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# Predation of juvenile tiger prawns in a tropical Australian estuary

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ABSTRACT: We investigated predation of juvenile penaeids, in particular the grooved tiger prawn *Penaeus semisulcatus* and the brown tiger prawn *P. esculentus*, by sampling prawns and their potential fish predators on 2 intertidal seagrass beds in the Embley River, Queensland, Australia. Despite large differences in above-ground biomass of seagrass, these beds are both critical nursery areas for postlarval [<3 mm carapace length (CL)] and juvenile (≥3 mm CL) tiger prawns. Thirty-seven species of fish were found to eat juvenile penaeids, but 76% of *P. semisulcatus* and 43% of *P. esculentus* (numbers) were found in the stomachs of 1 species of fish (*Scomberoides commersonianus*). Predation levels at the 2 seagrass beds did not appear to be related to the amount of seagrass present; rather the numbers of *Penaeus semisulcatus* eaten by fish increased with the numbers of *P. semisulcatus* on the seagrass beds. Compared to the size distributions of tiger prawns resident on the seagrass, postlarval and small juvenile tiger prawns were under-represented in the stomach contents of fish and only 17 of the 287 *P. semisulcatus* found in fish stomachs were ≤4 mm CL. Although we were unable to quantify the component of natural mortality attributable to predation by fish, we have identified the major fish predators of juvenile tiger prawns and provide evidence suggesting that fish are not significant predators of postlarval and small juvenile tiger prawns.

KEY WORDS: Predation · Penaeid · *Penaeus semisulcatus* · *Penaeus esculentus* · Diet

## INTRODUCTION

Intertidal and shallow subtidal seagrass and algal beds are critical nursery habitats for postlarval and juvenile tiger prawns (Loneragan et al. 1994) and, at times, very large numbers of postlarvae recruit to these habitats from offshore (Haywood et al. 1995). Some of the variation in numbers of juvenile tiger prawns can be explained by recruitment of the postlarvae and a small part can be explained by variation of environmental variables such as salinity and mean sea level (Vance et al. 1996). However, most of the variation is unexplained and is usually attributed to predation (Minello et al. 1989).

Predation by fish has been shown to be an important cause of mortality in various benthic invertebrates, e.g. blue crabs (Wilson et al. 1987), other crabs (Heck & Thoman 1981, Heck & Wilson 1987), sea urchins (Sala & Zabala 1996) and large juvenile penaeids (Minello et al. 1989, Salini et al. 1990, Brewer et al. 1995). However, field studies have found little evidence of fish feeding on recently settled prawns and other crustaceans. A 2 yr study on predation of juvenile penaeids in the Embley River in northern Australia found only 40 prawns that had a carapace length (CL) ≤4 mm from a total of 1620 fish stomachs (Salini et al. 1990). Similarly, although post-settlement loss of blue crab megalopae and small juveniles is considerable, none of the 35 fish species collected from the same habitat were significant predators of the newly settled blue crab (Metcalf et al. 1995).

Recent laboratory studies have shown that both postlarvae and small juvenile prawns are digested very rapidly in fish stomachs (reduced to ~30% of original dry weight 1 h after ingestion) and this may be why earlier work has not been able to identify major predators of small prawns (Haywood 1995). Coull et al. (1995) noticed this phenomenon in experiments in which whiting *Sillago maculata* were allowed to feed

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on meiofauna in microcosms. Although the numbers of nematodes in the microcosms were much lower after the whiting had fed for several hours, there were no nematodes present in the whiting guts. Previous work has shown that many penaeid predators are size selective, i.e. smaller fish eat smaller prawns (Brewer et al. 1995), so we examined predation on postlarval and small juvenile tiger prawns by using a range of sampling techniques to ensure we sampled a broad range of fish species of different sizes. We also focused our sampling in the critical nursery habitat, i.e. shallow seagrass (Loneragan et al. 1994). During a previous predation study in the Embley River, Salini et al. (1990) mainly used gill nets when sampling on the shallow seagrass beds. Since gill nets tend to capture larger fish, this may have been the reason they found few small tiger prawns in fish guts. We attempted to minimise the effects of post-capture digestion by regularly collecting fish from nets and immediately storing their stomachs in a brine/ice slurry. We monitored the juvenile tiger prawn population concurrently to compare mortality rates estimated from catch curves with the numbers of prawns found in fish stomachs.

Habitat structure (e.g. seagrass, algae, cobbles, saltmarsh) can reduce predation rates in marine environments (Wahle & Steneck 1992, Minello 1993, Irlandi 1994). In the case of small tiger prawns (4 to 5 mm CL), laboratory studies indicate that predation can be up to 3 times higher on bare sand than on broad-leaved seagrass (Kenyon et al. 1995). In the Embley River, above-ground biomass of seagrass ranges from <12 to 70 g $m^{-2}$, but large numbers of postlarval tiger prawns settle on these beds regardless of how much seagrass is present (Haywood et al. 1995). As well as searching for the fish predators of small prawns, we tested whether predation on juvenile tiger prawns varied between seagrass beds with different amounts of seagrass.

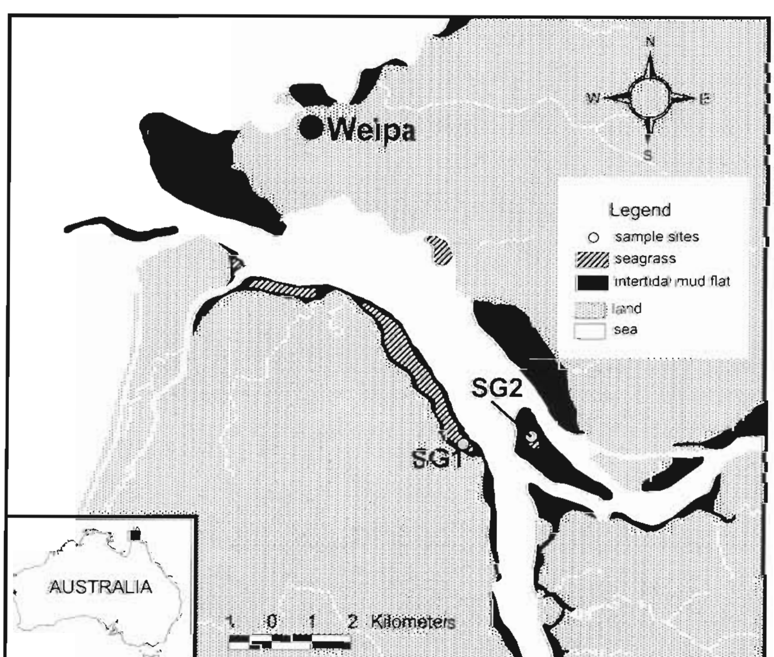


Fig. 1. Map of the Embley River area showing extent of seagrass beds and sample sites for fish and prawns

## MATERIALS AND METHODS

**Study area.** We sampled fish and prawns on 2 intertidal seagrass beds (SG1 and SG2) in the Embley River (Fig. 1). SG1 is located on the southern bank of the river about 10.6 km from the river mouth, while SG2 is on a mud bank in the middle of the river, 1 km further upstream. *Enhalus acoroides*, *Halophila ovalis* and *Halodule uninervis* were present at both beds. The dominant seagrass species (by weight) at SG1 was the long (0.5 to 1.0 m), broad-leaved (12 to 15 mm) *E. acoroides* (67.6 ± 4.5 g $m^{-2}$; mean above-ground biomass ± SE) and at SG2 was the short (40 to 75 mm), thin-leaved (1 to 2 mm) *H. uninervis* (3.1 ± 0.8 g $m^{-2}$; mean above-ground biomass ± SE) (see Haywood et al. 1995 for further details).

In this region the year can be divided into 4 tropical seasons: wet = January to March, early dry = April to June, dry = July to September and pre-wet = October to December. During this investigation, water temperatures at the seagrass sites ranged from 26.4 to 33.3°C during the pre-wet season and from 26.0 to 34.0°C during the early dry season. Salinity ranged from 33.7 to 37.2‰ during the pre-wet season and from 26.5 to 37.9‰ during the early dry season. Maximum tidal amplitudes during the investigation were 2.29 m in the pre-wet and 1.98 m in the early dry season.

**Sampling.** At both sites techniques for collecting fish included gill nets, beach seining, beam trawling and rotenone. Sampling was done during October 1993 (pre-wet season) and April 1994 (early dry season) to coincide with the peaks in abundance of juvenile *Penaeus semisulcatus* in this area (Vance et al. 1996).

