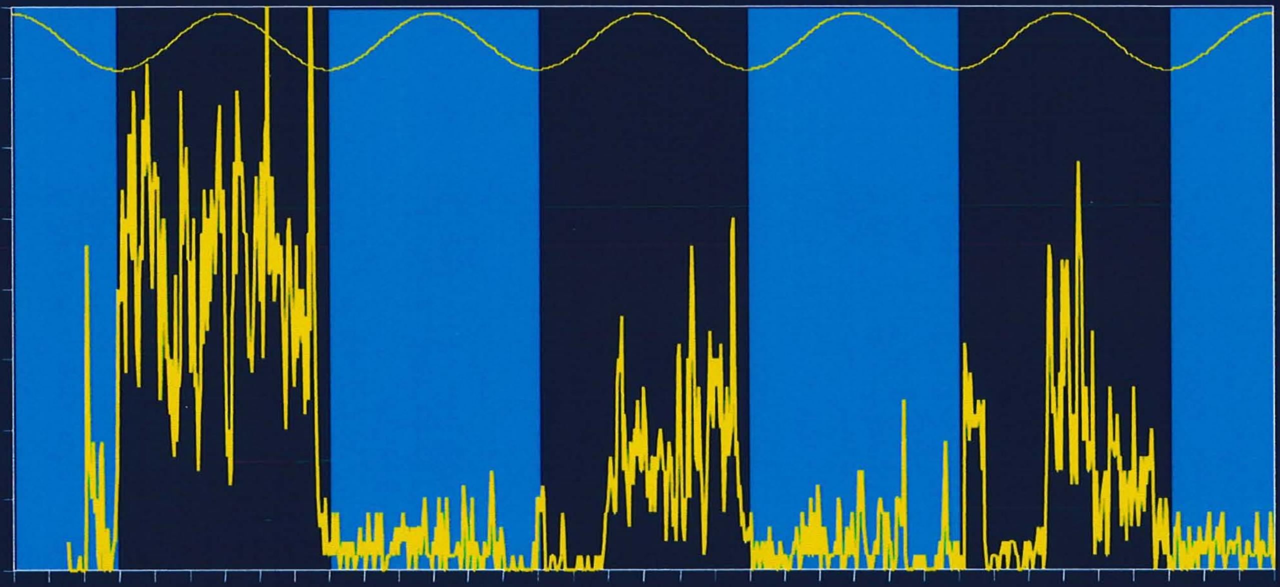
The definition of effective spawning stocks of commercial tiger prawns in the Northern Prawn Fishery and king prawns in the eastern king prawn fishery – behaviour of postlarval prawns



Mr D. J. Vance and Mr R. C. Pendrey

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97/108 **The definition of effective spawning stocks of commercial tiger prawns in the Northern Prawn Fishery and king prawns in the eastern king prawn fishery – behaviour of postlarval prawns**

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OBJECTIVES:

1. Measure the critical vertical migration behaviour of postlarval tiger and king prawns that determines their inshore advection patterns.

2. Incorporate this behaviour into hydrodynamic models to accurately estimate the effective spawning stocks of tiger and king prawns.

1. NON TECHNICAL SUMMARY

OUTCOMES ACHIEVED:

The project has contributed to the ecologically sustainable management of the Northern Prawn Fishery (NPF) by providing information on the likely distribution of effective spawning stocks. The specific outputs are:

1. Improved understanding of the response of postlarval penaeid prawns to tidal cycles and day-night cycles at different water depths.
2. A more accurate definition of the likely size and location of effective spawning areas for penaeid prawns in the NPF.

To effectively manage most fisheries, including penaeid prawn fisheries in northern and eastern Australia, it is important to know the relationship between the size of the spawning population and the number of young adults that recruit to a fishery in the next generation. In the tiger prawn fishery in the Gulf of Carpentaria, it has been assumed for management purposes that the total adult population at a particular time is the effective spawning stock, i.e. all spawners contribute to the next generation's stock. This is not necessarily correct and is particularly unlikely for many species of penaeid prawns, whose larvae and postlarvae have to migrate from offshore spawning areas to coastal and estuarine nursery areas. The area that contains spawners that actually contribute offspring to subsequent adult populations has been termed the “effective spawning area”.

Hydrodynamic modelling of water currents in the south-eastern Gulf of Carpentaria has shown that most of the banana prawn larvae (*Penaeus merguiensis*) produced during the autumn fishing season (when adult banana prawns are most abundant) are lost to the population due to unfavourable currents. The hydrodynamic model has also been used to estimate the size of the effective spawning areas for tiger prawns in the Gulf. Recent research has emphasised the importance of the vertical migration behaviour of the postlarvae themselves in enabling the postlarvae to be advected towards the coastal nursery areas. In particular, if postlarvae cue their behaviour to the tidal cycle, i.e. they move up into the water column on flood tides and settle on the seabed during ebb tides, they will be advected more quickly to the coastal areas than if they do not respond to the tides. We know that postlarvae of some penaeid prawn species are cued to flood tides when they are in relatively shallow estuarine waters (< 5 m) but not in deeper offshore waters (> 20 m).

The depth at which postlarvae start to cue to flood tides (the "transition depth") has a major impact on the estimates of effective spawning area calculated by the hydrodynamic model. For example, if the depth at which postlarvae become tidally cued is reduced from 20 to 7 m then effective spawning areas in different regions of the Gulf of Carpentaria decline by between 20 and 60%.

The main aim of our project was to investigate the vertical migration behaviour of postlarval penaeid prawns that enables them to recruit from offshore spawning areas to the coastal nursery areas. We used two strategies to achieve this aim: field sampling in estuaries in southern and northern Queensland and laboratory experiments.

Field sampling

The aim of the field sampling was to determine at what stage of the tidal and day-night cycles postlarvae in inshore waters are most active in the water column. We sampled for four 24-hour periods in the Nerang River, Southport and six 24-hour periods in the Embley River, Weipa in 1998 and 1999. During each sampling period, we trawled once every hour with a 1-mm mesh plankton net at the surface and with a beam trawl with three separate vertical compartments on and just above the seabed. At Southport we made good catches of the eastern king prawn, *Penaeus plebejus* and at Weipa we obtained data for two species of tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, and for the banana prawn, *P. merguiensis*.

The overall pattern of catches was very similar for all the species. The largest catches of postlarvae at the estuary surface were usually made on flood tides at night. Much smaller catches were made at the surface on flood tides during the day and very few postlarvae were caught there on ebb tides. Patterns of catches of postlarvae in the beam trawls near the seabed were less clear and less consistent between species. The response to both tide and day-night was strongest for the eastern king prawn. The results showed clearly that both tide and day-night cycles affect the vertical migration behaviour of penaeid postlarvae when they are in relatively shallow inshore waters.

Laboratory experiments

The aim of the laboratory experiments was to determine at what water depth postlarvae of the tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, begin to recognise and respond to simulated tidal cycles. We developed computer-controlled apparatus that allowed us to use pressure changes to simulate a sinusoidal tidal cycle with a period of 12 hours and a range of 2 metres. This tidal cycle was superimposed on simulated water depths of 4, 8, 12 and 16 m - again mediated by pressure changes. A day-night cycle of 12-hour days and 12-hour nights was maintained during the tidal experiments. We designed and built a small flow-through activity chamber that allowed us to run experiments for up to 4 days so that the response of postlarvae to a sequence of several tidal cycles could be tested. The activity of the postlarvae was recorded onto videotape using an infrared-sensitive video camera.

We were able to carry out and analyse a total of 64 experiments on postlarvae of the brown tiger prawn, *P. esculentus*, and 17 experiments on postlarvae of the grooved tiger prawn, *P. semisulcatus*. For all species and sizes of postlarvae and all water depths tested, the day-night cycle had a substantial effect on postlarval activity; postlarvae were always more active at night.

We were not able to collect enough data on the smallest sizes of postlarvae to analyse statistically, but medium-sized brown tiger postlarvae clearly responded to the tidal cycle when the water depth was set to 4 m. However, they did not respond to the tide when the water depth was 8 m or greater. Large postlarvae responded to the tidal cycle at 4 and 8 m but not at 12 or 16 m. Large grooved tiger postlarvae also responded to the tidal cycle at 4 and 8 m but not at 12 or 16 m.

We carried out further short-term experiments on a larger size range of brown tiger postlarvae to more clearly understand their response to water depth. The activity of the postlarvae was monitored while water depth was increased linearly from 3 to 7 m over 1 hour, held at constant water depth for 2 hours, and then decreased linearly from 7 to 3 m over 1 hour. We found that small postlarvae did not change their activity levels in response to the depth changes at all. However, medium and large postlarvae were significantly more active when the depth was decreasing and just after the pressure had decreased.

Conclusions

Our results suggest that medium-sized tiger prawn postlarvae would start to detect tidal cycles at water depths somewhere between 4 and 8 m and small postlarvae probably do not recognise the tides at all. The effective spawning areas for tiger prawns in the Gulf of Carpentaria are therefore probably quite small compared to the total area fished commercially and are mostly inshore of the commercial fishing grounds. Based on the hydrodynamic model of larval and postlarval advection, it was estimated that only about 2% of the commercial tiger prawn catch in October (when spawning levels in the fishery were highest) was taken in the effective spawning area if the transition depth was 7 m. Field sampling for adult tiger prawns is needed to confirm that adequate numbers of spawning tiger prawns occur in these relatively shallow inshore waters at the appropriate time of year to constitute an effective spawning stock.

KEYWORDS: **Effective spawning, prawns, postlarvae, behaviour, vertical migration.**

2. BACKGROUND

A knowledge of the relationship between the size of the spawning population and the number of young adults that recruit to a fishery in the next generation is important for the effective management of most fisheries. Most stock-recruitment relationships (SRRs) assume that the total adult population or the total adult population at a particular time is the effective spawning stock, i.e. all spawners contribute to the next generation's stock. This is not necessarily correct. For example, CSIRO modelling work in the south-eastern Gulf of Carpentaria has shown that most of the larvae produced during the autumn fishing season (when adult banana prawns are most abundant) are lost to the population. This is because spawning occurs too far offshore, and the currents are unfavourable for transporting the larvae and postlarvae to estuarine nursery areas.

If larvae and postlarvae from only one small area of the adult fishing grounds will become next year's recruits to the fishery, it would be meaningless to use total adult stocks to detect effects of fishing pressure on the spawning stock. We need to understand the behaviour patterns of larvae and postlarvae that determine their movement into the nursery areas, so that we can clearly identify the critical spawning areas in fisheries. This will allow us to improve strategies for protecting these spawning stocks and to determine whether annual variations in recruitment are due to variations in the size of the spawning stock.

Northern Prawn Fishery

The Northern Prawn Fishery is Australia's second most valuable fishery, generating about $100 - $200 million annually in exports and over half of this value is from tiger prawns. Tiger prawn catches in the fishery declined during the 1980s and, following advice from CSIRO on the probability that excessive fishing effort was reducing the spawning stock to critical levels, management measures were implemented. These measures included reducing fishing effort by about 30%. Given some evidence of a stock-recruitment relationship for tiger prawns, management adopted a conservative approach and limited fishing effort directed at adult tiger prawns in order to maintain recruitment to the fishery. Since this strategy was adopted, catches of tiger prawns have stopped declining but have not recovered to the levels predicted from the somewhat ill-defined SRR. It is likely that one of the reasons is that estimates of spawning indices are not accurate because they assumed that all spawning tiger prawns contribute to recruitment of juveniles and to the next year’s catch.

CSIRO subsequently carried out a six-year study of tiger prawn recruitment in Albatross Bay and confirmed that there is not a good relationship between total adult spawning stock and subsequent recruitment. This led to more specialized approaches to defining the effective spawning stock. One of these was the development of a hydrodynamic model of Albatross Bay to estimate how much of the adult prawn population produces postlarvae that recruit to the nursery grounds (FRDC 95/14, tiger prawn stock recruitment, Rothlisberg et al. 1996). Prawn larvae and postlarvae rely on tidal and wind-driven currents to reach inshore nursery areas. We also know that the vertical migration behaviour of the larvae and postlarvae is critical for determining the direction and distance they are moved. It is only while the animals are off the bottom that they are moved any distance by the ocean currents.

In offshore waters the vertical migration behaviour of many penaeid postlarvae is influenced by day-night cycles (moving off the bottom only at night) (Rothlisberg 1982). However, previous studies have shown that by the time postlarvae of some species have reached the nursery grounds their behaviour has changed and they are influenced by tidal cycles (moving off the bottom only on flood tides) (Staples and Vance 1985). This change in postlarval behaviour has not yet been shown for tiger prawns. Also, we don't know exactly when the change in behaviour occurs for any prawn species, although it is likely that it is associated with a particular water depth (the “transition depth” - Rothlisberg et al. 1995, Condie et al. 1999). In most areas of the Gulf of Carpentaria, variation in this parameter has a substantial impact on the effective spawning area calculated by the model. For example, at Groote Eylandt, if the depth at which postlarvae change from being day/night cued to tidally cued is decreased from 20 to 7 m then the effective spawning area is confined to relatively inshore areas and decreases from about 8500 to 3600 km^2 (Condie et al. 1999) (Figure 2.1, 2.2). It is clearly critical for the accuracy of predictions of the extent of the effective spawning population, that we know exactly when postlarvae switch from a day-night influence to a tidal influence.

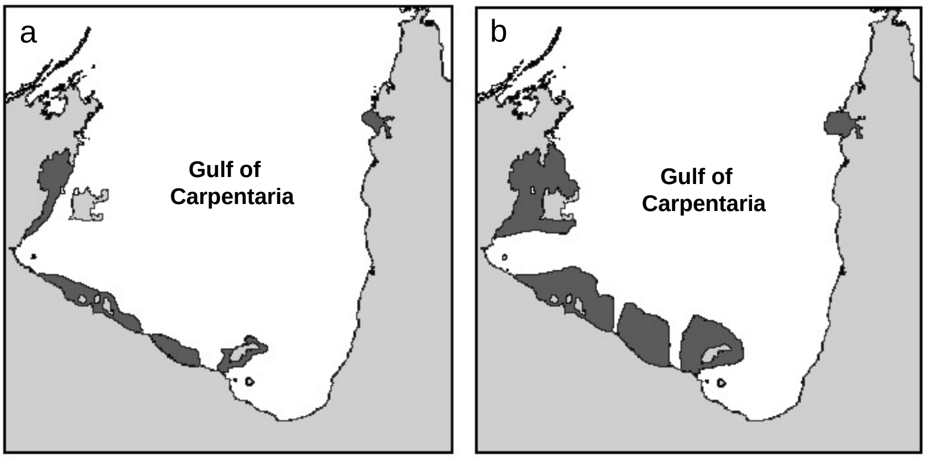

Figure 2.1. Gulf of Carpentaria showing the effective spawning areas (dark shading) based on the hydrodynamic model of Condie et al. (1999) for a) transition depth of 7 m, and b) transition depth of 30 m. Re-drawn from Condie et al. (1999).

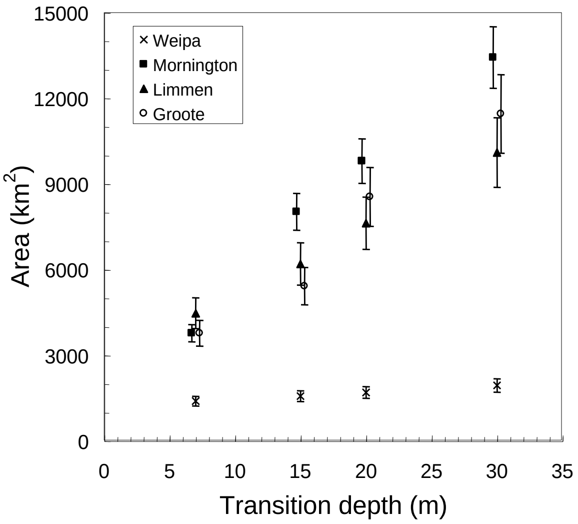

Figure 2.2. Effective spawning area plotted against transition depth for 4 regions of the Gulf of Carpentaria. Re-drawn from Condie et al. (1999).

East Coast King Prawn Fishery
On Australia's east coast, the fishery for eastern king prawns extends from Botany Bay (NSW) to the Swains Reef (Qld) and is worth $30-40 million annually. Catch rates of adult eastern king prawns (Penaeus plebejus) have declined since the 1970s and a recent study has found that catch rates of juvenile prawns are also lower in some nursery areas in Moreton Bay (Masel and Smallwood, 2000). This change is thought to be due to a decline in the size of the effective spawning stock possibly because of excessive fishing effort.

Recently, Rothlisberg et al. (1995) have shown that the vertical migration behaviour of Penaeus plebejus postlarvae is cued by the day-night cycle at water depths of 20 m but changes to being cued by the tidal cycle at the entrance to an estuary. They have also developed a descriptive model to explain the advection of postlarvae into east-coast nursery areas. This model predicts that only those larvae spawned close to the estuary entrances will be likely to recruit to the nursery areas. This would suggest that a large proportion of adult eastern king prawns caught in the offshore fishery do not contribute to the spawning stock. Therefore, fishing sub-adult king prawns in estuaries and adult king prawns in the entrances of these estuaries would have the most impact on spawning stocks, rather than fishing for adult eastern king prawns in offshore waters. Before these results can be used to recommend management measures aimed at protecting eastern king prawn stocks, it is necessary to test some of the assumptions of the model by Rothlisberg et al. (1995), particularly those related to the behaviour and spatial distribution of postlarvae.

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3. NEED

In the Northern Prawn Fishery and the East Coast King Prawn Fishery managers have concerns about declining levels of recruitment to the fishery, and the lack of knowledge of the relationship between spawning stock and recruitment to the fishery. In both fisheries, the increase in effective fishing effort due to the use of GPS plotters and other modern technologies means that measures will inevitably have to be taken to reduce effort in the future. A more accurate definition of the real spawning stock would allow management to more effectively protect spawning stock and maximize catches by ensuring that critical areas were not overfished while allowing fishing in non-critical areas. Clear identification of the critical spawning areas would also allow managers to determine if changes in annual recruitment were due to changes in levels of spawning stocks.

The CSIRO hydrodynamic model of Albatross Bay (and models being developed for the entire Gulf of Carpentaria) have the potential to allow managers to more accurately define the effective spawning stocks for tiger prawns, but are limited by our lack of knowledge of a critical piece of postlarval behaviour: the timing of the change in vertical migration behaviour from being day-night cued to tidally cued.

The research proposed for eastern king prawns is particularly important, not only because it provides information relevant to improving the management of the East Coast King Prawn Fishery, but also because it will allow us to validate the techniques used in obtaining the behavioural data on tiger prawns for the Northern Prawn Fishery (see Methods).

4. OBJECTIVES

1. Measure the critical vertical migration behaviour of postlarval tiger and king prawns that determines their inshore advection patterns.

2. Incorporate this behaviour into hydrodynamic models to accurately estimate the effective spawning stocks of tiger and king prawns.

5. VERTICAL MIGRATION BEHAVIOUR OF POSTLARVAL PENAEID PRAWNS IN TWO AUSTRALIAN ESTUARIES: THE EFFECT OF TIDE AND DAY/NIGHT

5.1 Introduction

To effectively manage most fisheries, it is important to have an accurate knowledge of the relationship between the size of the spawning population and the number of young adults that recruit to a fishery in the next generation. In many fisheries, including the tiger prawn fishery in Australia's Gulf of Carpentaria, it has been assumed for management purposes that the total adult population at a particular time is the effective spawning stock, ie. all spawners contribute to the next generation's stock. This is not necessarily correct and is particularly unlikely for many species of penaeid prawns. Their life cycle requires that the larvae and postlarvae move from offshore spawning areas to coastal and estuarine nursery areas, with associated high mortality rates and variability in survival, before they eventually contribute to subsequent adult populations. The area that contains spawners that actually contribute offspring to subsequent adult populations has been termed the "effective spawning area".

Hydrodynamic modelling in the south-eastern Gulf of Carpentaria has suggested that most of the banana prawn larvae (*Penaeus merguiensis*) produced during the autumn fishing season (when adult banana prawns are most abundant) are lost to the population (Rothlisberg et al. 1983). At this time of year the currents are unfavourable for transporting the larvae and postlarvae to the estuarine nursery areas. More recent research has emphasised the importance of the vertical migration behaviour of the postlarvae in enabling the postlarvae to be advected towards the coastal nursery areas (Rothlisberg et al. 1996; Condie et al. 1999). In particular, if postlarvae cue their behaviour to the tidal cycle, i.e. they move up into the water column on flood tides and settle on the seabed during ebb tides, they will be advected more quickly to the coastal areas than if they do not respond to the tides.

Many species of penaeid postlarvae in several countries respond to tidal cycles when they are entering estuaries (see Dall et al. 1990 for review). Most of the studies found that the postlarvae were in the water column during flood tides but the duration of time in the water column and the influence of the diel cycle on the vertical migration behaviour sometimes varied substantially between species and different studies. For example, in southern Queensland, Australia, Young and Carpenter (1977) sampled 1 m below the water surface and found that more postlarvae of the eastern king prawn, *Penaeus plebejus*, were caught in the first part of the flood tide at night than during the day. However, Rothlisberg et al. (1995) sampled in the same estuary but concluded that highest catches in the surface waters were on the flood tide, irrespective of the time of day or night.

In order to more accurately define the effective spawning areas for penaeid prawns we need to understand the behaviour of penaeid postlarvae that allows them to be advected into the coastal nursery areas. In southern Queensland, there is uncertainty regarding the relative importance of diel and tidal cycles in determining the vertical migration behaviour of *Penaeus plebejus* in estuarine waters. In the Gulf of Carpentaria, there is no information available on the vertical migration behaviour of the postlarvae of tiger prawns *P. semisulcatus* and *P. esculentus*. All the above species contribute to valuable commercial prawn fisheries in Australia. We have therefore sampled throughout a series of 24-hour periods at the mouth of the Nerang River, southern Queensland, and the mouth of the Embley River, northern Queensland to investigate the vertical migration behaviour of the postlarvae. In this paper, we have reported the variation in postlarval catches at four locations in the water column in response to diel and tidal cycles.

5.2 Materials and methods

Locations of sampling

We sampled at two locations; just inside the mouth of the Nerang River at Southport in southeastern Queensland and inside the mouth of the Embley River at Weipa in northern Queensland (Figure 5.1). It was not possible to sample the exact location sampled in earlier studies at Southport (Rothlisberg et al. 1995) because the river entrance has been modified for safety reasons, resulting in changes to topography inside the river mouth. In both locations, sampling was done near the edge of the main channel in water of 4 to 6 m depth. At both locations we sampled as close as possible to each river mouth where the seabed was suitable for operating a small beam trawl. At each location a 100 m trawl site was measured out parallel to the edge of the river and marked with moored buoys at either end. The substrate at Southport was mostly sand whereas at Weipa it was muddy sand.

