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Activity patterns of juvenile penaeid prawns in response to artificial tidal and day-night cycles: a comparison of three species

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ABSTRACT: Activity patterns of *Penaeus merguiensis*, *P. esculentus* and *Metapenaeus endeavouri* were studied in response to simulated tidal and day-night cycles in the laboratory. When these cycles were imposed separately, each species was more active at night and near the times of high tide. However, when the tidal and day-night cycles were imposed together, the relative strengths of the responses to the 2 factors differed among species. *M. endeavouri* was strongly influenced by the day-night cycle; virtually no activity occurred during the day but peaks of activity at night occurred near high tide. *P. merguiensis* and *P. esculentus* displayed some activity during the day with peaks around and just after high tide. However, for these 2 species, the peaks of activity near high tide at night were higher than the peaks during the day. All species were more active at night and, in the prawn's natural habitat, there is probably less risk of predation involved in being active at this time. Highest activity occurred near high tide and in the wild this is probably associated with feeding for all species. Decreased activity occurred at low tide, probably to avoid predation and, at times, dessication. The overall activity level of *P. merguiensis* was the highest of these species. The highest activity levels recorded for each species were similar but the lowest levels varied markedly. *M. endeavouri* remained buried for many hours during the day, whereas the lowest mean activity levels recorded for *P. merguiensis* were relatively high compared with the other species.

INTRODUCTION

The catch rates of penaeid prawns within a 24 h period are often extremely variable. A knowledge of this short-term variability is important in designing sampling strategies to estimate long-term changes in prawn abundance. As part of a study on the prawn fisheries of the Gulf of Carpentaria, Australia, the catchability of juveniles of several of the main commercial species was investigated in the Embley River (Vance & Staples 1992). Statistical analysis of the catch variation of juvenile *Penaeus merguiensis*, *P. esculentus* and *Metapenaeus endeavouri* showed that, in general, catches of these species were greater at night and at lower tide levels. There were, however, differences in the relative importance of each factor. *P. merguiensis* catches were most strongly related to the daily tidal cycle: catches were highest on the last stage of the ebb tide having the greater range of the 2 daily tides, irrespective of the day-night cycle. *M. endeavouri* was dominated by the day-night cycle: virtually no prawns were caught during the day. Although catches of *P. esculentus* were not as strongly influenced by either cycle, catches were higher at night and near low tide.

Several factors affect prawn catchability and activity, and of these, light and tide are the most widely reported influences. Day-night variability in prawn catches is well documented (e.g. Trent 1966, White 1975, Young 1975, Coles 1979) and Staples & Vance (1979) found a strong tidal periodicity in catches of juvenile *Penaeus merguiensis*. However, in some field studies (e.g. Clark & Caillouet 1975, Gamba & Rodriguez 1987) it has been difficult to decide on the relative importance of tidal and day-night cues in determining observed variations in the abundance of penaeids. Several laboratory studies have shown that penaeids are more active at night (e.g. Hughes 1968, Moller & Jones 1975, Reynolds & Casterlin 1979). Fuss

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& Ogren (1966) reported an inhibitory effect of moonlight on the nocturnal activity of *P. duorarum*, while Minello et al. (1987) showed that increased turbidity was associated with decreased burying of *P. aztecus*. Tidal rhythms in the direction in which *P. duorarum* swims have been shown by Hughes (1972), while Wickham (1967), Hindley (1975), Subrahmanyan (1976) and Natarajan (1989a, b) found evidence of behavioural responses of several penaeids to day-night and tidal cycles in the laboratory. Prawns became more active as water level or pressure was increased. At constant water levels, prawns showed endogenous tidal cycles, with increased activity near expected high tide. When combined day-night and tidal cycles were observed, less activity occurred at expected day high tides than at night high tides. Temperature (Aldrich et al. 1968, Reynolds & Casterlin 1979, Hill 1985) and salinity (Hughes 1969, Lakshmi et al. 1976) also influence prawn behaviour and endogenous 24 h feeding rhythms have been found in laboratory conditions by Hughes (1968) and Kutty & Murugapoopathy (1968).

Although the main factors associated with catch variation of juvenile penaeids in the Embley River were identified by Vance & Staples (1992) there was unexplained variation and the patterns of catches in relation to day-night and tidal cycles were not consistent over all sampling periods. This may have been due to environmental variables cycling at different periods (e.g. times of tidal peaks occurred at different times of the day for each sampling period) or modification of cycles by less predictable variables (e.g. day-night effects may have been modified by water turbidity, cloud cover or moonlight). Therefore, the present study examines the responses of juvenile *Penaeus esculentus*, *P. merguiensis* and *Metapenaeus endeavouri* to simulated day-night and tidal cycles imposed separately and simultaneously in controlled laboratory experiments. The relationships between activity responses and the different habitat types used by the 3 species and the effects on field catchability are discussed.

METHODS

Artificial tide regime. Several studies have shown that penaeid prawns exhibit endogenous tidal cycles without being able to identify the physical factor or factors that entrain the rhythm in the field (e.g. Subrahmanyan 1976). Natarajan (1989b) found that tidal rhythms could be synchronized with artificial cycles of salinity, temperature and water movements and with field variation in hydrostatic pressure but the quickest entrainment occurred with pressure cycles. Staples & Vance (1979) found that the strong tidal catchability cycle of juvenile *Penaeus merguiensis* in an estuary was not noticeably influenced by temperature or salinity and was maintained during the wet season when water was flowing downstream for several weeks, i.e. catches were dependent on tide height rather than current direction. In this study, therefore, cycles of hydrostatic pressure were used to represent the tidal cycle.

