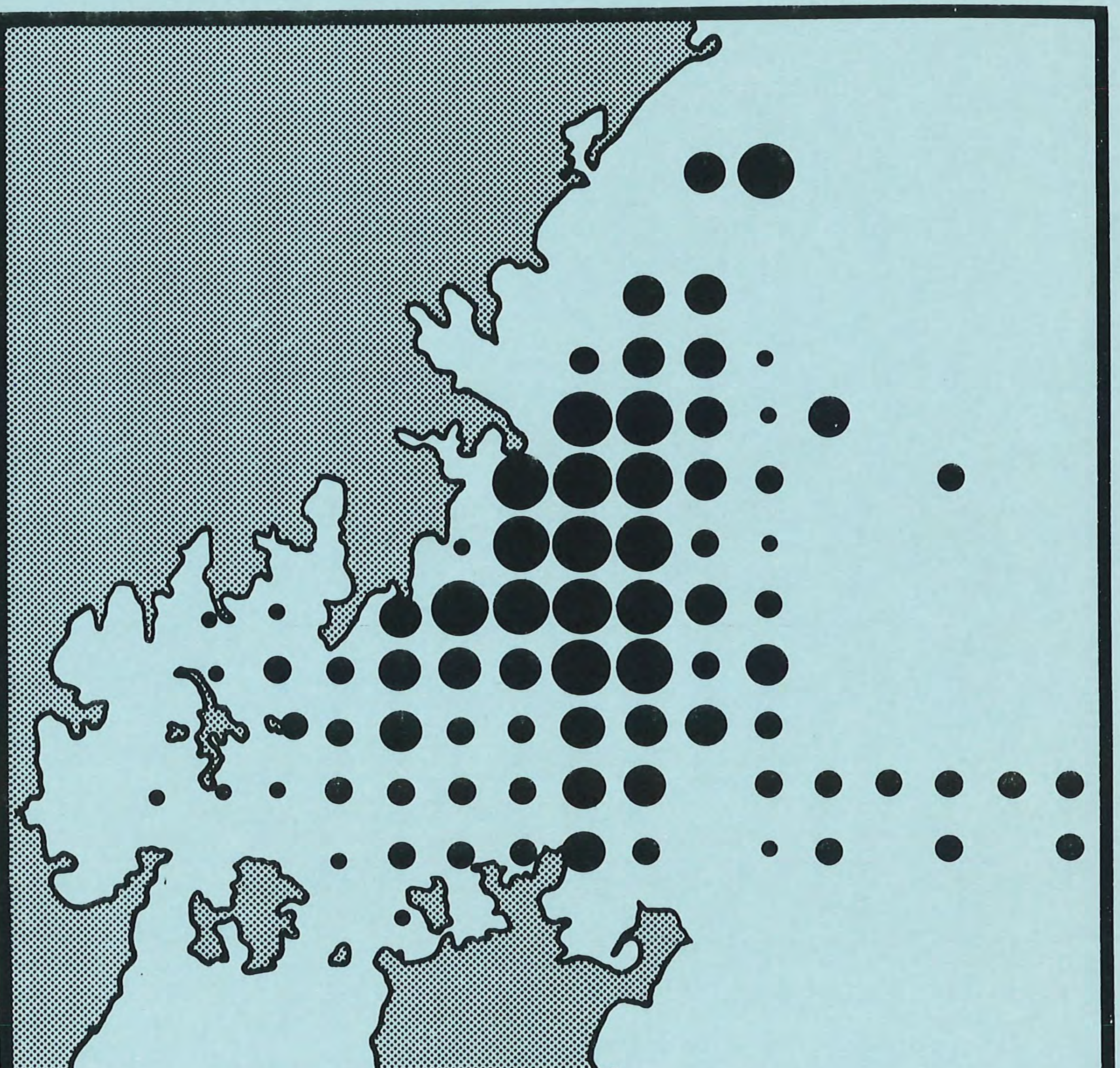
Investigation of the Biology of Tiger Prawns in the Western Gulf of Carpentaria

Final Report Project 82/13



CSIRO Marine Laboratories, Cleveland

Investigation of the Biology of Tiger Prawns
in the Western Gulf of Carpentaria

CSIRO Division of Fisheries Research
Cleveland Marine Laboratories

Final Report: FIRTA Project 82/13

CONTENTS Page

1. SUMMARY

A project to investigate the biology of tiger prawns in the western Gulf of Carpentaria was carried out over a three year period from 1982 to 1985. The main study area was in the commercial fishing area and adjacent nursery grounds north of Groote Eylandt. The commercial fishery for tiger prawns in this area is based on two species which are not distinguished by fishermen. Prior to this study, because of this difficulty, it was not possible to identify trends in catch rates or study the population dynamics. Therefore, stock assessment and rational management were not possible. The overall objective of the study was to obtain sufficient information on both species of tiger prawns to enable CSIRO to provide sound management advice to the Northern Fisheries Committee. The study as a whole concentrated on the dynamics of one complete generation, including spawning, larvae, postlarvae, juveniles and the exploited fishery stage.

Brown tiger prawns were found to spawn inshore, the whole year round, whereas grooved tigers spawned in deeper water offshore, but mainly from July to December. However, larvae were most common only in the summer months for both species. Settlement of postlarvae into seagrass nursery areas occurred mainly from October through February. It was concluded that the effective spawning period, resulting in recruitment of both species, occurs in August and September. Postlarvae settled in seagrass nursery areas but not all seagrass areas were utilised equally, the postlarvae being restricted to limited areas in more sheltered habitats. Cyclone damage to the beds was found to be a major factor affecting juvenile prawn survival and subsequent commercial catches.

About six months after spawning (December to February) prawns arrive on the fishing grounds. As they grow, the prawns move offshore and the two species separate; the grooved tiger move further into deeper water where substrates are finer. This spatial separation has allowed species resolution in the commercial catch data from logbooks dating back to 1970. The prawns are fished from April and the fleet concentrates initially on brown tiger prawns because they are found in waters sheltered from the winter winds. In spring, the fishing effort is

redirected to the offshore stocks of grooved tigers. The populations decline rapidly through the August-September spawning period and few prawns survive beyond one year.

Annual recruitment of both tiger species in the western Gulf of Carpentaria has declined in recent years by about 50%. The decline was initially in brown tigers, probably because of the impact of fishing of this species before spawning. In more recent years, effort on grooved tigers has also increased as a consequence of the decline of brown tiger stocks.

The project has been highly successful in all respects. Virtually all of the objectives have been achieved; population dynamics of the two species have been examined, the times and places of spawning have been described, nursery areas delimited and factors affecting recruitment identified. Most importantly, this information was critical in understanding the fishery's recent decline and timely in formulating the current revised management regime. Results have been transmitted directly to NORMAC, and to the industry through the CSIRO Information Notes, seminars and workshops. In addition, six papers have been published in scientific journals, three in CSIRO Information Notes (Appendix 4) and another nine are in preparation (Appendices 1, 2 & 3).

The results from this research will become part of a more extensive on-going data collection process, from both past and current research (e.g. FIRTA 85/85), enabling the Gulf of Carpentaria prawn fishery as a whole to be better understood and thus better managed. The new special issue of the Australian Journal of Marine and Freshwater Research (Vol. 38(1), 1987) on Prawn Ecology and Biology demonstrates how this process takes place.

2. MANAGEMENT IMPLICATIONS

The study revealed significant declines in recruitment of each species, associated with major increases in fishing effort. From the preliminary analysis of exploitation levels and the estimate of commercial catch, it was possible to determine an annual recruitment index for tiger prawns in the western Gulf of Carpentaria for 1984. This was extrapolated to earlier years based on standardised fishing effort levels and thus it was possible to carry out a preliminary stock assessment for the two species in the region. The results indicated that a reduction of at least 25% in fishing effort was required to restore recruitment levels (Somers 1987a, Appendix 4.6). Identification of nursery areas resulted in extensive permanent closures to protect juveniles. Seasonal closures, based on detailed knowledge of the life history dynamics, have also been implemented to prevent the taking of uneconomical small prawns in December and to reduce the capture of prawns in June and July before the effective spawning season (Hill 1987, Appendix 4.3). These conclusions were reported to NORMAC in October, 1986, and enabled immediate management measures to be implemented.

3. OBJECTIVES

The overall aim of the project was to obtain sufficient information on tiger prawns and the tiger prawn fishery to enable CSIRO to provide sound management advice to the Northern Fisheries Committee. Specific objectives were as follows:

1. Describe the population dynamics over the whole life cycle of both species of tiger prawns. There were three aspects to this study. Firstly, attempt to enhance the value of logbook catch and effort data which did not distinguish between the two species of tiger prawns, by investigating the seasonal and area distribution of the two species. Secondly, to estimate the level of exploitation within the fishery independently of commercial fishery catch and effort data. Thirdly, to determine the optimum size for capturing tiger prawns so that suitable management measures could be invoked to protect prawns of an uneconomic size and maximise economic return to the fishery.

2. Determine the times and places of spawning of the two species of tiger prawns together with the links between these spawning sites and nursery grounds.

3. Delimit the tiger prawn nursery grounds and determine which areas contribute most to the commercial stocks.

4. Investigate factors affecting recruitment of juvenile prawns to offshore fishing areas as a mean of developing a stock prediction model similar to that for the banana prawn fishery.

The research was divided into three sections, each supervised by a senior research scientist. Each section covered a separate phase of the prawns' life cycle:

1. Adult ecology - the exploited phase on the fishing grounds;
2. Juvenile ecology - the nursery ground phase;
3. Larval ecology - the planktonic phase.

Full reports, including the attainment of objectives and the main conclusions are be given under each of these headings. Detailed results are included in the appendices.

4. SECTION REPORTS

4.1. Adult ecology

Objectives:

The research reported here comes under Objectives 1, 2.

Field work completed:

Survey cruises, which each encompassed an average of 73 trawl stations, were carried out every lunar month in the area north of Groote Eylandt in the western Gulf of Carpentaria. In all, 21 trawl cruises were carried out between August 1983 and March 1985. All prawns collected were identified, sexed and measured, and samples of females of both tiger prawn species were examined histologically to ascertain ovarian development. A sediment survey was carried out over 360 sites covering the whole of the western Gulf fishing grounds in order to establish the sediment type in each 6 nautical mile grid square. Approximately 14,000 tiger prawns were tagged and released during the project to estimate rates of growth and patterns of migration.

Objectives attained:

1. Population dynamics

1.1 Logbook data enhancement:

Juveniles of both species of tiger prawn (*P. esculentus* and *P. semisulcatus*) share common seagrass nursery areas but once they move offshore onto fishing grounds, it was found that the distribution of each species showed little overlap. This effective separation in the adult phase was linked to differences in sediment/depth preferences between the species. *P. semisulcatus* was found mainly on very muddy sediments (>70% mud) in depths of between 20-50 m, whereas *P. esculentus* was found on sediments with a lower mud content and in depths of 10-30 m. This aspect of the study has been documented in more detail in the paper by Somers (1987a, Appendix 4.7) who examines which factors influenced the distribution of all the commercial species caught in the study.

The sediment survey carried out over the whole western Gulf enabled individual tiger prawn species to be separated from the logbook data for this region. Furthermore, because these factors (sediment/depth) are permanent, the allocation of commercial catch data between the two species has been extended back to the commencement of the fishermen's logbook program (1970). There are now 17 years of commercial fisheries data for the two species. This has facilitated stock assessments for the two species at a time when this information is crucial for management.

The objective of this aspect of the study has been achieved in full and it is already clear that the results (species/sediment associations) can be applied to other prawn fisheries. The results therefore, provide a sound foundation for enhancement of the commercial tiger prawn data of the whole Northern Prawn Fishery.

1.2 Estimation of exploitation level independent of commercial data:

Preliminary analysis of the data collected from the surveys indicates annual exploitation levels in excess of 50% and hence there is little scope for increasing yield per recruit with increased effort. Further analysis on mortality rates was delayed when it became clear that increased fishing effort was already having a detrimental effect on annual recruitment levels. A more detailed analysis is being completed.

1.3 Determination of optimum size at first capture

The industry prefers to regulate size at first capture through seasonal closures rather than with knife-edge methods such as mesh size or minimum legal sizes. A model was developed which, given information on exploitation and growth rates together with market prices for the various size grades, provided a tool for calculating the optimum opening date based on the size composition of the population rather than calculating an optimum size at first capture. The model has now been successfully applied to the banana prawn fishery in the eastern Gulf of Carpentaria where all the required input parameters were previously known. The equivalent modelling of the tiger prawn fishery will be carried out as soon as the analysis of mortality rates is completed (see 1.2 above).

2. Determination of the times and places of spawning of the two species of tiger prawns

Both the time and place of spawning was accurately measured for both species using an index of population egg production to describe reproductive output. Seasonal and spatial spawning patterns were markedly different for the two tiger prawn species.

Brown tiger prawns, *P. esculentus*, were found to spawn mainly in the area immediately to the north of Groote Eylandt, with spawning occurring in shallow inshore areas including North West Bay. In contrast, grooved tiger prawns, *P. semisulcatus*, were found to spawn further offshore in deeper water to the north-east of Groote Eylandt.

Seasonality of spawning also differs between the two species. Brown tiger prawns spawned over a prolonged period from July to March with some year to year variation, but the pattern of recruitment of sub-adults suggest that effective spawning is restricted to the spring months. The grooved tiger prawn has two discrete spawning periods; spring (Aug-Oct) and autumn (Feb-Mar), with the clearly defined and dominant spring spawning being the most important for stock renewal.

Results in detail:

Appendix 4. Publications 1,2,3,5,6,7,8.
Appendix 1. Synopses of unpublished results

4.2. Juvenile ecology

Objectives:

The research reported here comes under Objectives 2, 3, and 4.

Field Work Completed:

Sampling for juvenile prawns commenced in August 1983 and finished in September 1985. During this period samples were taken at fortnightly intervals from 10 locations around Groote Eylandt resulting in a total of 1,610 samples. A further 181 samples were collected from monthly sampling from Blue Mud Bay on the adjacent mainland in Arnhem Land. Large juvenile prawns were sorted from the samples at the field station at Groote Eylandt. Specimens were identified to species, measured and sexed where possible. Smaller specimens (postlarvae and small juveniles) were subsampled, freighted to Cleveland where several detailed measurements of each specimen were made in order to identify them to species using numerical taxonomic techniques; approximately 16,000 individuals were processed in this way. All results were then collected and entered into a Database Management package on CSIRONET.

Objectives attained:

2. Link between spawning sites and nursery grounds

The seasonal dynamics of tiger prawn postlarval recruitment and changes in juvenile prawn poulations were studied over two successive years. When combined with data collected on prawn spawning activity and recruitment into coastal waters, the main temporal links between the times of spawning, period of residence on nursery areas and subsequent recruitment into the fishery were established. In both species of tiger prawns, although spawning can occur throughout most of the year, the main time of effective spawning is during the late winter to spring months because juvenile prawns occur in greatest numbers on the nursery areas from September to March. These prawns then recruit into the fishery from November through until May, giving a mean time from spawning until recruitment on to the fishing grounds of approximately 6 months.

3. Nursery area definition

The importance of seagrass as a nursery area for juvenile tiger prawns was established in a previous FIRTA project (No. 81/237). As part of the present project, detailed maps and descriptions of the seagrass areas within the Gulf of Carpentaria have been produced. The major nursery areas for the tiger prawns occur mainly along the western coast of the Gulf of Carpentaria. It was found that the distribution of seagrass controls the distribution of offshore tiger prawn populations and, therefore, the presence or absence of commercial fisheries.

It has also been possible to define more exactly the habitat requirements of the juvenile stage of the two species of tiger prawns with respect to seagrass species, density, height and substrate and to relate the distribution and abundance of prawns to the distribution of these parameters around the western Gulf. Areas supporting large populations of juvenile prawns are, in fact, extremely limited in the Gulf of Carpentaria.

4. Factors affecting offshore recruitment

Two factors have been identified as having major impacts on the recruitment of prawns into the fishery. Firstly, the size of the spawning stock, a parameter which is sensitive to fishing pressure, and secondly, the size and extent of seagrass beds. Seagrass beds appear to be relatively stable from year-to-year except for major periodic disturbance during cyclones. Because of the unpredictable nature of this disturbance, it is difficult to model mathematically this type of impact. Cyclone Sandy in March 1985, however, removed 20% of the Gulf's seagrass resources. Taking the type of seagrass destroyed into account it can be calculated that this should result in a 15% decrease in the total Gulf catches and decreases of up to 35% in the Limmen Bight region. The brown tiger prawn, P. esculentus, will probably be more affected than the grooved tiger prawn, P. semisulcatus.

Results in detail:

Appendix 4. Publication 4,9
Appendix 2. Synopses of unpublished results.

4.3. Larval ecology

Objectives:

The research reported here comes under Objective 2. The larval part of this research was further divided into objectives:

1. Study the large-scale dispersal pathways that link spawning grounds and nursery grounds in the western Gulf of Carpentaria.

2. Study the mechanisms used by penaeid postlarvae to enter nearshore and estuarine nursery grounds.

Field Work Completed:

To study the differential vertical migratory behaviour and larval dispersal of the two tiger prawns, three locations were chosen for discrete depth sampling of the larvae: An inshore site intermediate between the spawning locations of the two species, an offshore site, in deep water where P. semisulcatus is known to spawn and a site at the entrance to Northwest Bay, a nursery ground used by both species. A total of 412 of the proposed 416 samples (99%) were obtained.

In order to study the dynamics of postlarval recruitment the eastern king prawn (Penaeus plebejus) entering the Southport Broadwater was chosen as a suitable system because of the high and predictable abundance of postlarvae at this location. Two, five day, cruises were held in May/June, 1984, to simultaneously sample the vertical distribution of postlarvae offshore, the abundance of postlarvae arriving in the mouth of the estuary and the abundance of postlarvae settling out in the nursery ground habitat. At the same time current meters were deployed to assess the cross-shelf and alongshore currents.

Objectives attained:

2.1 Large-scale dispersal pathways

While the descriptions of the vertical distribution patterns and vertical migratory behaviours have been completed the modelling of the current patterns in the western Gulf is still underway. The model, used in the past to describe the dispersal of the larvae of the banana prawn, P. merguiensis, in the eastern Gulf, will be upgraded with tidal, hydrographical and meteorological data that is currently being obtained and analysed. Much more detailed hydrographic data is, however, needed for dispersal pathways of tiger prawns to be determined by modelling the interaction between biological events and the physical environment. Steps are being taken to obtain this data in the future.

2.2 Postlarval recruitment mechanisms

The tidal rhythms of postlarval influx have been verified and shown to vary from one tidal cycle to the next and from one lunar phase to the next. The origin of postlarvae entering the estuary on any one tidal cycle is probably within a few hundred metres of the estuary mouth. The offshore location of the effective spawning stock however, is harder to pinpoint given the complex cross shelf and alongshore currents. Initial estimates would indicate that it is probably 10-15 km offshore and less than 400 km alongshore.

Results in detail:

Appendix 3. Synopses of unpublished results

Appendix 1.

Appendix 1 Papers in preparation - Adult ecology

1. Population dynamics of the tiger prawns in the northwestern Gulf of Carpentaria, Australia. I: Penaeus semisulcatus. I. Somers

Growth rates and offshore migration patterns are described on the basis of the tagging experiments carried out during the study. Mortality rates are estimated on the basis of decline in catch per unit effort (CPUE) from the trawl surveys as well as from analysis of the catch curve. Fishing effort on P. semisulcatus varies considerably during the life span of one generation and this is used to divide total mortality into natural and fishing components. The estimation of mortality rates from temporal changes in CPUE necessitated a detailed analysis of the factors which may influence these measures of relative abundance.

The population size structure for P. semisulcatus clearly shows modal progression of annual cohorts (Fig. 1). The data pertaining to the main generation under study was isolated using modal separation techniques. This cohort entered the fishery over the period from November 1983 to April 1984 and traces were still discernible in the population at the end of the survey program in March 1985 (Fig. 2). The temporal and spatial distribution of this cohort indicated a general migration offshore in the summer/autumn months with an unknown proportion of the population spread over the area outside the fishing grounds in waters deeper than 50 m in winter. These animals appear to move back into shallower water (<40m) in early spring (Fig. 3), thereby recruiting to the commercial fishery a second time and contributing to the spring increase in CPUE (Fig. 2). This movement to shallower water coincided with the formation of a thermocline at around 40m depth which persisted throughout the summer months, eventually breaking down in autumn (Somers et al. 1987, Appendix 4.8).

Fishing effort on the P. semisulcatus cohort was greatest from August to November which corresponded to the concentration of the population in the 30-40 m depth range after being widespread throughout deeper waters in winter. Female P. semisulcatus generally moved earlier and further inshore than males and, because they are larger and represent potentially higher catch rates (in kg per unit effort), suffered higher fishing mortality. This is evident in the changes which occur in the sex ratio from August onwards (Fig. 4) and the differential mortality can be measured in both the decline in CPUE from August on (Fig. 5) as well as in the catch curve (Fig. 6).

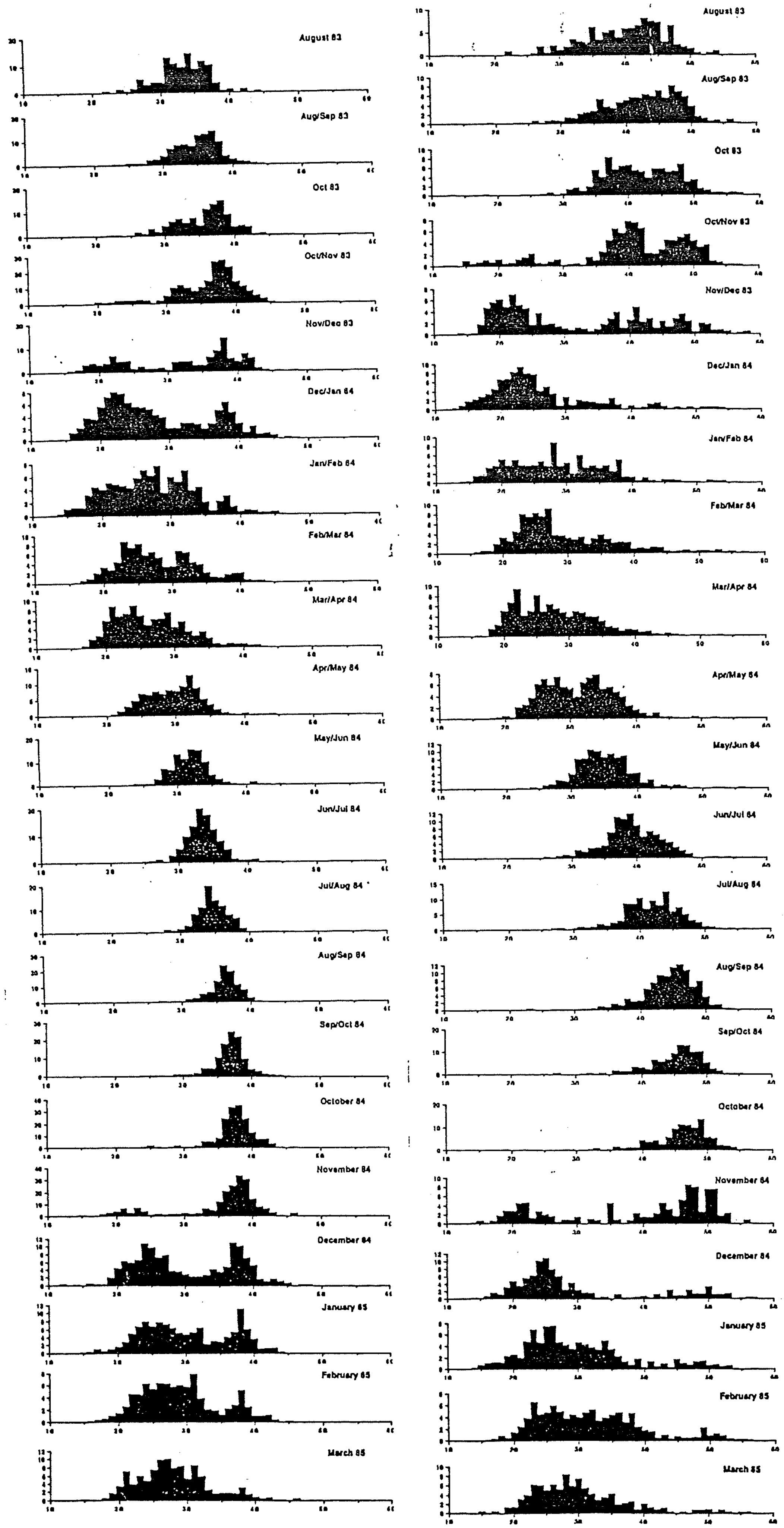


Figure 1. Size composition of P. semisulcatus in the north-western Gulf of Carpentaria from each of 21 trawl surveys carried out between August 1983 and March 1985.

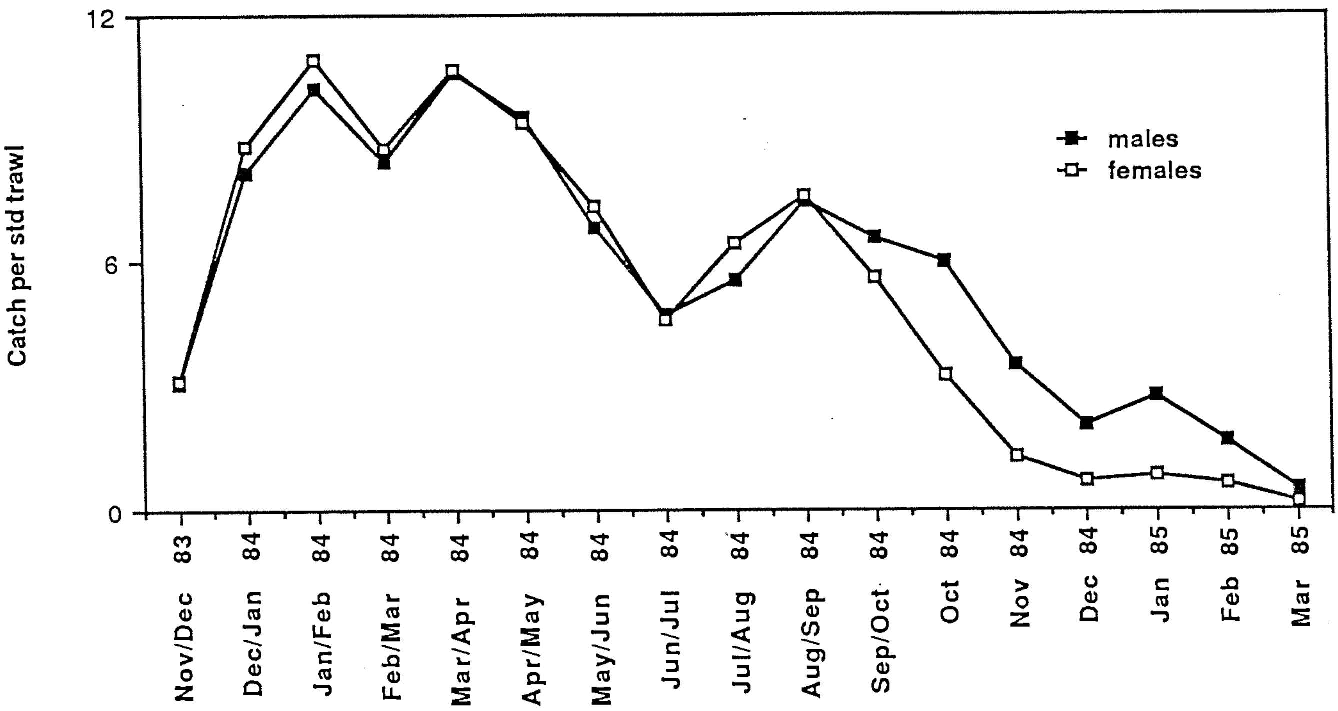


Figure 2. Catch per standard trawl of P. semisulcatus in the 1983/84/85 generation from November 1983 to March 1985.

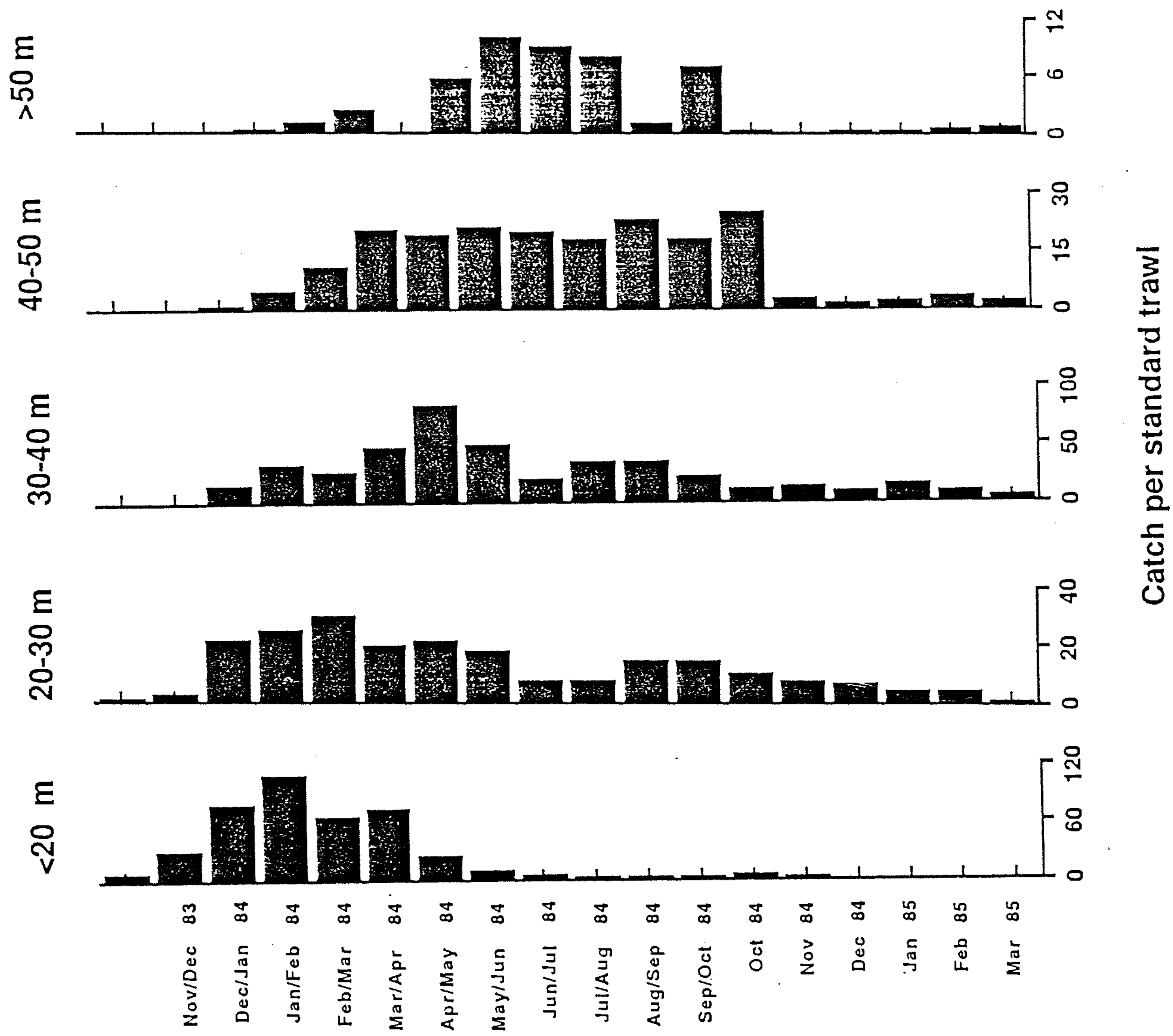


Figure 3. Catch per standard trawl of P. semisulcatus in the 1983/84/85 generation taken at various depth strata from November 1983 to March 1985.

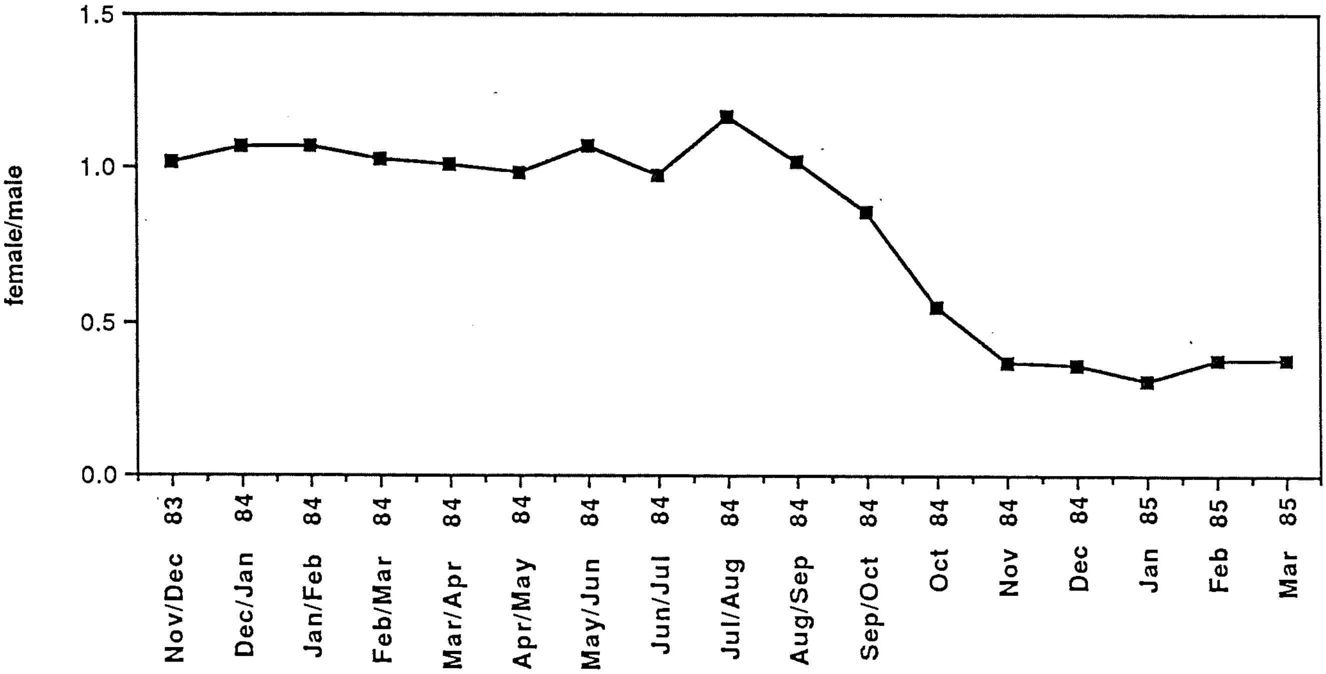


Figure 4. Ratio of female/male P. semisulcatus in the 1983/84/85 generation from November 1983 to March 1985.

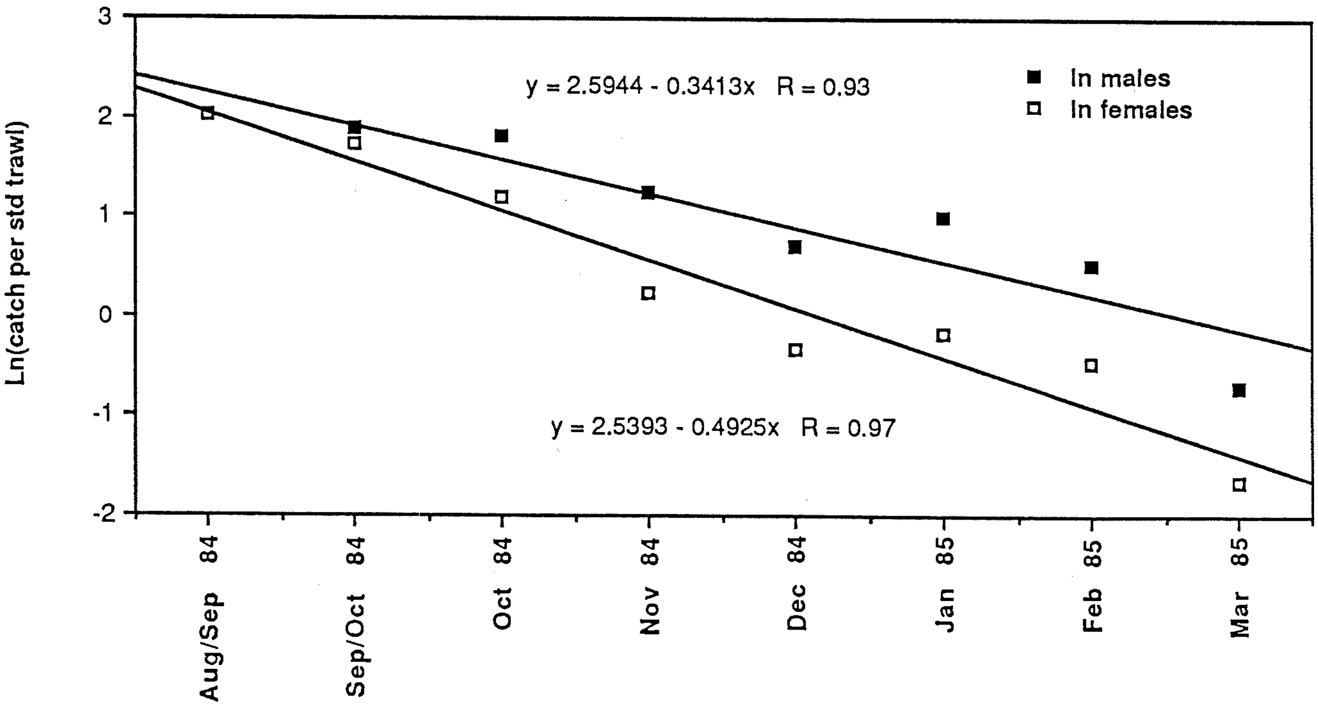
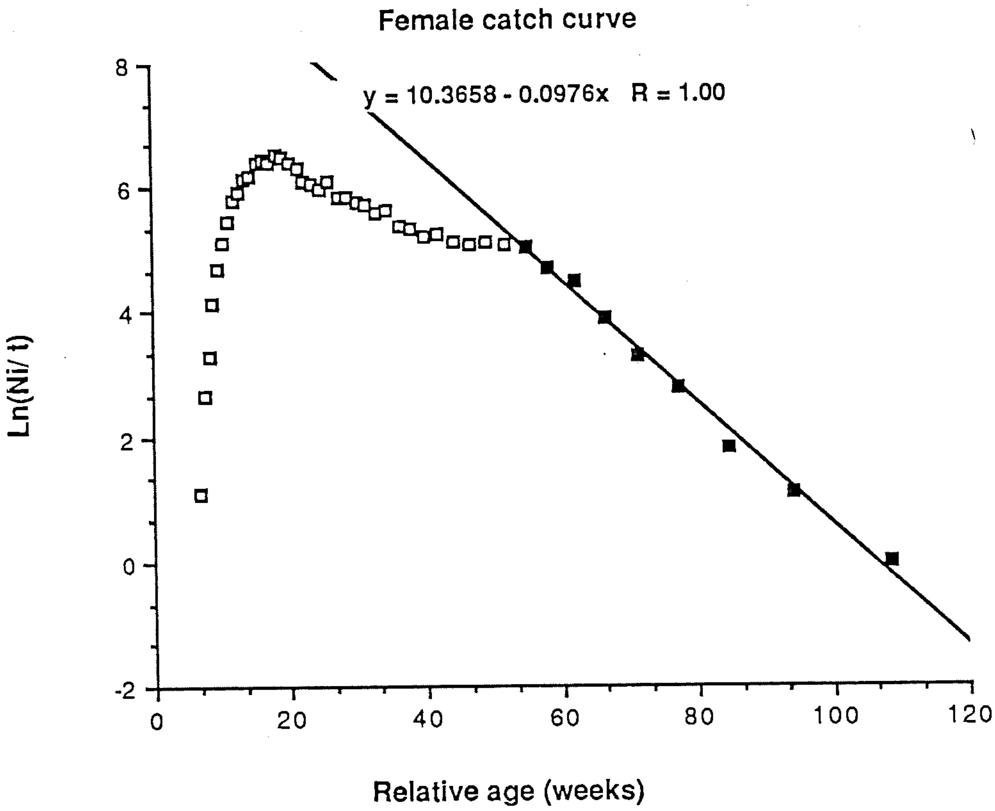


Figure 5. Regression of $\log_e$(CPUE) of P. semisulcatus in the 1983/84/85 generation against time from August/September 1984 to March 1985.



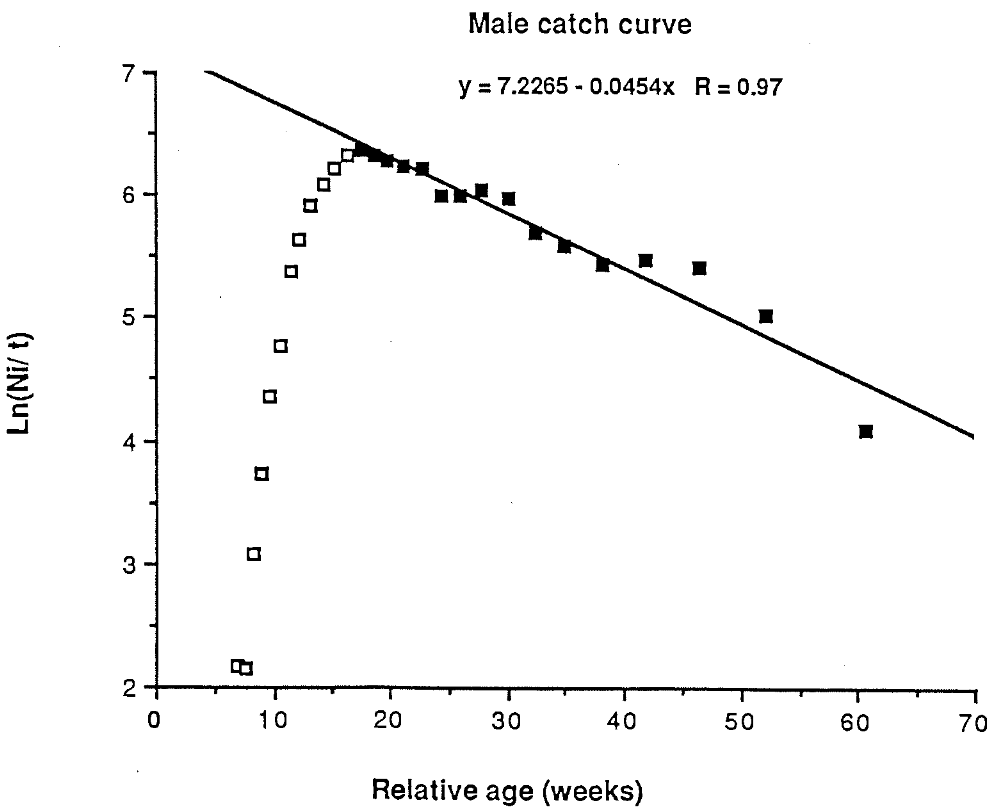


Figure 6. Regression of $\log_e(N_i/\Delta t_i)$ against relative age for *P. semisulcatus* caught during the trawl surveys, where N_i is the number caught in size class i and Δt_i is the time taken to grow through the size class.

2. Population dynamics of the tiger prawns in the northwestern Gulf of Carpentaria, Australia. II: *Penaeus esculentus* I. Somers

As with *P. semisulcatus*, growth rates and migration patterns for *P. esculentus* are described using the data obtained during the tagging experiments carried out during the study. Recruitment to the fishery took place over a more extended period than that for *P. semisulcatus* and as a result mortality rates are estimated from the size composition of the trawl survey catch rather than decline in CPUE. Analysis of these data are still underway.

3. Stock assessment of the tiger prawns *Penaeus semisulcatus* and *P. esculentus* in the western Gulf of Carpentaria, Australia. I. Somers.

Spawning stock, recruitment and fishing effort relationships are being examined for each species of tiger prawn in the western Gulf of Carpentaria. Preliminary findings have been summarised and given to the fishing industry and the fishery managers (Somers 1987a).

4. Population dynamics of the endeavour prawn, *Metapenaeus ensis*, in the northwestern Gulf of Carpentaria, Australia. I. Somers

Although not a primary component of the FIRTA project, endeavour prawns are an important commercial species and incidental component of the tiger prawn fishery. Records were kept of all *M. ensis* caught during the trawl surveys and this manuscript will summarise the growth rates, migration patterns and mortality rates from the combination of the population size composition data with seasonal and spatial distribution data obtained from the trawl surveys. Enhancement of endeavour prawn logbook data in a similar manner to that of tiger prawns will also be documented.

Appendix 2.

Appendix 2 Papers in preparation - Juvenile ecology

1. Seasonal cycles of recruitment of postlarval and juvenile penaeids within seagrass nursery areas in the western Gulf of Carpentaria. D.J. Staples, D.J. Vance and R.A. Kenyon.

Methods

Juvenile prawns were collected fortnightly from six sites around Groote Eylandt, and monthly, from two sites in Arnhem Land in the western Gulf of Carpentaria (Fig. 1.1). Trawls were taken on each occasion with two different sized beam trawls at several stations along transects extending from the intertidal zone to the 10m depth contour. Most trawls were taken near to the time of high tide at night although several 24h sampling periods were included to standardise for sampling time. A total of 2,100 samples were taken over the study period and all prawns were sorted, measured and identified to species. Species identification for small specimens (<3mm carapace length) required detailed measurements of 8 characters for each individual and processing using numerical taxonmomy techniques.

Fortnightly abundance estimates of postlarvae and juveniles were then combined with spawning and subadult data collected by the Adult Ecology Group (refer to attached papers) and the main periods of spawning, juvenile abundances and offshore recruitment compared.

Results

Abundance of juvenile prawns varied considerably among sites around northern Groote Eylandt (Fig. 1.2). As in earlier studies tiger prawn juveniles were almost exclusively confined to shallow intertidal seagrass areas. The seasonal cycle of prawn abundance showed similar patterns on all sites where sufficient juveniles were caught. Juveniles of both Penaeus esculentus and P. semisulcatus occurred mainly from September through to April with little recruitment of postlarvae during the winter months.

Data from the adult ecology group showed that the grooved tiger prawn, *P. semisulcatus* has two main periods of spawning each year. The main peak occurred during spring (September-October) with a smaller peak in autumn (February-March). Only the spring spawning was effective in producing postlarvae and juveniles in the nusery areas along the northern Groote coastline. The subsequent year's fishery, therefore, was derived almost entirely from this spring spawning activity (Fig. 1.3). The main difference between the northern Groote (NWB) and the Arnhem Land sites (BMB) was that postlavae were more abundant in autumn in the latter (Fig. 1.4). It follows from this analysis that the time taken between spawning and subsequent recruitment into the fishery is approximately six months and recruitment occurs mainly during the summer-autumn period.

Spawning in the brown tiger prawn, *Penaeus esculentus* was more protracted throughout the year, but despite this lack of sharp seasonality both juvenile and subadult abundances showed similar patterns to those observed for *P. semisulcatus* with an effective spawning season occurring during late winter and spring and recruitment occurring during summer and autumn (Figs. 1.5 and 1.6).

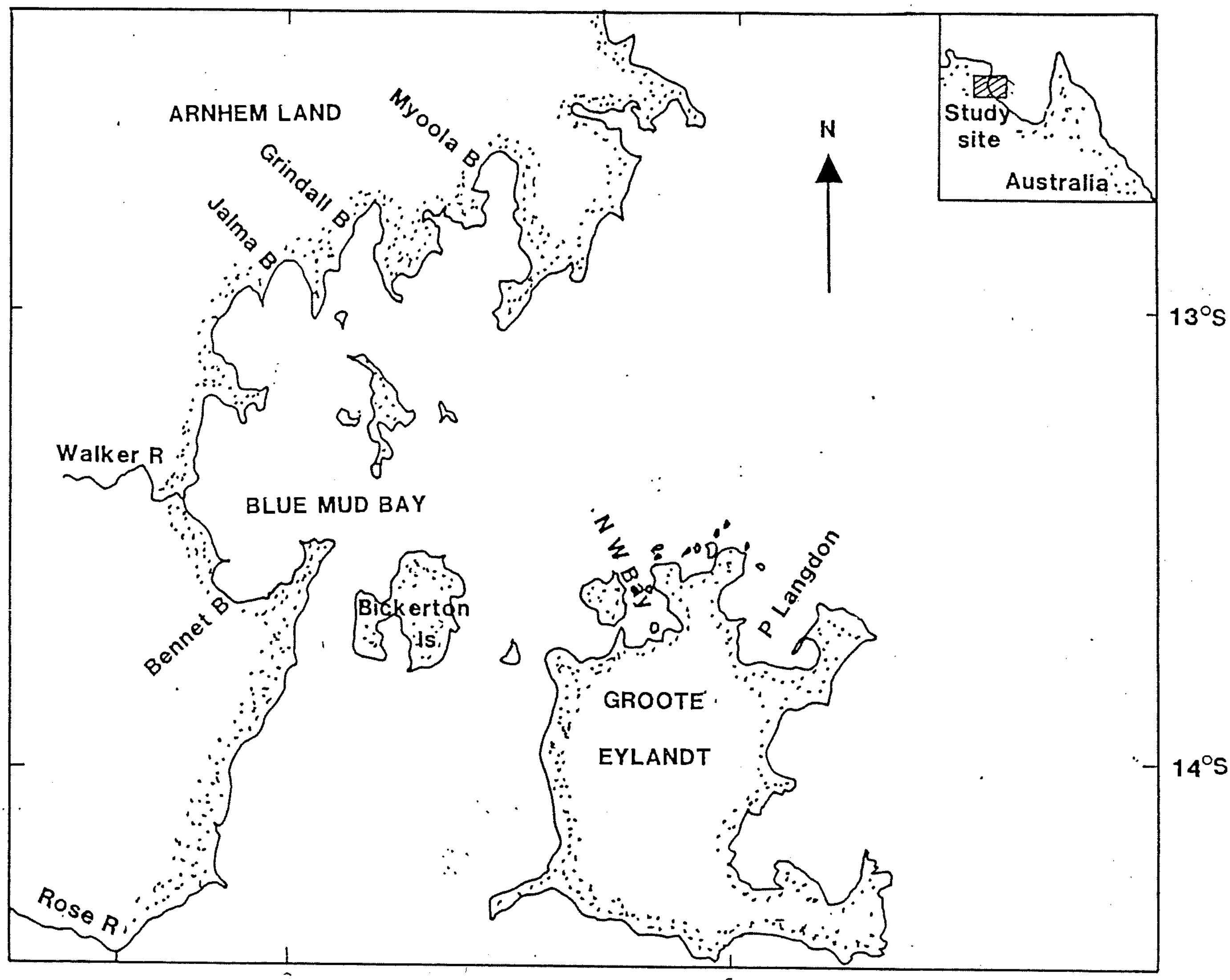


Fig. 1.1 Map of the western Gulf of Carpentaria showing study sites in northern Groote Eylandt and Blue Mud Bay.