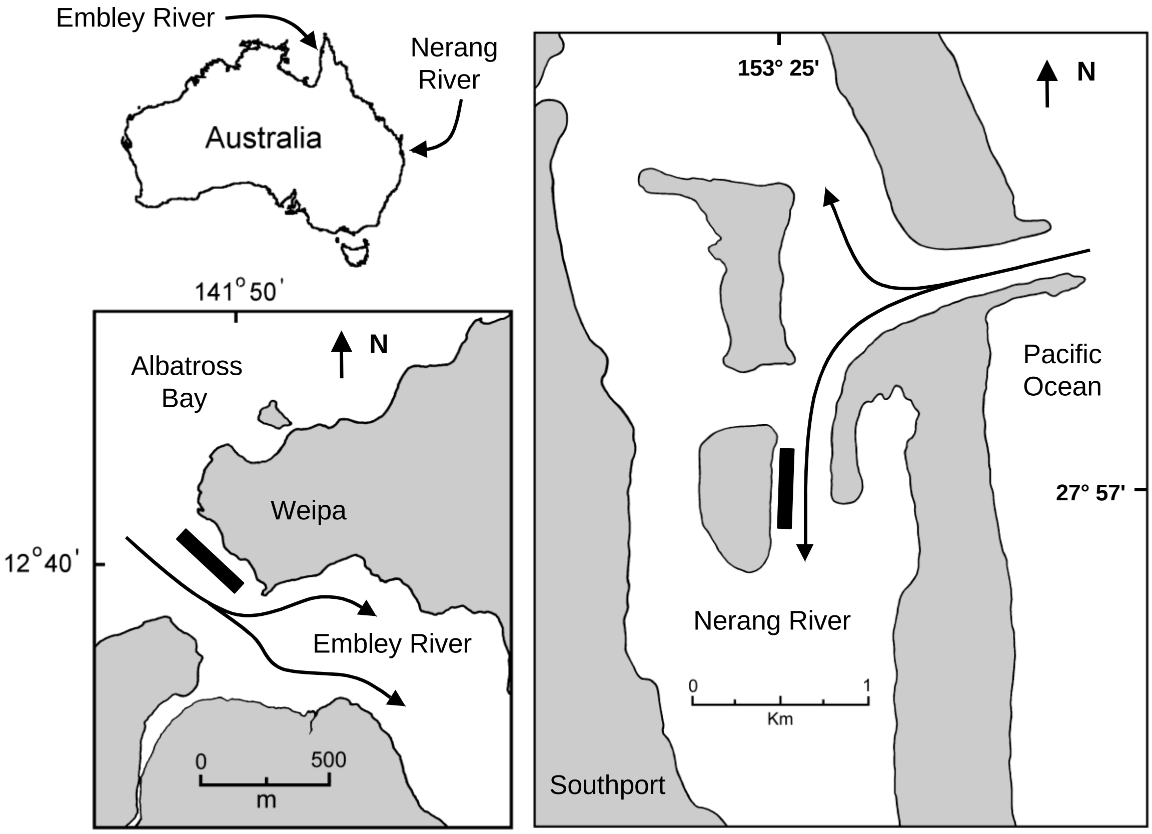

Figure 5.1. Sampling sites (black rectangles) in the Embley River and the Nerang River. The arrows show the direction of the flood tide currents.

Nets

We used a towed plankton net with mouth size of 0.25 by 0.25 m to sample postlarvae near the surface of the water column and a beam trawl to sample postlarvae on and near the seabed. The beam trawl had 3 separate nets fixed to a frame 1.0 m wide and 0.75 m high and was towed along the seabed into the current, along or close to the 100 metre marked site. The beam trawl had a loose chain stretched across the front of the base of the net to disturb postlarvae buried in or clinging to the substrate. The configuration of the nets was such that the bottom net of the beam trawl fished from the seabed to about 24 cm above the seabed. The middle beam trawl net fished from 24 to 48 cm above the substrate and the top beam trawl net fished from 48 to 72 cm above the substrate (Figure 5.2). The mesh size of the nets on the surface and beam trawls was 1 mm. All trawls were made into the current and the water flow through each net was measured individually using flowmeters.

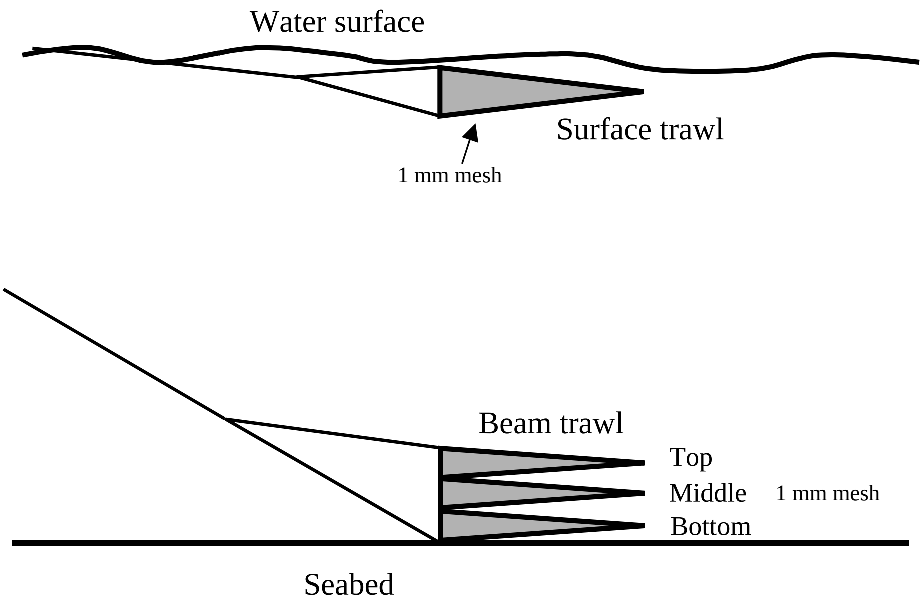

Figure 5.2. Schematic diagram of the four nets used to sample postlarvae

Sampling procedures

During each sampling period, trawling was carried out every hour for 25 hours, from 1200 on the first day through to about 1230 on the following day. The plankton net was towed first for 10 minutes, immediately followed by the beam trawl for 100 m. Samples from Southport were all preserved immediately in 10% Formalin in seawater buffered with Borax. Samples from Weipa needed to be frozen as soon as possible to enable the tiger prawn postlarvae to be identified to species using gel electrophoresis. On the boat they were initially chilled in an ice water slurry and then transferred to a mixture of ice and saturated brine that rapidly froze them. Every hour, we measured surface water temperature and salinity, water depth, and used a secchi disc to estimate light penetration.

In the laboratory, samples were sorted using a binocular microscope and postlarvae of the genus *Penaeus* were identified to species while other penaeids were identified to genus only (Heales et al. 1995). All postlarvae were measured to 0.1 mm carapace length (CL) using an ocular micrometer fitted to the microscope. Tiger prawn postlarvae from Weipa samples were identified to either *Penaeus semisulcatus* or *P. esculentus* using gel electrophoresis (Lavery & Staples 1990).

Timing of sampling

We sampled at Southport on two occasions in 1998 when dusk and dawn both coincided approximately with times of tide change so that each flood tide occurred almost completely during either day or night (Table 1). In 1999 we sampled on another two occasions but selected periods when the flood tides spanned both day and night (i.e. dusk and dawn occurred part way through flood tides).

At Weipa, we sampled on two occasions in 1998 when dusk and dawn both coincided approximately with times of tide change (Table 5.1). In 1999 we sampled on four occasions. On two of these occasions, dusk and dawn both coincided approximately with times of tide change but the night flood tide ranges were much smaller than the day tide ranges. On one of the other periods, dusk and dawn occurred part way through flood tides and on the final period, there was only one flood tide during the 24-hour period and it occurred completely during the day. There was no flood tide at night.

Table 5.1. Tide and day-night details for all the sampling periods at Southport and Weipa.

Location	Date	Flood tide Ranges (m)		Ebb tide Ranges (m)		Comments
Southport	7 May 1998	1.04	0.92	0.91	1.09	Dusk and dawn coincided with times of tide change
	21 May 1998	1.17	1.13	1.00	1.38	Dusk and dawn coincided with times of tide change
	16 Apr 1999	1.72	1.51	1.65	1.56	Dusk and dawn occurred part way through flood tides
	12 Jul 1999	1.84	1.12	1.75	1.21	Dusk and dawn occurred part way through flood tides
Weipa	19 Oct 1998	1.03	0.69	0.94	0.67	Dusk and dawn coincided with times of tide change
	21 Oct 1998	0.92	0.95	1.31	0.47	Dusk and dawn coincided with times of tide change
	10 Sep 1999	1.45	0.71	0.51	1.39	Dusk and dawn coincided with times of tide change
	14 Sep 1999	1.03	0.86	0.85	1.16	Dusk and dawn occurred part way through flood tides
	19 Oct 1999	1.25	1.21	1.21		Only one flood tide in 24 hours – all during the day
	22 Oct 1999	1.16	0.33	0.46	0.97	Dusk and dawn coincided with times of tide change

Analyses

We investigated differences in catches between sampling period and stages of the tide and day/night cycle using ANOVA for each net type separately (GLM procedure of the SAS statistical package) (SAS Institute 1990). For each sample in the analysis, tide was either coded as flood or ebb and day/night was coded as day or night. Because the data were non-normal and there were several zero and near-zero values, the catches were transformed by taking the 4th root of the variable. The four sampling periods at Southport in 1998 and 1999, and the two sampling periods at Weipa in 1998 were treated in two separate analyses. Data from 1999 at Weipa were not used in the analyses because catches were very low.

5.3 Results

Nerang River

Surface net
The most abundant penaeid prawn caught in samples taken at the mouth of the Nerang River was *Penaeus plebejus* and there was always a clear pattern of catch variation throughout each 24-hour period, particularly in the surface net. For example, on 21-22 May 1998, each flood

and ebb tide occurred either completely during the day or night (Figure 5.3). At the surface, almost all postlarvae (> 90%) were caught on the night flood tide. Only 1% of postlarvae were caught on the ebb tide and only 7% of postlarvae were caught on the day flood tide. There was no cloud cover during this sampling period. The moon was towards the end of the last quarter and rose at about 0220 on 22 May, so moonlight had no effect on catches in the first ¾ of the night.

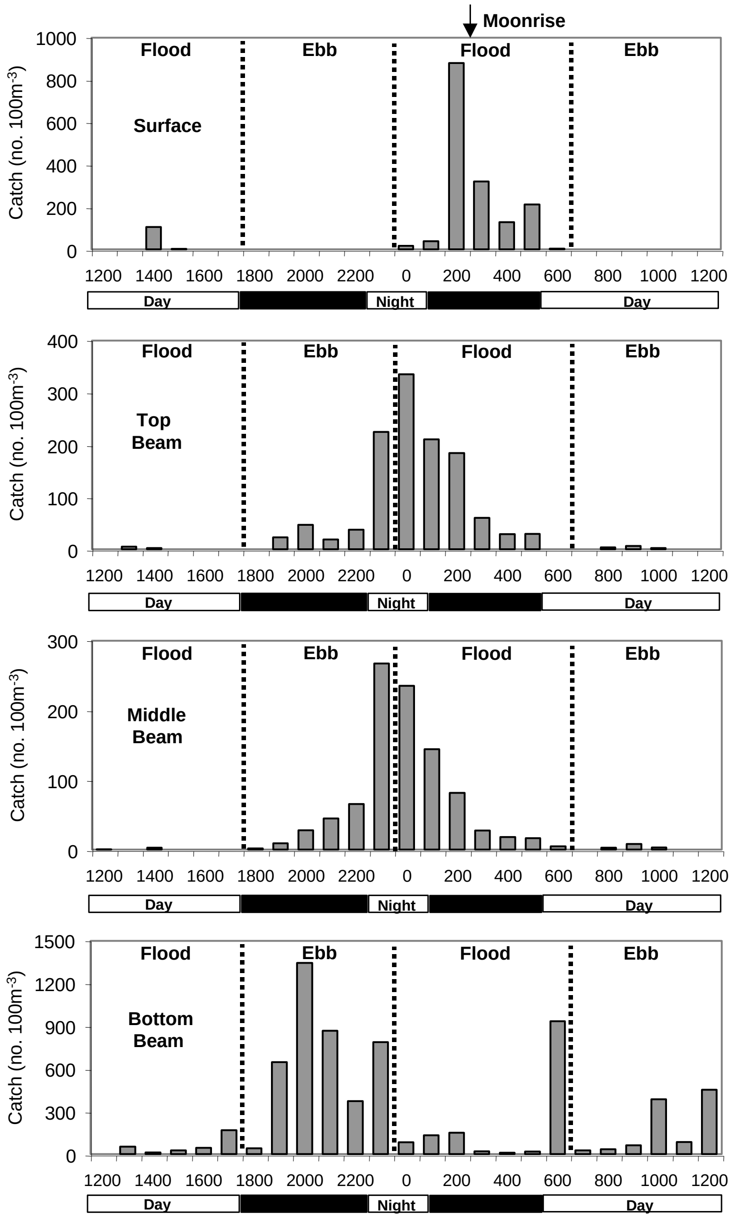

Figure 5.3. Catches of *Penaeus plebejus* postlarvae (< 3.0 mm CL) at the mouth of the Nerang River, Southport throughout 24 hours in four nets on 21-22 May 1998

On 16-17 April 1999, sunset occurred about halfway through one flood tide and sunrise occurred halfway through the next flood tide and, overall, the number of postlarvae caught in all nets was much lower than in May (Figure 5.3, 5.4). However, most of the *P. plebejus* postlarvae caught at the surface (81%) were still caught on flood tides at night (Figure 5.4). Only 14% of the postlarvae were caught on the night ebb tide and most of them were in the first hour of the night ebb tide. No postlarvae were caught at the surface during the day on the first flood tide but postlarvae were caught there within an hour of sunset. Catches at the surface during the second flood tide decreased after sunrise. During this sampling period the cloud cover increased gradually from almost zero when sampling commenced to almost complete, but light, cloud cover at the end of the period. The new moon was not visible at all during the night.

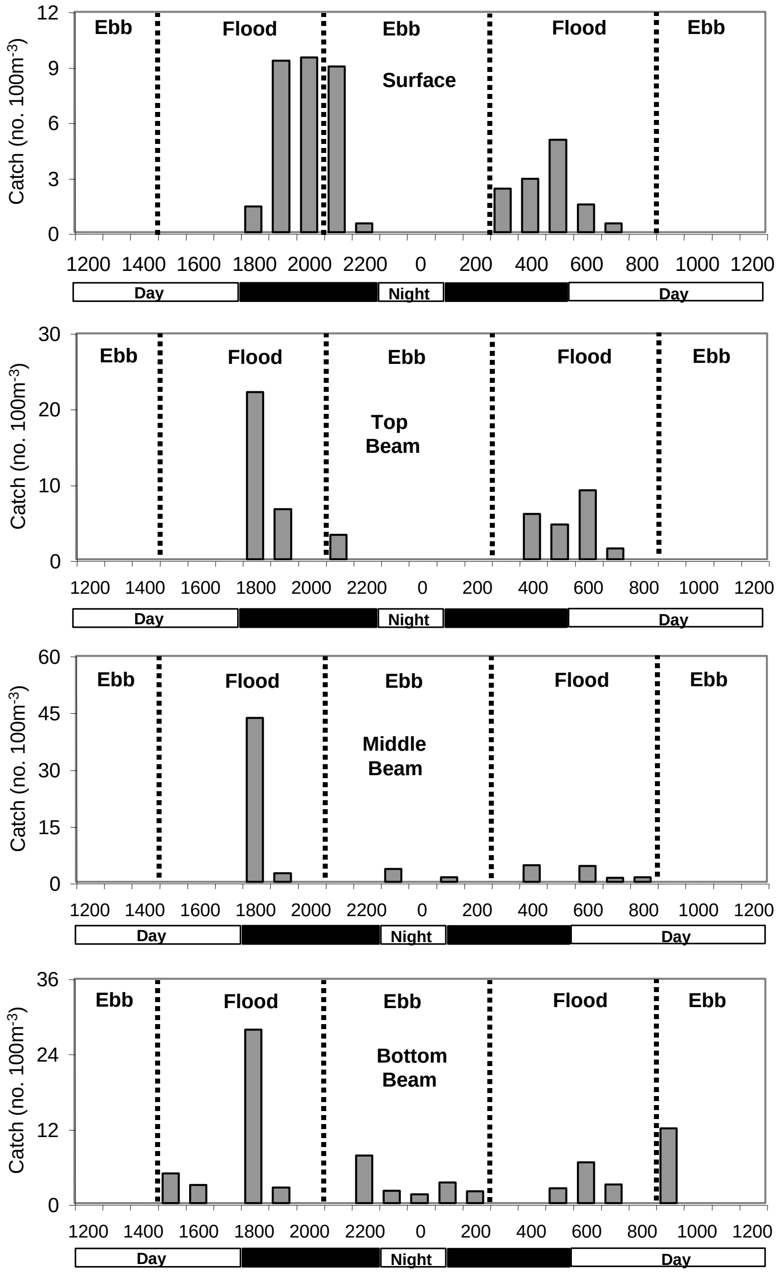

Figure 5.4. Catches of *Penaeus plebejus* postlarvae (< 3.0 mm CL) at the mouth of the Nerang River, Southport throughout 24 hours in four nets on 16-17 April 1999

When we combined the results from all four sampling periods in the Nerang River, by far the majority of postlarvae caught in the surface net were on the flood tide at night (Figure 5.5). Tide was the most significant variable in the ANOVA while day/night was also highly significant (Table 5.2).

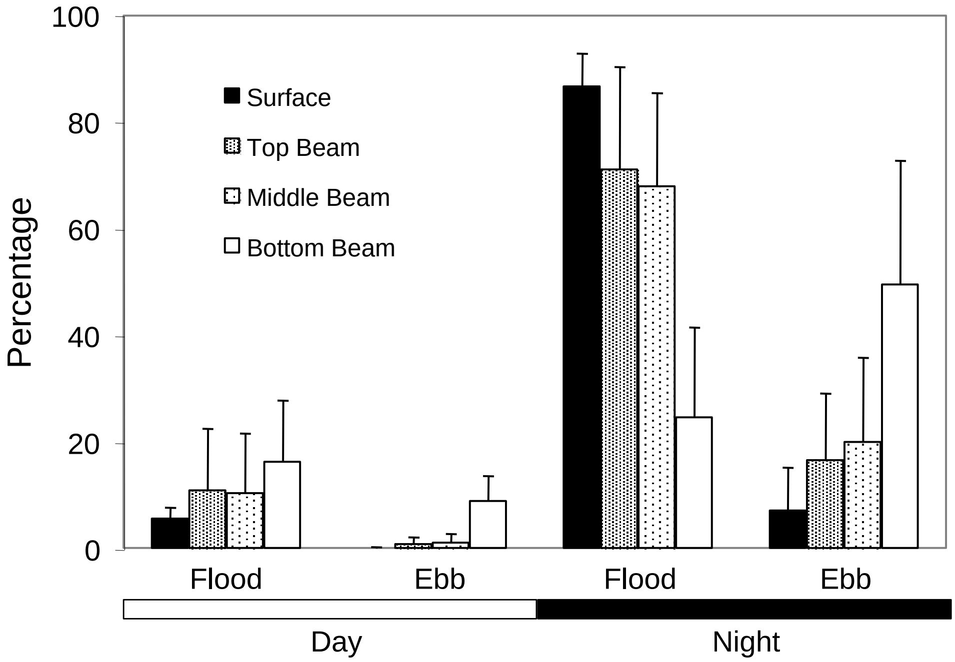

Figure 5.5. Mean percentage catches of *Penaeus plebejus* for four categories of day-night and tide for four nets over four sampling periods in 1998, 1999.

Table 5.2. Significant sources of variation and mean squares of catches of *Penaeus plebejus* for four nets over four sampling periods at the mouth of the Nerang River, Southport. Catches were transformed by taking the 4th root for each sample. df, degrees of freedom ;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

			Beam	
Source of variation (df)	Surface	Top	Middle	Bottom
Period (3)	2.98***	4.46***	3.97***	22.57***
Day/night (1)	8.10***	13.85***	11.40***	9.93***
Tide (1)	10.53***	4.79***	3.49***	2.00*
Period x day/night (3)	0.65*	2.28***	1.67***	0.89
Period x tide (3)	1.19**	0.05	0.44	3.39***
Day/night x tide (1)	3.83***	1.79**	0.28	4.23**
Period x day/night x tide (3)	0.40	0.25	0.06	1.13
Error (83)	0.22	18.99	19.55	44.70

Beam trawls

The pattern of variation in catches in the bottom beam trawl differed markedly from the surface net. On 21-22 May 1998, some postlarvae were caught throughout the 24-hour period, however, the majority of postlarvae (60%) were caught on the ebb tide at night (Figure 5.3). Catches in the middle and top beam trawls were intermediate between the surface and bottom nets. Most of the postlarvae were caught throughout the night, but peak catches in the middle and top beam trawls were taken on the late ebb and early flood tides.

On 16-17 April 1999, catches in the bottom beam trawl were again more spread out over the 24-hour sampling period than in the surface net, although more were caught at night (Figure 5.4). In all beam trawls the highest catches were on the flood tide in the first trawl after sunset.

When all four sampling periods in the Nerang River were combined there was a clear pattern of catches in the four categories of day/night and tide stage (Figure 5.5). For night flood tides, catches in all beam trawls were less than the surface net. However, catches in the beam trawls were highest in the top beam trawl and decreased with increasing depth of net to be lowest in the bottom beam trawl. For night ebb tides catches were highest in the bottom trawl. In contrast to the surface net, day/night was the most significant variable in the ANOVA for all beam trawls (Table 5.2). The mean squares for tides were highly significant in the ANOVA for surface plankton and for the top and middle beam trawls but were less significant for the bottom beam trawl.

Period

There was great variation between catch rates on different sampling periods (Table 5.2). Period was significant in the ANOVA for all nets. For example, the largest catch at the surface during the sampling on 21-22 May 1998 was 880 postlarvae 100 m^{-3} (Figure 5.3), while the largest surface catch on 16-17 April 1999 was only 9.6 postlarvae 100 m^{-3} (Figure 5.4).

Size of postlarvae

The smallest *P. plebejus* postlarvae caught was 0.9 mm CL. The largest prawn caught at the surface was 11.3 mm CL and the largest in the bottom net was 17.5 mm CL. There were a small number of prawns larger than 2.9 mm CL caught at all water depths, but they have not been included in the analyses as they have probably been resident in the estuary for some time. There were some significant differences between the sizes of postlarvae caught in the different nets and between sizes at different levels of day/night and tide. However the differences were not consistent between periods and unlikely to be biologically meaningful. We repeated the ANOVA with respect to day/night and tide for all samples using two size categories; 1.0 – 1.9 mm CL and 2.0 – 2.9 mm CL, but there was no difference in the pattern of results for the two size categories.

Embley River 1998

Several species of penaeid prawn postlarvae were caught in samples taken at the mouth of the Embley River. However, only two tiger prawns (*P. semisulcatus* and *P. esculentus*) and the banana prawn (*P. merguiensis*) were caught in sufficient numbers to analyse in detail. The most abundant species caught in two 24-hour sampling series in 1998 was *P. semisulcatus* (mean catch rate over all samples was 16.6 postlarvae 100m^{-3}). *P. merguiensis* and *P. esculentus* were caught at lower rates (4.9 and 3.9 postlarvae 100 m^{-3} respectively).

Surface net

The general pattern of catches throughout each 24-hour period in 1998 was similar for each species (Figure 5.6, 5.7, 5.8). Over the two 24-hour periods in 1998, more than half the total catches of postlarvae in the surface trawl were on the night flood tides, ranging from 64% for *P. esculentus* to 53% for *P. merguiensis* (Figure 5.9). Between 22% (*P. semisulcatus* and *P. esculentus*) and 26% (*P. merguiensis*) of surface trawl catches were taken on the night ebb tides. In contrast to *P. plebejus*, day/night was the most significant variable in the ANOVA of surface trawl catches for all three species at Weipa but tide was also highly significant (Table 5.3, 5.4, 5.5).