In the natural environment used by the prawns in this study, the tidal regime is complex. The tidal period averages 12.4 h but because of local hydrological and environmental variations, the time between tidal peaks is not the same from day to day. Furthermore, tide heights vary substantially from semi-diurnal tides of approximately equal range on the neaps to semi-diurnal tides of widely differing ranges or only a diurnal tide on the springs. Because of the large variation in day to day response patterns for individuals and between individuals seen in preliminary experiments and to reduce the complexity of combinations of day-night and tidal cycle stages, I used a constant 12 h tidal cycle so that the tidal cycle remained in phase with the day-night cycle for each experiment. I also maintained a constant tidal range for all experiments. Systems devised by Graham et al. (1987) and Reid et al. (1989) have enabled much more flexible control of variation in tidal period and tide ranges throughout an experiment and their approach would be valuable for measuring more subtle interactions between tidal and day-night cycles.

Experimental prawns. Juvenile *Penaeus esculentus* were collected from Moreton Bay, southern Queensland, and *P. merguiensis* and *Metapenaeus endeavouri* from the Embley River, northern Queensland, using small beam trawls. They were held in a 1000 l outdoor holding tank at the Cleveland Marine Laboratories under a natural day-night cycle in a constant depth of water (40 cm). Seawater was pumped from about 1 km offshore into a 120 000 l storage tank before circulation to the prawn holding tank to prevent tidal and day-night cycles of salinity and temperature in the water used in experiments. The prawns were held for up to 3 mo prior to experiments and were between 6.0 and 9.9 mm carapace length (CL) when used in most experiments. To assess the effect of prawn size on the behavioural response, a series of experiments were done with *P. esculentus* of small (4.0 to 5.9 mm CL), medium (6.0 to 9.9 mm CL) and large (10.0 to 12.9 mm CL) sizes. Each prawn was used only once in the series of experiments.

Experimental apparatus and procedure. Prawn activity was monitored individually, using activity chambers and an electronic infrared light system (Fig. 1a). Each activity chamber consisted of a circular channel

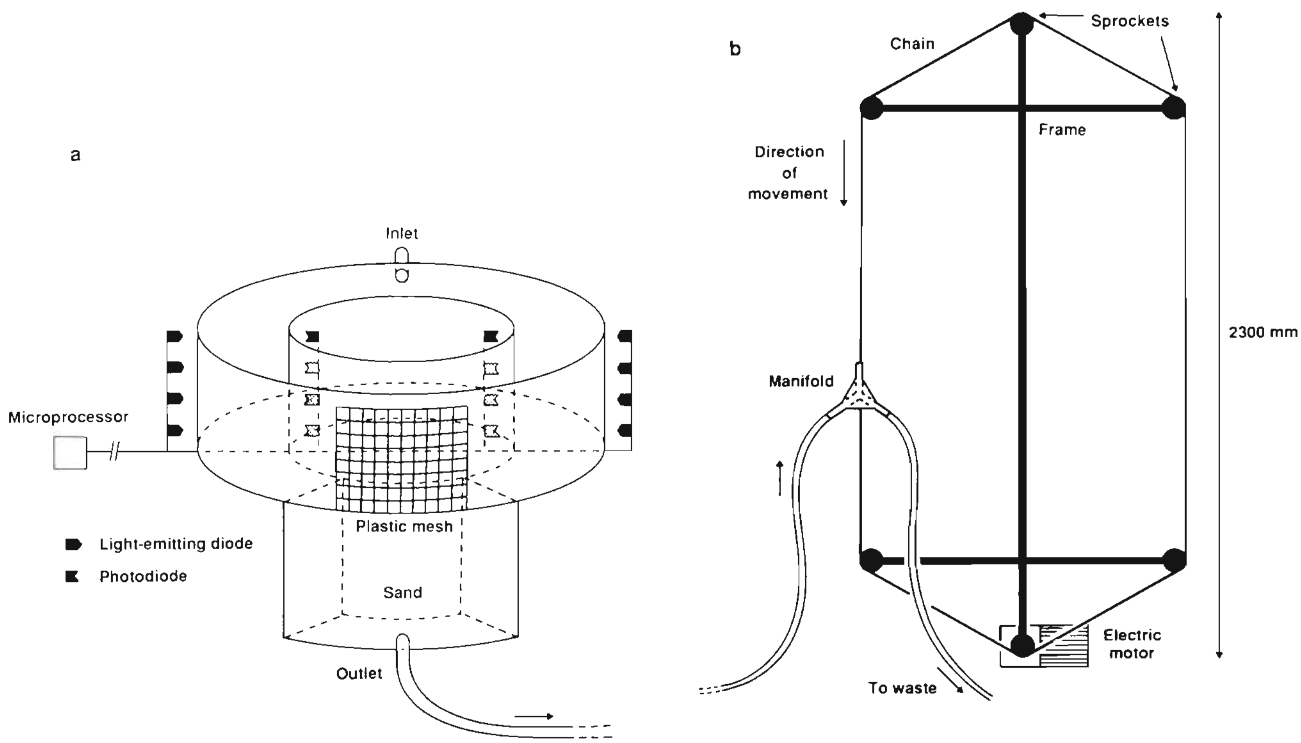

Fig. 1. Schematic diagram of (a) one prawn activity chamber, and (b) apparatus used to create the pressure cycle

constructed from 2 perspex cylinders placed one inside the other such that the diameter of the outer wall of the chamber was 120 mm, the width was 25 mm and the depth was 30 mm. The chamber had a fixed base and a removable water-tight and pressurized lid. Racek (1959) and Moller & Jones (1975) found that the rhythmic activity patterns of prawns were influenced by the presence or absence of substrate. Juvenile *Penaeus esculentus* and *Metapenaeus endeavouri* are mostly caught in habitats where some vertical structure (seagrass) is abundant (Staples et al. 1985). A segment of the chamber was therefore provided with a marine-sand-filled compartment and plastic mesh to allow the prawns to bury or cling to a vertical structure when they were inactive. Water flowed continuously into the chamber through an inlet near the top and exited diagonally opposite near the bottom of the sand compartment.