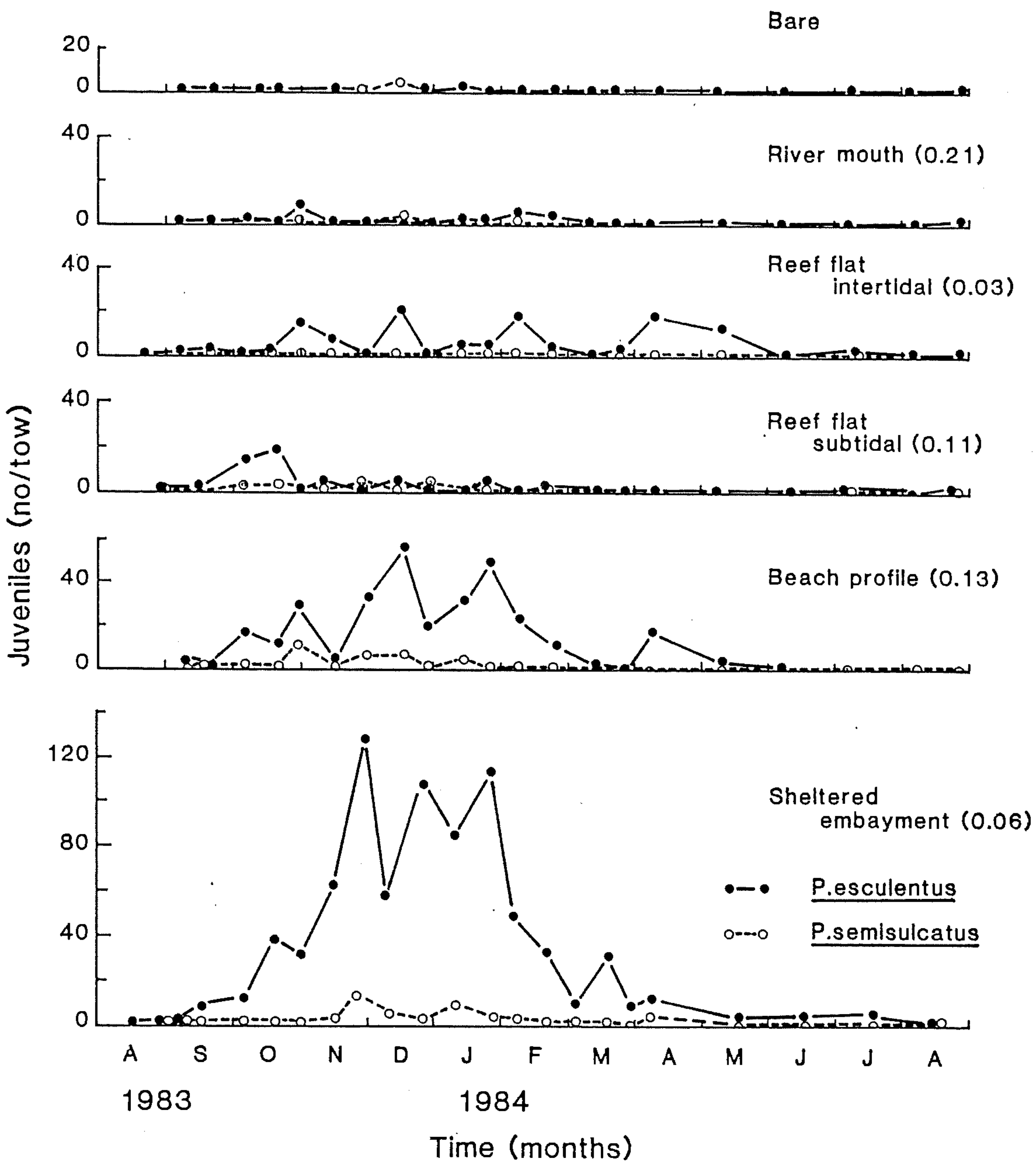


Fig. 1.2 Seasonal cycle of abundance of juvenile tiger prawns <u>Penaeus esculentus</u> and <u>P. semisulcatus</u>, on 6 sites around northern Groote Eylandt from August 1983 to August 1984.

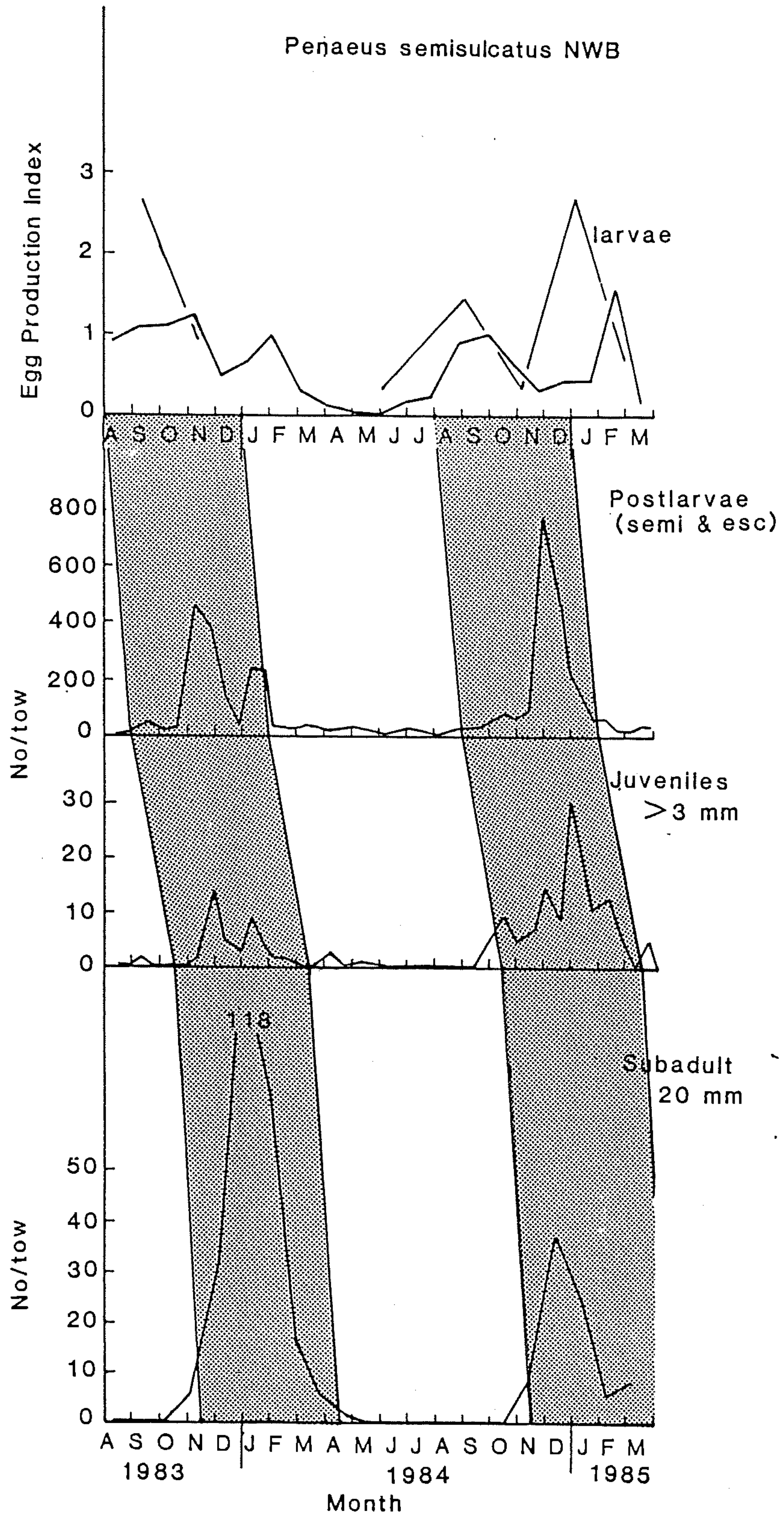


Fig. 1.3 Life history dynamics of Penaeus semisulcatus in Northwest Bay, northern Groote Eylandt.

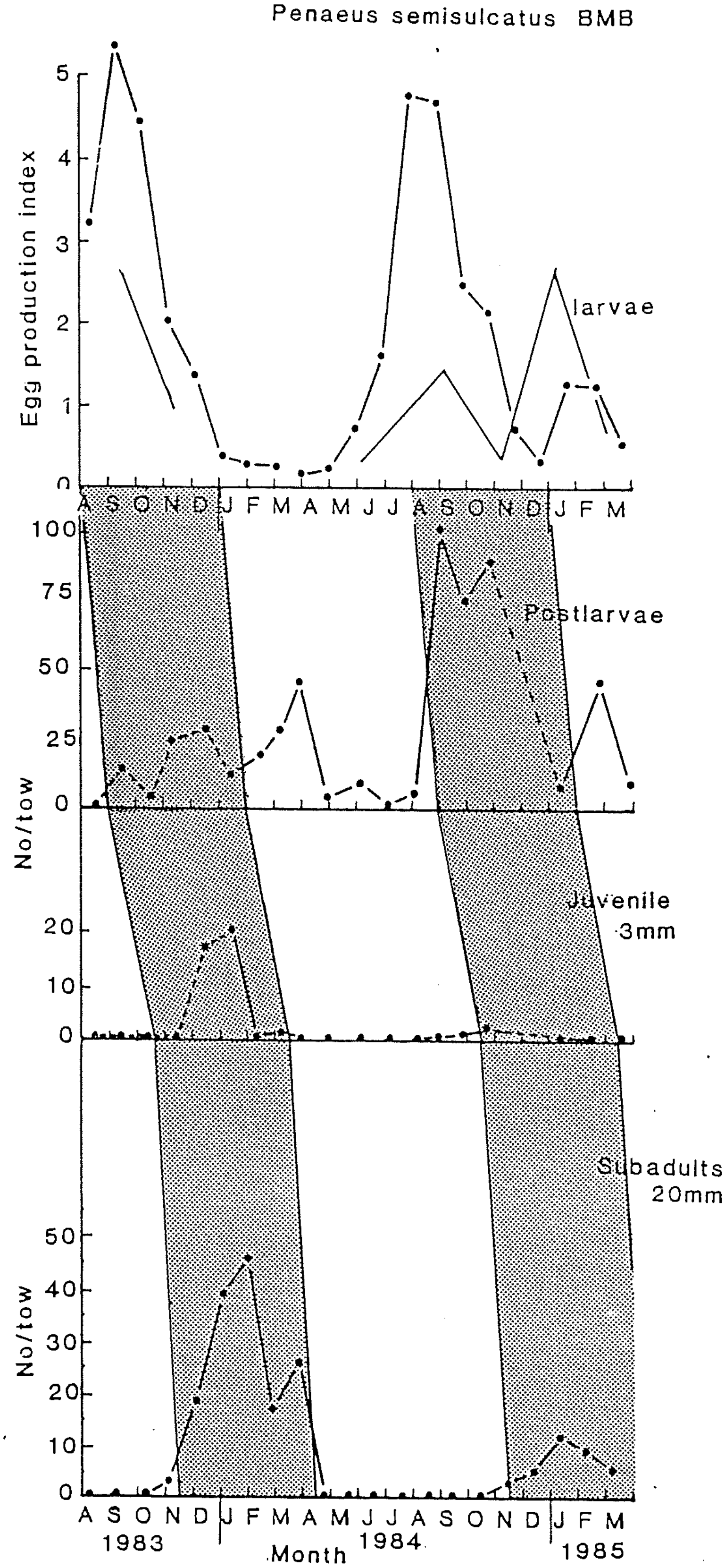


Fig. 1.4 Life history dynamics of Penaeus semisulcatus in Blue Mud Bay, Arnhem Land.

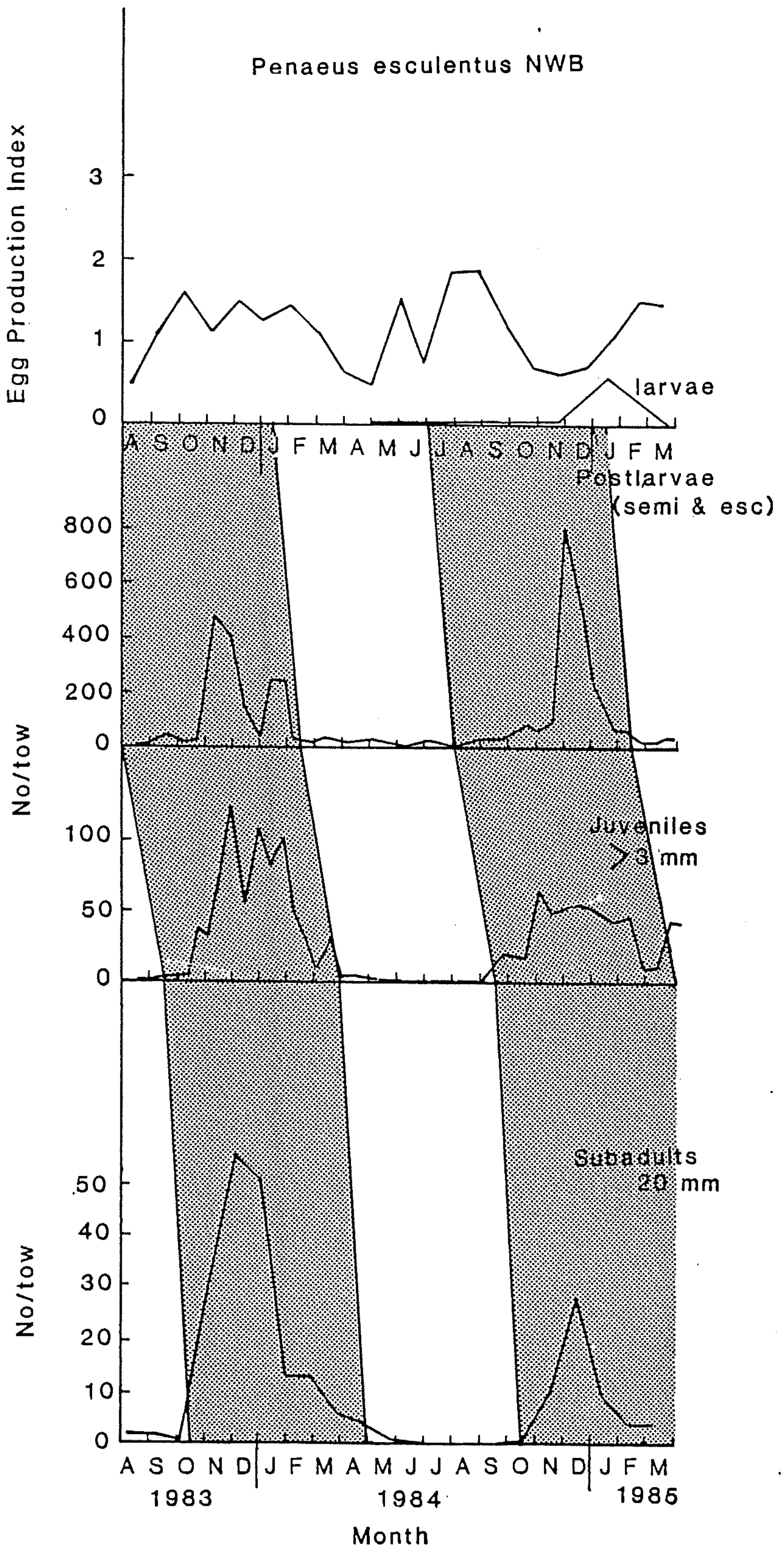


Fig 1.5 Life history dynamics of <u>Penaeus esculentus</u> in Northwest Bay, northern Groote Eylandt.

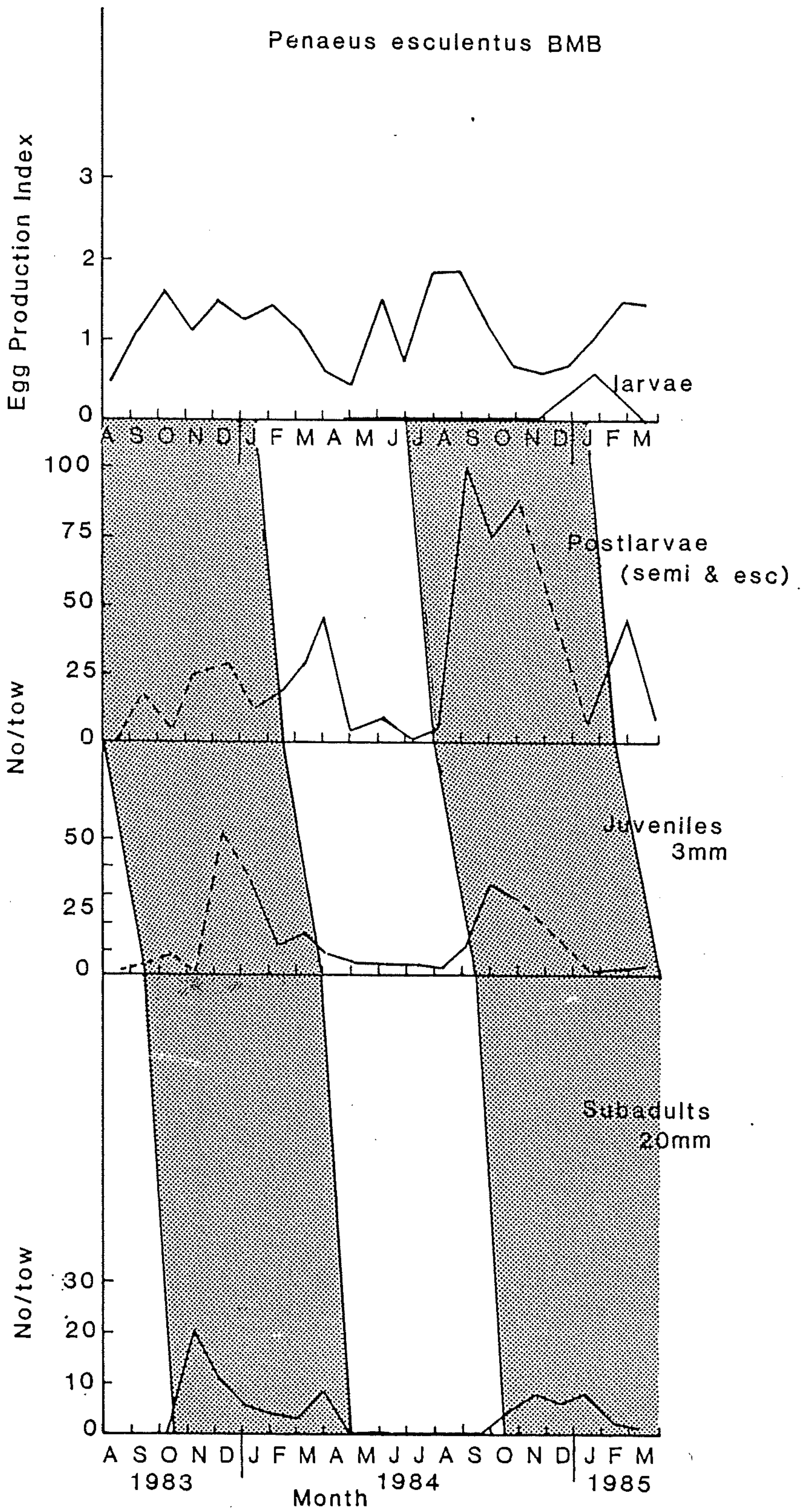


Fig. 1.6 Life history dynamics of <u>Penaeus</u> <u>esculentus</u> in Blue Mud Bay, Arnhem Land.

2. Net efficiency of beam trawls and sampling for juvenile tiger prawns. D.J. Staples and R.A. Kenyon

Methods

A series of 15 trawls were made at each of four seagrass sites to test the efficiency of the beam trawl in capturing juvenile prawns in different species and densities of seagrass. The beam trawl used in all sampling measured 1.0m x 0.5m and was fitted with a 2mm mesh netting and a 1mm mesh codend. All trawls were taken within fenced enclosures of 33m x 3m. which were staked out in the seagrass 1h prior to sampling. Each new trawl was started at alternate ends of the enclosure, the path being randomly chosen within the 3m width. All samples were returned to the laboratory where the postlarve and juvenile prawns were sorted, measured and identified.

As an additional check, the seagrass areas were also sampled using drop traps which successfully enclose all prawns within a 2m diameter enclosure. All prawns were removed from the enclosure using dip nets and their population density compared with estimates made using beam trawls.

Results

The number of prawns taken per trawl reduced exponentially over the 15 trawls. This decline in catch per unit effort provides an estimate of the catchability of prawns which can be compared by analysis of covariance between sites, species and size groups (Table 2.1). Preliminary analyses have indicated that no significant differences occurred between sites but that the net was twice as efficient in catching *Penaeus esculentus* as *P. semisulcatus*.

Drop trap sampling also revealed that sampling with beam trawls was biased towards *P. esculentus*. Obviously samples of juvenile prawns, collected with beam trawls, will need to be corrected by the appropriate factor before analyses.

Table 2.1. Catches of juvenile tiger prawns in 15 successive tows within an enclosure on seagrass. Decline in catches provides an estimate of net efficiency.

Tow No.	Penaeus esculentus	Penaeus semisulcatus	Total
1	41.0	13.0	54.0
2	35.0	10.0	45.0
3	17.0	9.0	26.0
4	16.0	5.0	21.0
5	13.0	8.0	24.0
6	18.0	7.0	25.0
7	32.0	5.0	37.0
8	26.0	14.0	30.0
9	8.0	4.0	12.0
10	10.0	3.0	13.0
11	10.0	2.0	12.0
12	1.0	5.0	6.0
13	4.0	0.0	4.0
14	7.0	4.0	11.0
15	1.0	0.0	1.0

Estimate of net efficiency *Penaeus esculentus* 0.35

Estimate of net efficiency *Penaeus semisulcatus* 0.19

3. Role of seagrass as a nursery area for juvenile tiger prawns in the western Gulf of Carpentaria. D.J.Staples, D.J. Vance, D.S Heales and R.A. Kenyon.

Methods

Ten sampling sites covering a range of seagrass species and densities in North West Bay at Groote Eylandt (Fig. 3.1)were sampled at fortnightly intervals for juvenile tiger prawns from November 1984 to February 1985. All samples were taken in replicate using a small (1.0m x0.5m) beam trawl fitted with a 2mm mesh net and 1mm mesh codend. Prawns were sorted, measured and identified to species in the laboratory.

Fifty one sites extending from the northern extremity of Blue Mud Bay in Arnhem Land to the eastern coast of Groote Eylandt were also sampled for juvenile tiger prawns during December 1984. As with the North West Bay sampling replicate tows were made at each site and information was collected on seagrass species composition, density and leaf area index (an index derived from seagrass shoot density and leaf area estimates). Samples of substrate were also taken for sediment analyses.

Results

On all sampling occasions in North West Bay, more juvenile tiger prawns were caught in the sheltered embayment sites than in either the beach profiles or reef flat or river mouth sites (Fig. 3.2). Samples combined over all sampling dates clearly show the differences between the less favoured sites and the more productive sheltered embayment sites (Fig. 3.3). It is also interesting to note that the two species were not present in the same proportions over all sites; some sites favouring *P. esculentus* and some sites favouring *P. semisulcatus*.

Because of the stability in the results over all sampling occasions it was considered valid to make wider geographic comaprisons based on one sampling date in December. Over the 51 sites sampled during the study, the same general conclusions reached in North West Bay were applicable (Fig. 3.4). More juvenile prawns were found in sheltered embayment sites than in the others, with beach profiles ranking second in importance. Riverine sites were again generally of low importance. Sheltered bay seagrass communities make up only 4% of the total Gulf seagrasses, whereas beach profile communities are much more common and account for 67%. Taking the area of seagrass and the density of prawns each type supports shows that the beach profile grasses are the most important nursery area in the Gulf.

A more detailed analysis of why some areas are more important nursery areas than others was also carried out. The abundance of juvenile prawns of both species was significantly correlated with both the amount of seagrass present on a given site (as measured by the leaf area index) and the percentage of silt in the substrate surrounding the seagrass shoots (Table 3.1). Taking each species separately showed that the distribution of P. esculentus in nursery areas could be explained by the amount of seagrass present within a site (Table 3.2; $r = 0.848$; $P<0.01$). The distribution of P. semisulcatus on the other hand, was more complicated and depended also on the amount of silt in the sediment, and the height of the seagrass shoots (Table 3.3; $R = 0.786$; $P<0.01$). Richer seagrass meadows were better for both species but P. semisulcatus also appeared to require softer sediments for successful settlement and survival. Good nursery areas for P. semisulcatus, therefore, are more limited in the Gulf of Carpentaria compared with P. esculentus areas.

Table 3.1 Correlation matrix for relating juvenile tiger prawn distribution with sediment and seagrass parameters.

Juveniles	juveniles	P.esc	P.semi	Silt	LAI	HT
P.esc	0.922	-				
P.semi	0.747	0.442	-			
Silt	0.777	0.527	0.879	-		
LAI	0.551	0.473	0.498	0.342		
HT	0.493	0.534	0.214	0.452	-0.242	-

LAI = Leaf area index
HT = Height of seagrass

Table 3.2 Stepwise multiple regression for describing the relationship between Penaeus esculentus distribution and seagrass parameters.

Variable	R	F value to enter	R change	
LAI	0.849	75.2	0.722	$p<0.001$

Table 3.3 Stepwise multiple regression for describing the relationship between Penaeus semisulcatus distribution, substrate and seagrass parameters

Variable	R	F value to enter	R change	
Silt	0.473	8.35	0.224	
LAI	0.570	4.20	0.101	
Silt	0.732	12.21	0.210	
HT	0.786	5.62	0.080	$p<0.001$

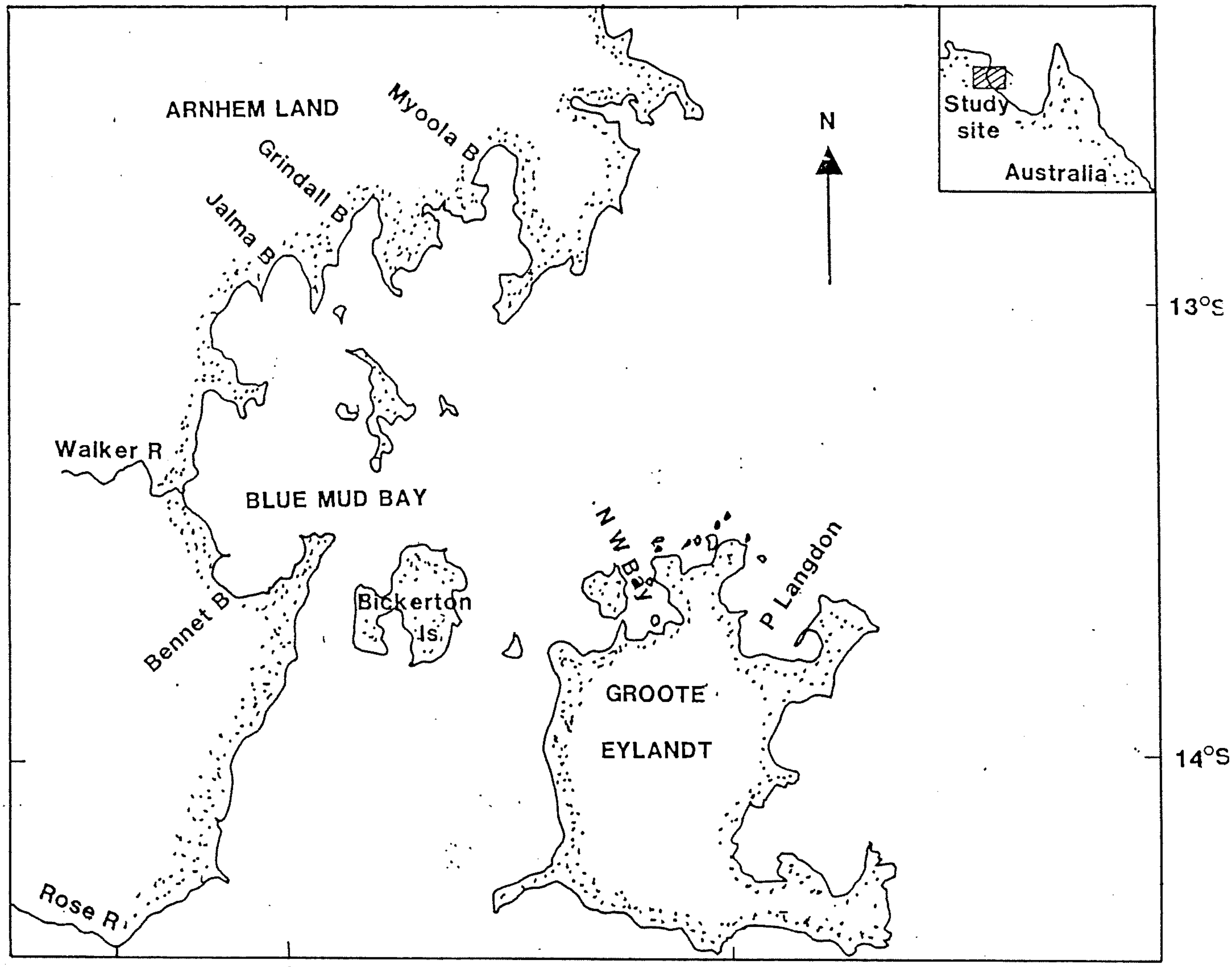


Fig. 3.1 Map of the western Gulf of Carpentaria showing the main study areas of Blue Mud Bay and northern Groote Eylandt.

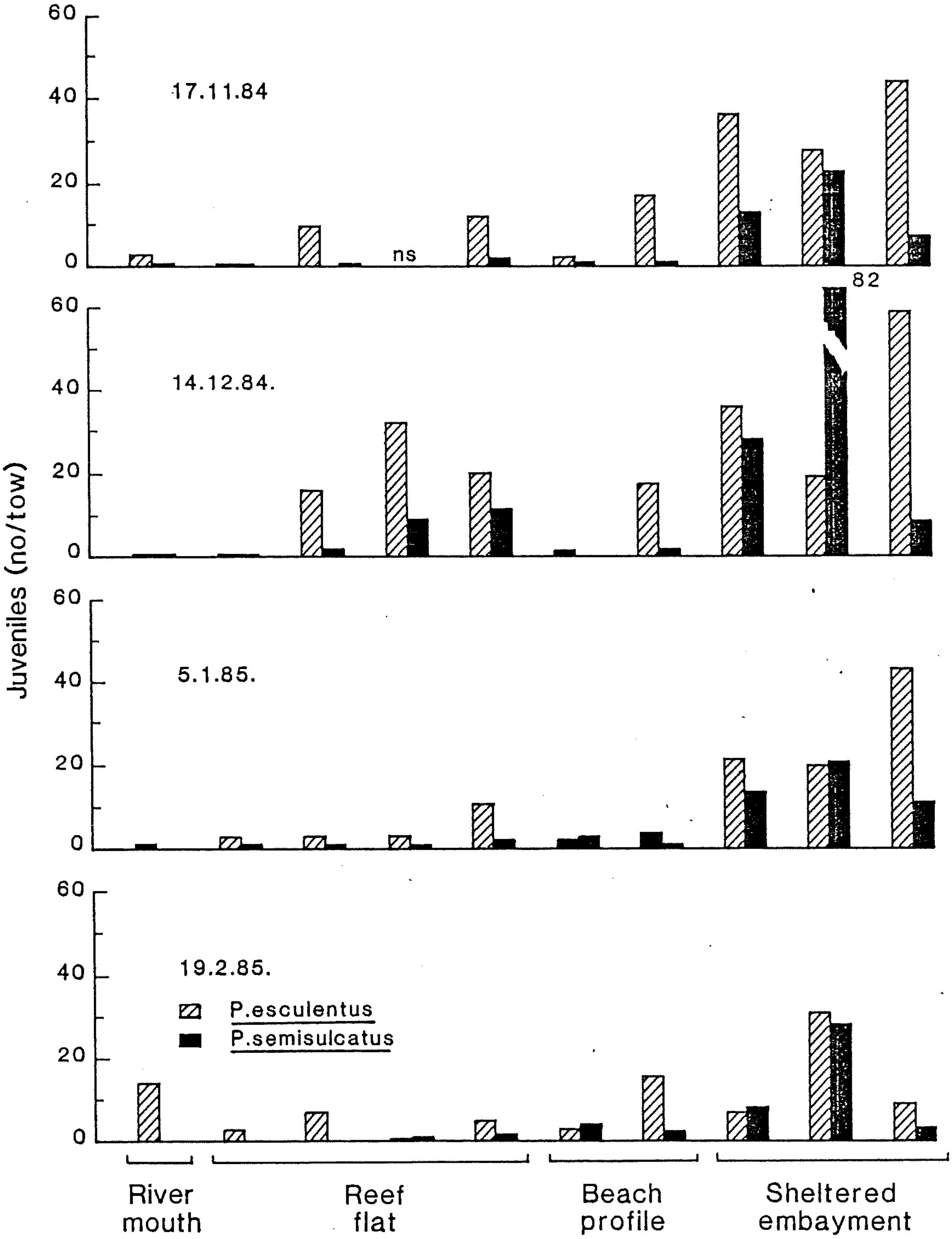


Fig. 3.2 Monthly changes in the distribution of juvenile tiger prawns within 10 sites around North West Bay, northern Groote Eylandt.

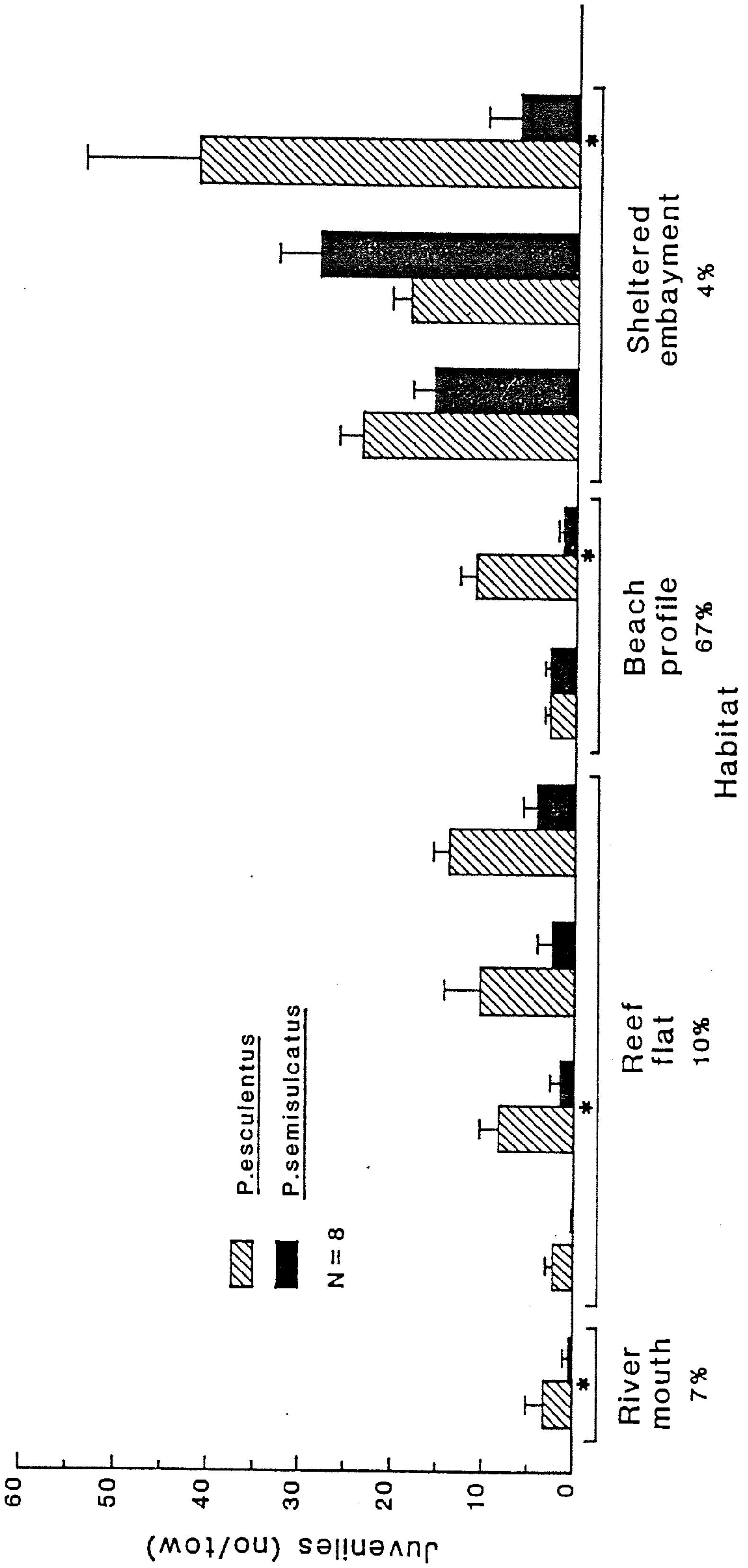


Fig. 3.3 Mean relative abundance of juvenile tiger prawns across four main habitat types in northern Groote Eylandt.

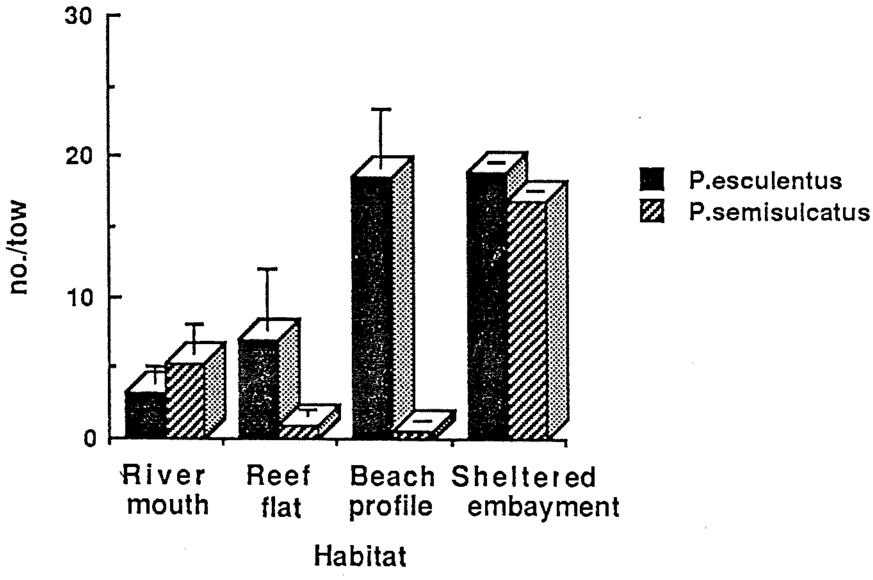


Fig. 3.4 Changes in the distribution of juvenile tiger prawns across four main habitat types around Blue Mud Bay and northern Groote Eylandt.

Appendix 3.

Appendix 3 Papers in preparation - Larval Ecology

1. Differential vertical migratory behaviour and larval advection of two species of tiger prawns in the western Gulf of Carpentaria. P.C. Rothlisberg and J.A. Church

Introduction

Two species of tiger prawns, P. esculentus and P. semisulcatus, occur in the fishery north of Groote Eylandt, western Gulf of Carpentaria. The species seem to use the same seagrass nursery areas yet have geographically distinct spawning habitats and different spawning periods. The hypothesis that the two species have different larval trajectories from the spawning grounds to the nursery grounds was investigated.

Methods

Discrete depth sampling at three or four depths, using a plankton pump was employed. Sampling was at two-hourly intervals for four days at each location. Three locations were chosens: an inshore site intermediate between the spawning locations of the two species, an offshore site, in deep water where P. semisulcatus is known to spawn and a site at the entrance to Northwest Bay, a nursery ground used by both species.

Results

Only the vertical distribution of P. semisulcatus zoeae at the nearshore sampling station are presented here. Zoeae were present in the water column at all times (Fig. 1.1). Numbers varied over the 2 h time intervals within and between days. The increases at night were due largely to the greater numbers of larvae at the surface and middle levels. During the day larvae were generally absent from the surface layer and were found at mid-depth or in the bottom layers.

While the descriptions of the vertical distribution patterns and vertical migratory behaviours have been completed the modelling of the current patterns in the western Gulf is still underway. The model, used in the past to describe the dispersal of the larvae of the banana prawn, P. merguiensis, in the eastern Gulf, will be upgraded with tidal, hydrographical and meteorological data that is currently being obtained and analysed. Much more detailed hydrographic data is, however, needed for dispersal pathways of tiger prawns to be determined by modelling the interaction between biological events and the physical environment. Steps are currently being taken to obtain this data.

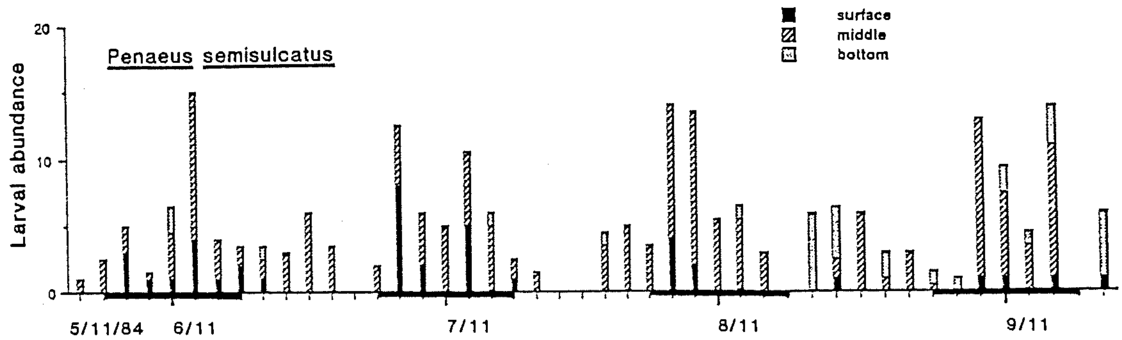


Figure 1.1 Vertical distribution of the zoeal stages of P. semisulcatus over four days in November 1984, north of Groote Eylandt, western Gulf of Carpentaria.

2. Larval transport and postlarval recruitment processes of the eastern king prawn, Penaeus plebejus. P.C. Rothlisberg, J.A. Church, C.J. Jackson and R.C. Pendrey.

Introduction

In order to study the dynamics of postlarval recruitment the eastern king prawn (Penaeus plebejus) entering the Southport Broadwater was chosen as a suitable system because of the high and predictable abundance of postlarvae at this location.

Methods

Two, five day, cruises were held in May/June, 1984, to simultaneously sample the vertical distribution of postlarvae offshore (plankton pump), the abundance of postlarvae arriving in the mouth of the estuary (plankton net) and the abundance of postlarvae settling out (beam trawl) in the nursery ground habitat. At the same time current meters were deployed offshore at two depths (30 and 60 m) to assess the cross-shelf and alongshore currents.

Results

Offshore postlarvae were most abundant in the water column at dusk and through the night at both the 20 and 50 m station (Fig. 2.1, Pump). In the estuary however, postlarvae had changed their behaviour and were most abundant on a tidal periodicity (Fig. 2.1, Plankton and Trawl). The abundance of the postlarvae varied from cycle to cycle. Numbers were very low on the first three cycles and then a dramatic peak occurred in the plankton samples, which tapered off through the next four cycles; this pattern was mirrored in the trawl samples one tidal cycle later. The peak abundance of the postlarvae occurred within 3 to 4 h of the start of the flood tide (Fig. 2.2). In order to estimate the postlarval origin the incurrent and excurrent water exchange of the estuary was modelled (Fig. 2.3). For postlarvae to arrive at our sampling station in the mouth of the estuary within 3 h they had to be within 500 m of the mouth at the start of the flood tide. Cues to elicit the postlarval acitivity cycle (e.g. tidal height, tidal flow etc.) are currently being investigated with laboratory-based experiments.

To estimate the offshore origin (spawning location) of these postlarvae estimates of larval age, as well as, cross-shelf and alongshore currents had to be made. These analyses are still proceeding, as the models are currently being refined with more detailed hydrographic and meteorological data. Estimates of postlarval age of 2 to 3 weeks have been obtained from laboratory rearings. Based on initial estimates of cross-shelf tidal currents the effective spawning area was not more than 10 to 15 km offshore in 50 to 55 m of water; this is well inshore of the centre of the offshore distribution of population. The longshore current field is very complex, incorporating eddies and counter-currents inside the southerly-flowing East Australian Current. Again, initial estimates indicate that southerly alongshore drift on the order of 350 to 400 km are likely. Therefore, postlarvae entering the Southport nursery ground were probably spawned 3 to 4 weeks earlier, 15 km off Fraser Island.

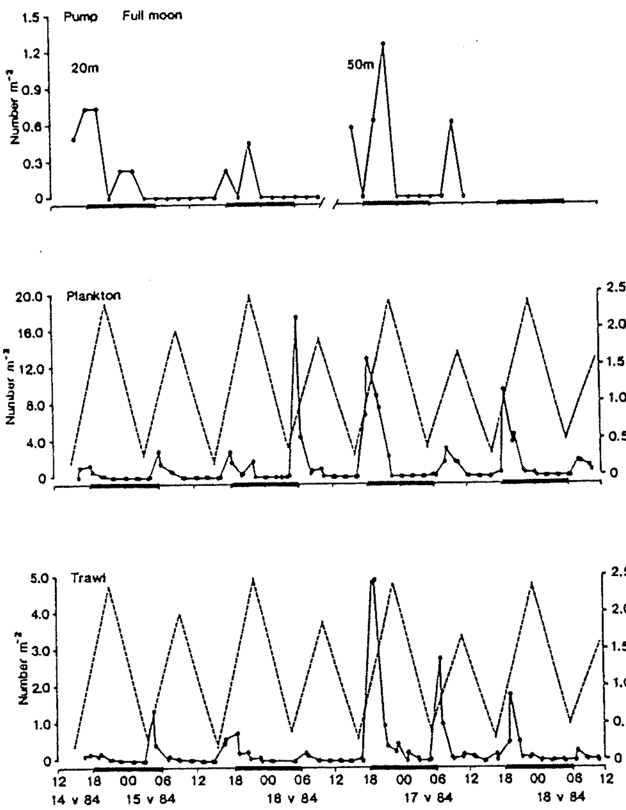


Figure 2.1 Postlarval Penaeus plebejus abundance over four days during the full moon at four sites: Offshore pump stations (20 and 50 m), plankton samples in the mouth of the Southport Broadwater and benthic beam trawl samples just inside the estuary mouth. Dark bars indicate night, dashed lines are predicted tidal height.

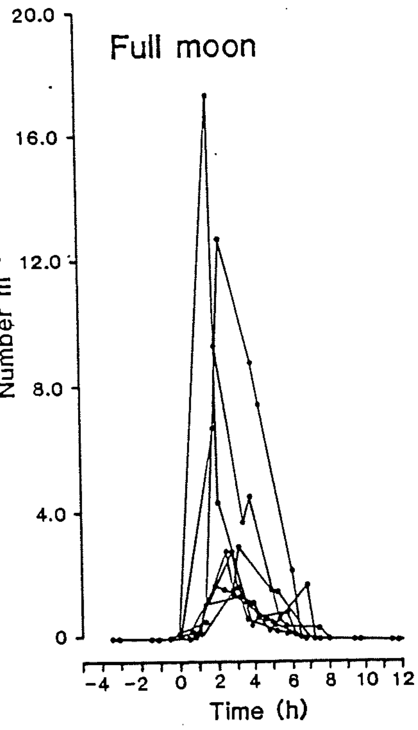


Figure 2.2 Postlarval abundance over all full moon tidal cycles sampled, normalised to a standard tidal cycle.

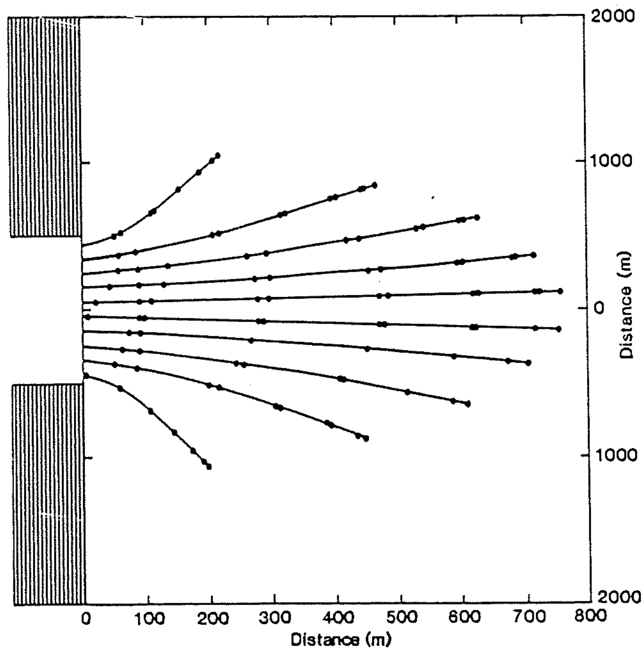


Figure 2.3 Modelled offshore particle trajectory over an ebb and flood tidal cycle of the Southport Broadwater.

Appendix 4 Publications

4.1. Crocos, P.J. (1987a) Reproductive dynamics of the grooved tiger prawn, Penaeus semisulcatus, in the north-western Gulf of Carpentaria. Aust. J. Mar. Freshw. Res. 38, 79-90.

4.2. Crocos, P.J. (1987b) Reproductive dynamics of the tiger prawn, Penaeus esculentus, and a comparison with P. semisulcatus, in the north-western Gulf of Carpentaria. Aust. J. Mar. Freshw. Res. 38, 91-102.

4.3. Hill, B.J. (1987) Biological aspects of management of the Declared Management Zone. Northern Prawn Fishery Information Notes Number 10 February 1987.

4.4. Poiner, I.R., Staples, D.J. and Kenyon, R. (1987). Seagrass communities of the Gulf of Carpentaria. Aust. J. Mar. Freshw. Res. 38: 121-131.

4.5. Somers, I.F. (1985) Movements of tagged tiger prawns in the Groote Eylandt region. Northern Prawn Fishery Information Notes Number 8 October 1985.

4.6. Somers, I.F. (1987a) The status of tiger prawn stocks in the western Gulf of Carpentaria. Northern Prawn Fishery Information Notes Number 10 February 1987.