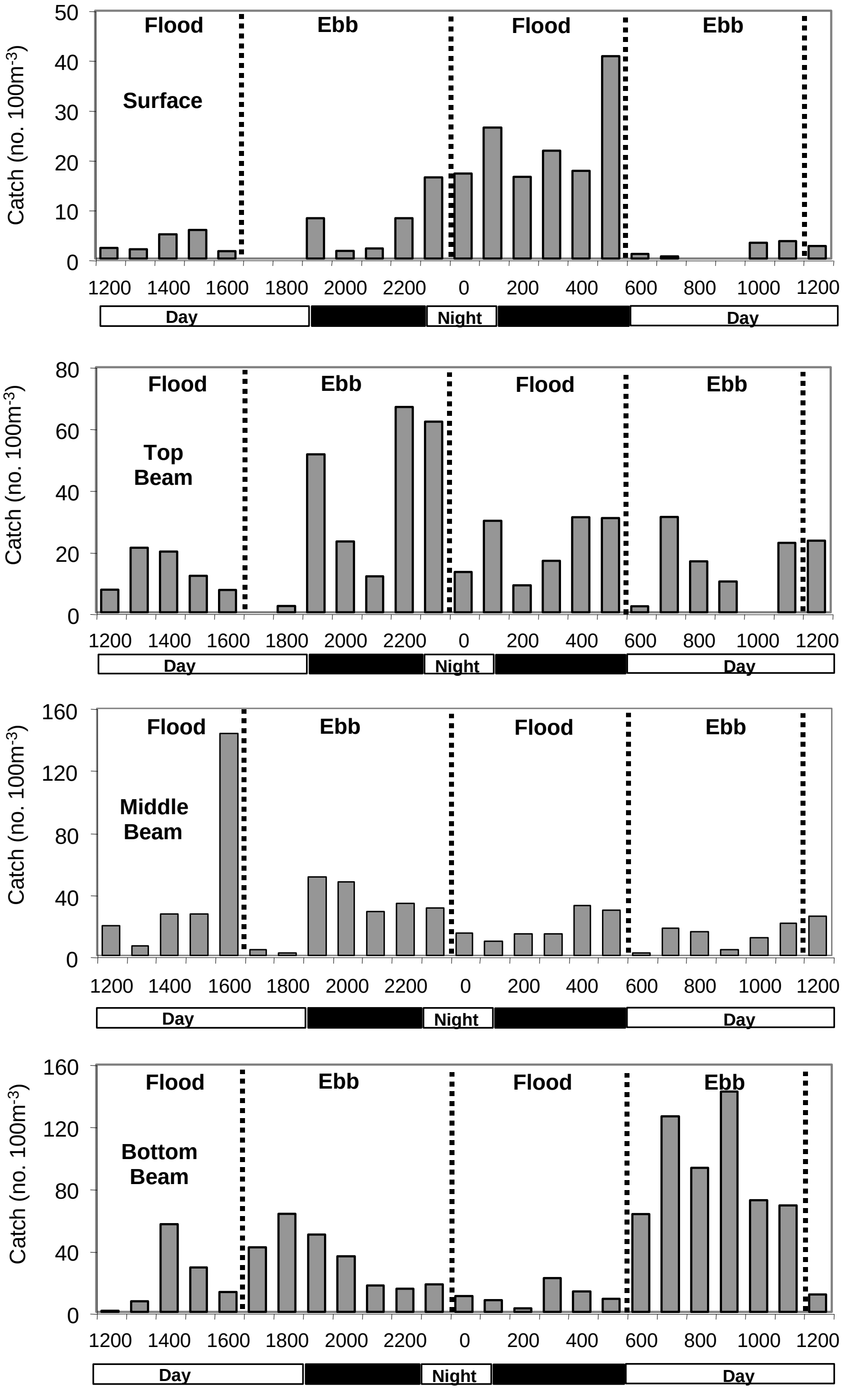

Figure 5.6. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 19-20 October 1998

Beam trawls

The highest catches in the bottom trawl were on the ebb tides for all species; on day ebb tides for *P. semisulcatus* (44%) and *P. esculentus* (51%) and on the night ebb tide for *P. merguiensis* (44%). Tide stage was significantly associated with catches of all species in the bottom trawl but day/night was much less strongly related (Table 5.3, 5.4, 5.5).

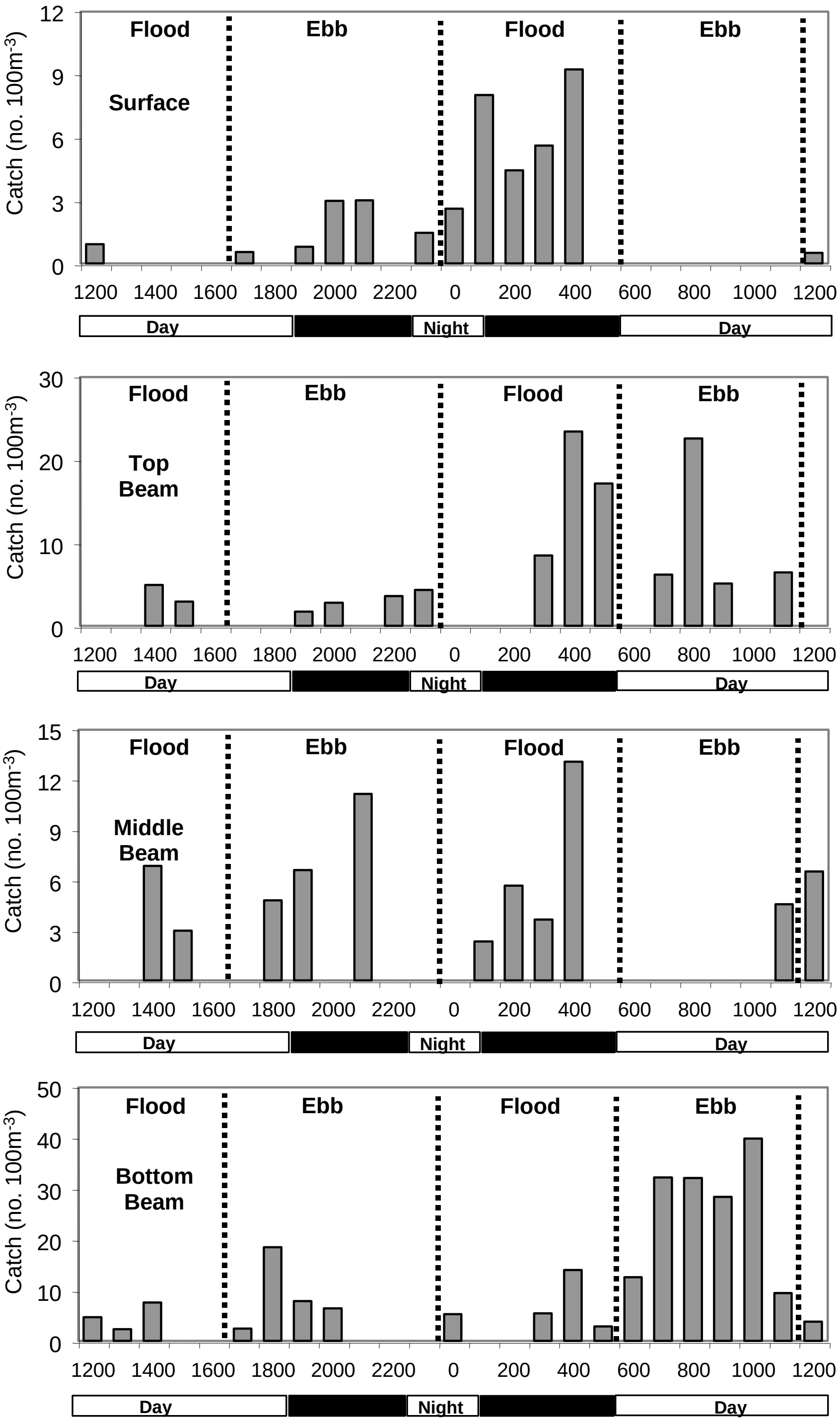

Figure 5.7. Catches of *Penaeus esculentus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 19-20 October 1998

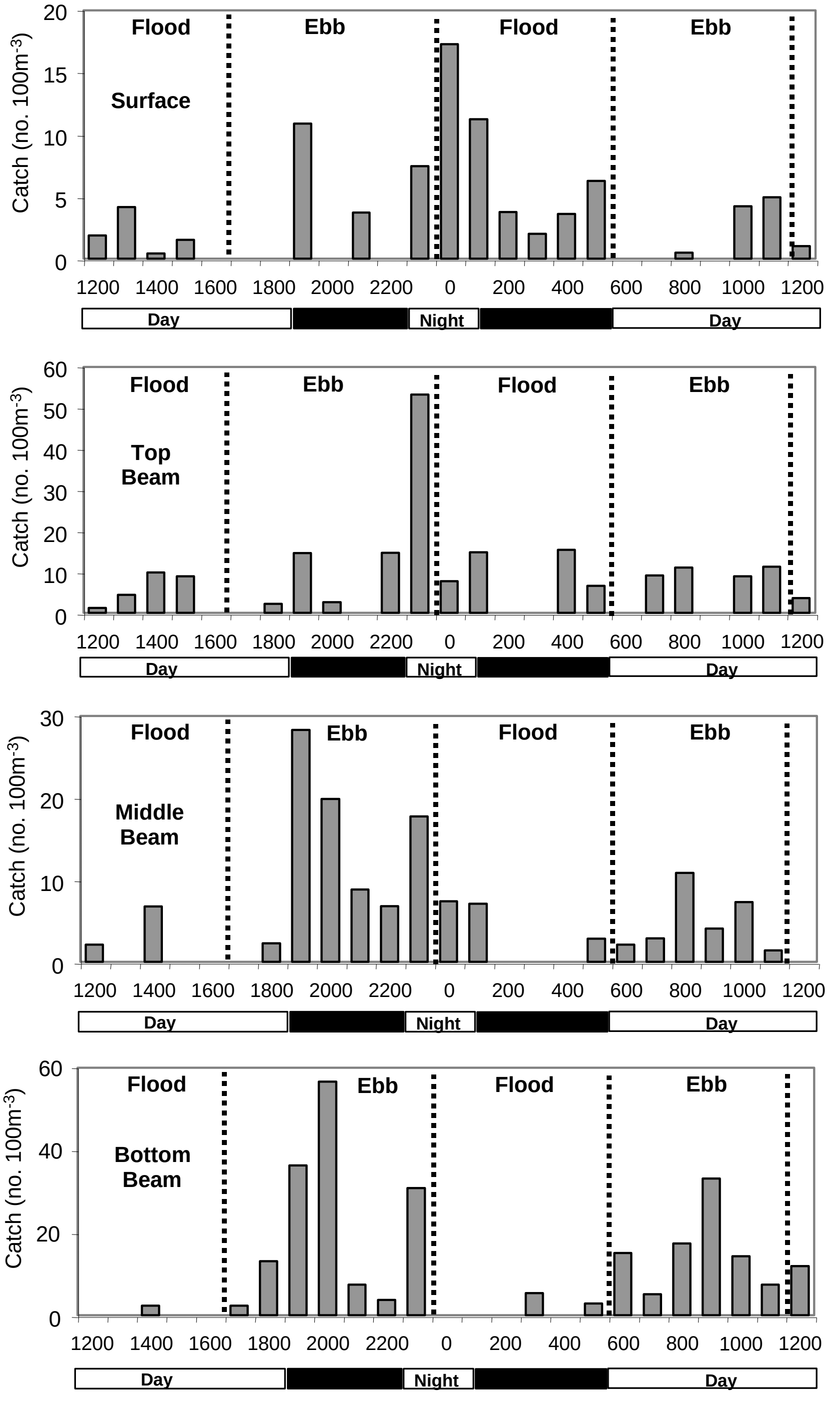

Figure 5.8. Catches of *Penaeus merguiensis* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 19-20 October 1998

The pattern of variation in top and middle beam trawl catches was less clear than for the surface or bottom trawls; catches were, in general, more evenly spread throughout the 24-hour periods. However, a large proportion of postlarval catches in the top and middle beam trawls were taken on ebb tides during the day and night, ranging from 75% for *P. merguiensis* to 49% for *P. esculentus* in the middle beam trawl. Catches in the top and middle beam trawl were often high around the change in tide direction. Neither day/night nor tide stage were significant in the ANOVA of catches for top and middle beam trawls except for *P. merguiensis* catches in the middle beam trawl where catches were significantly higher on ebb than flood tides.

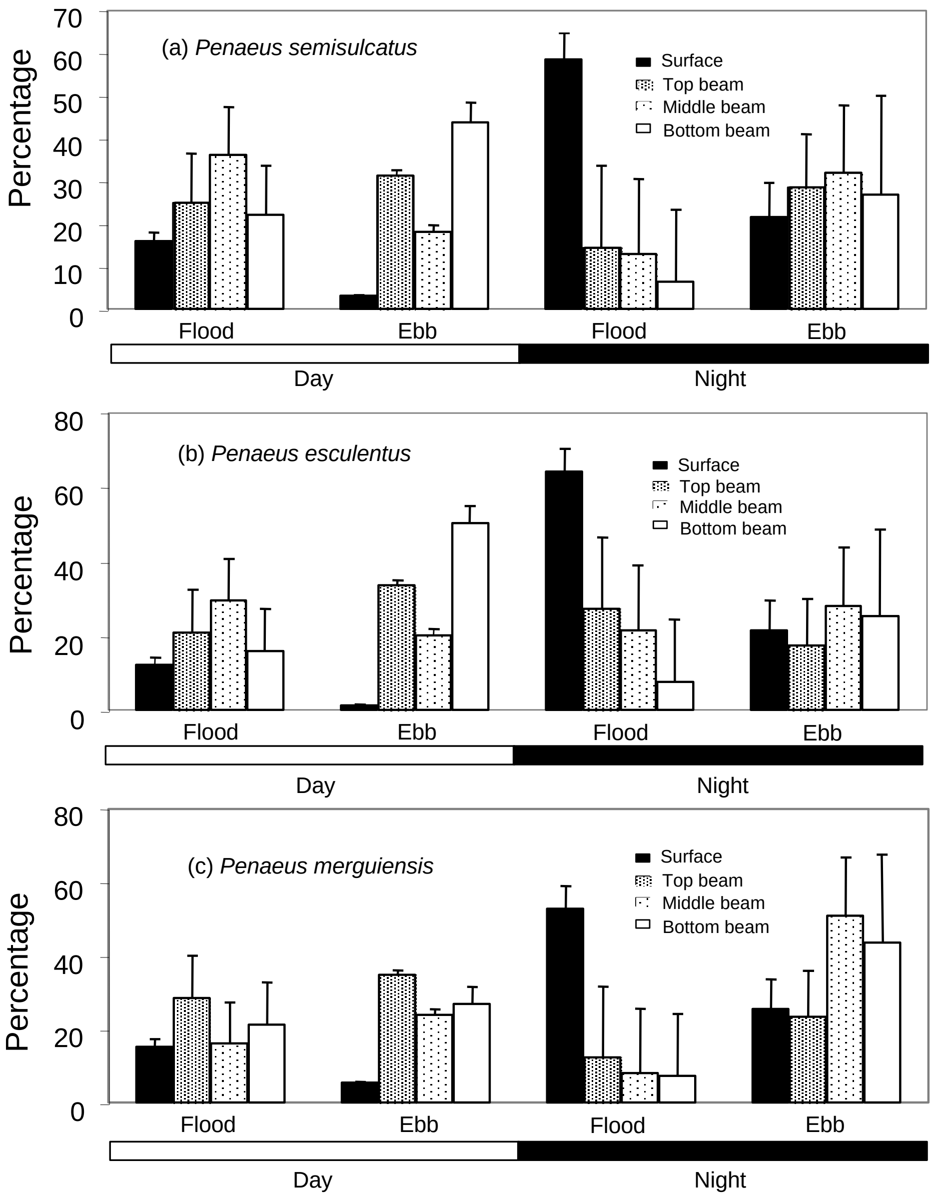

Figure 5.9. Mean percentage catches of *Penaeus semisulcatus*, *P. esculentus* and *P. merguiensis* for four categories of day/night and tide for four nets over two sampling periods in 1998.

Sampling in 1998 took place on the new phase of the moon so no moon was visible at night. There was a small amount of cloud cover during the day.

Table 5.3. Significant sources of variation and mean squares of catches of *Penaeus semisulcatus* for four nets over two sampling periods at the mouth of the Embley River, Weipa. Catches were transformed by taking the 4th root for each sample. df, degrees of freedom ;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

			Beam	
Source of variation (df)	Surface	Top	Middle	Bottom
Period (1)	0.41^{*}	1.79^{***}	3.78^{***}	6.74^{***}
Day/night (1)	4.42^{***}	0.04	0.14	0.75
Tide (1)	2.40^{***}	0.01	0.06	2.81^{**}
Period x day/night (1)	0.06	3.15^{***}	0.43	0.89
Period x tide (1)	0.01	0.10	0.04	0.48
Day/night x tide (1)	0.13	1.04^{*}	2.35^{***}	0.03
Period x day/night x tide (1)	0.01	0.21	0.14	0.96
Error (42)	0.06	0.21	0.20	0.25

Table 5.4. Significant sources of variation and mean squares of catches of *Penaeus esculentus* for four nets over two sampling periods at the mouth of the Embley River, Weipa. Catches were transformed by taking the 4th root for each sample. df, degrees of freedom ;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

			Beam	
Source of variation (df)	Surface	Top	Middle	Bottom
Period (1)	0.02	0.02	0.13	0.93^{*}
Day/night (1)	1.88^{***}	0.02	0.02	0.76^{*}
Tide (1)	0.64^{***}	0.01	0.03	1.09^{**}
Period x day/night (1)	0.01	0.17	0.21	0.63
Period x tide (1)	0.05	0.03	0.31	0.01
Day/night x tide (1)	0.18^{*}	0.01	0.31	0.20
Period x day/night x tide (1)	0.01	0.14	0.06	1.56^{**}
Error (42)	0.04	0.20	0.15	0.16

Table 5.5. Significant sources of variation and mean squares of catches of *Penaeus merguiensis* for four nets over two sampling periods at the mouth of the Embley River, Weipa. Catches were transformed by taking the 4th root for each sample. df, degrees of freedom ;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

Source of variation (df)	Surface	Top	Beam Middle	Bottom
Period (1)	0.39*	1.92**	0.57*	2.12***
Day/night (1)	1.50***	0.01	0.49	0.03
Tide (1)	0.68**	0.03	2.14***	2.49***
Period x day/night (1)	0.01	0.77	0.31	0.01
Period x tide (1)	0.02	0.01	0.22	2.48***
Day/night x tide (1)	0.08	0.19	0.67	0.44
Period x day/night x tide (1)	0.01	0.11	0.01	0.01
Error (42)	0.22	0.27	0.14	0.16

Size of postlarvae

The smallest postlarvae caught was 0.9 mm CL (*P. semisulcatus*) and the minimum sizes for *P. esculentus* and *P. merguiensis* were 1.5 and 1.3 mm CL respectively. Maximum sizes were 2.4 for *P. semisulcatus* and *P. esculentus* and 2.0 for *P. merguiensis*. Postlarval size was not significant in most analyses with day/night and tide. There was no strong or consistent relationship seen with size.

Embley River 1999

In most of the sampling periods in 1999, catches of all species were too low to provide reliable analyses. However, on 19-20 October 1999, catches of *P. semisulcatus* were high enough to analyse further. For several days either side of this 24-hour period, tides at Weipa were diurnal, i.e. there was only one flood and ebb tide each day. Furthermore, the ebb tide was almost completely at night while the flood tide was completely during the day. At the surface, almost equal numbers of *P. semisulcatus* postlarvae were caught on flood and ebb tides, 48% on the flood tide and 52% on the ebb tide (Figure 5.10). Catches in all the other nets were far higher on the ebb tide than on the flood tide, ranging from 83% in the bottom beam to 93% in the middle beam.

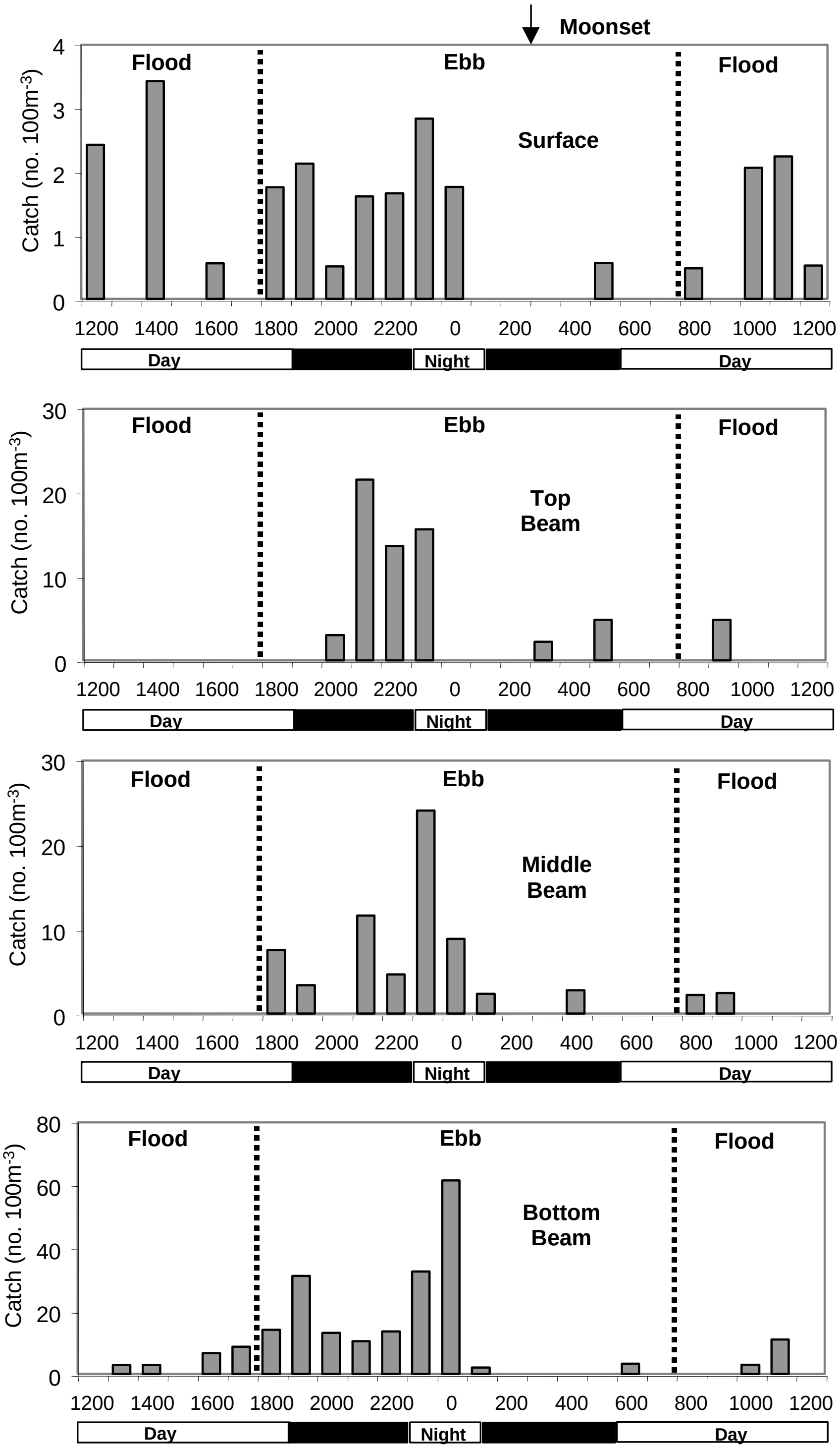

Figure 5.10. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 19-20 October 1999

Long-term variations in tidal timing

There are substantial differences in the timing of tidal cycles with respect to the day/night cycle throughout the year and also between regions. At Weipa the number of hours of flood tide at night is greater than the number of hours of ebb tide at night from February to July. However, at Karumba, in the southern Gulf of Carpentaria, the night flood hours are greater than night ebb hours from June to September (Figure 5.11).

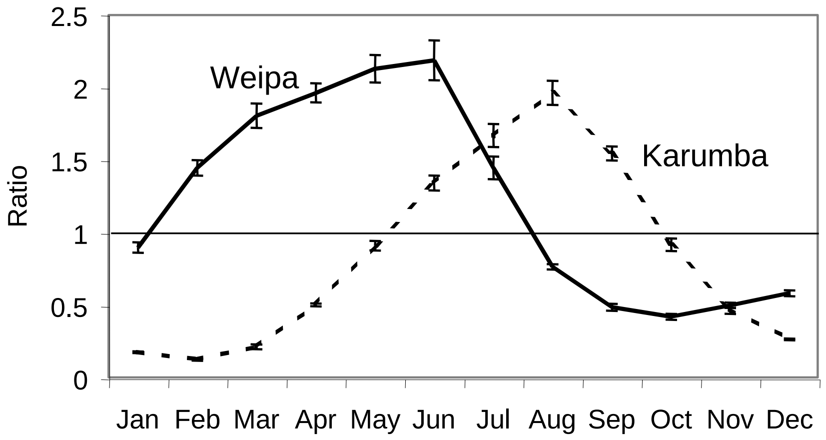

Figure 5.11. Ratio of hours of night flood tide to night ebb tide for each month for Weipa and Karumba. Each monthly value for Weipa is a mean over six years and for Karumba, a mean over three years. Error bars are one standard error.

There is much less annual variation in the timing of the tides. For example, over six years at Weipa for the months October to December, the variation in total number of night flood hours each year varied within a range of only 8% of the mean number. We found no significant correlation between the mean seasonal night flood hours and seasonal catches of benthic postlarvae at Weipa, as reported by Vance et al. (1996, 1998).