The apparatus used to create the pressure cycle was a variation of the tide models which create a sinusoidal change in water level by attaching the end of the outlet pipe from an experimental chamber to an arm rotating in a vertical plane (e.g. Underwood 1972). In this study, the water outflow from all chambers passed through ca 5 m of high-pressure tubing to a manifold which was open to the atmosphere and then overflowed to waste. The manifold was fixed to a drive chain, and an electric motor, working through 3 reduction gearboxes, drove the chain around a vertical frame, taking 12 h for 1 revolution (Fig. 1b). This created a cycle of height variation which was similar to the tidal height variation seen in the field. The difference in height between the top and bottom of the frame (2300 mm) represented the experimental tidal range; spring tide ranges in the areas from which the prawns were collected can reach 2500 mm while a typical neap tide range is about 1000 mm.

The basic activity recording unit was an array of 4 infrared light-emitting diodes (LEDs) and 4 corresponding photodiodes. The 4 LEDs were placed in a vertical line outside the circular channel and the 4 photodiodes in a parallel line on the inside of the channel so that a prawn moving through the array at any depth interrupted at least one of the beams of infrared light. Each activity chamber was fitted with 2 arrays on opposite sides of the circular chamber (Fig. 1a) and a prawn movement across either array was registered by a microprocessor. The microprocessor accumulated activity counts from up to 5 separate chambers continuously and output the individual totals to a printer at predetermined intervals (usually 30 min).

Prawns of each species were tested under 4 experimental regimes (Table 1). Each factor was tested with the other held constant (Regimes 1 and 2). To assess the effects of interactions of the 2 factors on prawn activity, 2 combinations of the factors were tested, with

Table 1. Experimental regimes used to assess activity responses of juvenile *Penaeus esculentus* (PE), *P. merguiensis* (PM) and *Metapenaeus endeavouri* (ME) to day-night and tidal cycles

Regime	Light on	Light off	Low tide	High tide	Species tested
1	Constant dark		09:00/21:00 h	03:00/15:00 h	PE, PM, ME
2	06:00 h	18:00 h	Constant low tide		PE, PM, ME
3	06:00 h	18:00 h	09:00/21:00 h	03:00/15:00 h	PE, PM, ME
4	06:00 h	18:00 h	03:00/15:00 h	09:00/21:00 h	PE, PM, ME
5	Constant light		09:00/21:00 h	03:00/15:00 h	PE
6	Constant light		03:00/15:00 h	09:00/21:00 h	PE

the tide cycle advanced by 6 h in one case (Regimes 3 and 4). In addition, *Penaeus esculentus* was tested under another 2 experimental regimes in which prawns were held under constant light (Regimes 5 and 6). Between 7 and 18 prawns were used and between 28 and 88 24 h activity periods were recorded for each experimental regime.

No attempt was made to synchronize the timing of the laboratory tidal cycle with the timing of tides in the field at time of capture. Lighting was provided by 2 white 40 W fluorescent tubes that were switched on and off by a timer. Light intensity when the lights were on was ca 1.8 µE m^{-2} s^{-1}. Temperature in the prawn chambers was maintained between 28 and 30 °C. Salinity varied from 30 to 37 ppt over all experiments and in any one experiment salinity varied by less than 2 ppt. This variation was a result of rainfall runoff, and was not synchronized with the natural tidal cycle.

In all experiments prawns were placed in individual acclimation chambers (similar in size to the activity chambers but without the electronics) 6 to 7 d before being placed into the activity chambers. The appropriate day-night and tidal regime was maintained in both the acclimation and test chambers. Activity was then recorded for 5 to 7 d in most cases. Prawns were fed at 12:00 h each day through an inlet line with a pressure lock to maintain the pressure cycle in the chambers. Hughes (1968) and Kutty & Murugapoopathy (1968) found that, by feeding *Penaeus duorarum* and *P. semisulcatus*, respectively, at the same time each day, 24 h activity rhythms could sometimes be induced with increased activity at the time of feeding. By feeding at 12:00 h each day in this study I hoped that any induced feeding rhythm would be identified as such and the activity resulting from feeding would be, to a certain extent, separate from activity changes due to day-night and tidal cycles. The chambers were not opened during an experiment but were inspected at least once a day to assess the health of the prawns and functioning of the apparatus. During constant-dark experiments a red-filtered torch was used for the short daily checks.

Analyses of activity. For all experiments, activity counts were summed over 1 h periods. Initial inspection and analysis of the results for individual prawns showed large variation between individuals and for individuals from day to day. Activity was, therefore, standardized across individuals by expressing each prawn's hourly activity as a proportion of the maximum hourly activity measured for that prawn over the 24 h period. The proportional data were then transformed using the arcsine of the square root of each proportion (Snedecor & Cochran 1978). Because several individuals were measured simultaneously (up to 5 per experimental run) a further mean was calculated for all individuals for each experimental run and these means were used in further analyses. Hourly mean activity counts were analysed with the General Linear Models procedure of the SAS statistical package (SAS Institute Inc. 1988). One-way analysis of covariance was used with day-night as the class variable and tide height as the continuous variable, and a more complex 2-way analysis of covariance used day-night and experimental regime as the class variables. Other continuous variables used in the 2-way analysis were: a day-night switch variable (which took the value −1 for the first 4 h of light, +1 for the first 4 h of dark and 0 for all other times); tide lagged by 1 h; and the previous hour's activity count.

The significance of the day-night cycle was more rigorously tested by calculating a single mean activity for each day and night period for each individual and then calculating a further mean value for each experimental run. The experimental run means were used in an analysis of variance with day-night as the class variable.

Figures of activity patterns were drawn using untransformed data. Activity was standardized across individuals by expressing each prawn's hourly activity as a percentage of the maximum hourly activity measured for that prawn over the 24 h period. Means of the hourly percent activities of all prawns and combined for all days for each experimental regime were then used for the figures but because several individuals were measured simultaneously (up to 5 per experimental run) the number of experimental runs was used as the sample size for calculating standard errors.