4.7. Somers, I.F. (1987b) Sediment type as a factor in the distribution of the commercial prawn species of the western Gulf of Carpentaria, Australia. Aust. J. Mar. and Freshw. Res. 38, 133-149.

4.8. Somers, I.F., Crocos, P.J. and Hill, B.J. (1987) Distribution and abundance of the tiger prawns P. esculentus and P. semisulcatus in the north-western Gulf of Carpentaria, Australia. Aust. J. Mar. and Freshw. Res. 38, 63-78.

4.9. Staples, D.J., Vance, D.J. and Heales, D.S. (1985) Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. pp. 47-54 In: P.C. Rothlisberg, B.J. Hill and D.J. Staples (Editors) Second Australian National Prawn Seminar. NPS2, Cleveland, Australia.

Appendix 4.

Appendix 4.1

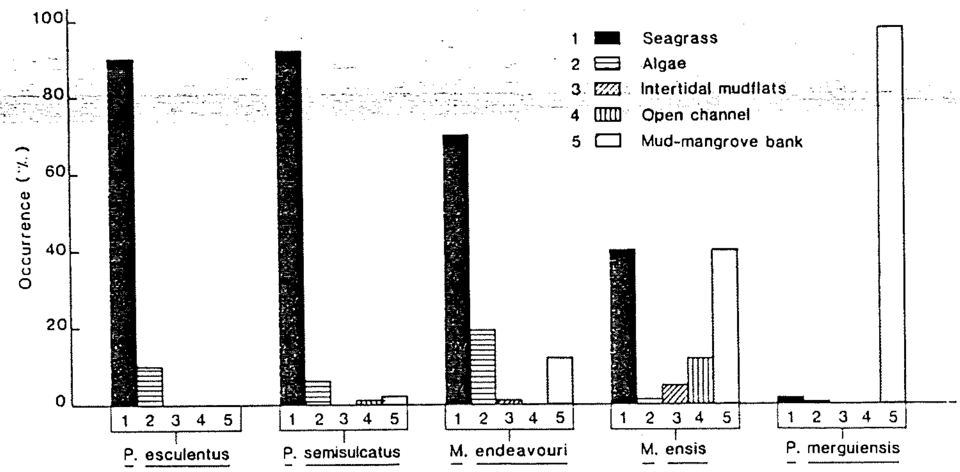


Figure 3. Percentage distribution of the catch of the five major commercial prawn species in each of five habitats in the Embley River estuary, 1981-82.

where k is the total number of samples taken, n_i is the number of individuals in sample i, and T is the total number of individuals taken. The significance of the departure from random is given by the variance ratio—

$$F = \frac{I_\delta (T-1) + k-T}{T-1}$$

for k-1 and ∞ degrees of freedom.

On a regional scale, the mean annual catch of banana and tiger prawns was estimated from landing figures and logbook returns for the 10 year period, 1973 to 1982 (data of Commonwealth Department of Primary Industry, Canberra). Geographic distribution of prawn catches was obtained from figures published by the Australian Fisheries Council (AFC 1982). The size of the estuarine mangrove systems within each region of the Gulf was estimated from Australian Topographic Survey Maps (1:100,000) for the Gulf coastal regions. The linear distance of the estuary fringed with mangroves, rather than mangrove area, was used as the best index of the available mangrove nursery area. Seagrass distributions within the Gulf were established from aerial surveys and subsequent transect sampling carried out in collaboration with I.R. Poiner (unpublished data[2]).

[2] I.R. Poiner, CSIRO Marine Laboratories, PO Box 120, Cleveland, Qld 4163, Australia

Results

Between-habitat distribution

Because habitats were in close proximity, temperature and salinity differences between habitats were negligible. Strong spatial partitioning existed among the five species, however, with all species, with the exception of *M. ensis* found predominantly in one habitat type (Fig. 3). *Penaeus esculentus, P. semisulcatus* and *M. endeavouri* had their highest occurrence on the seagrass site while *P. merguiensis* was largely confined to the mud bank immediately adjacent to the mangrove fringe (mud-mangrove bank). The percentage occurrence within these habitats was more than 90% for the two tiger prawn species, 70% for the endeavour prawn and approximately 97% for the banana prawn. In terms of total habitats occupied, *P. esculentus* and *P. merguiensis* showed the narrowest range followed by *P. semisulcatus, M. endeavouri* and then *M. ensis*. Approximately 20% of *M. endeavouri* occurred on the algal bed and 10% were on the mud-mangrove bank while *M. ensis* was even more widespread occurring equally on the seagrass and mud-mangrove sites. *Metapenaeus ensis* was the only commercial species to occupy the bare intertidal mudflats and open channel locations.

Within-habitat distribution

In both the seagrass area and on the mud-mangrove bank, the index of dispersion used to describe the dispersion pattern of the different prawn species, did not differ significantly from

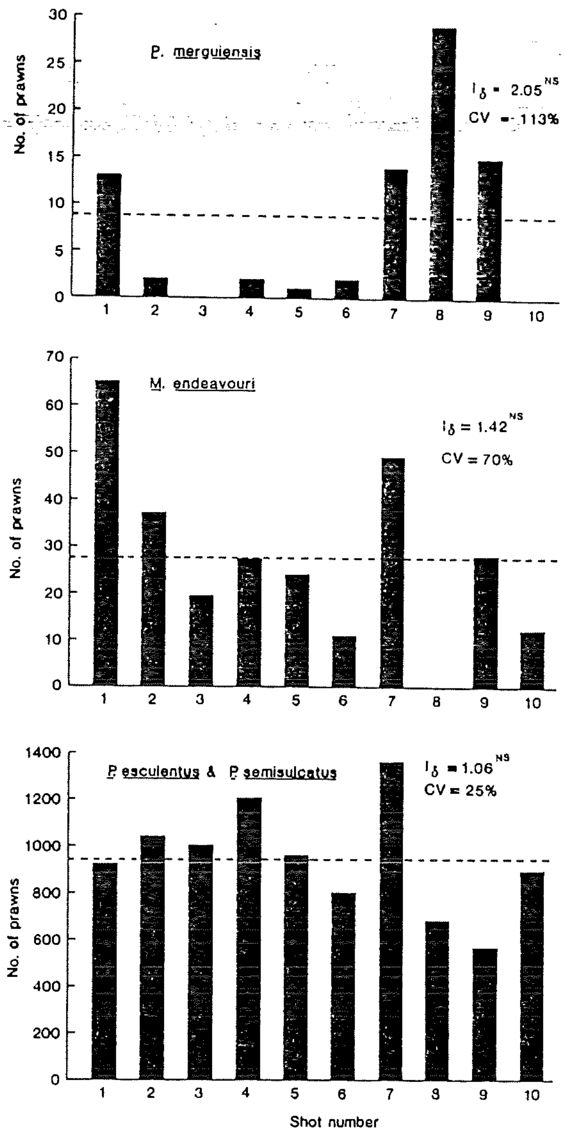


Figure 4. Catch of prawns in a series of trawls made within habitats, showing the mean catch for all trawls (broken line), index of dispersion (I_δ) and coefficient of variation (CV). Indices not significantly different from 1.0 marked NS.

1.0 (Fig. 4), indicating random distribution within these habitats. Both the coefficient of variation and the dispersion index, however, were greater for *P. merguiensis* than for either of the other groups indicating a greater tendency for clumping (Fig. 4). When juvenile and postlarval *P. merguiensis* were analysed separately, the dispersion index was significantly higher than unity within each stage ($P<0.05$). Because of the low sample numbers involved in this analysis we also tested 40 sets of random trawls taken in the Norman River between 1977 and 1979. The average dispersion index was 1.76 and ranged from 0.94 to 5.85. It was significantly greater than 1.0 on three occasions. We concluded that all species were essentially randomly distributed within habitats, although *P. merguiensis* was more variable and had a greater tendency for aggregation.

Distribution of nursery areas and catches

The main nursery area for juvenile *P. merguiensis* near the Embley River mouth was the mud-mangrove banks. Further sampling showed that both mangroves and juvenile banana prawns extended approximately 30 km inland, close to the upper limit of tidal influence. Similar mangrove lined estuarine rivers and creeks extend around the Gulf with a major concentration in the southeastern region (Fig. 5). Commercial catches of banana prawns are also widespread around the Gulf with the exception of a small area within the Limmen Bight region. Mean annual catch taken from 1973 to 1982 from each region of the Gulf was positively correlated with the size of the nursery area present inshore, calculated as the total length of available mangrove lined estuary ($r=0.76$, $df=5$, $P<0.05$; Fig. 6). The Limmen Bight region of the Gulf did not fit this relationship, and factors other than available nursery area presumably have more effect on catches in this region. Omitting Limmen Bight from the analysis resulted in a correlation coefficient of 0.96, ($df=4$, $P<0.01$) for the other five regions.

Seagrass areas in the Gulf are much patchier than mangroves in their distribution and are confined largely to the western Gulf. Catches of tiger prawns are also more discontinuous than banana prawns and are restricted to regions where seagrass nursery areas occur (Fig. 7). Complete quantitative data on seagrass areas are not yet available although considerable mapping and some analyses have been carried out. Preliminary analyses suggest that regional catches of tiger prawns are related to the area of available seagrass habitat with again the exception of the Limmen Bight region.

Discussion

Four of the five commercially most important species of prawns in the Gulf of Carpentaria, were closely associated with some form of vegetation during the juvenile phase of their life

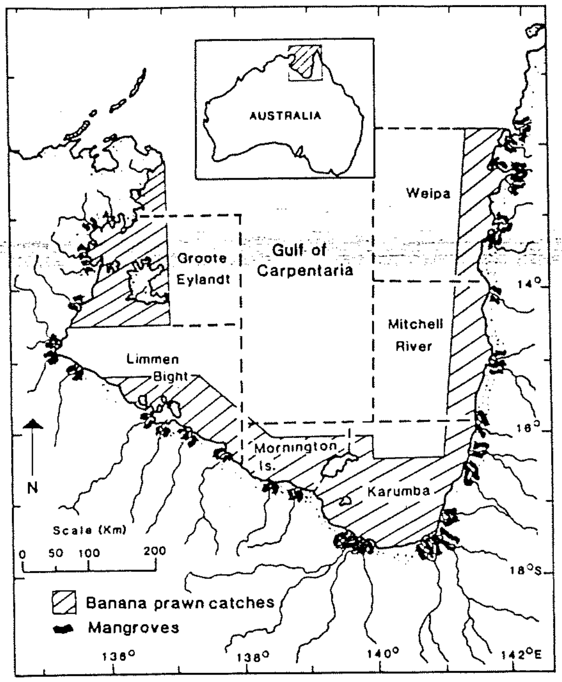


Figure 5. Distribution of mangrove lined rivers and extent of commercial catches of banana prawns *Penaeus merguiensis* in the Gulf of Carpentaria. Boundaries of the statistical catch regions are defined by broken lines.

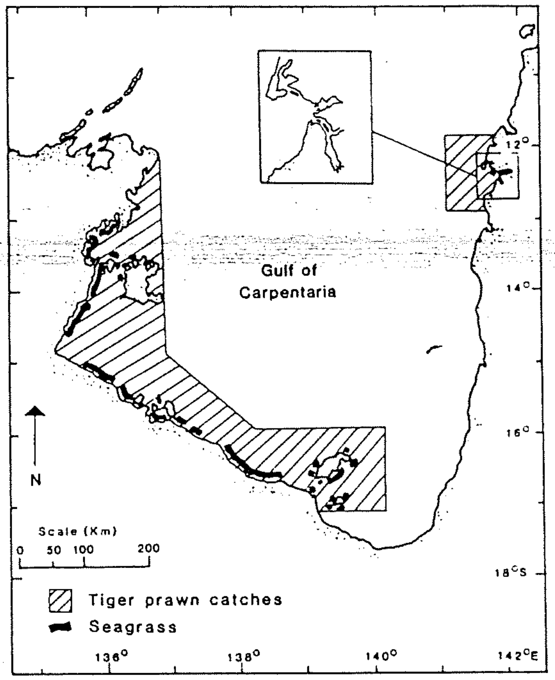


Figure 7. Distribution of seagrass areas and extent of commercial catches of tiger prawns *Penaeus esculentus* and *P. semisulcatus* in the Gulf of Carpentaria. Seagrass areas in the northeastern Gulf are mainly confined to estuaries and are shown in the inset.

history in the Embley River estuary. The most important nursery habitats were the intertidal seagrass flats, algal beds and mud-mangrove banks of the estuary. The three species of the

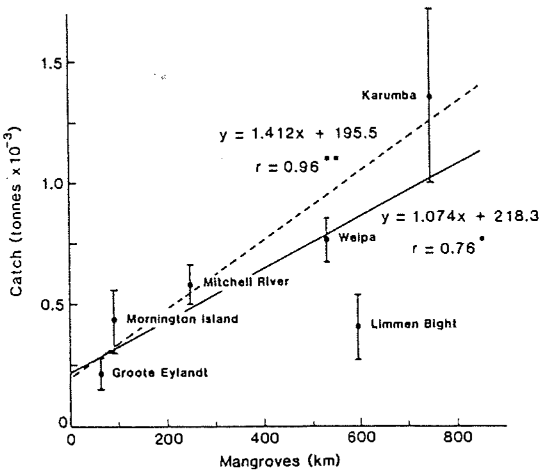


Figure 6. Mean annual commercial banana prawn catch (± standard error) and total length of mangrove lined rivers in each region of the Gulf of Carpentaria. The regression lines for all regions (solid line) and for all regions except Limmen Bight (broken line) are shown. $^{*}P<0.05$, $^{**}P<0.01$.

genus *Penaeus* were more restricted in their habitat requirements than the two *Metapenaeus* species. Within the *Penaeus* species there was little overlap between tiger prawns (both species) which were found mainly on seagrass, and banana prawns which were largely confined to the mud-mangrove banks. Of the two *Metapenaeus* species, *M. endeavouri* was found most commonly in the typical tiger prawn seagrass habitat but a significant percentage was also found in the algal and mud-mangrove areas. *Metapenaeus ensis* occurred equally in the seagrass and mud-mangrove areas and was also the only species to occur in any numbers on the bare intertidal mudflat and open channel. In comparing the distribution of the different species among habitats, it must be remembered that not all habitats are equally stable in time. The relatively low use of algal areas by the tiger and endeavour prawns, for example, is in part a reflection of the instability of algal areas in the estuary. Good algal cover occurred only in spring (September to November) and autumn (March to May) and because prawn occurrence was calculated on an annual basis the importance of algal areas may be underestimated. The more dynamic interactions between prawn abundances and preferred habitats will be reported elsewhere.

Many species of the genera *Penaeus* and *Metapenaeus* utilise the inshore coastal waters and estuaries as nursery areas during the juvenile phase of their life history (Kutkuhn 1966; Kirkegaard 1975). There is also considerable evidence to show that different species exhibit a strong spatial separation within this nursery area zone. Gunter (1961) and Gunter et al (1964) concluded that salinity was the most important factor in controlling the distribution of juvenile *P. setiferus*, *P. aztecus* and *P. duorarum* in nursery areas of the Gulf of Mexico, although more recent studies have suggested preferences of some species, in particular *P. aztecus*, for different vegetation types (Turner 1977; Zimmerman et al in press). It is obvious that salinity, vegetation type and prawn distribution will all be inter-related and arguments as to which is the controlling factor will tend to be circular. In the present study, however, study sites within the same estuary were in close proximity and temperature and salinity differences between sites were within ± 1%. On this scale, vegetation and substrate differences appeared to control prawn distribution. Similar observations have been made for some of these species in other parts of their range. *Penaeus esculentus*, in Moreton Bay in southeastern Queensland (27° 30′ S, 153° 20′ E), for example, occurred more commonly in seagrass areas than in adjacent bare substrates in areas of intermediate salinities (Young 1978). Basson et al (1977) suggested that *P. semisulcatus* in Saudi Arabia is dependent on algal and seagrass beds during its postlarval and juvenile stages. Price and Jones (1975) and Price (1979a, b) also recognised certain areas of Saudi Arabia as being important nursery areas for *P. semisulcatus* on the basis of their extensive algal and seagrass beds. In the Mediterranean, *P. semisulcatus* were also found over seagrass beds by Tom et al (1984). Mohamed et al (1981) reported that postlarval and juvenile *P. semisulcatus* were common in floating algal masses. In contrast, *P. merguiensis*, like the morphologically and ecologically similar *P. indicus*, appears to be much more closely associated with the mud-mangrove environment throughout much of its range (Hall 1962; Hynd 1974; Munro 1975; Chong 1979; Motoh 1981). These consistencies in the literature suggest that generalisations can be made concerning the habitat requirements of several species. Penn (1981) warns that considerable variation in nursery area requirements can occur in some instances and gives the example of White (1975), who reported that *P. esculentus* utilises highly turbid waters of Exmouth Bay in Western Australia (22° 20′ S, 114° 15′ E) in areas where little seagrass exists.

Based on our findings on the restricted nature of the habitat requirements of the main commercial species in the Embley River, especially for the genus *Penaeus*, we examined whether the large-scale distribution of the adult stocks of these species was in any way related to the distribution of their nursery grounds. For both tiger and banana prawns, the distribution of the main fishing grounds in the Gulf coincided with the presence of the appropriate nursery habitat inshore to the fishery. Thus, on a regional scale, nursery area distribution appeared to be controlling the major distributional patterns of the different prawn species. As a corollary, we suggest that the generalisations concerning the habitat requirements of these species appear to hold within the Gulf of Carpentaria, at least on a qualitative basis. Other factors, such as substrate and the distribution of food organisms will then affect the smaller scale distribution of prawns within these wider limits.

On a more quantitative basis, there is evidence that the mean catch of banana prawns over 10 years in each region of the Gulf depended on the amount of mangrove habitat available in estuaries within the region. While considerable year-to-year variation in catches has occurred, the highest mean catches have been made in regions with more available mangrove estuaries. A similar relationship for prawn catches (total of several species) and mangrove area has been found in Indonesia (Matsubroto and Naamin 1977) and the catch of several species and the area and type of estuarine vegetation in several regions of North America (Turner 1977). In our study, the Limmen Bight region of the Gulf was an obvious outlier with a much lower mean catch than expected on the basis of its rather extensive mangrove system. Catches fluctuated from 0 to 1400 t over the 10 years which could only in part be explained by rainfall fluctuations (Vance et al in press). The behaviour of prawns in this region serves as a useful reminder that the distribution and abundance of animal populations cannot be described on the basis of one or two physical parameters observed in only one part of their range. Further work in the Limmen Bight region should elucidate which factors affect long-term catches of *P. merguiensis* throughout its range.

The relationship between mangroves, seagrass and prawn catches has obvious implications for the management and future wellbeing of Australian prawn fisheries. The first conclusion is that, because these nursery areas are limited in their distribution, the offshore prawn fisheries are also limited resources. Any changes to the nursery habitat will have a corresponding effect on the offshore catch. Apart from the five main commercial species, many other species of penaeid prawns utilised the Embley estuary during part of their life history. The more common species included *M. dalli*, *M. conjunctus*, and *M. eboracensis*, all of which were often found on the wide bare intertidal mudflats. If the amount of vegetation in an estuary is reduced through its destruction for alternative land use (eg housing canals, aquaculture) then a corresponding decrease in the commercial species offshore can be expected and a replacement by less important non-commercial species is possible.

The restricted niche of each species must also be borne in mind in the consideration of pond siting and design in future aquaculture applications. It should also be considered in any re-stocking scheme of natural populations from hatchery postlarvae. Because only limited areas of suitable habitat are available around the Australian coast, and these areas will have upper limits to their carrying capacity, indiscriminate release of hatchery-reared postlarvae could be wasteful and costly.

Acknowledgements

Mr S. Garland, formerly of the CSIRO Marine Laboratories, Cleveland, Australia, provided invaluable assistance in the collection and sorting of all field samples. The present study was funded by the Fishing Industry Research Trust Account.

References

AFC 1982. Development and management of the Northern Prawn Fishery. AGPS, Canberra, 64 pp.

Basson, P.W., Burchard, J.E., Hardy, J.T. and Price, A.R.G. 1977. Biotopes of the western Arabian Gulf: marine life and environments of Saudi Arabia. Aramco, Bahrain, Saudi Arabia, 284 pp.

Braley, R.D. 1979. Penaeid prawns in Fanga uta Lagoon, Tongatapu. Pacific Science 33: 315-321.

Chong, V.C. 1979. The biology of the white prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Pulau Angsa-Klang Strait waters (Straits of Malacca). MSc thesis, Univ. of Malaya, 141 pp.

Dall, W. 1985. A review of prawn biological research in Australia. In: P.C. Rothlisberg, B.J. Hill and D.J. Staples (Editors), Second Aust. Nat. Prawn Sem., NPS2, Cleveland, Australia.

Grey, D.L., Dall, W. and Baker, A.G. 1983. A guide to the Australian penaeid prawns. NT Dept. of Primary Production, Darwin, 140 pp.

Gunter, G. 1961. Habitat of juvenile shrimp (Family Penaeidae). Ecology 42: 598-600.

Gunter, G., Christmas, J.Y. and Killebrew, R. 1964. Some relations of salinity to population distributions of motile estuarine organisms, with special reference to penaeid shrimp. Ecology 45: 181-185.

Hall, D.N.F. 1962. Observations on the taxonomy and biology of some Indo-west-Pacific Penaeidae (Crustacea, Decapoda). Colonial Office Fishery Publn. 17: 229 pp.

Heales, D.S., Polzin, H.G. and Staples, D.J. 1985. Identification of the postlarvae of the commercially important *Penaeus* species in Australia. In: P.C. Rothlisberg, B.J. Hill and D.J. Staples (Editors) Second Aust. Nat. Prawn Sem., NPS2, Cleveland, Australia.

Hughes, D.A. 1966. Investigations of the 'nursery areas' and habitat preferences of juvenile prawns in Mozambique. J. Appl. Ecol. 3: 349-354.

Hynd, J.S. 1974. Year round fishery possible in the Gulf. Aust. Fish. 33(5): 2-5.

Kirkegaard, I. 1975. Observations on penaeid larvae around Australia. pp. 54-59. In: P.C. Young (Editor), First Aust. Nat. Prawn Sem. AGPS, Canberra.

Kutkuhn, J.F. 1966. The role of estuaries in the development and perpetuation of commercial shrimp resources. Am. Fish. Soc. Spec. Publ. 3: 16-36.

Matsubroto, P. and Naamin, N. 1977. Relationship between tidal forests (mangroves) and commercial shrimp production in Indonesia. Marine Research in Indonesia 18: 81-86.

Mohamed, K.H., El-Musa, M. and Abdul-Ghaffer, A.R. 1981. Observations on the biology of an exploited species of shrimp, *Penaeus semisulcatus* de Haan, in Kuwait. Kuwait Bull. Mar. Sci. 2: 33-52.

Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E(Biol.) 2: 215-235.

Motoh, H. 1981. Studies on the fisheries biology of the giant tiger prawn, *Penaeus monodon*, in the Philippines. SEAFDEC Tech. Rep. 7. 1-128.

Munro, I.S.R. 1975. Biology of the banana prawn (*Penaeus merguiensis*) in the south-east corner of the Gulf of Carpentaria. pp. 60-78. In: P.C. Young (Editor), First Aust. Nat. Prawn Sem. AGPS, Canberra.

Noor-Hamid, S. 1976. The occurrence and abundance of shrimp fry at Jepara in 1975 and 1976. Bull. Shrimp Cult. Res. Cent. 2: 158-168.

Penn, J.W. 1981. A review of mark-recapture and recruitment studies on Australian penaeid shrimp. Kuwait Bull. Mar. Sci. 2: 227-247.

Price, A.R.G. 1979a. Temporal variations in abundance of penaeid shrimp larvae and oceanographic conditions off Ras Tanura, western Arabian Gulf. Estuarine Coastal Mar. Sci. 9: 451-465.
Price, A.R.G. 1979b. Saudi Arabian Gulf shrimp resources. Proc. Saudi. Biol. Soc. 3: 293-302.
Price, A.R.G. and Jones, D.A. 1975. Commercial and biological aspects of the Saudi Arabian Gulf fishery. Bull. Mar. Res. Cent., Saudi Arabia 6: 1-48.
Silas, E.G., George, M.J. and Jacob, T. 1984. A review of the shrimp fisheries of India: a scientific basis for the management of the resources. pp. 83-103. In: J.A. Gulland and B.S. Rothschild (Editors), Penaeid shrimps—their Biology and Management. Fishing News Books, Farnham, UK.
Staples, D.J. and Vance, D.J. 1979. Effects of changes in catchability on sampling of juvenile and adolescent banana prawns, *Penaeus merguiensis* de Man. Aust. J. Mar. Freshw. Res. 30: 511-519.
Tom, M., Shlagman, A. and Lewinsohn, C. 1984. The benthic phase of the life cycle of *Penaeus semisulcatus* de Haan (Crustacea Decapoda) along the southeastern coast of the Mediterranean. PSZNI: Mar. Ecol. 5: 229-241.
Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Trans. Amer. Fish. Soc. 106: 411-416.
Vance, D.J., Staples, D.J. and Kerr, J. in press. Factors affecting the year-to-year variation in the catch of banana prawns, *Penaeus merguiensis*, in the Gulf of Carpentaria. J. Cons. int. Expl. Mer.
Van Zalinge, N.P. 1984. A review of the shrimp fisheries in the Gulf between Iran and the Arabian Peninsula. pp. 71-82. In: J.H. Gulland and B.S. Rothschild (Editors), Penaeid Shrimps—their Biology and Management. Fishing News Books, Farnham, UK.
White, T.F.C. 1975. Population dynamics of the tiger prawn *Penaeus esculentus* in the Exmouth Gulf prawn fishery and implications for the management of the fishery. PhD thesis, Univ. of Western Australia.
Young, P.C. and Carpenter, S.M. 1977. Recruitment of postlarval prawns to nursery areas in Moreton Bay, Queensland. Aust. J. Mar. Freshw. Res. 28: 745-773.
Young, P.C. 1978. Moreton Bay, Queensland: a nursery area for juvenile penaeid prawns. Aust. J. Mar. Freshw. Res. 29: 55-75.
Zimmerman, R.J., Thomas, T.J. and Gilbert, Z.(Jr) in press. Selection of vegetated habitat by *Penaeus aztecus* in a Galveston Bay salt marsh. US Fish Wildl. Serv. Fish. Bull.

Appendix 4.9

D.J. Staples, D.J. Vance and D.S. Heales
CSIRO Division of Fisheries Research,
PO Box 120, Cleveland, Qld 4163, Australia

Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries

Abstract: The habitat requirements of the juvenile stage of five major commercial penaeid prawn species and the resource partitioning of an estuary by these species were studied in the Embley River in northeastern Gulf of Carpentaria during 1981-82. Sampling was carried out over a series of 24h stations with a small beam trawl. The maximum catch recorded during the 24h period was taken as a measure of the relative abundance of prawns. For the five commercial species, seagrass flats, algal beds and mud banks immediately adjacent to the mangrove fringe (mud-mangrove banks) formed the main nursery areas. All species, with the exception of *Metapenaeus ensis*, were found predominantly in one habitat type. Juvenile tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, were most common in seagrass whereas the juvenile banana prawn, *P. merguiensis*, was largely confined to mud-mangrove banks. *Metapenaeus endeavouri* occurred commonly on seagrass but with some spread to other habitats while *M. ensis* was widespread, occurring on seagrass, mud-mangrove, bare intertidal mud and open channel locations. Because of these specialised habitat requirements, especially of the *Penaeus* species, the regional distribution and long-term abundance of adult prawns of this genus in the Gulf appears to be related to the geographic distribution and size of their nursery areas.

Introduction

Five species of penaeid prawns make up more than 98% of the total commercial catch of prawns in the Gulf of Carpentaria (data of Commonwealth Department of Primary Industry for 1980 to 1983, Canberra). These are the banana prawn, *Penaeus merguiensis*, the tiger prawns, *P. semisulcatus* and *P. esculentus*, and the endeavour prawns, *Metapenaeus endeavouri* and *M. ensis*. The Gulf fishery commenced in the late 1960s and catches of banana prawns were high in the early years due to favourable environmental conditions and the discovery of new fishing grounds. Over the last decade, the catch of banana prawns has declined and tiger and endeavour prawns have become increasingly exploited. Tiger prawns now form the main component of the catch (Fig. 1). Initial research in the Gulf of Carpentaria concentrated on banana prawns but as the importance of tiger prawns increased, more research effort has been directed into tiger prawn life history and population dynamics.

A considerable amount of information is now available on juvenile stages of the banana prawn in the Gulf of Carpentaria (for review see Dall 1985) but little information exists on juvenile stages of the other important commercial species. A few studies on these species have been carried out in other areas, however, including the recruitment and distribution of *P. esculentus* in Moreton Bay, Queensland, Australia (Young and Carpenter 1977; Young 1978), postlarval and juvenile stages of *P. semisulcatus* and *M. ensis* in India (Silas et al 1984), Tongatapu (Braley 1979), Indonesia (Noor-Hamid 1976), and some work has been reported on *P. semisulcatus* in the Arabian Gulf (Van Zalinge 1984) and the Sinai Peninsula region (Tom et al 1984). The habitat requirements of several related species were examined in Mozambique by Hughes (1966).

The present study was initiated to examine the temporal and spatial variation in the distribution

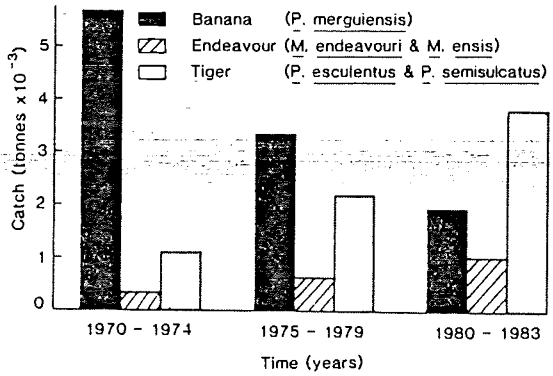


Figure 1. Mean annual commercial prawn catch for the three main species groups in the Gulf of Carpentaria, 1970 to 1983. (Data from Commonwealth Department of Primary Industry, Canberra).

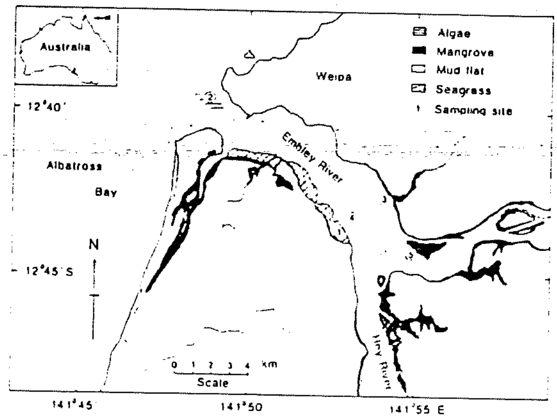


Figure 2. The Embley River estuary at Weipa. Sampling sites shown as: (1) intertidal seagrass flat, (2) shallow algal bed, (3) intertidal non-vegetated mud flat, (4) deepwater channel, (5) intertidal mud-mangrove bank.

of penaeid prawns inhabiting an estuarine system in the Gulf of Carpentaria. The Embley River in the northeastern Gulf was chosen as a study site mainly because of the presence of the five main commercial species in the offshore Albatross Bay region (Grey et al 1983). The seasonality in the distribution and abundance of these species has also been examined (CSIRO, unpublished data[1]) and the estuary contains a wide range of habitats likely to be suitable as nursery areas for juvenile prawns. Further, the narrow mouth of the estuary facilitated the monitoring of immigration and emigration of prawns.

This paper reports on some preliminary findings on the spatial distribution of the five major commercial species over scales ranging from within habitats (m) to Gulf-wide comparisons ($m \times 10^5$). Findings for other species and the temporal distribution of prawns on scales ranging from tidal and diel cycles (h) to seasonal comparisons ($h \times 10^3$) will be reported elsewhere.

Materials and methods

Juvenile prawns were collected from the Embley River estuary at three-weekly intervals from September 1981 to September 1982 using a 1x0.5m beam trawl fitted with a 2mm mesh net and a 1mm mesh codend. Five habitat types were selected for detailed sampling:
(1) seagrass flat, *Enhalus acoroides,* (2) shallow algal bed, mainly *Laurencia* sp. and *Sarconema* sp., (3) intertidal bare mud flat, (4) deep subtidal channel and (5) steep intertidal mud bank immediately adjacent to the mangrove fringe (mud-mangrove bank) (Fig. 2). Trawls on the wide gently shelving intertidal banks were made at right angles to the shore while other samples were taken parallel to the shore in the direction of the prevailing current. Trawls were repeated every 2h throughout a 24h period and the maximum catch taken during the 24h period was used as the index of relative abundance. Larger specimens, >5 to 7mm carapace length (CL), were identified to species using morphological characters revised from Grey et al (1983). Smaller specimens were identified using numerical taxonomy methods based on known reference material (Heales et al 1985). For the between-habitats comparisons, only prawns >5mm CL were used.

Dispersion within a habitat was estimated from a series of 10 parallel 200m long trawls taken at random within a 20m wide strip on the intertidal flats and 10 consecutive 30m trawls along the steeper bank. All trawls were taken at the time of day and tide stage known to maximise catches (eg low tide for *P. merguiensis*—Staples and Vance 1979). Similar samples in the Norman River in the southeastern Gulf (17° 30′ S, 140° 50′ E) were also analysed for banana prawn dispersion patterns. In this case, eight random trawls were made each week for 40 weeks within a 500m length of the estuarine bank. Morisita's index of dispersion (Morisita 1959) was used to describe dispersion patterns of all species and was calculated as—

$$I_\delta = \frac{k \sum_{i=1}^{k} n_i (n_i - 1)}{T (T-1)}$$

[1] CSIRO Marine Laboratories,
PO Box 120, Cleveland, Qld 4163, Australia

Coles, R. G., and Lee Long, W. J. (1985). Juvenile prawn biology and the distribution of seagrass prawn nursery grounds in the southeastern Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 55-60. (NPS2: Cleveland, Australia.)

Crocos, P. J. (1987*a*). Reproductive dynamics of the grooved tiger prawn, *Penaeus semisulcatus*, in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 79–90.

Crocos, P. J. (1987*b*). Reproductive dynamics of the tiger prawn *Penaeus esculentus*, and a comparison with *P. semisulcatus* in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 91–102.

FAO (1982). Report of the workshop on assessment of the shrimp stocks of the west coast of the Gulf between Iran and the Arabian Peninsula (Kuwait, 12–22 October 1981). 'Fisheries development in the Gulf. (Bahrain, Iran, Iraq, Kuwait, Oman, Qatar, Saudi Arabia, United Arab Emirates)'. (FAO: Rome.)

Fuss, C. M., and Ogren, L. H. (1966). Factors affecting activity and burrowing habits of the pink shrimp, *Penaeus duorarum*. *Biol. Bull. (Woods Hole)* **130**, 270–191.

Garcia, S. (1974). Biologie de *Penaeus duorarum notialis* en Côte d'Ivoire. IV. Relations entre la répartition et les conditions du milieu. Étude des variations du sex-ratio. *Doc. Sci. Rech. Oceanogr. Abidjan* **5**, 1–39.

Garcia, S. (1985). Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 139–58. (NPS2: Cleveland, Australia.)

Garcia, S., and LeReste, L. (1981). Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. 203.

Hall, D. N. F. (1962). Observations on the taxonomy and biology of some Indo-West Pacific Penaeidae (Crustacea, Decapoda). *Colonial Office Fish. Publ.* **17**, 1–229.

Hill, B. J. (1985). Effect of temperature on duration of emergence, speed of movement and catchability of the prawn *Penaeus esculentus*. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 77–84. (NPS2: Cleveland, Australia.)

Holthuis, L. B. (1980). FAO species catalogue. Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Synop. (125) Vol. 1.

Munro, I. S. R. (1975). Biology of the banana prawn (*Penaeus merguiensis*) in the south-east corner of the Gulf of Carpentaria. In 'First Australian National Prawn Seminar'. (Ed. P. C. Young.) pp. 60–78. (AGPS: Canberra, Australia.)

Penn, J. W. (1976). Tagging experiments with western king prawns, *Penaeus latisulcatus* Kishinouye. II. Estimation of population parameters. *Aust. J. Mar. Freshw. Res.* **27**, 239–50.

Penn, J. W., and Caputi, N. (1985). Stock recruitment relationships for the tiger prawn, *Penaeus esculentus*, fishery in Exmouth Gulf, Western Australia, and their implications for management. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 165–73. (NPS2: Cleveland, Australia.)

Penn, J. W., and Hall, N. G. (1974). Morphometric data relating to commercial prawns from Shark Bay, Western Australia. *Fish. Res. Bull. West. Aust.* **15**, 1–7.

Poiner, I., Staples, D., and Kenyon, R. (1987). Seagrass communities of the Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 121–31.

Robertson, J. W. A., Coles, R. G., and Goeden, G. B. (1985). Distribution patterns of commercial prawns and reproduction of *Penaeus esculentus* around the Wellesley Islands in the southeastern Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 71–75. (NPS2: Cleveland, Australia.)

Somers, I. F. (1987). Sediment type as a factor in the distribution of commercial prawn species in the western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* **38**, 133–49.

Somers, I. F., and Kirkwood, G. P. (1984). Movement of tagged tiger prawns, *Penaeus* spp., in the western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* **35**, 713–23.

Somers, I. F., and Taylor, B. R. (1981). Fishery statistics relating to the declared management zone of the Australian northern prawn fishery, 1968–1979. *Aust. CSIRO Mar. Lab. Rep.* **138**, 1–13.

Staples, D. J. (1984). Habitat requirements of juvenile prawns. In 'The Potential of Aquaculture in Queensland'. (Eds B. R. Pollock and R. H. Quinn.) pp. 87–102. (Queensland Conference Workshop Series QC83012: Queensland Department of Primary Industries, Brisbane.)

Staples, D. J., Vance, D. J., and Heales, D. S. (1985). Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 47–54. (NPS2: Cleveland, Australia.)
White, T. (1975). Factors affecting the catchability of a penaeid shrimp *Penaeus esculentus*. In 'First Australian National Prawn Seminar'. (Ed. P. C. Young.) pp. 115–37. (AGPS: Canberra.)
Williams, T. (1977). The raw material of population dynamics. In 'Fish Population Dynamics'. (Ed. J. A. Gulland.) pp. 27–45. (Wiley: New York.)

Manuscript received 3 September 1986, accepted 13 November 1986

Aust. J. Mar. Freshw. Res., 1987, 38, 79-90

Reproductive Dynamics of the Grooved Tiger Prawn, *Penaeus semisulcatus*, in the North-western Gulf of Carpentaria, Australia

P. J. Crocos

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 120, Cleveland, Qld 4163.

Abstract

The reproductive cycle of female *P. semisulcatus* was investigated in the region north of Groote Eylandt in the Gulf of Carpentaria from August 1983 to March 1985. Approximately 1750 trawls were carried out over 21 monthly sampling cruises, and 13 748 females were examined. The minimum size at maturity was 29 mm carapace length (CL), and 50% of the population were mature at 39 mm CL. The proportion of females which had mated increased sharply above 34 mm CL with a maximum of 80% of females inseminated in the size range 38-54 mm CL. An index of population egg production, calculated from female abundance, the proportion of females spawning and fecundity according to size, was used as an indicator of reproductive output. Egg production was markedly seasonal, with a major spawning peak in August-September, and a minor one in February. Spawning occurred in a limited area within the study area. The spawning stock of *P. semisulcatus* is likely to be vulnerable to fishing pressure because the area and time of major spawning coincides with the major fishing effort in the region.

Introduction

The biological management of prawn stocks is frequently limited by inadequate knowledge of factors affecting production. An understanding of the dynamics of the reproductive process, as the basis of resource renewal, provides a background for management direction. Many studies of penaeid prawn population reproductive dynamics have been far from satisfactory because they rely solely upon the percentage of females with mature ovaries as an index of population reproduction (for example, Cummings 1961; Rao 1967; Teng 1971; Thomas 1974; Munro 1975; Chong 1979; Buckworth 1985), but this parameter by itself can give a biased picture and must be combined with an index of adult abundance and fecundity according to size (Garcia 1977; Le Reste 1978; Penn 1980; Crocos and Kerr 1983; Crocos 1985). In Australia, detailed accounts of population reproduction, taking account of abundance of spawners and fecundity with size, have been provided for *Penaeus latisulcatus* Kishinouye by Penn (1980), and for *P. merguiensis* de Man by Crocos and Kerr (1983).

The study area north of Groote Eylandt is an important commercial fishery for the grooved tiger prawn *P. semisulcatus* (de Haan) and the brown tiger prawn *P. esculentus* (Haswell). The reproductive biology of *P. semisulcatus* in the Groote Eylandt area was investigated during an intensive study of the biology of this species and *P. esculentus* (Somers *et al.* 1987), in which the life history stages were monitored throughout the generation span of a particular cohort. The commercial prawn catch in the Groote Eylandt region of the western Gulf of Carpentaria is currently around 4000 t, with *P. semisulcatus* and *P. esculentus* being the most important component of this catch (Somers *et al.* 1987). Like many other penaeid prawn species, *P. semisulcatus* spawns offshore and postlarvae and juveniles use coastal and estuarine nursery areas for growth (for review see Garcia and Le Reste 1981; Garcia 1985).

0067-1940/87/010079$02.00

Buckworth (1985) summarized the monthly percentage of *P. semisulcatus* females with visible ovaries found in commercial catches in the western Gulf of Carpentaria, but did not investigate reproduction from the population fecundity viewpoint.

This paper presents data on the reproductive biology and, in particular, the seasonal and spatial reproductive patterns of *P. semisulcatus*.

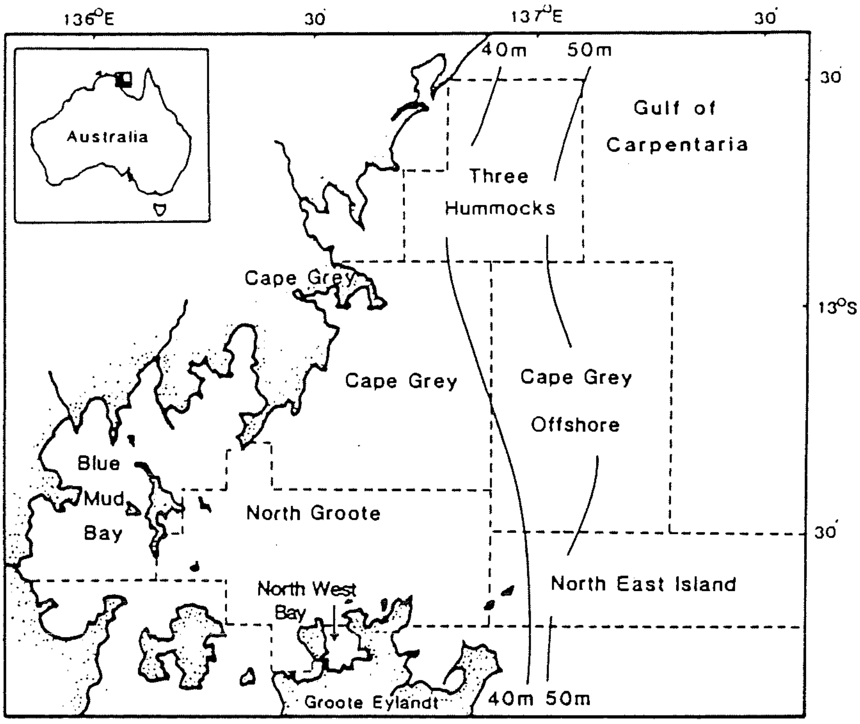


Fig. 1. Study area north of Groote Eylandt, western Gulf of Carpentaria, showing zones used in the analysis. Location of individual stations is given in Somers *et al.* (1987).

Materials and Methods

The sampling regime is described in detail by Somers *et al.* (1987). Briefly, approximately 1750 trawls were carried out over 21 monthly sampling cruises undertaken between August 1983 and March 1985. To eliminate any catchability changes related to the lunar cycle, sampling was standardized about the lunar month, the cruises generally extending from 5 days before to 5 days after the night of the new moon. Seventy-three trawl stations were established on a grid pattern of 6 nautical miles, incorporating inshore stations from 5 m depth to offshore stations of 55 m depth, the latter being beyond the limit of the commercial fishery. All stations were sampled at night with a standard trawl of 20 min duration using twin, 11-m headrope, otter trawls. The prawns from each trawl were separated by species and sex before measurement of carapace length (CL). A sample of up to 50 female *P. semisulcatus* was collected at each station, frozen to −40°C, and returned to the laboratory. Hydrographic data were collected from selected stations (Somers *et al.* 1987). On selected cruises, fresh female specimens were moult staged on board ship (Drach and Tchernigovtzeff 1967; Smith and Dall 1985).

In the laboratory, the insemination status of each female was recorded (Crocos and Kerr 1983). Tissue samples were dissected from the ovary in the region of the first abdominal segment and prepared, sectioned and stained for microscopic determination of maturity status (Crocos and Kerr 1983). As the ovary begins to mature the posterior lobes become visible and green in colour; at this stage (early ripe) vitellogenesis occurs. The post-vitellogenic oocytes then develop to the ripe stage, which is clearly characterized by the cortical specialization in the oocyte (Tuma 1967; Anderson *et al.* 1985). Histological examination is required to determine whether a visible, green-coloured ovary is in the early-ripe or ripe stage, since neither the colour nor the shape of the ovary provides a precise boundary. Presence of the cortical specialization in the oocytes indicates that spawning will usually occur within

7–9 days (Anderson *et al.* 1985; Crocos 1985). The spent ovary stage is recognizable histologically for 1–3 days after spawning (Crocos 1985). The combined number of females in the ripe and spent stages (i.e. within approximately 7–12 days of spawning) was recorded for each sample and regarded as the number of active spawners in the sample.

The relationship between fecundity and carapace length for *P. semisulcatus* was established with a sample of 63 ripe females over the size range 36–54 mm CL. Fecundity was calculated from the ovary weights of the 63 females and a mean number of ripe ova per gram of ovary (established from 33 of these females, using the counting method described in Crocos and Kerr 1983).

The description of spawning seasons and spawning areas was based on a calculated index of population egg production (Crocos and Kerr 1983). To analyse egg production on a regional basis, the study area was divided into zones on the basis of species and size distributions of the tiger prawn populations described in Somers (1987), and Somers *et al.* (1987). To examine seasonal spawning patterns, the egg production index was calculated on a monthly basis for data pooled over the whole study area and for data pooled for stations within each of the defined zones (Fig. 1). Spatial spawning patterns were ascertained by calculating the index on a per station basis, representing each 6 by 6 nautical mile grid (for station locations see Somers *et al.* 1987). The egg production index for a particular grid was calculated as the number of spawners (percentage of the female population actively spawning × abundance) multiplied by their individual fecundity (egg production as a function of size). Accordingly, for a specified zone,

$$I = \left[\sum_{i=1}^{N} a_i p_i \frac{1}{n_i} \sum_{j=1}^{n_i} f(l_{ij})\right] \Big/ N,$$

where I = egg production index, N = number of grids in a specified zone, a_i = abundance of females in grid i, p_i = proportion of actively spawning females in the sample from grid i, n_i = number of spawners in the sample from grid i, $i = 1, 2, \ldots N$, l_{ij} = carapace length of the jth active spawner caught in grid i, $j = 1, 2, \ldots n_i$, $i = 1, 2, \ldots N$, and $f(l)$ = fecundity of an active spawner with carapace length l, estimated from the fecundity–carapace length relationship. A mean of grid estimates for a specified zone provided the zone estimate. Standard errors for the egg production index within each zone were estimated assuming each grid sample was a random sample from the zone.

Results

Mating

Fewer than 8% of females with CL less than 30 mm were carrying a spermatophore (Fig. 2). The proportion of inseminated females increased rapidly with size, from 20% at 32 mm CL, to 70% at 38 mm CL, and 80% for females over 38 mm CL. The level of

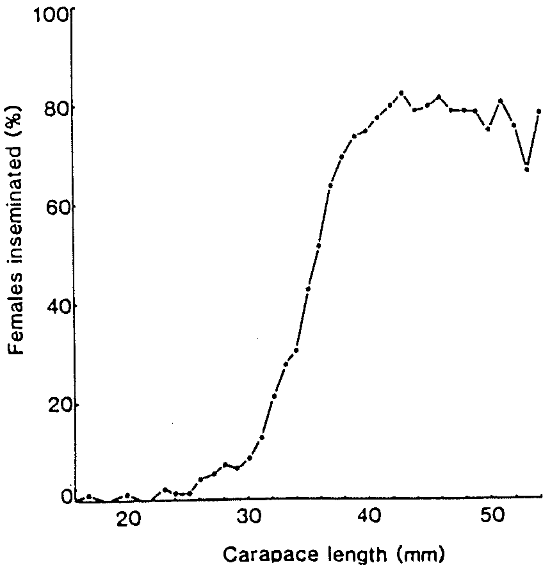


Fig. 2. Relationship between percentage of female *P. semisulcatus* inseminated and size (mm CL). (Total number of females examined, 13 748; mean number of females in each 1-mm CL size-class, 319.)

mating activity for females greater than 34 mm CL varied seasonally. The proportion of inseminated females above 34 mm CL was around 80% during September to December of the first year, but the proportion inseminated was much lower throughout late summer and dropped to around 30% in March to May (Fig. 3). In the second year, the proportion of mated females was between 60 and 80% from July to the following February, then declined to 50% in March. In closed-thelycum penaeids such as *P. semisulcatus*, mating occurs immediately after moulting while the exoskeleton of the female is soft (Crocos and Kerr 1983; Crocos 1985). Since the spermatophore deposited at this time is lost at the next moult, the high proportion of inseminated females in the adult population indicates that mating occurs several times during the adult phase, potentially at each moult. There is, however, an additional seasonal factor which modifies the proportion of females which are mated.

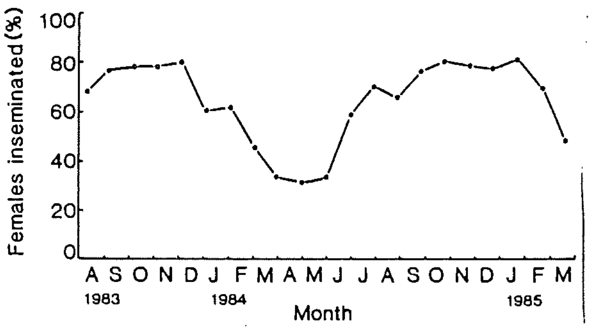


Fig. 3. Monthly percentage of inseminated female *P. semisulcatus* (≥34 mm CL), August 1983 to March 1985. (Total number of females ≥34 mm CL examined, 7736; mean number of females ≥34 mm CL in each monthly sample, 368.) Data points plotted according to central date of each sampling cruise.