Gill netting was conducted using a fleet of four 60 m long monofilament nets (50, 75, 100 and 150 mm stretch mesh). At both sites, nets were deployed at 17:00 h on a flooding tide for 2 nights during each sampling period (22 to 25 October 1993 and 14 to 17 April 1994). Fish were removed from the nets once between 20:00 and 21:00 h, and again when the nets were lifted at around midnight. Water depth ranged from 0.5 to 2.6 m during the periods the nets were deployed. All fish were identified, standard lengths and weights were measured, and the stomachs were removed, bagged and immediately placed in a slurry of frozen seawater and salt. Clearing the gill nets generally took about 30 min and measuring, weighing and removing stomachs from the catch took up to 2 h.

We used a 60 m long beach seine (19 mm mesh) with cod-end fitted midway along the seine. The net was deployed from a 5 m punt fitted with a submersible net-roller that kept the lead line on the bottom while the net was being retrieved. The net-roller was needed because the seagrass beds at SG1 and SG2 are not adjacent to beaches and so the beach seine could not be operated in the normal way. The punt was moored across the prevailing current and the net-roller was attached to the downstream side of the punt. The seine was laid in a circle on the downstream side using a 2.8 m punt powered by an electric outboard motor. This method sampled a swept area of about 285 $m^2$. The lead lines of the seine were kept close to or on the seabed by the net-roller. Although a seine used like this may not be as efficient as when used in the traditional way, we still captured good samples of fish, including some species that were not present in either beam trawl or gill net catches. Four seine samples were taken from each site during each season (28 and 29 October 1993, 26 and 27 April 1994). Samples were taken at dusk on a flooding tide, and water depths ranged between 1.0 to 1.5 m during seining. As with the gill net catches, all fish were identified, standard lengths and weights were measured, and the stomachs were removed, bagged and immediately placed in a slurry of frozen seawater and salt.

A small beam trawl (1.0 × 0.5 m mouth, 2.5 m long, 2 mm mesh net in the body, 1 mm mesh cod-end) was also used at both seagrass beds. Beam trawl samples were taken weekly during the periods from 30 September to 3 November 1993 and 27 March to 24 April 1994. On each sampling date, 2 trawls (at ~0.5 m $s^{-1}$) were made from a 4.8 m dinghy between 2 permanent markers placed 100 m apart on each of the seagrass beds. Trawls were made at night as close to high tide as possible. Two sites were trawled at SG1 and 1 site was trawled at SG2. Beam trawl samples were bagged and stored in a salt/ice slurry until arrival at the laboratory, where they were frozen until sorting and analysis. All fish and prawns were collected from the beam trawls.

Beam trawl samples were taken to estimate tiger prawn (*Penaeus semisulcatus* and *P. esculentus*) abundance. Juvenile tiger prawns were identified to species level (Grey et al. 1983), but postlarval tiger prawns could not be identified to species using morphological characteristics. Therefore, we estimated the catches of postlarval *P. semisulcatus* and *P. esculentus* by multiplying the total number of tiger prawn postlarvae in each sample by the ratio of 3 and 4 mm CL *P. semisulcatus*: *P. esculentus* from the following week's catch. This is a valid approximation because juvenile tiger prawns grow at a rate of approximately 1 mm $wk^{-1}$.

Fish were sampled with rotenone during the pre-wet but not in the early dry season because catches were very low. Three samples were taken from each seagrass bed during the first third of the flood tide, just after dawn. A 6 mm square mesh net was laid around a square defined by 4 steel stakes set into the seagrass bed, enclosing an area of 25 $m^2$. Water depth at the time was between 10 and 15 cm. Rotenone powder was scattered over the water enclosed by the net and fish were scooped from the enclosure using dip nets. Fish were placed in a salt/ice slurry and identification, weighing, standard length measurements and gut examination were done back at the laboratory.

We hypothesised that predators of small [<30 mm total length (TL)] prawns and 'prawn-like' animals might have a wider choice of prey species than predators of large (≥ 30 mm TL) 'prawn-like' animals. To test this hypothesis we estimated densities of benthic animals (including tiger prawns) on the seagrass beds by sampling with a 'drop-trap' that consisted of a cubic 0.8 m aluminium frame, 4 sides of which were covered in 2 mm mesh. The top and bottom were open and the frame was set into the substrate (~10 cm) while the water depth was between 0.4 and 0.7 m. We then used scoop nets to catch the animals enclosed by the frame. Ten drop-trap samples were taken across a 150 m transect at SG1 in the pre-wet season (16 October 1994). Samples were placed in a salt/ice slurry and returned to the laboratory for sorting. Penaeids were identified, as far as possible, to species; other taxa were identified to family and all invertebrates were measured (TL).

**Data analysis.** In the laboratory, fish stomach contents were sorted and prey items were identified to the lowest taxon possible and were dried to a constant weight. Stomach contents of specimens of all species were examined; however, in cases where >25 individuals from a single species were caught in the same sample, only stomachs from 25 individuals (representative of the size range present in the sample) were examined. Each prey type was expressed as a percentage of the dry weight of all prey types. The percent frequency of occurrence of each prey type was calculated as the percentage of fish of each species having at least 1 item of a particular prey type in its stomach (Hyslop 1981). For these analyses, prey types were grouped into 9 categories based on the dominant organisms found (Brewer et al. 1995).

We estimated a relative measure of predation on *Penaeus semisulcatus* and tiger prawn postlarvae as the product of the catch rate of each fish species and the proportion of *P. semisulcatus* in the diet of each species [Prawn Predation Index (PPI); following Salini et al. 1990]. PPI was not estimated for *P. esculentus* because the numbers found in fish stomachs were very low. The PPI was calculated separately for gill nets and the other fishing methods because gill-net catch rates are expressed in terms of g $h^{-1}$, whereas the beam trawl and beach seine catch rates are expressed as g $m^{-2}$.

We also estimated a total PPI (TPPI) for each site, season and fishing method. This index was a combination of the catch rate of each fish species at each site and in each season, and the proportion of *Penaeus semisulcatus* found in the diet of that fish species over the whole study. The TPPI gives a measure of the potential for predation of *P. semisulcatus* at each site and season. It was calculated as:

$$\text{TPPI} = \sum_{l} p_l \times c_l$$

where $p_l$ = the proportion of *P. semisulcatus* in the diet of fish species $l$ and $c_l$ = the catch rate of species $l$.

We calculated a mortality index for the juvenile tiger prawn populations by estimating the total mortality of prawns between 2 and 10 mm CL using catch curves (Gallucci et al. 1996) from the beam trawl data for each site and season. Prawns <2 mm CL were excluded because they were not fully recruited to the seagrass beds. Prawns >10 mm CL were excluded because at this size, some would be emigrating off the seagrass beds. Catch curves were generated by a linear regression of $N_{ijk}$ for each 1 mm CL size class against CL; where

$$N_{ijk} = \log\left(\sum_{k} n_{ijk} + 1\right)$$

and $n_{ijk}$ is the number of prawns within each size class caught over $k$ sampling dates at the $j$th site during the $i$th season. The mortality index was simply the slope of the regression line.

## RESULTS

### Overall diets

A total of 5321 fish from 132 species were caught. Of these, 4135 were kept for stomach analysis. The stomachs of the remainder were not examined because there were >25 individuals of the same species in a particular sample. Most fish were caught using the beam trawl and the fewest were caught with rotenone (Table 1). The mean size of fish caught also depended upon the fishing method; the largest fish were caught in the gill nets and the smallest were caught with rotenone (Table 1).

Table 1. Total number (N), number of different species and mean total length of fish caught using the different fishing gears

| Fishing method | N | No. of species | Mean size (mm) ± SE |
|---|---|---|---|
| Beam trawl | 2322 | 55 | 38 ± 0.6 |
| Beach seine | 1381 | 67 | 71 ± 1.6 |
| Gill nets | 1291 | 63 | 319 ± 5.4 |
| Rotenone | 327 | 23 | 25 ± 0.8 |

Of the 4135 stomachs examined, 2694 contained food and 1441 were empty. There were 40 species of fish in which ≥10 stomachs contained food. These comprised 3771 stomachs of which 2503 contained food.

For most fish species a particular prey type was dominant in the stomach contents, e.g. teleost prey in *Scomberoides commersonianus*, *Carcharhinus cautus*, *Platycephalus indicus* and *Eleutheronema tetradactylum* (Tables 2 & 3). However, some species ate a wide variety of prey types, e.g. *Acentrogobius caninus* and *Amniataba caudavittatus*. A few species ate only a single type of food, e.g. *Secutor ruconius*—copepods; *Siganus canaliculatus*—algae; *Nematolosa come*—unidentified digested remains.

