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.

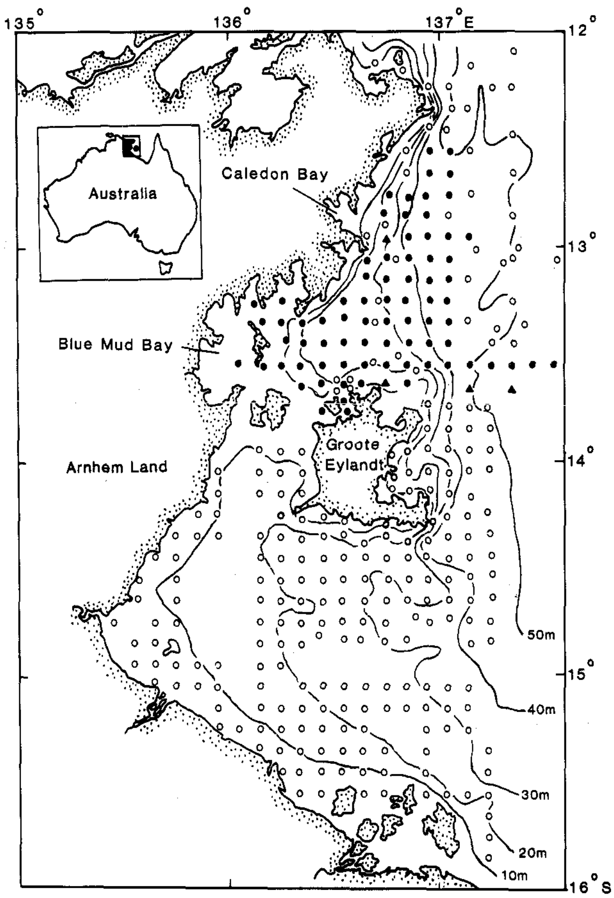

Fig. 1. Western Gulf of Carpentaria, showing the sampling sites for sediments (○), prawns and sediments (●), and prawns only (▲). The bathymetry is also shown.

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 $-1·5\phi$ 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 $\leqslant$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 $\leqslant$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 (>8ϕ) (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

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.

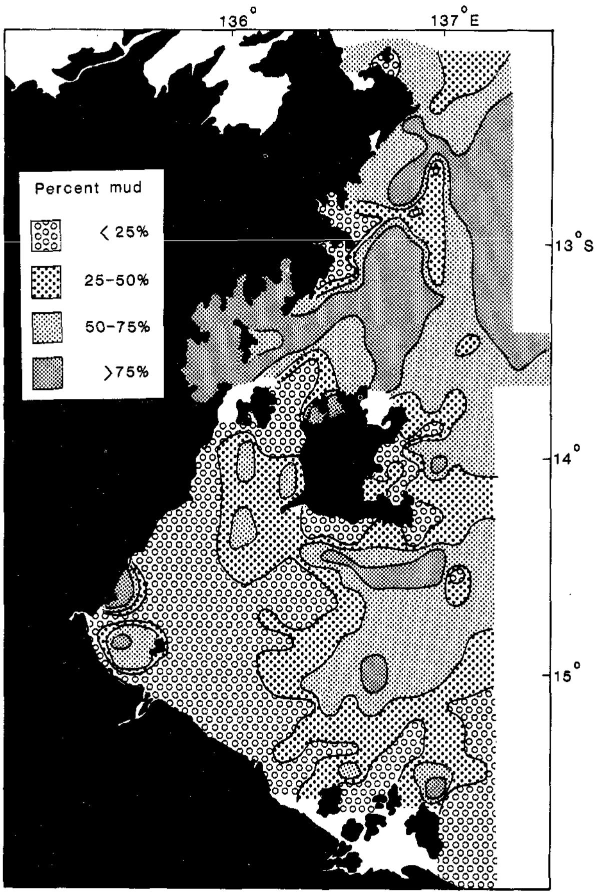

Fig. 3. Geographic distribution of sediments of the western Gulf of Carpentaria on the basis of the percentage of mud (<63 μm). Contours are drawn at the 25, 50 and 75% mud boundaries.

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).