See Appendix 3.1 to 3.8 for detailed figures of other 24-hour samples taken in the Nerang and Embley Rivers.

5.4 Discussion

Our study has shown a clear effect of both tide and day/night cycles on the vertical migration behaviour of four penaeid prawn species caught in our 24-hour samples. The basic response to tide and day/night for all species was to move up in the water column on flood tides and also during night time. For all species, on most sampling occasions, the highest catches at the surface were made during the flood tide at night. Conversely, the highest catches in the bottom beam trawl were always on the ebb tide, either during the day or night. However, there were differences in the strengths of the responses to the tidal and day/night cycles between species. *P. plebejus*, caught only at Southport, was the most strongly effected by the tide and day/night cycles; very few postlarvae were caught during the day at all. Catches of the three species at Weipa were not as strongly affected by tide and day/night; only 53% of *P. merguiensis* caught in the surface trawl were caught on the night flood tide. In fact, quite large densities of postlarvae were found in the water column in the top and middle beam trawls for all species at Weipa on night ebb tides.

The differences found between the four species are likely to be real despite the fact that *P. plebejus* was caught at a different location to the other three species. The same nets and sampling procedure was used at both sites: tide ranges were similar, cloud cover was low for most samplings and moonlight was either low or zero for all sampling periods. Although we did not accurately measure light levels below the water surface with a light metre we did estimate light penetration using a secchi disc: day time readings were not significantly different between the two sites but night time readings were substantially lower at Weipa.

This may be a reflection of the more intense lights of civilisation at Southport compared to the more isolated Weipa as well as slightly more turbid water at Weipa.

Our results for *P. plebejus* broadly agree with most of the previous studies on this species. However, we disagree with Rothlisberg et al. (1995) who concluded that the day/night cycle was not important in determining vertical migration behaviour of postlarvae at the estuary mouth. We believe that the disagreement in our conclusions may be due to different weather conditions at the time of sampling. Although light levels were not recorded during the Rothlisberg et al. (1995) study, conditions were very overcast with heavy rain for much of the sampling period (Pendrey, R. C., CSIRO Marine Research, personal observation). It is possible that the decreased light levels during the day may have altered the behaviour of the postlarvae and masked the underlying day/night activity pattern. It should also be noted that the catches in our bottom beam trawl are not directly comparable with the beam trawl results of Rothlisberg et al. (1995). The tickler chain on our net was designed to help estimate the abundance of postlarvae that were either buried in or resting on the substrate, whereas their beam trawl had no chain and would have probably mostly caught postlarvae that were on or just above the seabed.

Other authors have also caught substantial numbers of postlarvae in the water column on ebb tides as well as flood tides. Forbes and Benfield (1986) suggested that high catches of *P. japonicus* on night ebb tides in South Africa may have been because the substrate was not suitable for settlement of the postlarvae. This may also be the case for some of the postlarvae caught at Weipa on day ebb tides. The concept of physiological readiness to settle has been discussed for crabs in the USA, ie. the possibility that crabs may reach a physiological stage where they need to settle out on the substrate (Lipcius et al. 1990, Metcalf and Lipcius 1992). It is possible that postlarval prawns may reach this state and if they don't find suitable habitat at that time, their normal activity pattern may be modified. Postlarval *P. semisulcatus* in the laboratory changed their behaviour at about 1.7 mm CL and began to spend more time perched on seagrass leaves rather than swimming in the water column (Liu and Loneragan 1997). However, it is also highly likely that there is a tension between the responses to the tidal and day/night cycles with a high degree of variation between individual postlarvae. For postlarvae in the water column on the night ebb tides, the response to day/night was apparently stronger than the response to tide.

Our results suggest that there is a continual interaction between the response to tide and day/night. We have seen that postlarval *P. plebejus* in the Nerang River did not move off the seabed during the flood tide until night fell. (Figure 5.4). However, the results of Rothlisberg et al.(1995) suggested that postlarvae will move to the surface waters during the day if weather conditions are overcast. Whether the majority of postlarvae respond to tide or day/night at any particular time, and therefore the rate of recruitment of postlarvae into coastal nursery areas will probably be influenced by short-term environmental factors as well as regular tidal and day/night cycles. For example, increased water turbidity due to storm activity may increase the numbers of postlarvae in the water column during day time flood tides.

It is clear from our results that sampling at the surface does not give a complete indication of the vertical distribution of penaeid postlarvae in the water column. We have seen that the pattern of postlarval abundance at the surface is not always the same as the pattern in the water column but closer to the seabed. For example, very few *P. semisulcatus* were caught at the surface on the night ebb tide, but large numbers were caught in the top beam trawl at the same time (Figure 5.6). It was clear from our flowmeter readings that water currents were similar at the top and bottom of the water column and therefore, many postlarvae during the 24-hour period were probably being advected out of the estuary.

Diurnal tides

The results for *P. semisulcatus* when only one flood tide occurred during the 24-hour period and there was no flood tide at night suggests that there could be net emigration of postlarvae rather than immigration under these conditions. These tidal circumstances are unusual for the northeastern Gulf of Carpentaria, but are more common in the southeastern Gulf where diurnal tides are the norm. The results for *P. semisulcatus* contrast with results for *P. merguiensis* in the southern Gulf. Staples (1980) sampled extensively in the Norman River and found large catches of postlarvae on flood tides during the day when there was no flood tide at night. It is probable that water turbidity is much higher in rivers of the Southern Gulf, resulting in more daytime vertical migration of postlarvae.

Seasonal and annual variation in recruitment

Since night time flood times are clearly times when most advection of penaeid postlarvae towards the coastal nursery areas will occur, it would seem logical that there should be a relationship between the frequency of night-time flood tides and recruitment of postlarvae into estuaries.

In fact there is a strong seasonal and geographical variation in the timing of flood tides. In Weipa, the number of night flood hours was greater than the night ebb hours from February to July whereas at Karumba in the southern Gulf of Carpentaria, night flood hours were less than night ebb hours from February to May (Figure 5.11). This may partly explain why there is more recruitment of postlarval *P. merguiensis* to the Embley River at Weipa at this time of year than there is to the Norman River in the southern Gulf (Rothlisberg et al. 1985, Vance et al. 1998).

We compared the annual variation in the number of hours of night flood tides by season with the abundance of benthic postlarvae of *P. merguiensis* and *P. semisulcatus* as reported by Vance et al. (1996, 1998) over six years, but there was no significant relationship. This may be because there is actually only a small annual variation in the number of night flood hours. For example, over six years, for the three months from October to December, the total number of night flood hours only varied within ±4% of the mean for six years.

5.5 Conclusions

It is clear that both tide and day/night cycles affect the vertical distribution of the four penaeid postlarvae assessed in this study. However, the behaviour of the postlarvae is probably also modified by short-term environmental factors that affect light levels in the water, such as water turbidity and cloud cover. It is also clear that to accurately assess migration patterns of postlarval prawns it is necessary to sample in more than one location in the water column.

Condie et al. (1999) used their hydrodynamic model of larval and postlarval advection in the Gulf of Carpentaria to calculate the size of the effective spawning areas in the Gulf. However, they assumed that once postlarvae were cued to the flood tides, the day-night cycle was no longer important. Our results have shown that this assumption is not correct. Because the postlarvae spend less time in the water column on day flood tides than night flood tides, they will take longer to reach the coastal and estuarine nursery areas than predicted by the model. The effective spawning areas calculated by the model will therefore be slightly over-estimated.

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6. VERTICAL MIGRATION BEHAVIOUR OF POSTLARVAL PENAEID PRAWNS: A LABORATORY STUDY OF THE EFFECT OF TIDE, WATER DEPTH AND DAY/NIGHT

6.1 Introduction

Hydrodynamic modelling has been used to estimate effective spawning areas for all regions of the tiger prawn fishery in the Gulf of Carpentaria. However, the present hydrodynamic model of postlarval prawn advection from the spawning grounds to the nursery grounds is limited in its accuracy because we do not know when the postlarvae begin to recognise and start cuing their vertical migration behaviour to the flood tides (the “transition depth”) (Rothlisberg et al. 1996, Condie et al. 1999). In most areas of the Gulf of Carpentaria, variation in this parameter has a substantial impact on the effective spawning area calculated by the model. For example, at Groote Eylandt, if the depth at which postlarvae change from being day/night cued to tidally cued is decreased from 20 to 7 m then the effective spawning area is confined to relatively inshore areas and decreases from about 8500 to 3600 km^2 (Condie et al. 1999).

Rothlisberg et al. (1995) suggested that postlarval prawns respond to the tides by recognising the changes in water pressure associated with the tidal cycle. In deep waters (> 20 m) the change in pressure due to the tidal cycle is only small compared to the total water pressure and the postlarvae cannot detect the tidal cycle. As postlarvae move closer inshore and water depth decreases, a point is reached where the tidal range becomes large enough in proportion to the water depth that postlarvae can detect the tide cycle.

Although there are other possible cues that postlarvae could use to detect change in tide stage, for example, change in water current direction, we believe that a response to pressure change is the simplest and most likely mechanism for detection of tide change. If postlarvae were to use water currents to differentiate between flood and ebb tides, they would not only have to be able to detect the change in current direction but also be able to know the absolute direction of the current with respect to the coastline. This is a much more complicated response than simply responding to a pressure change.

Laboratory studies have shown that many crustacean species, including some penaeid prawns, are sensitive to pressure changes, either single pressure pulses or changes of tidal frequency (Rice 1964, Knight-Jones & Morgan 1966, Sulkin 1984, Forward & Buswell 1989). Juvenile *Penaeus duorarum* in the laboratory became more active when the water level was raised (Wickham 1967) and Hindley (1975) found that the activity of juvenile *Penaeus merguiensis* in laboratory studies increased as the water pressure increased. However, the response was confounded by changes in the water flow at the same time. Vance (1992) used cyclical pressure changes to simulate a tidal cycle in a study on juvenile penaeid prawns and noted behavioural responses that helped explain patterns of field catchability. Postlarval *P. japonicus* moved up in the water column in response to increased pressure changes (Forbes & Benfield 1986). However, very few studies have tested the response of crustacea to simulated tidal cycles over several days and no studies have examined postlarval penaeid prawns under these conditions.

In this section of the project, we used pressure changes to simulate tidal cycles and have tested the response of two species of tiger prawns, *Penaeus esculentus* and *P. semisulcatus* to a sinusoidal tidal cycle at simulated water depths of 4, 8, 12 and 16 m over three and four day periods. We have also tested the response of a range of sizes of postlarvae to short-term pressure changes to see if the sensitivity to pressure changes with size.

6.2 Materials and methods

Supply of experimental postlarvae
Mature female prawns with visible ovaries were collected from several offshore locations. Most of the tiger prawns (*Penaeus semisulcatus* and *P. esculentus*) were supplied by a commercial fisherman from Cairns in northern Australia but some were collected from Weipa, also in northern Australia, by CSIRO staff working on another research project. Some *P. plebejus* were caught by commercial fishermen working offshore from Brisbane in eastern Australia. Prawns were caught at night and transported by air or road during the next day to the CSIRO laboratory at Cleveland.

The prawns were placed in large holding tanks at CSIRO and their spawning condition monitored: prawns thought likely to spawn were placed in individual spawning tanks. Offspring from successful spawnings were reared through to the postlarval stage in aerated tanks. They were fed a diet of either algae, brine shrimp or formulated dried food appropriate to their size and kept under artificial lighting with a cycle of 12 hours day and 12 hours night.

Wild postlarvae
We also carried out some experiments with postlarvae caught from the field as they were migrating upstream. Towards the end of one of the 24-hour field sampling sessions in the Nerang River, Southport, (Chapter 5) we placed the catch from several beam trawls into a shallow container with seawater and removed about 50 live postlarvae from the samples. These postlarvae were kept alive in 20-litre drums of aerated seawater for about three hours until we returned to the laboratory. Some of the postlarvae were then placed immediately into an experimental chamber and their response to tide and day/night was tested as for laboratory-reared postlarvae (see below).

Experimental apparatus
The aim of the experiments was to determine when postlarvae were in the water column with respect to day/night and tidal cycles. We placed the postlarvae in a small doughnut-shaped chamber with water circulating around the chamber. The current would not move postlarvae that were resting on the substrate but postlarvae that had moved off the substrate would be moved around the chamber by the current. A video camera and recorder fixed outside one section of the chamber was used to record the number of postlarvae passing its field of view and therefore provide an estimate of the number of postlarvae in the water column.

In the following section, the numbers in brackets refer to corresponding numbers in Figure 6.1. See Appendix 4 for technical specifications of apparatus. Seawater from the Cleveland laboratory reticulated water supply (1) was fed to a 20-litre storage tank (2) to give a buffer against brief interruptions to the water supply. A 1000W centrifugal pump (3) pressurised water in the experimental system to 220 kPa and excess pressure was released back to the storage tank through an adjustable pressure release valve (4). The water flow rate into the drum, which was constantly overflowing to waste, was high enough that the water in the drum was not heated excessively by the operation of the pump. The water for the experiment then passed through about 5 metres of flexible hose, a diaphragm airlock accumulator and a one-micron cartridge filter (5). A device that maintained a constant pressure drop across an adjustable valve (6) controlled the water exchange rate through the experimental system. The flow rate at this point was measured by a paddle wheel sensor (7), logged and displayed on a computer (PC). Water was circulated through the experimental chamber (11) by a small magnetic drive pump (8) at a rate determined by manual control valve (9). The flow rate through the chamber was measured by a sensor (10) and logged and displayed on the computer. The jet of water entered the chamber at a tangent and created a current around the doughnut-shaped chamber. Postlarvae above the substrate in the chamber were moved by the current past a video camera (12) and recorded using a time lapse video recorder.

Water left the chamber through a coarse sand substrate and then rejoined the loop through the circulation pump. If the exchange rate was higher than the circulation rate the water flowed from left to right in the central link (13). If the exchange rate was lower than the circulation rate some water could return to the pump (8) from right to left. Outlet water from the experimental chamber was filtered again through a 25-micron cartridge filter (14). Water pressure was sensed by a transducer (15) and logged and displayed on the computer. The computer software compared the actual water pressure in the system with an expected value based on the time and the parameters preset for each experiment and the needle valve (16) was closed or opened by a stepper motor to raise or lower the actual pressure.

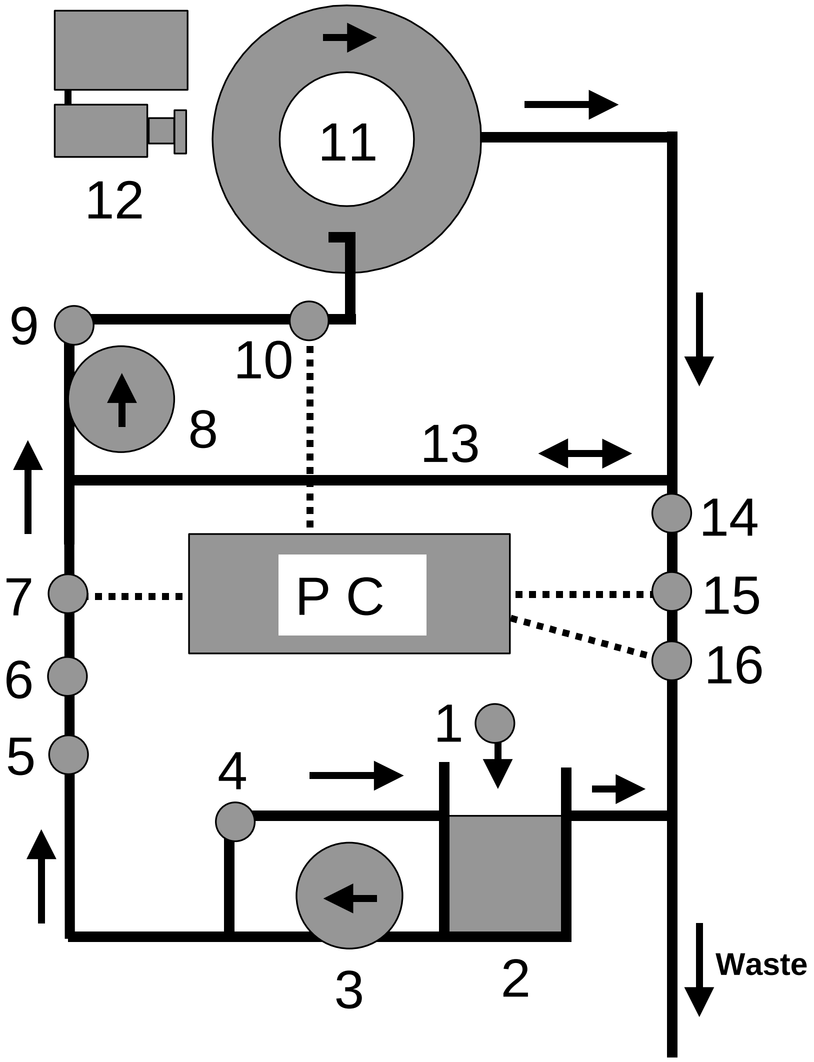

Figure 6.1. Schematic diagram of apparatus used to monitor postlarval behaviour: **1** Laboratory seawater supply, **2** Storage tank, **3** Pressure pump, **4** Pressure release valve, **5** 1-micron filter, **6** Flow regulating device, **7** Flow sensor, **8** Circulation pump, **9** Circulation control valve, **10** Flow sensor, **11** Experimental chamber, **12** Camera and video recorder, **13** Central link, **14** 25-micron filter, **15** Pressure sensor, **16** Needle valve, **PC** Computer. Solid lines are water lines and dashed lines are communication cables.

Day light was simulated by two 20 W halogen lights and an infrared light was on continuously so that the video camera could record activity at night. Prawns do not detect infrared light. The experimental chamber and light sources were kept in a light-proof enclosure during each experiment so that the postlarvae would not be disturbed by people working in the experimental room. Light levels in the experimental enclosure as well as water temperature from the top of the experimental chamber were continuously logged to the computer.

An important aspect of the experimental apparatus was that it was constructed to allow water to flow constantly through the experimental chamber while pressure in the system changed in a controlled manner. This water exchange allowed us to run experiments over several days without undue mortality of postlarvae.

The donut-shaped experimental chamber was constructed from two Perspex cylinders placed one inside the other such that the diameter of the outer wall of the chamber was 150 mm and the width was 35 mm (Figure 6.2). The height of the chamber was 60 mm and the bottom 20 mm was filled with coarse sand. The base of the chamber was fixed with an outlet below the sand level while the lid was removable but watertight.

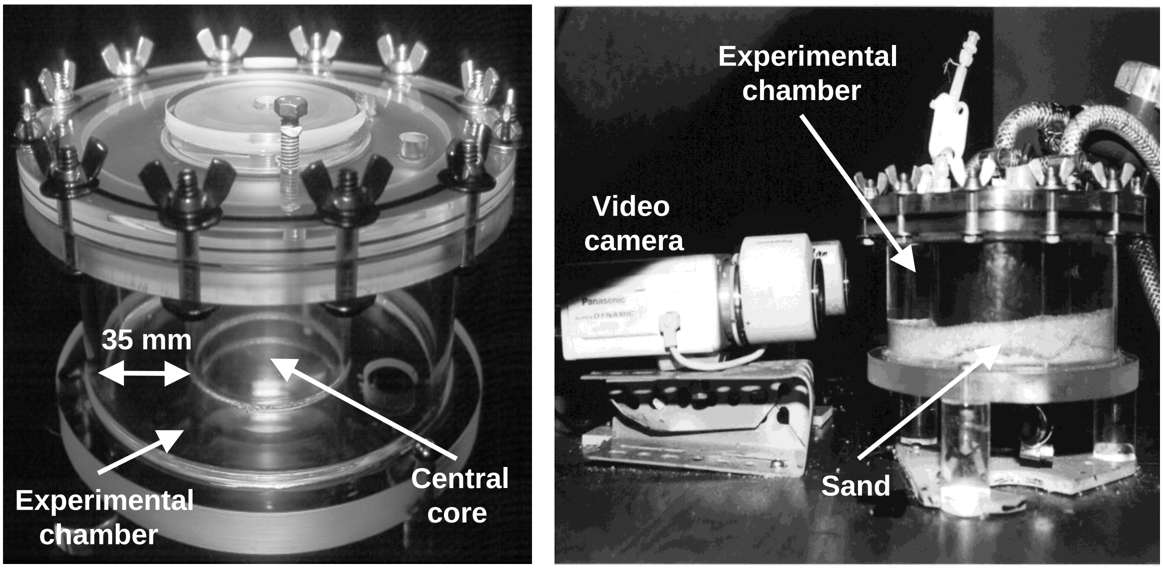

Figure 6.2. The donut-shaped experimental chamber and the video camera used to record postlarval activity.

Computer system
The computer was fitted with an interface card to allow input from the various sensors and to enable the computer to control the needle valve. A custom-written Visual Basic program logged input from all the sensors and also controlled water pressure in the experimental chamber. We have used water pressure to simulate water depth and the tidal cycle in this apparatus. The software allowed us to simulate any water depth between 0 and 20 m and the appropriate depth was entered to the computer at the beginning of each experiment. The tidal cycle was created by specifying an equation for the shape of the tidal curve. For all experiments where we attempted to simulate a natural tidal cycle, we used a simple sinusoidal curve with a period of 12 hours, so that two full cycles of high and low tide were completed in 24 hours, and a tidal amplitude of 2 m. This meant, for example, that for a water depth of

12 m, the simulated water depth inside the experimental chamber ranged from 11 to 13 m. The software continuously compared the actual pressure in the experimental system with the expected pressure and made adjustments to the needle valve at 2 or 20 second intervals depending on whether the two values were trending away or towards each other. In most experiments the actual pressure in the system kept very close to the target pressure (Figure 6.3). When a day/night cycle was simulated for experiments, the computer software also simulated dawn and dusk by changing light levels over a period of one hour.

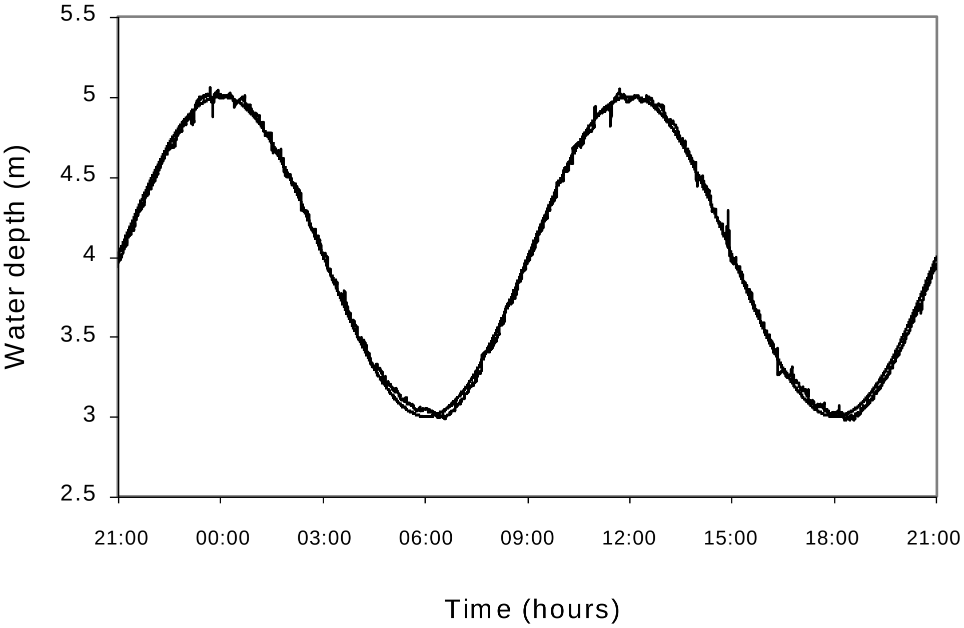

Figure 6.3. Target and actual water depth for one 24-hour period with a tide range of 2 m recorded at 10 second intervals. The simulated water depth ranged from 3 to 5 m.

Experimental procedures – simulated tidal and day/night cycles

For each experiment, 10 postlarvae were scooped from the large rearing tanks, usually in the early afternoon, and placed into the experimental chamber. The chamber was immediately sealed, the water pumps were started and the tidal software was initiated. The light cycle was always set so that dawn was from 0500 to 0600 and dusk was from 1700 to 1800 hours. For all experiments, the tidal period was 12 h and the tidal range was 2 m, while the simulated water depth was set to either 4, 8, 12 or 16 m.