Crustaceans other than penaeids, brachyurans and stomatopods were the dominant prey type in terms of frequency of occurrence and dry weight, with over half (23) of the 40 fish species examined having a frequency of occurrence of crustaceans of 50% or more (Table 2). In 19 fish species, the percentage dry weight of crustaceans was 25% or more (Table 3).

Teleost prey were dominant in 8 of the species in terms of percent dry weight, and in 4 species in terms of percent frequency of occurrence. Molluscs other than cephalopods were important in the diets of *Drombus palackyi*, *Chelonodon patoca*, *Gerres abbreviatus*, *G. oyena* and *Monocanthus chinensis*. Annelids were well represented in the diets of many of the smaller species, in particular *Chelonodon patoca*, *Herklotsichthys lippa*, *G. oyena*, *Leiognathus decorus*, *L. equulus*, *L. splendens* and *Thryssa hamiltoni*. In terms of dry weight, penaeids were dominant in the diet of only a single species of fish (*T. hamiltoni*). However, more than half of all the *Cymbacephalus nematophthalmus*, *Eleutheronema tetradactylum* and *Gnathanodon speciosus* caught had eaten penaeids (Tables 2 & 3).

### Penaeid diet

A total of 896 penaeid prawns were found in the stomachs of 382 fish of 37 different species (Table 4).

Table 2. Percentage frequency of occurrence of prey items in the stomach contents of fish from intertidal seagrass beds in the Embley River. This only includes those species of fish in which 10 or more stomachs contained food. $N_f$: number of stomachs containing food; $N_e$: number of empty stomachs; Ann: Annelida; Bra: Brachyura; Cep: Cephalopoda; Cru: Crustacea; Mol: Mollusca; Oth: other; Pen: Penaeidae; Sto: Stomatopoda; Tel: Teleostei

| Fish species | $N_f$ | $N_e$ | Ann | Bra | Cep | Cru | Mol | Oth | Pen | Sto | Tel |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acentrogobius caninus* | 19 | 10 | 21.1 | 10.5 | – | 36.8 | 21.1 | 26.3 | – | – | 10.5 |
| *Ambassis nalua* | 40 | 30 | 7.5 | – | – | 81.1 | – | 50 | 22.5 | – | 20 |
| *Ambassis vachellii* | 74 | 54 | 16.2 | 1.4 | – | 87.5 | 1.4 | 28.4 | – | – | 1.4 |
| *Amniataba caudavittatus* | 16 | 10 | 37.5 | 12.5 | – | – | 6.3 | 37.5 | 18.8 | 12.5 | – |
| *Anodontostoma chacunda* | 46 | 3 | – | – | – | 97.5 | – | 100 | – | – | – |
| *Apogon ruppelli* | 121 | 30 | 13.2 | 0.8 | – | 62.3 | – | – | 2.5 | – | 1.7 |
| *Arius proximus* | 257 | 103 | 18.7 | 36.2 | – | 92.6 | 8.6 | 23.7 | 22.2 | 14 | 24.1 |
| *Butis butis* | 162 | 74 | 6.2 | – | – | 11.1 | 0.6 | 1.9 | 6.8 | – | 4.3 |
| *Carcharhinus cautus* | 18 | 3 | – | 5.6 | 16.7 | 79.3 | 11.1 | – | 16.7 | 27.8 | 77.8 |
| *Centrogenys vaigiensis* | 92 | 29 | 27.2 | 13 | – | 60 | – | 3.3 | 15.2 | – | 2.2 |
| *Chelonodon patoca* | 10 | 1 | 30 | – | – | 21.7 | 90 | 70 | – | – | – |
| *Cymbacephalus nematophthalmus* | 23 | 8 | – | 26.1 | – | 40 | – | 8.7 | 52.2 | – | 47.8 |
| *Drombus palackyi* | 20 | 6 | 10 | 5 | – | 3.7 | 50 | 15 | – | – | 5 |
| *Eleutheronema tetradactylum* | 54 | 8 | 1.9 | 5.6 | 3.7 | 66.7 | 3.7 | 1.9 | 51.9 | 16.7 | 83.3 |
| *Epinephelus suillus* | 63 | 52 | 1.6 | 7.9 | – | 70.6 | 1.6 | 1.6 | 19 | – | 17.5 |
| *Favonigobius melanobranchus* | 17 | 30 | 5.9 | – | – | 30.4 | 5.9 | 47.1 | – | – | 5.9 |
| *Gerres abbreviatus* | 23 | 19 | 52.2 | 13 | – | 80.6 | 39.1 | 17.4 | – | – | – |
| *Gerres* spp. | 36 | 114 | 16.7 | – | – | 14.5 | 8.3 | 11.1 | – | – | – |
| *Gerres oyena* | 55 | 49 | 74.5 | – | – | 87.5 | 50.9 | 23.6 | – | – | – |
| *Gnathanodon speciosus* | 24 | 34 | – | 12.5 | – | 53.1 | 12.5 | 20.8 | 58.3 | 4.2 | 58.3 |
| *Herklotsichthys lippa* | 49 | 12 | 93.9 | – | – | 98.3 | 4.1 | 6.1 | – | – | – |
| *Leiognathus decorus* | 60 | 7 | 51.7 | 1.7 | – | 78.3 | 31.7 | 26.7 | – | – | – |
| *Leiognathus equulus* | 92 | 28 | 59.8 | – | – | 95 | 10.9 | 35.9 | – | – | – |
| *Leiognathus splendens* | 60 | 20 | 51.7 | 1.7 | – | 52.6 | 8.3 | 33.3 | – | – | 1.7 |
| *Lethrinus lentjan* | 19 | 56 | 21.1 | – | – | 70.9 | 5.3 | 42.1 | – | – | 10.5 |
| *Lutjanus russelli* | 78 | 16 | 8.9 | 3.8 | – | 28.6 | – | 7.6 | 29.1 | – | 15.2 |
| *Monocanthus chinensis* | 21 | 72 | 9.5 | – | – | – | 42.9 | 76.2 | – | – | – |
| *Nematolosa come* | 34 | 4 | – | – | – | 64.2 | – | 100 | – | – | – |
| *Pelates quadrilineatus* | 137 | 111 | 13.1 | 0.7 | – | 2.3 | 5.8 | 54.7 | 0.7 | – | 0.7 |
| *Pelates sexlineatus* | 43 | 5 | 7 | 2.3 | – | 23.5 | 2.3 | 95.3 | – | – | – |
| *Platycephalus indicus* | 17 | 23 | – | – | – | 11.3 | – | 5.9 | 23.5 | – | 70.6 |
| *Rhizoprionodon acutus* | 62 | 10 | – | 1.6 | 1.6 | 55 | 3.2 | 1.6 | 40.3 | 30.6 | 61.3 |
| *Sardinella albella* | 20 | – | 15 | – | – | 7.7 | 5 | 55 | – | – | – |
| *Scomberoides commersonianus* | 231 | 41 | – | – | 1.3 | 100 | 8.2 | 3.4 | 48.5 | – | 77.3 |
| *Secutor ruconius* | 14 | 4 | – | – | – | – | – | – | – | – | – |
| *Siganus canaliculatus* | 25 | 15 | – | – | – | 16.7 | – | 100 | – | – | – |
| *Sillago lutea* | 12 | 2 | 41.7 | 25 | – | 100 | – | 25 | 8.3 | 16.7 | 16.7 |
| *Stolephorus carpentariae* | 10 | 1 | 10 | – | – | 79.1 | 20 | – | – | – | – |
| *Terapon puta* | 321 | 160 | 18.7 | 1.2 | – | 53.6 | 5.3 | 45.2 | 2.5 | – | 4.4 |
| *Thryssa hamiltoni* | 28 | 14 | 32.1 | – | – | – | – | – | 32.1 | – | 10.7 |

The most common species of prawns found in fish stomachs were *Penaeus semisulcatus* (287) and unidentified *Metapenaeus* spp. (268), compared with only 28 *P. esculentus*. Ninety-seven percent of the fish stomachs that contained penaeids had ≤5 penaeids in each stomach; however, 1 *Scomberoides commersonianus* stomach contained 72 juvenile *P. semisulcatus* and a *Rhinobatus typus* stomach contained 39 juvenile *Metapenaeus* spp. In some cases prawns from stomach contents were digested to a state where identification to species was not possible.

Unidentified *Metapenaeus* spp. were present in the stomach contents of most of the penaeid predators and were the dominant (≥50%) penaeid in 12 species of fish. Tiger prawns accounted for ≥25% of the dry weight of penaeids in 15 species of fish (*Penaeus semisulcatus*: 9 species; *P. esculentus*: 5 species; unidentified tiger prawns: 1 species).