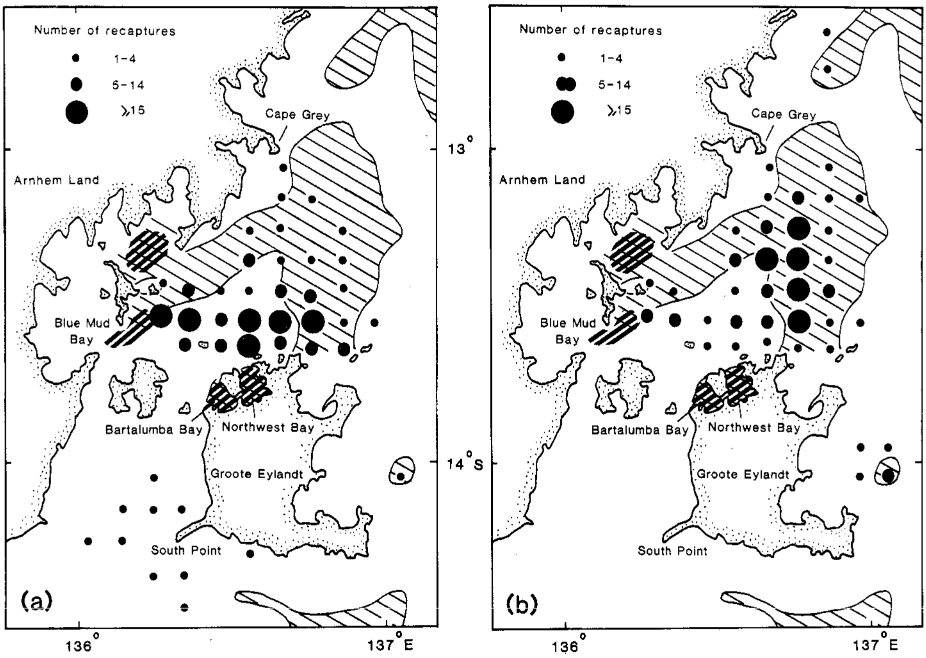

Fig. 4. Distribution of tagged tiger prawn recaptures in the western Gulf of Carpentaria from release areas (heavy cross-hatching) in Blue Mud Bay, North West Bay and Bartalumba Bay. The distribution of fine sediment (>75% mud) is given for comparison (light cross-hatching). (*a*) *P. esculentus.* (*b*)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

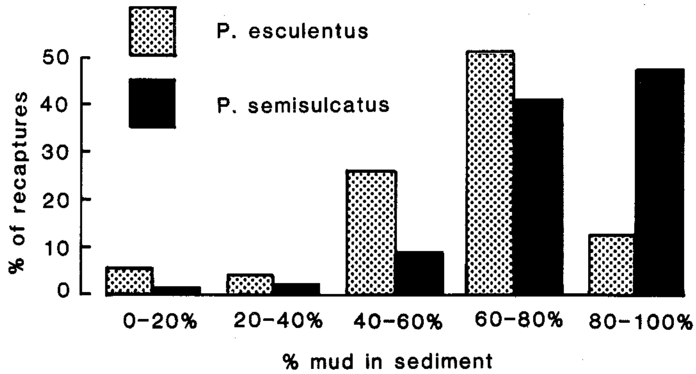

Fig. 5. Distribution of tagged tiger prawns in relation to the mud content of the sediment on which they were recaptured.

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	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
0–10							**	**	—
10–20				**		**	—	—	—
20–30	**	**		*	*	*	*	—	*
30–40		*		—			—	—	—
40–50			—	—	—	—	—	—	—
50–60				—		—			

P. semisulcatus

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

M. endeavouri

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

M. ensis

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

P. latisulcatus

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

P. longistylus

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

P. merguiensis

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

S. australiana

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

Juveniles (all species)

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

Adults (all species)

Depth (m)	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	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 $\log_e(\mathrm{CPUE}+1)$ 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: *D*1	*D*2	*M*1	*M*2	*DM*	R^2
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

