri* from Torres Strait had developed ovaries by the time they had reached 20 mm CL and by 26 mm CL over one-third of all females had mature ovaries. The smallest vitellogenic female for this species from the present study was 25.6 mm CL suggesting that *M. endeavouri* start maturing at a smaller size in Torres Strait than in the central Queensland region. This has also been noted for other species from these two regions. Somers et al. (1987) found that *P. longistylus* begins yolk production at 24 mm CL in Torres Strait while Courtney and Dredge (1988) found that the smallest female *P. longistylus* producing yolk from the central Queensland east coast was 33 mm CL.

Metapenaeus endeavouri was taken from a broad range of stations but was generally absent from the deepest (stations 9-12, see Fig. 1). Somers et al. (1987) also found *M. endeavouri* to be evenly distributed across their study area and equally abundant on all substrate types from Torres Strait where depths were in the 20-40 m range. Although *M. ensis* was limited in its distribution it was very abundant and approximately 2.5 times more so than *M. endeavouri*. Because a) there was limited distribution of *M. ensis* within the study area, b) low frequency of mature females and, c) no ripe (stage 4) females sampled over the two-year period, it may indicate that none of the sites were representative of preferred spawning areas for this

species. Distribution of *M. ensis* and its spawning areas may be restricted to areas with depths of 17 m or less.

Small and immature female *M. endeavouri* were found in greater depths than larger, more mature females (Tables 1 and 2) indicating that there is a general inshore migration to mature and spawn. This differs significantly from *Penaeus* species' life cycles, such as those described for *P. merguensis* by Munro (1975) and Crocos and Kerr (1983) which undertake a seaward migration to mature and spawn. Generally, *Metapenaeus* species are more dependent upon an estuarine phase than *Penaeus* species (Kutkuhn 1966; Coles and Greenwood 1983) and some may even spend entire life cycles within rivers and estuaries (Morris and Bennett 1951; Racek 1959). The present results support the speculations of Kirkegaard (1975) that adult females must place larvae in their most suitable zones and the inshore migration of mature females may result in eggs being released in or near estuaries. If, as the data suggest, some *Metapenaeus* species move shoreward to mature and spawn, it may also explain why so few *M. ensis*, which appear to have been at their deepest and most seaward limits in this area, were found in a mature condition. The distribution of small and large *M. endeavouri*, described by Somers et al. (1987) in Torres Strait differed from results of the present study and suggested that larger shrimp move into deeper water. This discrepancy between the two studies may be partly due to the complex bathymetry of Torres Strait, where small *M. endeavouri* were not associated with shallow coastal areas, but rather an oceanic area west of the main fishing grounds.

Population fecundity indices (Fig. 5) for *M. ensis* were reduced during the cooler, winter months when temperatures fell below about 24.5°C and peaked during early summer, September to December. The seasonality in reproductive output would be even more distinct if the influence of spermatophore availability was considered on egg viability. Because almost no female *M. ensis* were found inseminated from May to September in both years (Fig. 3) it is unlikely that there would have been any viable eggs spawned during this period, even though the PFI suggested a low level of egg production.

When compared with other shrimps from the same fishery the reduced PFIs during winter for *M. endeavouri* and *M. ensis* contrast with the winter peaks (July-August) in maturation and ovary weight for *Penaeus longistylus* and *P. latisulcatus* (Courtney and Dredge 1988).

From their four surveys of Torres Strait, which were approximately three months apart, Somers et al. (1987) recorded the lowest proportion of female *M. endeavouri* with visible ovaries during June, which is consistent with results of the present study. Coles and Lee Long (1985) recorded the abundance of postlarval *M. endeavouri* from dense seagrass nursery areas in the southeastern Gulf of Carpentaria over a period of fifteen months. Their results also support those of the present study and imply that spawning took place during the summer, from October to January. Postlarval abundance was consistently low from March to August. Therefore, there appears to be little geographic variation in reproductive periodicity between populations of *M. endeavouri* from Torres Strait, the southeastern Gulf of Carpentaria and the central east coast region of Queensland.

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