We targeted smaller fish by using the beam trawl, beach seine and rotenone and caught 3929 fish with these gears compared with 1291 fish caught using the gill nets. However, 77% of all penaeids found in fish stomachs were from fish caught in the gill nets (Fig. 2). Only 17 of the 287 *Penaeus semisulcatus* found in fish stomachs were ≤4 mm CL and they were eaten by the following species of fish: *Scomberoides commersonianus* (5), *Arius proximus* (4), *Butis butis* (3), *Centrogenys vaigiensis* (1), *Epinephelus suillus* (1), *Ter-*

Table 3. Percentage contribution by dry weight of prey items in the stomach contents of fish from intertidal seagrass beds in the Embley River. This only includes those species of fish in which 10 or more stomachs contained food. Ann: Annelida; Bra: Brachyura; Cep: Cephalopoda; Cru: Crustacea; Mol: Mollusca; Oth: other; Pen: Penaeidae; Sto: Stomatopoda; Tel: Teleostei

| Fish species | Length range (mm) | Ann | Bra | Cep | Cru | Mol | Oth | Pen | Sto | Tel |
|---|---|---|---|---|---|---|---|---|---|---|
| *Acentrogobius caninus* | 28–92 | 39.5 | 13.1 | – | 19.4 | 21.2 | 3.4 | – | – | 3.5 |
| *Ambassis nalua* | 32–85 | 1.5 | – | – | 9.8 | – | 16.7 | 30.8 | – | 41.2 |
| *Ambassis vachellii* | 17–48 | 49 | – | – | 26.5 | – | 24 | – | – | 0.5 |
| *Amniataba caudavittatus* | 71–170 | 23.9 | 5.6 | – | 33.6 | 0.2 | 19.2 | 9 | 8.5 | – |
| *Anodontostoma chacunda* | 63–82 | – | – | – | – | – | 100 | – | – | – |
| *Apogon ruppelli* | 15–63 | 5.5 | 0.1 | – | 83 | – | – | 10.7 | – | 0.7 |
| *Arius proximus* | 110–665 | 3.8 | 45.9 | – | 17.1 | 1 | 7 | 3.2 | 10.9 | 11.3 |
| *Butis butis* | 16–76 | 1.5 | – | – | 60.8 | 0.1 | 2.3 | 26.7 | – | 8.7 |
| *Carcharhinus cautus* | 418–1300 | – | 0.4 | 0.1 | 0.5 | 0.2 | – | 0.3 | 2.5 | 96 |
| *Centrogenys vaigiensis* | 14–70 | 12.6 | 18.7 | – | 55.2 | – | 0.2 | 11.5 | – | 1.9 |
| *Chelonodon patoca* | 17–54 | 66.4 | – | – | 2.4 | 27 | 4.2 | – | – | – |
| *Cymbacephalus nematophthalmus* | 69–257 | – | 13 | – | 6.7 | – | 0.1 | 25.7 | – | 54.4 |
| *Drombus palackyi* | 20–37 | 5.6 | 4.5 | – | 25.4 | 42.4 | 7.5 | – | – | 14.6 |
| *Eleutheronema tetradactylum* | 290–465 | – | 0.7 | 2.2 | 0.4 | 0.2 | 0.5 | 17.9 | 5.2 | 72.8 |
| *Epinephelus suillus* | 18–270 | 0.1 | 21.2 | – | 37.9 | – | – | 15.4 | – | 25.3 |
| *Favonigobius melanobranchus* | 17–29 | 8.5 | – | – | 44.2 | 1.6 | 40.4 | – | – | 5.3 |
| *Gerres abbreviatus* | 44–195 | 1.8 | 23.3 | – | 0.2 | 74.6 | 0.1 | – | – | – |
| *Gerres* spp. | 13–36 | 26.5 | – | – | 64.7 | 2.6 | 6.3 | – | – | – |
| *Gerres oyena* | 40–77 | 73.3 | – | – | 0.1 | 23.4 | 3.2 | – | – | – |
| *Gnathanodon speciosus* | 230–360 | – | 8.3 | – | 87.1 | 0.2 | 1.5 | 2 | 0.1 | 0.7 |
| *Herklotsichthys lippa* | 46–65 | 89.3 | – | – | 9.3 | 0.1 | 1.3 | – | – | – |
| *Leiognathus decorus* | 21–73 | 38.8 | 0.2 | – | 52.8 | 7.3 | 1 | – | – | – |
| *Leiognathus equulus* | 32–58 | 46.8 | – | – | 28.5 | 2.2 | 22.6 | – | – | – |
| *Leiognathus splendens* | 21–58 | 31.2 | 0.1 | – | 66.3 | 0.5 | 1.8 | – | – | 0.1 |
| *Lethrinus lentjan* | 14–90 | 17.9 | – | – | 43.3 | 17.5 | 10.6 | – | – | 10.8 |
| *Lutjanus russelli* | 17–140 | 0.4 | 0.2 | – | 22.9 | – | 1.1 | 23 | – | 52.5 |
| *Monocanthus chinensis* | 12–87 | 1.2 | – | – | 1.6 | 37.1 | 60 | – | – | – |
| *Nematolosa come* | 41–180 | – | – | – | – | – | 100 | – | – | – |
| *Pelates quadrilineatus* | 15–180 | 0.4 | 0.1 | – | 1.4 | 1.7 | 96.2 | 0.1 | – | 0.1 |
| *Pelates sexlineatus* | 27–140 | 1.2 | 0.7 | – | 0.3 | – | 97.7 | – | – | – |
| *Platycephalus indicus* | 121–410 | – | – | – | 3.1 | – | – | 0.8 | – | 96 |
| *Rhizoprionodon acutus* | 418–687 | – | 0.2 | 2.4 | 3.1 | 0.4 | 0.1 | 10.5 | 16.1 | 67.3 |
| *Sardinella albella* | 52–60 | 16.2 | – | – | 48.4 | – | 35.4 | – | – | – |
| *Scomberoides commersonianus* | 105–880 | – | – | 0.2 | 0.4 | 0.6 | 0.3 | 18.9 | – | 79.5 |
| *Secutor ruconius* | 25–32 | – | – | – | 100 | – | – | – | – | – |
| *Siganus canaliculatus* | 23–44 | – | – | – | – | – | 100 | – | – | – |
| *Sillago lutea* | 82–210 | 5.5 | 7.3 | – | 50.4 | – | 0.3 | 3.3 | 21.4 | 12 |
| *Stolephorus carpentariae* | 37–46 | 1.2 | – | – | 98.4 | 0.4 | – | – | – | – |
| *Terapon puta* | 14–142 | 15.7 | 2.2 | – | 32.7 | 2.6 | 15.5 | 5.2 | – | 26 |
| *Thryssa hamiltoni* | 85–175 | 31.1 | – | – | 11.7 | – | – | 34.6 | – | 22.5 |

*apon puta* (1), *Elops machnata* (1) and *Polydactylus multiradiatus* (1).

In terms of the PPI, which takes into account the proportion of *Penaeus semisulcatus* in the diet and the catch rate of the fish species, *Scomberoides commersonianus* caught in gill nets were the most important predator of tiger prawns. Seventy-six percent of *P. semisulcatus* and 43% (numbers) of *P. esculentus* found in fish stomachs were from this species. *Eleutheronema tetradactylum*, *Lates calcarifer* and *Rhizoprionodon acutus* were also important predators that were caught using gill nets (Fig. 3a). *Cymbacephalus nematophthalmus*, *Terapon puta*, *Epinephelus suillus* and *Lutjanus russelli* were the dominant tiger prawn predators that were caught using the beam trawl, beach seine and rotenone (Fig. 3b). *Penaeus semisulcatus* and unidentified tiger prawns ≥3 mm CL were found in the stomachs of 18 different species of fish; however, the top 4 species of fish caught in the gill nets ate 87.5% of all the *P. semisulcatus* found in fish stomachs.