Size at Maturity

Fewer than 1% of females smaller than 29 mm CL (20–22 g) were mature, but the proportion rose rapidly above this size (Fig. 4). Accordingly, 29 mm CL was regarded as the size at first maturity. The proportion of mature females in the population increased rapidly to 20% mature at 35 mm CL and 80% mature at 44 mm CL, with 50% of the population having mature ovaries at 39 mm CL (50–55 g) (Fig. 4). Although arbitrary, the size at 50% mature provides a good indicator of size at large-scale spawning in the population, hence 39 mm CL was regarded as the size at maturity of *P. semisulcatus*.

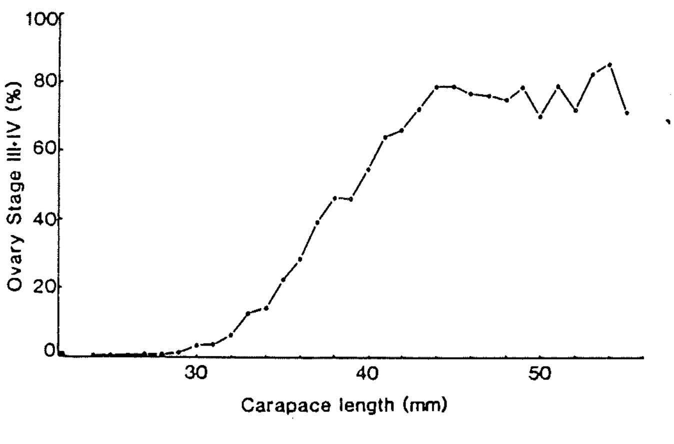


Fig. 4. Relationship between ovary maturation (stage III + IV) of female *P. semisulcatus* and length (mm CL), n = 13 748.

Fecundity

The overall mean number of ova per gram of ovary for the subset of 33 females (38–54 mm CL) for which egg count was determined was 76 150 (s.d. = 10 654). Using this estimate in combination with ovary weights obtained from 63 females between 38 and 54 mm CL, the relationship between number of ripe ova, V, and carapace length, l, in millimetres is given by the equation:

$$V = 28\,268l - 737\,782,$$

$r = 0{\cdot}77$, $n = 63$, s.e. of slope = 2987. The relationship is highly significant (Student's t test, $t = 9{\cdot}46$, $P < 0{\cdot}01$), explaining 60% of the error variance in egg number. According to this model, fecundity varies from approximately 336 000 ova at 38 mm CL to 790 000 ova at 54 mm CL. Since retained ripe ova were rarely seen in histological sections of spent ovaries, these values are considered to represent the number of eggs released at a single spawning.

Seasonality in Spawning

Overall study area

The peak relative abundance of *P. semisulcatus* females occurred in January or February of each year (Fig. 5*a*), when the mean size of females spawning was 40–42 mm CL (Fig. 5*b*).

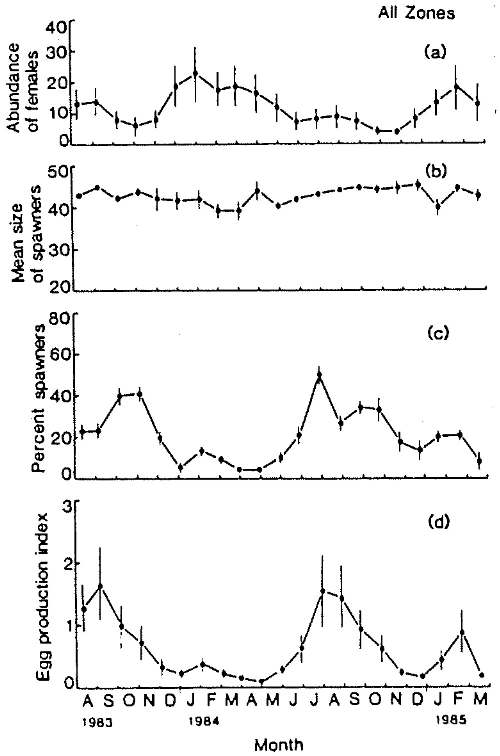


Fig. 5. Reproductive dynamics of *P. semisulcatus*, over the entire study area (all zones, 73 stations): (*a*) relative abundance of females (mean of catch per standard trawl, over the specified zone); (*b*) mean size of spawning females (mm CL); (*c*) percentage of females spawning; (*d*) mean egg production index. Data points are plotted according to central date of each sampling cruise. Vertical bars indicate standard errors of means. Where error bars are not shown, standard errors were smaller than the symbols used.

However, the percentage of females spawning in the population was lower in January and February, in both years, than during the August to November period in 1983 or the August to October period in 1984 (Fig. 5*c*). The seasonal egg production pattern of *P. semisulcatus* suggests two peaks of differing magnitude occurring each year, and that these peaks are area-dependent. In the spring months of 1983, egg production was high from August to late October, with a peak in September, followed by a drop and then a slight increase in February of 1984 (Fig. 5*d*). [When the data are split by area it can be seen that a strong February peak occurs only in the North Groote zone (Fig. 7), so the contribution of this peak is minimal when averaged over the whole study area.] Egg production increased sharply in July 1984 and remained high until October, with a peak in early August 1984, one month earlier than for the corresponding spring peak in 1983. Again, a secondary peak of egg production occurred in February 1985, which was of greater magnitude than the slight peak in February 1984. During spring 1983, even though the percentage of females spawning was highest in October and November (approximately 40%), peak egg production occurred in September as a consequence of the higher September abundance (Fig. 5*a*), and larger mean size of spawners (Fig. 5*b*), compared to October and November. During spring 1984, the early August peak was mainly due to the higher percentage of spawners at this time, since abundance and size of spawners were similar over the July to October period. Similarly, the secondary February peak of egg production observed in both 1984 and 1985 was of greater magnitude in 1985 due to a higher percentage of spawners (Fig. 5*c*).

Cape Grey, Cape Grey Offshore, Three Hummocks, and North East Island

In the Cape Grey zone the high abundance of females during September and October 1983 (Fig. 6*a*), in combination with the high proportion (55%) of large (mean 45 mm CL) and highly fecund spawning females (Figs 6*b*, 6*c*), resulted in very intense egg production from early August to late October, with a peak in September 1983 (Fig. 6*d*). During 1984, egg

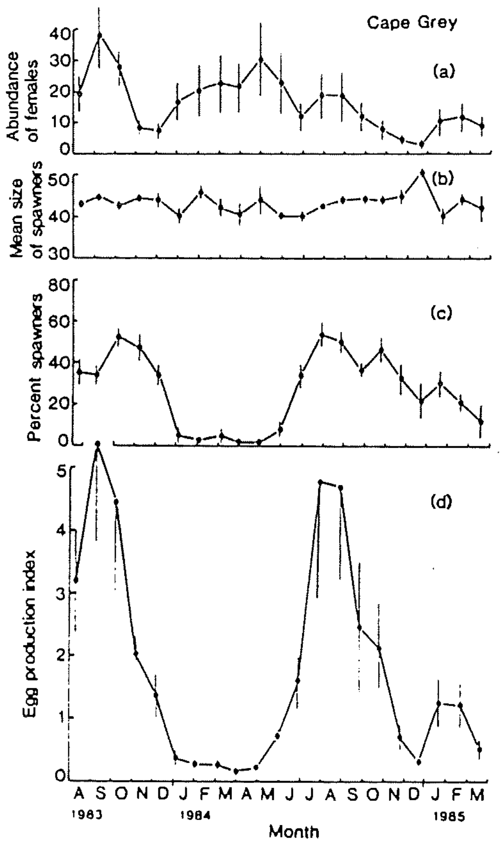


Fig. 6. Reproductive dynamics of *P. semisulcatus*, Cape Grey zone (17 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 5.

production was high from July to October, and peaked strongly in early August and September (Fig. 6*d*). The maximum egg production index (EPI) values of 5·5 and 4·8 for September 1983 and August 1984, respectively, were the highest recorded in the study. A secondary peak of egg production occurred in January and February 1985, but was not evident for this period in 1984, even though the relative abundance of females was higher during January to March 1984 than for January to March 1985 (Fig. 6*a*). The proportion of spawners at this time in 1984 was extremely low (Fig. 6*c*) hence the low level of egg production.

The seasonal egg production patterns of the Three Hummocks, Cape Grey Offshore and Cape Grey zones (Fig. 1) were identical. However, egg production in September 1983 in the Cape Grey Offshore zone was lower (EPI 2·5) than that for Cape Grey (EPI 5·5); similarly, for August 1984 EPI values were 2·3 and 4·8 respectively, and for February 1985, 0·5 and 1·2 respectively. The Three Hummocks zone, which was only sampled from June 1984 to March 1985, showed peak egg production in August 1984 (index value 4·0) and a second peak in February 1985 (index value 1·0).

Egg production of *P. semisulcatus* was relatively low in the North East Island zone, mainly due to low abundances of females. Peak EPI values were 1·8 in September 1983 and 0·9 in July 1984, with values of less than 0·2 at other times during the study period.

North Groote

In the North Groote zone (Fig. 1), abundance of female *P. semisulcatus* peaked in February of both years of the study (Fig. 7*a*). Although the proportion of spawners in this population was low in February 1984 (Fig. 7*c*), the mean size of these spawners at 42 mm CL resulted in relatively high fecundity (Fig. 7*b*), and resultant egg production was comparable to the

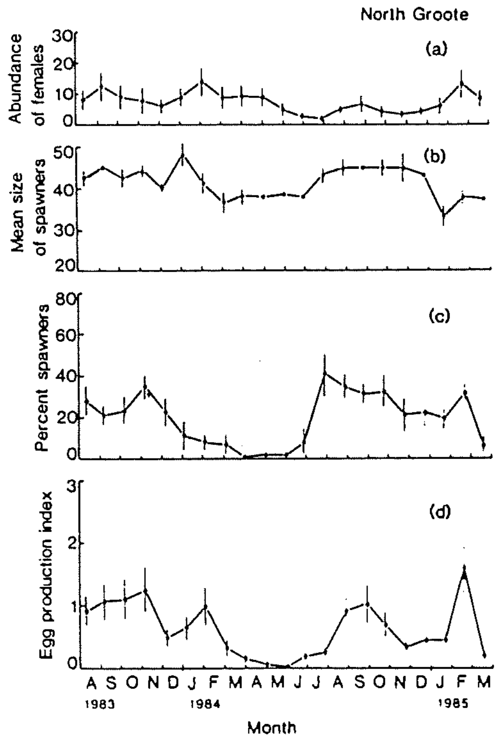


Fig. 7. Reproductive dynamics of *P. semisulcatus*, North Groote zone (23 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 5.

August–November peak for this zone (Fig. 7*d*). In February 1985, despite the spawners being smaller in size (37 mm CL), the combination of high female abundance with a high proportion of spawners in the population produced a larger peak of egg production than that for the previous spring spawning period (August–October) (Fig. 7*d*).

North West Bay, Blue Mud Bay

The highest abundances of female *P. semisulcatus* in North West Bay occurred in the summer months: January and February of 1984, and December 1984 to March 1985 (Fig. 8*a*). For most of the study period there were no spawners in this area, with only a very small percentage (2–7%) of females being reproductively active in August–September 1983, July–August 1984 and January–February 1985 (Fig. 8*c*). The few spawning females present in January–February were close to the minimum size of maturity for *P. semisulcatus* (Figs 4, 8*b*), and hence represented the earliest maturing females of this particular cohort.

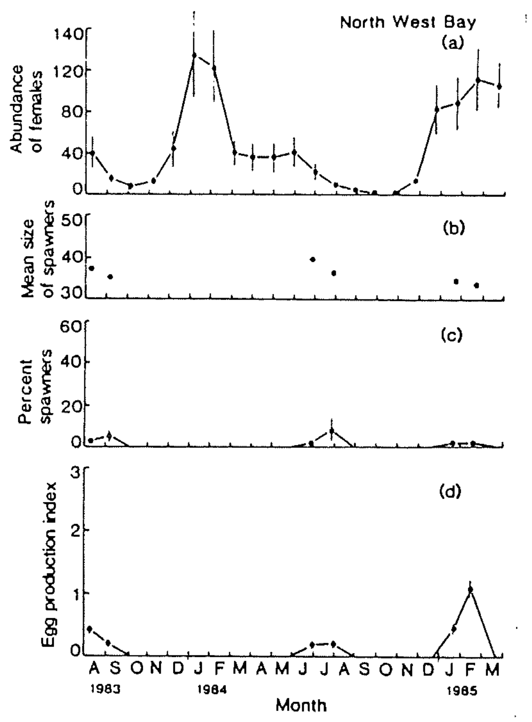


Fig. 8. Reproductive dynamics of *P. semisulcatus*, North West Bay zone (4 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 5.

Consequently, only small pulses of egg production were evident in August 1983, July–August 1984, and February 1985. In Blue Mud Bay, abundances were high between December and March for both 1984 and 1985, but these prawns were not large enough to be mature, and very few prawns were present at other times, so virtually no spawning activity occurred in this area at any time of year.

Spawning Areas

Analysis of mean egg production in each grid over the whole of the study period from August 1983 to March 1985 shows that the greatest spawning activity occurred generally offshore from Cape Grey, and to the south towards Groote Eylandt (Fig. 9). Egg production decreased markedly towards the outer edge of the study area, generally beyond the 40-m depth contour, as adult abundances declined. Inshore areas, particularly Blue Mud Bay, North West Bay, and the western part of the North Groote zone, contributed very little to the egg production of the *P. semisulcatus* population.

During the major seasonal spawning period, July to October, egg production was more intense in the Cape Grey zone (Fig. 10), resulting in higher values for the egg production index for that period compared to the annual mean egg production (Fig. 9). Egg production from July to October was minimal in the inshore areas, North West Bay and North Groote zones, and in the offshore areas beyond the 40-m depth contour except in the northernmost part of the study area.

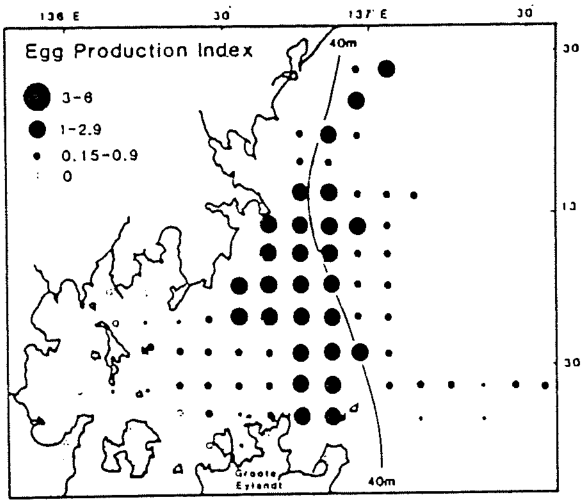


Fig. 9. Mean egg production index for *P. semisulcatus* by grid (mean index values over all cruises, August 1983–March 1985).

Discussion

P. semisulcatus matures at a larger size than do other penaeids in the region, with a minimum size at maturity of 29 mm CL, compared with 23 mm CL for *P. merguiensis* and 25 mm CL for *P. esculentus* (Crocos and Kerr 1983; Crocos 1987). The size at which 50% of the population is mature is 39 mm CL for *P. semisulcatus*, and 32 mm CL for both *P. merguiensis* and *P. esculentus*. At 39 mm CL, *P. semisulcatus* females have a relatively high fecundity of *c.* 365 000 eggs per spawning, whereas *P. merguiensis* and *P. esculentus* at the 50% maturity size (32 mm CL) have lower fecundities of *c.* 197 130 and 186 050 respectively. Thus, individual fecundities for *P. semisulcatus* are very high at the time of major spawning of the population during August and September, when individuals are approximately 10–12 months old.

Estimates of the relative abundance of prawns in this study were based on changes in CPUE. Typically, CPUE values for penaeid prawns tend to decline as water temperatures reach winter minimum values (Fuss and Ogren 1966; White 1975; Penn 1976; Buckworth 1985), suggesting that catchability is reduced at lower temperatures. In laboratory studies, Hill (1985) observed reduced emergence time for *P. esculentus* at temperatures below 24°C, and suggested that this would contribute to a decrease in CPUE in winter. Hill (unpublished data) found that emergence time for *P. semisulcatus* was also reduced at temperatures below 26°C. In the present study, temperatures fell below 24–26°C during May to July and the relative abundance of *P. semisulcatus* may have been underestimated in this period (Somers *et al.* 1987). However, since the proportion of active spawners was very low (mean 8%) at this time, any effect of underestimation of the EPI would be minimal.

A double-peaked pattern of reproductive output appears to be typical for many penaeid prawns: Garcia (1977) reviewed seasonal spawning patterns for several penaeids and, despite shortcomings in the methods used at that time to quantify spawning activity, found the double-peaked pattern to be most common. In the Gulf of Carpentaria, Australia, Rothlisberg *et al.* (1987) observed a bimodal seasonal pattern of abundance for the larval stages of *P. semisulcatus*, *P. merguiensis*, and *P. latisulcatus*. For *P. merguiensis* in the Gulf of Carpentaria, Crocos and Kerr (1983) observed a bimodal pattern of seasonal egg production, although the dominance of either the spring or autumn peak varied according to geographic location. Similar regional differences were found for *P. semisulcatus* in the present study. Egg production in the *P. semisulcatus* population suggests a bimodal pattern, with a dominant August–September peak and a lesser peak in February, with the magnitude of these peaks being related to geographic location. The August–September peak is strongly dominant in the Cape Grey zone, but the February peak can be equivalent or even larger in the North Groote zone (Figs 6 and 7). The highest levels of egg production occur in the Cape Grey zone during spring, so this is considered to be the major spawning for *P. semisulcatus*.

Buckworth (1985) pooled data for *P. semisulcatus* from commercial catch samples taken over a 4-year period from the whole of the western Gulf of Carpentaria, and used the monthly percentage of females with visible ovaries as an indicator of spawning activity. From these data he proposed a unimodal pattern of spawning activity, with a prolonged spawning period from July to December. Buckworth did observe a slight increase in the proportion of adult-sized females in February, which, if combined with spawning data, may have shown an increase in population fecundity at this time. Also, much of the reproductive activity observed during February in the present study was a result of younger, smaller-sized females spawning further inshore where they may not have been included in Buckworth's commercial catch samples, as these samples are inherently biased towards heavily fished adult populations.

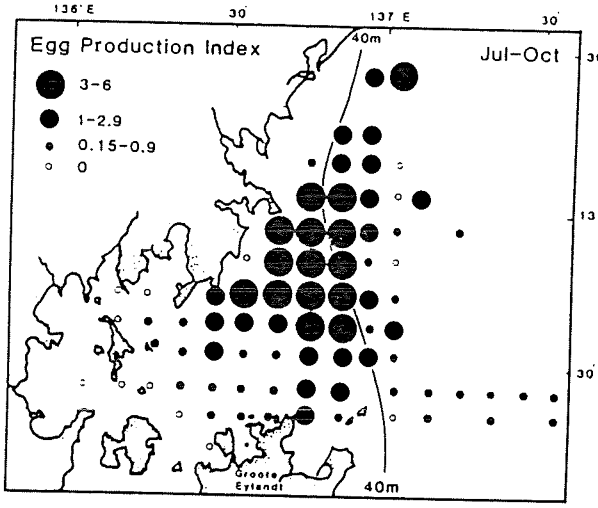


Fig. 10. Mean egg production index for *P. semisulcatus* by grid during the main spawning season (July to October, 1983 and 1984).

High abundances of sub-adult (<20 mm CL) *P. semisulcatus* occur in both North West Bay and Blue Mud Bay (Somers *et al.* 1987), these areas being regarded as nursery areas for *P. semisulcatus*. Tagging studies by Somers and Kirkwood (1984) showed that *P. semisulcatus* pass through the North Groote zone during migration from inshore nursery areas to offshore grounds. The February peak of egg production is strongest in the inshore area of the North Groote zone, as prawns migrating from these inshore nursery areas reach maturity. The mean size of spawners at this time is as low as 36 mm CL (Fig. 7*b*), compared with 45 mm CL for females spawning in September. The February spawners represent the early maturing group of this cohort, and constitute the first spawners of this population. From March onwards, the percentage of active spawners in the population, and hence egg production, began to decline sharply (Figs 7*c*, 7*d*), possibly as a consequence of water temperatures falling from a maximum of 31°C in February to a minimum of 24°C in July (Somers *et al.* 1987). Concomitant with rising water temperatures from August onwards, the proportion of active spawners in the population increased. As these females were large, with high fecundity, egg production showed a major peak in August–September (Figs 5 and 6).

The basic pattern of spawning for *P. semisulcatus* is therefore an initial spawning when the first individuals of a cohort breed at approximately 6 months of age, then a massive spawning at about 10–12 months of age. The success of these spawnings can be estimated from the subsequent recruitment of juveniles. Staples (D. Staples, Division of Fisheries Research, CSIRO, Cleveland, Qld, personal communication) observed waves of high abundance of juvenile *P. semisulcatus* in coastal nursery areas within the study area from September to

March, with peak abundance in December. Data currently available on recruitment to the fishery indicate a late summer ingress of small prawns to the adult population (Kirkwood and Somers 1984; Buckworth 1985; Somers *et al.* 1987). This suggests that the larger spring (August–September) spawning period is more important for stock renewal than the February period.

The most intense egg production for *P. semisulcatus* occurs in the Cape Grey zone and the Three Hummocks zone to the north-east, during the major spawning period from August to October (Fig. 10). At other times of the year, egg production is less intense and slightly more widespread, but these two areas are still the dominant spawning zones. The resultant distribution of spawning stock is consistent with a migration from the nursery areas to offshore spawning grounds (Somers and Kirkwood 1984). The Cape Grey zone was the area of highest abundances of adult *P. semisulcatus* in the study area (Somers *et al.* 1987) and is also the area of most intense commercial fishing activity. The period of major spawning coincides with the time of heaviest fishing pressure, and this has the effect of reducing reproductive output at a stage of the life history which is critical for stock renewal. Over-exploitation of this spawning stock has the potential to result in reduced reproductive output which could become a limiting factor for production in this fishery.

Acknowledgments

I would like to thank B. J. Hill for his assistance and encouragement during the course of the study, and Tonya Cahill for her able technical assistance, both in the laboratory and in the field. John Kerr, Division of Mathematics and Statistics, CSIRO, provided valuable input to the data analysis. The cooperation and assistance from Steve Ivicic and the crew of the FV *Maxim* are gratefully acknowledged. W. Dall, B. J. Hill and P. C. Rothlisberg, all of CSIRO, constructively commented on the manuscript. The study was funded in part by a grant from the Australian Fishing Industry Research Trust Account.

References

Anderson, S. L., Clark, W. H., and Chang, E. S. (1985). Multiple spawning and moult synchrony in a free-spawning shrimp (*Sicyonia ingentis*: Penaeoidea). *Biol. Bull. (Woods Hole)* **168**, 377–94.

Buckworth, R. C. (1985). Preliminary results of a study of commercial catches, spawning and recruitment of *Penaeus esculentus* and *Penaeus semisulcatus* in the western Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 85–93. (NPS2: Cleveland, Australia.)

Chong, V. C. (1979). The biology of the white prawn *Penaeus merguiensis* de Man (Crustacea : Penaeidae) in the Palau Angsa-Klang Strait waters (Straits of Malacca). M.Sc. Thesis, University of Malaya, 141 pp.

Crocos, P. J. (1985). Appraisal of some factors relevant to the development of penaeid prawn population reproductive models. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 159–164. (NPS2: Cleveland, Australia.)

Crocos, P. J. (1987). Reproductive dynamics of the tiger prawn *Penaeus esculentus*, and a comparison with *P. semisulcatus* in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 91–102.

Crocos, P. J., and Kerr, J. D. (1983). Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea : Penaeidae) in the Gulf of Carpentaria. *J. Exp. Mar. Biol. Ecol.* **69**, 37–59.

Cummings, W. C. (1961). Maturation and spawning of the pink shrimp, *Penaeus duorarum*. *Trans. Am. Fish. Soc.* **90**, 462–8.

Drach, P., and Tchernigovtzeff, C. (1967). Sur la méthode de détermination des stades d'intermue et son application générale aux Crustacea. *Vie Milieu* **18A**, 595–610.

Fuss, C. M. Jr, and Ogren, L. H. (1966). Factors affecting activity and burrowing habits of the pink shrimp *Penaeus duorarum* Burkenroad. *Biol. Bull. (Woods Hole)* **130**, 170–91.

Garcia, S. (1977). Biologie et dynamique des populations de crevettes roses (*P. duorarum notialis*, Perez-Farfante, 1967) en Côte d'Ivoire. *Trav. Doc. ORSTOM* **79**, 1–271.

Garcia, S. (1985). Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 139–158. (NPS2: Cleveland, Australia.)

Garcia, S., and Le Reste, L. (1981). Life cycles, dynamics, exploitation and management of coastal penaeid Shrimp stocks. FAO Fish. Tech. Pap. No. 203.

Hill, B. J. (1985). Effect of temperature on duration of emergence, speed of movement, and catchability of the prawn *Penaeus esculentus*. In 'Second National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 77–83. (NPS2: Cleveland, Australia.)

Kirkwood, G. P., and Somers, I. F. (1984). Growth of two species of tiger prawn, *Penaeus esculentus* and *P. semisulcatus*, in the Western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* **35**, 703–12.

Le Reste, L. (1978). Biologie d'une population de crevettes *Penaeus indicus*, H. Milne-Edwards, sur la côte nord ouest de Madagascar. *Trav. Doc. ORSTOM* **99**, 1–291.

Munro, I. S. R. (1975). Biology of the banana prawn, *Penaeus merguiensis*, in the south east corner of the Gulf of Carpentaria. In 'First Australian National Prawn Seminar'. (Ed. P. C. Young.) Maroochydore, 1973, pp. 60–78. (AGPS: Canberra.)

Penn, J. W. (1976). Tagging experiments with western king prawn *Penaeus latisulcatus* Kishinouye. II. Estimation of population parameters. *Aust. J. Mar. Freshw. Res.* **27**, 239–50.

Penn, J. W. (1980). Spawning and fecundity of the western king prawn, *Penaeus latisulcatus* Kishinouye, in Western Australia waters. *Aust. J. Mar. Freshw. Res.* **31**, 21–35.

Rao, P. V. (1967). Maturation and spawning of the penaeid prawns of the south west coast of India. *FAO Fish. Rep.* **57**, 285–302.

Rothlisberg, P. C., Jackson, C. J., and Pendrey, R. C. (1987). Larval ecology of penaeids of the Gulf of Carpentaria, Australia. I. Assessing the reproductive activity of five species of *Penaeus* from the distribution and abundance of the zoeal stages. *Aust. J. Mar. Freshw. Res.* **38**, 1–17.

Smith, D. M., and Dall, W. (1985). Moult staging the tiger prawn *Penaeus esculentus*. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill, and D. J. Staples.) pp. 85–93. (NPS2: Cleveland, Australia.)

Somers, I. F. (1987). Sediment type as a factor in the distribution of commercial prawn species of the western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 133–??.

Somers, I. F., and Kirkwood, G. P. (1984). Movement of tagged tiger prawns, *Penaeus* spp., in the Western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* **35**, 713–23.

Somers, I. F., Crocos, P. J., and Hill, B. J. (1987). Distribution and abundance of tiger prawns *Penaeus esculentus* and *P. semisulcatus* in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 63–78.

Teng, Seng Keh (1971). Observations on certain aspects of the biology of *Metapenaeus brevicornis* (H. Milne-Edwards) and *Penaeus merguiensis* (de Man) in the Brunei estuary system. M.Sc. Thesis, University of Singapore. 125 pp.

Thomas, M. M. (1974). Reproduction, fecundity and sex ratio of the green tiger prawn, *Penaeus semisulcatus* de Haan. *Indian J. Fish.* **21**, 152–63.

Tuma, D. J. (1967). A description of the development of primary and secondary sexual characteristics in the banana prawn *Penaeus merguiensis* de Man (Crustacea : Penaeidae). *Aust. J. Mar. Freshw. Res.* **18**, 73–88.

White, T. (1975). Factors affecting the catchability of a penaeid shrimp *Penaeus esculentus*. In 'First Australian National Prawn Seminar'. (Ed. P. C. Young.) Maroochydore 1973, pp. 115–37. (AGPS: Canberra.)

Manuscript received 21 July 1986, accepted 2 October 1986

Appendix 4.2

Aust. J. Mar. Freshw. Res., 1987, 38, 91-102

Reproductive Dynamics of the Tiger Prawn *Penaeus esculentus*, and a Comparison with *P. semisulcatus*, in the North-western Gulf of Carpentaria, Australia

P. J. Crocos

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 120, Cleveland, Qld 4163.

Abstract

The reproductive cycle of female *P. esculentus* was investigated in the Groote Eylandt region of the Gulf of Carpentaria from August 1983 to March 1985. The minimum size at maturity for *P. esculentus* was 25 mm carapace length (CL), and 50% of the population were mature at 32 mm CL. The proportion of females which had mated increased sharply above 28 mm CL to a maximum of 80% inseminated in the size range 32-50 mm CL. An index of population egg production, calculated from female abundance, the proportion of females spawning and fecundity with size, was used as an indicator of reproductive output. Egg production tended to be spread throughout the year, but with eggs being produced most consistently in late winter and early spring. Spawning occurred in a limited area within the study area. A comparison of *P. esculentus* and *P. semisulcatus* showed that *P. esculentus* matures at a smaller size (50% at 32 mm CL) than *P. semisulcatus* (50% at 39 mm CL), fecundity is lower, spawning is nearer inshore and egg production is less strongly seasonal.

Introduction

The two species of tiger prawns, *Penaeus esculentus* (Haswell, 1879), and *P. semisulcatus* (de Haan, 1850) co-occur in Northern Australia. *P. esculentus* appears to be restricted largely to Australia, with a distribution in tropical and subtropical waters from the north-west coast to the east coast of Australia, while *P. semisulcatus* occurs throughout the Indo-West-Pacific (Grey *et al.* 1983). In the western Gulf of Carpentaria, these two species account for most of the commercial catch, currently about 4000 t. In the region north of Groote Eylandt, *P. esculentus* comprises between 35 and 66% of this catch (Buckworth 1985).

Information for biological management of these species has in the past been scant because the main source has been fishermen's log-book records, which do not distinguish between the two species of tiger prawns. A broad spectrum of biological information is required to ascertain whether or not these two similar species can be managed as a single entity. To date, Somers and Kirkwood (1984) have described contrasting migration patterns for the two species, Buckworth (1985) has provided commercial fishery data on the species distribution, and Somers *et al.* (1987) have provided comparative data on the species distribution for both fished and non-fished areas within the region north of Groote Eylandt. Further, distribution patterns of *P. esculentus* and *P. semisulcatus* have been shown to be related to bottom sediment type, which implies that these species have different substrate preferences (Somers 1987).

Information available on reproduction in *P. esculentus* has been limited to a summary of occurrence of females with visible ovaries provided by Buckworth (1985) from commercial catch data for the whole of the western Gulf of Carpentaria pooled over 4 years, a record of the percentage of females with visible ovaries in 1 year in the south-eastern Gulf (Robertson *et al.* 1985), and a record of the percentage of females with visible ovaries in

0067-1940/87/010091$02.00

the commercial catch from Exmouth Gulf, Western Australia (Penn and Caputi 1986). For *P. esculentus* on the east coast of Australia, O'Connor (1979) described seasonal changes in female gonadosomatic index as an indicator of spawning activity. However, these data may not adequately express the reproductive output of a population as they do not take specific account of population size and fecundity (Penn 1980; Crocos and Kerr 1983; Crocos 1985, 1987; Garcia 1985).

The detailed account of the seasonal and spatial reproductive dynamics of *P. esculentus* presented in this paper was part of an intensive ecological investigation of both *P. esculentus* and *P. semisulcatus* (Somers *et al.* 1987), in which both species were monitored throughout a generation of a particular cohort. As differences were observed in several aspects of the biology of these two species, it was also considered appropriate to compare some aspects of the reproductive dynamics of *P. esculentus* and *P. semisulcatus*. Detailed information on the reproductive dynamics of the latter species has been presented in Crocos (1987).

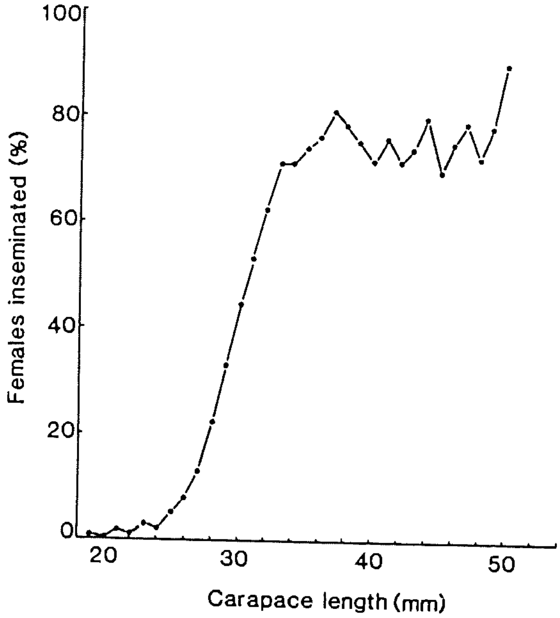


Fig. 1. Relationship between percentage of female *P. esculentus* inseminated and size (mm CL). (Total number of females examined, 10 307.)

Materials and Methods

The study area north of Groote Eylandt was sampled with 73 trawl stations established on a grid pattern of 6 by 6 nautical miles (11 by 11 km), which included both inshore stations from 5 m depth and offshore stations of 55 m depth, the latter being beyond the limit of the commercial fishery (fig. 1 of Crocos 1987 and fig. 1 of Somers *et al.* 1987). A detailed rationale for the selection of the study area and of the sampling regime is given by Somers *et al.* (1987). Briefly, approximately 1750 trawls were carried out over 21 monthly sampling cruises, each cruise of typically 11 days' duration, between August 1983 and March 1985, using the chartered trawler FV *Maxim*. All stations were sampled at night with a standard trawl of 20 min duration, using twin 11-m-headrope otter trawls. Sampling was carried out 5 days either side of the new moon.

Up to 50 female *P. esculentus* were collected from each station. In the laboratory, determination of impregnation status and the relationship between fecundity and size were carried out as detailed in Crocos (1987). Tissue samples were dissected from the ovary of each female in the region of the first abdominal segment, fixed, sectioned and stained for microscopic assessment of reproductive status. Characterization of actively spawning females was determined according to criteria detailed in Crocos (1987).

The description of spawning seasons and spawning areas was based on an index of population egg production (Crocos and Kerr 1983). Egg production was analysed on a regional basis as described in Crocos (1987).

Results

Mating

Fewer than 5% of females smaller than 25 mm carapace length (CL) were carrying a spermatophore (Fig. 1). The proportion increased rapidly with size: 22% at 28 mm CL, 72% at 34 mm CL, and up to 80% of females larger than 34 mm CL were inseminated. The proportion of females over 32 mm CL which were inseminated was relatively constant throughout the year at 60–80%, which suggests that adult females mate continuously, since the presence of a spermatophore indicates that mating has taken place within the current moulting cycle.

Size at Maturity

Although females as small as 21 mm CL were found with developed ovaries (at least stage III), fewer than 1–2% of females smaller than 25 mm CL were mature. The minimum size at which *P. esculentus* mature was taken as 25 mm CL (Fig. 2). The proportion of mature females rose rapidly from 6% at 27 mm CL to 70% at 36 mm CL, with 50% of females mature at 32 mm CL. The latter size was regarded as the size of maturity of *P. esculentus*.

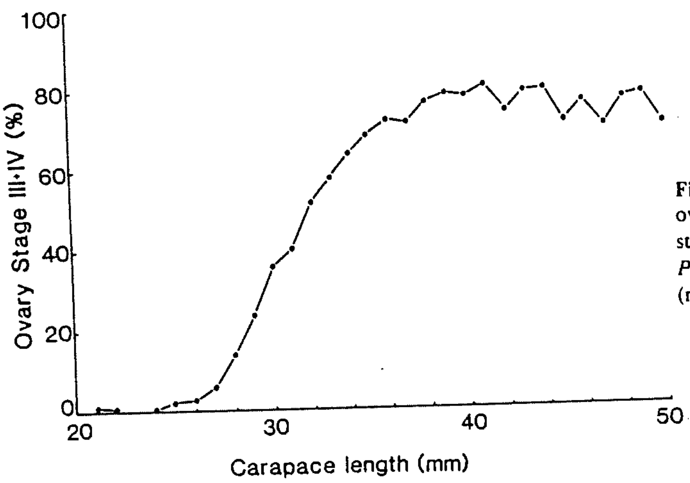


Fig. 2. Relationship between ovary maturation (ovary stage III + IV) of female *P. esculentus* and length (mm CL), $n = 9954$.

Fecundity

The number of ova in weighed subsamples of ripe ovaries from 42 females (28–51 mm CL) was counted. A mean of 77 181 (s.d. = 6496) ova per gram of ovary was found. Using this estimate in combination with ovary weights of 131 ripe females over the size range 28–51 mm CL, the number of ripe ova (V) can be expressed as the function of carapace length (l):

$$V = 22\,573l - 536\,291\,,$$

where l is measured in millimetres ($r = 0 \cdot 91$, $n = 131$, s.e. of slope = 905). The relationship is highly significant ($t = 24 \cdot 93$, $P < 0 \cdot 01$), with 83% of the variance in egg numbers explained by carapace length. According to this relationship, mean fecundity varies from 95 750 to 614 930 for females of 28 and 51 mm CL respectively. Since retained ripe ova were rarely seen in histological sections of spent ovaries, these values are considered to represent the number of eggs released at a single spawning.

Spawning Areas

A summary of mean egg production in each grid over the period from August 1983 to March 1985 indicates that egg production was most intense in the area corresponding to the North Groote zone, and including North West Bay (Fig. 3). Egg production was very low towards the outer edge of the study area to the north and east. An isolated pocket of high egg production occurred in one grid to the north-east of Cape Grey; egg production was otherwise confined to the area close to the north of Groote Eylandt. Inshore areas within Blue Mud Bay contributed little to the egg production of the population.

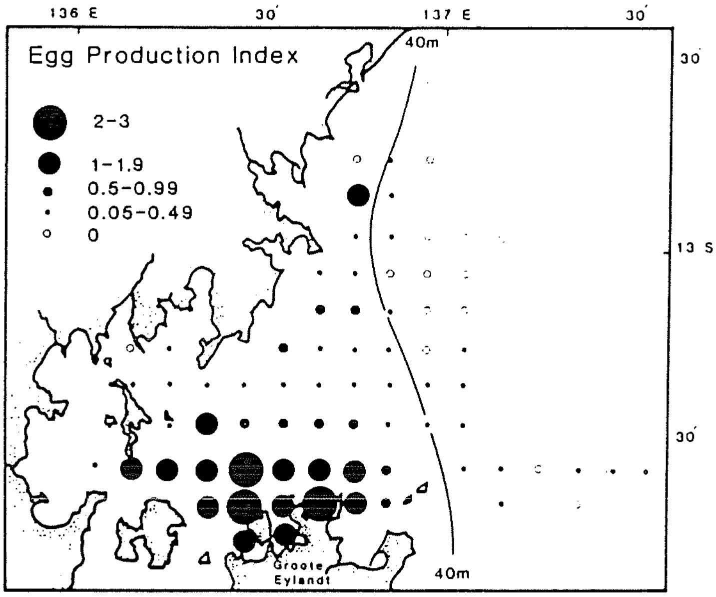


Fig. 3. Spatial distribution of egg production of *P. esculentus* between August 1983 and March 1985 (mean egg production index values by grid over all cruises).

Seasonality in Spawning

Entire study area

Female *P. esculentus* were most abundant in late spring and summer [November 1983 to February 1984 and December 1984 to March 1985, with peaks in December 1983 and January 1985 (Fig. 4*a*)]. During this same period the mean size of spawners was smallest; 34 mm CL during November 1983 to January 1984, and December 1984 to February 1985 (Fig. 4*b*), and therefore represent the contribution of the first reproduction of the late summer recruitment to the adult population. The percentage of females spawning was low in January 1984 (10%) and December 1984 (13%), but much higher in October 1983 (36%), late July 1984 (55%) and February 1985 (35%) (Fig. 4*c*). Rather than having a distinct seasonal pattern, mean egg production for *P. esculentus* tends more to be continuous at a fairly low level.

In 1983–84 the egg production index (EPI) from August to February was fairly constant (range 0·4–0·7), but egg production in 1984–85 was high from June to August (EPI 0·8), decreased until early summer and then peaked in February (EPI 1·0) (Fig. 4*d*). Even so, the range of the EPI values over the whole study period was narrow (0·3–1·0) (Fig. 4*d*).

The distinct peak in the percentage of females spawning (36%), which occurred in early October 1983 (Fig. 4*c*), did not result in a commensurate peak of egg production, as the population abundance was low at this time. By December 1983 the percentage of females spawning was much lower (15%) (Fig. 4*c*), but as the population was more abundant at this time (Fig. 4*a*) egg production reached a similar level to that in September. Similarly, in late July 1984 the peak in the percentage of females spawning (55%) (Fig. 4*c*) did not result in a commensurate peak of egg production, as abundance was relatively low (Fig. 4*a*).

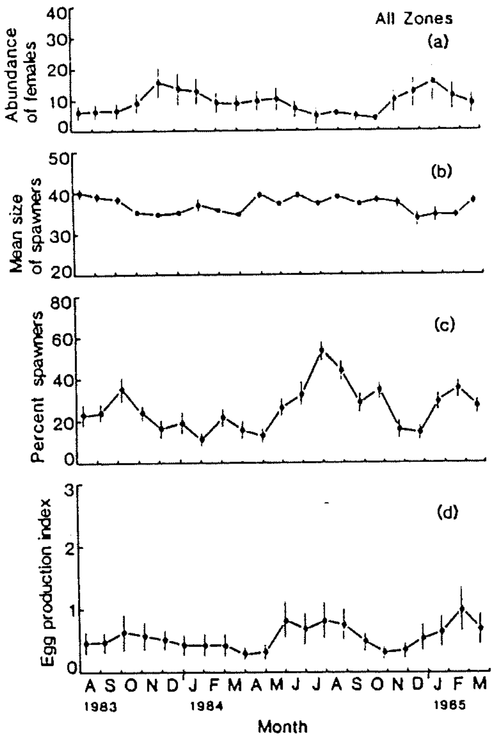


Fig. 4. Reproductive dynamics of *P. esculentus* over the entire study area (all zones, 73 stations): (*a*) relative abundance of females (mean of catch per standard trawl, over the specified zone); (*b*) mean size of spawning females (mm CL); (*c*) percentage of females spawning; (*d*) mean egg production index. Data points plotted according to central date of each sampling cruise. Vertical bars indicate standard error of means. Where error bars are not shown, standard errors were smaller than the symbols used.

North Groote zone

This area supported the highest mean annual abundance of adult *P. esculentus* in the overall study area (Somers *et al*, 1987), and the highest concentration of egg production (Fig. 3). It is therefore most representative of the reproductive pattern for *P. esculentus* in the present study. Abundance of females was highest during the summer and autumn months, with a peak in January of both 1984 and 1985 (Fig. 5*a*). The mean size of females spawning varied from a summer minimum of 34 mm CL in January 1984 and December 1984–February 1985, to 41 mm CL in August and October 1983, and 39–40 mm CL in the winter and early spring months of 1984 (Fig. 5*b*). The percentage of females spawning reached a peak in October 1983, declined to 30% during January and February 1984, and then declined further to a low of 10% by late April 1984 (Fig. 5*c*). The percentage then increased to a peak (60%) in late July, declined slowly to 30% by October and 25% in December, and had increased to 38% by March 1985.

Egg production for *P. esculentus* in this zone was very low in August 1983 (EPI 0·5), then increased (EPI fluctuating around 1·3) over the spring and summer period (September 1983 to early March 1984) (Fig. 5*d*). By early May 1984, egg production had declined to the level of the previous August. A pulse of egg production occurred in late May 1984 (EPI 1·4), followed by a decline in late June, and then a peak (EPI 1·9) in late July to late August. Egg production was low (EPI 0·6) throughout October–December 1984, increasing to an EPI of 1·5 in February 1985. Thus the patterns of egg production were slightly different in spring–summer in 1983–84, compared with those of spring–summer

1984–85. In 1983–84, egg production was relatively high throughout spring and summer, but in 1984–5 egg production peaked earlier (July–August) and then declined during spring before another peak in late summer.

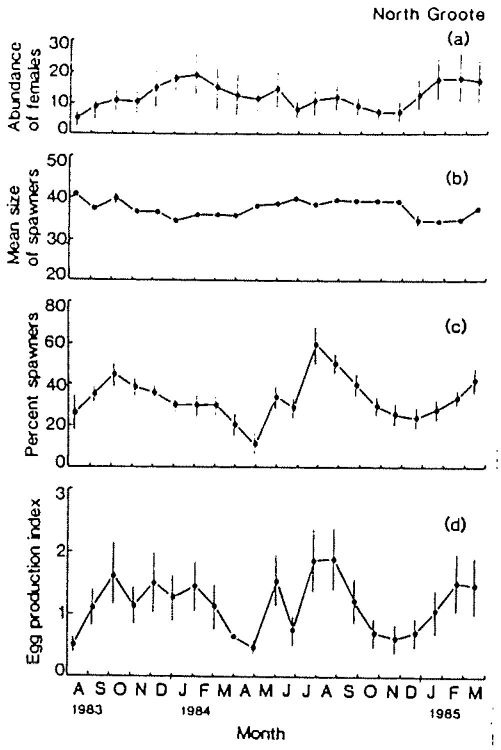


Fig. 5. Reproductive dynamics of *P. esculentus*, North Groote zone (23 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 4.

North West Bay

North West Bay is a very small (50 km^2) inshore area regarded as a nursery area for *P. esculentus* (Somers *et al.* 1987). Females were most abundant in December and January of both years of the study (Fig. 6*a*), mainly as a result of recruits entering the area at this time (Somers *et al.* 1987). Spawners present in this area in November–February, when population abundance was high, tended to be small (mean 32 mm CL) (Fig. 6*b*), with the exception of December 1983 when the mean size of spawners was 40 mm CL. However, less than 1% of the females in this population were spawning (Fig. 6*c*). The percentage of females spawning in North West Bay showed peaks in October 1983, late July 1984, and February 1985. The resultant egg production was high from August to November 1983 (mean EPI 1·5) and then declined (Fig. 6*d*); December 1983 to February 1984 levels were very low (EPI 0·2) despite the high population abundance, as the percentage of females spawning was very low (1%). Egg production by late May was again high (EPI 1·5) when larger (38 mm CL) spawners were moderately abundant (Figs 6*a*, 6*b*), and remained high until September, with a peak (EPI 2·2) in late July when a high proportion of females was spawning (Figs 6*c*, 6*d*). Egg production peaked again in January 1985 (EPI 1·7) when 18% of the small (30 mm CL) but abundant female population was spawning.

Other zones

The Cape Grey, Cape Grey Offshore, Three Hummocks and North East Island zones were not important areas for either adult abundance (Somers *et al.* 1987) or egg production

(Fig. 3). Mean annual abundance of *P. esculentus* in the Cape Grey zone was extremely low (Fig. 7*a*), so although the spawners present were large (mean 40 mm CL) (Fig. 7*b*), the actual numbers of spawners and hence egg production remained generally low (Fig. 7*d*).

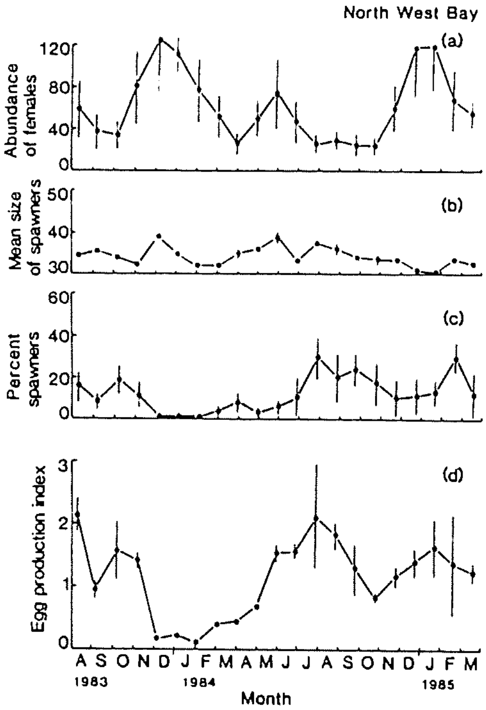


Fig. 6. Reproductive dynamics of *P. esculentus*, North West Bay zone (4 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 4.

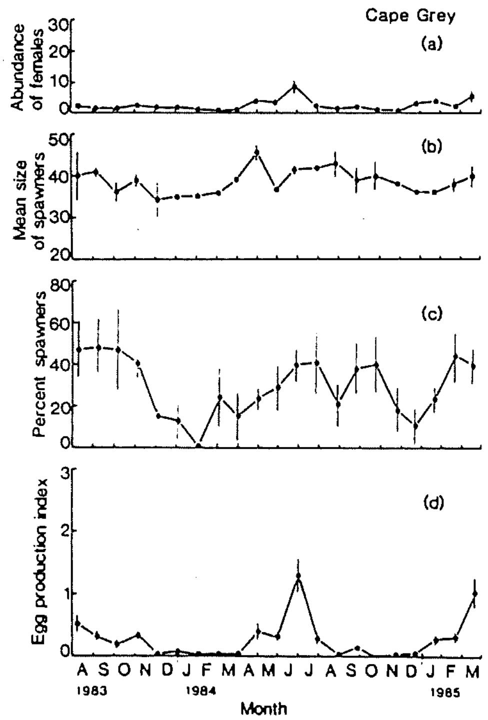


Fig. 7. Reproductive dynamics of *P. esculentus*, Cape Grey zone (17 stations): (*a*), (*b*), (*c*), (*d*) as for Fig. 4.