RESULTS

Penaeus esculentus

In all experiments where hydrostatic pressure was varied, medium-sized *Penaeus esculentus* became more active around high tide (when hydrostatic pressure was highest), with peaks 1 to 2 h after high tide (Figs. 2a, c, d & 3a, b). The lowest activity periods were around or just after the times when pressure was lowest ('low tide'). When prawns were exposed to a day-night cycle (Fig. 2b, c, d), either with or without a tidal cycle, they were more active during the dark periods.

Under constant dark conditions and with a simulated tidal cycle imposed (Fig. 2a), peaks of approximately equal height were observed just after each high tide. Activity then decreased quickly, was lowest around or just after low tide, and increased more gradually as the tide rose. Prawns held under constant light also showed activity peaks of approximately equal height just after high tide, irrespective of the time of high tide (Fig. 3a, b). However the levels of maximum activity were lower under constant light conditions (about 100 counts h^{-1}) than constant dark (about 240 counts h^{-1}).

In the absence of a tidal cycle (constant low tide; Fig. 2b) overall activity levels were higher at night than during the day. Activity was lowest in the first 4 h after the lights were switched on, increased throughout the rest of the day and then increased sharply after dark. Peak activity was in the second hour after dark and decreased gradually throughout the night.

When tidal and day-night cycles were imposed simultaneously with high tide at 03:00 and 15:00 h (Fig. 2c) activity again peaked just after high tide, but the night peak was higher than the day peak. Similarly when the tidal cycle was shifted by 6 h relative to the day-night cycle so that high tide was at 09:00 and 21:00 h (Fig. 2d) the night high-tide activity peak was nearly twice the day peak. However, when high tide occurred early in the night period the high-tide activity level was almost twice that when high tide occurred late in the night period.

In some experiments activity increased around 12:00 h, which may be associated with the introduction of food to the chambers (Figs. 2b, c & 3a). Prawns were often seen to arouse from an apparently resting state and begin feeding within 5 min of food being added. A small increase in activity 1 to 2 h before the lights were switched on is also apparent in some experiments (Fig. 2b, d).

Rhythms of prawn activity were clearly influenced by both day-night and tide cycles (Fig. 2). A simple analysis of variance using only day-night and using a single estimate for day and night activity for each experimental run was carried out on data from the first 4 experimental regimes. Day-night was highly significant and explained 35.8 % of the variation in activity (Table 2a). In an analysis of covariance using hourly

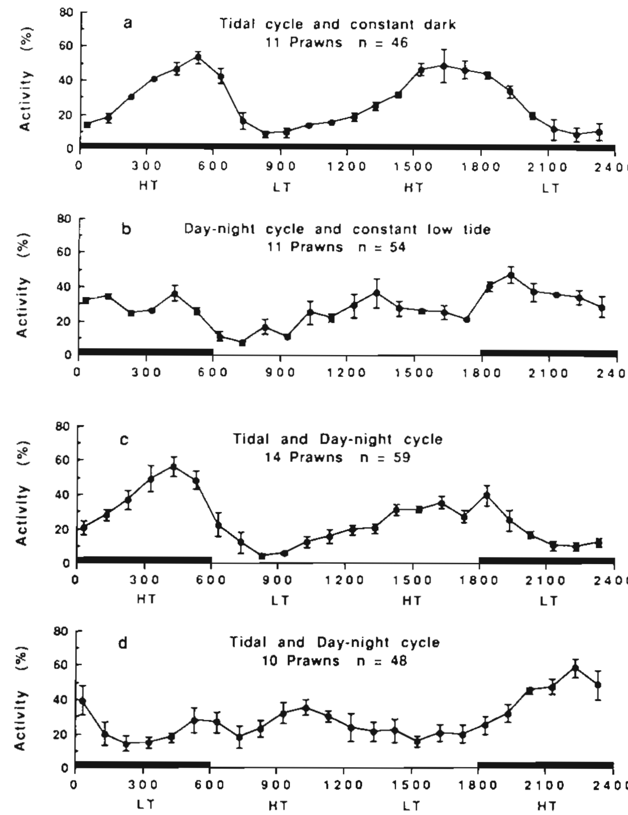

Fig. 2. *Penaeus esculentus*. Mean percent activity (see 'Methods') of medium-sized prawns (6.0 to 9.9 mm CL) throughout a 24 h period for (a to d) Regimes 1 to 4 (Table 1). Vertical bars: standard errors; horizontal bars: hours of darkness; HT: high tide; LT: low tide; n: no. of 24 h records

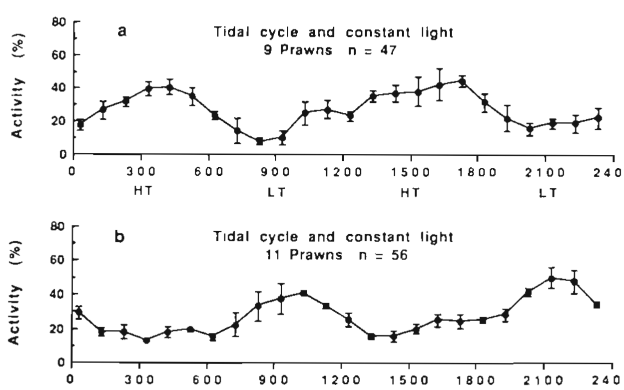

Fig. 3. *Penaeus esculentus*. As in Fig. 2 but (a) Regime 5 and (b) Regime 6

Table 2. *Penaeus esculentus*. Analysis of covariance of arcsine-transformed activity counts of juveniles with (a) day-night, (b) day-night and tide height, and (c) day-night, day-night switch, tide height lagged by 1 h, previous hour's activity and experimental regime. df: degrees of freedom; SS: sums of squares; % variation: percentage of the total activity variation explained by each variable

	Source of variation	df	SS	*F*-ratio	% Variation
(a)	Day-night	1	0.073	17.90***	35.8
	Error	32	0.131		
(b)	Day-night	1	1.019	46.45***	10.4
	Tide height	1	1.976	90.07***	20.1
	Day-night × Tide height	1	0.062	2.82	0.6
	Error	308	6.756		
(c)	Day-night	1	1.019	98.00***	10.4
	Day-night switch	1	0.435	41.82***	4.4
	Tide height lagged	1	2.625	252.46***	26.7
	Previous activity	1	2.069	199.01***	21.1
	Experimental regime	3	0.505	16.18***	5.1
	Error	304	3.161		

***$p < 0.001$

estimates of activity and using day-night and tide height, light accounted for 10.4 % of the hourly variation in activity, while tide height explained 20.1 % (Table 2b). There was no significant interaction between tide and light.

