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Lunar Periodicity in Catch Rate and Reproductive Condition of Adult Eastern King Prawns, *Penaeus plebejus*, in Coastal Waters of South-eastern Queensland, Australia

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Abstract. This study examined the lunar and diel variation in catch rates and reproductive condition of adult eastern king prawns, *Penaeus plebejus*, in relatively deep (160 m) coastal waters off south-eastern Queensland. Females numerically dominated catches over most of the lunar cycle and constituted 76% of the weight of the catch. Analysis of variance (ANOVA) revealed an interaction between lunar phase and sex; catches peaked during Lunar Phase 3 (full moon ± 3 days) and were particularly marked for males. This was the only period during the lunar cycle when the sex ratio approached 1:1. There was also an interaction between trawl-time and sex; male catch rates were at a minimum early in the evening, whereas female catch rates were at a maximum then and declined throughout the night. Trawler logbook catch rate data from the same area over a similar period indicated an interaction between lunar cycle and lunar phase. ANOVA revealed an effect of the interaction between phase and sex on the incidence of soft prawns; the incidence of soft males increased during Phase 4 (half moon waning to new moon ± 3 days). Ovary weight also varied between phases and was higher during Phases 2 (half moon waxing to full moon ± 3 days) and 4 (half moon waning to new moon ± 3 days). Trends in the ovary weight and the incidence of histologically mature and ripe females suggested there are two periods of increased spawning activity during each lunar cycle. A cyclic regression fitted to the data explained 93% of the variation in the incidence of ripe females between samples. The influence of these cyclic trends in catch rate and reproductive condition should be considered when monitoring the spawning stock in the fishery and when planning sampling strategies in any future reproductive studies.

Introduction

Many coastal marine organisms exhibit physiological and behavioural rhythms that are synchronized with changes in their environment (Neumann 1981). DeCoursey (1983) found examples of tidal, diurnal, semilunar, lunar and annual periodicities in locomotor activity, moulting and reproduction in crustaceans. Most published examples refer to relatively highly visible intertidal organisms, such as fiddler crabs (*Uca* spp.). There are fewer examples for neritic species, and fewer still for oceanic species.

For penaeid prawns, although endogenously controlled nocturnal activity has been reported for a few species, persistent tidal, daily and semilunar rhythms have generally been poorly demonstrated (Natarajan 1989). Most studies supporting the existence of such rhythms have been based upon catch rates of early life-history stages (postlarvae and juveniles), which occur in shallow inner-littoral nursery habitats (Barber and Lee 1975; Young and Carpenter 1977; Staples and Vance 1985; Vance and Staples 1992; Vance *et al.* 1994). Little is known of the behavioural and physiological rhythms of adults, which generally occur in deeper, mid-to-outer littoral habitats.

Such rhythms may bias abundance estimates (owing to variations in catchability) and other population parameters that are derived from periodic sampling programmes. Whenever populations are sampled for stock assessment purposes, the influence of such rhythms needs to be considered (Vance and Staples 1992). This can be achieved by *(a)* using sampling gear that is not susceptible to the changes in behaviour, *(b)* setting the sampling periodicity to coincide with specific physiological or behavioural events, *(c)* standardizing the data after they have been obtained, or *(d)* a combination of *a*, *b* and *c*. The last three alternatives require some understanding of the physiological and behavioural rhythms of the organisms examined.

Eastern king prawns (*Penaeus plebejus*) are the largest of Australia's endemic penaeid prawns and constitute a major otter-board trawl fishery off the east coast (Glaister *et al.* 1990). Evidence for behavioural or physiological rhythmicity in adults is scant. This is partly because the species is highly migratory (Potter 1975; Ruello 1975; Glaister *et al.* 1987; Montgomery 1990) and partly because adults occur in relatively deep water (100–300 m).

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Trawler operators targeting adult *P. plebejus* report that their catch rates are influenced by lunar phase and consequently regulate their fishing activities on a lunar phase basis. This suggests that the prawns exhibit behavioural rhythms that are synchronized with specific phases within the lunar cycle and that influence their catchability. The aim of this study is to determine if the catch rate and reproductive biology of adult *P. plebejus* are independent of lunar phase. The results are discussed in relation to monitoring abundance of adults and defining a suitable spawning stock index for the fishery.

Materials and Methods

Data on catch rates were obtained from two sources: a compulsory logbook programme and a research sampling programme. Samples obtained from the research programme were also used to provide information on reproductive condition. The logbook programme provided information on individual vessel catch rates (catch per unit of effort (CPUE), kg boat^{-1} night^{-1}) from two (pooled) 30′ × 30′ logbook grids (Fig. 1). The period examined from the logbook database was from 1 May to 31 July 1993, which included two consecutive lunar cycles.

Research Sampling

Three transects were established within the logbook grids (27°02′S,153°37′E) in a depth of 160 m, 9 n miles east of Cape Moreton (Fig. 1). Each transect was approximately 4·4 n miles long and orientated north–south. Previous sampling in the area indicated that prawn catches consisted almost entirely of adult *P. plebejus*. The transects were located with radar and an on-board global positioning system.

Sampling trips were undertaken every 72 h (weather permitting) for 2·25 consecutive lunar cycles from 24 May to 21 July 1993 (59 days, inclusive). On each trip, all transects were sampled once and the order in which they were sampled was randomized. The duration of each trawl was 2 h bottom time. Trawling was restricted to three periods each night (three trawl-times). The first trawl (Trawl-time 1) was undertaken early in the evening (from 1800 to 2000 hours), the second (Trawl-time 2) in the middle of the night (from 2200 to 2400 hours), and the third (Trawl-time 3) in the early hours of the morning (from 0200 to 0400 hours) before sunrise. The trawl gear consisted of three 13-m Florida Flyer nets with 50-mm-mesh codends.