High tides were set to occur at either 0600 and 1800 or 0000 and 1200 so that each flood and ebb tide occurred completely during the day or night period. By carrying out experiments with high tide set at different times of the day/night cycle, we hoped to more clearly separate the effects of day/night and tide on postlarval behaviour. Each experiment ran for either 3 or 4 days, after which postlarvae were removed from the chamber and the apparatus was cleaned in preparation for the next experiment.

The postlarvae were fed each day at about 1500 through a small inlet in the lid of the chamber using a syringe. This could be accomplished with only small disruptions to the pressure cycle.

Experimental procedures – short-term pressure change
We also carried out shorter experiments to test the response of postlarvae to pressure changes over a shorter time, which enabled us to increase the replication of the results. For these experiments, the parameters of the tidal software were changed so that the simulated water depth remained constant for 2 hours at 4 m, then increased linearly to 7 m over one hour, remained constant at 7 m for 2 hours, then decreased to 4 m over 1 hour. This cycle was repeated 3 times (Figure 6.4).

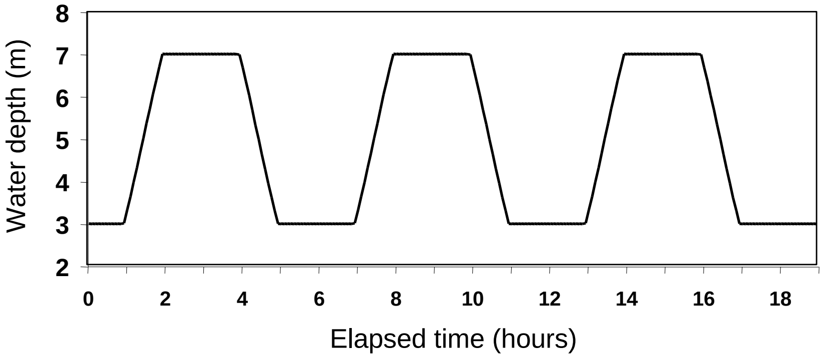

Figure 6.4. Simulated water depth regime used in experiments to test the response of postlarvae to short-term pressure changes.

Ten postlarvae were placed in the chamber as for the longer-term experiments and the tidal software was initiated immediately. White lights were kept on for the duration of these experiments and the postlarvae were not fed at all.

At the end of all experiments, postlarvae were measured under a binocular microscope to the nearest 0.1 mm carapace length (CL).

For both short and long-term experiments, the activity of the postlarvae in one section of the chamber was continuously recorded onto video tape for the duration of the experiment.

Analyses
The video tapes were later replayed in the laboratory and analysed. The total number of passes of postlarvae across the field of view of the camera were recorded for each 5-minute period of the experiment and entered onto a computer file.

Simulated tidal and day/night cycles
For each experiment, a tide variable was created with values of flood or ebb and a day/night variable with values of day or night. Inspection of the raw data plotted at 5-minute intervals showed that there was no apparent response of postlarvae to tidal cycles within the first 24-hour period so the data sets used for further analyses and summary graphs began at 1200 on the second day of each experiment. We summed the activity counts for each category of tide and day/night – resulting in 4 separate 6-hourly totals for each 24-hour period. Combining data into 6-hourly totals removed the auto-correlation that was clearly evident from inspection of the raw data. It was also clear that the overall activity levels varied substantially between experiments and sometimes between days of the same experiment. We therefore standardised activity across days and experiments by expressing activity for each 6-hourly period as a proportion of the total activity for that 24-hour period. A mean activity for each 6-hourly

period was then calculated for each experiment. The proportional data were transformed using the arcsine of the square root of each proportion.

We used ANOVA on the transformed proportional data to test for differences in activity between the four categories of tide and day/night for each of the water depths tested.

Short-term pressure change
For each experiment a pressure variable was created with six categories, each representing one hour of the experimental cycle. The categories were:

1. Constant low pressure – 1 hour before pressure increase
2. Increasing pressure
3. Constant high pressure – 1 hour after pressure increase
4. Constant high pressure – 1 hour before pressure decrease
5. Decreasing pressure
6. Constant low pressure – 1 hour after pressure decrease

We standardised activity across cycles and experiments by expressing activity for each pressure category as a proportion of the total activity for each six-hour cycle. A mean proportional activity was then calculated for each pressure category for each experiment. The proportional data were transformed using the arcsine of the square root of each proportion.

We used ANOVA on the transformed proportional data to test for differences in activity between the six categories of pressure.

Table 6.1. Mean, minimum and maximum sizes (mm CL) of postlarvae, measured at the end of each experiment. SD standard deviation.

Experiment type and species	Size group	Mean size ± SD	Size range
Sinusoidal tidal cycle *Penaeus esculentus*	Medium	1.7 ± 0.2	1.1 - 2.4
	Large	2.3 ± 0.3	1.0 - 3.5
Penaeus semisulcatus	Medium	1.9 ± 0.1	1.6 - 2.2
	Large	2.4 ± 0.4	1.2 - 3.2
Linear pressure change *Penaeus esculentus*	Small	1.2 ± 0.2	0.8 - 1.7
	Medium	1.8 ± 0.1	1.4 - 2.1
	Large	2.5 ± 0.3	1.7 - 3.4

Size groups
We attempted to carry out experiments on three size groups of postlarvae, covering the range of sizes that we saw in the field sampling. However, because of fast growth rates and high mortality rates of the very small postlarvae (possibly associated with high moulting rates) we

were not able to carry out enough experiments using the tidal simulations on our smallest size group. Because it was virtually impossible to measure the postlarvae accurately before each experiment without damaging them most experiments began with a larger size range of postlarvae than would have been ideal. For this reason and because of high growth rates, there is some overlap in sizes of postlarvae recorded for each size group (Table 6.1). The details of the size groups are presented in Table 6.1.

6.3 Results

Simulated tidal and day/night cycles

Penaeus esculentus

An example of the pattern of postlarval activity in 5-minute blocks for a typical 3-day experiment where the postlarvae showed a response to the tidal cycle is shown in Figure 6.5. In this experiment high tide was at 0000/1200 and low tide was at 0600/1800. The activity of postlarvae in the chamber was initially low but then increased substantially straight after dusk. Activity remained high and variable for most of the first night but decreased quickly at dawn. The postlarvae were mostly inactive for the next day and activity levels only started to increase about 2/3 of the way through the flood tide on the second night. Activity was high for the rest of the night with highest activity on the ebb tide. Activity was again low during the following day, followed by a brief burst of activity straight after dusk. The main period of activity during the night was again on the ebb tide. Activity levels were always higher at night than during the day and, if the postlarvae responded to the tidal cycle, the response was usually first seen during the second 24-hour period of the experiment.

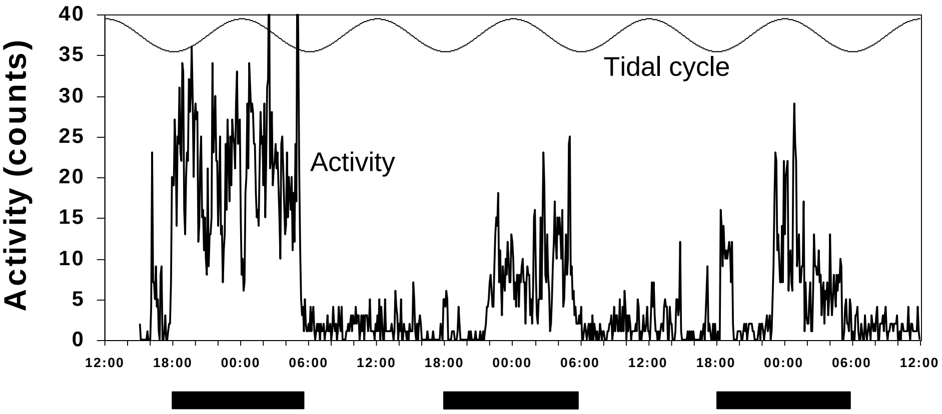

Figure 6.5. Activity of *Penaeus esculentus* in 5-minute blocks and tidal cycle for one 3-day experiment from 24-27 March 2000. The black bars represent periods of darkness. High tide was at 0000 and 1200; low tide was at 0600 and 1800.

Medium postlarvae

The mean size of postlarvae for all of these experiments was 1.7 mm CL (individual sizes ranged from 1.1 to 2.4 mm CL) (Table 2.1). When all experiments for postlarvae tested at a water depth of 4 m with high tide at 0600 and 1800 were combined, the highest activity levels occurred during the first few hours of darkness on the ebb tide (Figure 6.6a). There was also a small peak in activity in the two hours before dawn. When the tidal cycle was shifted by six hours so that high tide was at 0000 and 1200, most of the activity occurred in the last half of the night, but again on the ebb tide (Figure 6.6b). There was also a small activity peak just after dusk and a small burst of activity at about 1500 when the postlarvae were fed.

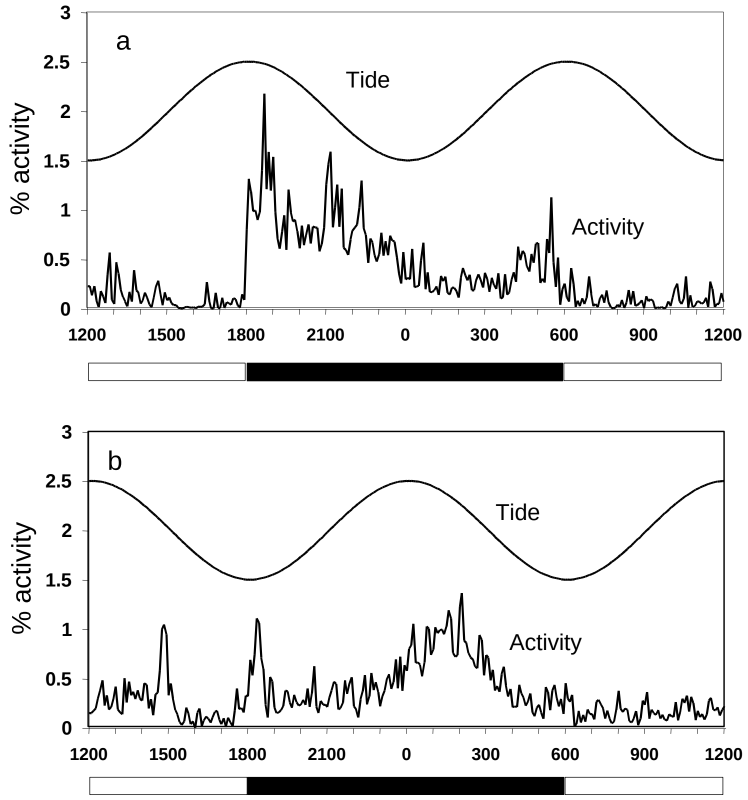

Figure 6.6. Mean activity of medium sized *Penaeus esculentus* postlarvae at a simulated water depth of 4 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.

ANOVA showed that activity differed significantly between day/night and tide (Table 6.2). The interaction between day/night and tide was also significant because the strong difference in activity between flood and ebb tides was only at night: overall activity levels during the day were very low.

Table 6.2. Mean squares and significance levels for two-way analyses of variance of activity of medium postlarval *Penaeus esculentus* with day-night and tide for four simulated water depths. The proportional activity in each category was transformed using the arcsine of the square root of each proportion. df, degrees of freedom;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

		Source of variation (df)			
Depth (m)	Number of experiments	Day-night (1)	Tide (1)	Day-night x Tide (1)	Error (20-40)
4	9	0.970^{***}	0.165^{***}	0.184^{***}	0.009
8	11	1.186^{***}	0.005	0.008	0.023
12	6	0.943^{***}	0.043	0.002	0.029
16	7	1.486^{***}	0.006	0.001	0.013

When the water depth was set at 8 m and high tide at 0600 and 1800, there was a sharp peak in activity at dusk but there were no significant increases in activity during the rest of the night period (Figure 6.7a). When high tide was at 0000 and 1200, the largest peak of activity was again at dusk with slightly higher levels of activity in the few hours before dawn (Figure 6.7b). The activity of postlarvae at 8 m differed significantly only between day and night but not between tide stage (Table 6.2).

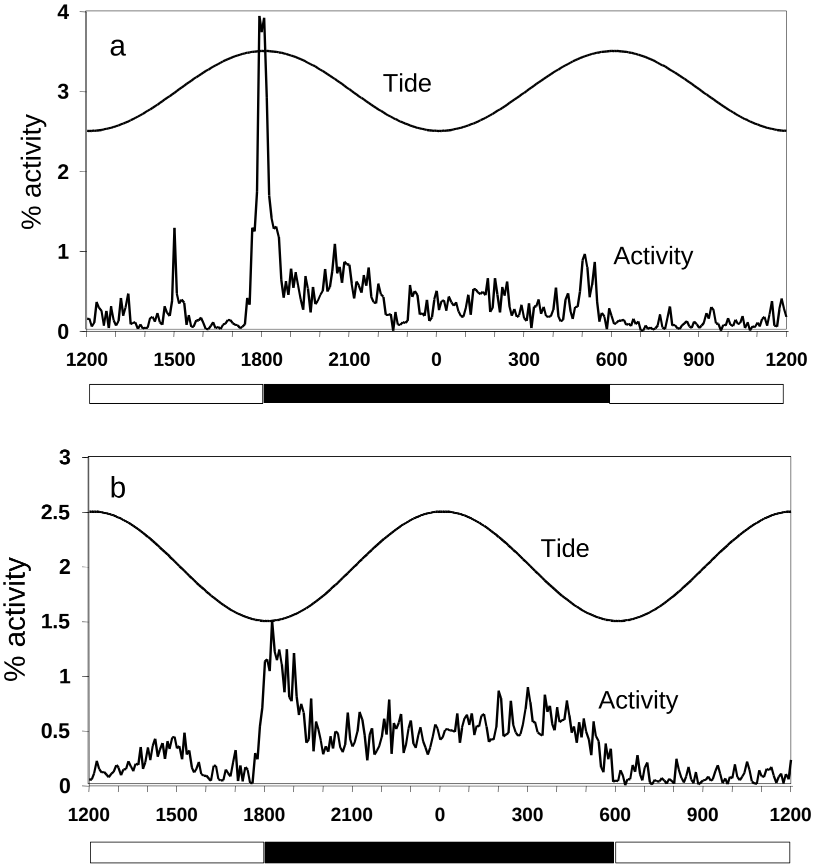

Figure 6.7. Mean activity of medium sized *Penaeus esculentus* postlarvae at a simulated water depth of 8 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200. Note the different scales.

For water depths of 12 and 16 m the patterns of activity were similar to those for 8 m (See Appendix 3.9 and 3.10 for Figures). There was always more activity at night and there was always a peak of activity at dusk and in the pre-dawn period. There was no increased activity associated solely with any particular stage of the tidal cycle. The activity of postlarvae at these depths differed only between day and night (Table 6.2).

Large postlarvae

The mean size of postlarvae tested in the large size group was 2.3 mm CL and individual sizes ranged from 1.0 to 3.5 mm CL (Table 6.1). In general, the activity patterns for large postlarvae were similar to those for medium postlarvae. Prawns were more active at night in all experiments. At a water depth of 4 m, the highest activity levels occurred on ebb tides at night (Figure 6.8). However, in contrast to the medium prawns, there was also a response to the tidal cycle at a water depth of 8 m (Figure 6.9). At 8 m, postlarvae were more active on the ebb tides at night, and tide as well as day/night was significant in the ANOVA (Table 6.3). However, at 12 and 16 m tide was not significant in the analyses (See Appendix 3.11 and 3.12 for Figures).

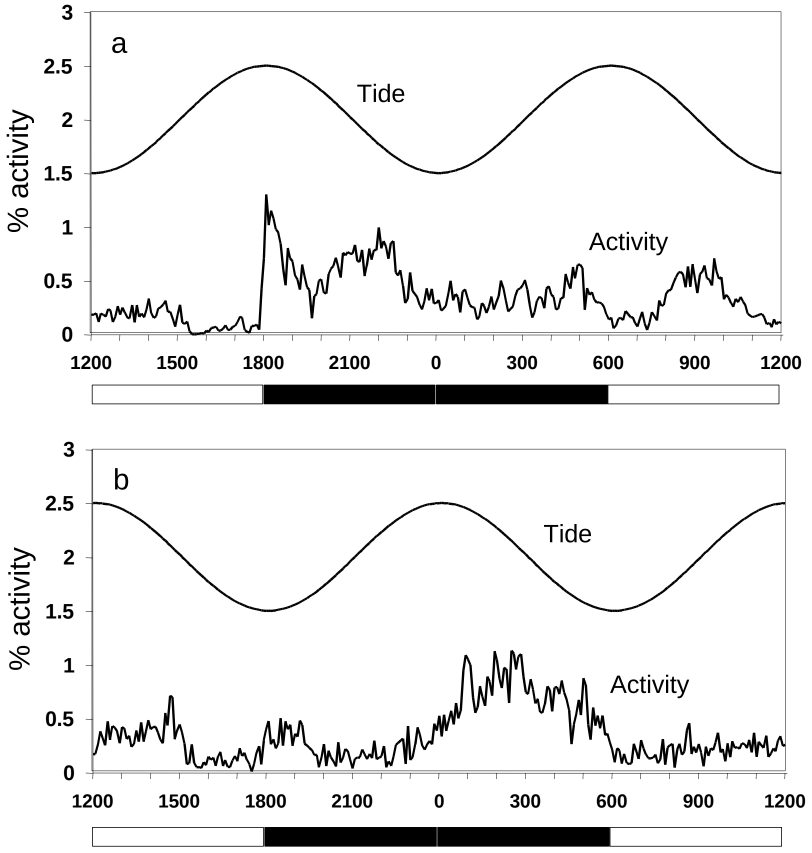

Figure 6.8. Mean activity of large *Penaeus esculentus* postlarvae at a simulated water depth of 4 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.

Table 6.3. Mean squares and significance levels for two-way analyses of variance of activity of large postlarval *Penaeus esculentus* with day-night and tide for four simulated water depths. The proportional activity in each category was transformed using the arcsine of the square root of each proportion. df, degrees of freedom;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

		Source of variation (df)			
Depth (m)	Number of experiments	Day-night (1)	Tide (1)	Day-night x Tide (1)	Error (4-44)
4	10	0.371^{***}	0.441^{***}	0.152^{***}	0.012
8	12	1.262^{***}	0.299^{***}	0.069^{*}	0.016
12	2	0.451^{**}	0.001	0.016	0.002
16	7	0.943^{***}	0.032	0.091^{*}	0.021

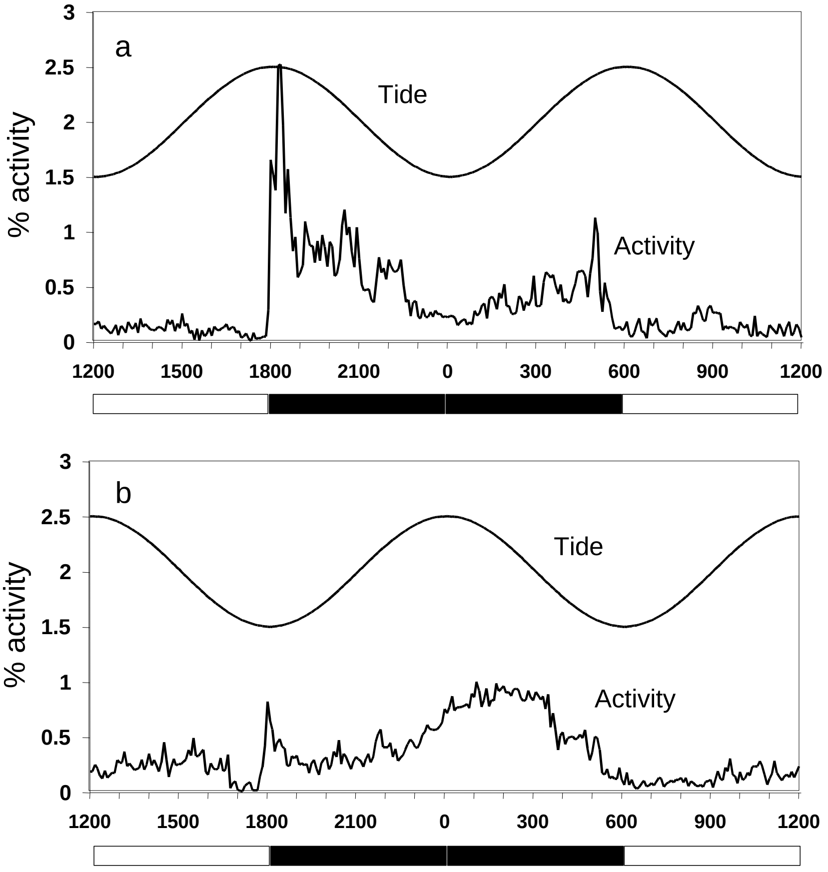

Figure 6.9. Mean activity of large *Penaeus esculentus* postlarvae at a simulated water depth of 8 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.

Penaeus semisulcatus

Because of the difficulty in obtaining successful spawnings of this species less data were obtained for *P. semisulcatus* than for *P. esculentus* and all the results for *P. semisulcatus* are for large postlarvae. The activity patterns, however, were quite similar to those obtained for large *P. esculentus*. Most activity occurred at night and at 4 m water depth the highest activity levels occurred on the ebb tide at night (Figure 6.10). At 8 m, the postlarvae still appeared to be responding to the tidal cycle although the level of significance was less than for 4 m (Figure 6.11, Table 6.4). Tide was not significant at a water depth of 12 m and also did not appear to affect activity levels at 16 m although we only carried out one experiment at 16 m and therefore could not analyse the results statistically (See Appendix 3.13 and 3.14 for Figures).

Penaeus plebejus

We were not able carry out experiments on *P. plebejus* at different water depths but we were able to briefly compare the behaviour of postlarvae of *P. plebejus* reared in the laboratory with those caught in the field at Southport. The majority of the activity of the lab-reared postlarvae occurred on the ebb tide at night, with a smaller peak in activity on the ebb tide during the day (Figure 6.12a). There was also an increase in activity around dusk. Postlarvae brought back to the laboratory from the field showed a very similar pattern of activity except that activity during the night ebb tide was more accentuated than for the lab-reared postlarvae (Figure 6.12b).

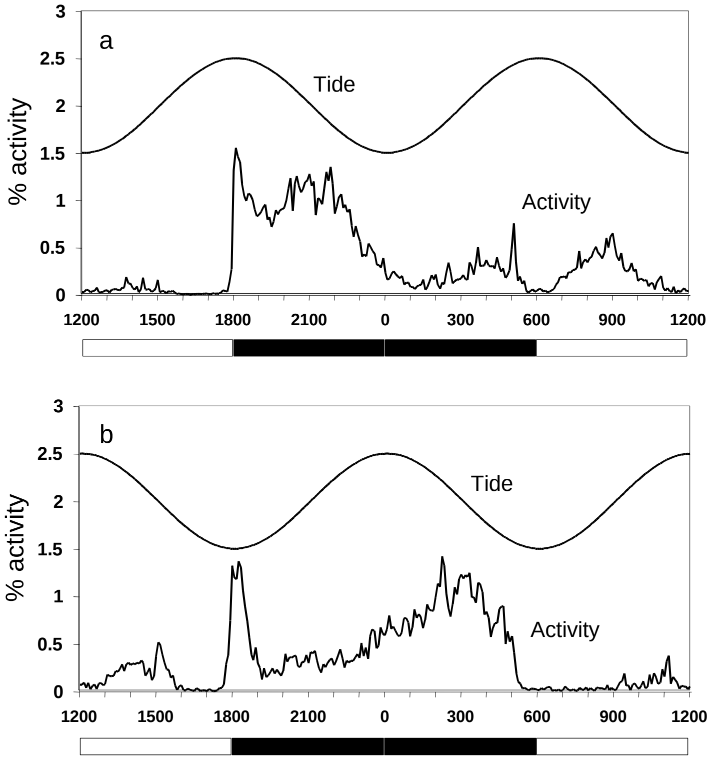

Figure 6.10. Mean activity of large *Penaeus semisulcatus* postlarvae at a simulated water depth of 4 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.