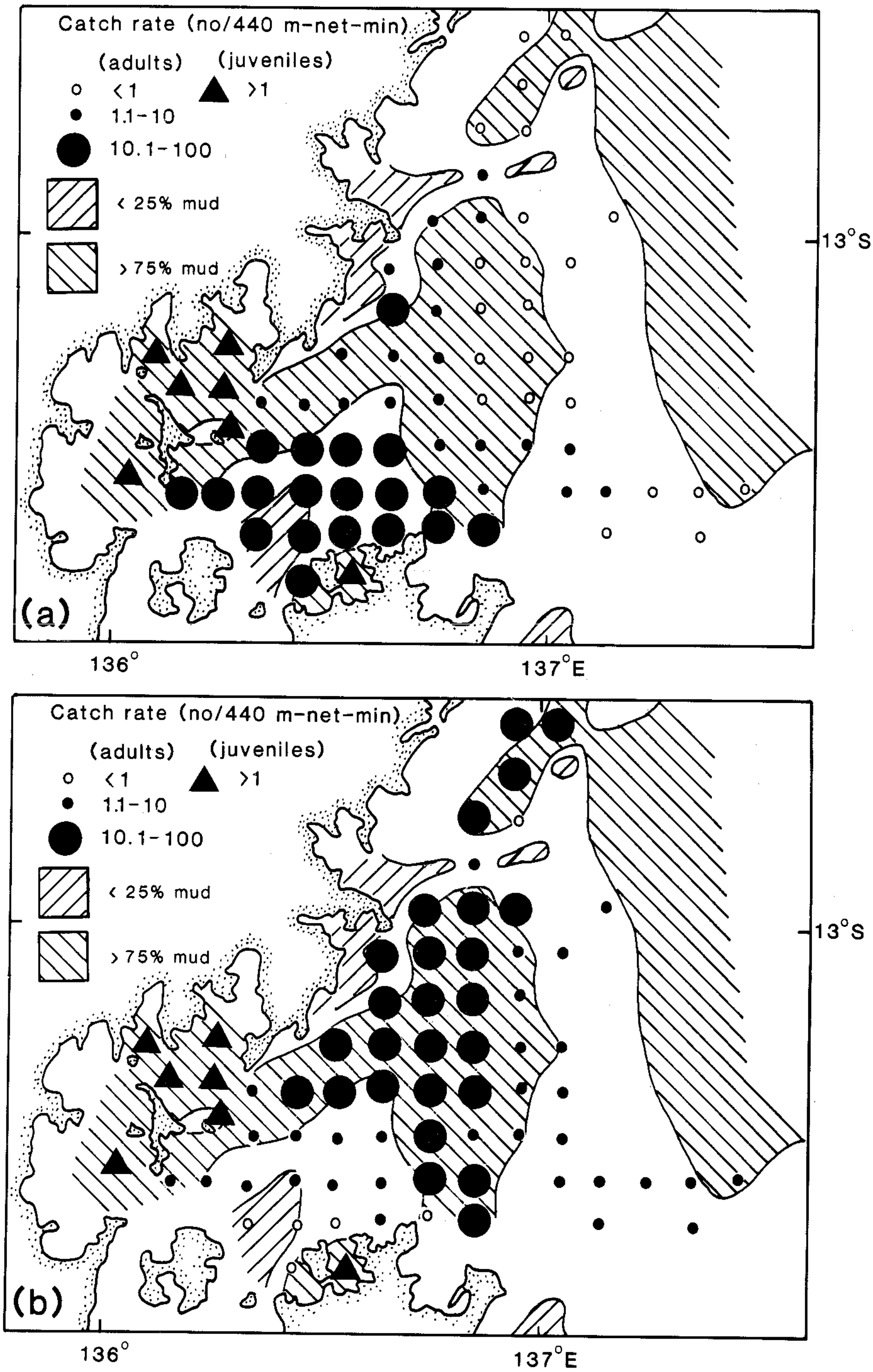

Fig. 6. Catch-per-unit-effort of adult tiger prawns (*a*) *P. esculentus* (n = 17792) and (*b*) *P. semisulcatus* (n = 13941), from the trawl surveys in the north-western Gulf of Carpentaria.