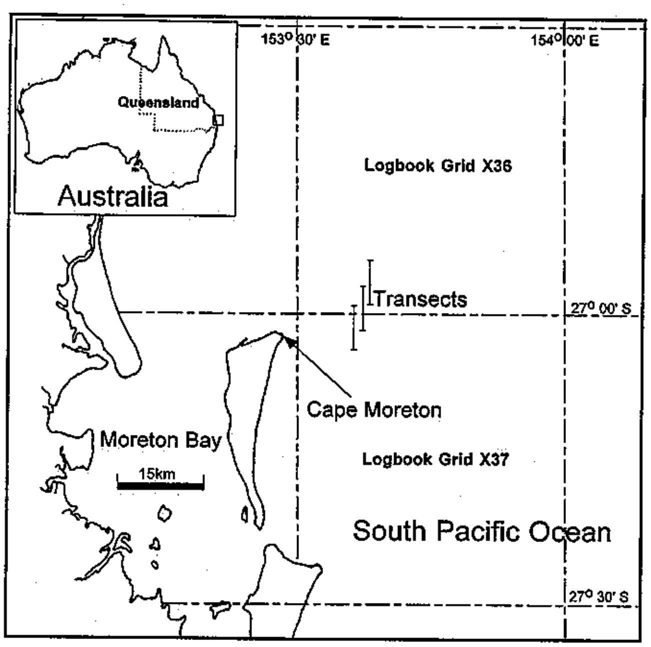

Fig. 1. Coastal region of south-eastern Queensland, showing the positions of the three transects east of Moreton Island and the two logbook grids that were used to provide information on commercial catch rates.

The direction in which each transect was trawled (north or south) was determined randomly. Two assumptions were implicit in the research sampling. The first was that any differences between catch rates that may have been due to the prevailing current strength or direction were negligible. The second assumption was that the size of the population being sampled remained largely unchanged over the sampling period (59 days). For this to occur, any depletion that may have occurred because of the research sampling, commercial fishing in the vicinity, natural mortality or emigration would have to have been negligible or offset by recruitment and immigration.

Sample Processing

The catch from each trawl was sorted immediately after the nets were brought to the surface. Each time a transect was sampled, the prawns from the three nets were pooled, placed in a labelled plastic bag, and frozen on board. After each night of sampling the vessel returned to port. Samples were then transported to the laboratory, where the number and size of all prawns in each sample were determined. Each prawn had its carapace length (CL) measured to the nearest millimetre and was assigned an approximate moult stage (soft or hard).

Three characteristics were used to determine female reproductive condition: *(1)* spermatophore insemination, *(2)* ovary weight and *(3)* ovarian histological development. The presence or absence of a spermatophore was determined for every female by opening the thelycum and removing the spermatophore, when present. Ovaries from 45 randomly selected females from each sample were weighed to the nearest 0·1 g. In samples with fewer than 45 females, the ovaries from all females were weighed. A histological section of ovarian tissue from the first abdominal somite was prepared for every female sampled. Exceptions were made for samples with a large number of females, for which the number of sections was limited to 100. Ovarian tissue used in the histological sections was preserved in 4% (v/v) formaldehyde, embedded in paraffin, sectioned at 6 μm, and stained with haematoxylin and eosin. The developmental stage was determined according to a histological description of maturation in *P. plebejus* (Courtney *et al.* 1995*b*).

Statistical Design

Split-plot analysis of variance (ANOVA) was used to determine if logbook catch rates differed between lunar cycles and lunar phases. Four consecutive cycles were examined. Within each complete cycle, four phases were identified as the split factor in the analysis: *(1)* new moon (± 3 days), *(2)* half moon waxing to full moon (± 3 days), *(3)* full moon (± 3 days), and *(4)* half moon waning to new moon (± 3 days). The statistical model was cycles(4) split for phases(4) (with replication, the extent of which varied between days depending on the number of vessels working). The variate was catch rate (CPUE, kg boat^{-1} night^{-1}).

For analysis of the research sampling data, catches from two complete, consecutive lunar cycles were compared. Four phases within each cycle were identified, as for the logbook data analysis. Trawl-time was also considered as a possible treatment effect. Where appropriate, these data were analysed by a triple split-plot ANOVA. The model was cycles(2) split for phases(4) (with replication, which varied depending on the number of trips undertaken), split for trawl-times(3), and further split for individual prawns within trawls to investigate this level of variability. The variates were catch rate (number of prawns per sample), mean prawn size (mm CL), sex ratio (males : females), incidence of soft (early post-moult) individuals, incidence of spermatophore insemination, individual female ovary weight, and incidence of females in specific stages of ovarian development.

Before ANOVA, catch rates from the research sampling were transformed—$\log_e$(number caught per trawl + 1). Estimates of the total weight and sex-specific weight of each sample were made from length–weight conversions. Data expressed as percentages were arcsine-transformed when the data set, or a portion of the data set, was in the ranges <30% (0·3) or >70% (0·7) (Sokal and Rohlf 1981). Neither ovary weight nor the gonosomatic index (ovary weight/total body weight) is independent of carapace length in *P. plebejus* (Courtney *et al.* 1995*b*), and therefore to remove the effect of prawn size on ovary weight, the ANOVA was undertaken with carapace length as a covariate. Ovary weight and carapace length were also transformed ($\log_e$) for this analysis.