Egg production was highest in winter 1984 (July, EPI 1·2) and March 1985 (EPI 1·0), when abundances were also highest. In the Cape Grey Offshore zone, egg production was extremely low (maximum EPI 0·03) from June to August 1984, and negligible at other times. Similarly, egg production was at very low levels in the North East Island zone over the period March to June 1984 (mean EPI 0·1), with a small peak in May (EPI 0·3). In the Three Hummocks zone, sampled from June 1984 to March 1985, eggs were produced in June and July only (mean EPI 0·9) and only in an area restricted to two or three grids (Fig. 3). In Blue Mud Bay, eggs were produced sporadically and at a very low level (mean EPI 0·3) over the period September–February.

Discussion

Penaeus esculentus

Egg production for *P. esculentus* does not show the strong bimodal seasonal pattern observed for *P. merguiensis* in the eastern Gulf of Carpentaria (Crocos and Kerr 1983) and *P. semisulcatus* (Crocos 1987) in the north-western Gulf. Over the entire study area, egg production shows considerable interannual variation, with fairly constant egg production over the spring–summer period in 1983–84, followed by increased egg production in winter 1984, and a peak in February 1985 which did not occur in 1984. The mean monthly estimate of egg production over the entire study area (Fig. 4) results in some attenuation of the magnitude of the EPI values as a consequence of the large number of grids with low egg production (Fig. 3). However, this effect is largely removed if the North Groote zone, where the majority of egg production occurs, is considered separately. In this zone, the egg production pattern for *P. esculentus* is complex, with an indication of considerable interannual variation. In both 1983 and 1984, egg production was high in late winter or early spring. The timing of this egg production is consistent with recruitment of sub-adults (<20 mm CL) to the trawl grounds over the period November–March (Somers *et al.* 1987). Recruitment at other times was minimal, which suggests that eggs produced outside the spring period do not contribute markedly to stock renewal. Therefore, despite almost equivalent levels of egg production at other times, effective reproductive output may be restricted to the spring period.

From commercial catch samples taken in the western Gulf of Carpentaria over 4 years (1979–82), including the present study area, Buckworth (1985) found a high level (33–68%) of *P. esculentus* females with visible ovaries throughout the year, with peaks in February, July and October. He proposed that *P. esculentus* has a protracted spawning period; however, pooling the 4 years' data would have masked a seasonal pattern in any 1 year, given the interannual variation observed in the present study. Buckworth (1985) also noted that major recruitment of sub-adults to the fishery was restricted to a short period (November–February); hence the timing of spawning was not the main factor affecting the timing of recruitment.

For *P. esculentus* in the south-eastern Gulf of Carpentaria, Robertson *et al.* (1985) recorded about 40% of females with ripe ovaries throughout 1983, and suggested potential year-round spawning. However, these authors also noted that the combination of the percentage of ripe females with relative abundance data indicated a greater potential for egg production in the period July–September.

In Exmouth Gulf, Western Australia, Penn and Caputi (1986) found that the proportion of females with visible ovaries (stages III and IV) from commercial fishery samples of *P. esculentus* was consistently high from July to November (after which samples were unavailable) and still high in March when sampling resumed. These data suggest that spawning continued throughout the summer; however, the timing of subsequent recruitment suggests that the period August–October is the most important for stock renewal.

In the Low Islets area on the east coast of Australia, O'Connor (1979) observed *P. esculentus* females with visible ovaries throughout the year but, on the basis of a gonado-somatic index as an indicator of spawning activity, proposed that reproduction would be highest in autumn. This pattern is markedly different from that observed for *P. esculentus* in the Gulf of Carpentaria. However, some aspects of O'Connor's study suggest that the results he presented may not be representative of the pattern of reproductive output of this population. Firstly, although O'Connor stressed the effects of population abundance and size composition on reproductive output, he did not include these parameters in the analysis. Secondly, the sampling was constrained by the limited availability of trawlable grounds in the study region, and O'Connor recognized the possibility of migration of *P. esculentus* through the study area with a large proportion of the adult population existing beyond the limits of the study.

All these studies indicate the tendency for protracted spawning of *P. esculentus*, with moderate peaks generally occurring in spring and autumn, based on the percentage of females with visible ovaries. The present study confirmed that the percentage of active spawners was highest in spring, with a major peak occurring during July–October and a secondary peak in February or March (Figs 4–6). However, this parameter alone is not a good indicator of reproductive output, as the population abundance and hence the number of spawners and the variable fecundity of different-sized spawners will determine the level of egg production. The overall reproductive pattern for *P. esculentus* is one of protracted egg production but the spring spawning is the one which contributes most to subsequent recruitment.

Comparison of P. esculentus *and* P. semisulcatus

Size at maturity and fecundity

P. esculentus does not grow to the same maximum size as *P. semisulcatus* (Kirkwood and Somers 1984), and is not as fecund. In all, 50% of *P. esculentus* females were mature at 32 mm CL with a mean fecundity at this size of 186 045 eggs per spawning, whereas for *P. semisulcatus* 50% were mature at 39 mm CL with a mean fecundity of 364 670 eggs per spawning. The average maximum sizes of females in the present study were 45 mm CL for *P. esculentus* and 52 mm CL for *P. semisulcatus*. At these sizes, the estimated mean fecundity for *P. esculentus* is 479 494, and for *P. semisulcatus* 732 154 eggs per spawning. Further, female *P. semisulcatus* were more abundant (20–40 CPUE units, Crocos 1987) in their major spawning areas during spawning periods than were *P. esculentus* (10–20 CPUE units, Fig. 5*a*). For females spawning at a similar age, when *P. semisulcatus* females are larger, the fecundity of the *P. semisulcatus* population north of Groote Eylandt was potentially several times higher than that of *P. esculentus* during the period of the study.

Spawning areas

Spawning areas for a population are largely determined by the factors affecting the spatial distribution of adults. Somers and Kirkwood (1984) have shown that *P. esculentus* and *P. semisulcatus* exhibit a strong degree of separation in the offshore fishery as a result of different directions of movement from nursery areas. Further, Somers (1987) demonstrated that adults of the two species have specific preferences of different substrate types, which explains the adult distribution patterns. In the present study, the major spawning areas of *P. esculentus* in the North Groote zone (Fig. 3), and of *P. semisulcatus* in the Cape Grey zone (Crocos 1987), coincide with adult distribution patterns (Somers 1987; Somers *et al.* 1987). In North West Bay, where both *P. esculentus* and *P. semisulcatus* occur in high abundance, *P. esculentus* shows intense spawning activity (Fig. 6), whereas spawning in *P. semisulcatus* is minimal, even though female *P. semisulcatus* above the size at maturity occur in this area (Crocos 1987; Somers *et al.* 1987). *P. esculentus* spawners are found from close inshore areas (North West Bay) to deeper offshore areas (Cape Grey, Fig. 3), whereas *P. semisulcatus* was not found spawning in the inshore areas.

Seasonality in spawning

Egg production of *P. semisulcatus* fluctuates seasonally, with an EPI range of 0·2–5·5 in the major spawning area in the Cape Grey zone (Crocos 1987). The EPI range for *P. esculentus* in the major spawning area in the North Groote zone is narrower (0·4–0·9) (Fig. 5), and the strong and consistent seasonal timing of egg production observed for *P. semisulcatus*, with a major peak in August–September and a minor peak in February (Crocos 1987), is not evident for *P. esculentus*. Both Buckworth (1985) and Robertson *et al.* (1985) noted that the percentage of ripe *P. esculentus* females remained fairly constant through the year. In the present study, the EPI indicated a complex pattern of egg release with considerable interannual variation over the period studied, and with less distinct peaks in the EPI than shown for *P. semisulcatus*.

The bimodal egg production pattern observed in *P. semisulcatus* is also apparent in *P. merguiensis* in the eastern Gulf of Carpentaria (Crocos and Kerr 1983), while Penn (1980) observed a bimodal pattern (autumn and spring) of egg production in *P. latisulcatus* in Shark Bay and Exmouth Gulf on the Western Australian coast. In the Gulf of Carpentaria, Rothlisberg *et al.* (1987) found a bimodal seasonal pattern of abundance for the larval stages of *P. semisulcatus*, *P. merguiensis* and *P. latisulcatus*, but *P. esculentus* larvae were present throughout the year.

P. semisulcatus were reported to have a double-peaked spawning pattern on the east coast of India and in Kuwait waters, with maxima in spring and autumn (Thomas 1974; FAO 1982). Al-Attar and Ikenoue (1974) observed an April spawning peak for *P. semisulcatus*, but their data only covered the period February–May. Garcia (1977, 1985) reviewed the seasonal spawning patterns of other penaeids, including *P. aztecus* in the Gulf of Mexico (Berry and Baxter 1969), *P. notialis* in North Senegal (Lhomme and Garcia 1984), *P. indicus* in Madagascar (Le Reste 1978), and *P. monodon* in the Philippines (Motoh 1981), and found the double-peaked pattern the most common. With this pattern, the first spawning occurs soon after recruitment at 5–7 months of age, and is followed by a massive spawning by the bulk of the cohort when 10–12 months old. This is the general pattern observed for *P. semisulcatus* in the present study, but it appears that *P. esculentus* in the Groote Eylandt region differs markedly from *P. semisulcatus* in the same region. The potential effects of fishing pressure on the observed egg production pattern in *P. esculentus* are unknown, but since the protracted egg production in *P. esculentus* is due in part to the prolonged period when there is a high proportion of spawning females in the population, the effect of variable stock levels on the egg production pattern in *P. esculentus* would be to alter the magnitude of egg production rather than the inherent seasonal pattern.

The observed differences between *P. esculentus* and *P. semisulcatus* indicate that management regimes aimed at protecting the spawning stocks of these species would need to be tailored to their different reproductive patterns. The wider interannual variation and the generally lower level of egg production in *P. esculentus* tend to make any seasonality of reproductive output less distinct, particularly when compared with *P. semisulcatus*. In terms of vulnerability of the spawning stock to fishing pressure, the inherently higher egg production for *P. semisulcatus* must be balanced against the more restricted seasonal pattern of reproductive output for this species. Despite the protracted spawning and interannual variation of egg production in *P. esculentus*, the important period of spawning for stock renewal in both species of tiger prawns, based on the timing of subsequent recruitment (Somers *et al.* 1987), is early spring (July–August to September). This coincides with the major spawning peak in *P. semisulcatus* and a period of comparatively high egg production in *P. esculentus*.

Acknowledgments

I would like to thank B. J. Hill for his assistance and encouragement during the course of the study, and Tonya Cahill for her able technical assistance, both in the laboratory and in the field. John Kerr, Division of Mathematics and Statistics, CSIRO, provided valuable input to the data analysis. The cooperation and assistance of Steve Ivicic and the crew of the FV *Maxim* are gratefully acknowledged. W. Dall, B. J. Hill, and P. C. Rothlisberg, all of CSIRO, constructively commented on the manuscript. The study was funded in part by a grant from the Australian Fishing Industry Research Trust Account.

References

Al-Attar, M. H., and Ikenoue, H. (1974). Spawning season of shrimp *Penaeus semisulcatus* in the sea along the coast of Kuwait. Kuwait Institute of Scientific Research, July, MAB 1. VII.

Berry, R., and Baxter, K. N. (1969). Predicting brown shrimp abundance in the northwestern Gulf of Mexico. FAO Fish. Rep. No. 57, 775–98.

Buckworth, R. C. (1985). Preliminary results of a study of commercial catches, spawning and recruitment of *Penaeus esculentus* and *Penaeus semisulcatus* in the western Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 85–93. (NPS2: Cleveland, Australia.)

Crocos, P. J. (1985). Appraisal of some factors relevant to the development of penaeid prawn population reproductive models. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 159–64. (NPS2: Cleveland, Australia.)

Crocos, P. J. (1987). Reproductive dynamics of the grooved tiger prawn, *Penaeus semisulcatus*, in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* 38, 79–90.

Crocos, P. J., and Kerr, J. D. (1983). Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea : Penaeidae) in the Gulf of Carpentaria. *J. Exp. Mar. Biol. Ecol.* 69, 37–59.

FAO (1982). Report of the Workshop on Assessment of the Shrimp Stocks of the West Coast of the Gulf between Iran and the Arabian Peninsula (Kuwait, 12–22 October 1981). Fisheries Development in the Gulf (Bahrain, Iran, Kuwait, Oman, Qatar, Saudi Arabia, United Arab Emirates). FI/DP/RAB/80/015:163.

Garcia, S. (1977). Biologie et dynamique des populations de crevettes roses (*Penaeus duorarum notialis*, Perez-Farfante, 1967) en Côte d'Ivoire. *Trav. Doc. ORSTOM* 79, 1–271.

Garcia, S. (1985). Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 139–58. (NPS2: Cleveland, Australia.)

Grey, D. L., Dall, W., and Baker, A. (1983). 'A Guide to the Australian Penaeid Prawns.' (Northern Territory Department of Primary Production: Darwin.)

Kirkwood, G. P., and Somers, I. F. (1984). Growth of two species of tiger prawn, *Penaeus esculentus* and *P. semisulcatus*, in the Western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* 35, 703–12,

Le Reste, L. (1978). Biologie d'une population de crevettes *Penaeus indicus*, H. Milne-Edwards, sur la côte nord ouest de Madagascar. *Trav. Doc. ORSTOM* 99, 1–291.

Lhomme, F., and Garcia, S. (1984). Biologie et exploitation de la crevette penaeid *Penaeus notialis* (Perez-Farfante, 1967) au Sénégal. In 'Penaeid Shrimps: their Biology and Management'. pp. 111–41. (Fishing News Books: Farnham, U.K.)

Motoh, H. (1981). Studies on the fishery biology of the giant tiger prawn, *Penaeus monodon*, in the Philippines. SEAFDEC Tech. Rep. No. 7, pp. 1–128.

O'Connor, C. Y. (1979). Reproductive periodicity of a *Penaeus esculentus* population near Low Islets, Queensland, Australia. *Aquaculture* 16 , 153–62.

Penn, J. W. (1980). Spawning and fecundity of the western king prawn, *Penaeus latisulcatus* Kishinouye, in Western Australian waters. *Aust. J. Mar. Freshw. Res.* 31, 21–35.

Penn, J. W., and Caputi, N. (1986). Spawning stock recruitment relationships and environmental influences on the tiger prawn *Penaeus esculentus* fishery in Exmouth Gulf, Western Australia. *Aust. J. Mar. Freshw. Res.* 37, 491–505.

Robertson, J. W. A., Coles, R. G., and Goeden, G. B. (1985). Distribution patterns of commercial prawns and reproduction of *Penaeus esculentus* around the Wellesley Islands in the southeastern Gulf of Carpentaria. In 'Second National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 71–5. (NPS2: Cleveland, Australia.)

Rothlisberg, P. C., Jackson, C. J., and Pendrey, R. C. (1987). Larval ecology of penaeids of the Gulf of Carpentaria, Australia. I. Assessing the reproductive activity of five species of *Penaeus* from the distribution and abundance of the zoeal stages. *Aust. J. Mar. Freshw. Res.* 38, 1–17.

Somers, I. F. (1987). Sediment type as a factor in the distribution of commercial prawn species of the western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 133-49 149

Somers, I. F., and Kirkwood, G. P. (1984). Movement of tagged tiger prawns, *Penaeus* spp., in the Western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* 35, 713-23.

Somers, I. F., Crocos, P. J., and Hill, B. J. (1987). Distribution and abundance of tiger prawns, *Penaeus esculentus* and *P. semisulcatus*, in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* **38**, 63-78.

Thomas, M. M. (1974). Reproduction, fecundity and sex ratio of the green tiger prawn, *Penaeus semisulcatus* de Haan. *Indian J. Fish.* 21, 152-63.

Manuscript received 3 September 1986, accepted 2 December 1986

Appendix 4.3

BIOLOGICAL ASPECTS OF MANAGEMENT OF THE DECLARED MANAGEMENT ZONE

BURKE HILL, CSIRO MARINE LABORATORIES, CLEVELAND

Although the management of prawn fisheries involves the use of non-biological means such as licence limitation and controls on the size of fishing vessels and gear, much of the management has a biological base. Until recently, it was thought that because prawns produce vast numbers of eggs — about 250,000 per female per month in the spawning season — it was unlikely that the number of spawning females could be reduced to the point where insufficient eggs would be produced to maintain the population at a reasonable level (see Somers article). It was considered that prawn fishing would become uneconomic before the number of adults had been reduced to the point where insufficient eggs would be produced. Increasing catching efficiency, coupled with factors such as extremely high prices, have changed the situation. Far more effort is being put into the Northern Prawn Fishery now as compared with even 5 years ago (see Buckworth article). The experience in Exmouth Gulf and now in the Northern Prawn Fishery (see Somers article) has caused a rapid change in thinking and consequently, in management techniques.

We now have to accept that heavy fishing pressure on the stock can lead to a dangerous decline in recruitment. The measures taken to rectify the situation in the Northern Prawn Fishery consist largely of reducing effort. This reduction is not however, aimed simply at reducing the total catch but rather at ensuring that as many prawns as possible survive to spawning age. After spawning, fishing pressure can theoretically be increased.

All the larger commercially fished Australian prawns have a similar life cycle (see Fig. 8). Unlike other crustaceans such as crabs and lobsters, female prawns do not carry their eggs attached to the body. Spawning occurs offshore where the eggs are released directly into the water to hatch into the first of many larval stages. The vast majority do not survive but are eaten by fish, jelly fish and other small predators.

Larvae reaching the nursery grounds settle out as post-larvae. Banana prawns settle in muddy mangrove areas whereas tiger prawns settle in seagrass beds. These nursery areas are critical for prawn populations and as they have been identified, many have been closed to trawling to protect both the habitat and the young prawns. These permanent nursery closures form the first level of biological management.

The young prawns grow rapidly and after a few months leave the nursery areas and move into deeper water. In the case of banana prawns, the mechanism which initiates this movement is associated with rainfall. The trigger starting tiger prawn movement is not known but the prawns appear to leave the seagrass when they reach a critical size. Once they leave the closed nursery area the prawns become vulnerable to fishing. They are at a small, uneconomic size at this stage and so closures were introduced to allow them to grow and reach maximum economic value. This introduces the second biological management tool — seasonal closures. The end of the closure period, i.e. the opening date of the fishing season, is dictated by three factors. These are the growth rate of prawns, the rate at which they are dying off and the export value of prawns at different sizes. Whilst the opening of the season is based upon banana prawns, the long closure also gives tiger prawns an opportunity to grow to an economic size.

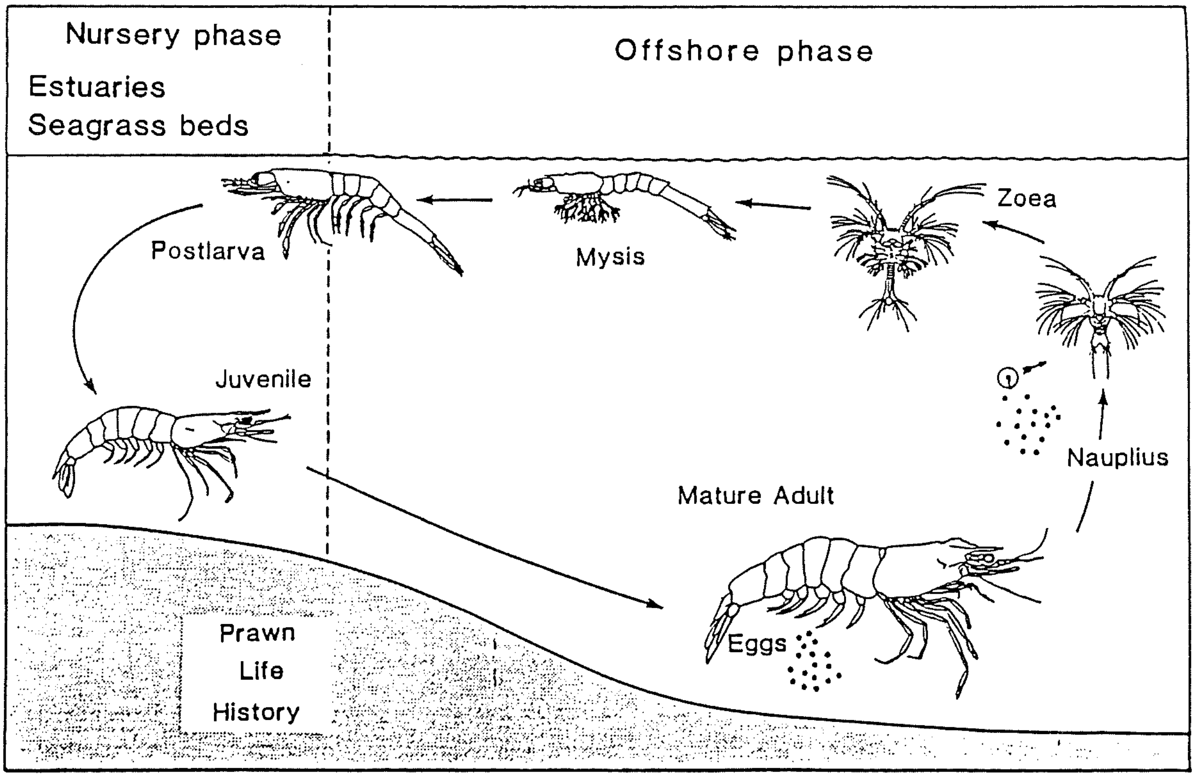


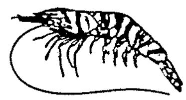
FIGURE 8: Generalised life history of northern commercial prawn species.

Because fishing pressure on tiger prawns is regarded as excessive, NORMAC decided additional protection was required to ensure that more prawns survived to spawning. A closure during the spawning season would serve no purpose if the prawns had already been caught. It was not feasible to close only the spawning grounds and leave the rest of the fishery open because the main fishing grounds are also the spawning grounds. This is illustrated by the situation north of Groote Eylandt where CSIRO studies have identified the spawning grounds for brown and grooved tigers (see Fig. 9). The only feasible alternative was to close the whole fishery before spawning commenced, hence the mid-season closure.

Identification of the spawning season was not easy. Examination of female brown tiger prawns showed prolonged spawning for most of the year. The grooved tiger prawn showed a marked August-October spawning season. Sampling of juveniles in the nursery areas and sub-adult recruits in the fishery showed that the most important spawning time for both tiger species in from August to October. The best time for the mid-season closure was therefore June/July. Banana prawns also spawn around August-October and so closing the fishery in July may also benefit the banana prawn populations.

Restrictions on daytime trawling arose from concern expressed by fishermen. There was no scientific information on the matter available as the effects of daytime trawling had not been investigated. There was however, data showing that the ratio of females to males in the remaining prawn population declined during the year as fishing intensity reached a peak. Fishermen suggested that daytime trawling yielded a higher proportion of females than males. As a result of this information, together with the overall state of the stock, NORMAC decided to take a conservative approach and ban daytime trawling before the spawning season.

Measures such as the mid-season closure, gear restrictions and the ban on daytime trawling are seen as being short-term measures to reduce effort. As the longer term measure of reducing the size of the fleet takes effect, it may be possible to remove the short-term measures. The main December-March closure will probably remain in place because of its economic benefit.



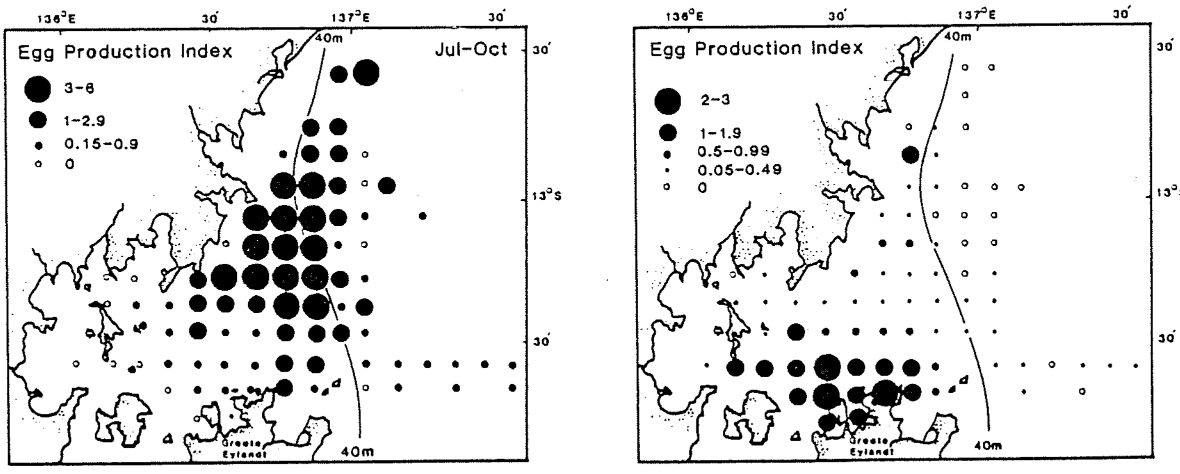


FIGURE 9: Grooved and brown tiger prawn spawning areas north of Groote Eylandt.

Appendix 4.4

Aust. J. Mar. Freshw. Res., 1987, 38, 121–31

Seagrass Communities of the Gulf of Carpentaria, Australia

I. R. Poiner, D. J. Staples and R. Kenyon

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 120, Cleveland, Qld 4163.

Abstract

The seagrass communities of the Gulf of Carpentaria were mapped and classified in terms of their species composition, their areas of shoot surface and their above-ground biomass. A total of 906·4 km^2 of seagrass habitat, fringing 671·1 km of coastline was identified, mapped and sampled. Eleven seagrass species (approx. 20% of all known species) were recorded. In all, 74% of the seagrass communities occur along open coastlines and are characterized by depth-zoned species distributions (intertidally and subtidally), variable shoot-surface areas and variable above-ground biomass values. Each zone was dominated by one or two of the following species: *Syringodium isoetifolium*, *Cymodocea serrulata*, *Halodule uninervis*, *Halophila ovalis* and *Halophila spinulosa*. Of the remaining seagrass, 10% occurred on reef flats in mixed-species communities, 13% in a regionally restricted monospecific community of *Halodule uninervis*, and 4% in communities dominated by *Enhalus acoroides*.

Introduction

Seagrass communities are important nursery grounds for juvenile tiger (*Penaeus esculentus* and *P. semisulcatus*) and endeavour (*Metapenaeus endeavouri*) prawns (Staples *et al.* 1985). These prawns are of major importance in the penaeid prawn catch from northern Australia, especially the Gulf of Carpentaria (Somers and Taylor 1981). Seagrasses are also the primary food resource of dugongs (*Dugong dugong*) and the green turtle (*Chelonia midas*).

Apart from Coles and Lee Long's (1985) brief description of the seagrasses around the Wellesley Islands (Fig. 1), there are no published reports on the distribution and composition of the seagrass communities of the Gulf of Carpentaria. In fact, there is a paucity of information of this type for the whole tropical Indo-West Pacific. The few published studies include: Johnstone (1978*a*, 1978*b*, 1979, 1982) and Brouns and Heijs (1985) for the south coast of Papua New Guinea; Tsuda *et al.* (1977) for Micronesia; Bridges *et al.* (1982) for the southern portion of the Torres Strait; and Young and Kirkman (1975), Kirkman (1978) and Poiner (1984) for Moreton Bay, Queensland.

The aims of this study were, firstly, to map quantitatively and sample the seagrass communities of the Gulf of Carpentaria and, secondly, to classify the seagrasses into community types in terms of their species composition and structural diversity. Staff of the Division of Fisheries Research, CSIRO, are presently examining the seasonal and inter-annual variability of a representative subset of the identified seagrass communities to identify the factors that determine their distribution.

0067-1940/87/010121$02.00

Study Area

The Gulf of Carpentaria (Fig. 1) is a large rectangular (approx. $3 \cdot 7 \times 10^5$ km^2), shallow (<70 m), tropical embayment between 11–17·5°S. latitude and 136–142°E. longitude (Rothlisberg and Jackson 1982). Its abiotic environment has been described by Forbes (1984), Staples (1983), Vance and Staples (1985) and Newell (1973). A brief summary of their results is presented below.

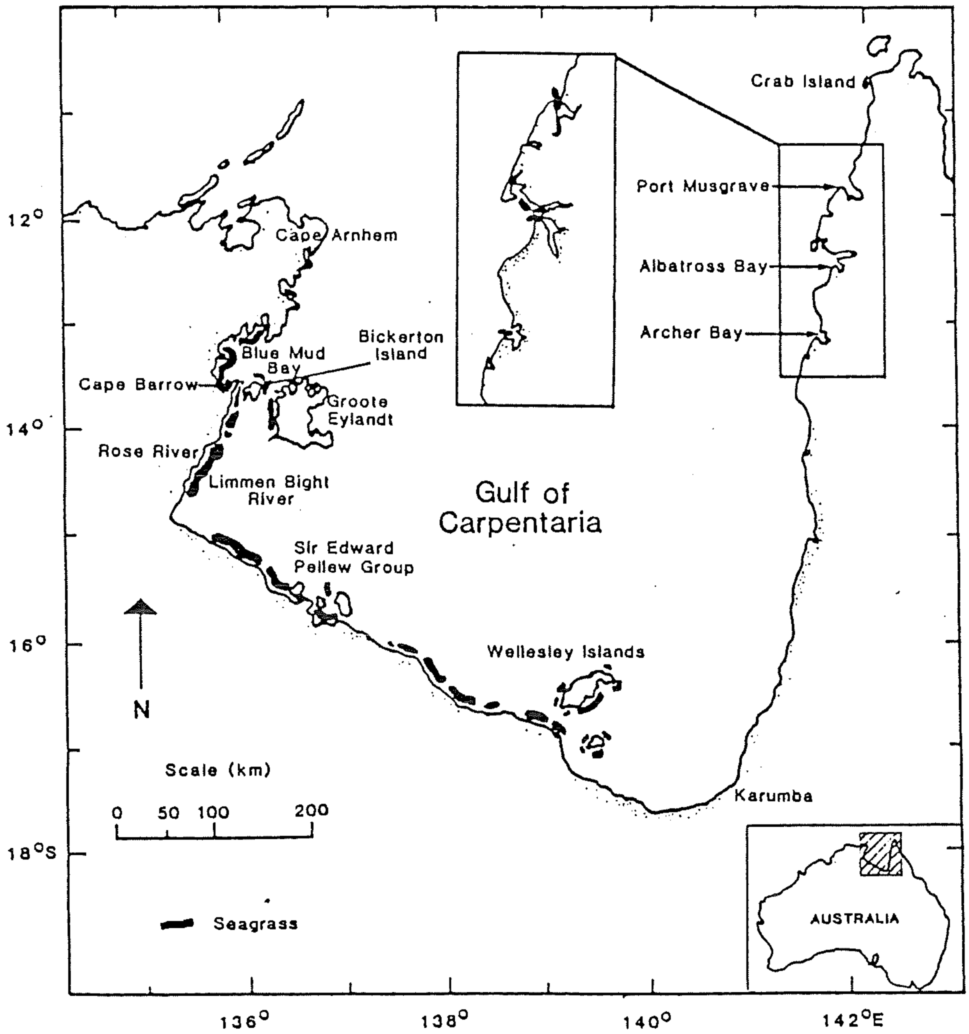


Fig. 1. Gulf of Carpentaria, showing study areas and location of seagrass habitat (not drawn to scale).

The area has marked seasonality in temperature, salinity, rainfall and wind regimes. The dominant features are seasonal wind events, with rainfall restricted to the north-western monsoon in the austral summer (December to February) and a very dry period during the south-east trades (May to October). Most variation in hydrometeorological conditions is in coastal waters (seasonal temperature range 10°C and salinity range 12), largely influenced by runoff, but the central Gulf of Carpentaria can have seasonal ranges of 5°C and 3. This variation offshore, though largely locally generated, can be modified by intrusions of water from the Coral and Arafura Seas. The western Gulf of Carpentaria is different from the rest of the Gulf in having smaller drainage basins and fewer rivers, which results in it being less affected by river run-off.

Methods

Aerial Surveys

For the initial mapping of the seagrasses, we used satellite imagery (Classen *et al.* 1984) and low-level aerial photography (Poiner 1984). The resolution of the satellite imagery was too low for our purposes. Low-level aerial photography was useful, but its high cost prevented us from applying it to such a large area as the Gulf of Carpentaria.

A low-level (152–300 m) aerial survey technique was developed whereby a trained observer in a high-winged aircraft (Cessna 185) allocated the inshore environments to one of three categories: 'seagrass'; 'no-seagrass'; and 'unknown'. At the same time, the dimensions of the along-shore distribution of the 'seagrass' and of the 'unknown' category were plotted onto 1 : 100 000 Australian Topographical Survey maps. The technique was tested and verified at Albatross Bay and Groote Eylandt (Fig. 1) before it was applied to the Gulf of Carpentaria generally. The surveys undertaken (Fig. 1) were Crab Island to Karumba in October 1982; Groote Eylandt to the Sir Edward Pellew Group in November 1983 and Karumba to the Sir Edward Pellew Group and Blue Mud Bay to Cape Arnhem in October 1984.

Verification

Following the aerial surveys, all areas were visited to verify the survey results and to sample the seagrass communities. A series of transects perpendicular to the coast were selected at intervals of 3–5 nautical miles (1 nautical mile = 1·852 km) for the 'seagrass' and 'unknown' categories, and at intervals of 5–30 nautical miles for the 'no-seagrass' category. At each transect, the presence and position of any fringing reef was recorded and the associated coastline was categorized as: open coastline, sheltered embayment, estuarine, or river or creek mouth.

Along each transect, sample sites were selected at intervals of 50–500 m, depending on the rate of change in the composition of seagrass species. At each site, the species of seagrass present and the water depth were recorded, and the distance from shore and the state of the tide were estimated visually.

A subset of the sites (52%) was sampled quantitatively for shoot density per species per site, biomass per site and shoot surface area per site. The quantitative samples were collected when it was subjectively decided that the species composition of the communities had changed. At each site five replicated 0·07-m^2 samples were extracted with a garden shovel, sieved wet through a 5-mm mesh, packaged and stored on ice for later processing. In the laboratory, the samples were sorted into species, and the number of shoots per species per sample were recorded. The five replicates were averaged and the averaged value for each species converted to shoot density per square metre. *Enhalus acoroides*, an unusually large species, was sampled using a 0·25-m^2 quadrat. For this species the number of shoots per quadrat was counted *in situ* and 15 shoots with their associated erect stems were randomly selected for estimating biomass and shoot surface area. Its shoot density values were converted to shoot density per square metre.

Above-ground Biomass

The above-ground biomass was estimated for each species sampled in each replicate after removal of the rhizomes and roots. The remaining erect stems, shoots, flowers and fruits were washed in 10% (v/v) orthophosphoric acid to remove epiphytes, dried to a constant weight at 70°C and weighed. The above-ground biomass for each site was then estimated from the mean of the five replicates after pooling the values of the individual species (within each replicate). For *E. acoroides*, the above-ground biomass was calculated (biomass per shoot) from the collected shoot sample. The contribution to the site value was then estimated by multiplying the biomass per shoot by the measured shoot density per square metre.

Shoot Surface Area

Shoot surface area per site was estimated from 15 randomly selected shoots (including erect stems) of each species sampled at a site. Each shoot was separated into leaves, old leaf bases and erect stem. The length and diameter of the stem, length and width of the outermost old leaf base, and length and width of each leaf were measured. For all species, the erect stem was assumed to be cylindrical.

The old leaf bases and the leaves were assumed to be rectangular in the strap-like species (*Halodule* spp., *Cymodocea* spp., *Enhalus* sp., *Thalassia* sp.), cylindrical in *Syringodium isoetifolium*, and elliptical in the *Halophila* spp. The surface area per shoot was estimated by summing (*a*) the area of erect stem, (*b*) double the area of the outer old leaf base and (*c*) double the total area of leaves above the ligule. For each species the surface area per shoot was estimated from the mean of the 15 measured shoots. The site value was calculated from the sum of shoot density per square metre multiplied by the surface area per shoot for each species sampled.

Species Identifications in the Field

Two statistically significant size-morphs, *Halophila ovalis* (small) and *H. ovalis* (large), over the tidal gradient in Moreton Bay, Queensland, were reported by Poiner (1984). A similar analysis of *H. ovalis* and *Halodule uninervis* in the Gulf of Carpentaria demonstrated the same morphs for *H. ovalis* and a similar set for *H. uninervis* (thin and broad leaf). Both species were separated into their two morphs in the current study.

The differences between the *Halophila ovalis* (large) morph and *H. decipiens*, and between the *H. ovalis* (small) morph and *H. ovata*, were not sufficient to separate these taxa in the field and all references to these taxa will be given by *H. ovalis* (large) for *H. ovalis* (large) plus *H. decipens* and *H. ovalis* (small) for *H. ovalis* (small) plus *H. ovata*. A similar problem was found for the *Halodule uninervis* (thin) morph and *H. pinifolia*, and all further references to these two taxa will be given as *H. uninervis* (thin).

Analytical Procedures

Differences and similarities in the distributions of the seagrass species both at a locality and between localities were investigated through pattern analysis (Clifford and Stephenson 1975). An agglomerative hierarchical classification was used to detect groups of biotically similar sites (normal analysis) and groups of species that tend to be found together in the same site (inverse analysis). These methods are discussed fully in Poiner (1977, 1980).

Classification was performed on the presence–absence data using the TAXON library of programs (Lance and Williams 1967*a*, 1967*b*; Dale *et al.* 1981). The Canberra Metric coefficient of similarity, with double-zero matches omitted, and flexible sorting with intense clustering were used. The sorting coefficients *a* and *b* were set to 0·625 and −0·25 (Clifford and Stephenson 1975; Williams 1976).

Sites grouped by numerical classification were in geographically and/or tidally restricted areas and are referred to as 'site groups'. The spatial distributions of site groups and of commonly occurring species in each group were compared using the biological data (shoot densities per species per site, above-ground biomass per site and shoot surface area per site) collected from the subset of quantitatively sampled sites and the abiotic data collected at all sample sites (bottom depth, distance offshore and the coastal topography).

Results

Seagrass Map

A total of 906·4 km^2 of intertidal and shallow subtidal areas fringing 671·1 km of coastline were found to be supporting seagrass communities (Fig. 1). The area of seagrass and length of coastline for selected geographical subsets of the Gulf of Carpentaria are given in Table 1.

A total of 93% of the seagrasses of the Gulf of Carpentaria occurred in large patches in the western Gulf between the Wellesley Islands and the northern end of Blue Mud Bay. The remaining 7% occurred in small patches in the estuaries north of the Archer Bay (on the east coast) and north of Blue Mud Bay (on the west coast).

Classification

Of 13 taxa (11 species) recorded from the Gulf of Carpentaria, 10 were used in the analysis. These are listed in Table 2 together with a species code used throughout. The 11 species sampled represent approximately 20% of the known seagrass species in the world.

Table 1. Area of seagrass and percentage of the total area and the length of bordering coastline for selected geographical localities of the Gulf of Carpentaria. Principal site group(s) for each area are also presented

Locality	Area (km²)	Area (%)	Length (km)	Site group A	B	C	D	E	F	G
Crab Island	2·3	0·3	1·5		+					
Port Musgrave	4·8	0·5	11·5		+					
Albatross Bay	6·8	0·8	15·0	+	+	+				
Archer Bay	4·8	0·5	6·7		+					
Wellesley Islands	108·4	12·0	90·7		+	+	+	+		
Wellesley Islands to Sir Edward Pellew Group	56·4	6·2	90·8		+			+	+	
Sir Edward Pellew Group	99·9	11·0	41·7	+						
Sir Edward Pellew Group to Limmen Bight River	183·0	20·2	117·9		+			+	+	
Rose River to Cape Barrow	293·7	32·4	99·7		+			+	+	
Bickerton Island	28·5	3·1	23·7		+	+	+			
Groote Eylandt	32·4	3·7	62·1		+	+	+	+	+	
Blue Mud Bay	81·1	8·9	79·9		+	+		+	+	
Blue Mud Bay to Cape Arnhem	4·3	0·5	5·9		+	+				
Total	906·4		671·1							

Site Groups

Of 343 sites classified, 164 were quantitatively sampled. The results of the classification, together with the number of sites and species in each site group, are presented in Fig. 2.

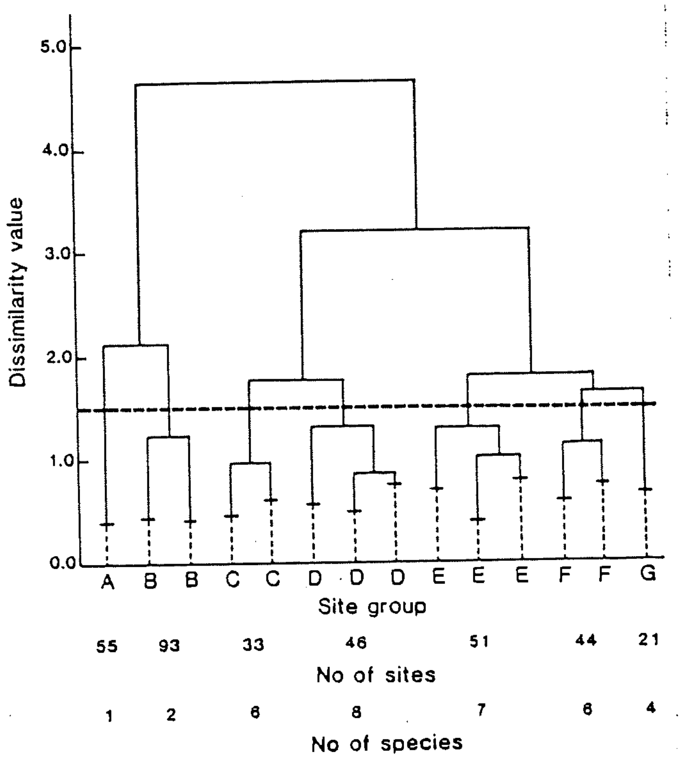


Fig. 2. Dendrogram of the classification of sites by species. Site groups ordered from A to G. Number of sites and total number of species sampled are given for each site group.

Optimal clarity was obtained by subjectively truncating the dendrogram at the level of 1·5, which gave seven unequal groups, designated A to G. Three major clusters of sites were apparent: site groups A and B (located in the shallow intertidal); site groups C and D [located either behind fringing reefs (C) or in sheltered embayments (D)]; and site groups E and F (located in the subtidal along the more open coastlines). Site group G was usually seawards of river or creek mouths but also offshore of site groups E and F along the more open coastlines.

Table 2. Species and species morph list, together with the code used in the classification analyses

Code	Species/morph
1	*Cymodocea serrulata* (R.Br.) Aschers. & Magnus
2	*Cymodocea rotundata* Ehrenb. et Hempr. ex Aschers.
3	*Halodule uninervis* (broad) (Forsk.) Aschers. in Bolssier
4	*Halodule uninervis* (thin); *Halodule pinifolia* (Miki) den Hartog
5	*Enhalus acoroides* (L.F.) Royle
6	*Thalassia hemprichii* (Ehrenb.) Aschers.
7	*Syringodium isoetifolium* (Aschers.) Dandy
8	*Halophila ovalis* (small) (R.Br.) Hook. F.; *Halophila ovata* Gaud. in Freycin
9	*Halophila spinulosa* (R.Br.) Aschers.
10	*Halophila ovalis* (large); *Halophila decipiens* Ostenfeld

Table 3. Mean ($\bar{x}$), standard error (s.e.) and sample size (n) of depth, ratio of shoot surface area per site and above-ground biomass for each of seven site groups. The area and percentage of total Gulf of Carpentaria seagrasses in each site group are also presented

Parameter		Site groups						
		A	B	C	D	E	F	G
Depth (m)	$\bar{x}$	0·9	1·1	1·0	1·6	2·1	3·7	4·3
	s.e.	0·14	0·08	0·24	0·30	0·24	0·95	0·67
	n	12	35	19	28	24	18	12
Shoot surface area (m^2)/site area (m^2)	$\bar{x}$	1·03	1·11	3·44	1·95	1·51	5·90	1·58
	s.e.	0·30	0·17	0·68	0·25	0·43	1·54	0·43
	n	10	25	16	32	23	19	12
Above-ground biomass (g/m^2)	$\bar{x}$	11·9	27·3	158·3	68·0	87·6	112·8	58·4
	s.e.	3·44	8·63	33·60	9·29	24·43	20·24	15·75
	n	12	37	20	39	22	18	12
Area (km^2)		114·8	131·0	33·4	99·0	134·2	331·1	64·9
Percentage of total		13	15	4	10	15	37	7

The mean values of depths, shoot surface area per site and above-ground biomass per site for the seven site groups are given in Table 3. Site groups A, B and C occurred in the shallow intertidal region (A, mean depth = 0·9 m; B, mean depth = 1·1 m; C, mean depth = 1·0 m). Site group A was primarily confined to the landward side of the Sir Edward Pellew Group of islands (48 of 55 sites; Fig. 1; Table 1), site group B occurred along more open coastlines, and site group C was confined to sheltered embayments or estuaries. Site groups D and E occurred lower down the tidal gradient and extended into the shallow subtidal (D, mean depth = 1·6 m; E, mean depth = 2·1 m), while site groups F and G were subtidal (F, mean depth = 3·7 m; G, mean depth = 4·3 m). All the sites in the site groups E and F occurred along open coastlines seawards of site group B. The sites in group D were located behind fringing reefs, and most of the sites in group G occurred along open coastlines, seawards of the mouths of rivers and creeks (16 of 21 sites).

Site groups A and B had the smallest above-ground biomass and shoot surface areas per site; site groups D and G had moderate values; and, site groups C, E and F were noticeably higher than the other site groups (Table 3).

Species Groups

Four unequal species groups, designated 1–4, were accepted at a level of 0·25 on the dendrogram (Fig. 3). Cramer values (Lance and Williams 1977) calculated on the binary

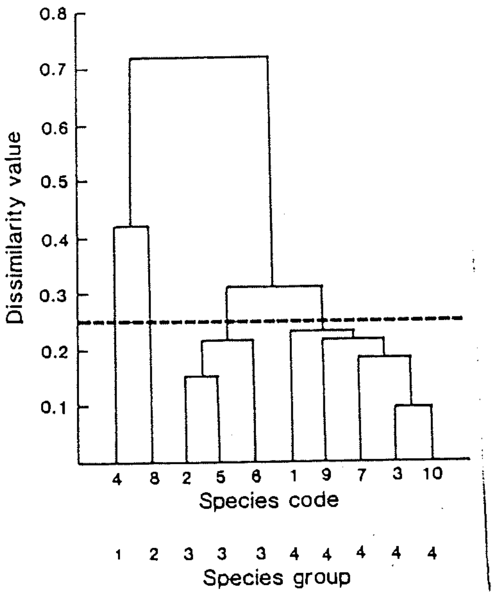


Fig. 3. Dendrogram of the species classification by sites. Species groups are ordered from 1 to 4.

Table 4. Species groupings, characterizing site groups and the site groups from which each species was sampled for seagrass species from the Gulf of Carpentaria

Species group	Species	Level of significance (P) Cramer	Pseudo-F	Characterizing site groups	Site group where species sampled
1	*H. uninervis* (thin)	<0·001	<0·001	A B	A B C D
2	*H. ovalis* (small)	<0·001	<0·01	B D	B C D
3	*C. rotundata*[A]	–	–	D	D
	E. acoroides	<0·001	<0·05	C D	A B C D
	T. hemprichii	n.s.	<0·05	D	C D E F
4	*C. serrulata*[B]	<0·001	<0·001	D E F	B C D E F
	H. uninervis (broad)[B]	n.s.	<0·05	E F	C E F
	S. isoetifolium	n.s.	<0·01	E F	C D E F G
	H. spinulosa	<0·001	<0·001	G	E F G
	H. ovalis (large)	<0·001	<0·05	F G	E F G

[A] *C. rotundata* was only sampled from site group D.
[B] Pseudo-*F* tests were only significant for site group E.

data, and Pseudo *F*-tests (Poiner 1977; Stephenson *et al.* 1978) calculated on the quantitative data (log n + 1 transformed shoot densities of the species), were performed to highlight noticeable differences in species distributions between the seven site groups. Table 4 gives the species groups, the site group (or groups they characterize) and their level of significance for each test. All species and morphs showed noticeable differences when compared by the Pseudo *F*-test. Three species, *T. hemprichii*, *H. uninervis* (broad) and *S. isoetifolium*, had non-significant Cramer values. Although all three had been sampled from many site groups, a comparison of the quantitative data showed that they dominated one or two site groups (Table 4).

Site groups A and B had only two species, *H. ovalis* (small) and *H. uninervis* (thin). Five of the seven site groups had six to eight species, though they differed in the number and type of characterizing species (Fig. 3; Table 4). Site G had three species. Site group D had seven species, five of which occurred in noticeably high shoot densities (Table 4), with *T. hemprichii* the most common species, though no one species dominated. In all the other site groups, one or two species dominated: C, *E. acoroides*; E, *C. serrulata* and *H. uninervis* (broad); F, *S. iseotifolium*; and G, *H. spinulosa* and *H. ovalis* (broad).

Community Types and their Relative Importance

The relative importance of each site group in relation to the total area of seagrass habitat recorded for the Gulf of Carpentaria is presented in Table 3, which shows that 74% (661·2 km^2) of the seagrass occurred along open coastlines in depth-zoned distributions (site groups B, E, F and G). Each zone was dominated by one or two of the following species: *S. isoetifolium*, *C. serrulata*, *H. uninervis*, *H. ovalis* and *H. spinulosa*, with 37% of the seagrasses of the Gulf of Carpentaria occurring in the subtidal zone dominated by *S. isoetifolium* (site group F).

Of the remaining seagrass, 10% (99·9 km^2) occurred in mixed-species communities on reef flats (site group D) and 13% (114·8 km^2) in monospecific *H. uninervis* communities (site group A) in the shelter of large islands, principly the Sir Edward Pellew Group (99·9 km^2; Table 1; Fig. 1). The remaining 4% of the seagrass were *E. acoroides*-dominated communities which had been sampled from sheltered embayments (site group C).

Discussion

Comparisons with Other Tropical Seagrass Floras

Significant areas of the western Gulf of Carpentaria supported well-developed seagrass communities and a large proportion of all known seagrass species (20%). The species sampled have strong taxonomic affinities with those in the Indo-West Pacific area and are generally the same as those sampled in studies within this area (Bridges *et al.* 1982; Ogden and Ogden 1982; Birch and Birch 1984; Brouns and Heijs 1985).