### Site/season comparison

Mean numbers of *Penaeus semisulcatus* caught in the beam trawls were greater during the pre-wet season and were higher at the *Enhalus acoroides* site

Table 4. Mean percentage composition (by dry weight) of penaeids in the diets of fish caught in the Embley River. Psem: *Penaeus semisulcatus*; Pesc: *P. esculentus*; Tig: unidentified tiger prawns; Pen: *Penaeus* spp.; Pmerg: *P. merguiensis*; Plat: *P. latisulcatus*; Penaeid: unidentified penaeids; Met: unidentified *Metapenaeus* spp.; CUP: commercially unimportant penaeids

| Fish species | No. of fish stomachs | No. of prawns | Psem | Pesc | Tig | Pen | Pmerg | Plat | Penaeid | Met | CUP |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Absalom radiatus* | 1 | 1 | – | 100 | – | – | – | – | – | – | – |
| *Ambassis nalua* | 9 | 9 | – | – | – | 0.3 | – | – | 2.8 | 96.9 | – |
| *Amniataba caudavittatus* | 3 | 4 | – | – | – | – | – | – | 64.3 | 35.7 | – |
| *Apogon ruppelli* | 3 | 3 | – | – | – | – | – | – | 1.4 | 98.6 | – |
| *Arius proximus* | 57 | 79 | 14.7 | 9.7 | 0.7 | 6.8 | 14.9 | – | 9.2 | 20.3 | 23.7 |
| *Butis butis* | 11 | 12 | 8.6 | 58.7 | 11.6 | – | – | – | 8.6 | 12.5 | – |
| *Caranx bucculentus* | 1 | 1 | – | – | – | – | – | – | 100 | – | – |
| *Carcharhinus amblyrhynchoides* | 1 | 1 | – | – | – | 100 | – | – | – | – | – |
| *Carcharhinus cautus* | 3 | 3 | – | – | – | – | – | – | 19 | 7.8 | 73.2 |
| *Carcharhinus dussumieri* | 4 | 6 | 28.1 | – | 16.9 | – | – | – | 12.4 | 9.2 | 33.4 |
| *Carcharhinus sorrah* | 1 | 1 | – | – | – | – | – | – | – | – | 100 |
| *Centrogenys vaigiensis* | 14 | 17 | – | – | 4.3 | – | – | – | – | 95.7 | – |
| *Cymbacephalus nematophthalmus* | 12 | 16 | 43.5 | 2.6 | 33.2 | – | – | – | 0.2 | 20.4 | – |
| *Eleutheronema tetradactylum* | 28 | 46 | 16.5 | 2.6 | 6.4 | – | 39.9 | – | 1.2 | 8.1 | 25.3 |
| *Elops machnata* | 3 | 3 | 1.6 | – | – | – | – | – | – | – | 98.4 |
| *Epinephelus suillus* | 12 | 13 | 21 | 35.1 | 2.6 | – | – | – | 15 | 26.3 | – |
| *Gnathanodon speciosus* | 14 | 28 | 29.7 | 52 | 4 | 2.1 | – | – | 11.8 | 0.4 | – |
| *Lates calcarifer* | 5 | 11 | 75.7 | 10.9 | 1.6 | – | – | – | 1.4 | 10.4 | – |
| *Lutjanus russelli* | 23 | 41 | 45.3 | – | – | – | – | – | 20.9 | 33.8 | – |
| *Nibea microgenys* | 1 | 14 | – | – | – | – | – | – | – | 100 | – |
| *Pelates quadrilineatus* | 1 | 1 | – | – | – | – | – | – | 100 | – | – |
| *Platycephalus endrachtensis* | 1 | 1 | – | – | – | – | – | – | 100 | – | – |
| *Platycephalus indicus* | 4 | 4 | 37.1 | – | – | – | – | – | 0.4 | 62.4 | – |
| *Polydactylus multiradiatus* | 1 | 10 | 10.4 | – | 4 | – | – | – | – | 85.7 | – |
| *Polydactylus sheridani* | 1 | 5 | 29.4 | – | – | – | – | – | – | 21.3 | 49.2 |
| *Pseudorhombus arsius* | 2 | 3 | – | – | – | – | – | – | 15.7 | 84.3 | – |
| *Rhinobatus typus* | 1 | 39 | – | – | – | – | – | – | – | 100 | – |
| *Rhizoprionodon acutus* | 25 | 40 | 21 | – | – | 0.5 | 30 | – | 2.3 | 16.9 | 29.2 |
| *Rhynchobatus djiddensis* | 2 | 19 | 7.1 | – | 8.5 | – | – | – | 35.8 | 22.6 | 25.9 |
| *Scomberoides commersonianus* | 113 | 435 | 25.8 | 3.4 | 2.6 | 0.9 | 33.4 | 0.4 | 5.3 | 8.2 | 19.9 |
| *Sillago analis* | 3 | 3 | – | – | – | – | – | – | 22 | 78 | – |
| *Sillago lutea* | 1 | 1 | – | – | – | – | – | – | – | 100 | – |
| *Strongylura strongylura* | 2 | 2 | – | – | – | – | – | – | 11.7 | 88.3 | – |
| *Sygnathoides* spp. | 1 | 1 | – | 100 | – | – | – | – | – | – | – |
| *Terapon jarbua* | 1 | 2 | – | – | – | – | – | – | – | 100 | – |
| *Terapon puta* | 8 | 8 | 74.1 | 4.7 | – | 1.4 | – | – | 19.8 | – | – |
| *Thryssa hamiltoni* | 9 | 13 | – | – | – | – | – | – | 8.8 | 91.2 | – |
| Total number | 382 | 896 | 287 | 28 | 34 | 21 | 27 | 1 | 139 | 268 | 91 |

(SG1) than at the *Halophila/Halodule* site (SG2; Table 5). This pattern matches that shown for these sites during 1990–1992 (Haywood et al. 1995). Mean catches of *P. esculentus* were always higher at SG1 than SG2, but there was no consistent seasonal pattern.

The numbers of *Penaeus semisulcatus* found in stomachs of predatory fish were higher during the pre-wet season at both sites, even though numbers were always greater at SG1 than at SG2. The number of *P. semisulcatus* found in the stomachs during both seasons at both sites increased as the number of *P. semisulcatus* caught on the seagrass beds increased (Fig. 4). The numbers of *P. esculentus* in fish stomachs was generally low compared with the numbers of *P. semisulcatus*, but were greatest at SG1 in the early dry season (Table 5).

The $TPPI_{gill\ nets}$ was higher during the early dry than the pre-wet season at SG1, but higher during the pre-wet at SG2 (Table 5). The very high $TPPI_{gill\ nets}$ for SG2 in the pre-wet was largely because 218 queenfish were caught, compared with 35 from SG1 during the same season. The $TPPI_{gill\ nets}$ did not bear any clear relationship to the numbers of prawns in stomachs.

The *Penaeus semisulcatus* mortality index (highest negative number indicates highest mortality) was higher at SG1 than SG2 and higher in the early dry season at SG1 and during the pre-wet season at SG2

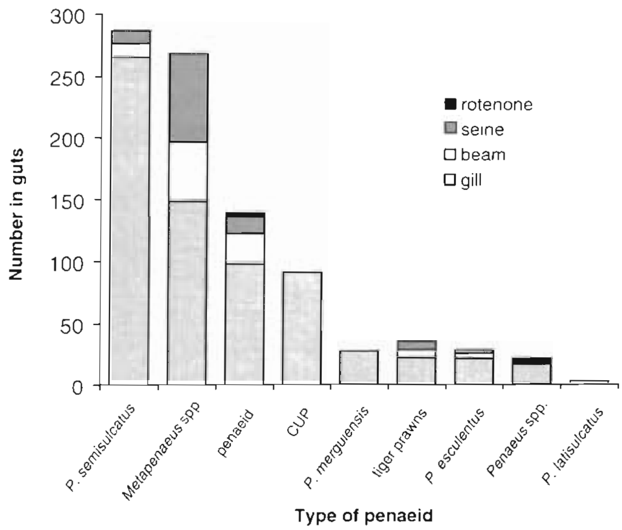


Fig. 2. Summary of the type of penaeid found in fish stomachs (total number of penaeids = 896). CUP: commercially unimportant penaeid; tiger prawns: unidentified *Penaeus semisulcatus* and *P. esculentus*

b). *P. esculentus* from fish guts ranged from 2 to 18 mm CL, 17% of which were postlarvae (Fig. 5d).

Although we caught 3 times as many fish in the beam trawl, beach seine and rotenone as we caught in the gill nets, only 22 of the 287 *Penaeus semisulcatus* and 4 of the 28 *P. esculentus* found in fish stomachs were caught in the former methods, and they were all ≤8 mm CL. Nevertheless, our strategy of using a variety of fishing gears and focusing the fishing effort on the critical nursery areas for tiger prawns resulted in a higher proportion of small tiger prawns being found in fish stomachs than in an earlier study in the western Gulf of Carpentaria, Australia (Fig. 6).