Results

Variation in Catch Rate and Prawn Size

Logbook data. Mean daily catch rates varied considerably over the period examined (Fig. 2); the highest mean daily CPUE was 129 (± 15·4 s.e.) kg boat^{-1} night^{-1} and the lowest was 40 (± 8·0 s.e.) kg boat^{-1} night^{-1}. Some trends associated with lunar phase were evident, the most consistent being a decline in CPUE over the seven days following the full moon. Mean daily CPUE was generally high two to three days before the full moon and low in the period between seven days after the full moon and five days before the new moon (Fig. 2). ANOVA indicated a significant ($P < 0·01$) interaction between cycle and phase.

Research sampling data. Of the 21 research sampling trips, two were completely abandoned and a third had only one transect completed because of poor weather. Fifty-five samples (18 trips with three samples, one trip with one sample) were obtained, containing 7972 *P. plebejus* specimens. Males and females accounted for 36·8% (2935) and 63·2% (5037) of the total number of *P. plebejus* sampled, respectively (Fig. 3). Neither the individual transects nor the direction in which each transect was trawled had a significant ($P > 0·05$) effect on the catch rate (number per sample) of either sex.

The mean number of females caught on each trip varied considerably (Fig. 4*a*). The maximum mean female catch rate per sample (160 ± 40·3 s.e.) occurred on Trip 14 (1 July), two nights before the full moon. The minimum mean catch rate (24 ± 5·0 s.e.) occurred on Trip 9 (16 June), three days before the new moon. There was a consistent decline in the catch rate of females during the seven days following the full moon, and there were two periods within each cycle when catch rates increased; one occurred about three days before the full moon, the other was more variable in its timing but generally occurred around the time of the new moon.

Although male catch rates showed similar trends (Fig. 4*a*), they were generally lower and more variable than female catch rates. Male catch rates exhibited one major peak during each cycle approximately two to three days before the full moon. A second minor peak occurred within three days either side of the new moon. The decline in catch rate during the seven days following the full moon was similar to, but more marked than, that observed for females. The maximum (165 ± 56·1 s.e.) and minimum (3±1.2 s.e.) mean male catch rates per sample occurred on the same nights as those for the females.

The sex ratio varied considerably over the sampling period but was generally well below 1.0. On more than 50% of trips the ratio was less than 0.5, and it exceeded 1·0 on only one sampling trip (30 May, Fig. 4*b*). Peaks in the ratio occurred two to three days before the full moon and were followed by declines during the seven to eight days following the full moon. Troughs occurred five to six days before the new moon. Lunar phase had a significant effect on the ratio ($P < 0·05$). Adjusted means were 0·24, 0·61, 0·81 and 0·42 for Lunar Phases 1, 2, 3 and 4, respectively.

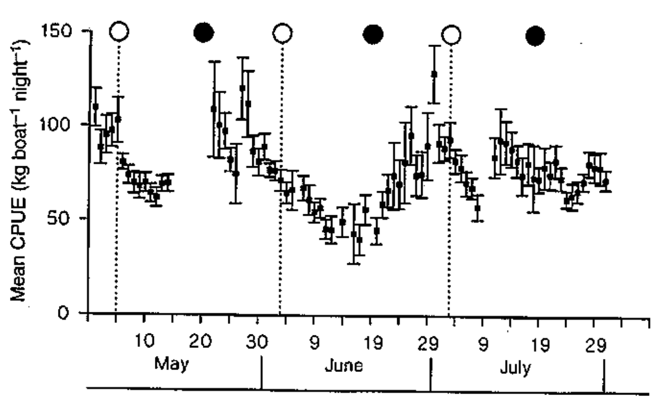

Fig. 2. Mean daily commercial catch rates of *Penaeus plebejus* from trawlers fishing in offshore areas (commercial trawl logbook grids ×36 and ×37) from May to July 1993. Vertical lines represent one standard error either side of the mean. Data are presented only for those days when four or more vessels were working. ●, New moon; ○, full moon.

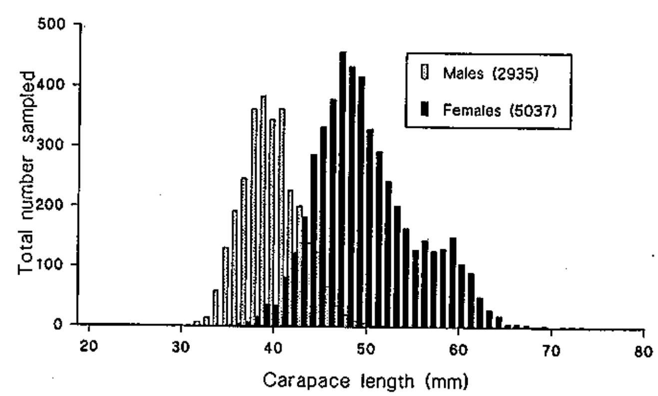

Fig. 3. Size-class–frequency distribution of *Penaeus plebejus* obtained from 19 sampling trips over approximately 2·25 consecutive lunar cycles. Samples from all trips and transects were pooled.