Further statistical analysis was undertaken to look at factors more subtle than simply tide height and day-night levels. The importance of the switch between day and night phases, the rising compared to the falling stage of the tide, and a lagged response to tide height were tested by analysis of covariance. Day-night, a day-night switch variable, tide with a high-tide lag of 1 h, the previous hour's activity and the experiment number were all highly significant ($p < 0.001$) in a model that explained 67.7 % of the variation in activity (Table 2c).

Size effects. The effect of prawn size was assessed with a single experimental regime incorporating a day-night and tidal cycle with high tides at 03:00 and 15:00 h. All the size groups seemed to react to the day-night and tide cycles in a similar way, but the relative strength of the reactions was different for each group (Fig. 4). The response to day-night was very strong in the small prawns, while tide seemed to be less important; the peak of activity near the day high tide was almost negligible. With increasing size, the day-night effect decreased and the tidal response became more pronounced. In the largest prawns a day-night response was only noticeable in the slight increase in activity just after lights off and the trough in activity just after lights on. The highest activity was late in the day around high tide.

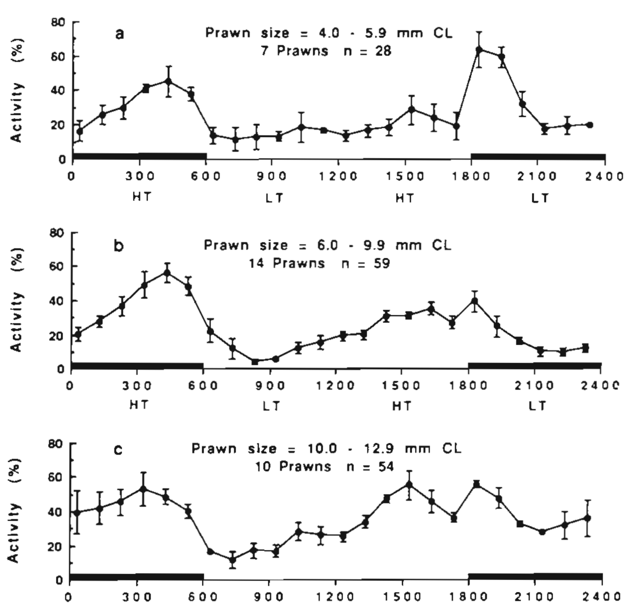

Fig. 4. *Penaeus esculentus*. Mean percent activity (see 'Methods') of 3 size groups of prawns throughout a 24 h period for Regime 3 (Table 1). Symbols and abbreviations as in Fig. 2

Penaeus merguiensis

In all experiments where tide height was varied, activity was mostly high around or just after high tide (Fig. 5a, c, d). When a day-night cycle was imposed, either with or without a tidal cycle, prawns were more active at night (Fig. 5b, c, d). Under constant dark and with a tidal cycle imposed, activity

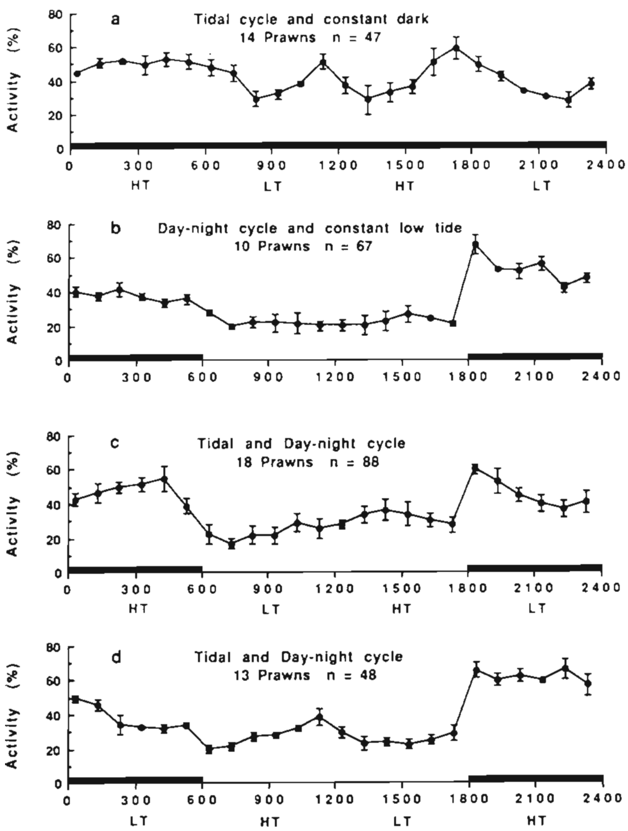

Fig. 5. As in Fig. 2 but for *Penaeus merguiensis*

was high just after high tide and lowest near low tide, although there was also a peak just before 12:00 h (Fig. 5a). With no tidal cycle (constant low tide; Fig. 5b) activity increased sharply after dark, remained high for 4 h, and then decreased gradually throughout the night. Activity remained low throughout the day.

When tidal and day-night cycles were imposed simultaneously, activity again increased sharply when the lights were switched off (Fig. 5c, d). When high tide occurred at 03:00 and 15:00 h, activity peaked just after or just before high tide but the night peak was higher than the day peak (Fig. 5c). When high tide was at 09:00 and 21:00 h, the night activity peak was twice the day peak.