### By site and season

Since the majority (92.3%) of the *Penaeus semisulcatus* found in fish stomachs were from fish caught in the (Table 5). It was not related to the number of *P. semisulcatus* found in fish stomachs (Table 5). At SG1, the mortality index for *P. esculentus* was lower than for *P. semisulcatus*. At SG2, it was slightly higher in the pre-wet season and was not estimated for SG2 in the early dry season because numbers were too low.

## Size range of tiger prawns on seagrass beds and in fish stomachs

### All sites and seasons pooled

The size of *Penaeus semisulcatus* caught in beam trawls on the seagrass ranged from 1 to 20 mm CL. Forty-eight percent of the catch were postlarvae (1 to 2 mm CL) and there was a smaller mode of about 5 mm CL (Fig. 5a). Juvenile *P. semisulcatus* found in fish stomachs from both sites and seasons ranged from 1 to 18 mm CL, with a mode of 6 mm CL (Fig. 5c); however, only 2.5% of these were postlarvae.

*Penaeus esculentus* caught in beam trawls showed a similar size-distribution pattern to that of *P. semisulcatus*, ranging in size from 1 to 17 mm CL (Fig. 5b). Forty-five percent of these were postlarvae and there was a mode of about 6 mm CL. More of the larger (≥10 mm CL) *P. esculentus* were caught on the seagrass than was the case for *P. semisulcatus* (Fig. 5a,

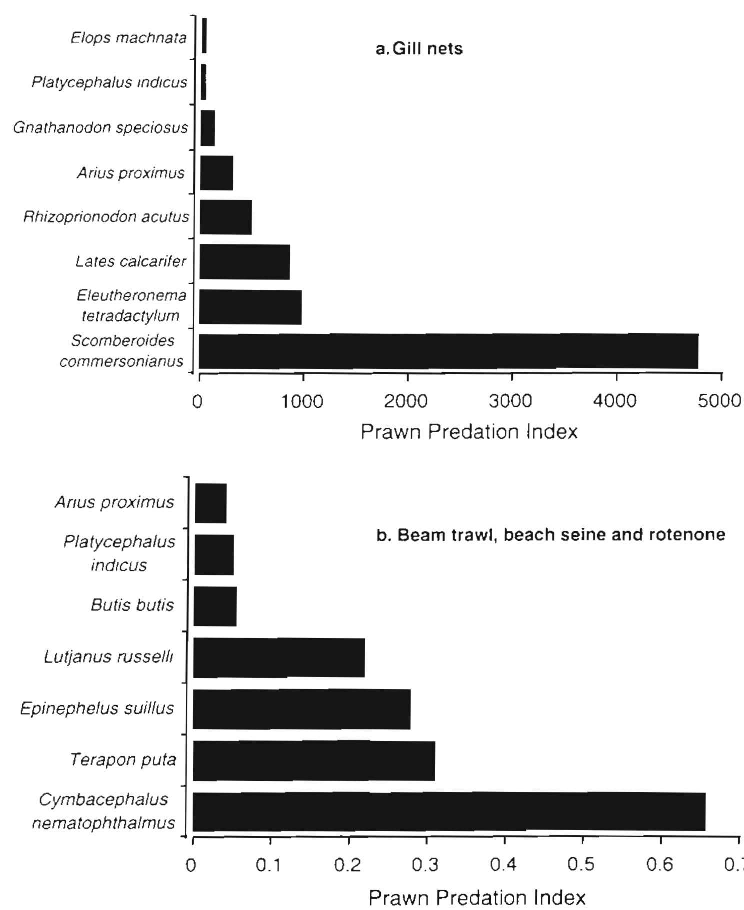


Fig. 3. *Penaeus semisulcatus*. Prawn Predation Indices (PPI) for fish species caught in (a) gill nets and (b) beam trawl, beach seine and rotenone. Only fish species in which at least 5 stomachs contained food are included in this analysis

Table 5. *Penaeus semisulcatus* and *P. esculentus*. Mean density (per 100 $m^2$) ± SE of postlarvae and juveniles, total numbers found in fish stomachs, mean number per fish stomach ± SE (excluding the stomach containing 72 *P. semisulcatus*), Total Prawn Predation Indices (TPPI) and mortality indices at sites in the Embley River during the pre-wet and early dry seasons 1993–94. The values for $TPPI_{gill\ nets}$ are scaled by dividing by 1000. PPI was not estimated for *P. esculentus* because the numbers of this species found in fish guts was so low. Mortality index was not estimated for *P. esculentus* at SG2 during the early dry season because numbers caught were too low. Other methods: beach seine and beam trawl

| Species | Estimate | SG1 | | SG2 | |
|---|---|---|---|---|---|
| | | Pre-wet | Early dry | Pre-wet | Early dry |
| *P. semisulcatus* | Mean density (per 100 $m^2$) | 585 ± 108.9 | 168 ± 13.9 | 304 ± 77.3 | 21 ± 9.6 |
| | Total no. in stomachs | 129 | 62 | 92 | 6 |
| | Mean no. per stomach | 2.8 ± 0.56 | 1.6 ± 0.21 | 1.8 ± 0.21 | 1.3 ± 0.27 |
| | $TPPI_{gill\ nets}$/1000 | 4.3 | 8.7 | 16.7 | 6.6 |
| | $TPPI_{other\ methods}$ | 13.7 | 10.5 | 0.4 | 2.7 |
| | Mortality index | −0.46 | −0.53 | −0.36 | −0.26 |
| *P. esculentus* | Mean density (per 100 $m^2$) | 47 ± 11.0 | 58 ± 10.3 | 20 ± 4.4 | 9 ± 2.6 |
| | Total no. in stomachs | 7 | 17 | 0 | 6 |
| | Mortality index | −0.29 | −0.19 | −0.40 | – |

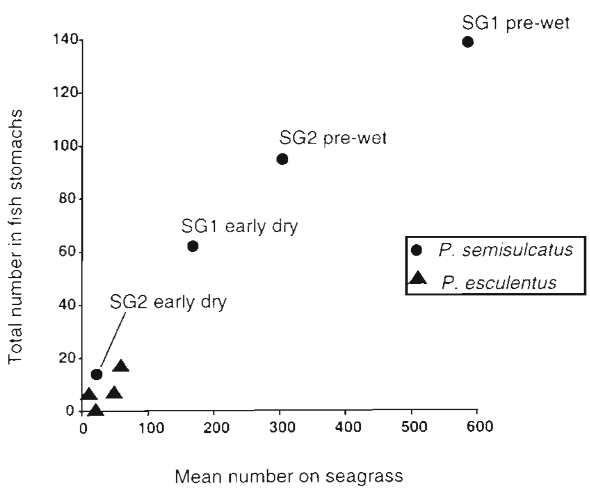


Fig. 4. *Penaeus semisulcatus* and *P. esculentus*. Mean number caught in beam trawls on seagrass beds (SG1 and SG2) and total number found in predatory fishes' stomachs

gill nets, we only used gill net data for the site–season comparison. The numbers of *P. esculentus* in fish stomachs was too low to perform this analysis. Gill nets were only used for 2 nights at each site and season, and beam-trawl data used in this comparison were from the sampling dates immediately before and after the gill-netting dates.

The size distributions of *Penaeus semisulcatus* caught in the beam trawls were similar at both sites during the same seasons (Fig. 7). *P. semisulcatus* caught on 18 and 26 October 1993 (pre-wet season) ranged from 1 to 13 mm CL, with modes at about 1 and 5 mm CL. Length frequencies of *P. semisulcatus* found in fish stomachs during this period (22 to 25 October 1993) appeared similar to those from the beam trawls in that they had a mode at about 6 mm, but there were very few postlarvae (Fig. 7a, b). Stomach and beam-trawl length distributions of *P. semisulcatus* from both sites were significantly different (Kolmogorov-Smirnov test; SG1, p = 0.0001; SG2, p = 0.0001) during the pre-wet season. Length distributions from the early dry seasons were different at SG1 (Kolmogorov-Smirnov test; SG1, p = 0.0001). Prawns caught by the beam trawl were predominantly between 1 and 5 mm CL, whereas those from fish stomachs during the same period had modes of about 6 and 12 mm CL. The number of prawns at SG2 in the early dry season was too low to perform the test, but the distributions appear quite different (Fig. 7d). The mean size of *P. semisulcatus* for any given site and season was always greater in fish stomachs than in the beam trawl (Fig. 7).

### Drop-trap sampling

The density of tiger prawns (i.e. *Penaeus semisulcatus*, *P. esculentus* and unidentified tiger prawns) on the seagrass beds during the pre-wet season was very low (1.1%) compared to the total density of prawns and 'prawn-like' animals (Table 6). Densities taken with the drop-traps ranged from 0.3 ± 0.21 $m^{-2}$ (mean ± SE) for *P. esculentus* and *P. semisulcatus* to 59.8 ± 7.63 $m^{-2}$ for carids (Table 6).