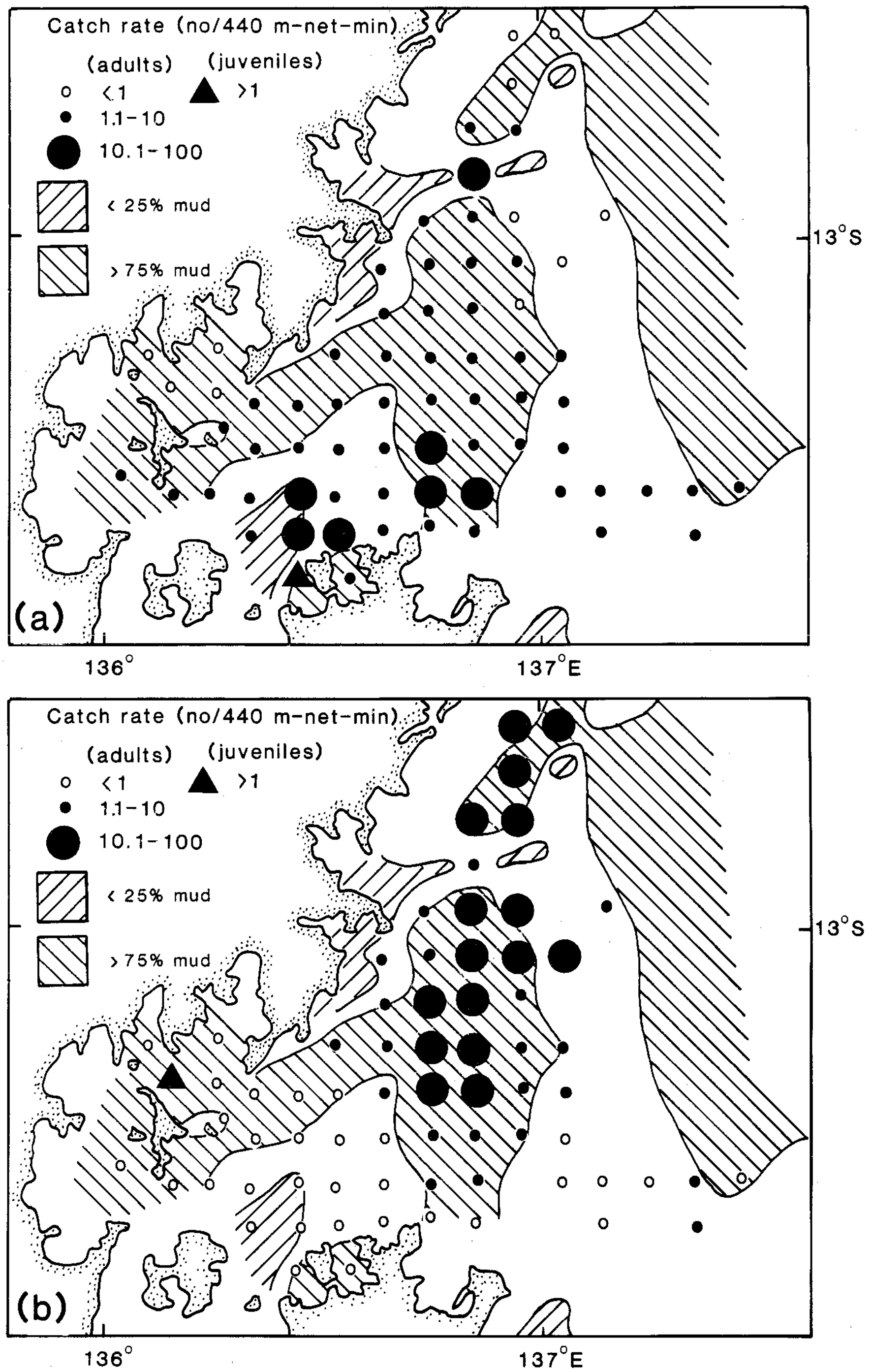

Fig. 7. Catch-per-unit-effort of adult endeavour prawns. (*a*) *Metapenaeus endeavouri* (n = 7923) and (*b*) *M. ensis* (n = 5616), from the trawl surveys in the north-western Gulf of Carpentaria.

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.