The seagrasses of the southern portion of the Torres Strait, which borders the Gulf of Carpentaria to the north-east, were described by Bridges *et al.* (1982). These mixed-species communities are confined to intertidal areas fringed by coral reefs similar to the reef-flat communities identified in the present study (site group D). Bridges *et al.* (1982) did not identify other community types and found no species that conformed to depth gradients or sediment characteristics. As in the Gulf of Carpentaria, the seaward edges of these communities were fringed by coral reefs that dropped abruptly into unvegetated offshore channels with fast currents and high turbidity. Bridges *et al.* (1982) postulated that the distribution patterns and community structure of the Torres Strait seagrasses were primarily due to exposure stress associated with an intertidal existence which overrides the competitive advantage of such potentially dominant species as *S. isoetifolium*, *C. serrulata* and *T. hemprichii*. In the Gulf of Carpentaria, environmental stress is probably important in determining the distribution and structure of the 10% of seagrass communities associated with fringing coral reefs. In other seagrass communities of the tropical Indo-West Pacific reef, associated mixed-species communities are reported to dominate the seagrass flora, e.g. Johnstone (1978*a*, 1978*b*, 1979) and Brouns and Heijs (1985) on the south coast of Papua New Guinea; Birch and Birch (1984) on Magnetic Island, Townsville, Australia; and Ogden and Ogden (1982) on the Western Caroline Islands, Micronesia.

The Gulf of Carpentaria has a greater diversity of seagrass communities than the nearby Torres Strait and elsewhere in the tropical Indo-West Pacific. As well as the commonly reported reef-flat communities, three other communities were recognized: an *E. acoroides*-dominated community sampled from shallow, sheltered embayments; an intertidal, thin-leaved *H. uninervis* community restricted to the landward side of the Sir Edward Pellew Group (Fig. 1); and depth-zoned open coastline communities. In contrast to the rest of the Indo-West Pacific, most of the seagrasses of the Gulf of Carpentaria occurred along open coastlines (74%), where they formed characteristic zonation patterns, with 37% being sampled from the *S. isoetifolium*-dominated community.

The predominance of open-coastline communities dominated by monospecific stands of *H. ovalis* and *H. uninervis* intertidally, and *C. serrulata* and *S. isoetifolium* subtidally, has not been reported elsewhere in the Indo-West Pacific. The difference may possibly be attributed to the presence in the western Gulf of Carpentaria, an area less affected by river runoff (Forbes 1984), of extensive and stable offshore subtidal habitats, with suitable light regimes, which allow the stronger competitors to dominate and segregate into zoned distributions. Current studies by Division of Fisheries Research, CSIRO, in the western Gulf are testing this hypothesis.

The seagrass communities of the Gulf of Carpentaria are similar to the lush, vigorous and usually subtidal meadows reported for the tropical western Atlantic and the Caribbean (Taylor 1928; Voss and Voss 1955; Humm 1956; Phillips 1960; den Hartog 1970; Taylor *et al.* 1973) and for subtropical Moreton Bay, Queensland (Young and Kirkman 1975; Poiner 1984). In these studies, subtidal stands of *Syringodium* species, *Thalassia testudium* and/or *C. serrulata* either dominated the seagrass communities or were well represented in a depth-related zonation pattern of distribution within the seagrass communities. We would predict that patterns of seagrass communities similar to those of the Gulf of Carpentaria will be found on the northern and north-western tropical Australian coast and the northern portions of the Torres Strait when these areas are investigated. In these areas open coastlines are a prominent geomorphological feature.

Seagrasses and Prawns

The habitat requirements of the juvenile stages of the four prawn species (*P. esculentus*, *P. semisulcatus*, *M. endeavouri* and *M. ensis*) important in the commercial fishery in the western Gulf of Carpentaria were studied by Staples *et al.* (1985). Three of the species (*M. ensis* was the exception) have restricted habitat requirements; most juveniles were found associated with seagrass communities.

The population dynamics of the two tiger prawn species, *P. esculentus* and *P. semisulcatus*, were examined at several seagrass sites around Groote Eylandt (Staples 1987). Four of the seagrass community types recognized in the present study were examined: a mixed-species reef flat, and open coastline (characterized by *C. serrulata* and *S. isoetifolium*), a sheltered embayment (dominated by *E. acoroides*) and a river-mouth area (dominated by *H. ovalis* and *H. spinulosa*). Noticeable differences in the abundance of juvenile prawns in the four communities were observed: the lowest abundance was in the river mouth, the highest in the sheltered embayments, with intermediate numbers on the reef flat and open-coastline communities. The difference in relative abundances appeared to result from differences in both the level of settlement of postlarvae into these areas and the subsequent survival of juveniles (Staples 1987).

The abundance of the juvenile prawns correlated well with above-ground biomass and shoot surface area. It was highest in the *E. acoroides*-dominated seagrass community and lowest in the river-mouth community. The complexity and amount of seagrass were probably of critical importance in determining juvenile prawn numbers. Many studies of epifauna in seagrass communities have found strong correlations between abundance and plant biomass (Heck and Orth 1980; Gore *et al.* 1981; Lewis and Stoner 1983; Leber 1985). The important question now is whether these correlations reflect habitat preferences, food availability, refuge from predation (Leber 1985) or other factors such as sediment type, which also correlates with seagrass biomass.

Acknowledgments

This work was funded by the Fishing Industry Research Trust Account (Grant 82/13), Australian Department of Primary Industry and Division of Fisheries Research, CSIRO. Thanks to D. Harrison and the crew of the F.V. *Maxim* for assistance with field work, Dr I. Stejskal for help in data-sorting and some analysis and G. Roberts for critical comments on the manuscript.

References

Birch, W. R., and Birch, M. (1984). Succession and pattern of tropical intertidal seagrasses in Cockle Bay, Queensland, Australia: a decade of observations. *Aquat. Bot.* 19, 343–67.

Bridges, K. W., Phillips, R. C., and Young, P. C. (1982). Patterns of some seagrass distributions in the Torres Strait, Queensland. *Aust. J. Mar. Freshw. Res.* 33, 273–83.

Brouns, J. W. M., and Heijs, M. L. (1985). Tropical seagrass ecosystems in Papua New Guinea. A general account of the environment, marine flora and fauna. *Proc. K. Ned. Akad. Wet.* (Series C) *Biol. Med. Sci.* 88, 145–82.

Claasen, D. van R., Jupp, D. L. B., Bolton, J., and Zell, L. D. (1984). An initial investigation into the mapping of seagrass and water colour with CZCS and Landsat in north Queensland, Australia. In 'Proceedings of the 10th International Symposium for Machine Processing of Remotely Sensed Data'. (Purdue Univ. Press, West Lafayette, Indiana.)

Clifford, H. T., and Stephenson, W. (1975). 'An Introduction to Numerical Classification.' (Academic Press: New York.)

Coles, R. G., and Lee Long, W. J. (1985). Juvenile prawn biology and the distribution of seagrass prawn nursery grounds in the southeastern Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 55–60. (NPS2: Cleveland, Australia.)

Dale, M., Hain, D., Lance, G., Milne, P., Ross, D., Thomas, M., and Williams W. (1981). 'TAXON User's Manual.' Edn 2.1. [Aust. CSIRO Div. Comput. Res. Manual No. 6.]

Forbes, A. M. G. (1984). The contribution of local processes to seasonal hydrology of the Gulf of Carpentaria. *Oceanogr. Trop.* 19, 193–201.

Gore, R. H., and Gallaher, E. E., Scotto, L. E., and Wilson, K. A. (1981). Studies on the decapod crustacea from the Indian River region of Florida. *Estuarine Coastal Shelf Sci.* 12, 485–508.

Hartog, C. den (1970). 'The Seagrasses of the World.' (North-Holland Publ. Co.: Amsterdam.)

Heck, K. J., Jr, and Orth, R. J. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea. *Estuaries* 3, 289–95.

Humm, H. J. (1956). Seagrasses of the northern Gulf coast. *Bull. Mar. Sci. Gulf Caribb.* 6, 305–8.

Johnstone, I. M. (1978*a*). The ecology and distribution of Papua New Guinea seagrasses. I. Additions to the seagrass flora of Papua New Guinea. *Aquat. Bot.* 5, 229–33.

Johnstone, I. M. (1978*b*). The ecology and distribution of Papua New Guinea seagrasses. II. The Fly Islands and Raboin Island. *Aquat. Bot.* 5, 232–43.

Johnstone, I. M. (1979). Papua New Guinea seagrasses and aspects of the biology and growth of *Enhalus acoroides* (L.F.) Royle. *Aquat. Bot.* 7, 197–208.

Johnstone, I. M. (1982). Ecology and distribution of seagrasses. *Monogr. Biol.* 42, 497–512.

Kirkman, H. (1978). Decline of seagrass in northern areas of Moreton Bay, Queensland. *Aquat. Bot.* 5, 63–76.

Lance, G. N., and Williams, W. T. (1967*a*). A general theory of classificatory sorting strategies. I. Hierarchical systems. *Aust. Comput. J.* 9, 373–90.

Lance, G. N., and Williams, W. T. (1967*b*). Mixed data classificatory programs. I. Agglomerative systems. *Aust. Comput. J.* 1, 15–20.

Lance, G. N., and Williams, W. T. (1977). Attribute contributions to a classification. *Aust. Comput. J.* 9, 128–9.

Leber, M. L. (1985). The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66, 1951–64.

Lewis, F. G., III, and Stoner, A. W. (1983). Distribution of macrofauna within seagrass beds: an explanation of patterns of abundance. *Bull. Mar. Sci.* 33, 116–24.

Limpus, C. J., and Reed, P. C. (1984). The green turtle *Chelonia mydas* in Queensland. Population structure in a coral reef feeding ground. In 'The Biology of Australasian Frogs and Reptiles'. (Eds G. Grigg, R. Shine and H. Ehmann.) pp. 53–61. (Surrey Beatty and Sons: Australia.)

Marsh, H., Barker-Hudson, B., Heinson, G., and Kinboy, F. (1984). Status of the dugong in the Torres Strait area. Report to Australian National Parks and Wildlife Service, April 1984.

Newell, B. S. (1973). Hydrology of the Gulf of Carpentaria. Aust. CSIRO Div. Fish. Oceanogr. Tech. Pap. No. 35.

Ogden, J. C., and Ogden, N. B. (1982). A preliminary study of two representative seagrass communities in Palua, Western Caroline Islands (Micronesia). *Aquat. Bot.* 12, 229–44.

Phillips, R. C. (1960). Observations on the ecology and distribution of Florida seagrasses. Fl. Board Conserv. Mar. Lab. Prof. Pap. Ser. No. 2.

Poiner, I. R. (1977). Microvariation in the fauna of a sublittoral sand bank, Moreton Bay, Queensland. *Aust. J. Ecol.* 2, 297–308.

Poiner, I. R. (1980). A comparison between species diversity and community flux rates in the macrobenthos of an infaunal sand community and a seagrass community of Moreton Bay, Queensland. *Proc. R. Soc. Queensl.* 91, 21–36.

Poiner, I. R. (1984). Interspecific interactions: their role in structuring multispecific seagrass communities. *AES Monograph* 1, 55–82.

Poiner, I. R. (1985). A re-examination of the seagrass communities of North Stradbroke Island with an evaluation of their longterm stability. In 'Focus on Stradbroke: New Information on North Stradbroke Island and Surrounding Areas 1974–1984'. (Eds R. Coleman, J. Covacevich and P. Davie.) pp. 228–37. (Boolarong Press: Queensland.)

Rothlisberg, P. C., and Jackson, C. J. (1982). Temporal and spatial variation of plankton abundance in the Gulf of Carpentaria, Australia 1975–1977. *J. Plankton Res.* 4, 19–40.

Somers, I. F., and Taylor, B. R. (1981). Fishery statistics relating to the declared management zone of the Australian northern prawn fishery, 1968–1979. Aust CSIRO Mar. Lab. Rep. No. 138.

Staples, D. J. (1983). Environmental monitoring: Climate of Karumba and hydrology of the Norman River estuary, southeast Gulf of Carpentaria. Aust. CSIRO Mar. Lab. Rep. No. 156.

Staples, D. J. (1987). Effects of environmental variability and fishing pressure on the catches of penaeid prawns in the Gulf of Carpentaria, Australia. In 'Proceeding of the First Asian Fisheries Forum, Manila, May 1986'. (In press.)

Staples, D. J., Vance, D. J., and Heales, D. S. (1985). Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 47–54. (NPS2: Cleveland, Australia.)

Stephenson, W., Cook, S. D., and Newlands, S. J. (1978). The macrobenthos of the Middle Banks area of Moreton Bay. *Mem. Queensl. Mus.* 18, 185–212.

Taylor, J. L., Saloman, C. H., and Prest, K. W. (1973). Harvest and regrowth of turtle grass (*Thalassia testudinum*) in Tampa Bay, Florida. *U.S. Nat. Mar. Fish. Serv. Fish. Bull.* 71, 145–8.

Taylor, W. R. (1928). The marine algae of Florida, with special reference to the Dry Tortugas. Carnegie Inst. Wash., Publ. No. 379.

Tsuda, R. T., Fosberg, F. R., and Sachet, M. H. (1977). Distribution of seagrasses in Micronesica. *Micronesica* 13, 191–8.

Vance, D. J., and Staples, D. J. (1985). Factors affecting year-to-year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia. *J. Cons. Cons. Int. Explor. Mer* 42, 83–97.

Voss, G. L., and Voss, N. (1955). An ecological study of Soldier Key, Biscayne Bay, Florida. *Bull. Mar. Sci. Gulf Caribb.* 5, 203–29.

Williams, W. T. (1976). Hierarchical agglomerative strategies. In 'Pattern Analysis in Agricultural Science'. (Ed. W. T. Williams.) pp. 84–95. (Elsevier and CSIRO: Oxford and Melbourne.)

Young, P. C., and Kirkman, H. (1975). The seagrass communities of Moreton Bay, Queensland. *Aquat. Bot.* 1, 191–202.

Manuscript received 29 July 1986, accepted 5 November 1986

Appendix 4.5

MOVEMENTS OF TAGGED TIGER PRAWNS IN THE GROOTE EYLANDT REGION

Ian Somers
CSIRO Division of Fisheries Research
Cleveland

An extensive tagging program carried out in 1981 by CSIRO, with the assistance of Northern Territory and Queensland Fisheries, revealed much about the tiger prawn migration patterns in the Groote Eylandt region. In that study, approximately 13000 brown tiger prawns and 7000 grooved or green tiger prawns were tagged and released. The patterns of movement observed during the study have been documented by Somers and Kirkwood (1984) — see the publication list at the end of these *Information Notes*. In that paper the authors described the general offshore movement of the tiger prawns, noting that differences in the patterns for each species resulted in effective separation of the two species in the offshore fishery.

Building on the knowledge gained in that tagging program, an intensive study of the tiger prawn populations north of Groote Eylandt (Figure 2) was carried out from August 1983 until March 1985 using the chartered commercial prawn trawler *FV Maxim*. Although this more recent research program primarily involved the monitoring of a generation of tiger prawns over its life span, it also included the release of a further 14000 tagged tiger prawns.

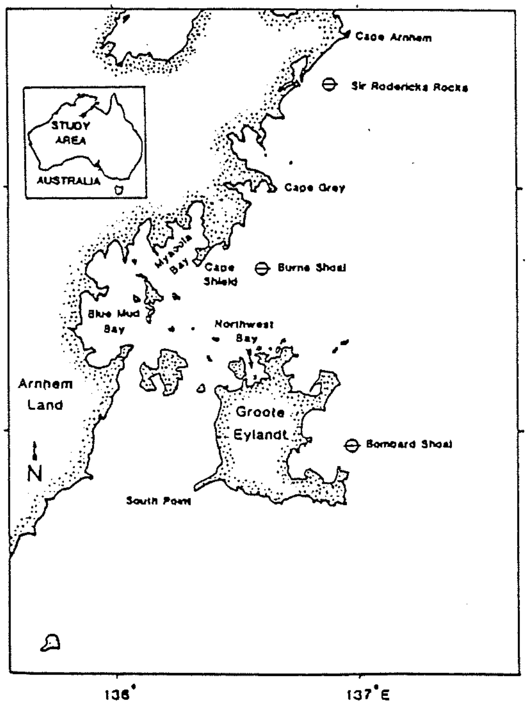


FIGURE 2 — Map of the Groote Eylandt region of the western Gulf of Carpentaria.

Unlike the earlier program however, most of the prawns were tagged and released within waters closed to fishing (Blue Mud Bay and Northwest Bay) and the results may be of direct interest to fishermen in that they give some indication of which fishing grounds are most influenced by these inshore closures.

An exception to the inshore releases was a series in August 1984 when releases were made in the area southeast of Cape Grey.

Blue Mud Bay Releases

The distribution of recaptures from releases in the Blue Mud Bay/Myaoola Bay region (Figure 3) was similar to those of the 1981 tagging experiments with the two species separating offshore through generally different directions of movement. The movement of grooved or green tiger prawns was generally northeast toward Cape Grey, one prawn being recaptured near Sir Rodericks Rocks (120 km from the point of release). In contrast to this, the distribution of brown tiger prawn recaptures was south and east of the release area with the majority being recaptured between Nicol Island and Groote Eylandt.

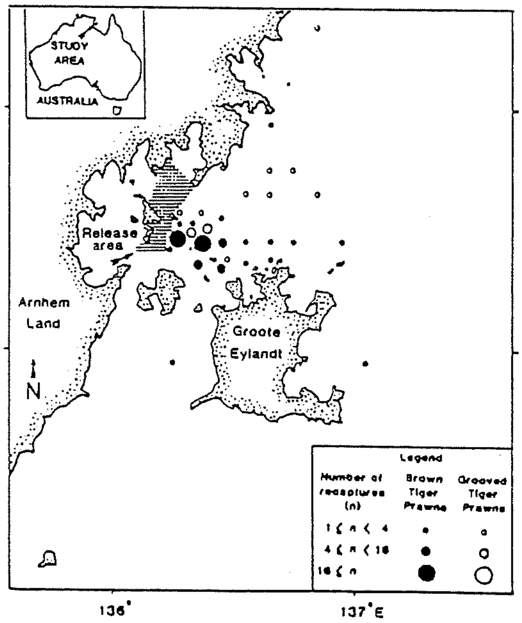


FIGURE 3 — Distribution of recaptures of brown and grooved tiger prawns from releases in Blue Mud Bay and Myaoola Bay.

Northwest Bay Releases

During the 1981 tagging program, Northwest Bay was open to fishing. The results from tag releases in Northwest Bay during that study showed that very few prawns were reaching the offshore fishery. All but 2 of the 207 recaptures were taken in Northwest Bay. What happens to the prawns of Northwest Bay now that it is closed to fishing? The distribution of recaptures of prawns released in Northwest Bay and the adjacent Bartalumba Bay (Figure 4) from the most recent study gives an indication of their relative contribution to the various offshore fishing grounds. It is interesting to note that although most of the brown tiger prawn recaptures were immediately adjacent to the northern part of Groote Eylandt, several recaptures were taken on the fishing grounds around South Point. Grooved or green tiger prawn recaptures however, were generally taken further northward towards Burns Shoal and Cape Grey as well as several recaptures east of Groote Eylandt near Bombard Shoal.

Cape Grey Releases

Virtually all prawns tagged in the releases near Cape Grey were grooved or green tiger prawns. As there are no significant nursery grounds for tiger prawns between Cape Shield and Cape Arnhem, it is reasonable to assume that the prawns had previously migrated north from nursery grounds in either Blue Mud Bay or from along the north coast of Groote Eylandt. However, from the distribution of recaptures (Figure 5), it would appear that the prawns do not necessarily continue with this northern movement. Rather they would seem equally likely to move north or south. Three recaptures were recorded near Bombard Shoal while four were recorded near Three Hummocks. Another significant feature of these releases was the percentage recaptured (40%), the highest we have recorded for tiger prawns. The releases did however coincide with the peak in fishing intensity (August) in this region.

Acknowledgements

The success of the tagging program has required the full support and co-operation of all sectors of the fishing industry as well as various research organisations. The tagging of prawns was completed with a great deal of assistance from the skipper (Steve Ivicic) and crew of the *FV Maxim* while the collection and processing of recaptures has been meticulously carried out by officers of Northern Territory Fisheries. The program was funded from the Fishing Industry Research Trust Account.

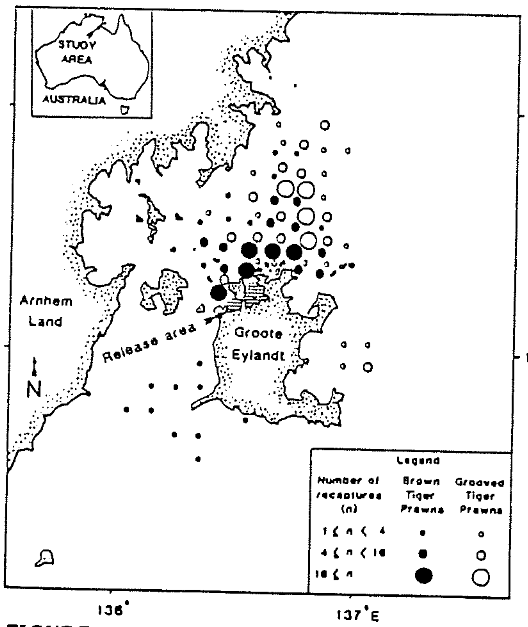


FIGURE 4 — Distribution of recaptures of brown and grooved tiger prawns from releases in Northwest Bay and Bartalumba Bay.

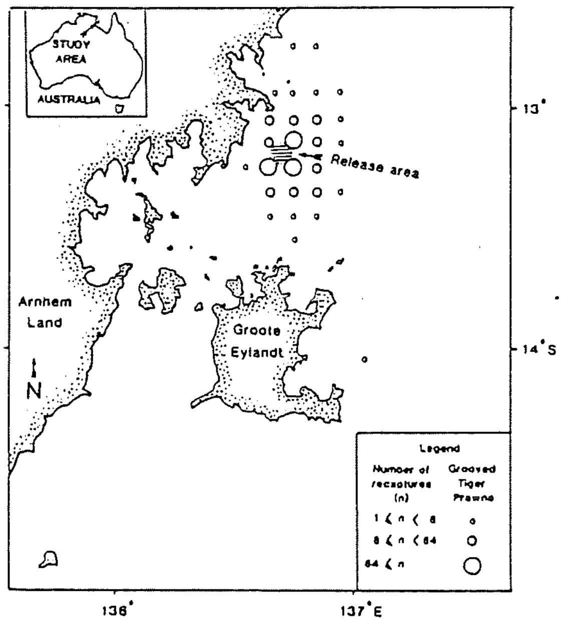


FIGURE 5 — Distribution of recaptures of grooved tiger prawns from releases in the area southeast of Cape Grey.

Appendix 4.6

THE STATUS OF TIGER PRAWN STOCKS IN THE WESTERN GULF OF CARPENTARIA

IAN SOMERS, CSIRO MARINE LABORATORIES, CLEVELAND

Resiliance to Fishing Pressure

Prawn fisheries are generally believed to be very resilient to fishing pressure. The main reason behind this belief is related to the very large number of eggs which are produced by each spawning female. A small change in the high natural mortality rate in the larval and juvenile stages can have a much larger effect on recruitment to a fishery than can the actual number of spawning females.

To demonstrate this, consider the hypothetical situation of a tiger prawn population before any commercial fishing (see Table 3): Suppose the recruitment of small prawns to the unfished population in January each year was 150 million individuals. With a drop in this population of 18% each month, the population would decline to about 30 million individuals by the time of the main effective spawning period (August-October). From what we know about reproduction, we would expect a population of this size to produce in the order of 15000 billion eggs. Of these, 99% do not survive through to the planktonic postlarval stage (the first month) and close to 99% of these survivors do not reach suitable nursery grounds (seagrass beds) because of unfavourable currents, winds, etc. Over the next three months on the nursery grounds, another 90% of the postlarval and juveniles will be lost to predition etc., leaving 150 million recruits to complete the cycle.

With the development of an intensive fishery on this population, the number of spawners might be reduced to half that of the hypothetical unfished population (i.e. 15 million rather than 30 million). With correspondingly fewer eggs being produced, some compensation in mortality rates occurs (or the Gulf prawn fishery would have long been extinct). It is possible that compensation may occur in the larval and juvenile stages through reduced competition for food, shelter etc. The important point to note is that a drop of as little as 1% in either larval or postlarval mortality would be sufficient to compensate for the 50% drop in egg production.

TABLE 3: Hypothetical tiger prawn life table for the western Gulf of Carpentaria prior to the establishment of a commercial fishery.

	First Generation			Second Generation		
Month	Stage	Number in each stage (million)	Mortality between stages (%)	Stage	Number in each stage (million)	Mortality between stages (%)
January	recruits	150	18			
February		122	18			
March		100	18			
April		82	18			
May		67	18			
June		55	18			
July		45	18			
August	spawners	37	18			
September	spawners	30	18	eggs	15000000	99
October	spawners	25	18	postlarvae[1]	150000	99
				postlarvae[2]	2140	80
November		20	18	juveniles	428	50
December		17	18	pre-recruits	214	30
January		14	18	recruits	150	18
February		11	18		122	18

1. Planktonic postlarvae having survived through the earlier larval stages.
2. Postlarvae which have settled on seagrass nursery areas.

Present Situation

In recent years, the degree of resilience of prawn fisheries (in particular tiger prawn fisheries) to fishing pressure has been increasingly questioned. Significant declines in tiger prawn stocks have recently been documented for fisheries in the Arabian Gulf (grooved tiger prawn) as well as Exmouth Gulf and Shark Bay in Western Australia (brown tiger prawn). In each of these fisheries, annual recruitment gradually dropped over years of heavy fishing pressure to levels of about 20% of that of early years.

Catches of tiger prawns in the western Gulf of Carpentaria, after reaching a peak of 2758 tonnes in 1980, have gradually declined to a 1985 catch of only 1427 tonnes (see Table 4). This decline followed a dramatic increase in fishing effort which occurred in the late 1970's (see article by Buckworth). Indications are that the 1986 catch was even less than that of 1985.

As we do not yet have a quantitative knowledge of the mechanisms which regulate survival at each of the pre-recruit stages in the life cycle, we must at this stage restrict analysis to the simple relationships between recruitment, fishing effort and spawning stock. However, with the level of recruitment so sensitive to small changes in pre-recruit mortality, relatively large natural fluctuations in annual recruitment must be expected. As a result, the relationship between spawning stock and subsequent recruitment will show a large degree of variability.

Theoretical Model

One way to understand the rather complicated way a natural population of prawns responds to being exploited is to develop simple theoretical models to describe the processes. The first of these involves the reduction in the number of spawning females as a result of increased fishing pressure. For a given level of fishing effort, the number of prawns which reach spawning age should be proportional to the number which recruit to the fishery. However, if the level of effort was to increase, more females will be caught before spawning, in which case the number of spawners would be less for the same recruitment level (see Fig 2).

TABLE 4: History of tiger prawn catch, effort and CPUE in the western Gulf of Carpentaria. Trawl survey results ((FV *Maxim*) and commercial catch sampling (NT Department of Ports and Fisheries) have been used to separate the information relating to the two species making up the tiger prawn catches. Although the splitting is based on only 18 months data, the separation of the two species in the fishery is thought to be stable because of their association with different sediment types. Effort is allocated to one species of the other dependent on which is predominant in the area. Because effort is calculated on a monthly basis using an extrapolitan technique, total annual effort may differ slightly from the sum of the effort on each species.

Year	Tiger Prawns			Brown Tiger Prawns			Grooved Tiger Prawns		
	Catch (tonnes)	Effort (days)	CPUE (kg/day)	Catch (tonnes)	Effort (days)	CPUE (kg/day)	Catch (tonnes)	Effort (days)	CPUE (kg/day)
1970	558	3355	166	420	2769	151	137	611	224
1971	806	4106	196	496	2679	185	309	1461	211
1972	746	3513	212	573	2676	214	173	939	184
1973	1176	4370	269	780	2938	265	396	1431	276
1974	522	2019	258	306	1257	243	215	801	269
1975	443	2795	158	345	2166	159	98	638	153
1976	633	3570	177	401	2219	180	232	1369	169
1977	1741	6956	250	1119	4399	254	621	2557	243
1978	2243	10780	208	1319	6937	190	924	3843	240
1979	1722	8303	207	1121	5927	189	601	2378	252
1980	2758	16418	167	1635	10944	149	1123	5474	205
1981	2364	13274	178	1359	8574	158	1004	4700	213
1982	1766	12290	143	1144	8579	133	621	3710	167
1983	2270	13884	163	1221	8197	148	1049	5686	184
1984	1750	13123	133	877	7064	124	872	6059	143
1985	1427	10853	131	806	6402	125	620	4617	134

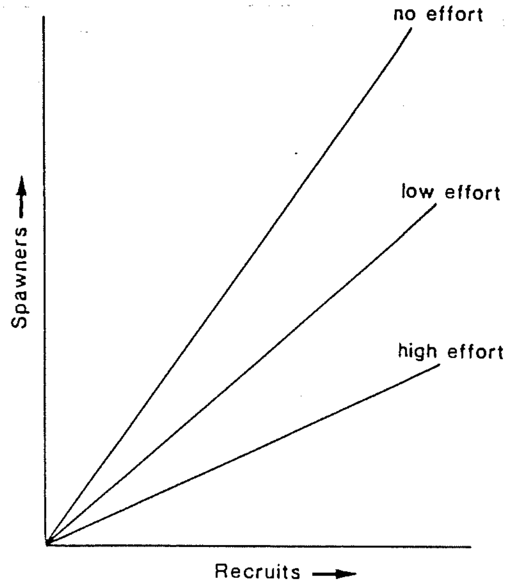


FIGURE 2: Conceptual relationship between the abundance of recruits, fishing effort and the subsequent abundance of spawners.

These surviving prawns, in turn, give rise to the next generation of recruits. Our conceptual model of the relationship between the size of the spawning population and that of subsequent recruitment is one where recruitment is zero with no spawning stock, where recruitment increases with increasing spawning stock, but where recruitment eventually levels out when the spawning stock is no longer the limiting factor (see Fig. 3). With sufficient levels of spawning stock, tiger prawn populations are generally thought to be largely regulated by the amount of available nursery ground (seagrass beds) and hence would conform to this type of model.

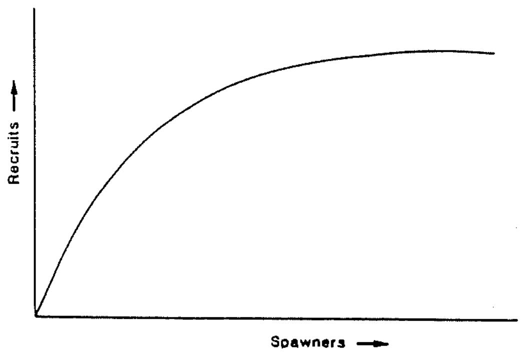


FIGURE 3: Conceptual relationship between the abundance of spawners and the subsequent abundance of recruits.

Combining two models (see Fig. 4) gives an appreciation of what constitutes recruitment overfishing and when management measures need to be introduced. The points at which the lines describing the recruit to spawner model cross over the curve describing the spawner to next recruit model, represent stable situations where the number of spawners balance the number of recruits and the population neither increases nor declines. At no fishing effort, the average spawning stock and recruitment remain high. With increasing fishing effort, both the number of spawners and the number of recruits move to a lower but stable level. This will occur in all fisheries. However, if the effort increases beyond a critical level, the line will not intersect the curve (high effort line of Fig. 4) and the population will simply collapse.

Methods of Analysis

To obtain suitable recruitment estimates for each of the two tiger species in the western Gulf of Carpentaria requires a knowledge of current levels of exploitation together with the history of fishing effort. Preliminary indications of 1985 exploitation levels are that around 50% of recruits are being caught. Exploitation levels for earlier years were estimated from the relative levels of fishing effort. Catch and effort for the individual species was estimated using logbook data, processing returns, and the results of CSIRO's trawl survey program in 1983/85 (see Table 4). Annual effort was standardised to make earlier boat-days equivalent to a 1985 boat-day; the effective increase in a nominal boat-day has been at least 100% over the period from 1970 to 1985 (see Buckworth article).

Annual recruitment of both tiger species in the western Gulf of Carpentaria has declined in recent years by about 50% (see Table 5). Recruitment of brown tiger prawns has decreased from about 110 million individuals in 1977 to around 50 million in 1985. Recruitment of grooved tiger prawns has decreased from around 60 million in 1980 to just over 30 million in 1985.

The effective spawning period for both species is in late winter and early spring (August, September, October) and the mean catch rate for these three months was chosen as a suitable measure of the relative size of the annual spawning stock (see Table 6).

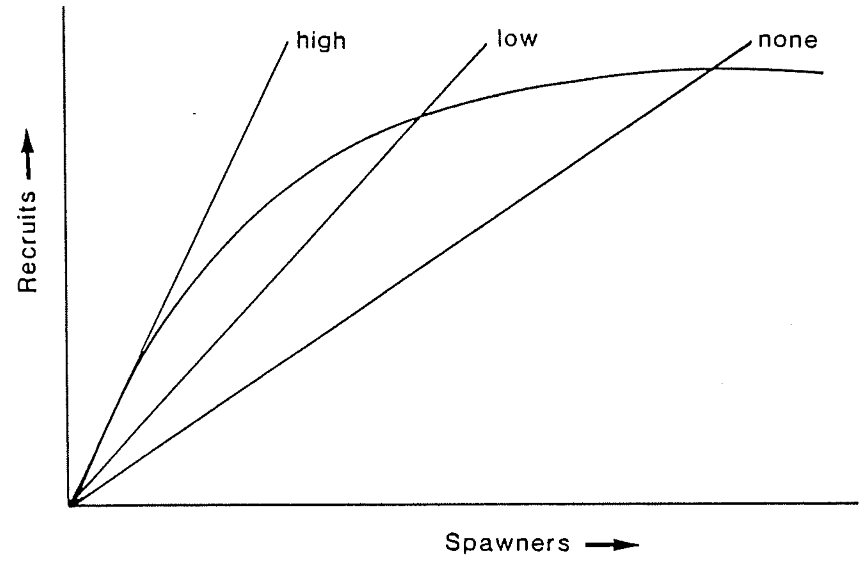


FIGURE 4: Conceptual stock-recruitment model under different levels of fishing effort (high, low and none).

Over the years 1970-1985, the average monthly fishing effort on brown tigers has dropped during the banana season (March) and immediately picked up as the banana season has drawn to a close (May) (see Fig. 5). Much of the effort is expended prior to August and hence before the effective spawning season. Effort on grooved tigers, however, has historically been later than that on brown tigers with most of the effort from August to November which may account for the fact that the decline in recruitment was initially in brown tiger prawns. However, in recent years there has been a re-direction of effort from brown to grooved tiger prawns (probably as recruitment declined on brown tigers). In 1984, 40% of the effort on grooved tiger prawns was expended before August compared to an average of 14% in earlier years.

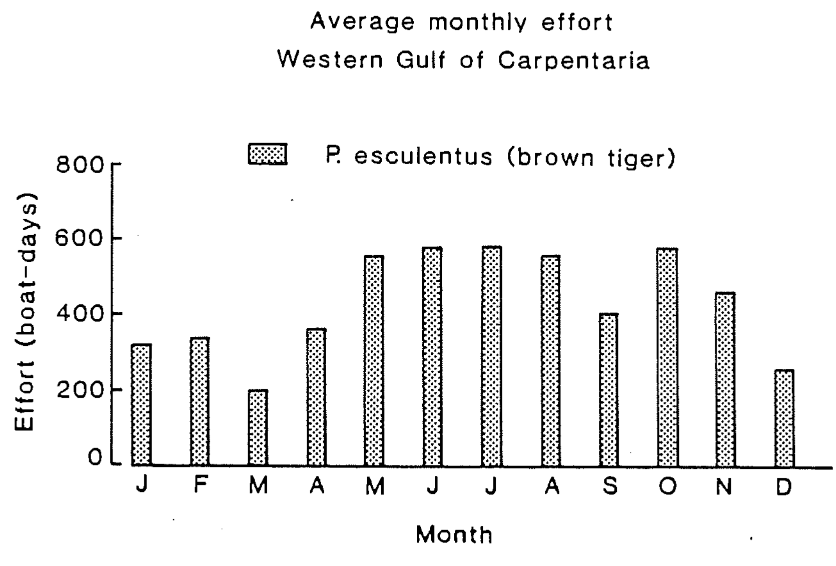


FIGURE 5: Monthly fishing effort (boat-days) on each of the tiger prawn species in the western Gulf of Carpentaria, averaged over the years 1970–1985.

TABLE 5: Estimates of effective effort, level of exploitation and recruitment for tiger prawns in the western Gulf of Carpentaria for the years 1970 to 1985. Effective effort has been standardised to 1985-boat-days assuming that there has been an increase of 100% in the effectiveness of a nominal boat day since 1970.

Year	Nominal effort (boat-days)	Effective effort (1985-boat-days)	Level of exploit-ation (%)	Number caught (million)	CPUE (thousand per 1985-boat-day)	Number of recruits (million)
Brown Tiger Prawns						
1970	2769	1384	17	13	10	78
1971	2679	1429	18	17	11	93
1972	2676	1516	19	19	12	99
1973	2938	1763	21	25	14	119
1974	1257	796	11	10	12	92
1975	2166	1444	18	11	8	64
1976	2219	1553	19	12	8	66
1977	4399	3226	33	36	11	110
1978	6937	5318	45	44	8	98
1979	5927	4741	42	36	7	86
1980	10944	9120	58	55	6	93
1981	8574	7430	53	45	6	84
1982	8579	7721	54	38	5	71
1983	8197	7650	54	41	5	76
1984	7064	6828	51	29	4	57
1985	6402	6402	50	26	4	53
Grooved Tiger Prawns						
1970	611	305	6	3	11	58
1971	1461	779	14	8	10	56
1972	939	532	10	5	9	48
1973	1431	859	15	11	13	72
1974	801	507	9	5	10	56
1975	638	425	8	2	5	29
1976	1369	958	17	5	6	34
1977	2557	1875	28	16	9	58
1978	3843	2946	38	24	8	61
1979	2378	1902	29	14	7	50
1980	5474	4561	49	30	6	61
1981	4700	4073	46	28	6	60
1982	3710	3339	41	17	5	42
1983	5686	5307	53	28	5	53
1984	6059	5857	55	27	4	49
1985	4617	4617	50	16	3	32

Thus for each species, the recruitment decline has followed a substantial increase in the level of pre-August (pre-spawning) fishing effort which reduced the size of the spawning stock.

Present Status of the Fishery

The data on the spawning stock, fishing effort and recruitment for the tiger prawns of the western Gulf of Carpentaria have been analysed with respect to our conceptual stock-recruitment model (see Figs. 6 and 7). For the recruitment to remain at a high level (i.e. in line with the high part of the curve), an appropriate limit on pre-August effort in the western Gulf should be around 3000 boat-days (2000 on brown tigers, 1000 on grooved tigers). On this basis, overfishing has been occurring on brown tigers since 1978 with pre-spawning effort reaching a peak in 1980 (5230 boat-days). For grooved tigers, overfishing would only be evident since 1983. Effort on tiger prawns in 1985 prior to August was around 4000 boat-days, which is the lowest that it has been since 1979.

TABLE 6: Annual recruitment, effort prior to August and index of spawning stock for the years 1970 to 1985. Effort has been standardised to 1985-boat-days and the measure of spawning stock abundance used is the mean CPUE (kg per 1985-boat-day) for the months August, September and October.

Year	Brown Tiger Prawns			Grooved Tiger Prawns		
	Number of recruits (million)	Spawning stock index (kg/boat-day)	Fishing effort pre-August (boat-days)	Number of recruits (million)	Spawning stock index (kg/boat-day)	Fishing effort pre-August (boat-days)
1970	78	280	622	58	449	60
1971	93	329	717	56	497	130
1972	99	274	1064	48	331	188
1973	119	416	1167	72	386	329
1974	92	485	418	56	458	93
1975	64	217	919	29	232	33
1976	66	296	1194	34	265	98
1977	110	385	1873	58	345	543
1978	98	262	3502	61	372	620
1979	86	307	2376	50	380	234
1980	93	202	5230	61	282	1212
1981	84	233	4077	60	311	1143
1982	71	157	4086	42	200	746
1983	76	199	4448	53	248	1430
1984	57	160	3472	49	154	2079
1985	53	170	3171	32	163	1082

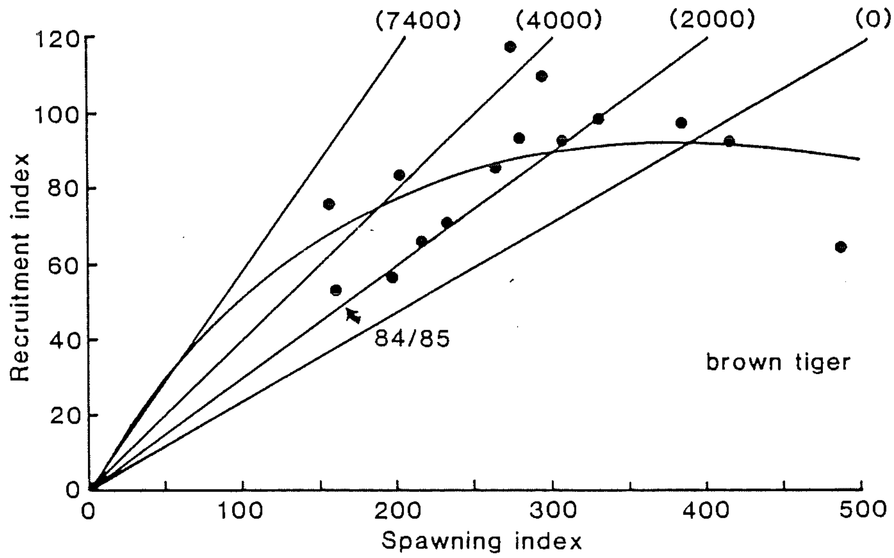


FIGURE 6: Stock-recruitment relationship for the brown tiger prawn in the western Gulf of Carpentaria. Numbers in brackets give the fishing effort in boat-days for each of the recruit to spawner lines.

The rate of recovery of the stocks is dependent on the degree of curtailment of fishing effort. A total ban on trawling before the spawning season would be expected to achieve the desired population levels in two to three generations (two to three years) if the conceptual model correctly describes the current situation.

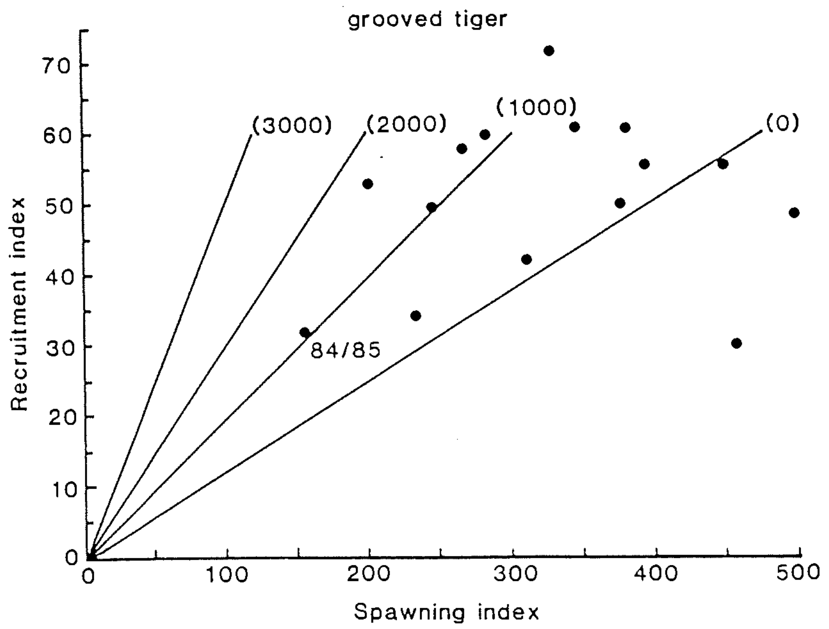


FIGURE 7: Stock-recruitment relationship for the grooved tiger prawn in the western Gulf of Carpentaria. Numbers in brackets give the fishing effort in boat-days for each of the recruit to spawner lines.

Comparison with Exmouth Gulf

To provide some wider perspective to the situation in the western Gulf of Carpentaria, it is interesting to compare the situation with that of Exmouth Gulf in Western Australia. The fishing intensity in Exmouth Gulf prior to recent restrictions was estimated as being the equivalent of each square metre of trawlable bottom being trawled more than four times per year. The comparable figure for the western Gulf of Carpentaria is just over twice per year. Whereas the tiger prawn recruitment decline in Exmouth Gulf was around 80%, the decline (so far) in the western Gulf has been around 50%. Monitoring of the tiger population in Exmouth Gulf since effort restrictions were imposed has shown the predicted increase in the size of the spawning population, indicating that prawn fisheries can bounce back with suitable management measures.

Appendix 4.7

Aust. J. Mar. Freshw. Res., 1987, 38, 133–49

Sediment Type as a Factor in the Distribution of Commercial Prawn Species in the Western Gulf of Carpentaria, Australia

I. F. Somers

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 120, Cleveland, Qld 4163.

Abstract

The relationship between sediment type and the distribution of the commercial prawn species of the western Gulf of Carpentaria was examined. The distribution of sediments was described on the basis of the mud content while the spatial distributions of the adult populations of all the commercial species were described from the results of trawl surveys. The main species caught were the tiger prawns *Penaeus esculentus* and *P. semisulcatus*, the endeavour prawns *Metapenaeus endeavouri* and *M. ensis*, and king prawns *P. latisulcatus* and *P. longistylus*, the banana prawn *P. merguiensis*, and the coral prawn *Solenocera australiana*.

The individual species were caught in varying depth ranges and, in order to assess the influence of sediment type on the spatial distributions, a stepwise multiple regression analysis was carried out in which variation due to depth was considered before that due to percentage mud. Although depth generally accounted for most of the variation in catch-per-unit-effort (CPUE), percentage mud was also found to be a significant factor for all species except *P. merguiensis*. Three species, *P. semisulcatus*, *M. ensis* and *S. australiana*, showed a preference for sediments with a high mud content while the abundances of *P. esculentus*, *M. endeavouri* and *P. latisulcatus* were each negatively correlated with percentage mud. *P. longistylus* showed a strong depth–mud interaction, being largely found on sediments of 40–60% mud in depths of 40–50 m. *P. merguiensis* was found in depths <20 m but, because the trawl stations in this depth range were all high in mud content, there was no significant correlation with sediment type. The distribution of the CPUE of all the commercial species combined was relatively even and showed no correlation with sediment type (either percentage mud or percentage organic carbon) and only 13% of the variation could be explained by a preferred depth range. Unlike the adults, juveniles were largely confined to shallow inshore waters (<20 m). Tagging experiments carried out on the major commercial species, *P. esculentus* and *P. semisulcatus*, in common inshore nursery grounds demonstrated the preferences for different sediment types; *P. semisulcatus* recaptures were mainly in areas with the finest sediments (>75% mud) whereas those of *P. esculentus* were associated with coarser sediments (50–75% mud).

Introduction

The commercial prawn fishery in the Gulf of Carpentaria presently yields around 10 000 tonnes annually. Most of this catch is taken in the western Gulf and is made up of at least nine penaeid species. The six most important commercially are the tiger prawns *Penaeus esculentus* Haswell and *P. semisulcatus* de Haan, the endeavour prawns *Metapenaeus endeavouri* Schmitt and *M. ensis* de Haan, the banana prawn

0067-1940/87/010133$02.00

P. merguiensis de Man and the western king prawn *P. latisulcatus* Kishinouye. The red spot king prawn *P. longistylus* Kubo and the leader prawn *P. monodon* Fabricius are also caught but rarely in commercial quantities. The coral prawn, *Solenocera australiana* Perez Farfante & Grey, is caught in significant numbers but its relatively small size restricts its commercial value.

The juvenile habitat requirements for tiger, endeavour and banana prawns in the Gulf of Carpentaria were described by Staples *et al.* (1985) based on a study of the Embley River estuary in the eastern Gulf. They found that offshore commercial fishing areas were adjacent to suitable nursery grounds: mangrove-lined rivers for juvenile banana prawns; expanses of seagrass for juvenile tiger and endeavour prawns. Commercial fishery statistics show that within the tiger–endeavour prawn fishing grounds, the ratio of tiger prawns to endeavour prawns varies from region to region (Somers and Taylor 1981), as do the individual species within a group (Buckworth 1985; Robertson *et al.* 1985). Although different nursery grounds are responsible for the differences in the distribution between adult banana prawns and tiger and endeavour prawns, no differences in nursery ground for the individual tiger and endeavour prawn species have been described. Furthermore, a study of the offshore movement patterns of *P. esculentus* and *P. semisulcatus* in the Groote Eylandt region showed that, although these two species shared common inshore areas adjacent to nursery grounds, the adults separated in the offshore commercial fishery (Somers and Kirkwood 1984). This observation prompted a study of the relationships between the adults of the various commercial species and their habitats in this region of the western Gulf.

Links between sediment types and particular penaeid species have previously been identified by several authors. The three major commercial species of the Gulf of Mexico, *P. setiferus*, *P. duorarum* and *P. aztecus* showed substrate preferences in laboratory tanks (Williams 1958). The substrate preferences of *P. esculentus* and *P. latisulcatus* enabled Hall and Penn (1979) to assess the effective fishing effort on each species in the Shark Bay prawn fishery in Western Australia. Relationships between sediment characteristics and individual species abundance for *P. semisulcatus*, *P. latisulcatus* and *M. monoceros* in the Sudanese Red Sea were demonstrated by Branford (1981).

The spatial and temporal distributions of *P. esculentus* and *P. semisulcatus* in the north-western Gulf of Carpentaria have been described by Somers *et al.* (1987*a*) from data collected during 21 trawl surveys carried out between August 1983 and March 1985. To discover whether a relationship between sediment type and prawns species existed in the region, data on all the commercially important species caught during these surveys were recorded and sediment samples were collected as vessel time permitted. In addition, tiger prawns of both species were tagged and released in common inshore nursery grounds; the subsequent distribution of recaptures for each species was examined in relation to the sediment types to which they had migrated. Although the trawl surveys were confined to the northern half of the western Gulf, sediment samples from the south-western Gulf were obtained during other research cruises in order to cover southern migration of tagged tiger prawns. Thus the sediments of the whole of the western Gulf were mapped. From microscopic examination of these sediment samples, Jones (1987), in a complementary study, has suggested origins, transport pathways and depositional areas for the sediments in the western Gulf.

Methods

Sediment Analysis

Sediment samples were obtained throughout the western Gulf (west of 137°30′E.) at intervals of approximately 6 nautical miles (11 km) (Fig. 1). Position fixing was by use of radar or, occasionally, satellite navigator. Sediment samples were obtained with a 0·01 m^2 Van Veen grab and approximately 200 ml of material from the top 1–2 cm of the sample was kept for analysis. Each subsample was frozen before transportation to the laboratory. Twenty-eight samples were collected in March 1982; a further 331 samples were obtained between April 1984 and March 1985.