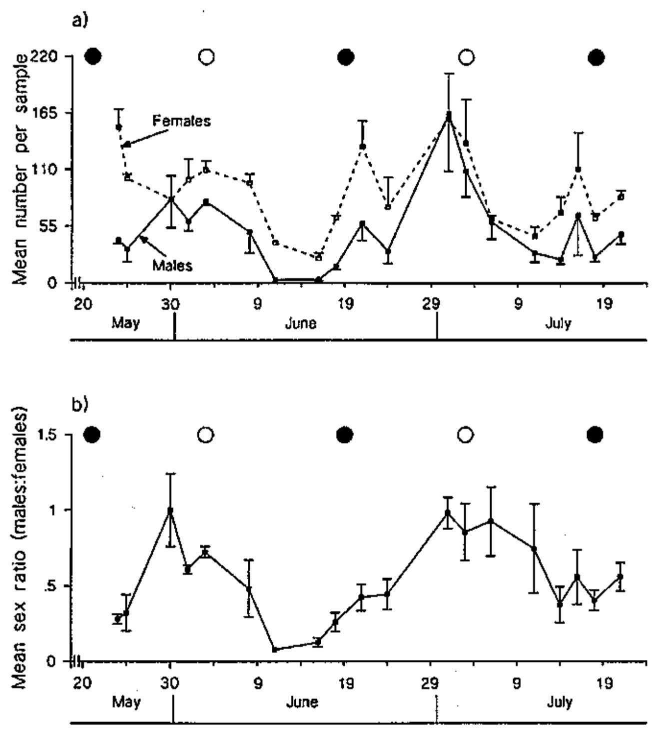

Fig. 4. Variation in the *(a)* catch rate and *(b)* sex ratio of adult *Penaeus plebejus* in samples obtained from 19 sampling trips over approximately 2·25 consecutive lunar cycles. Each point is the mean of three samples obtained each sampling night. Vertical bars represent one standard error either side of the mean. ●, New moon; ○, full moon.

The significant effect of lunar phase on the sex ratio indicated that any possible effects from the other treatment factors (lunar cycles and trawl-times) on catch rates may also differ between sexes. For this reason, sex was considered as an additional treatment in the split-plot ANOVA of catch rates. Although this analysis suggested that the catch rates did not differ between cycles, phases or trawl-times, it confirmed that there were significant ($P < 0{\cdot}01$) differences between sexes (females were more numerous) and that there was a significant ($P < 0{\cdot}01$) phase by sex interaction. Back-transformed adjusted means indicated that although the catch rates for both sexes peaked during Phase 3, the increase was particularly marked for males and was at least twice that for the other phases.

The analysis also revealed a significant ($P < 0{\cdot}05$) interaction between trawl-time and sex. Male catch rates were at a minimum early in the evening (Trawl-time 1, 1800–2000 hours), whereas female catch rates were at a maximum then and declined throughout the night. The back-transformed adjusted means were 24·2, 34·9 and 34·3 males per sample and 75·6, 68·9 and 64·7 females per sample for Trawl-times 1 (1800–2000 hours), 2 (2200–2400 hours) and 3 (0200–0400 hours), respectively. The analysis also revealed a significant ($P < 0{\cdot}05$) interaction among phase and trawl-time and sex, as might be expected given the two previous interactions.

The mean CL of the prawns in each sample differed significantly ($P < 0{\cdot}01$) between the sexes; adjusted means were 38·6 mm CL for males and 48·4 mm CL for females. There was also a relatively small but significant ($P < 0{\cdot}05$) variation in the size of the prawns between cycles; mean size declined by about 1·0 mm CL in both sexes from the first cycle to the second. There were no other significant effects on size.

Females comprised 76% of the total weight of the research samples. A mean sample weight, estimated for each trip from the three samples, was found to be positively correlated with the same-day mean daily logbook CPUE ($P < 0{\cdot}01$, Pearson correlation coefficient 0·61). ANOVA of the estimated sample weights revealed results similar to those obtained for the analysis of the numerical catch rates. This was expected owing to the relatively low variation in the size of the prawns. The sample weights differed significantly ($P < 0{\cdot}01$) between males and females, and there were significant interactions between phase and sex ($P < 0{\cdot}01$), and between trawl-time and sex ($P < 0{\cdot}05$). The interaction among phase and trawl-time and sex was marginal ($P = 0{\cdot}051$).

Variation in Incidence of Recently Moulted Prawns

The percentage of individuals in early post-moult (i.e. soft) at any one time was relatively low, generally ranging between 2% and 6%. Analyses of the arcsine-transformed percentage data revealed no significant differences between cycles or trawl-times. However, there was a significant interaction between phase and sex ($P < 0{\cdot}01$). The percentage of soft males peaked in Phase 4 (Fig. 5) for both lunar cycles. Results for the phase by trawl-time interaction were marginal ($P = 0{\cdot}08$).

Variation in Reproductive Condition

The insemination status and ovary developmental stage were determined for 85·8% (4324) of the 5037 females sampled. Of these, 55·1% (2384) also had their ovaries dissected out and weighed. The overall incidence of spermatophore insemination was high (96.6%), and variation between trips was low throughout the sampling period. The percentage inseminated in each sample was independent of cycles, phases and trawl-times ($P > 0{\cdot}05$).

For each of five size classes examined, mean ovary weight varied considerably over the sampling period (Fig. 6). There were no obvious trends with lunar phase, although some consistencies across size classes were present. Firstly, mean ovary weight minima occurred during either Phase 1 or Phase 3, mostly during Phase 1. Secondly, high mean ovary weight values were attained during Phases 2 and 4.