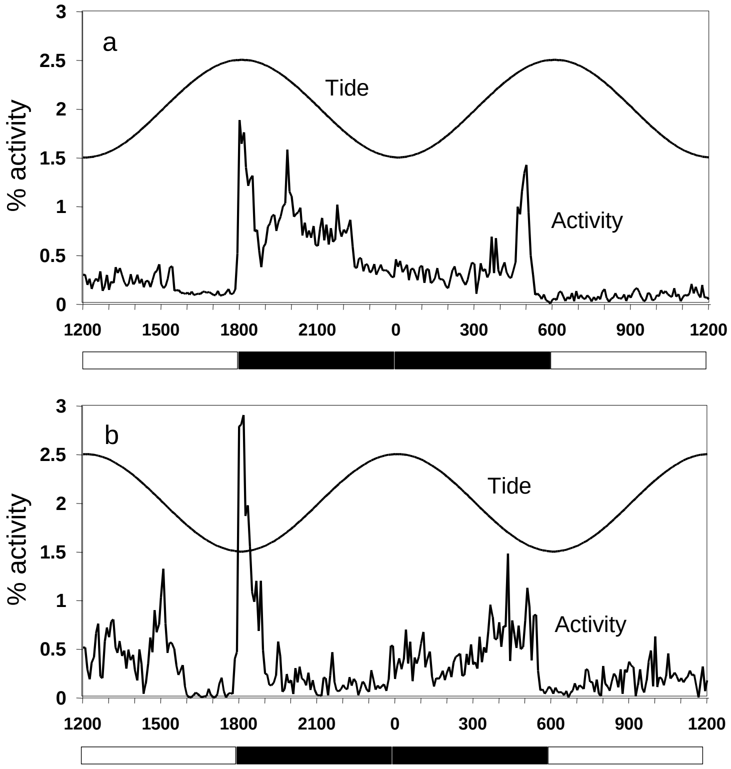

Figure 6.11. Mean activity of large *Penaeus semisulcatus* postlarvae at a simulated water depth of 8 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.

Table 6.4. Mean squares and significance levels for two-way analyses of variance of activity of large postlarval *Penaeus semisulcatus* with day-night and tide for three simulated water depths. The proportional activity in each category was transformed using the arcsine of the square root of each proportion. df, degrees of freedom;
*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$

		Source of variation (df)			
Depth (m)	Number of experiments	Day-night (1)	Tide (1)	Day-night x Tide (1)	Error (4-28)
4	8	1.206^{***}	0.594^{***}	0.083^{*}	0.018
8	7	0.363^{**}	0.044^{*}	0.071	0.033
12	2	0.109^{***}	0.005	0.001	0.019

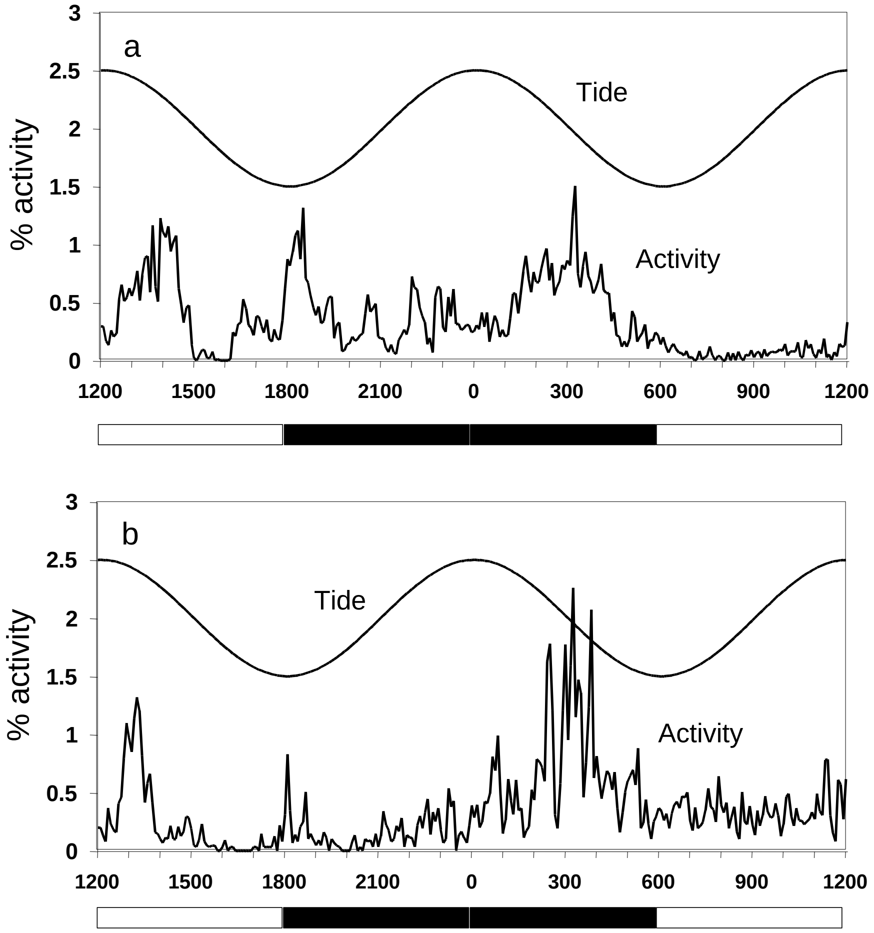

Figure 6.12. Mean activity of medium *Penaeus plebejus* postlarvae at a simulated water depth of 4 m for a) laboratory-reared postlarvae, and b) field-caught postlarvae. High tide was set at 0000 and 1200.

Short-term pressure change

Penaeus esculentus

Small postlarvae

The small postlarvae (mean size = 1.2 mm CL) (Table 2.1) showed no strong pattern of response to simulated depth change in these experiments. Activity levels were usually high for the first few hours of each experiment and then gradually decreased over several hours (Figure 6.13a).

Medium and large postlarvae

For both these size groups there was a very marked increase in activity levels during the decreasing depth phase and for the first hour of constant depth after the depth decrease (Figure 6.13b, c). When tested with ANOVA, depth category was highly significant for the medium and large postlarvae but was not significant for the small postlarvae (Table 6.5).

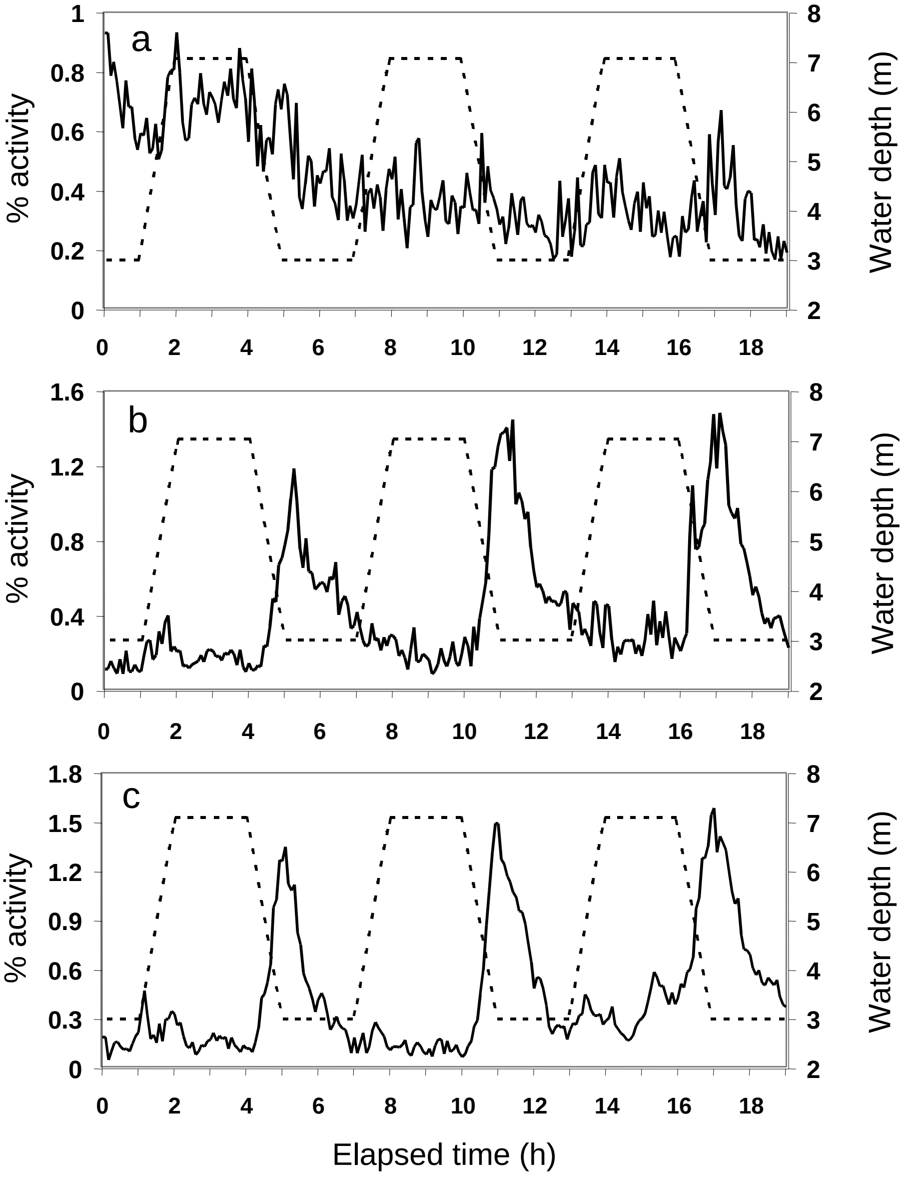

Figure 6.13. Mean activity in 5-minute blocks of a) small, b) medium, and c) large *Penaeus esculentus* postlarvae in response to short-term changes in water pressure. (- - -) water depth, (—) activity.

Table 6.5. Mean squares and significance levels for analyses of variance of activity of three size groups of postlarval *Penaeus esculentus* with depth category. The proportional activity in each category was transformed using the arcsine of the square root of each proportion. df, degrees of freedom; *** $p < 0.001$

		Source of variation (df)	
Size	Number of experiments	Depth (5)	Error (36-78)
Small	14	0.006	0.009
Medium	11	0.206***	0.005
Large	7	0.185***	0.004

6.4 Discussion

The results of these laboratory studies clearly showed that the activity levels of postlarval *Penaeus esculentus* and *P. semisulcatus* were strongly influenced by both the simulated day-night cycle and the tidal cycle. Furthermore, the response of postlarval *Penaeus esculentus* to simulated tidal cycles varied with respect to the simulated water depth and also the size of the postlarvae.

Day-night
Postlarvae of both species and all size groups spent far more time in the water column at night than during the day. This result is consistent with the results of other field and laboratory studies on penaeid prawns. Juveniles and adults of most penaeid prawns have been shown to be more active at night (see Dall et al. 1990 for review). Juvenile *P. esculentus* were more active at night when tested under simulated day-night cycles in the laboratory (Vance 1992). In the field studies described in Chapter Five of this project, postlarvae of several species of penaeid prawns including *P. esculentus* and *P. semisulcatus* were more abundant in the water column at night and concentrated on or close to the seabed during the day.

Tide/pressure
In our experimental apparatus, postlarval *Penaeus esculentus* of medium size could detect a simulated tidal cycle of 2 m amplitude when in relatively shallow simulated water depths (4 m) but not in deeper water (≥ 8 m). The pattern of response to tide was not as clear as for day-night, but when the postlarvae responded to the tidal cycle, they were more active on the ebb than the flood tide. Larger postlarvae of both *P. esculentus* and *P. semisulcatus* seemed to detect and respond to tide at greater depths than the medium-sized postlarvae. Their behaviour was significantly affected by the tidal cycle at 8 m as well as 4 m. However, no postlarvae reacted to the tidal cycle when the depth was set at 12 or 16 m. When postlarvae responded to the tidal cycle the response was evident during the second 24-hr period of the experiment, i.e. the postlarvae were cueing to tide after being exposed to only two tidal cycles.

The response of medium and large postlarvae to the short-term experiments was similar to the response for the long-term experiments; i.e. they were very active during and straight after a depth decrease. In contrast, the results of the short-term experiments on small postlarvae clearly show that they didn’t respond to either increasing or decreasing water depth.

There are no other studies that have examined the response of postlarval prawns to simulated tidal cycles over several days while superimposed on a range of simulated water depths so it is difficult to make direct comparisons of our results with other studies. Several authors, however, have reported ontogenetic changes in the response of other organisms to pressure. Larval sole were not sensitive to pressure cycles of 12 hour period but juveniles showed increased activity when the pressure decreased (Champalbert & Koutsikopoulos 1995). Jacoby (1982) and Sulkin (1984) reported on variation in response to pressure change with the developmental stage of several species of crab larvae.

Although the response of postlarvae to tidal cycles in our experiments is clear, the interpretation of the results is complicated. There is a discrepancy between the timing of activity of postlarvae in the laboratory compared with activity of postlarvae in field studies. Postlarvae were most active in the water column on flood tides in the field but were most active on ebb tides in the laboratory experiments. It is possible that the laboratory results are at least partly an artefact of the experimental apparatus but it also likely that the results provide an insight into the mechanism for the response of postlarvae to tide change.

Firstly, in the short-term experiments, postlarvae did not respond to an increase in pressure equivalent to 4 m of water depth over one hour but there was a substantial increase in activity during and after a corresponding decrease in pressure. This is consistent with the vertical migration behaviour we saw in the field studies where postlarvae moved into the water column at the beginning of the flood tide and sometimes at the end of the ebb tide. If postlarvae move off the seabed at the start of the flood tide they cannot be responding to an increase in pressure as their response occurs before the pressure has begun to rise. They may be responding to either a substantial period of pressure decrease associated with the ebb tide or a cessation of that pressure decrease at the time of low slack water. Our laboratory results suggest that, in the field, the postlarvae may be responding to a period of pressure decrease.

It is likely that the increased levels of activity on ebb compared to flood tides in the laboratory experiments using simulated tidal cycles are at least partly an artefact of the experimental apparatus. In our experiments, the postlarvae were confined in small chambers and did not have the freedom to move large distances in a vertical direction. In the wild, although water pressure at the seabed increases as the tide floods, postlarvae that respond to the tidal cycle and move towards the surface on the flood tide will actually move into an environment with lower pressure. In fact, postlarvae caught at the surface in field studies must have been continually swimming in a vertical direction as the pressure in their immediate environment decreased. In our experimental chambers they were not able to move into this decreased pressure environment during the flood tides, but were forced to remain in an increasing pressure environment. It is possible that this situation confused their response to the pressure (tidal) cycle and led to them being more active on the decreasing pressure phase of the cycle (ebb tide) in the laboratory.

It is not clear if this discrepancy in behaviour occurs with other species. Forward & Buswell (1989) tested crab larvae of several species in the laboratory and found that some swam upwards on pressure decrease while others descended on pressure decrease. Stage I *Uca pugnax* moved upwards on the pressure decrease. In a field study, however, *Uca* spp larvae were found to be higher in the water column on flood tides than ebb tides but it is not certain that the species were the same (Epifanio et al. 1988).

The results are not an artefact of using laboratory-reared postlarvae for the experiments as we observed the same increased ebb-tide activity in the laboratory when we tested postlarvae of

Penaeus plebejus that had been caught at the mouth of the Nerang River. These postlarvae were caught at the end of one of the 24-hour sampling series where postlarvae were found to be most active in the water column on flood tides.

6.5 Conclusions

Despite the difficulty in interpreting the form of the postlarval response to tide changes in the laboratory, it is clear that the postlarvae do respond to the cyclical pressure changes at shallow simulated water depths but do not respond at greater depths. This has substantial implications for the definition of effective spawning grounds of prawns in the Gulf of Carpentaria. Condie et al. (1999) calculated effective spawning areas for the Gulf of Carpentaria for transition depths (where postlarvae begin to detect the flood tides) of 7, 15, 20 and 30 m. Our results suggest that their shallowest transition depth (7 m) is most likely to be closest to the actual situation.

In fact, the effective spawning areas may be even less than those estimated by the Condie et al. (1999) model for a 7-m transition depth. They assumed that, if the prawns were located shallower than the transition depth, they would respond to the tidal cycle as soon as they moulted to postlarvae. This is unlikely to be true as we have shown that small postlarvae do not seem to respond to changes in water depth at all. Therefore, no matter what the water depth, the postlarvae will not respond to the tidal cycle as early as assumed by the model.

In our experiments, we have only tested the response of postlarvae to tides with a range of 2 m. In some regions of the Gulf of Carpentaria and for some periods during the monthly tidal cycle, the tide range is much less than 2 m. Presumably, the water depth required for postlarvae to detect smaller tides would be even shallower and consequently the average transition depth may be even less than our experiments have suggested.

Our overall conclusion is that the effective spawning areas are likely to be small and not include much of the commercial fishing grounds.

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7. BENEFITS

The Northern Prawn Fishery will be the main beneficiary of this research. The benefits may be seen in two main areas.

The results will allow managers to make more informed decisions about future closures aimed at protecting spawning stock. If it is believed that fishing effort has reduced the spawning stock to critical levels then a closure of inshore waters to fishing during the critical spawning period for tiger prawns in the NPF (September-October) may help rebuild spawning stocks. Offshore waters could remain open to fishing. This would be effective provided there is no substantial migration of prawns from offshore to inshore waters during this period.

The results may also allow researchers to construct more useful stock assessment models of prawn abundance in the fishery by identifying more accurately the real levels of spawning stock. Researchers should then be able to investigate the relationship between spawning stock and subsequent recruitment to the fishery using these more realistic estimates. This would then enable managers to more accurately detect the effects of fishing effort and environmental variation on prawn catches.

8. FURTHER DEVELOPMENT

The main conclusion from this research is that most of the effective spawning in the Northern Prawn Fishery must occur in relatively shallow inshore waters. Much of this area is not fished commercially at all or is only lightly fished. There has also been very little survey trawling carried out in these shallow waters (< 10 m deep) in the past. Because our conclusion is, to a large extent, based on a hydrodynamic model of the water currents in the Gulf of Carpentaria, we believe it is important to carry out some validation of this model. Research should be carried out to confirm that an effective spawning population does actually exist in these inshore areas. It would also be important to determine how many adult prawns migrate between the offshore fishing grounds and the effective spawning areas during the spawning season.

It is important that hydrodynamic models of larval and postlarval advection be developed for other prawn fisheries. The banana prawn fishery in Joseph Bonaparte Gulf (JBG) in the NPF occurs in an area of large tidal ranges (up to 9 m) and very strong tidal currents. The fishery for banana prawns apparently occurs at a substantial distance away from the juvenile nursery areas and research on the currents in JBG is essential to help identify the effective spawning stocks. Studies on the response of postlarvae to simulated tides would be useful as it is possible that they may detect the larger tides at greater depths than postlarvae in the Gulf of Carpentaria.

It is also critical that a hydrodynamic model of the water currents in central and southern Queensland be developed to help identify the critical spawning areas for East Coast King Prawns. Further behavioural research on the postlarvae of this species should be carried out to determine depths at which the postlarvae begin to detect flood tides.

9. CONCLUSION

Condie et al. (1999) modelled the advection of postlarvae in the Gulf of Carpentaria but their model was limited in its accuracy because they did not know when the postlarvae began to detect and respond to flood tides (the transition depth). They reported results for assumed transition depths of 7, 15, 20 and 30 m and, for most regions of the Gulf, found large differences in the size of the effective spawning area with each transition depth (Figure 2.1, 2.2). For example, the effective spawning area in the Mornington region, assuming a transition depth of 7 m, was calculated to be less than 30% of the effective spawning area if the transition depth was assumed to be 30 m.

There were two main objectives of our project and our achievements with respect to these objectives are summarised below:

1. Measure the critical vertical migration behaviour of postlarval tiger and king prawns that determines their inshore advection patterns.

Tiger prawns

Our laboratory results for *Penaeus esculentus* and *P. semisulcatus* showed that, as for most penaeid prawns, postlarvae of all sizes were far more active at night than during the day. The results also showed that small and medium-sized postlarvae cannot detect a simulated tidal cycle of 2 m range when the water depth is 8 m or greater. In fact small postlarvae do not seem to react to substantial pressure changes at all whereas medium and large postlarvae do respond in a predictable way. Larger postlarvae were able to respond to the 2-m tidal cycle at simulated depths of 8 m but not at 12 or 16 m.

The maximum size of the large postlarvae in our experiments was greater than the size at which tiger prawn postlarvae usually recruit to estuarine and coastal nursery areas (Vance et al. 1996, Liu & Loneragan 1997). Therefore, even if larger postlarvae can detect the tidal cycles at greater water depths, field results suggest that these larger postlarvae are not usually the main component of postlarval recruitment to nursery areas.

The field sampling at Weipa in northern Queensland showed that, in shallow, estuarine waters both the tide and the day-night cycle affected the vertical migration behaviour of tiger prawn postlarvae. Postlarvae were caught in the water column more during the night and on flood tides.

Eastern king prawns

We were not able to carry out sufficient laboratory experiments on *Penaeus plebejus* to determine the critical depth at which these postlarvae begin to respond to tidal cycles, although it was clear that they do respond to simulated tides at a water depth of 4 m. They were also clearly more active at night than during the day.

The patterns of vertical migration behaviour seen in field sampling at Southport were broadly similar to those seen for tiger prawns at Weipa, but the responses to tide and day-night were more accentuated than for tiger prawns. The postlarvae were caught in the water column more during the night and on flood tides.

Although we cannot be sure of the depth at which postlarval king prawns begin to detect tidal cycles, the similarities we have observed in vertical migration behaviour of tiger and king prawn postlarvae suggest that postlarval *P. plebejus* may also not be able to detect tidal cycles in relatively deep water.

2. Incorporate this behaviour into hydrodynamic models to accurately estimate the effective spawning stocks of tiger and king prawns.

Tiger prawns

Our laboratory and field results suggest that the effective spawning areas for prawns in the Gulf of Carpentaria will be at the low end of the scale of areas described by Condie et al. (1999) (Figure 2.1, 2.2). We believe that medium-sized postlarvae would start to detect the tidal cycle at water depths somewhere between 4 and 8 m, but we cannot determine the depth more accurately than this. This range of depths encompasses the smallest transition depth (7 m) used by Condie et al. (1999). The effective spawning areas would therefore be no larger and probably smaller than the areas defined for their transition depth of 7 m. Based on advice from Dr. Condie we have not attempted to run the hydrodynamic model again using slightly different assumptions. Even if we knew the transition depth more accurately, the depth used in the hydrodynamic model is only resolved on a 10 km square grid, so we would not be justified in attempting to examine differences between transition depths of, for example, 6 and 7 m.

The practical implications of not being able to resolve the transition depth more accurately are probably fairly minor from a fisheries-management point of view. When the transition depth was set at 7 m, it was estimated that only about 2% of the commercial tiger prawn catch in October (when spawning levels in the fishery were highest) was taken in waters shallower than this depth (Condie et al. 1999). A smaller transition depth could not decrease this catch percentage much further.

There are two reasons to believe that the effective spawning areas may be even less than those predicted by the hydrodynamic model. Firstly, the model assumed that, if the prawns were located shallower than the transition depth, they would respond to the tidal cycle as soon as they moulted from larvae to postlarvae. This is unlikely to be true as we have shown that small postlarvae do not seem to respond to changes in water depth at all. Therefore, no matter what the water depth, the postlarvae will not respond to the tidal cycle as early as assumed by the model.

Secondly, the hydrodynamic model made no allowance for day-night variability in activity once postlarvae had begun to cue to the flood tides. This is again clearly not correct and the fact that postlarvae, when cued to the flood tides are still more active on night flood tides than day flood tides means that they will move inshore more slowly than predicted by the model. Therefore the model has slightly overestimated effective spawning area based on these two factors.

Eastern king prawns

There is some disagreement on the relative importance of inshore versus offshore spawning/long-distance larval advection for eastern king prawns (see Rothlisberg et al. 1995 for review). However, it is not possible to identify effective spawning areas for eastern king prawns based on the results of this project. This subject is discussed more fully in the report of the linked FRDC project “Developing indicators of recruitment and effective spawner stock levels in eastern king prawns” (FRDC 97/145).