The proportion of tiger prawns eaten (by fish caught in all net types) compared with 'prawn-like' animals was much higher for large fish (>200 mm TL; 16.4% dry weight) compared with small fish (≤200 mm TL; 1.1% dry weight).

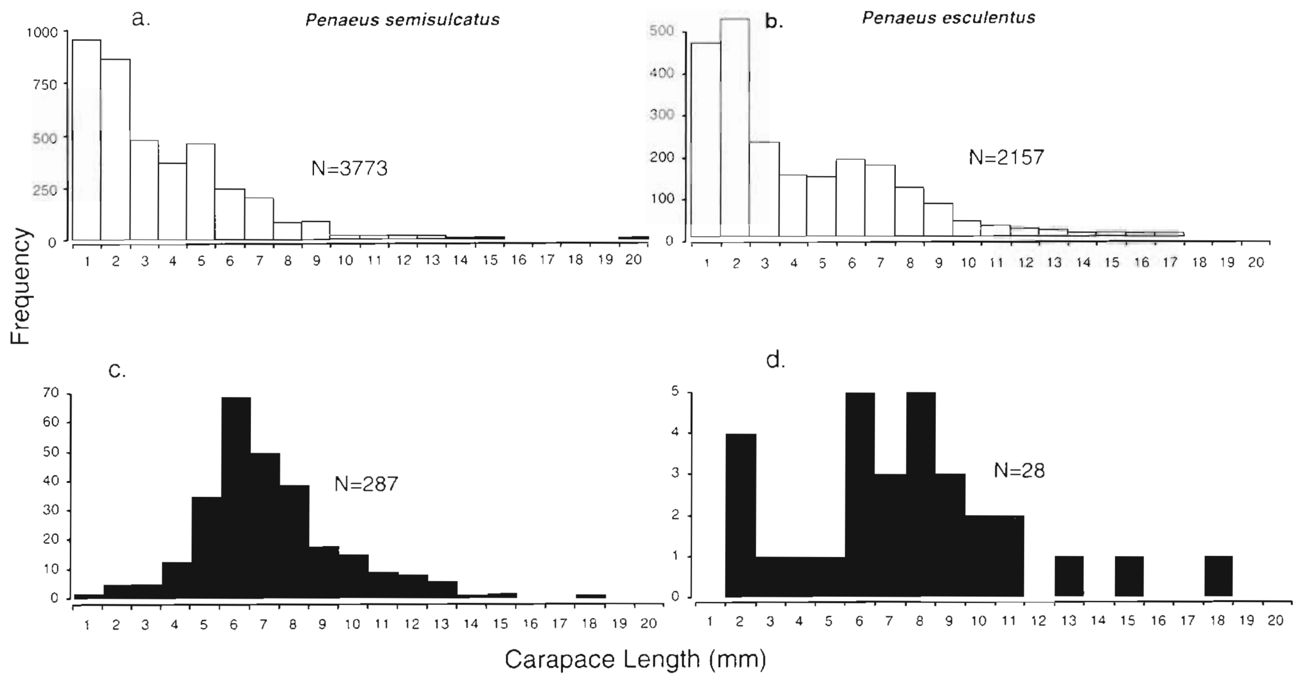


Fig. 5. Carapace length frequency of (a) *Penaeus semisulcatus* and (b) *P. esculentus* caught in the beam trawl from seagrass beds SG1 and SG2 and (c) *P. semisulcatus* and (d) *P. esculentus* recovered from the stomachs of fish caught on the seagrass beds during the same period

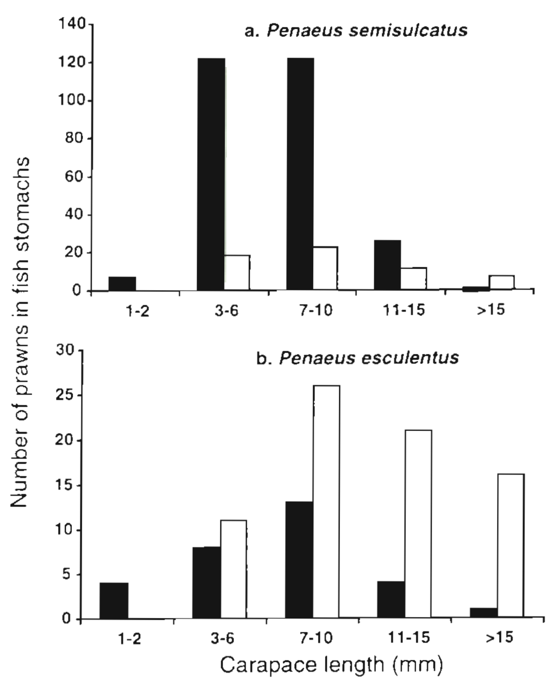


Fig. 6. *Penaeus semisulcatus* and *P. esculentus*. Carapace length frequency distributions of prawns from fish stomachs obtained from this study (filled bars) and from Groote Eylandt, Australia (open bars) (Brewer et al. 1995)

## DISCUSSION

Although crustaceans were the dominant prey group found in the stomachs of fish on seagrass beds, very few (<10%) of the fish stomachs that were examined contained penaeid prawns. Of the 37 fish species that ate prawns, 76% (numbers) of *Penaeus semisulcatus* and 43% of *P. esculentus* were eaten by a single species of fish (*Scomberoides commersonianus*). A previous study in the Embley River (Salini et al. 1990)

Table 6. Mean density (±1 SE) of prawns and 'prawn-like' animals (<30 mm total length) caught in a series of 10 drop-traps at SG1 on 16 October 1994

| Species | Mean density (no. $m^{-2}$) |
|---|---|
| *Penaeus esculentus* | 0.3 ± 0.21 |
| *Penaeus semisulcatus* | 0.3 ± 0.21 |
| Unidentified tiger prawn | 0.5 ± 0.24 |
| Stomatopod | 1.4 ± 0.75 |
| *Metapenaeus endeavouri* | 1.6 ± 0.52 |
| Mysid | 1.6 ± 0.47 |
| Tanaeid | 2.0 ± 0.47 |
| *Metapenaeus* spp. | 3.6 ± 0.9 |
| Sergestid | 3.6 ± 0.7 |
| Isopod | 4.8 ± 1.2 |
| Alphaeid | 5.6 ± 1.85 |
| Amphipod | 11.9 ± 2.57 |
| Carid | 59.8 ± 7.63 |