In general, *Penaeus merguiensis* seemed to be more active than *P. esculentus*: the peaks of activity were no higher but the lowest activity levels were not as low in most experiments except when the tide height was constant (Fig. 2b). As with *P. esculentus*, there is a suggestion of a feeding activity peak just before 12:00 h in some experiments (Fig. 5a, d) and a pre-dawn increase in activity (Fig. 5b, d).

An analysis of variance using day-night alone was highly significant and explained 70.0 % of the variation in activity (Table 3a). In an analysis of covariance using tide and day-night as variables and using hourly estimates of activity, 42.5 % of the activity variation was explained by day-night and 7.3 % by tide (Table 3b). Further analysis of covariance with a more complex model using the same variables as for *Penaeus esculentus* explained 67.9 % of the variation in activity (Table 3c).

Metapenaeus endeavouri

When subjected to a tidal cycle under constant dark *Metapenaeus endeavouri* showed peaks of activity around and just after high tide (Fig. 6a). The activity peak associated with the 15:00 h high tide is slightly later than the 03:00 h high-tide peak and also extends for longer. When prawns were kept at constant low tide (Fig. 6b), almost no activity occurred during the

Table 3. As in Table 2 but for *Penaeus merguiensis*

	Source of variation	df	SS	*F*-ratio	% Variation
(a)	Day-night	1	0.296	46.58***	70.0
	Error	20	0.127		
(b)	Day-night	1	3.667	281.02***	42.5
	Tide height	1	0.627	48.03***	7.3
	Day-night × Tide height	1	0.001	0.05	0.0
	Error	332	4.332		
(c)	Day-night	1	3.667	434.83***	42.5
	Day-night switch	1	0.540	64.08***	6.3
	Tide height lagged	1	0.674	79.94***	7.8
	Previous activity	1	0.959	113.72***	11.1
	Experimental regime	3	0.020	0.79	0.2
	Error	328	2.766		

***$p < 0.001$

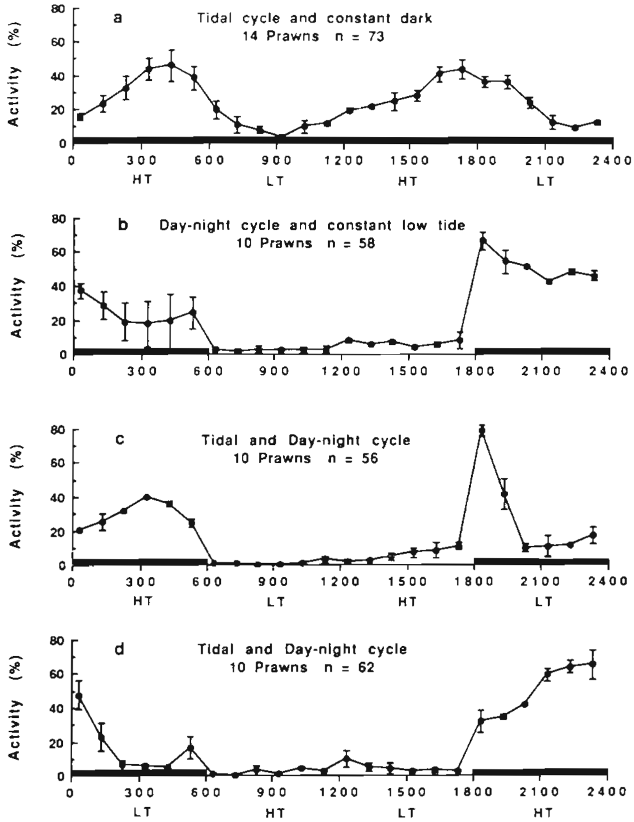

Fig. 6. As in Fig. 2 but for *Metapenaeus endeavouri*

day; most prawns were buried in the substrate. Activity increased immediately after dark, remained high until just before midnight and then gradually declined through the rest of the night, dropping to zero immediately after lights on.

When day-night and tide cycles were imposed together, virtually no activity occurred during daylight hours. However the night activity was modified substantially by the tide height, with activity dropping to zero around low tide (Fig. 6c, d). The slight rise in activity at 12:00 h in all experiments was associated with the time of feeding, and in some experiments there is a pre-dawn increase in activity (Fig. 6b, d).

Metapenaeus endeavouri responded to day-night and tide in a similar manner to the other species, but the strength of the day-night effect far outweighed the tidal effect when both cycles were imposed. Day-night alone in an analysis of variance explained 94.3 % of the variation in activity (Table 4a). When day-night and tide were considered in the analysis using hourly estimates of activity, 44.2 % of activity variation was explained by day-night and only 4.8 % by tide height (Table 4b). There was also a small but significant interaction between day-night and tide due to the almost complete lack of activity of *M. endeavouri* during the day high tide compared to the night high tide. (This interaction was not significant for *Penaeus esculentus* or *P. merguiensis*.) Although day-night was the strongest influence on activity, in the experiment where tide height alone was varied, tide height explained 46 % of the variation in activity ($p < 0.001$; Fig. 6a). A more complex analysis of covariance model explained 80.6 % of the total activity variation (Table 4c).

Comparison of activity levels

Comparison of activity levels between experiments and between species must be treated with caution as

Table 4. As in Table 2 but for *Metapenaeus endeavouri*

	Source of variation	df	SS	*F*-ratio	% Variation
(a)	Day-night	1	0.504	164.97***	94.3
	Error	10	0.031		
(b)	Day-night	1	5.853	193.10***	44.2
	Tide height	1	0.638	21.05***	4.8
	Day-night × Tide height	1	0.325	10.71***	2.5
	Error	212	6.426		
(c)	Day-night	1	5.853	468.04***	44.2
	Day-night switch	1	0.935	74.73***	7.1
	Tide height lagged	1	1.208	96.56***	9.1
	Day-night × Tide lagged	1	0.485	38.80***	3.7
	Previous activity	1	1.609	128.67***	12.2
	Experimental regime	3	0.563	15.02***	4.3
	Error	207	2.589		

***$p < 0.001$

Table 5. *Penaeus esculentus*, *P. merguiensis* and *Metapenaeus endeavouri*. Mean and maximum activity levels (counts h^{-1}) for each experimental regime. SE: standard error; Max: maximum