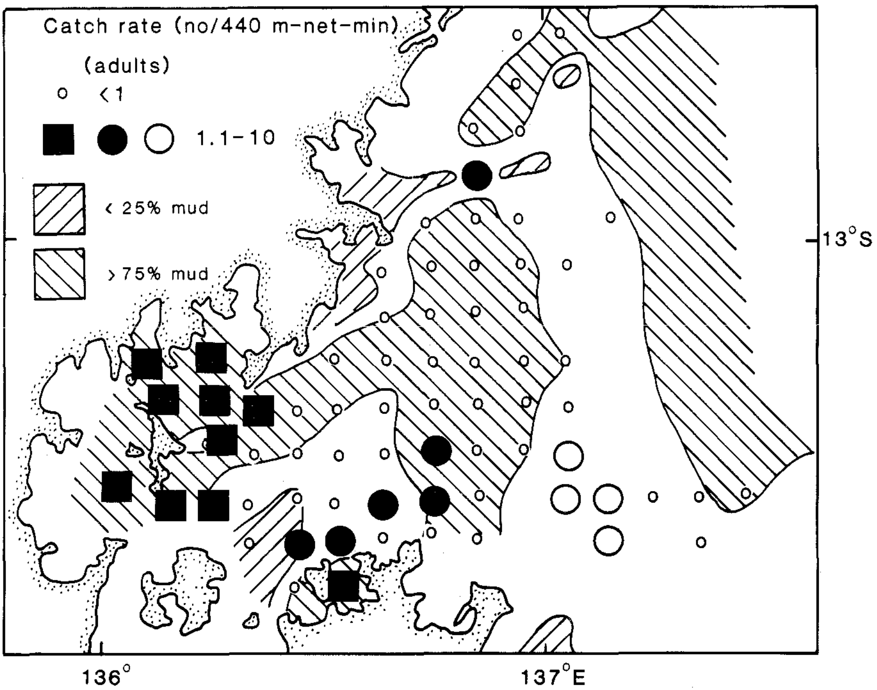

Fig. 8. Catch-per-unit-effort of adult banana prawns *Penaeus merguiensis* (■, n = 1536) and adult king prawns *P. latisulcatus* (●, n = 658) and *P. longistylus* (○, n = 315), from the trawl surveys in the north-western Gulf of Carpentaria.

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.

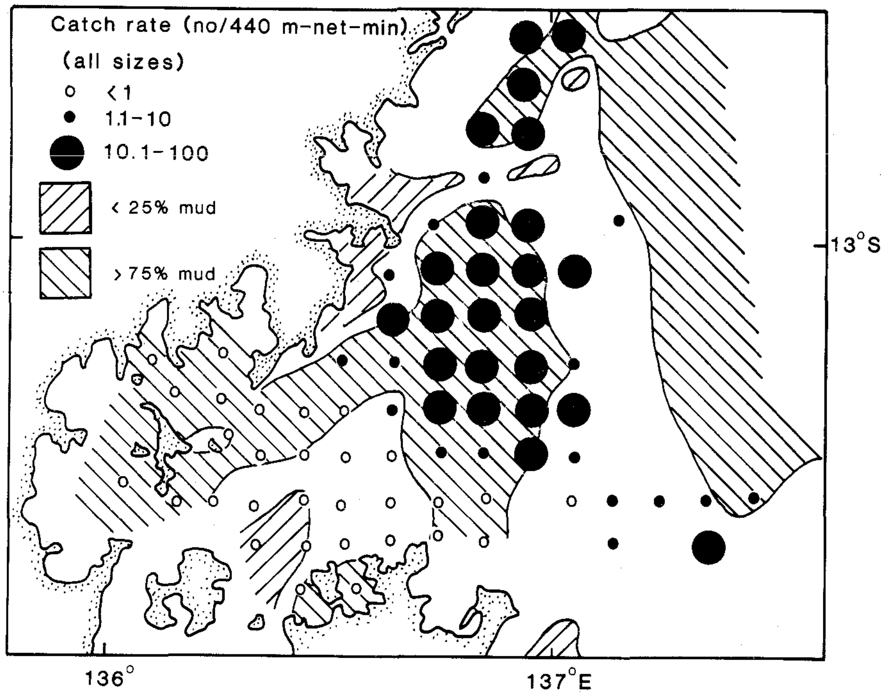

Fig. 9. Catch-per-unit-effort of coral prawns *S. australiana* ($n = 315$), from the trawl surveys in the north-western Gulf of Carpentaria.

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