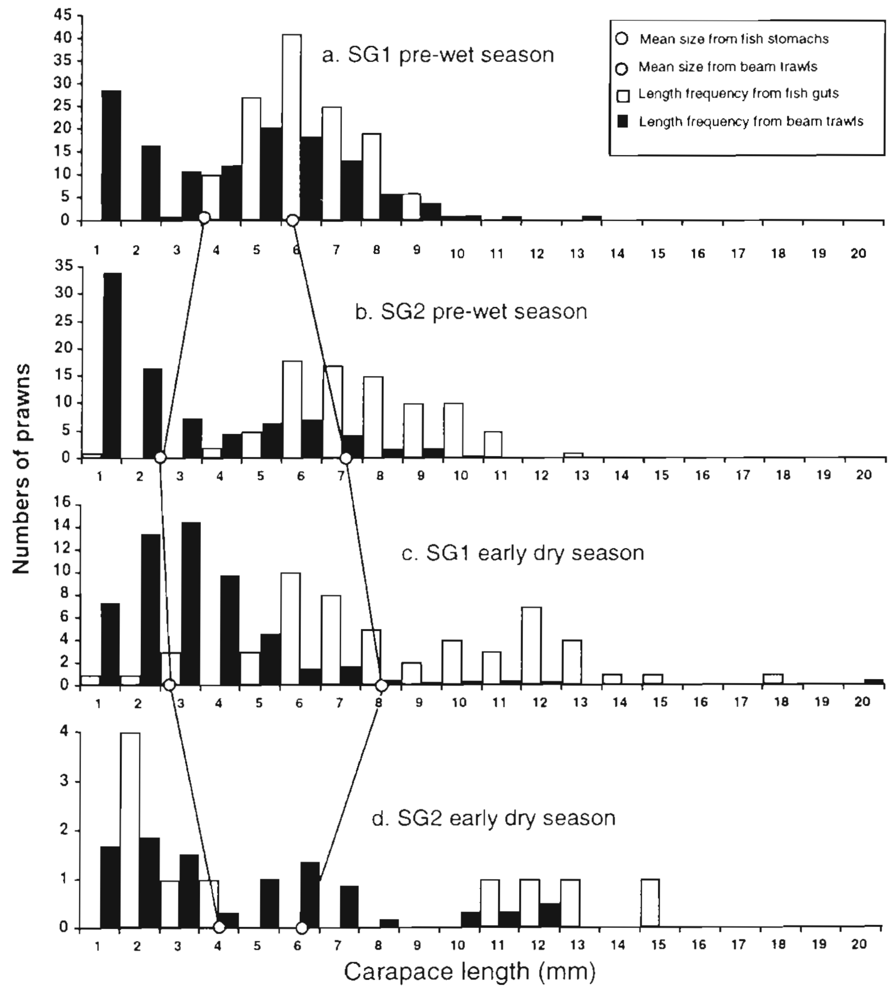


Fig. 7 *Penaeus semisulcatus*. Carapace length frequency distributions (histograms) and mean sizes of prawns caught in beam trawls (18 and 26 October 1993 = pre-wet season and 10 and 18 April 1994 = early dry season) and found in gill-netted fish stomachs (22–25 October 1993 and 14–17 April 1994) at sites SG1 and SG2. Numbers of prawns caught in beam trawls have been scaled so that the total is equal to the number found in fish stomachs

found *S. commersonianus*, *Polydactylus sheridani* and *Lates calcarifer* to be the most important penaeid predators. Salini et al. (1990) included *Penaeus merguiensis* in their PPI estimate and they also sampled fish from a variety of other habitats within the estuary. In our study we only caught 1 *Polydactylus sheridani* with food in its stomach so this species was not included in our estimates of PPI. We only caught 5 *L. calcarifer* that contained food; despite this, they were the third most important predator of *Penaeus semisulcatus* because of the relatively high proportion (75.7%) of *P. semisulcatus* in the penaeid part of their diet. *S. commersonianus* was also identified as the most important predator of juvenile tiger prawns on seagrass beds in the western Gulf of Carpentaria (Brewer et al. 1995). Several shark species, in particular *Rhizoprionodon acutus* and *Carcharhinus sorrah*, were also important in this region.

Despite the fact that we targeted small fish by using beam trawls and seines, the small tiger prawns were under-represented in the predators' stomach contents, which suggests that fish are not important predators of small tiger prawns. Postlarvae and small juvenile penaeids can be digested quickly by fish (Haywood 1995) and this could partly explain the low numbers of small prawns we found in fish stomachs. However, we minimised this effect by removing fish from the nets frequently and freezing the fish stomachs and their contents very soon after capture. While fish predation did not seem to be an important source of mortality of postlarval and small penaeids in this study, its effect was greater than previous studies had suggested, e.g. Brewer et al. (1995).

Another reason for the low numbers of postlarval and small juvenile tiger prawns found in fish stomachs could be that predators of small 'prawn-like' prey have a much larger choice of prey species than predators of larger 'prawn-like' prey. In a series of 10 drop-traps on the *Enhalus acoroides* beds (SG1), we found much higher densities of small (<30 mm total length) 'prawn-like' species (e.g. carids, amphipods, alphaeids, isopods, sergestids, tanaeids, mysids and stomatopods) than tiger prawns (Table 6), despite these samples being taken at a time of year when *P. semisulcatus* densities were likely to be high (Vance et al. 1996). Very few of these 'prawn-like' crustaceans (apart from the prawns) grow much larger than 30 mm TL, and so, at larger sizes, prawns are a larger proportion of the available suite of 'prawn-like' prey. Predators of larger crustaceans may, therefore, be more likely to prey on prawns than on other Crustacea. This idea is supported by the finding that large penaeid predators eat a larger proportion of tiger prawns than do small penaeid predators.

It is possible that fish are actively selecting for the largest prawns available. Foraging theory suggests that, in order to minimise the energy cost-benefit ratio, predators should select a few large prey rather than many smaller prey (Schoener 1971, Stephens & Krebs 1986). Other studies have demonstrated positive size selection in laboratory experiments. Main (1985) observed that 2 predatory fishes preferred large caridean shrimp over small shrimp. Using fish and meiofauna from South African rockpools, Gibbons (1988) found that fish typically took the largest prey available, and, unless they were starved, they ignored the smaller prey. In mesocosms and microcosms, fish and jellyfish predators generally selected the largest larval capelin (*Mallotus villosus*) available (Litvak & Leggett 1992).

If fish are not major predators of postlarval and small juvenile tiger prawns, then some other explanation must be found for the apparent high mortality rates observed in the field. Wading birds, in particular royal spoonbills *Platalea regia*, are an important predator of the palaemonid shrimp *Machrobracium intermedium* in Western Port Bay, in southeastern Australia (Howard & Lowe 1984). However, during a 6 yr study in this estuary we noticed very few wading birds on the seagrass beds. Cannibalism has been suggested as a source of mortality of blue crab megalopae (postlarvae; K. Metcalf pers. comm.); however, analysis of stomach contents of juvenile *Penaeus semisulcatus* did not reveal any evidence of cannibalism (Heales et al. 1996). Other invertebrate inhabitants of the seagrass beds may be important predators of postlarval and small juvenile tiger prawns and future predation studies should examine animals other than fish. Laboratory studies have demonstrated high levels of predation of blue crab megalopae by both sand shrimp *Crangon septemspinosa* and grass shrimp *Palaemonetes pugio* (Olmi & Lipcius 1991) and it is possible that some of the carids found in our drop-trap sampling are eating postlarval tiger prawns.

Many studies have reported that predation rates on small benthic animals are reduced in areas of increased habitat complexity (e.g. Wahle & Steneck 1992, Minello 1993, Irlandi 1994, Kenyon et al. 1995). It is not the presence of physical structure per se that results in decreased predation. Other factors that are important are: that the prey species demonstrate some behavioural characteristic which takes advantage of the physical structure (e.g. clinging to seagrass blades; Main 1987); the feeding mode of the predator (Minello & Zimmerman 1983); and the relative sizes of predator and prey (Ryer 1988). Although the number of data points is small, our results suggest that, for *Penaeus semisulcatus*, seagrass structure is not important in providing protection from predation. This may be related to the behaviour of juvenile *P. semisulcatus*. In night-time laboratory studies, juvenile *P. semisulcatus* spent equal amounts of time on bare sand and artificial seagrass (Hill & Wassenberg 1993). However, during dark nights in the field, we have observed many *P. semisulcatus* swimming up in the water column above the seagrass, where the seagrass is unlikely to offer any protection. Since our gill netting was always done shortly after the new moon and the major predators were *Scomberoides commersonianus*, which are pelagic, this may explain why seagrass was not important in reducing predation at the high seagrass biomass site (SG1). Similarly, laboratory studies have demonstrated increased predation rates on juvenile brown shrimp *P. aztecus* by southern flounder *Paralichthys lethostigma* in turbid water compared with clear water (Minello et al. 1987). They explained this finding as the result of a combination of the feeding tactics of the flounder and the increased activity and swimming behaviour of the brown shrimp under turbid conditions.

The mortality indices of *Penaeus semisulcatus* were generally higher than those of *P. esculentus*. If this is an accurate reflection of the difference in mortality rates between the 2 species, it may be explained by their behavioural differences. As noted previously, *P. semisulcatus* divide their night-time activity equally between seagrass and bare areas. In contrast, *P. esculentus* spend over 80% of their time at night within the seagrass (Hill & Wassenberg 1993), thereby gaining more protection from predation than *P. semisulcatus*.

The total number of *Penaeus semisulcatus* found in fish stomachs increased with the numbers of *P. semisulcatus* on the seagrass beds. In laboratory experiments, predation of juvenile brown shrimp *P. aztecus* also increased in proportion to prey density (Minello et al. 1989). There are 2 possible explanations for this observation: either increased prey numbers attract more predators into the area or individual predators respond to increased prey density by eating more prey individuals. Our results suggest the latter, since the mean number of *P. semisulcatus* per fish stomach increased with the density of *P. semisulcatus* on the seagrass beds, whereas there was no relationship between the mean number of *P. semisulcatus* on the seagrass and the $TPPI_{gill\ nets}$.

We were unable to quantify the component of natural mortality of *Penaeus semisulcatus* that was due to predation by fish because it is not possible to estimate the area sampled by gill nets. Despite this limitation, our study has identified the major fish predators of juvenile tiger prawns and provides evidence that fish predators do not significantly affect numbers of post-larval and very small juvenile tiger prawns. Future work in this area should focus on identifying alternative causes of mortality.

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