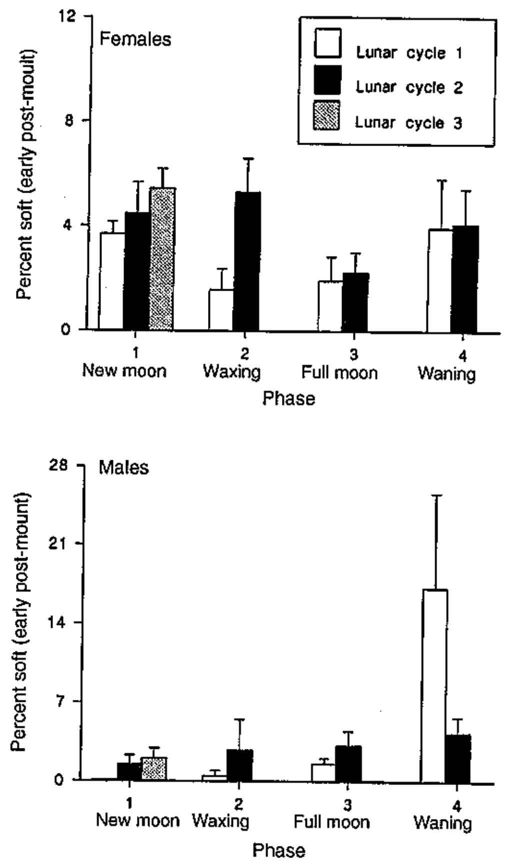

Fig. 5. Mean percentages of recently moulted (soft) *Penaeus plebejus* during the four lunar phases. The sampling period included lunar phases from two complete and one partial lunar cycle. The means are based on individual samples within each phase. Vertical bars represent one standard error either side of the mean.

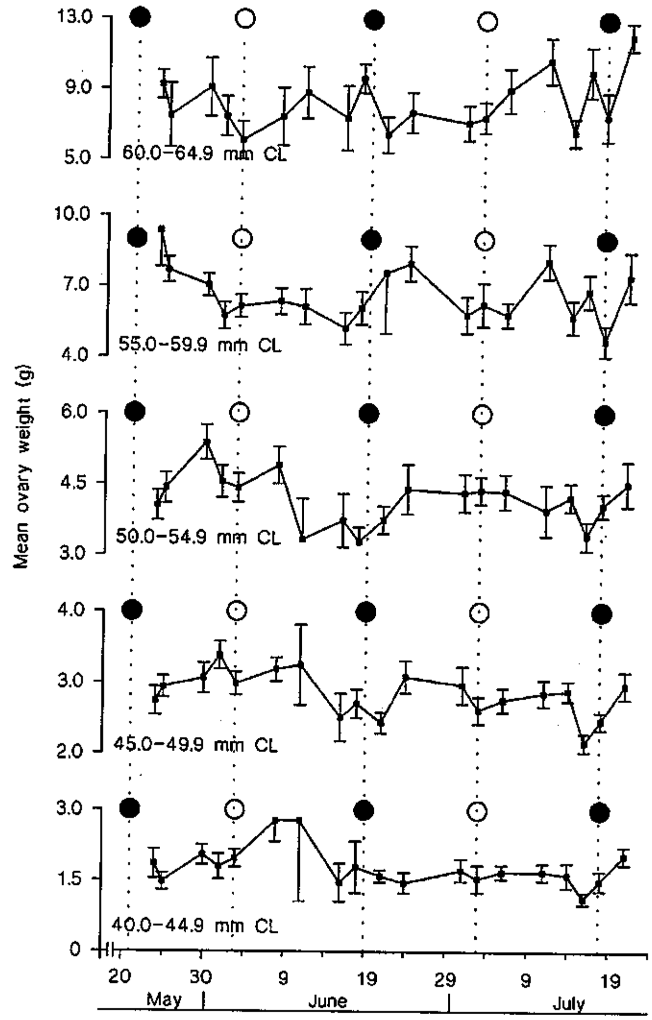

Fig. 6. Mean ovary weights from five size classes of female *Penaeus plebejus* in samples obtained from 19 sampling trips over approximately 2·25 consecutive lunar cycles. Samples were pooled on each trip. ●, new moon; ○, full moon. Vertical bars represent one standard error either side of the mean. Total number of individual female ovary weights in these size classes is 2351.

With female size (CL) as a covariate, ANOVA revealed that ovary weight differed significantly ($P < 0{\cdot}01$) between cycles; back-transformed adjusted means were 3·58 g and 3·13 g for Cycles 1 and 2, respectively. The analysis also indicated that ovary weight was not independent of phase ($P = 0{\cdot}05$); back-transformed adjusted means were 3·14, 3·41, 3.36 and 3.47 g for Phases 1, 2, 3 and 4, respectively. This result supports the above observations—that ovary weight was high during Phases 2 and 4 and low for the remaining phases, particularly for Lunar Phase 1. Results for the interaction between phase and trawl-time were marginal ($P = 0{\cdot}097$).

Of the 4324 females that had their ovary development assessed, 1·3% were pre-vitellogenic (immature or developing) and 87·2% were mature, ripe or in the germinal vesicle breakdown (GVBD) stage (Table 1). The histological characteristics of recently spawned (i.e. spent) females could not be confidently distinguished from those of females that may have resorbed their ovaries and therefore not spawned. For this reason, no detailed analysis of the incidence of spent females was undertaken. Together, spent and resorbed females accounted for 9·2% of the total. The incidence of very advanced developmental stages (GVBD and ovulation) was extremely low and therefore it was not possible to interpret the effects of the treatments on these stages or to make any inference about the imminent spawning time.

For mature (vitellogenic oocytes) and ripe (oocytes with peripheral bodies) females, however, some trends were apparent. The mean percentage of mature females ranged between 54.7% and 87.0% (Fig. 7*a*) and tended to peak on, or close to, each new moon (Phase 1) and full moon (Phase 3). The mean percentage of ripe females ranged between 2·5% and 25%, displayed a marked cyclic trend, and peaked

Table 1. Numbers and percentages of female *Penaeus plebejus* in different stages of ovarian development
All 55 samples pooled