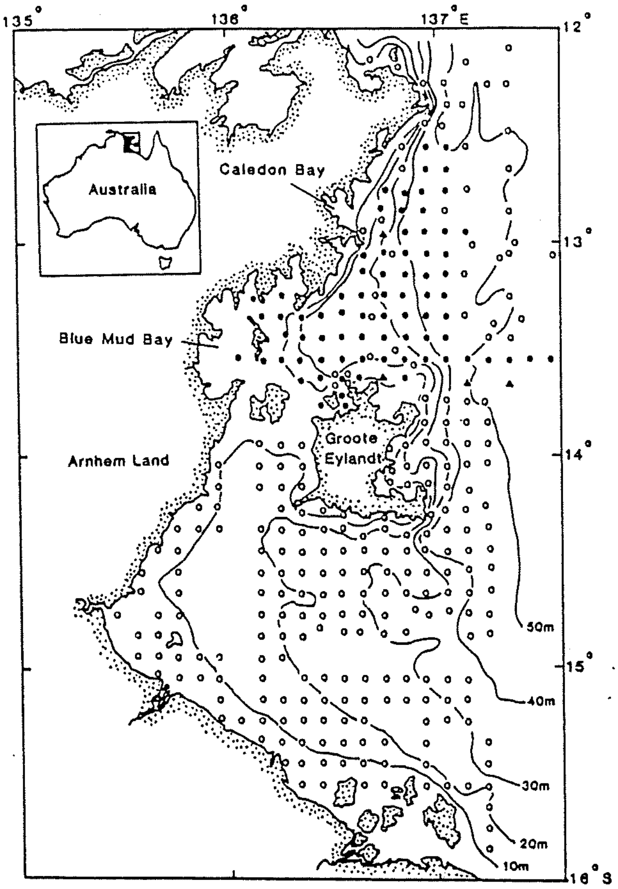


Fig. 1. Western Gulf of Carpentaria, showing the sampling sites for sediments (o), prawns and sediments (•), and prawns only (▲). The bathymetry is also shown.

The organic carbon and nitrogen contents were ascertained for the 28 samples collected in 1982. Three measurements were made for each sediment sample by combustion at 800°C in a Hewlett Packard CHN analyser (Telek and Marshall 1974). Because of the time-consuming nature of organic carbon and nitrogen determinations and because these preliminary results showed no discernible relationship with the total commercial prawn distribution, no organic carbon or nitrogen analyses were carried out on the remaining 331 samples.

The grain size of all samples was analysed using the technique of Folk (1968), as described in McLoughlin and Young (1985). Each sample was separated into sand and mud components by washing through a 63 μm nylon mesh. The sand fraction was dried and sieved at intervals of 0·5ϕ from −1·5ϕ to 4·0ϕ, where $\phi = -\log_2 D$ and D is the grain diameter (mm). The mud fraction was separated by pipette analysis into silt and clay fractions at size intervals of 0·5ϕ between 4ϕ and 6ϕ, and thereafter at size intervals of 1·0ϕ up to 9ϕ.

Tiger Prawn Tagging

The patterns of tiger prawn migration from nursery grounds to offshore fishing grounds was studied by tagging and releasing 7365 *P. esculentus* and 4034 *P. semisulcatus* in inshore areas adjacent to major nursery grounds north of Groote Eylandt, chiefly Blue Mud Bay, North West Bay and Bartalumba Bay (Fig. 4). The prawns were tagged with blue Hallprint streamer tags, which resemble the Floy tags described by Marullo *et al.* (1976) except that the needles used to insert the tag through the first abdominal segment are bonded to the vinyl streamer. The tagging methods were similar to those described by Somers and Kirkwood (1984). Tag recaptures were collected from the commercial fishing fleet together with the information on date and location of recapture.

Adult Prawn Surveys

The description of the distribution of individual species was confined to the region of the western Gulf north of Groote Eylandt and is based on catches obtained from 21 trawl surveys carried out between August 1983 and March 1985. The sampling procedures have been described in detail by Somers *et al.* (1987*a*). The sampling gear consisted of twin 11 m headrope trawl nets of 50 mm stretch mesh with 44 mm stretch mesh codends. Trawls were typically of 20 min duration and the catch-per-unit-effort (CPUE) for each station has been expressed in terms of the number of prawns per standard trawl (two 11 m nets towed for 20 min). The annual mean CPUE for each station was calculated as the mean of the CPUEs for each cruise, the stations being restricted to 73 which were sampled on at least eight occasions.

Distribution Analysis

In order to compare the sediment preferences of the adults of the various species, CPUE was calculated on the basis of the number of prawns above a certain size, which depended on species. In describing the spatial distribution of tiger prawns with respect to size, Somers *et al.* (1987*a*) defined size ranges for juveniles, subadults and adults. For convenience, they chose a minimum size for adults corresponding to that at which 20% of females are sexually mature. Where possible, the same convention has been adopted in this paper, with adult sizes, in terms of carapace length (CL), of 29 mm for *P. esculentus* and 35 mm for *P. semisulcatus* (Buckworth 1985), of 25 mm for *M. endeavouri* and 28 mm for *P. longistylus* (Somers *et al.* 1987*b*), 25 mm for *M. ensis* (Tenakanai 1980), and of 28 mm for *P. merguiensis* (Crocos and Kerr (1983). No such information could be found for *P. latisulcatus* and the division was set as for the other king prawn *P. longistylus* (28 mm). No subdivision was attempted for *S. australiana*. Juveniles of *Penaeus* spp. have been defined as <20 mm CL in line with the convention adopted by Somers *et al.* (1987*a*). The size chosen for the relatively smaller *Metapenaeus* species was <15 mm CL.

The individual species were caught in varying depth ranges and, in order to assess the relative importance of sediment type as a factor which might influence spatial distribution, both depth and percentage mud were included in a stepwise multiple regression of the form:

$$\mathrm{F(CPUE)} = a_0 + a_1 D1 + a_2 D2 + a_3 M1 + a_4 M2 + a_5 DM,$$

where F(CPUE) is $\log_e(\mathrm{CPUE}+1)$, $D1$ is the depth (m), $D2$ is $(D1-30)^2$, $M1$ is percentage mud, $M2$ is $(M1-70)^2$ and DM is $D1$ multiplied by $M1$. The terms $D2$ and $M2$ gave the model a potential quadratic form. The values 30 m and 70% are close to the mean values for depth and percentage mud respectively and were included to reduce the correlation between linear and quadratic components. One interactive term (DM) was also included. Variables were added to the equation one at a time in a specified order ($D1$, $D2$, $M1$, $M2$, DM) and were only included if significant at the 5% level.

Results

Sediment Distribution

The sediments were initially classified in terms of the proportions of sand (including gravel) ($-1\cdot5$–4ϕ), silt (4–8ϕ) and clay ($>8\phi$) (Fig. 2). The sediments north of Groote Eylandt including those obtained from the trawl sites, generally had a lower sand component than those south of Groote Eylandt. Many of the samples contained in excess of 75% sand, whereas none contained such high fractions of silt and only four samples exceeded 75% clay. As the ratio of silt to clay was relatively constant in the samples, the silt and clay components were subsequently combined and referred to as the mud fraction.

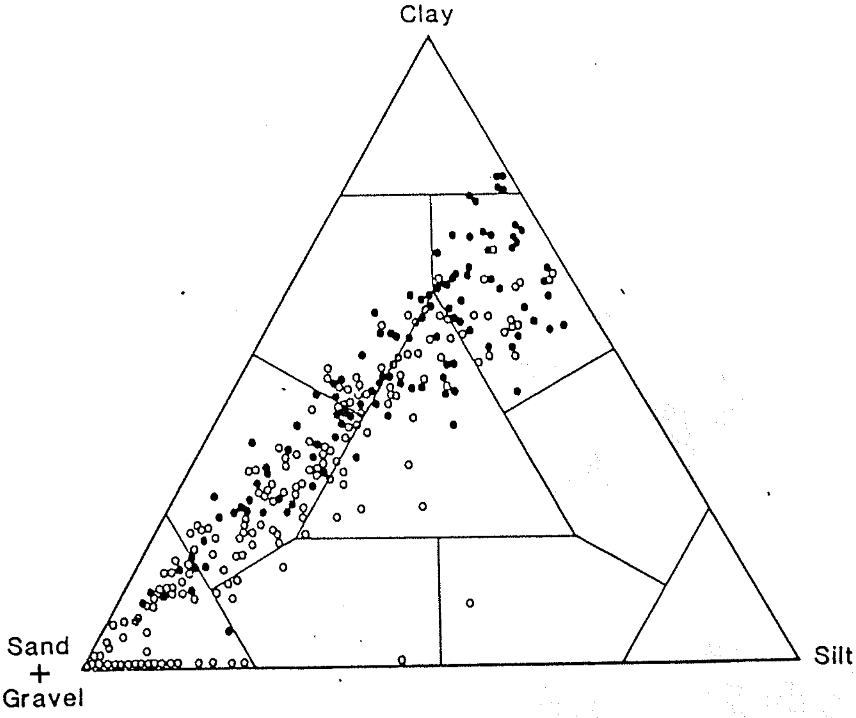


Fig. 2. Triangular diagram showing the percentage sand (including gravel) (−1·5–4ϕ), silt (4–8ϕ) and clay (>8ϕ) in the sediment samples from north (•) and south (o) of Groote Eylandt in the western Gulf of Carpentaria. After Shepard (1954).

The geographical distribution of sediments in the western Gulf on the basis of the percentage of mud is given in Fig. 3. The main feature of the distribution of sediments north of Groote Eylandt is the large expanse of fine sediment (>75% mud) extending seawards from Blue Mud Bay. The fine sediment in the bays at the northern end of Groote Eylandt is separated from this expanse by an intrusion of much coarser material, which runs from the channel between Groote Eylandt and the mainland. A tongue of coarser material also extends seawards from Caledon Bay for about 50 km and then spreads both north and south just beyond the 40 m depth contour, separating the seaward extension of fine material from Blue Mud Bay from a region of fine sediment further offshore. South of Groote Eylandt, there is an offshore gradation from coarse to fine sediment.

The percentage by weight of organic carbon in the sediment samples taken in 1982 ranged from 0·86 to 2·12%. Organic nitrogen in these samples ranged from 0·04 to 0·12%, with the ratio of carbon to nitrogen remaining relatively constant (20·79 with a standard deviation of 2·69). Both carbon and nitrogen showed significant correlations with the mud content of the sediment (R^2 = 0·66 and 0·56 respectively).

Distribution of Tag Recaptures of Adult Tiger Prawns

Of the adolescent tiger prawns released in Blue Mud Bay, North West Bay and Bartalumba Bay, 389 adult *P. esculentus* (5·3%) and 310 adult *P. semisulcatus* (7·7%) were subsequently recaptured in the offshore commercial fishery. The recapture distributions were very similar to those described by Somers and Kirkwood (1984): the two species moved into different areas in the offshore commercial fishery. Most of the *P. esculentus* recaptures were in the area adjacent to the northern end of Groote Eylandt although some moved south of Groote Eylandt, with 15 recaptured in the fishing grounds around South Point (Fig. 4*a*). *P. semisulcatus*, however, were generally recaptured further north, with two being recaptured north of Cape Grey (approximately 120 km north of their point of release) (Fig. 4*b*). An interesting departure from this northerly movement was the recapture of 12 *P. semisulcatus* east of Groote Eylandt.

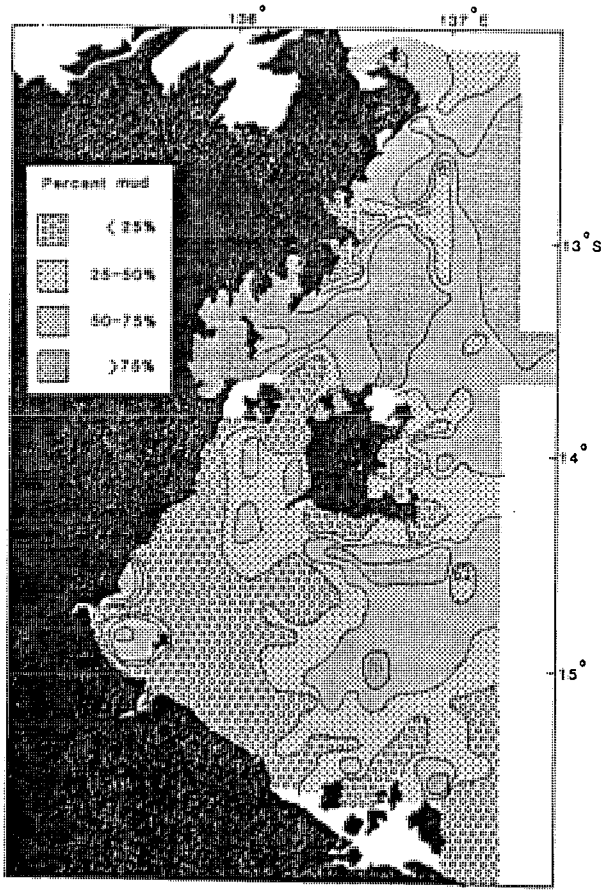


Fig. 3. Geographic distribution of sediments of the western Gulf of Carpentaria on the basis of the percentage of mud (<63 μm). Contours are drawn at the 25, 50 and 75% mud boundaries.

Comparison of these distributions with that of sediments shows that the two species were mostly recaptured on different sediment types: most *P. semisulcatus* recaptures were on sediments with a mud content greater than 75%; most *P. esculentus* recaptures were on sediments with a mud content less than 75% (Figs 4, 5). Even the departures from the general directions of movement reflect the same species–sediment associations (Fig. 4).

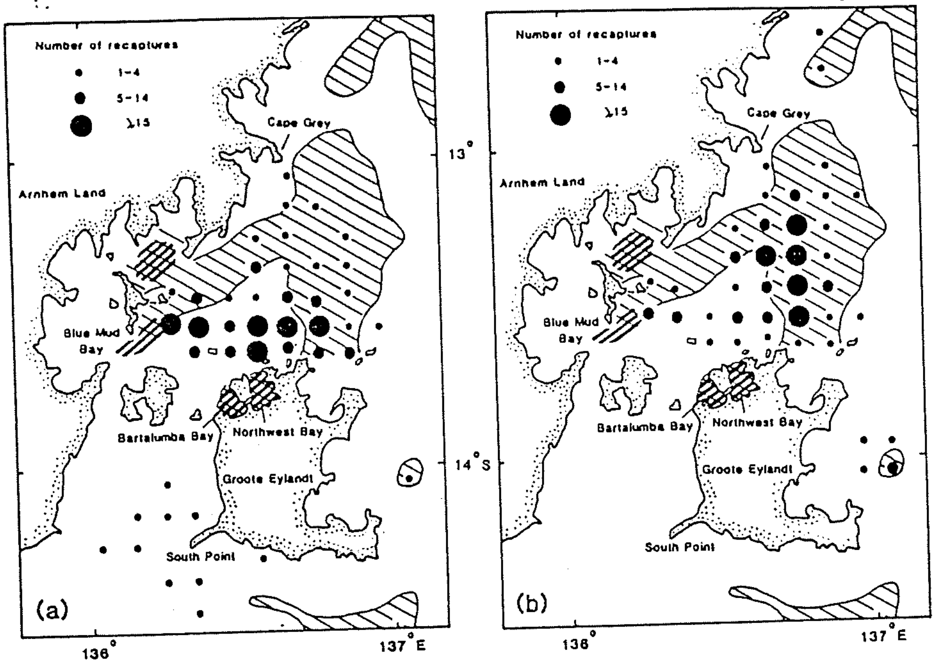


Fig. 4. Distribution of tagged tiger prawn recaptures in the western Gulf of Carpentaria from release areas (heavy cross-hatching) in Blue Mud Bay, North West Bay and Bartalumba Bay. The distribution of fine sediment (>75% mud) is given for comparison (light cross-hatching). (*a*) *P. esculentus*. (*b*) *P. semisulcatus*.

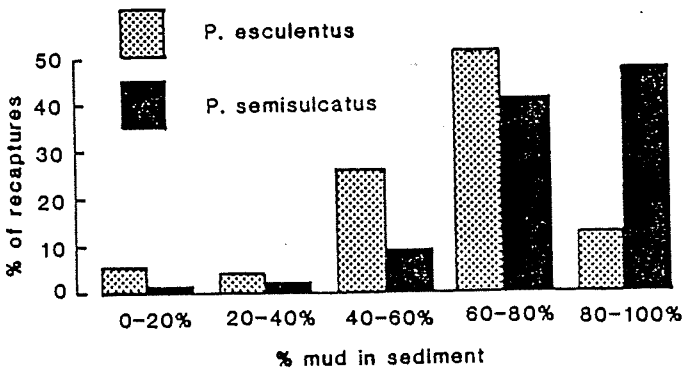


Fig. 5. Distribution of tagged tiger prawns in relation to the mud content of the sediment on which they were recaptured.

Distribution for Each Commercial Species from the Trawl Surveys

Tiger prawns

The adult population distributions of both species show the same spatial partitioning seen in the tag recapture results (Figs 4*a*, 4*b*). Highest catch rates of adult *P. esculentus*

Table 1. Distribution of relative catch-per-unit-effort (CPUE) for the main commercial species in the north-western Gulf of Carpentaria with respect to depth (m) and sediment type (% mud)
CPUE is expressed relative to the mean and standard deviation (s.d.): less than the mean (—), the mean to one s.d. above the mean (*), between one and two s.d. above the mean (**), greater than two s.d. above the mean (***). No symbol indicates no stations with that particular depth–sediment type

Depth (m) / Sediment type (% mud)

P. esculentus

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							**	**	—	
10–20				**		**	—	—	—	
20–30	**	**		*	*	*	*	—	*	
30–40		*		—			—	—	—	
40–50			—	—	—	—	—	—	—	
50–60				—		—				

P. semisulcatus

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10								—	—	—
10–20				—		—	—	—	—	
20–30	—	—		—	—	*	*	*	*	
30–40		**	—				*	**	**	
40–50			*	—	—	*	*	*	*	
50–60				—		—				

M. endeavouri

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							—	—	—	
10–20				*		*	—	—	—	
20–30	*	*		**	*	*	*	*	**	
30–40		*		*			*	*	—	
40–50			—	—	—	—	—	—	—	
50–60					*		*			

M. ensis

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							—	—	—	
10–20				—		—	—	—	—	
20–30	—	—		—	—	—	—	*	—	
30–40		*		*			***	*	**	
40–50			**	*	—	**	—	*	**	
50–60					—		—			

P. latisulcatus

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							*	—	—	
10–20				—		—	—	—	—	
20–30	***	*		**	*	—	—	*		
30–40		—		**			—	—	—	
40–50			—	—	—	—	—	—	—	
50–60					—		—			

P. longistylus

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							—	—	—	
10–20				—		—	—	—	—	
20–30	—	—	—	—	—	—	—	—		
30–40		—		—			—	—	—	
40–50			—	***	***	—	—	—	—	
50–60					—		*			

P. merguiensis

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							—	**	**	
10–20				*		**	*	***	***	
20–30	—	—		—	—	—	—	—	—	
30–40		—		—			—	—	—	
40–50			—	—	—	—	—	—	—	
50–60					—		—			

S. australiana

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							—	—	—	
10–20				—		—	—	—	—	
20–30	—	—		—	—	—	—	—	—	
30–40		*		*			*	*	*	
40–50			*	*	—	***	**	*		**
50–60					*					

Juveniles (all species)

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							*	***	**	
10–20				—		—	*	*	***	
20–30	—	—		—	—	—	—	—	—	
30–40		—		—			—	—	—	
40–50			—	—	—	—	—	—	—	
50–60					—		—			

Adults (all species)

Depth (m)	10	20	30	40	50	60	70	80	90	100
0–10							*	*	—	
10–20				*		*	—	—	—	
20–30	*	*		*	—	*	—	*	—	
30–40		*		*			*	*	*	
40–50			*	—	—	*	—	—	*	
50–60					—		—			

were found in relatively shallow water (<30 m) adjacent to the northern coast of Groote Eylandt (Fig. 6*a*), whereas *P. semisulcatus* were most abundant in deeper waters (30–40 m) further north (Fig. 6*b*).

Adult *P. esculentus* were found over a wide range of sediment types; however, the highest catch rates in each depth range sampled were at stations with the least mud content (Table 1). The adult *P. semisulcatus* population was generally found on sediments which contained >75% mud (Fig. 6*b*) and, even though high catch rates were obtained at depths less than 30 m, the species was effectively separated from *P. esculentus* through its preference for muddier sediments (Table 1). This is supported by the results of the stepwise multiple regression analysis which shows that after the effect of depth is removed, sediment type (percentage mud) has a significant effect on the CPUE of both species (Table 2). For *P. esculentus*, percentage mud has a negative effect on CPUE, whereas for *P. semisulcatus* it has a positive effect.

Juveniles (≤20 mm CL) of both *P. esculentus* and *P. semisulcatus* were mainly caught at the shallow water (<20 m) trawl stations in Blue Mud Bay and North West Bay (Figs 6*a*,6*b*). The sediments at these locations all contained >75% mud.

Table 2. Contribution of significant variables (absolute *t* values for the coefficients >2·0) to explained variation of $\log_e(\text{CPUE}+1)$ in the stepwise regression with depth (m) and sediment type (% mud)

The *t* values for the coefficients are given in brackets. $D1$ = depth (m), $D2 = (D1-30)^2$, $M1$ = % mud, $M2 = (M1-70)^2$, $DM = D1 \times M1$. The square of the multiple correlation coefficent (R) was used as a measure of the explained variation. The order of entry of variables into the equation was from left to right so that depth effects would be removed (if significant) before the analysis of mud. Note: the level of contribution to the R^2 was dependent on the order of entry.

Species	Variables used in regression:					R^2
	$D1$	$D2$	$M1$	$M2$	DM	
P. esculentus	0·56 (−7·2)		0·11 (−6·2)	0·03 (−2·8)	0·05 (+4·4)	0·75
P. semisulcatus	0·17 (+5·5)	0·27 (−7·3)	0·16 (+5·4)			0·60
M. endeavouri		0·14 (−3·7)	0·17 (−5·1)	0·07 (−2·9)		0·38
M. ensis	0·34 (+7·7)	0·09 (−4·1)	0·12 (+5·1)	0·04 (+2·5)		0·59
P. latisulcatus	0·05 (−4·4)		0·25 (−5·5)		0·12 (+3·8)	0·42
P. longistylus	0·16 (+5·1)		0·06 (+3·1)		0·17 (−4·3)	0·39
P. merguiensis	0·41 (−7·6)	0·15 (+4·9)				0·56
S. australiana	0·57 (+11·8)	0·02 (−2·2)	0·08 (+5·0)	0·03 (+2·8)		0·70
All species		0·13 (−3·2)				0·13

Endeavour prawns

Adult *M. endeavouri* were widely distributed throughout the study area (Fig. 7*a*). Catch rates were highest in the depth range 20–40 m and were lowest on sediments which contained >90% mud (Table 1). As with *P. esculentus*, removal of the effect

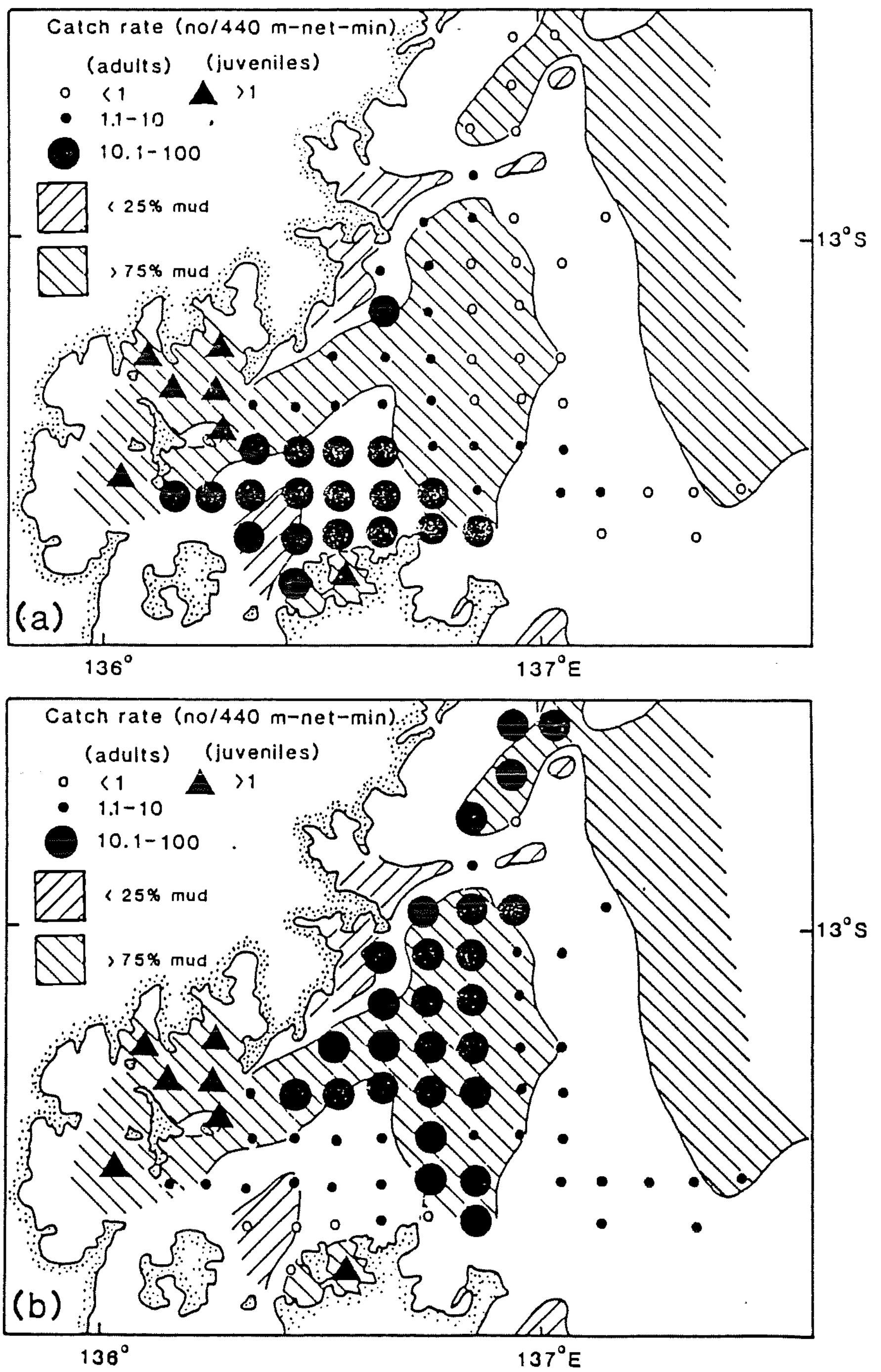


Fig. 6. Catch-per-unit-effort of adult tiger prawns (*a*) *P. esculentus* (n = 17792) and (*b*) *P. semisulcatus* (n = 13941), from the trawl surveys in the north-western Gulf of Carpentaria.

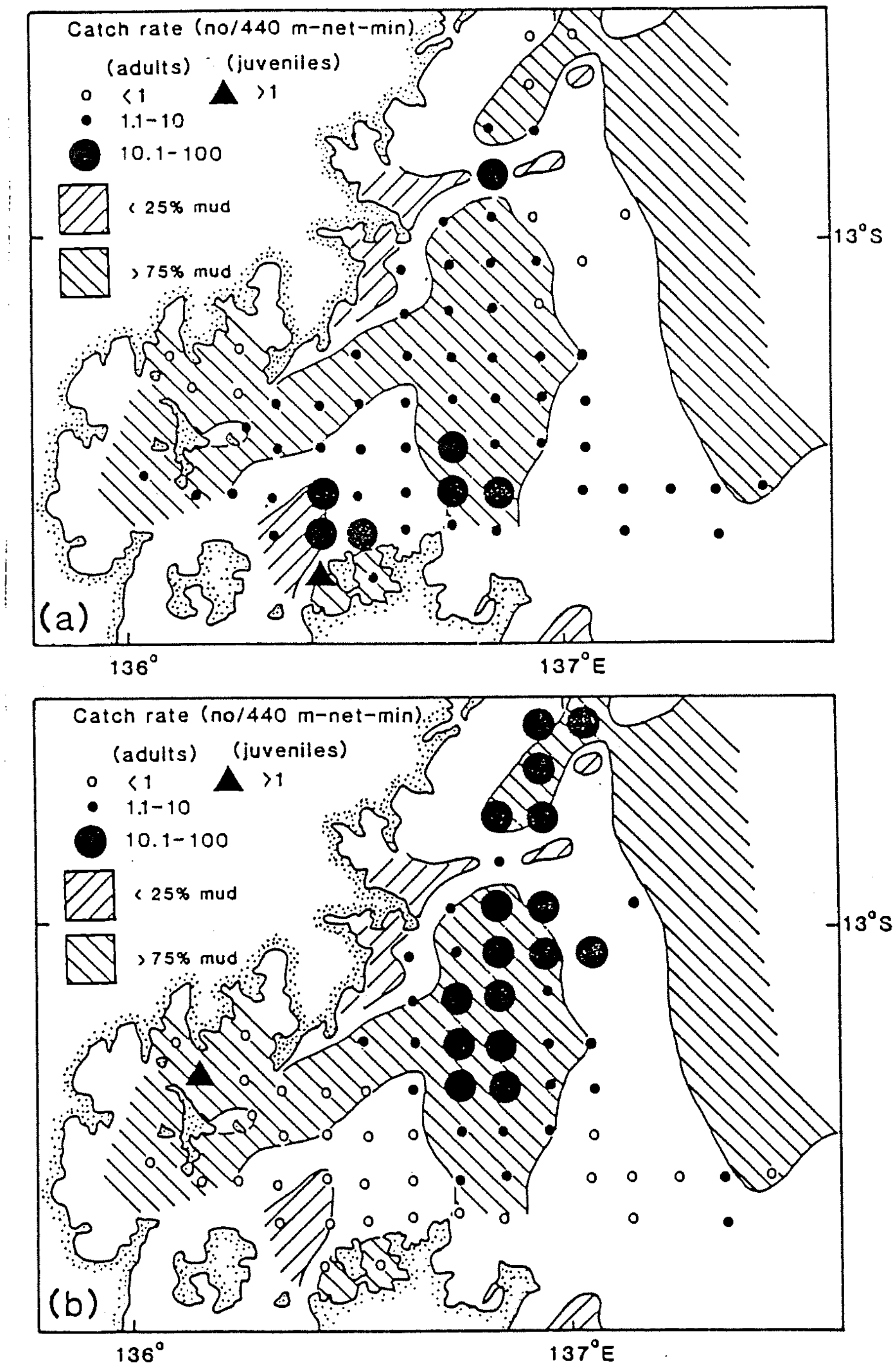


Fig. 7. Catch-per-unit-effort of adult endeavour prawns. (*a*) *Metapenaeus endeavouri* ($n = 7923$) and (*b*) *M. ensis* ($n = 5616$), from the trawl surveys in the north-western Gulf of Carpentaria.

of depth in the multiple regression results in a significant negative correlation between CPUE and percentage mud (Table 2).

Unlike *M. endeavouri*, *M. ensis* was far more restricted in its distribution, with most of the catch being taken on the finest sediments (>75% mud) (Fig. 7*b*) and the highest catch rates occurring in depths of 30–50 m (Table 1). Sediment type (percentage mud) was shown to be a significant factor in relation to CPUE and was positively correlated (Table 2).

Juvenile endeavour prawns (<15 mm CL) were mainly caught in Blue Mud Bay (*M. ensis*) and Bartalumba Bay (*M. endeavouri*) although rarely in large numbers (Figs 7*a*,7*b*). Slightly larger endeavour prawns (15–20 mm CL), unlike tiger prawns of the same size, were caught throughout their respective ranges.

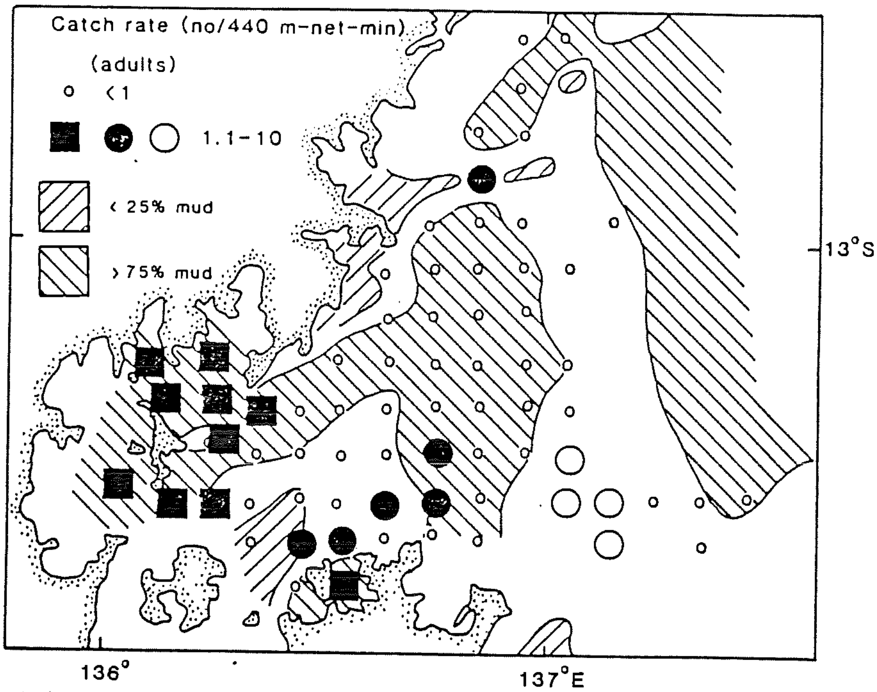


Fig. 8. Catch-per-unit-effort of adult banana prawns *Penaeus merguiensis* (■, $n = 1536$) and adult king prawns *P. latisulcatus* (●, $n = 658$) and *P. longistylus* (o, $n = 315$), from the trawl surveys in the north-western Gulf of Carpentaria.

Species of Minor Commercial Importance

The king prawns *P. latisulcatus* and *P. longistylus* constituted less than 2% of the prawns caught during the study. The results of the regression analysis suggest a significant sediment–depth interaction for both species (Table 2). Although both species were found on similar sediment types (<75% mud), adult *P. latisulcatus* were more abundant in shallower waters (<35 m), whereas *P. longistylus* were caught in only one area near the north-eastern tip of Groote Eylandt in 45–50 m of water (Fig. 8, Table 1). This area is outside the main commercial fishery; the by-catch there included sessile benthic fauna (sponges and soft corals). On the basis of commercial fishery statistics, the greatest concentration of king prawns in the region was in Caledon Bay (Somers and Taylor 1981). Although there was no trawl station in

Caledon Bay throughout the study, an exploratory trawl in August 1983 confirmed the species present to be *P. latisulcatus*. These differences between the king prawn habitats are consistent with those described by Penn (1980) for Western Australian waters.

The banana prawn *P. merguiensis* constituted less than 2% (by weight) of the prawns caught in the present study, but comprised between 5 and 10% (by weight) of the commercial catch in the Groote Eylandt region (Somers and Taylor 1981). This disparity in relative abundance arises from the schooling behaviour of the species. The species is usually caught commercially after first locating the schools with echo sounders and grid sampling by trawling is not, therefore, effective. However, sporadic catches of *P. merguiensis* were made, mainly in the shallow waters (<20 m) of Blue Mud Bay and North West Bay (Fig. 8, Table 1). Of all the species investigated, *P. merguiensis* was the only one which did not show any significant relationship with sediment type (percentage mud) after depth effects had been removed (Table 2).

The leader prawn *P. monodon* was extremely rare in the region. Only 15 individuals were caught during the study. Of these, 11 were taken in North West Bay.

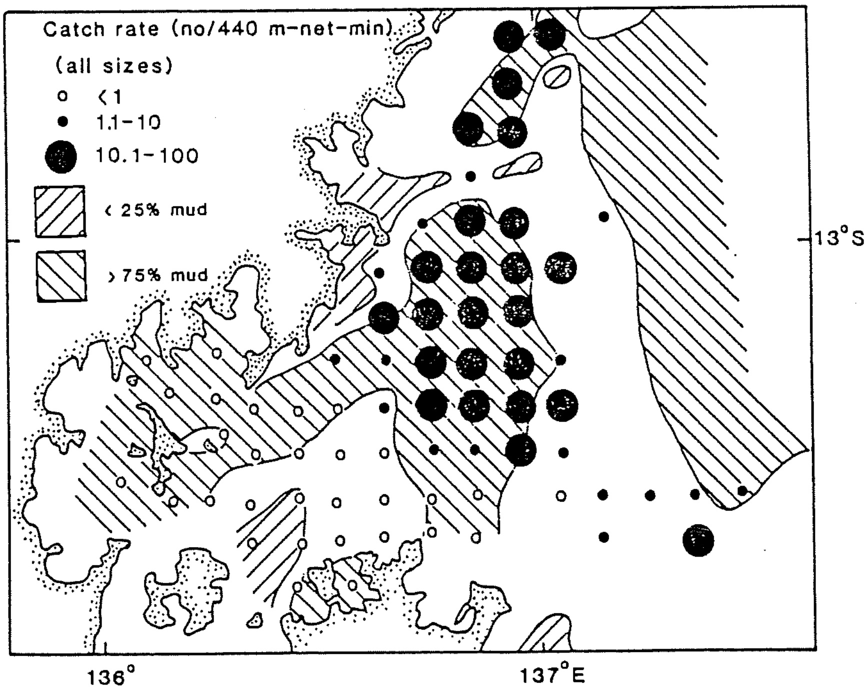


Fig. 9. Catch-per-unit-effort of coral prawns *S. australiana* (n = 315), from the trawl surveys in the north-western Gulf of Carpentaria.

The coral prawn *S. australiana* has only recently been described taxonomically (Perez Farfante and Grey 1980) and its biology is not well known. The species was most abundant in depths greater than 30 m and showed an affinity for sediments with a high mud content (Fig. 9, Table 1, Table 2). The species was caught in the eastern-most sampling sites (55 m). Occasionally a very small specimen (<10 mm CL) was caught in 15–20 m of water just outside Blue Mud Bay, although the sampling gear would have been very inefficient for prawns of this size.

Discussion

Variation in prawn abundance has been linked to the organic carbon content of the sediments in commercial fisheries in both the Gulf of Mexico (Grady 1971) and in the Sudanese Red Sea (Branford 1981). However, a similar relationship could not be demonstrated during this study of the commercial species in the western Gulf of Carpentaria. Although juvenile prawns were generally confined to the shallow muddy bays, the adult population was evenly distributed throughout the study area (Table 1) and catch rates showed no significant correlation with organic carbon content ($P = 0\cdot36$, $R^2 = 0\cdot04$). A noticeable difference in the Gulf of Carpentaria study was that organic carbon levels were between two to four times higher than those recorded in the fishing grounds in the Gulf of Mexico (Grady 1971) and the Red Sea (Branford 1981). The levels of organic carbon in the sediments of the north-western Gulf of Carpentaria may therefore have not been low enough to be a limiting factor in the distribution of the commercial species. In the stepwise multiple regression analysis, the only factor which was found to be significant in accounting for variation in the catch rate of the commercial species was the quadratic term in depth (*D*2 in Table 2). Although the variation explained was only 13%, the result suggests a preferred depth range of around 20–40 m for commercial species in the Gulf, which is consistent with the absence of a commercial fishery in deeper water (Somers and Taylor 1981).

Unlike the relatively even total prawn distribution, individual species showed marked differences in their spatial distributions (Figs 6–9), apparently corresponding to different depth and sediment preferences (Table 1). A stepwise regression analysis was used to evaluate the importance of these two factors in determining the individual species distributions. However, because depth and sediment type were not independent variables, their contribution to explained variation was dependent on their order of entry into the analysis. Therefore to guard against incorrectly attributing too much importance to the effect of sediment type when the variation may simply have been attributed to depth, the order of entry was fixed, with linear and quadratic depth terms being entered (if significant) before those of sediment type. The analysis showed depth to be a significant factor for all species examined while for all species except *P. merguiensis*, percentage mud was also shown to be significant (Table 2). Species which were more abundant on muddy sediments included *P. semisulcatus*, *M. ensis* and *S. australiana*, while *P. esculentus* and *M. endeavouri* showed a strong preference for more sandy sediments. The king prawns *P. latisulcatus* and *P. longistylus* both showed significant depth–sediment interactions (Table 2), being found on similar sediment types (sandy) but only in specific (and different) depth ranges (Fig. 8, Table 1). *P. merguiensis* was mainly found in shallow water (<20 m) where the range of percentage mud on the trawl stations was narrow and the mud content generally high. Even so, the highest catch rates were from the muddiest stations (Table 1), and the coefficient for the linear term in percentage mud was on the border line of significance ($t = +1\cdot88$, $P = 0\cdot064$). Hence, although many factors, such as suitable nursery habitat (Staples *et al.* 1985), may determine the distribution and abundance of a prawn species, suitable offshore habitat also appears to be an important factor in delimiting the distribution of the commercial species in the western Gulf of Carpentaria. The tag recapture study of tiger prawns demonstrated that even species which share the same inshore nursery areas as juveniles, can have separate adult distributions which may be influenced by sediment type (Figs 4*a*,4*b*,5).

It is not known whether the species–sediment associations described in this study are applicable to all other regions. *P. semisulcatus*, *M. ensis*, *P. merguiensis*, *P. latisulcatus*, *P. longistylus* and *P. monodon* are widely distributed throughout the Indo-west Pacific region, whereas *P. esculentus*, *M. endeavouri* and *S. australiana* are endemic to Australian waters (Grey *et al.* 1983). However, very limited information is presently available in the literature to test the species–sediment hypotheses. *P. esculentus* constitutes over 90% of the tiger prawn catch in the fishery south of Groote Eylandt (Buckworth 1985) where the sediments are generally low in mud content (Fig. 3). In the south-eastern Gulf where sediments of <50% mud predominate (Rhodes 1980), the tiger, endeavour and king prawn fishery is based on *P. esculentus*, *M. endeavouri* and *P. latisulcatus* (Robertson *et al.* 1985). The sediments in the Torres Strait prawn fishery have also been shown to be predominantly coarse (<50% mud) and the fishery there is based almost entirely on *P. esculentus*, *M. endeavouri*, *P. longistylus* and *P. latisulcatus* (Somers *et al.* 1987*b*). A few *P. semisulcatus* (<1% of the tiger prawn catch) are caught in the Torres Strait fishery but only in a very small area which has fine sediment (>65% mud) (Somers *et al.* 1987*b*). Branford (1981) showed that *P. semisulcatus* density in the Sudanese Red Sea was highest in sediments containing greater than 70% mud, while Mohammed *et al.* (1981) described the trawling grounds for *P. semisulcatus* in Kuwait waters as being 'soft and muddy'. Thus the information available elsewhere on species and sediments seems to be consistent with the findings of the study in the north-western Gulf of Carpentaria.

More tenuous evidence of the consistency of these relationships is the co-occurrence of species with similar sediment preferences throughout most of their respective geographic ranges. *P. semisulcatus* and *M. ensis* both showed an affinity for muddy sediments in the north-western Gulf of Carpentaria and both species co-occur in fisheries in the Gulf of Papua (Tenakanai 1980), Indonesia, Malaysia, Singapore, the Philippines, Japan and the east coast of India (Holthuis 1980). Although *P. semisulcatus* is also caught further west in the Red Sea and east Africa, *M. ensis* is replaced in these regions by a similar species, *M. monoceros*. Both *P. esculentus* and *M. endeavouri* have similar preferences for sandy sediments in the north-western Gulf of Carpentaria and both species apparently co-occur in Australian fisheries, being caught in tropical and subtropical waters from New South Wales in the east to Shark Bay in the west (Holthuis 1980).

The reasons for the substrate preferences of individual species are not clear. Gray (1974), in a general review of animal–sediment relationships, has discussed in detail the many and varied reasons for specific sediment preferences. With respect to grain-size relationships for burying species like prawns, the reasons usually revolve around an ability to bury effectively in the substsrate while still maintaining the efficient function of the gills when buried. Hall and Penn (1979) observed that *P. esculentus* buried less efficiently than *P. latisulcatus* in coarse beach sand. However, a sand substrate has been used successfully in laboratory experiments in which burying activity was monitored under controlled environmental conditions for *P. semisulcatus* and *P. merguiensis* (Hill, personal communication) as well as *P. esculentus* (Hill 1985). Sediment preferences for the prawn species may therefore be more complex than simply being related to an ability to bury or respire while buried.

The available evidence suggests that food does not appear to be a limiting or determining factor in the distributions of the species. Wassenberg and Hill (1987) examined the diet of tiger prawns caught during the trawl surveys in the north-western Gulf and found that virtually all individuals examined immediately after sunset had full foreguts and that there was no significant difference in the prey items between adult *P. esculentus* and *P. semisulcatus*.

The present study has not been designed to elucidate the mechanisms of substrate selection, a subject which would be more easily studied under controlled laboratory conditions. However, the signficance of depth and sediment type in determining the different spatial distribution of the various species suggests the relative permanancy of these distributions. An important implication of this is that the interpretation of commercial fishery data which is limited to species groups (e.g. tiger, endeavour and king prawns) will be possible on an individual species basis as long as the data are obtained with precise information on the area of capture.

Acknowledgments

Many people contributed to making this study possible. The study was initially conceived through useful discussions with Norm Carroll from the Fisheries Division, Northern Territory Department of Ports and Fisheries; Dr Burke Hill and Peter Crocos helped with planning and organizing the trawl program; Steve Ivicic and the crew of F.V. Maxim provided enthusiastic assistance; Brian Taylor, together with David Kelly, Rik Buckworth and Margo Sachse from the Fisheries Division, Northern Territory Department of Ports and Fisheries, helped with the tagging program and subsequent collection of recaptures from the commercial fishing fleet; Richard McLoughlin, June Hill and Doug Harding organized and carried out the sediment grain size analysis; John Kerr from the Division of Mathematics and Statistics, CSIRO, assisted with the statistical analysis. The study was funded in part from the Fishing Industry Research Trust Account.

References

Branford, J. R. (1981). Sediment and the distribution of penaeid shrimp in the Sudanese Red Sea. *Estuarine Coastal Shelf Sci.* 13, 349–54.

Buckworth, R. C. (1985). Preliminary results of a study of commercial catches, spawning and recruitment of *Penaeus esculentus* and *P. semisulcatus* in the western Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 213–20. (NPS2: Cleveland, Australia).

Crocos, P. J., and Kerr, J. D. (1983). Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentaria, Australia. *J. Exp. Mar. Biol. Ecol.* 69, 37–59.

Folk, R. L. (1968). 'Petrology of Sedimentary Rocks.' (University of Texas Press: Austin.)

Grady, J. R. (1971). The distribution of sediment properties and shrimp catch on two shrimping grounds on the continental shelf of the Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 23rd annual session. pp. 139–48.

Gray, J. S. (1974). Animal-sediment relationships. *Oceanogr. Mar. Biol. Annu. Rev.* 12, 223–61.

Grey, D. L., Dall, W., and Baker, A. (1983). 'A Guide to the Australian Penaeid Prawns.' (Department of Primary Production of the Northern Territory: Darwin.)

Hall, N. G., and Penn, J. W. (1979). Preliminary assessment of effective effort in a two species trawl fishery for Penaeid prawns in Shark Bay, Western Australia. *Cons. Int. Explor. Mer.* 175, 147–54.

Hill, B. J. (1985). Effect of temperature on duration of emergence, speed of movement, and catchability of the prawn *Penaeus esculentus*. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 77–83. (NPS2: Cleveland, Australia.)

Holthuis, L. B. (1980). FAO species catalogue. Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. *FAO Fish. Synop.* (125) 1, 1–261.

Jones, M. R. (1987). Surficial sediments of the western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* 38, 151–67.

McLoughlin, R. J., and Young, P. C. (1985). Sedimentary provinces of the of the fishing grounds of the North West Shelf of Australia: grain-size frequency analysis of surficial sediments. *Aust. J. Mar. Freshw. Res.* 36, 671–81.

Marullo, F., Emiliani, D. A., Caillouet, C. W., and Clark, S. H. (1976). A vinyl streamer tag for shrimp (*Penaeus* sp.). *Trans. Am. Fish. Soc.* 105, 658–63.

Mohammed, K. H., El-Musa, M., and Abdul-Gaffer, A. R. (1981). Observations on the biology of an exploited species of shrimp, *Penaeus semisulcatus* de Haan, in Kuwait. In 'Proceedings of the International Shrimp Releasing, Marking and Recruitment Workshop, 25–29 November 1978, Salmiya, State of Kuwait'. (Ed. A. S. D. Farmer.) [Kuwait Bulletin of Marine Science No. 2.] pp. 33–51.

Perez Farfante, I., and Grey, D. L. (1980). A new species of *Solenocera* (Crustacea : Decapoda : Solenoceridae) from northern Australia. *Proc. Biol. Soc. Wash.* 93, 421–34.

Penn, J. W. (1980). Observations on length-weight relationships and distribution of red spot king prawn, *Penaeus longistylus* Kubo, in Western Australian waters. *Aust. J. Mar. Freshw. Res.* 31, 547–52.

Poiner, I., Staples, D., and Kenyon, R. (1987). Sea grass communities of the western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* 38, 121–31.

Rhodes, E. G. (1980). Modes of holocene coastal progradation Gulf of Carpentaria. Ph.D. Thesis, Australian National University, Canberra.

Robertson, J. W. A., Coles, R. G., and Goeden, G. B. (1985). Distribution patterns of commercial prawns and reproduction of *Penaeus esculentus* around the Wellesley Islands in the southeastern Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.0 pp. 71–5. (NPS2: Cleveland, Australia.)

Shepard, F. P. (1954). Nomenclature based on sand–silt–clay ratios. *J. Sediment. Geol.* 24, 151–8.

Somers, I. F., and Kirkwood, G. P. (1984). Movements of tagged tiger prawns, *Penaeus* spp., in the western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* 35, 713–23.

Somers, I. F., and Taylor, B. R. (1981). Fishery statistics relating to the declared management zone of the Australian northern prawn fishery, 1968–1979. Australian CSIRO Marine Laboratories Report No. 138.

Somers, I. F., Crocos, P. J., and Hill, B. J. (1987*a*). Distribution and abundance of the tiger prawns *Penaeus esculentus* and *P. semisulcatus* in the north-western Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* 38, 63–78.