Experimental regime	*P. esculentus*		*P. merguiensis*		*M. endeavouri*	
	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE	Max
1. Constant dark High tide: 03:00/15:00 h	117.7 ± 4.5	240	151.8 ± 3.8	220	80.6 ± 3.8	182
2. Day-night cycle Constant low tide	67.1 ± 2.8	149	68.0 ± 2.3	147	77.7 ± 4.3	204
3. Day-night cycle High tide: 03:00/15:00 h	53.9 ± 2.0	122	111.9 ± 3.0	202	39.1 ± 2.7	206
4. Day-night cycle High tide: 09:00/21:00 h	85.9 ± 3.5	211	134.1 ± 3.7	253	54.6 ± 3.7	242
5. Constant light High tide: 03:00/15:00 h	34.4 ± 1.7	62	–		–	
6. Constant light High tide: 09:00/21:00 h	49.0 ± 1.8	97	–		–	

the experiments were carried out over several years and the prawns were collected from different locations and times of the year. Nevertheless some trends are apparent.

For experimental Regimes 1, 3 and 4, *Penaeus merguiensis* had the highest mean activity level and *Metapenaeus endeavouri* the lowest (Table 5). The ranking of these means is driven largely by the activity levels of each species in periods when activity is low; the highest activity level recorded for each species is very similar (240 to 253 counts h^{-1}). *M. endeavouri* activity levels are zero when in an inactive mode, the lowest activity levels of *P. esculentus* are slightly higher, and the lowest activity levels of *P. merguiensis* are relatively high. For every species, the highest mean activity level occurred under conditions of constant dark (Table 5). All species also registered a very high peak of activity when high tide was at 21:00 h (Regime 4); high tide and the first period of the night seemed to have an additive effect on activity levels (Figs. 2d, 5d & 6d).

DISCUSSION

Day-night activity

The results of this study have shown that when exposed to the artificial day-night cycle only, all 3 species of prawns were more active at night. *Metapenaeus endeavouri* was most clearly affected: virtually no activity occurred during the day. *Penaeus merguiensis* was less strongly affected: low levels of activity occurred during the day, while the activity of *P. esculentus* varied least between day and night. Furthermore, peak activity of all species was in the first half of the night period: for *P. esculentus*, activity was greatest in the second hour after dark, whereas for *P. merguiensis* and *M. endeavouri*, activity remained high for 4 and 7 h after dark, respectively, before decreasing. The activity levels of *P. esculentus* and *M. endeavouri* remained at their lowest levels for the first 4 and 6 h of daylight, respectively, and then increased throughout the remainder of the day. *P. merguiensis* showed no consistent change in activity levels during the day. These results are consistent with reports of many other researchers who have shown that prawns are more active at night (e.g. Hindley 1975, Moller & Jones 1975, Reynolds & Casterlin 1979).

Tidal activity

When a tidal cycle was imposed under constant 24 h light, the activity of all species increased as the tide height increased, with the prawns being most active 2 to 3 h after high tide. The lowest activity levels were within an hour of the time of low tide. Several other studies have recorded endogenous tidal rhythms of activity of penaeid prawns, with peaks near the time of expected high tide (e.g. Subrahmanyan 1976, Natarajan 1989a). Wickham (1967) found that juvenile *Penaeus duorarum* in the laboratory became more active when the water level was raised, but Hindley (1975) found no similar change with juvenile *P. merguiensis*. However, his pressure changes were sudden and did not simulate the gradual changes of a tidal cycle.

Day-night and tidal activity

Although Wickham (1967), Hindley (1975), Subrahmanyan (1976) and Natarajan (1989a, b) have observed interactions between day-night cycles and endogenous tidal rhythms, no studies have recorded the activity responses of penaeids to simulated day-night and tidal cycles together and therefore the relative importance of each factor in influencing behaviour patterns. In the present study, when tide and day-night cycles were superimposed, both factors clearly contributed to the overall activity patterns observed. In all species, highest activity levels were at night and peaks occurred either in the first 2 h of the night period or in the 2 to 3 h after high tide at night. For all species, activity was highest when high tide was in the first half of the night period. However, the relative strengths of the responses to tide and day-night were different for each species. The day-night cycle was the dominant influence on *Metapenaeus endeavouri*: virtually no activity occurred during the day regardless of the tide height. *Penaeus merguiensis* and *P. esculentus* were less influenced by the day-night cycle and were active during the day as well as night; however, the difference in activity between daytime high and low tides was greater for *P. esculentus* than for *P. merguiensis*.

These experiments were not designed to assess endogenous cycles of activity; the acclimation period was expected to remove the affects of any endogenous activity rhythms associated with the prawns' previous environment. However, it appears that in some experiments the prawns' behaviour was influenced by an endogenous rhythm associated with the day-night cycle. For example, for *Penaeus esculentus* (Fig. 2a) and for *Metapenaeus endeavouri (*Fig. 6a), under conditions of constant dark, the late afternoon peak of activity just after high tide was extended, compared to the early morning peak, and activity remained high for the first 2 h of expected night time. Also in all the experiments where activity was seen to be relatively low in the last half of the night, a small rise in activity was seen at 04:00 to 05:00 h, before the decrease in activity associated with the onset of daylight. This suggests that the prawns were anticipating the end of the night period. However, there was no sign of a pre-dusk rise in activity, which has been reported by Reynolds & Casterlin (1979) for juvenile *P. duorarum*.