Histology stage	No. of females	Percentage of total number of females sampled
Immature oocytes (oogonia stage)	5	0·1%
Developing (perinucleolus stage oocytes)	52	1·2%
Mature (vitellogenic oocytes)	3278	75·8%
Ripe (peripheral bodies present in oocytes; occurs within 96 h of spawning)	463	10·7%
Germinal vesicle breakdown (nucleus disintegrates; occurs within 24 h of spawning)	29	0·7%
Ovulation (oocytes with peripheral bodies, follicle cells absent; occurs within 4 h of spawning)	0	0%
Spent or resorbed (ovaries with large intercellular spaces, follicle cells, no vitellogenic oocytes)	398	9·2%
Unstaged (owing to problems in preparation or difficulty in allocating a specific stage of development)	99	2·3%
Total	4324	100%

in between the new and full moon phases (Fig. 7*b*). The dotted lines linking Figs 7*a* and 7*b* indicate possible progressive histological development of the ovary—peaks in the incidence of mature females were followed by peaks in the incidence of ripe females by approximately four to five days. Those periods associated with peaks in the percentage of ripe females (Fig. 7*b*) coincided with periods of increased mean ovary weight (Fig. 6). Interestingly,

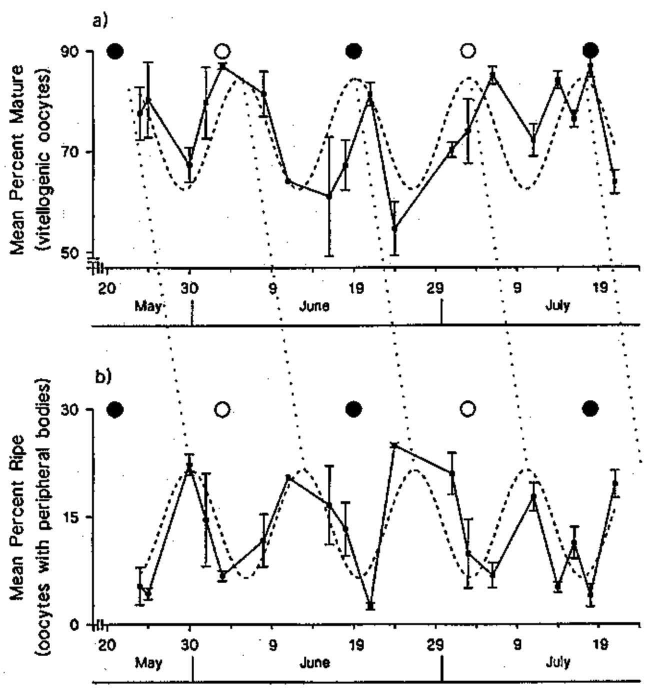

Fig. 7. Mean percentages of female *Penaeus plebejus* in different stages of ovarian development in samples obtained from 19 sampling trips over approximately 2·25 consecutive lunar cycles. *(a)* Percentage of females in mature stage; *(b)* percentage of females in ripe stage. Each point represents the mean of three samples obtained each sampling night. ●, new moon; ○, full moon. Dashed lines represent cyclic regression curves of best fit. Dotted lines represent possible progressive development of the ovary.

although the proportion of females in the mature stage was relatively high throughout the sampling period (Fig. 7*a*), only a relatively small proportion of females appeared to continue development through to the ripe stage (Fig. 7*b*) at any one time.

Although the split-plot ANOVA indicated that none of the developmental stages differed significantly between cycles, phases or trawl-times, cyclic regressions could be fitted to the incidence of mature and ripe females (dashed curves, Figs 7*a* and 7*b*, respectively). A sinusoidal regression explained 93% of the variation in the incidence of ripe females between samples. The independent variables included in the regression were time (in days after the new moon) and time of night (trawl-time). The regression was expressed thus:

$$\ln R = \ln[13{\cdot}315 - 8{\cdot}946\cos(0{\cdot}454T - 6{\cdot}036) + B_1X_1 + B_2X_2] + \varepsilon$$
$$\text{d.f.} = 54,\ P<0{\cdot}001,\ r^2 = 0{\cdot}93,$$

where R is the percentage of ripe females, T is the time in days after the first new moon phase, B_1 is a coefficient defining the difference in mean percentage ripe between the second and the first trawl shots ($B_1 = -0{\cdot}1096$), B_2 is a coefficient defining the difference in mean percentage ripe between the third and first trawl shots ($B_2 = -0{\cdot}0694$), X_1 and X_2 are indicator variables that take the value of 0 and 0, 1 and 0, and 0 and 1 for Trawl-times 1, 2 and 3 respectively, and ε is an error term.

Discussion

Variation in Catch Rates

The catch rates from the logbook and from the research sampling showed similar trends and were positively correlated. Both indicated peaks in catch rate shortly before the full moon (Phase 3), and both displayed declines for about seven days after the full moon. The interaction between cycles and phases for the logbook catch rate data is possibly due to the relatively high catch rates reported in the period immediately after the new moon in May (Fig. 2). These high catch rates had high standard errors and were associated with only very few vessels working immediately after a period of bad weather that had prevented fishing. It is possible that these catch rates were unusually high for that particular phase and cycle and were therefore largely responsible for the interaction. This explanation is supported by the fact that no such interaction was found for the research sampling data.

The research sampling data revealed that the increased catch rate during Phase 3 was due to an increase in both males and females, but particularly in males. The back-transformed adjusted means indicated that during Phase 3 the male catch rate increased by more than twice that of any other phase and slightly less than four times that of Phase 1. Thus, the study corroborates the reports by fishers—that catch rates of adult *P. plebejus* in deep water (>100 m) increase during the nights leading up to the full moon. The study also suggests that the increase is largely, but not exclusively, due to an increase in male catch rates at that time.