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Mr Peter Thomson carried out most of the development of the computer software needed to control the laboratory experimental apparatus. Ms Sandy Keys, Mr Stuart Arnold and Mr John Graffe maintained prawn brood stock and reared larvae through to postlarval stages for use in our experiments. Mrs Sue Cheers, Mr Quinton Dell, Ms Michelle Jones and Mr Clinton Muller spent many hours analysing videotapes of postlarval activity and entering the data onto computer. Ms Michelle Jones also helped carry out some of the experiments on postlarval behaviour. Mr Rob James, a CSIRO Vacation Student, provided valuable help with the short-term behavioural experiments. Dr Neil Loneragan, Dr Roland Pitcher and Mr Don Heales of CSIRO Marine Research provided many useful comments and suggestions on the draft report. We are also grateful for the support and encouragement of Dr Neil Loneragan, Dr David Die and Mr Don Heales of CSIRO Marine Research.

APPENDICES

Appendix 1: Intellectual property

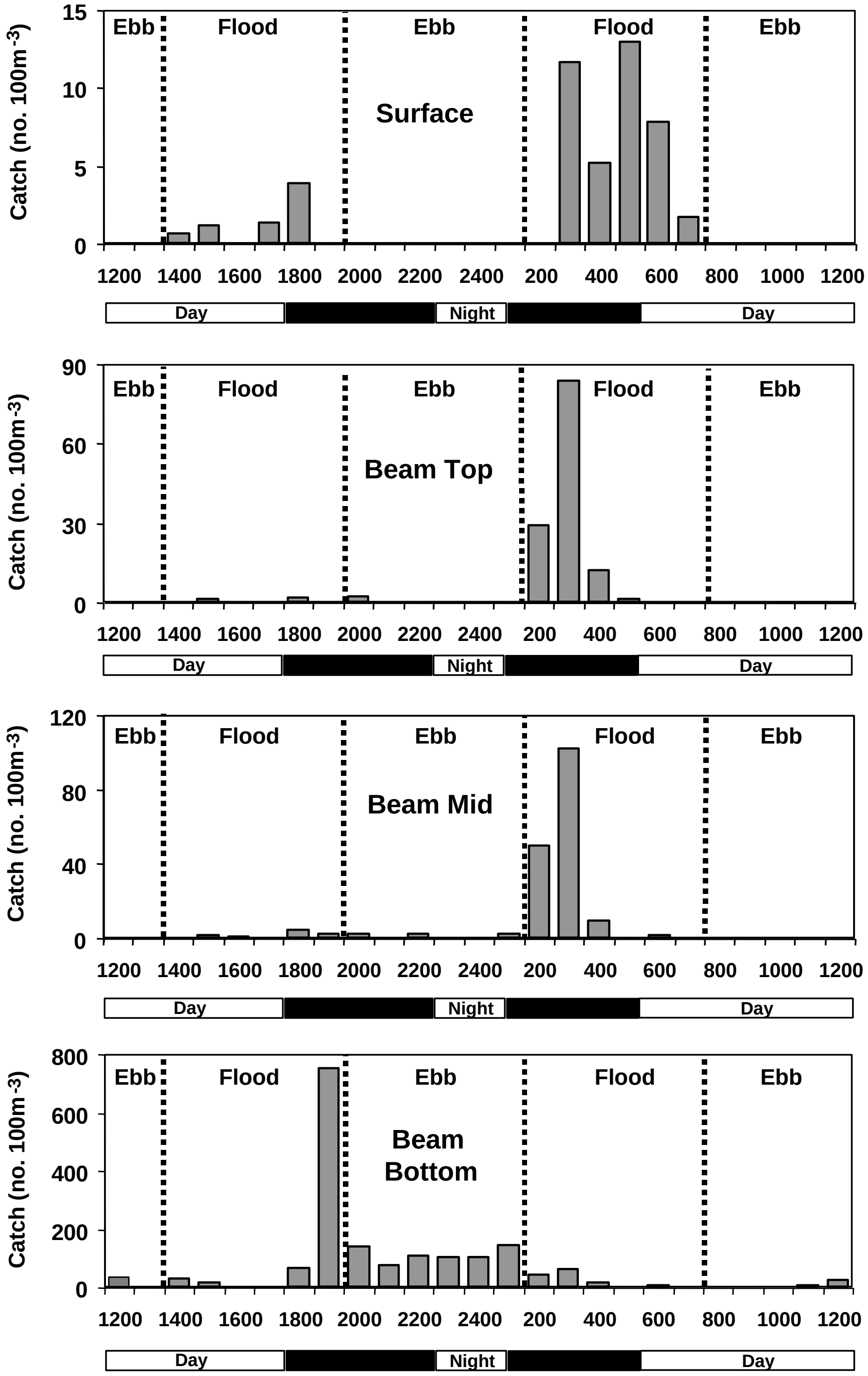
No commercial intellectual property arose from this work.

Appendix 2: Staff

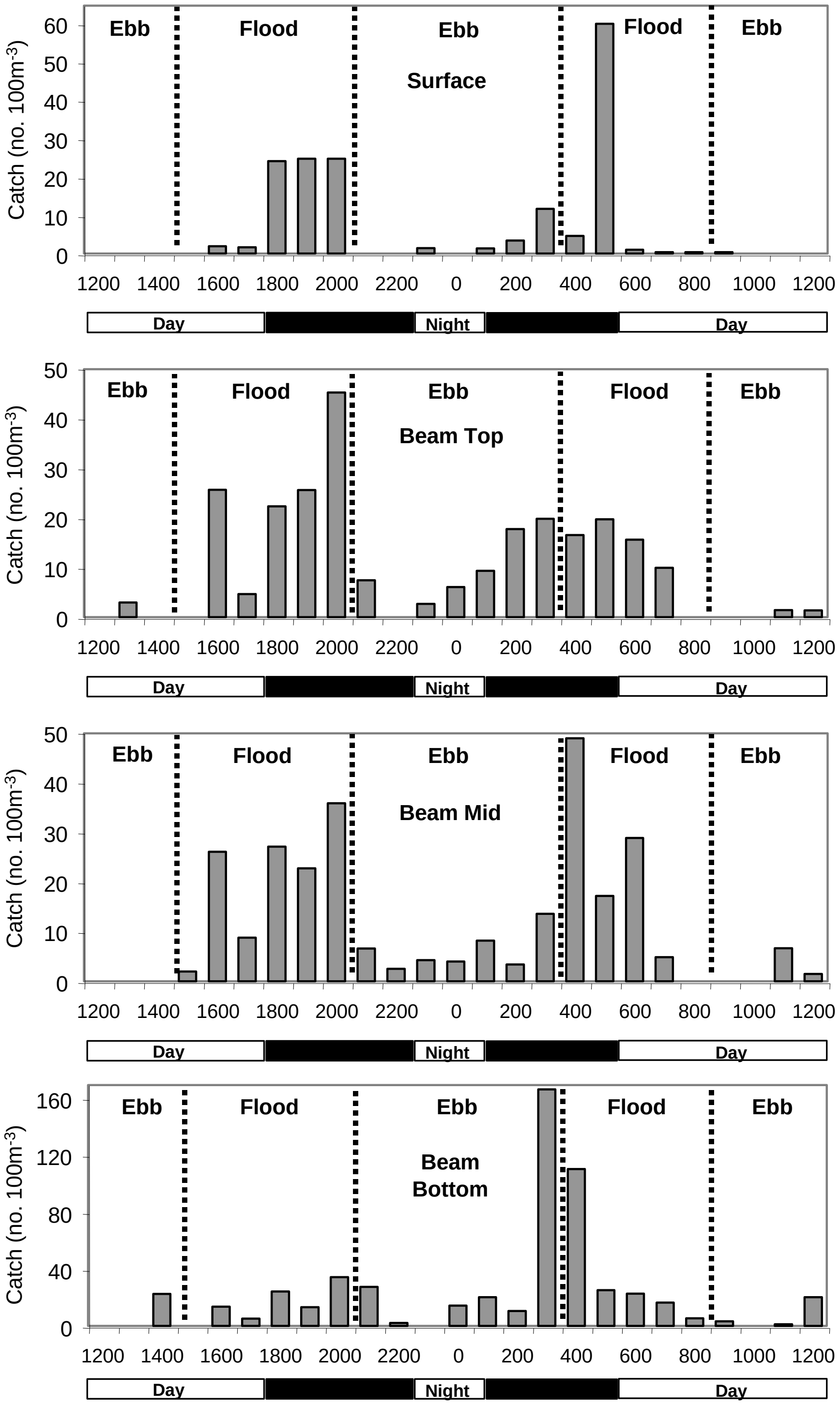
CSIRO Marine Research
Mr David Vance
Mr Bob Pendrey
Mr Greg Smith
Dr David Griffin
Dr Scott Condie

Qld QDPI
Dr Tony Courtney

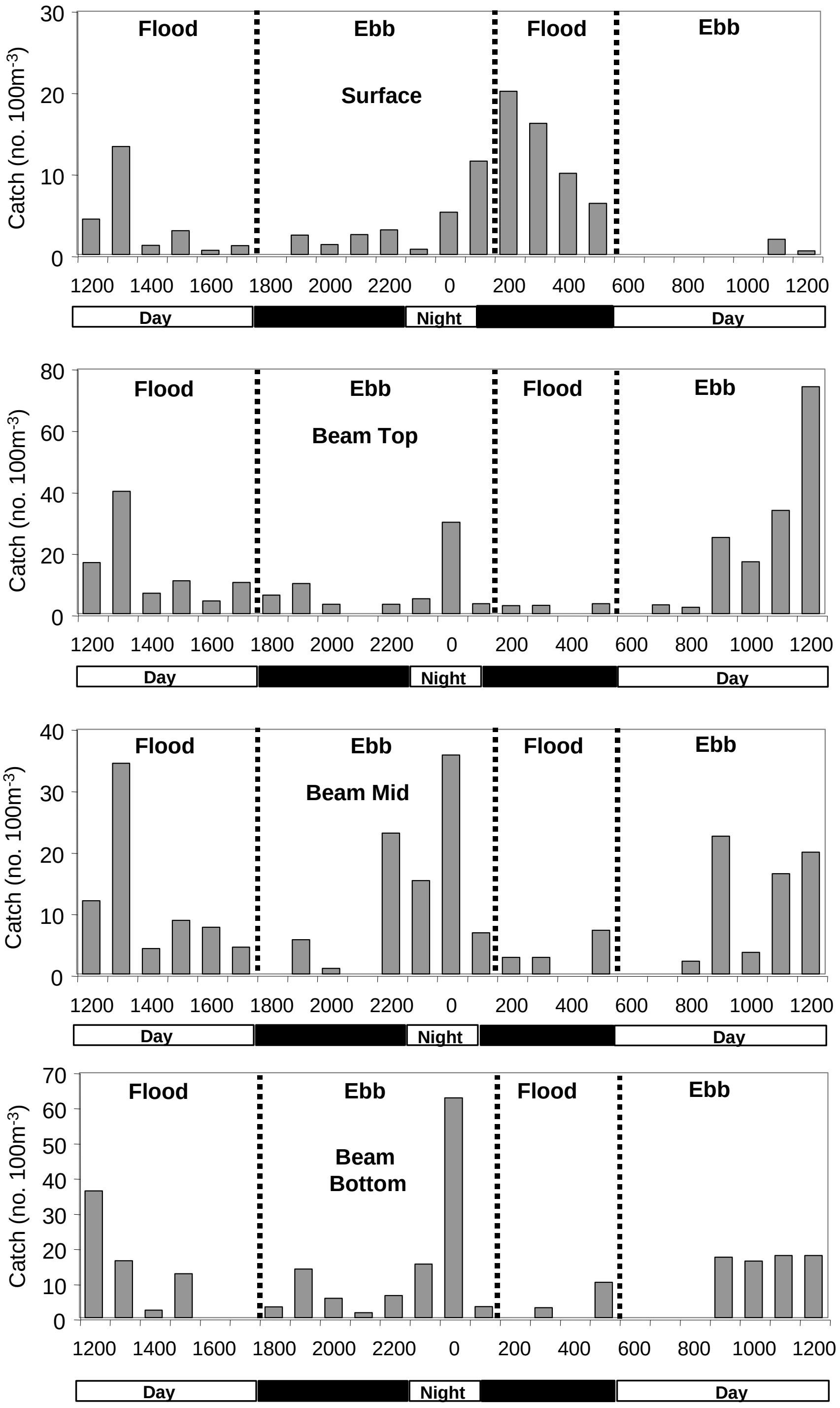
Appendix 3: Extra figures – field and laboratory results not included in main report



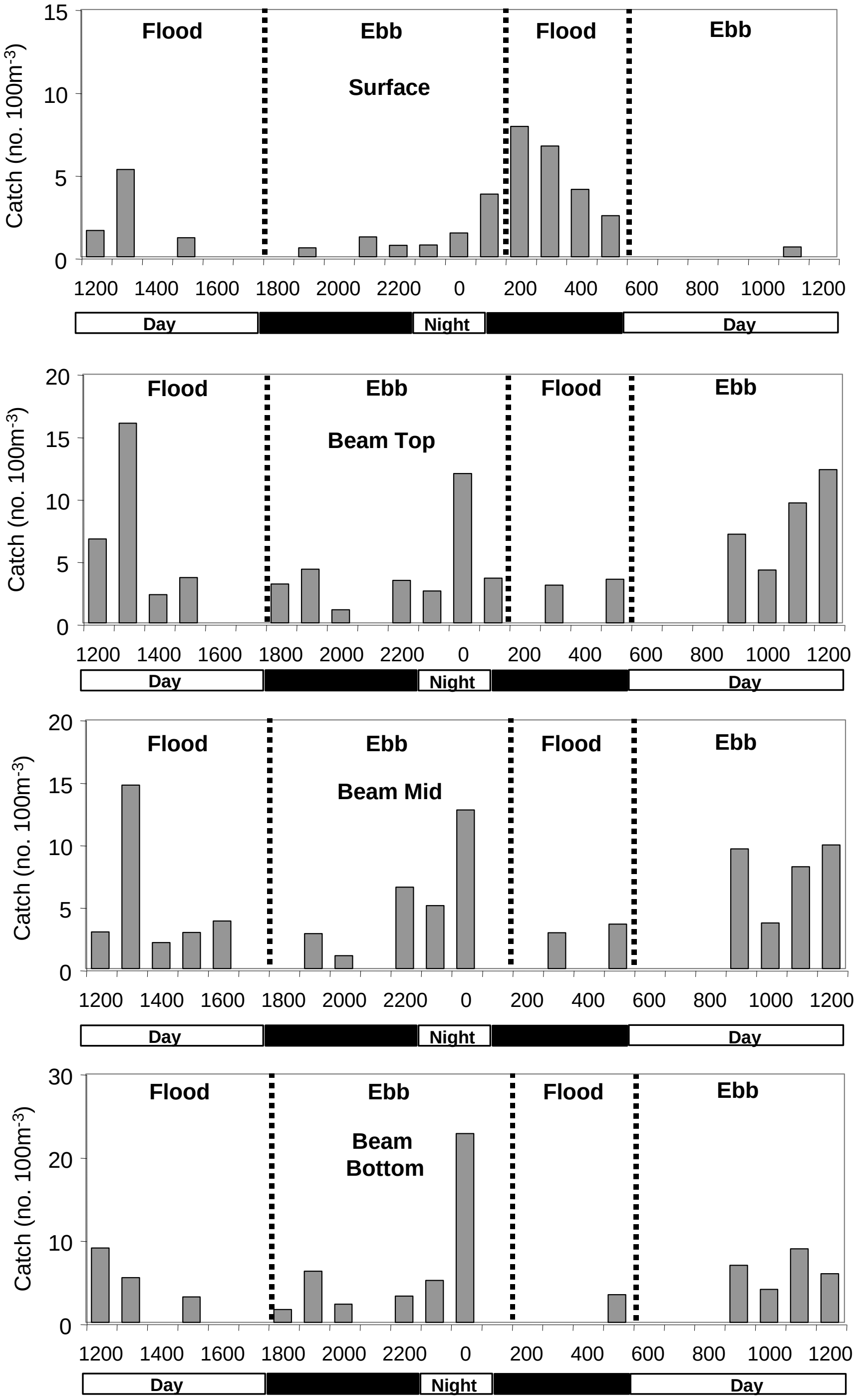
Appendix 3.1. Catches of *Penaeus plebejus* postlarvae (< 3.0 mm CL) at the mouth of the Nerang River, Southport throughout 24 hours in four nets on 7-8 May 1998.



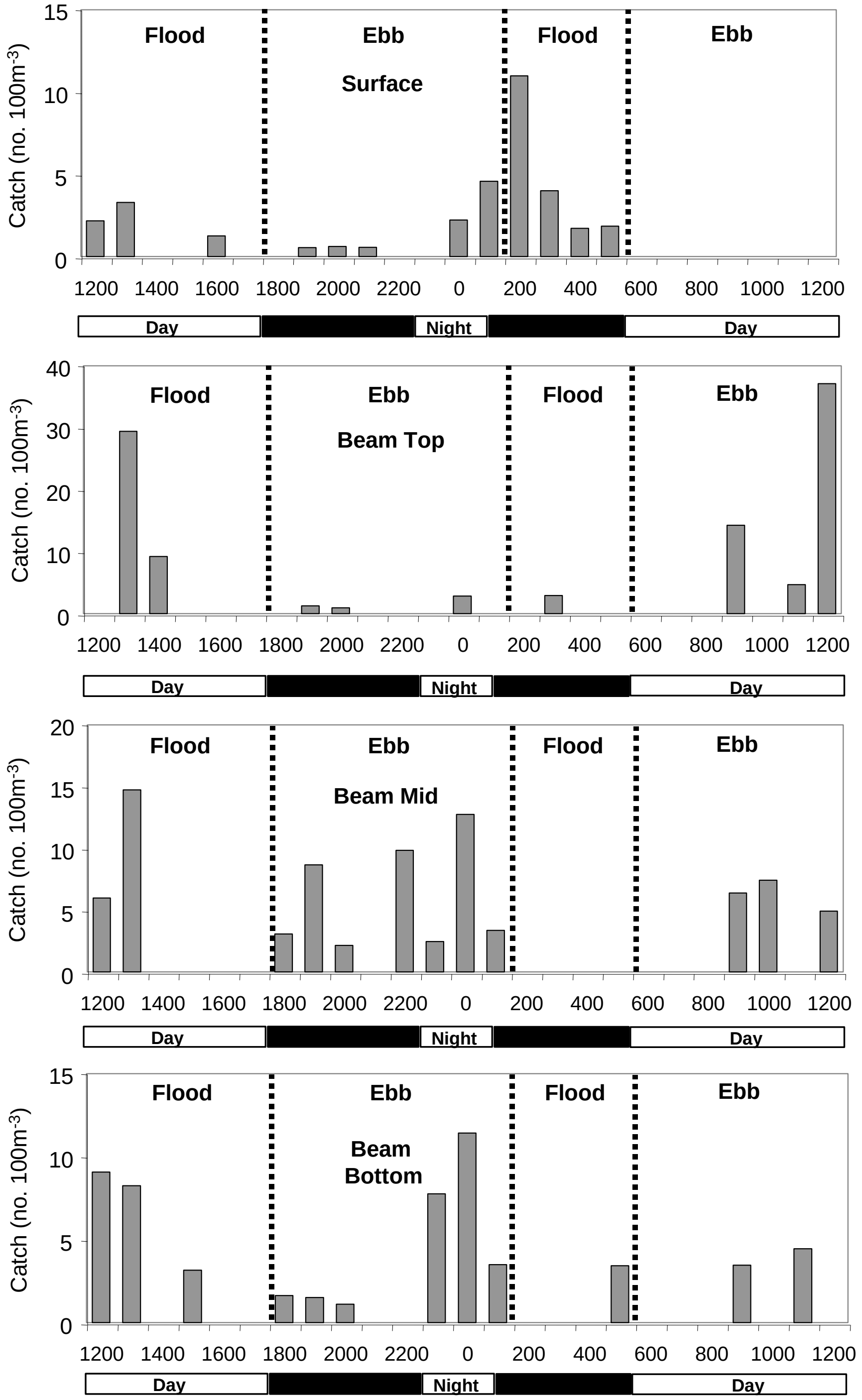
Appendix 3.2. Catches of *Penaeus plebejus* postlarvae (< 3.0 mm CL) at the mouth of the Nerang River, Southport throughout 24 hours in four nets on 12-13 July 1999.



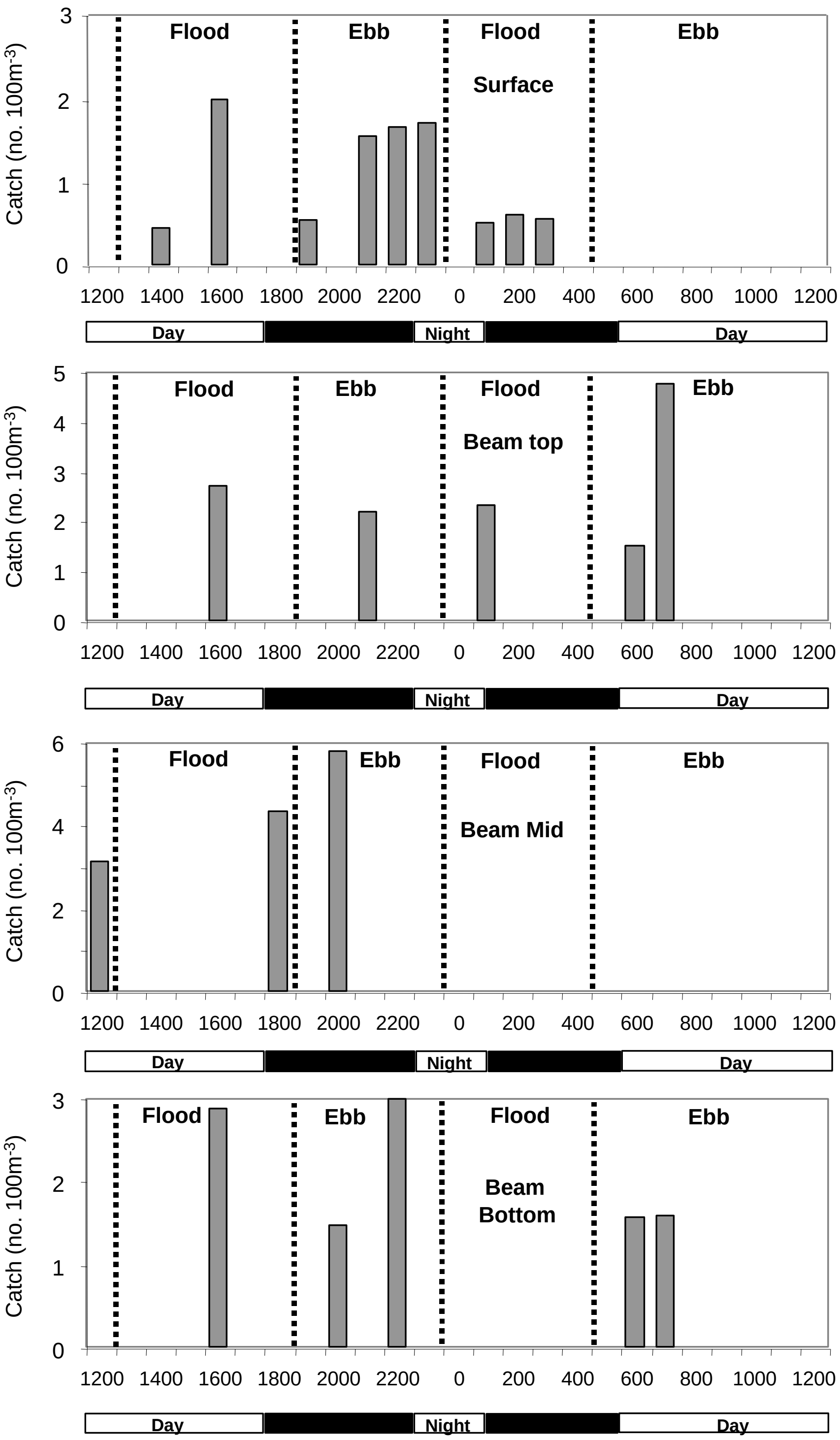
Appendix 3.3. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 21-22 October 1998.