Somers, I. F., Poiner, I., and Harris, A. (1987*b*). A study of the species composition and distribution of commercial penaeid prawns of Torres Strait. *Aust. J. Mar. Freshw. Res.* 38, 47–61.

Staples, D. J., Vance, D. J., and Heales, D. S. (1985). Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 47–54. (NPS2: Cleveland, Australia.)

Tenakanai, C. D. (1980). Some aspects of the biology and fishery for endeavour prawns (*Metapenaeus spp.*) in the Gulf of Papua. Research Bulletin No. 28, Department of Primary Industry, Port Moresby.

Telek, G., and Marshall, N. (1974). Using a CHN analyser to reduce carbonate interference in particulate organic carbon analyses. *Mar. Biol.* 24, 219–21.

Wassenberg, T. J., and Hill, B. J. (1987). Natural diet of the tiger prawns *Penaeus esculentus* and *P. semisulcatus*. *Aust. J. Mar. Freshw. Res.* 38, 169–82.

Williams, A. B. (1958). Substrates as a factor in shrimp distribution. *Limnol. Oceanogr.* 3, 283–90.

Manuscript received 19 June 1986, accepted 6 February 1987

Appendix 4.8

Aust. J. Mar. Freshw. Res., 1987, 38, 63–78

Distribution and Abundance of the Tiger Prawns *Penaeus esculentus* and *P. semisulcatus* in the North-western Gulf of Carpentaria, Australia

I. F. Somers, P. J. Crocos and B. J. Hill

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 120, Cleveland, Qld 4163.

Abstract

Trawl surveys in the north-western Gulf of Carpentaria were carried out each lunar month from August 1983 to March 1985 to assess the temporal and spatial distribution and abundance of *P. esculentus* and *P. semisulcatus*. The information obtained was then compared with that from fishermen's logbooks. Water temperature and salinity were monitored during the study and their possible influence on the distributions has been inferred.

The distributions of juveniles of less than 20 mm carapace length indicated that, for both tiger prawn species, the main nursery areas in the region were in Blue Mud Bay and in the bays along the northern coast of Groote Eylandt. Although the two species shared the same nursery areas, the juveniles were concentrated in different parts of Blue Mud Bay and were most abundant at different times. Catches of juvenile *P. esculentus* increased substantially in October and peaked in November, whereas catches of juvenile *P. semisulcatus* increased in November and peaked in January. Catches of both species showed a secondary peak in March 1984, coincident with the heaviest monthly rainfall of the summer monsoon season. The distribution of larger prawns showed spatial separation of the two species in the offshore fishery.

The monthly pattern of the catch-per-unit-effort (CPUE) of the two tiger prawn species combined was similar to that obtained from fishermen's logbooks; the logbook data are therefore generally reliable. Monthly CPUE from the trawl surveys for the individual species showed distinct peaks in late summer, which were apparently related to recruitment of small prawns into the fishery. CPUE for *P. semisulcatus* peaked in February and April (juvenile abundance had peaked in January and March); CPUE for *P. esculentus* peaked in January and May (juvenile abundance had peaked in November and March). However, a distinct CPUE peak in spring (August/September) for *P. semisulcatus* could not be related to a previous peak in juvenile abundance; this was presumably a result of an increase in catchability. Although there was evidence linking changes in the catchability of *P. semisulcatus* to changes in water temperature, a similar link was not as evident for *P. esculentus*.

Introduction

Commercial prawn fishing in the Gulf of Carpentaria, which began in the late 1960s following an exploratory trawl survey in the south-eastern Gulf (Munro 1975), initially concentrated on the banana prawn *Penaeus merguiensis* de Man. By 1970, fishing grounds around Groote Eylandt in the western Gulf were also being fished. The catch in this region consisted mainly of tiger prawns, *P. esculentus* Haswell and *P. semisulcatus* de Haan, and endeavour prawns, *Metapenaeus endeavouri* Schmitt and *M. ensis* de Haan. Fishing activity now extends around most of the Gulf coast, with an annual catch approaching 10 000 t. Tiger prawns have now become the most important single component and account for between 3000 and 4000 t, more than half of which is caught in the western Gulf.

Although exploratory trawl surveys are generally reliable in assessing the resources and potential development of major fisheries (Alverson and Pereyra 1969), long-term biological

0067-1940/87/010063$02.00

data are usually obtained through monitoring commercial catches. The reason for this is, as Williams (1977, p. 28) points out, 'the operation of a large number of commercial vessels, fishing continuously over a wide area, provides an invaluable sampling tool and has advantages in both cost and coverage over the limited number of observations that can be made by a single research vessel'. The Gulf prawn resource has been monitored since 1970 through a fishermen's logbook program (Somers and Taylor 1981). However, because the two tiger prawn species look alike, they are not separately identified in logbook records. Consequently, these logbooks do not indicate the separate distributions of the two species. Buckworth (1985) obtained more detailed information on the tiger prawns in the western Gulf by analysing samples from the commercial catches. He concluded that *P. esculentus* made up about 93% of the tiger prawn catch in the area south of Groote Eylandt, whereas north of Groote Eylandt, *P. semisulcatus* represented about 65% of the tiger prawn catch. Tagging experiments by Somers and Kirkwood (1984) showed that there was little interchange of tiger prawns between these two areas.

Data collected from a commerical fishery may present problems of interpretation (Garcia and LeReste 1981). For example, catch-per-unit-effort (CPUE) is generally assumed to be proportional to abundance, despite the potential bias when the distribution of the fleet is not random and changes over time. Furthermore, closed seasons and closed areas may prevent the fleet from providing samples that adequately represent the recruitment of juveniles from nursery grounds. In the case of tiger prawns in the western Gulf, because fishermen concentrated in the highest yielding areas, which limited the temporal and spatial coverage of catch samples, Buckworth (1985) was unable to give a complete description of their distribution. In addition, catch samples were unavailable from many inshore areas that were closed to fishing in order to restrict the capture of small prawns.

The present study was designed to provide a comprehensive description of the distribution and abundance of *P. esculentus* and *P. semisulcatus* in the region north of Groote Eylandt in the western Gulf. The data were collected on trawl surveys carried out each lunar month from August 1983 to March 1985. Because each trawl survey took at least 11 nights to complete, changes in catchability both within a night and between nights within a cruise were also studied. Water temperature and salinity were monitored and their influence on the distributions examined.

This study has also provided the opportunity to evaluate the information obtained from the logbooks of the commercial fishery by comparing it with our data from the trawl surveys. Comparisons were also made between our results and those of Buckworth (1985) which were based on fishermen's logbooks and commercial catch sampling in this region.

Methods

Study Area

The study area encompassed the commercial prawn fishery between Groote Eylandt and Cape Arnhem in the north-western Gulf. For ease of comparison with the data from the commercial fishery, trawl stations were established at intervals of approximately 6 nautical miles (11 km) throughout (Fig. 1). However, to monitor recruitment to the fishery, stations were also established in shallow inshore areas: Northwest Bay and Blue Mud Bay. To describe the outer limit of the population, stations were also established along two east-west transects at 13°03'S. and 13°33'S.; these extended to about 50 km beyond the eastern boundary of the fishery. The stations covered a depth range of 5-55 m, whereas the commercial fishery is largely confined to depths between 20 and 40 m.

Sampling

In all, 21 cruises were made. These were carried out each lunar month between August 1983 and March 1985. Each cruise, of approximately 11 nights' duration, began 5 nights before the new moon. In June 1984, additional stations were established between Cape Grey and Cape Arnhem (Fig. 1) to follow a northward movement of *P. semisulcatus*. However, to avoid any temporal bias in the abundance index of *P. esculentus*, the data obtained from these additional stations were not included in the analysis of seasonal patterns of abundance for either species.

One chartered commercial trawler was used for 19 of the 21 cruises; however, owing to mechanical problems, other vessels were used on the second and fourth cruises. Except for these two cruises, the sampling gear consisted of two 11·0-m (headrope length) nets although, on the first and third cruises, a single 7·3-m net was used on several trawl stations because of technical problems with the larger gear. The sampling gear used on the first of the substitute vessels consisted of four 6·4-m nets, while the second had four 7·3-m nets. Trawls were typically of 20 min duration, and CPUE has been standardized to the number of prawns per 440 m-net-min (i.e. the equivalent of two 11·0-m nets trawled for 20 min, here called a standard trawl). The net design (Florida Flyer) and stretch mesh size (50 mm with 44 mm codend) were the same for all boats. Although this trawl mesh combination is fairly standard in the Gulf fishery, the sizes refer to manufacturers' specifications measured from centre of knot to centre of knot, and internal measurements may vary with the thickness of the net material. Internal mesh size averaged 46 mm and the codends 38 mm.

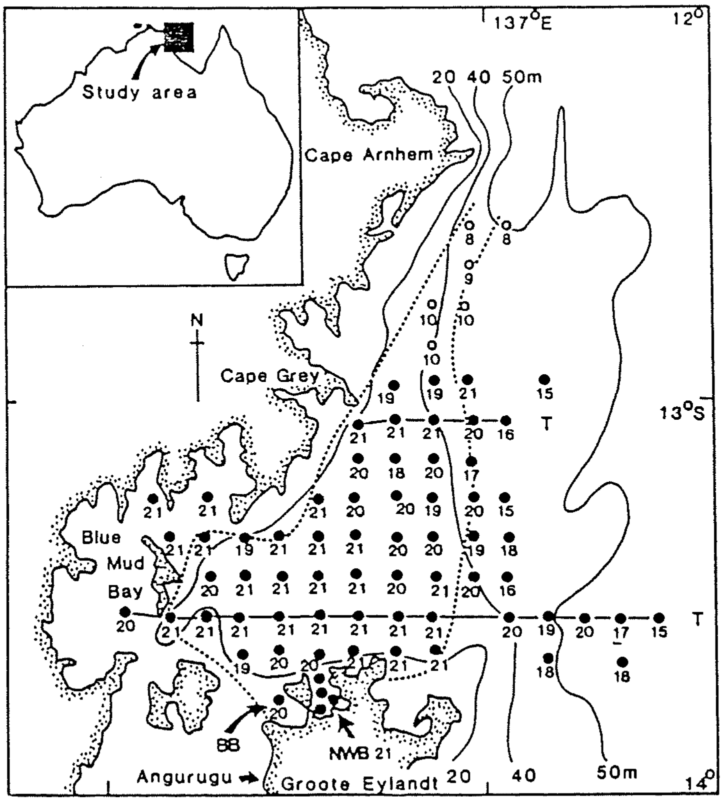


Fig. 1. Study area in the north-western Gulf of Carpentaria, showing bathymetry and place names mentioned in the text. Solid circles indicate stations sampled between August 1983 and March 1985; open circles indicate additional stations sampled between June 1984 and March 1985. Number of cruises on which the station was sampled is indicated. BB = Bartalumba Bay, NWB = Northwest Bay. T marks the station transects at which surface and bottom temperatures and salinities were measured. The dotted line indicates the general extent of the fishing grounds in 1984 based on logbook effort greater than 20 days' fishing per 6-nautical-mile grid square.

All survey trawls were carried out during the hours of darkness, from 1 h after sunset to 1 h before sunrise. The time and duration of each trawl were recorded along with the depth, latitude and longitude of the midpoint of the trawl station. Radar and a satellite navigator were used to fix position. Surface temperature and salinity were measured at each of the trawl stations using a Hamon portable salinity-temperature bridge. Readings were also made on the bottom at stations along each of the two east-west transects (Fig. 1).

The catch from all nets was combined for recording: the prawns were ascribed to species and each individual was sexed and its carapace length (CL) measured to the nearest millimetre; the moult stage for each prawn was subjectively classified as 'soft' or 'hard' depending on the flexibility of the cuticle; the occurrence of bopyrid parasites was also noted.

The distributions of juvenile, subadult and adult prawns were described on the basis of CPUE of three discrete size groups. The classification by size was designed to elucidate the movement patterns with increasing age and, by inference, the main nursery grounds for each species. Prawns of 20-mm CL and smaller were classified as juvenile; the size ranges for the other two classifications varied according to the species (Table 2). No information was available for size at maturity of male tiger prawns, and so the division was based solely upon the size at maturity of females. For convenience, the division between subadult and adult prawns was chosen to correspond to the size at which 20% of females are sexually mature. This occurs at 29-mm CL in *P. esculentus* and at 35-mm CL in *P. semisulcatus* (Buckworth 1985).

Special Studies

On each cruise, change in catchability over one night was tested by 14 consecutive trawls at 1-h intervals at a selected station. The first trawl of each series began at least 1 h before sunset, whilst the last began at least 1 h after sunrise. In order to represent the entire study area, a different station on each cruise was chosen for this sampling.

To test for any significant night-to-night variation in CPUE over the duration of a cruise, four stations in Northwest Bay (Fig. 1) were sampled twice on every cruise; once at the beginning of the cruise and again not less than 5 nights later (i.e. before and at or after the new moon). A Student's *t*-test was carried out using a pairwise comparison of the first and second series of samples from each cruise. The area of Northwest Bay is about 6 nautical miles square and the data from the four stations were averaged before their inclusion in the analysis of species distributions.

To check whether small prawns were escaping from the nets used during the study, a 25-mm stretch mesh (20 mm internal measurement) codend cover was added to the starboard trawl net for the duration of the cruise in December 1984. The size composition and abundance of the prawns in the starboard codend were compared with those in the codend cover. To check whether the codend cover had altered the catching efficiency of the starboard net, its catch was compared with that of the uncovered codend of the port side by using a Student's *t*-test with a pairwise comparison of the total catch in each size category.

Logbook Data

The logbook system in Australia's northern prawn fisheries provides information on daily fishing activity: the catch in weight for each of the species groups and the time spent trawling are recorded together with the fishing location on a 6-nautical-mile grid system (Somers and Taylor 1981). Over 80% of the estimated total landings in 1984 were accounted for in logbook returns (unpublished data, Australian Fisheries Service). The geographic extent of the commercial fishery in the north-western Gulf was estimated from these logbook returns.

To compare logbook and trawl survey data, mean monthly CPUE was calculated from both data sets for the area between Groote Eylandt and Cape Grey. The seasonal pattern of CPUE from each was compared after converting the trawl survey CPUE to the weight equivalent, using the length-weight relationships described by Hall (1962) for *P. semisulcatus* and by Penn and Hall (1974) for *P. esculentus*. Because the commercial fishery concentrates on the larger prawns, juveniles ($\leqslant 20$ mm CL) were omitted from this analysis.

Results

Hydrography

The climate of the region is characterized by distinct wet and dry seasons. Heaviest rainfall fell in the summer monsoon period between December and March (Fig. 2). As a result, mean surface salinity fluctuated seasonally, reaching 35 to 36 at the end of the dry season and dropping to around 33 at the end of the wet season (Fig. 2). The mean salinity remained low for about 2 months after the end of the summer monsoon. Inshore salinities showed much greater seasonal variation than did offshore salinities, reaching a peak of around 38 in December and a low of around 30 in March. Salinities at stations east of the 40-m depth contour remained between 34 and 36 throughout the study period. Generally there were no surface-to-bottom differences in salinity, even during the wet season.

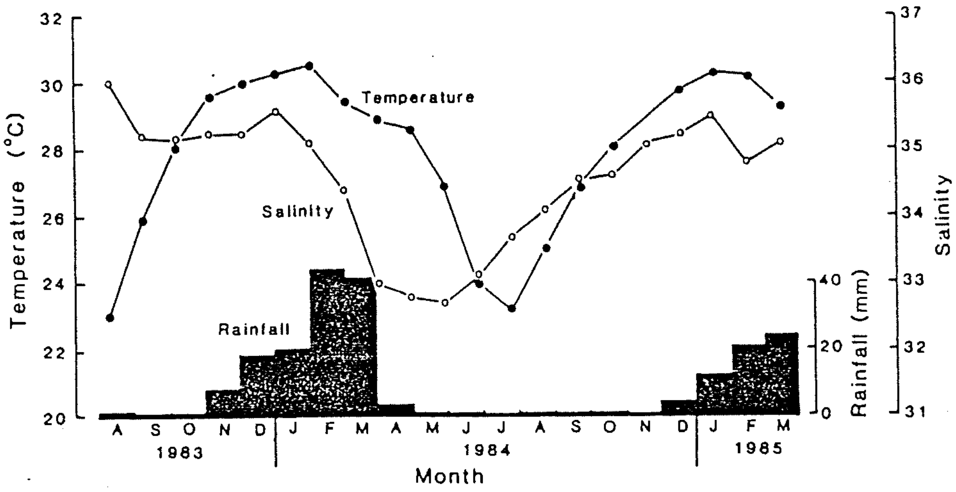


Fig. 2. Mean surface salinities and temperatures in the study area between August 1983 and March 1985. The number of stations per cruise range from 37 to 72. Monthly rainfall (mm) recorded at Angurugu on Groote Eylandt.

Mean surface water temperature also varied seasonally, reaching between 30 and 31°C in January and February but dropping sharply in May to a minimum of around 23°C in July (Fig. 2). Inshore waters were generally well mixed, but surface-to-bottom temperature differences were evident in offshore waters in spring and summer (Fig. 3): 2°C in August and September 1983, but almost 6°C by October/November (surface water at 29–30°C and bottom water around 24°C). The temperature along the two transects showed good agreement with respect to the depth of the station and indicated that a well-developed thermocline was present at between 20 and 40 m in summer. In February 1984, the thermocline broke down and by the beginning of March water offshore was well mixed vertically. In winter, despite vertical mixing, there was some horizontal variation, with a temperature gradient from below 23°C inshore to around 25°C offshore. Coincident with the spring warming, the temperature gradient was reversed: temperatures in October were around 29°C inshore and 27° offshore. By this time stratification was reappearing and it persisted until the end of the study period in March 1985.

Within-night and Within-cruise Variation in CPUE

Based on the repeated samples within a night from all of the selected stations pooled, mean CPUE of both *P. esculentus* and *P. semisulcatus* clearly showed rapid increases after sunset and decreases at sunrise (Fig. 4). However, no significant changes in CPUE during the night could be shown for either species. As a result, when comparing results from different stations, no account has been taken of the time of night at which they were collected.

A pairwise comparison between the CPUE at each of the four stations in Northwest Bay in the first and second series of trawls of each cruise showed no significant difference for either *P. semisulcatus* ($t = -0{\cdot}24$, $P = 0{\cdot}81$, 78 d.f.) or *P. esculentus* ($t = 0{\cdot}48$, $P = 0{\cdot}63$, 78 d.f.). This indicated that CPUE within Northwest Bay did not change significantly during a cruise and so, by extension, comparison of CPUE of all stations sampled over a cruise was legitimate.

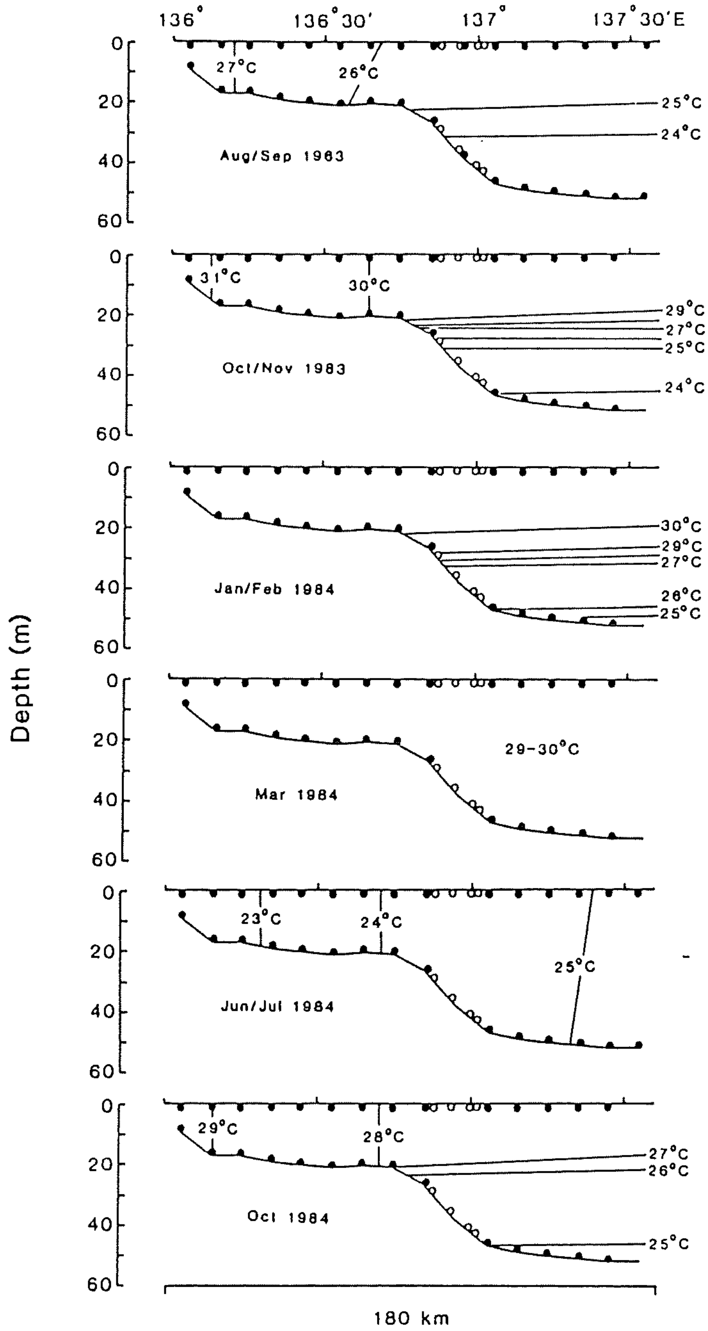


Fig. 3. Temperature profiles in the study area between August 1983 and March 1985. The cross-section represents the southernmost transect (13°33'S.) of hydrography stations in Fig. 1. Supplementary temperature data from the northern transect (13°03'S.) are indicated by hollow circles at the appropriate depth.

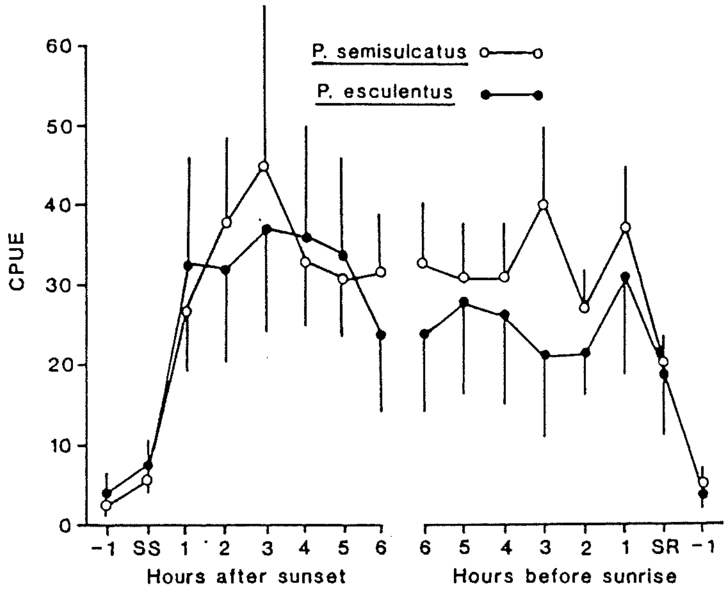


Fig. 4. Mean catch per unit effort (CPUE) and one standard error for *Penaeus semisulcatus* and *P. esculentus* over 14 successive trawls taken at hourly intervals on 18 separate cruises. Data have been standardized with respect to time of sunset (SS) and sunrise (SR).

Mesh Selectivity

All tiger prawns >30 mm CL were retained by the 44-mm codend mesh of the sampling gear (Table 1). Retention of smaller prawns was progressively lower, with approximately 80% retention at 20 mm CL for both species. Below this size, retention appears to drop more rapidly, although the low numbers caught prevent a more accurate assessment.

Table 1. Retention of tiger prawns *P. semisulcatus* and *P. esculentus* in the codend of 44-mm mesh net

Carapace length (mm)	*P. semisulcatus* No. in codend	No. in cover	No. retained in codend (%)	*P. esculentus* No. in codend	No. in cover	No. retained in codend (%)
11–12	1	1	50	0	0	–
13–14	2	2	50	0	0	–
15–16	11	4	73	6	2	75
17–18	23	10	70	19	15	56
19–20	70	14	83	59	15	80
21–22	112	5	96	92	8	92
23–24	183	6	97	146	4	97
25–26	188	5	97	188	4	98
27–28	124	1	99	186	3	98
29–30	45	1	98	111	0	100
>30	148	0	100	201	0	100

A pairwise comparison of the total catch of each size class in the port and starboard nets showed no significant differences for either *P. esculentus* ($t = 0\cdot83$, $P = 0\cdot41$, 23 d.f.) or *P. semisulcatus* ($t = 1\cdot59$, $P = 0\cdot13$, 23 d.f.), indicating that the codend cover on the starboard net did not affect its fishing efficiency.

Distribution of P. semisulcatus

Juvenile *P. semisulcatus* were found mainly at depths ≤20 m (Table 2). They were most abundant in Blue Mud Bay and in Northwest Bay, which indicates that these are important

Table 2. Depth distribution for the juveniles, subadults and adults of *P. semisulcatus* and *P. esculentus*

Species category	Distribution (%) of size categories for depths (m) of: 0–10	11–20	21–30	31–40	41–50	51–60	Total No. caught
P. semisulcatus							
Juvenile (≤20 mm CL)	64	31	3	2	0	0	1653
Subadult (21–34 mm CL)	25	12	33	23	7	0	25431
Adult (≥35 mm CL)	1	2	33	35	27	2	13941
P. esculentus							
Juvenile (≤20 mm CL)	68	26	6	0	0	0	2541
Subadult (21–28 mm CL)	40	26	32	2	0	0	13268
Adult (≥29 mm CL)	21	14	56	7	2	0	17792

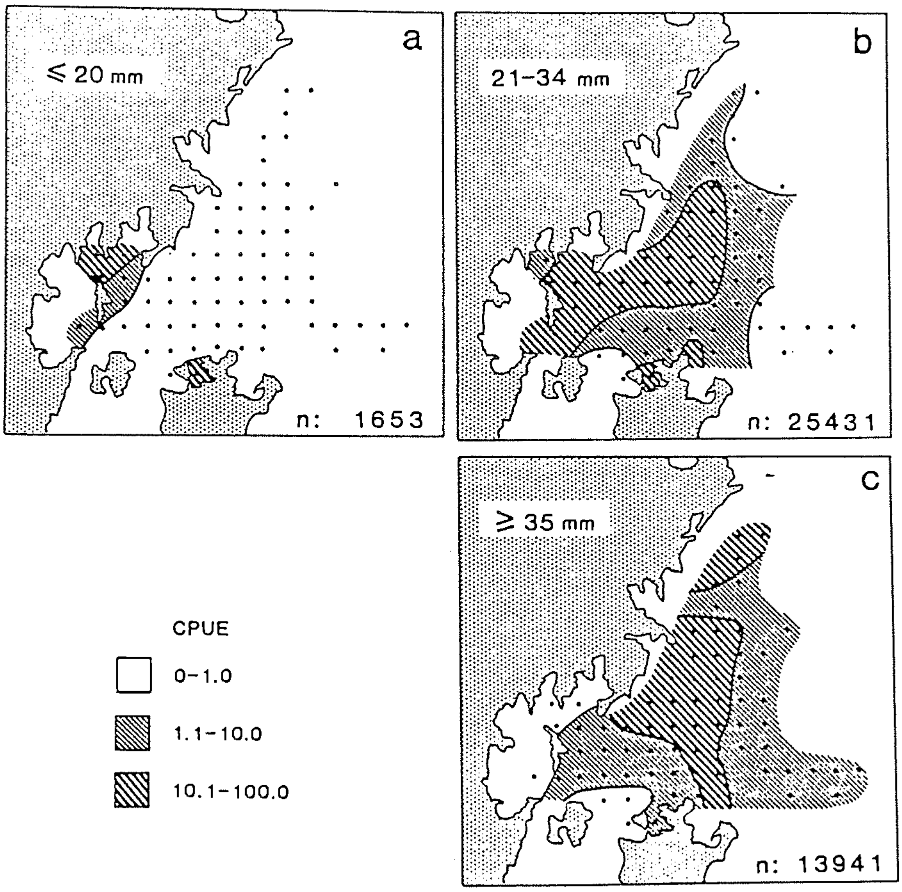


Fig. 5. Distribution of *Penaeus semisulcatus* in the study area from August 1983 to March 1985. Positions of sampling stations are indicated. CPUE for each station is expressed as number of prawns caught per standard trawl and represents the mean of all cruises. (*a*) Juveniles; (*b*) subadults; (*c*) adults.

nursery grounds (Fig. 5*a*). The distribution of subadult *P. semisulcatus* extended offshore and northward from these nursery areas with the major concentrations reaching Cape Grey (Fig. 5*b*). Although 37% of the subadult catch was also taken in waters ≤20 m, most prawns were caught between 21 and 40 m (Table 2). Adults were caught even further offshore and further northwards, with the main concentrations in the area between the north-eastern tip of Groote Eylandt and Cape Grey and in an area between Cape Grey and Cape Arnhem (Fig. 5*c*). Only 3% of the adult catch was from waters ≤20 m in depth, the bulk of the catch coming from depths between 20 and 50 m (Table 2).

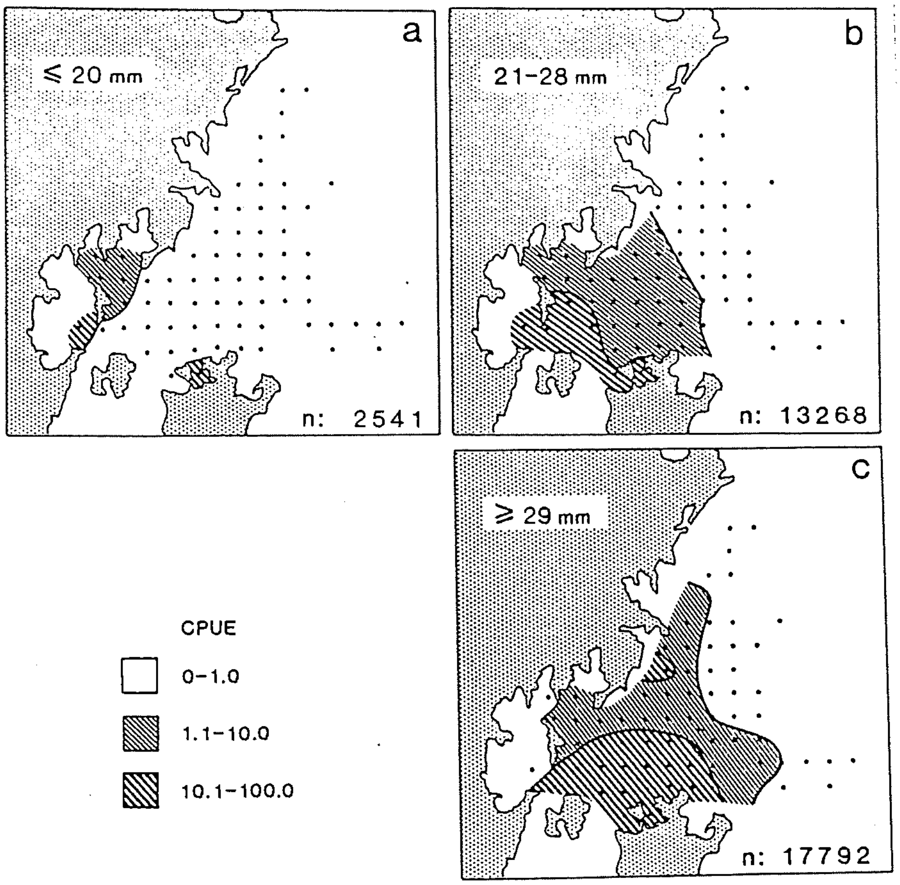


Fig. 6. Distribution of *Penaeus esculentus* in the study area from August 1983 to March 1985. CPUE for each station is expressed as number of prawns caught per standard trawl and represents the mean of all cruises. (*a*) Juveniles; (*b*) subadults; (*c*) adults.

Distribution of P. esculentus

The distribution of juvenile *P. esculentus* was similar to that of juvenile *P. semisulcatus*, in that they were restricted to Northwest Bay and Blue Mud Bay (Fig. 6*a*) and depths ≤20 m (Table 2). However, a noticeable difference in the two distributions was that, in Blue Mud Bay, *P. esculentus* was more heavily concentrated in the southern part (Fig. 6*a*), while *P. semisulcatus* was more abundant in the northern part (Fig. 5*a*). The distributions of subadult (Fig. 6*b*) and adult (Fig. 6*c*) *P. esculentus* indicated limited offshore movement with the highest concentrations of adults in the southern part of the study area adjacent to the northern coastline of Groote Eylandt and a small area south of Cape Grey. Most of the adult catch was taken in depths between 21 and 30 m, with less than 10% of the adult catch from deeper waters (Table 2). Adults were also present on the shallower trawl stations, with 35% of the adult catch coming from depths ≤20 m.

Recruitment Patterns

From the seasonal abundance of juveniles (≤20 mm CL), it was apparent that both tiger prawn species recruit to the fishery in the warmer months of the year (October–April); very few juveniles of either species were caught during the colder months (May–September) (Fig. 7). However, as well as some spatial separation in the main concentrations of the juveniles of the two species (Figs 5*a*, 6*a*), there was some temporal separation in peaks of abundance. Catches of juvenile *P. esculentus* in 1983–84 and 1984–85 increased substantially in October and peaked in November or December; catches of juvenile *P. semisulcatus* increased in November and peaked in January. A secondary peak in juvenile catches was evident for both species in March–April of 1984.

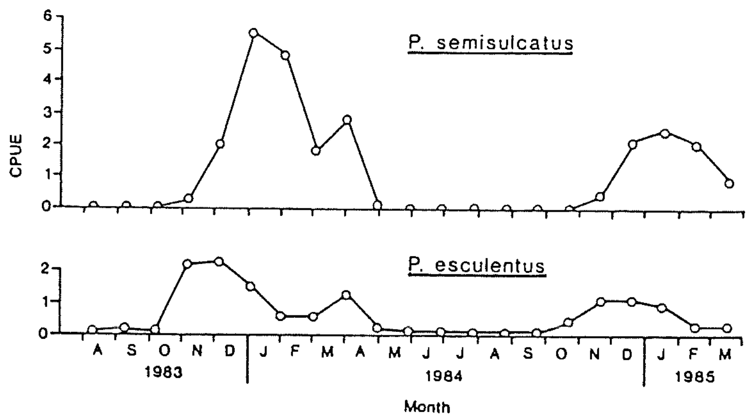


Fig. 7. Mean CPUE for juvenile (≤20 mm carapace length) *Penaeus semisulcatus* and *P. esculentus* at the trawl stations south of Cape Grey (closed circles on Fig. 1) on each of the monthly cruises between August 1983 and March 1985. CPUE is expressed as number of prawns per standard trawl.

Comparison of Logbook and Survey CPUE

The mean monthly logbook CPUE (kg per boat-day) for the area between Cape Grey and Groote Eylandt showed peaks in September 1983, January, April and August 1984 and in February 1985 (Fig. 8*a*). Each of these peaks was associated with an increase in commercial fishing effort (Fig. 8*a*).

The trawl survey CPUE of the combined catch of adult and subadult *P. semisulcatus* and *P. esculentus*, when converted to kilogram per standard trawl, showed a similar pattern to that obtained from the logbooks (Fig. 8*a*). Although absolute values of survey and logbook CPUE could not be directly compared because of different effort units, the number and timing of the peaks in the monthly survey CPUE corresponded closely to those from logbook data. The logbook data do, therefore, provide a meaningful representation of monthly CPUE for tiger prawns. However, because logbook records include both tiger prawn species and refer to catch in weight, the logbook data on their own do not describe the seasonal changes in relative population abundance of the individual species.

To describe the seasonal abundance of the individual species, the trawl survey CPUE has been expressed in numbers of prawns rather than weight and the two species have been presented separately (Fig. 8*b*). The monthly CPUE of *P. semisulcatus* showed peaks in

September 1983, February, April and August–September 1984 and February 1985. The CPUE peaks in late summer (February and April 1984 and February 1985) came about 1 month after respective peaks in juvenile abundance in shallow coastal waters (Fig. 7). However, the CPUE peaks in the early spring (September 1983, August–September 1984) followed periods of extremely low juvenile abundance. This indicates the possibility of increased catchability of subadult and adult *P. semisulcatus* in the spring months.

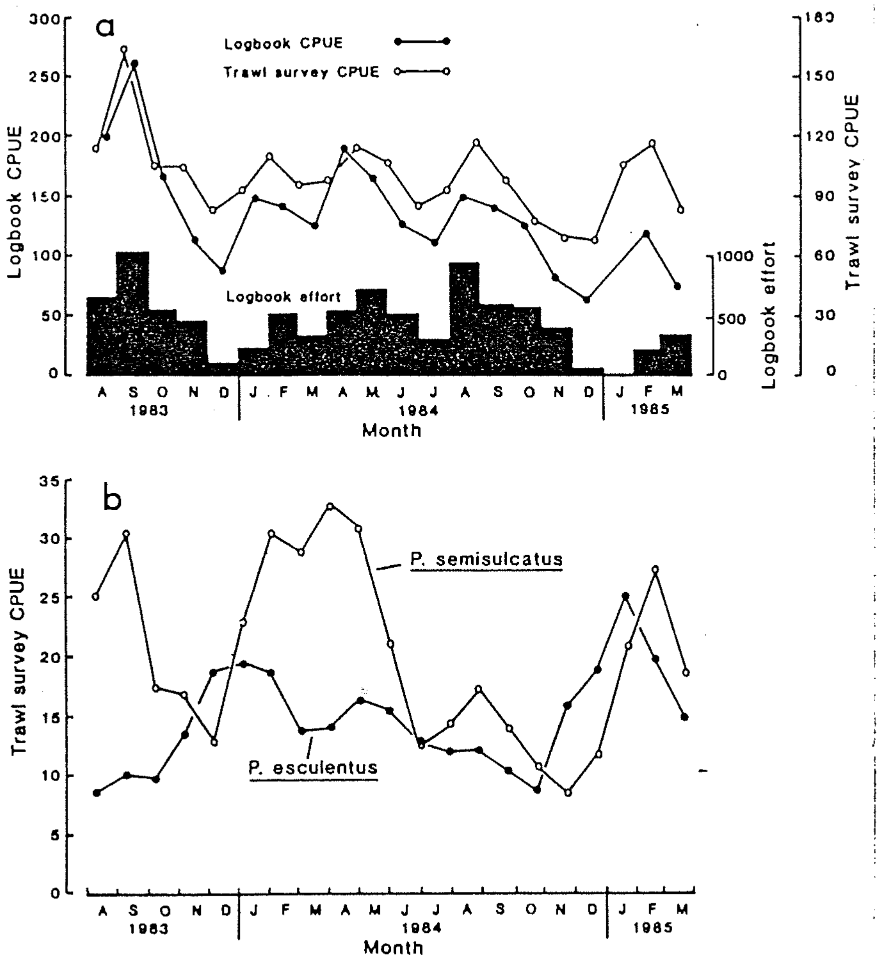


Fig. 8. CPUE for the area south of Cape Grey (closed circles on Fig. 1) from August 1983 to March 1985: (*a*) Logbook effort (boat-days) and CPUE (kilograms per boat-day) for tiger prawns in the commercial fishery and CPUE (kilograms per standard trawl) for tiger prawns [>20 mm carapace length (CL)] from the trawl surveys. The tiger prawns *Penaeus semisulcatus* and *P. esculentus* are combined. (*b*) CPUE (number per standard trawl) for each of *P. semisulcatus* and *P. esculentus* (>20 mm CL).

Monthly CPUE for *P. esculentus* (Fig. 8*b*) showed a similar pattern to that of *P. semisulcatus* except that the peaks differed slightly in timing, were not as pronounced and were not evident in spring. The two peaks in January and May in 1984 followed peaks in juvenile abundance in November 1983 and March 1984, respectively, while the peak in January 1985 followed a peak in juvenile abundance in November–December 1984 (Fig. 7).

Discussion

In a review of exploited prawn populations, Garcia (1985) suggested that most *Penaeus* stocks have a seasonal offshore recruitment pattern, with a main generation recruited during summer and autumn and a secondary generation recruited in spring. Seasonal recruitment patterns for *P. semisulcatus*, which is distributed throughout the Indo-West-Pacific region, and *P. esculentus*, which is endemic to northern Australia, have been described by various authors in various fisheries. The patterns vary considerably both within and between species. In the Arabian Gulf, recruitment of *P. semisulcatus* occurs in spring although secondary recruitment may occur in some years in late autumn (FAO 1982). Based on the abundances of juveniles on intertidal seagrass beds, Staples (1984) suggested that summer and winter recruitment peaks are of equal importance for both *P. semisulcatus* and *P. esculentus* in the north-eastern Gulf of Carpentaria. Robertson *et al.* (1985) found only an early summer recruitment peak for *P. esculentus* in the south-eastern Gulf of Carpentaria. In Exmouth Gulf (Western Australia), *P. esculentus* was found to have only an autumn recruitment peak (White 1975; Penn and Caputi 1985).

The seasonal recruitment patterns of *P. semisulcatus* and *P. esculentus* in the western Gulf have been described by Buckworth (1985) on the basis of the percentage of individuals $\leqslant$25 mm CL in samples taken from commercial catches between 1979 and 1982. He found seasonal recruitment patterns for both species, with only one peak per year. Recruitment of *P. esculentus* was mainly from November to February with the peak in December (early summer) while *P. semisulcatus* recruited 1–2 months later, from January to April, with a peak in February (late summer). In the present trawl survey study, recruitment has been described on the basis of relative abundance of prawns $\leqslant$20 mm CL in order to define more precisely the timing of recruitment and to describe the location of the main nursery areas. Nevertheless, the seasonal patterns are similar to those described by Buckworth (1985): the main recruitment of *P. esculentus* was in early summer (November–December) and of *P. semisulcatus* about 1 month later (December–January) (Fig. 7). However, the patterns described by Buckworth (1985) were unimodal, whereas a secondary peak in recruitment in March–April was evident in the trawl survey data for each species (Fig. 7). This occurred at a time of low inshore salinities following the heaviest rainfall of the wet season (Fig. 2). No evidence of a secondary spring recruitment was found for either species in either the present study or that of Buckworth (1985). Thus, despite some limitations, commercial catch sampling appears adequate for describing the general seasonal recruitment patterns for each species.

It is not possible to identify the various nursery grounds in the Gulf of Carpentaria, nor assess their relative importance, by sampling commercial catches because of the regulations introduced to prevent the capture of small tiger prawns (closed seasons and closed areas). However, the spatial distributions of juveniles of both tiger prawn species described from the trawl surveys (Figs 5*a* and 6*a*) show that Blue Mud Bay and Northwest Bay are important nursery areas in the region. Furthermore, tagging studies have demonstrated recruitment from these nursery areas into the adjacent offshore fishery (Somers and Kirkwood 1984; Somers 1987). The distributions of *P. semisulcatus* and *P. esculentus* of different sizes (Figs 5*a*–5*c* and 6*a*–6*c*; Table 2) show an offshore progression in abundance in relation to size, also indicating movement from these nursery areas into the offshore fishery. Although no shallow coastal stations were sampled along the mainland coast north of Blue Mud Bay, the lack of juvenile and subadult concentrations in nearshore stations suggest that this region of coastline has few, if any, important nursery areas. Coles and Lee Long (1985) and Staples *et al.* (1985) showed that postlarval tiger prawns of both species occur in coastal seagrass beds, and Poiner *et al.* (1987) reported very few seagrass beds along the northern coastline of our study area. Furthermore, Somers (1987) has shown that, on the basis of the northerly movement of tagged *P. semisulcatus*, the adults caught north of Cape Grey could have come from nursery areas in Blue Mud Bay and Northwest Bay.

The logbook data do not provide separate information on the two tiger species and, although Buckworth (1985) was able to describe the regional species composition from commercial catch samples, he was unable to provide more precise descriptions of the species distributions, presumably because of insufficient catch samples. The results of the present study show a noticeable spatial separation in the main concentrations of the adults of the two species in the offshore fishery (Figs 5*c* and 6*c*). Somers (1987) found that the two species had different substrate preferences: adult *P. semisulcatus* were found only on sediments with a high mud content while *P. esculentus* were found over a wider range of sediment types, but were most abundant on sediments with a lower mud content than that preferred by *P. semisulcatus*. Although there are suitable sediments in deeper water, *P. semisulcatus* were generally found in depths less than 50 m (Table 2). According to Holthuis (1980), *P. semisulcatus* has been recorded in depths of up to 130 m, which indicates that factors other than sediment type and depth may be limiting its offshore distribution in the study area. Garcia (1974), in a study of *P. notialis* on the Ivory Coast, showed that the depth distribution varied with the seasonal oscillation of a thermocline. The main concentration of the commercial catches of *P. notialis* were in depths where the thermocline contacted the bottom. In the present study, a thermocline was shown to exist in spring and summer months (October to February) at depths of between 20 and 40 m (Fig. 3). Although *P. semisulcatus* was caught in depths greater than 40 m (Table 2), catches in these depths were negligible during the existence of the thermocline, which suggests that the thermocline may be influencing the distribution of that species.

Buckworth (1985), using logbook records for 1979 to 1982, summarized the combined CPUE of both tiger prawn species in the western Gulf. He suggested that CPUE generally peaked twice each year: in late summer (February to May) and in spring (August to November). However, interpretation of the CPUE obtained from logbooks is difficult because it represents the catch rate in weight (kilograms per boat-day) of both species combined and because fishermen tend to concentrate in locations with highest prawn abundance. Over the duration of the study, the pattern of logbook CPUE north of Groote Eylandt was similar to the general pattern described by Buckworth (1985), with late summer and spring peaks. However, the late summer peak was bimodal, with separate peaks in January and April (Fig. 8*a*). The similarity of logbook CPUE (kilograms per boat-day) with the pattern of CPUE (kilograms per standard trawl) obtained from the trawl surveys (Fig. 8*a*) indicates the general reliability of the information obtained from the fishing industry. Garcia and LeReste (1981) point out that CPUE from logbook data may be a biased index of abundance at different levels of effort because fishermen tend to concentrate on higher abundances and disperse when abundance is low. This may be the situation in the study area as fishing effort varied substantially in relation to changes in CPUE (Fig. 8*a*), with the result that the logbook CPUE generally showed more pronounced differences in the relative magnitude of the peaks and troughs than CPUE from the trawl surveys.

The trawl surveys made it possible to ascertain the CPUE for each species in terms of the number of individuals per unit of effort. The CPUE of *P. semisulcatus* from the trawl surveys showed peaks in the early spring (August–September) and late summer (February–April) of each year (Fig. 8*b*), the latter reflecting earlier peaks of juvenile recruitment (Fig. 7). This pattern is similar to the general tiger prawn pattern suggested by Buckworth (1985), with the late summer peak in CPUE a result of offshore recruitment and the spring peak presumably resulting from an increase in catchability. CPUE of *P. esculentus* (Fig. 8*b*) also shows a close correspondence to the summer recruitment pattern of the juveniles (Fig. 7) but, unlike *P. semisulcatus*, no distinct additional spring peaks in CPUE were evident (Fig. 8*b*). Nevertheless, *P. esculentus* may also exhibit a similar changing catchability, for CPUE in early spring (August–September) did not decline (but actually increased slightly) at a time of increased commercial fishing effort (Fig. 8*a*) and an apparent absence of juvenile recruitment (Fig. 7).

A somewhat similar pattern in CPUE has been reported for *P. esculentus* in Exmouth Gulf (White 1975): CPUE declined to a minimum in winter (July) and then remained constant, or increased slightly, through spring and early summer (August–November). As the decline in winter might be partly due to the decrease in water temperature, White (1975) incorporated ambient temperature into the traditional mathematical model of exponential population decline in an attempt to explain these seasonal changes in CPUE. This approach did not account for all the changes in catchability, although Hill (1985) has since shown that the duration of nocturnal activity, and hence catchability, of *P. esculentus* is reduced when temperatures drop below 27°C. Unpublished observations by Hill on *P. semisulcatus* have shown a similar relationship. Mean water temperatures in the present study were below 27°C from May to September. The decline in CPUE of tiger prawns, which occurred from May to July (Fig. 8*b*), could have partly been temperature-related (Fig. 2). Possibly, too, the increase in CPUE of *P. semisulcatus* in August–September (Fig. 8*b*) was related to the increase in water temperature; however, in 1984, the CPUE began to rise 1 month before the temperature rose (Fig. 2). Fuss and Ogren (1966), when studying the activity patterns of *P. duorarum*, found a similar relationship with temperature, but concluded that rate of change in temperature was more important than actual temperature. In their study, the initial low temperature in winter significantly reduced activity, but the same temperature in late winter seemed to have little effect, possibly because of acclimation.

The ability to describe the CPUE for the individual tiger prawn species has made possible a more detailed analysis of population fecundity. Buckworth (1985) calculated the percentage of females in the population with visible ovaries from commercial catch sampling during the period 1979–82. Based on the females caught during the present study, Crocos (1987*a*, 1987*b*) has been able to describe reproductive patterns using a population egg production index for each species, thereby avoiding potential bias caused by seasonal recruitment of immature prawns.

The comparison between the trawl survey and commercial fishery data has shown that, despite some potential bias arising from the nature of fishing operations, the latter does provide a reasonable overall description of the distribution and abundance of the tiger prawn populations. Although the similarity in appearance of the two species will probably always make interpretation of logbook information on the individual species difficult, the spatial separation of the adults (Figs 5*c* and 6*c*) still offers the potential for the long-term assessment of the populations of the individual species from logbook data. The trawl survey results will make possible the estimation of mortality rates of the two tiger prawn species free from the bias associated with logbook CPUE.

Acknowledgments

We wish to thank Steve Ivicic and the crew of the F.V. *Maxim* for their enthusiastic assistance during the field program. Rob Kenyon, Tonya Cahill, Brian Taylor and Ted Wassenberg assisted on various cruises. The study was funded in part by a grant from the Australian Fishing Industry Research Trust Account.

References

Alverson, D. L., and Pereyra, W. T. (1969). Demersal fish explorations in the northeastern Pacific Ocean—an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. *J. Fish. Res. Board Can.* **26**, 1985–2001.

Buckworth, R. C. (1985). Preliminary results of a study of commercial catches, spawning and recruitment of *Penaeus esculentus* and *P. semisulcatus* in the western Gulf of Carpentaria. In 'Second Australian National Prawn Seminar'. (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 213–20. (NPS2: Cleveland, Australia.)