Glaister (1983) examined variation in the commercial catch rates (prawn weight per trawler per night) of three different size classes of *P. plebejus* from coastal waters of northern New South Wales. Although he concluded that there was no statistically significant periodicity, there were trends in the catch rate of the large (>22 g) size class that were similar to those of the present study; catch rates tended to be high around the time of the full moon and declined in the seven days following. Glaister (1983) also suggested that a 'mirror' trend was present for the smallest (<15 g) size class; catch rates peaked close to the new moon phase. This trend in the catch of the smaller size classes was supported by the earlier work of Racek (1959), who used set pocket-nets to sample seaward-migrating *P. plebejus* in coastal inlets and entrances.

Thus, there appears to be a complex relationship between catch rate and lunar phase for *P. plebejus*, which varies with prawn size and/or depth. In estuaries and inner littoral areas (<30 m depth) catch rates of subadults increase in the period leading up to and including the new moon (Racek 1959), whereas in the outer littoral areas (>100 m depth) catch rates of adults peak shortly before the full moon and decline over the following seven days (Glaister 1983; present study). Consequently, the lunar activity patterns of trawler operators targeting *P. plebejus* in shallow (<30 m) and deep (>100 m) water regions of the fishery differ. Fishers operating relatively small vessels in shallow water prefer fishing in the period leading up to and including the new moon, whereas fishers operating the larger vessels targeting adults in deeper waters prefer fishing in the period leading up to and including the full moon.

The trends in catch rate of adult *P. plebejus* reported here are similar to those reported by White (1975), who found a pronounced lunar cycle rhythm in daily catch rates of *Penaeus esculentus* from the Exmouth Gulf fishery in Western Australia, over three consecutive years. Catch rates peaked three to four days prior to the full moon and were at a minimum at or near the new moon phase.

In the present study, females were about 1·7 times more abundant than males. Such a dominance of one sex is uncommon in penaeid prawn fisheries (see Hyland 1985 and Somers *et al.* 1987 for comparisons) and resulted in 76% of the total weight of the research samples consisting of females. It is likely that a similar proportion of the commercial catch from the same general area consisted of females. One possible explanation for this could be differences in the selectivity of the mesh size between sexes. No information is available on the selectivity of the gear used on adult *P. plebejus*. Although sex-specific selectivity could account for the differences in the number of males and females captured over the entire sampling period, it does not explain the marked variation in the sex ratio observed within the cycles. Another possible explanation could be the general size–depth spatial distribution common to many penaeid prawn populations (Garcia and Le Reste 1981) combined with the fact that the maximum attainable size of female *P. plebejus* is much greater than that of males. At their maximum attainable sizes (L_∞ = 45·4 mm CL and 59·5 mm CL for males and females respectively; Glaister *et al.* 1987), females weigh more than twice as much as males and thus may prefer, or be better suited for, greater depths. A third possible explanation for the female predominance is that female catchability was generally higher than that of males owing to behavioural changes associated with increased reproductive activity. Monthly spawning patterns in adult *P. plebejus* in south-eastern Queensland (Courtney, unpublished data) indicate that during the study period (May to July), there is increased spawning activity. It is possible that female catchability may be enhanced during this time through increased behavioural activities associated with maturation and mating, but this is only speculation. Such a positive correlation between the relative monthly contribution of females to the catch and female maturation has been reported by Choy (1988) for *Penaeus canaliculatus*.

The predominance of females notwithstanding, the present study also revealed an interaction between phase and sex catch rate. A number of studies have reported on the sex ratio of *P. plebejus* catches. Racek (1959) found that females numerically dominated catches from estuarine and inner littoral areas during most seasons of the year. In the estuarine conditions of Moreton Bay adjacent to the current study area, the sex ratio of subadult *P. plebejus* remained close to 1 : 1 all year round (Courtney *et al.* 1995*a*). Glaister

(1983) likewise concluded that the sex ratio of *P. plebejus* off northern New South Wales did not differ significantly from 1:1.

The reason for the interaction between phase and sex catch rate is unknown. It may have been due to behavioural changes in activity, within and between sexes over the lunar cycle, which influenced the catchability of each sex but, again, this is only speculation. Such changes in catchability could explain the variation in the sex ratio, as well as the general trend in catch rates over the lunar cycle. White (1975) also attributed the pronounced lunar periodicity in the catch rate of *P. esculentus* to changes in catchability over the lunar cycle, but because of the nature of logbook data he did not examine sex-specific catch rates. Natarajan (1989) demonstrated in the laboratory that locomotory activity in *Penaeus indicus* and *Penaeus monodon* varied with moon phase. From this work Natarajan, too, inferred that the catch rates of these species in the field were influenced by lunar phase.

The difference in catch rates between males and females was not restricted to the interaction with lunar phase. The study also revealed a significant interaction between sex catch rate and trawl-time. The adjusted means indicated that male catch rates were at a minimum early in the evening whereas female catch rates were at a maximum then and declined as the night progressed. As a consequence of this, and of the large size and numerical dominance of females, there was a general decline in the total number and total weight of the prawns caught throughout the night. This may be partially explained by the work of Wassenberg and Hill (1994), who studied emergence patterns in eight species of penaeid prawns ranging in size from 25 to 30 mm CL in the laboratory. They found that, compared with the other species, *P. plebejus* spent the least amount of time emerged at night, that it began to bury itself again soon after emerging (within 2 h), and that the time spent emerged declined rapidly throughout the night. These results, albeit for smaller sizes than those in the present study, suggest that the general decline in total catch rate throughout the night was due to decreased emergence times as the night progressed. Wassenberg and Hill's results do not explain the variation observed in male catch rates throughout the night, and they did not comment on the sex of the prawns used in their study.