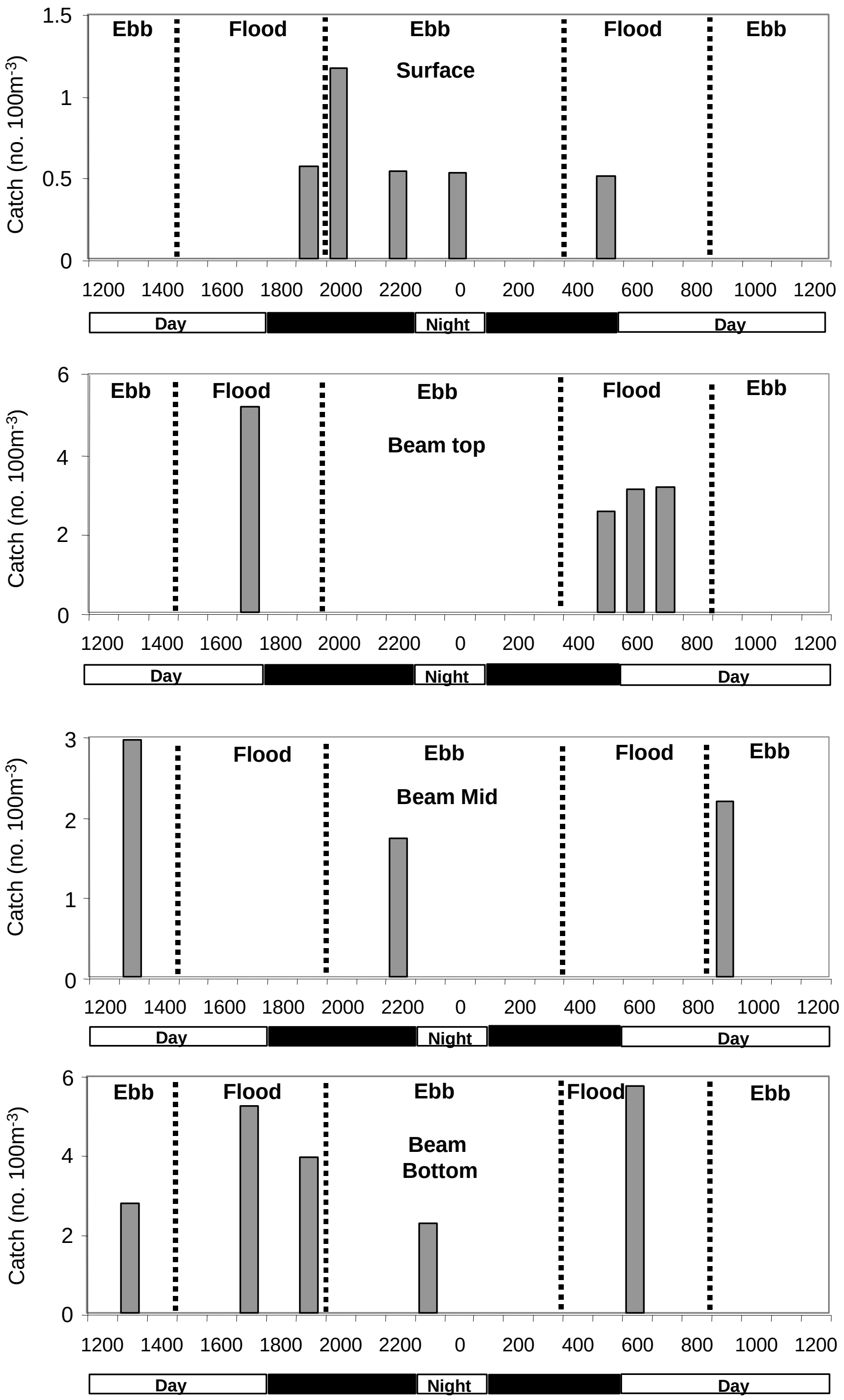
Appendix 3.4. Catches of *Penaeus esculentus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 21-22 October 1998.



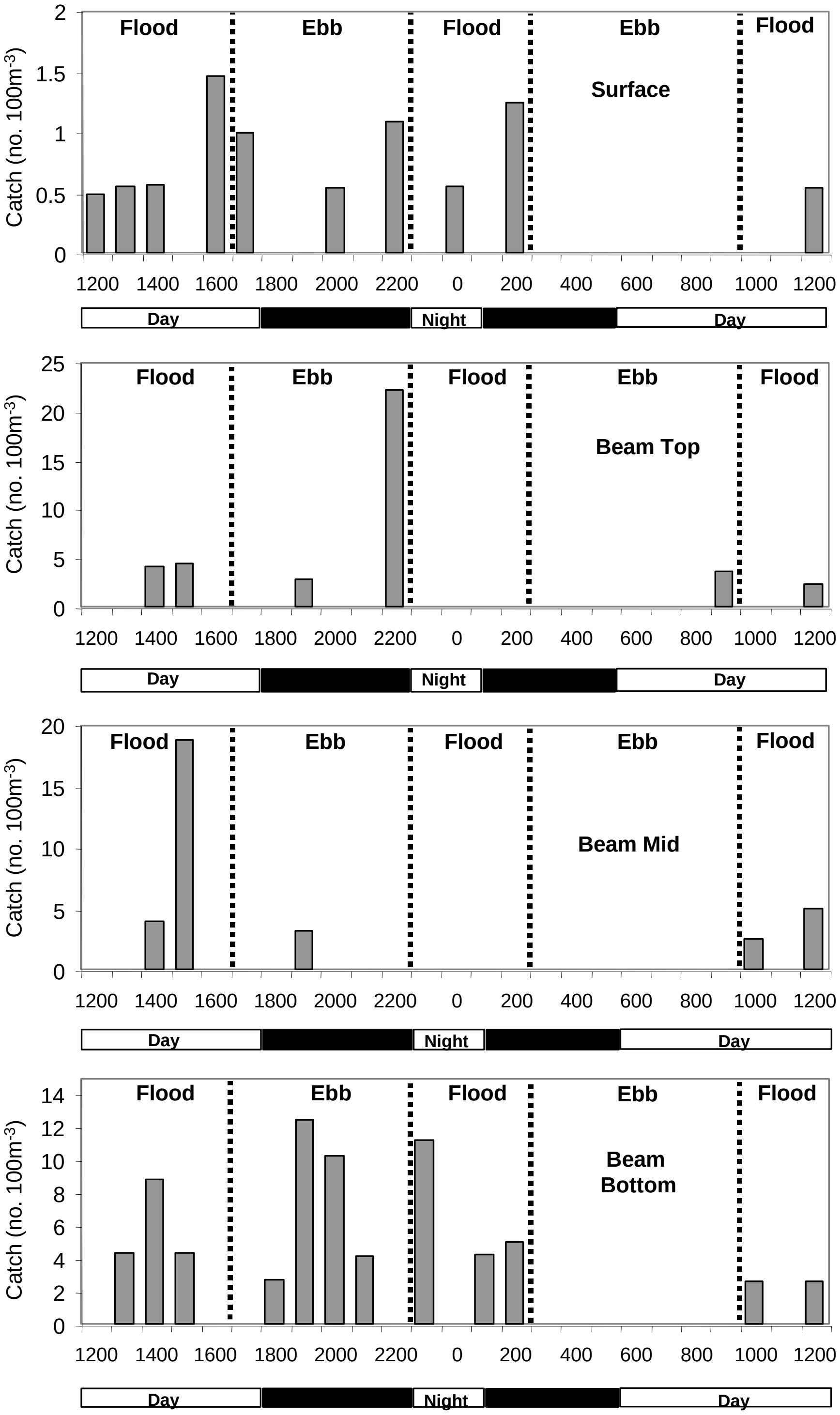
Appendix 3.5. Catches of *Penaeus merguiensis* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 21-22 October 1998.



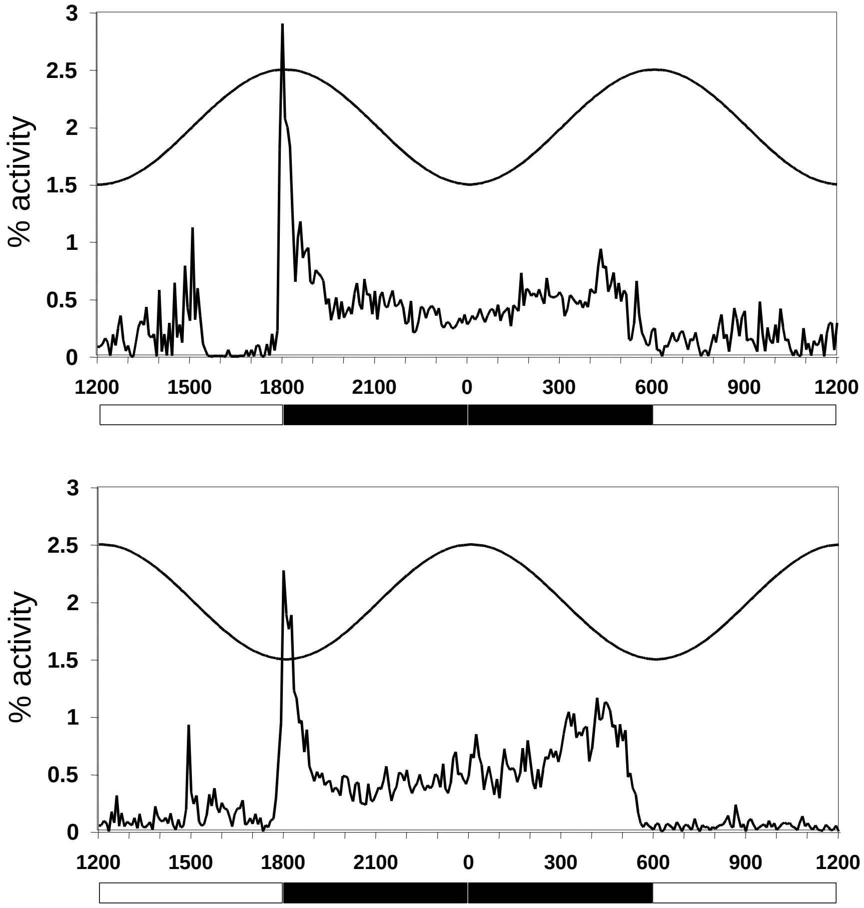
Appendix 3.6. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 10-11 September 1999.



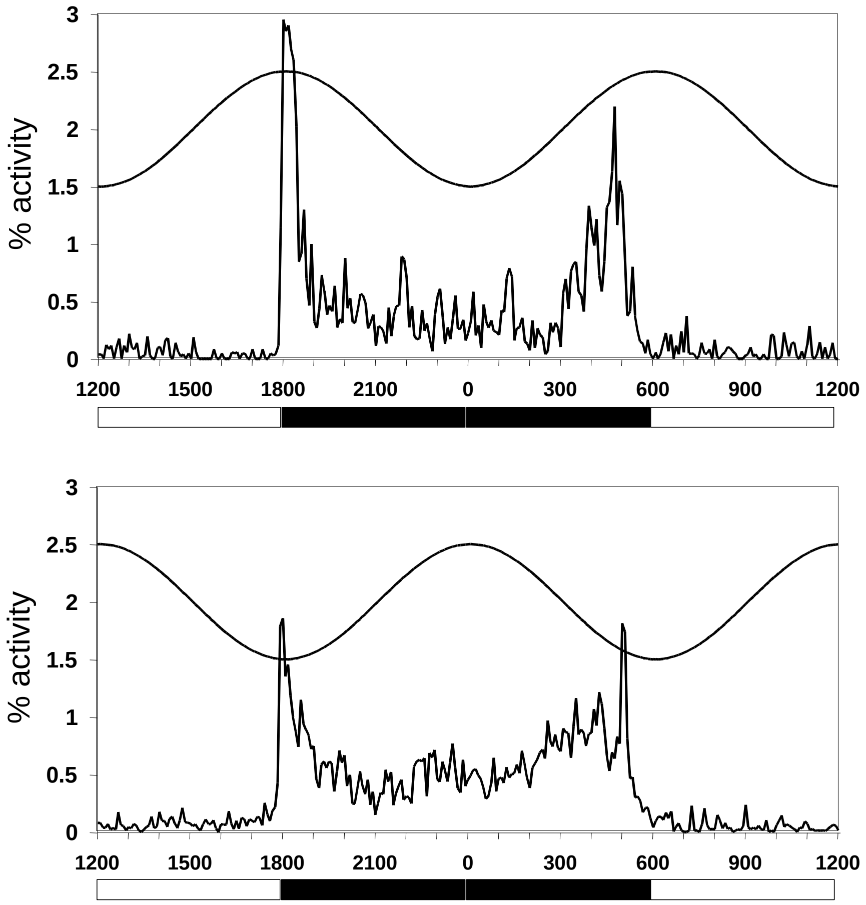
Appendix 3.7. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 14-15 September 1999.



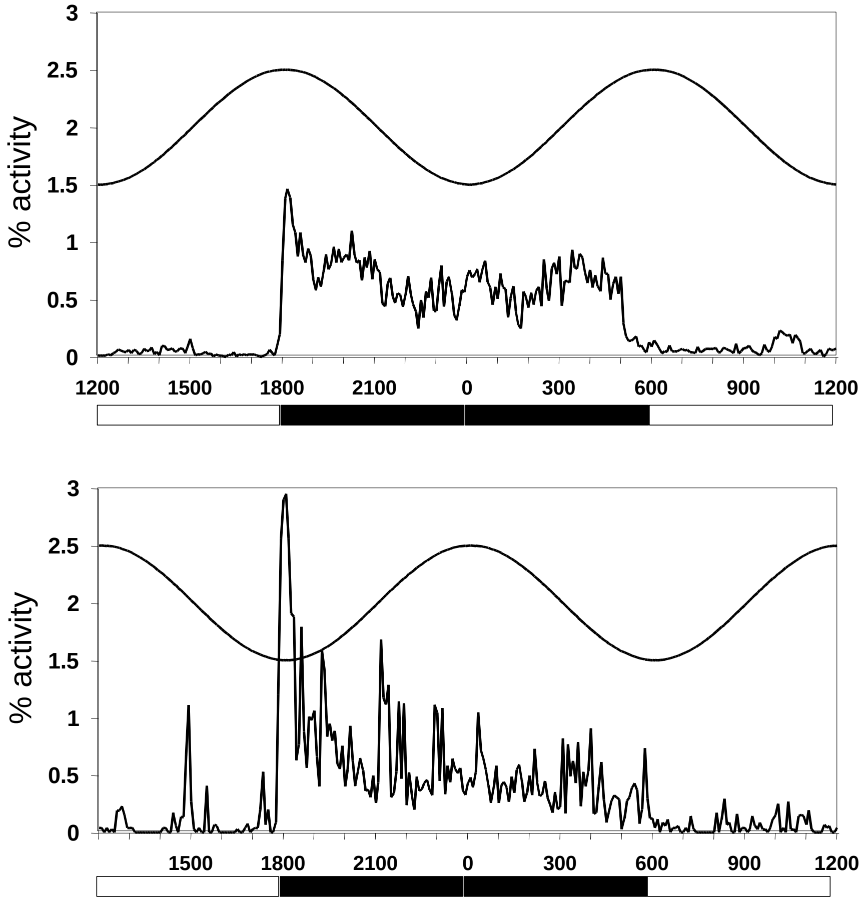
Appendix 3.8. Catches of *Penaeus semisulcatus* postlarvae (< 3.0 mm CL) at the mouth of the Embley River, Weipa throughout 24 hours in four nets on 22-23 October 1999.



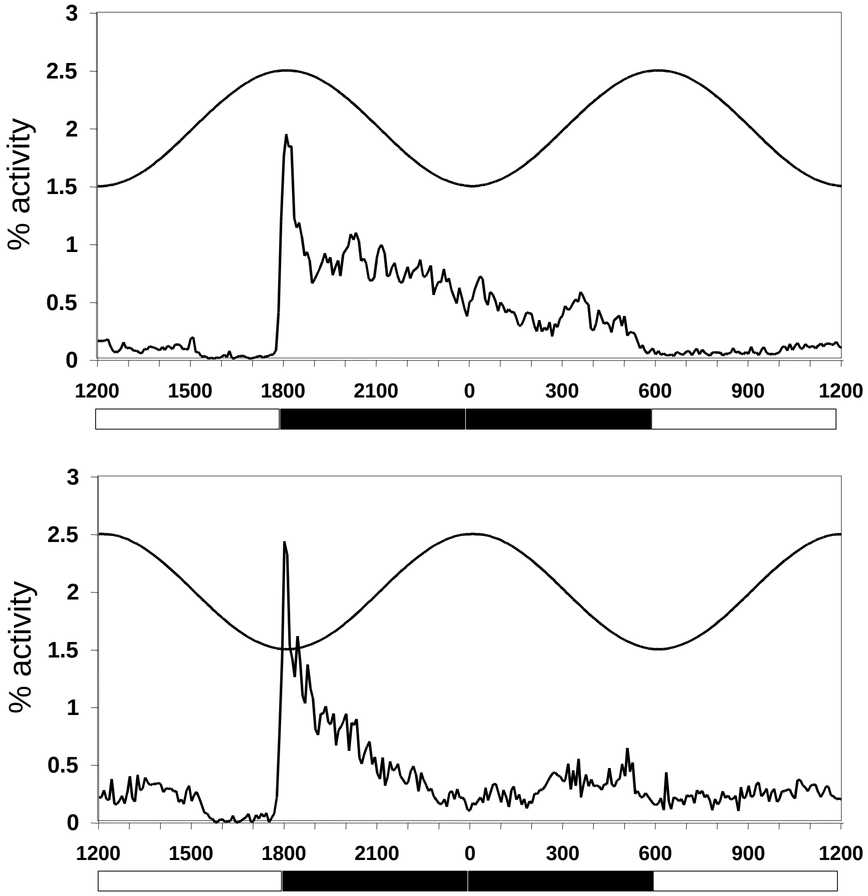
Appendix 3.9. Mean activity of medium sized *Penaeus esculentus* postlarvae at a simulated water depth of 12 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.



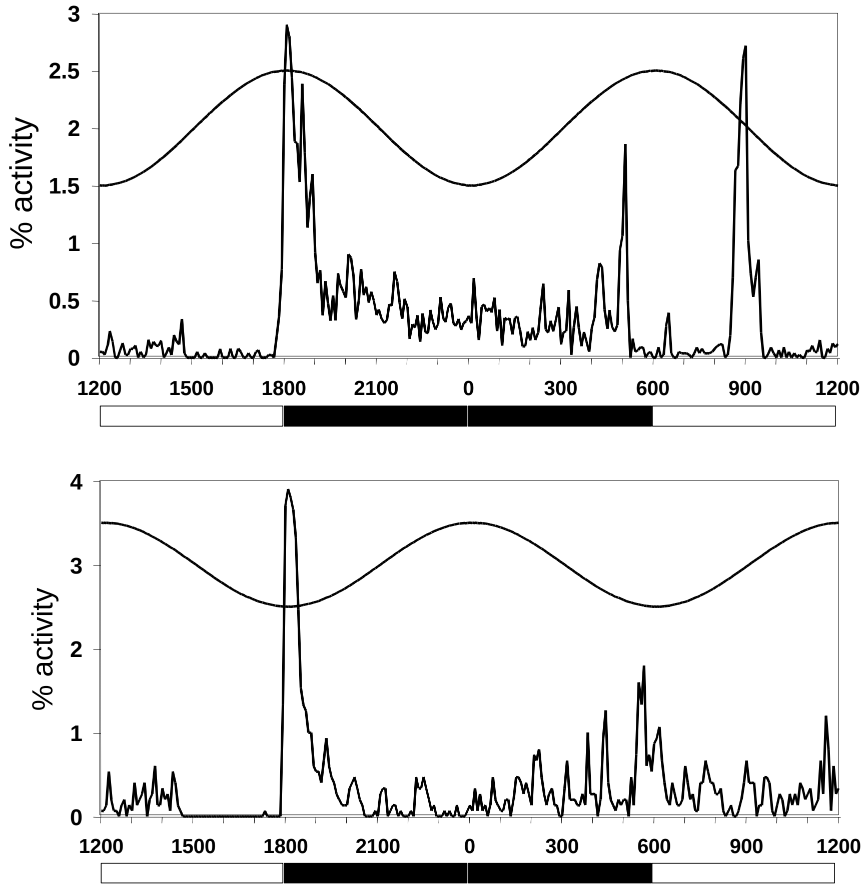
Appendix 3.10. Mean activity of medium sized *Penaeus esculentus* postlarvae at a simulated water depth of 16 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.



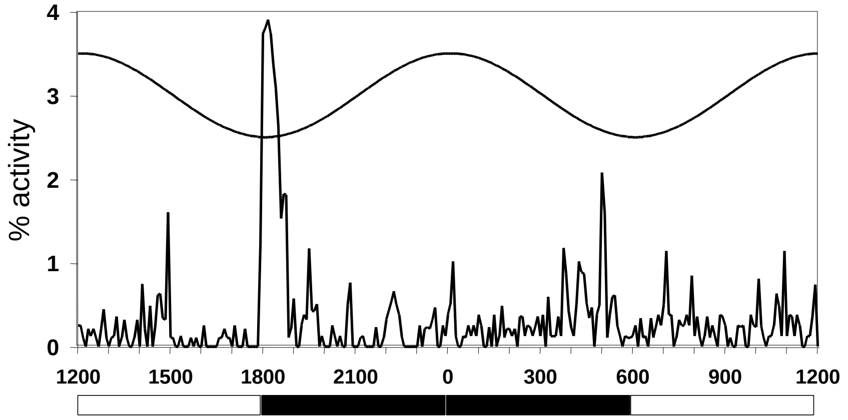
Appendix 3.11. Mean activity of large *Penaeus esculentus* postlarvae at a simulated water depth of 12 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.



Appendix 3.12. Mean activity of large *Penaeus esculentus* postlarvae at a simulated water depth of 16 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.



Appendix 3.13. Mean activity of large *Penaeus semisulcatus* postlarvae at a simulated water depth of 12 m with high tide set at a) 0600 and 1800, and b) 0000 and 1200.



Appendix 3.14. Mean activity of large *Penaeus semisulcatus* postlarvae at a simulated water depth of 16 m with high tide set at 0000 and 1200.

Appendix 4: Technical details of experimental apparatus

The item numbers in the following list refer to identifying numbers on Figure 6.1.

3. Pressure pump: Easy Pump Garden 1000. Plastic fountain pump draws 1000 watts and can pump to a 48-metre head.

4. Pressure release valve: a simple spring-operated valve available from irrigation shops.

6. Flow regulating device: Moore Flow controller 63-SD matched with Blue and White Flow Meter F 700E, operating range 100-700 ml/min.

7. Flow sensor: RS (Radio Spares) -256-225 Paddle wheel.

8 Circulation pump: Iwaki MD-10 magnetic drive pump.

9. Circulation control valve: a manually-operated gate valve.

10. Flow sensor: RS (Radio Spares) -256-225 Paddle wheel.

12. Camera and video recorder: Video Camera - Panasonic Super Dynamic WV-BP554 with 9 mm lens WV-LA-908-C3; Video Recorder – Panasonic Time Lapse Video Cassette Recorder AG-6730.

15. Pressure sensor: Pressure transducer Setra C206 0-350 kPa

16. Needle valve: Control valve Hoke 18 turn metering valve 1315M4Y-316SS attached by custom made sliding union to stepper motor RS 23 440-442 giving 200 steps per turn.

Light control
Clipsal C-bus software and hardware, supplied by Gerard Industries Pty Ltd, controlled the lighting in the experimental enclosure and allowed the simulation of dawn and dusk by gradually increasing and decreasing light intensity over a period of one hour.

Computer software
The software was written in Visual Basic. It continuously compared the actual pressure in the experimental system with the expected pressure and made adjustments to the needle valve at 2 or 20 second intervals depending on whether the two values were trending away or towards each other. To raise the pressure in the chamber the software closed the needle valve (16 in Figure 6.1) in steps; to lower the pressure it opened the valve. When the pressure values were approaching each other, response time was slowed and the number of steps constrained. When the values were diverging, the response was quicker and the number of steps greater.

The software allowed these parameters to be easily edited on screen before or during the experiments to allow for different valve settings for different pressures (depths) and water exchange rates. With an experimental depth range of from 3 to 5 metres and a water flow rate of about 150 ml/min, it required about 290 needle valve steps to change the water depth by one metre.

The computer was interfaced with the experimental apparatus via a DAQ-801 interface card with a DCC10-P counter time card.