Comparisons with field catchability

Vance & Staples (1992) have discussed in detail the significance of these results in relation to trawl catches of the 3 species in the field. All 3 species were more catchable at night and the relative catchabilities with respect to day-night were very similar to the laboratory changes in activity. *Metapenaeus endeavouri* were virtually only caught at night whereas *Penaeus esculentus* and *P. merguiensis* were also caught during the day. It was suggested that prawns are more catchable at night because they are less able to detect and therefore avoid the net, and in the case of *P. esculentus* and *M. endeavouri*, they have emerged from the substrate. Catches of all species were lowest at high tide. *P. merguiensis* were least catchable because they entered the mangrove forests at high tide where trawling was not possible. *P. esculentus* and *M. endeavouri* may have been able to avoid the net when they were more active near high tide but also may have been swimming in the water column above the path of the net. As the water level dropped, all species became more concentrated in the water column and possibly tended to settle to the bottom as their activity decreased; their catchability by the beam trawl increased. *P. esculentus* and *M. endeavouri* remain on the seagrass flats at low tide and bury in the substrate and catches are therefore very low at this time (CSIRO Division of Fisheries, unpubl. data). *P. merguiensis*, however, do not bury at low tide but follow the water level down on each tide cycle. They are concentrated close to the water's edge and are, therefore, more catchable to a beam trawl at this time.

Comparisons of activity levels

The lowest activity levels of *Penaeus merguiensis* under all laboratory conditions were considerably higher than the lowest levels for *P. esculentus* or *Metapenaeus endeavouri*; this is probably related to the habitat utilized by each species. *P. merguiensis* inhabits mangrove-lined small creeks and rivers with steeply sloping mud banks and moves large distances during a tidal cycle as the water level changes (Vance et al. 1990). Towards low tide they aggregate in the very shallow turbid water close to the river edge, which presumably affords them protection from predation. Because the tidal currents in this habitat are often strong, some activity is probably required to maintain position close to the water's edge. In contrast, *P. esculentus* and *M. endeavouri* mainly inhabit wide seagrass flats (Staples et al. 1985) where the tidal currents are not as strong and where they can avoid or reduce predation by burying in the substrate or by remaining motionless amongst or on the seagrass. Therefore the lowest activity levels for these 2 species would be virtually zero.

Effect of size

The variation in response to day-night and tide with size of *Penaeus esculentus* is difficult to interpret. Because only 1 combination of day-night and tide was tested, the results were not as definite as for the comparisons among species. However, it appears that the day-night cycle was most important in determining the small prawns' activity while the tidal cycle was more important for the larger prawns. It is unlikely that the change is related to immigration or settlement behaviour as the smallest prawns tested would have been settled on the seagrass beds for about 2 wk when collected.

The difference may be related to feeding behaviour of the prawns. A recent study on the diet of juvenile *Penaeus esculentus* (C. J. O'Brien pers. comm.) showed that postlarval and small juvenile prawns mainly ate diatoms and filamentous algae but as the prawns increased in size they used less vegetation and more live animal matter in their diet. The larger prawns, therefore, probably have to forage over a far greater area to find the diverse food items which comprise their diet. The intertidal nature of the seagrass beds would make it extremely difficult for larger prawns to forage at low tide whereas smaller prawns could still be active in the 2 to 5 cm deep pools which are left at low tide. The reason is still uncertain and more detailed studies on the feeding behaviour, area of foraging and use of the seagrass itself are needed.

Activity patterns and habitat

The activity patterns of juvenile prawns resident in an estuarine environment are probably influenced by 2 main factors: the need to have regular access to food sources and to gain protection from predators. Although the 3 species studied in these experiments usually utilize 2 distinct habitat types, the use of each habitat is similar in relation to the tidal cycle. The seagrass beds used by *Penaeus esculentus* and *Metapenaeus endeavouri* are often exposed at low tide, when the prawns are almost certainly buried in the substrate: they are not found in deeper water adjacent to the seagrass at low tide. It is, therefore, often only possible for the prawns to forage for food on the higher tide levels. Wading birds, which are significant predators of shrimp on seagrass beds in other areas (e.g. Howard & Lowe 1984) and on penaeid prawns in estuaries (Mukherjee 1971), fish in shallow water. Therefore it would be advantageous to the prawns to feed near high tide and avoid predation either by burying in the substrate or hiding amongst the seagrass near low tide. Also on spring low tides, when the seagrass is exposed, the prawns would bury to avoid desiccation. Similarly, for *P. merguiensis*, the mangrove forests in which juvenile *P. merguiensis* feed are only inundated towards high tide (T. J. Wassenberg & B. J. Hill, CSIRO Division of Fisheries, unpubl. data). Less feeding appears to take place near low tide, when the prawns tend to aggregate in the very shallow turbid water close to the banks rather than burying in the substrate.

All 3 species of prawns are eaten by several species of fish in the Embley River (Salini et al. 1990). Although some of the fish feed at night, many feed primarily in the day and so decreased prawn activity during the day would probably decrease the chances of predation by fish and birds. *Penaeus esculentus* was least affected by the day-night cycle but its colouration (brown and green bands and patches) would help it to merge with the seagrass. This colouration and close association with seagrass may give *P. esculentus* more protection from predation during the day than the other species.

Studies on several other penaeid species from Australia (Racek 1959), North America (e.g. Fuss & Ogren 1966, Hughes 1968, Reynolds & Casterlin 1979), India (Kutty & Murugapoopathy 1968, Natarajan 1989a) and Venezuela (Gamba & Rodriguez 1987) have all shown that penaeids are most active at night. A few studies have also shown that penaeids were more active under increased water pressure or showed endogenous cycles of increased activity near the times of expected high tide. In one of the few studies to consider both tidal and day-night cycles, Subrahmanyan (1976) suggested that an endogenous day-night rhythm was a stronger influence on the overall activity pattern of *Penaeus duorarum* than was an endogenous tidal rhythm. This result is similar to what we observed for *Metapenaeus endeavouri*. Juvenile *P. duorarum* are found in similar vegetated habitat, have similar patterns of colouring and probably utilize the habitat in a similar way.

All the penaeid species examined in this and other studies have been shown to respond similarly to tidal and day-night cycles: in general, they are more active near high tide when food sources would be accessible to them, and also more active at night when the risk of predation is less. For the species in the present study, the adaptive significance of these similar responses is clear although the habitats utilized by the prawns are different.

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