Further differences between sexes were reflected in the analysis of the incidence of recently moulted prawns. The interaction between phase and sex revealed that the incidence of soft males was highest during Phase 4 for both lunar cycles. Racek (1959) also stated that ecdysis in adolescent and adult prawns displayed a pronounced rhythm, coinciding with the lunar phase, but he did not present any data for *P. plebejus*. Glaister (1983) examined the incidence of soft *P. plebejus* in commercial landings from northern New South Wales. He found no statistical significance but concluded that there was some indication of a cycle that may be size-dependent. White (1975), using logbook data, found a lunar-based rhythm in the incidence of soft *P. esculentus*. He concluded that the highest incidence occurred on or near the new moon phase and was partially responsible for the low catch rates at that time. In the present study, the highest incidence of soft males occurred during a different phase (Phase 4) from that associated with lowest male catch rates (Phase 1).

Variation in Reproductive Condition

The relatively high abundance of females in the samples, combined with the high incidences of insemination (>96·6%) and advanced ovarian development (>87·2% for mature, ripe and GVBD stages), was indicative of high egg production in the population throughout the sampling period (May to July).

Not all ovarian developmental stages were well represented. The low incidence of the GVBD and ovulation stages suggests that they are of short duration, that they are rare events, or that the catchability of such females is reduced. Anderson *et al.* (1984) and Clark and Pillai (1991) have shown under laboratory conditions that certain histological stages in another penaeid prawn (*Sicyonia ingentis*) occur at specific intervals prior to spawning. The GVBD and ovulation stages occur within 24 and 4 h of spawning, respectively. Because of the low incidence of these stages in the present study, it is difficult to define the precise (i.e. within hours) time of spawning. However, the ripe stage, which occurs within 96 h of spawning, had a higher incidence of occurrence (10·7%, Table 1) and displayed an obvious cyclic trend. The most common developmental stage was the mature stage (75·8%), which also displayed a cyclic trend, but this was less pronounced than that of the ripe females. The lagged time between peaks in the incidences of the two stages (Fig. 7) suggests that the development of the ovary can be observed as the lunar cycle progresses and that it takes about four to five days for females to develop from mature to ripe.

Trends in ovary weight and the incidence of ripe females were well correlated. Both sets of data indicated that there were two periods of increased ovarian development each lunar month (during Phases 2 and 4). The effect of phase was significant for ovary weight but not for the incidence of ripe females, despite the obvious cyclic trend in the latter. The reason for this was probably the way phases were defined, which resulted in the cyclic trend in the incidence of ripe females being slightly out of synchrony with the four lunar phases. The definition and allocation of phases is partially subjective and likely to influence statistical outcomes. Thus, it is likely that very different statistical results would have been obtained in this study if the phases had been defined differently (e.g. if Phase 1 had been defined as the period from the new moon to the first quarter instead of as the new moon ± 3 days, and so on for the remaining phases). It should be noted that the lunar cycle consists of a continuum of different lunar stages, and the allocation of four (or more) discrete phases within the cycle is subjective.

The trends in the incidence of mature and ripe stages contrast with those of Crocos (1985), who examined lunar variation in the proportion of *P. esculentus* spawning in Moreton Bay. He concluded that the proportion of spawners showed no significant effects from moon phase and that there was no evidence to suggest a spawning cycle within the period studied. Some researchers have inferred spawning periodicity from studies of prawn larvae catch rates. Price (1979) sampled surface plankton in the western Persian Gulf and found two peaks in the abundance of early *Penaeus* spp. planktonic stages that occurred on or close to the quarter-moon phases (Phases 2 and 4). Although his results tend to support those of the present study—that there are two periods of increased spawning activity each lunar month—cautious interpretation of the data is required, as noted by Price. This is because the early planktonic stages comprised two *Penaeus* species, which may have contributed differently to the peaks, and because peaks in abundance may have been due to increased catchability associated with the planktonic response to varying light intensities over the lunar cycle and not to any variation in spawning activity. Rothlisberg *et al.* (1987) sampled plankton at three different depths over 18 months in the Gulf of Carpentaria, Australia, and concluded that, for all penaeid species examined, the occurrence of the first zoeal stage was unaffected by moon phase.

Implications for Fisheries Assessment and Management

Determining the status of the eastern king prawn fishery requires close monitoring of the catches. The relationship between spawning stock and recruitment is poorly understood, and therefore it is difficult to determine whether the fishery is experiencing recruitment overfishing. Indices of spawning stock and recruitment have yet to be identified. A suitable index of spawning stock should be representative of the egg production by the population, which is largely a function of the size, abundance and proportion of females spawning and the ability of those females to fertilize eggs. This study has provided some insight into the short-term variation in these parameters within and between lunar cycles.

In the Exmouth Gulf tiger prawn fishery (Western Australia), logbook catch rate data from specific months and areas are used as an index of spawning stock and thus as an annual measure of egg production (Penn and Caputi 1986). The results from the present study suggest that it would be prudent to consider the effects of lunar phase on both catch rate and catch composition if commercial catch rate data are used as an index of spawning stock in the eastern king prawn fishery. Mean lunar monthly catch rates may vary by a factor of two to three within a single lunar cycle, depending on the phase in which the fishers choose, or are able, to work.

This study has revealed a number of significant variations and interactions in the catch rate and reproductive condition of adult *P. plebejus* with lunar phase and sampling time-of-night. It is important to note that no causes or effects were investigated, nor should any be assumed. Nevertheless, the variations and interactions have the potential to influence how results from sampling programmes are interpreted, and therefore they should be considered in the design and interpretation of results of any future reproductive studies of *P. plebejus*, and possibly other *Penaeus* spp. In this respect, the assumptions made by Penn (1980) and the conclusions of Crocos (1985) pertaining to the asynchronous spawning of *P. esculentus* with lunar phase do not apply to adult *P. plebejus*.

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