Marine Biology 96, 193–205 (1987)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia*

A. I. Robertson and N. C. Duke

Australian Institute of Marine Science; P.M.B. No. 3, Townsville MC, Queensland 4810, Australia

Abstract

Daytime sampling of mangrove and seagrass (*Halophila/Halodule* community) habitats every 7 wk at Alligator Creek, Queensland, Australia, over a period of 13 mo (February 1985–February 1986) using two types of seine net, revealed distinct mangrove and seagrass fish and crustacean faunas. Total abundance of fish and relative abundance of small and large fish also varied between habitats and seasonally. Post-larval, juvenile and small adult fish captured with a small seine-net (3 mm mesh) were significantly more abundant (4 to 10 times) in the mangrove habitat throughout the 13 mo of sampling. Mangrove fish abundance showed significant seasonality, greatest catches being recorded in the warm, wet-season months of the year. Relative abundances of larger fish (captured in a seine net with 18 mm mesh) in the two habitats varied throughout the year, but did not show a seasonal pattern. At the same site, small crustaceans were significantly more abundant in the mangroves in all but one dry-season sample. Similar comparisons for three riverine sites, sampled less frequently, in the dry and wet seasons of 1985 and 1986, respectively, showed that in general mangrove habitats had significantly more fish per sample, although the relative abundance of fish in mangroves and other habitats changed with season. Crustacean catches showed a similar pattern, except that densities among sites changed with season. Fish and crustacean abundance in mangroves varied among sites, indicating that estuaries differ in their nursery-ground value. The juveniles of two commercially important penaeid prawn species (*Penaeus merguiensis* and *Metapenaeus ensis*) were amongst the top three species of crustaceans captured in the study, and both were significantly more abundant in the mangrove habitat. By contrast, mangroves could not be considered an important nursery for juveniles of commercially important fish species in northern Australia. However, based on comparisons of fish catches in other regions, the results of the present study indicate the importance of mangroves as nursery sites for commercially exploited fish stocks elsewhere in South-East Asia.

* Contribution No. 378 from the Australian Institute of Marine Science

Introduction

As Boesch and Turner (1984) have pointed out, it is almost an article of faith amongst estuarine scientists that coastal wetlands, such as mangrove forests, are important nursery sites for juvenile fish and crustaceans. However, despite the extensive literature on the nekton of mangrove habitats (e.g. Austin, 1971; Lindall *et al.*, 1973; Odum and Heald, 1975; Blaber, 1980; Staples, 1980a, b; Yanez-Arancibia *et al.*, 1980; Bell *et al.*, 1984), the nursery-ground value of mangroves remains unclear. This is because few studies have used balanced sampling stategies which provide concurrent data on the densities of fish and crustaceans in mangroves and control (non-mangrove) sites.

In Florida, Lindall *et al.* (1973) have provided some of the best evidence for the importance of nearshore, mangrove-dominated areas as refuges for juvenile fish and crustaceans by comparing catches per unit effort of nekton for stations on transects perpendicular to the south-west coast of Florida. They showed that average catches were up to an order of magnitude greater in inshore sites near mangroves than at sites just outside the land fringe in 1 to 2 m water depth. Unfortunately, it is difficult to determine the exact role of mangroves in that region, since small mangrove islands are intimately mixed with shallow seagrass beds (Lindall *et al.*, 1973). Whether the preferred habitat of nektonic species is mangroves, seagrass or a combination of both is problematical in such a complex habitat. In Australia, only Blaber *et al.* (1985) have attempted to compare fish densities in mangroves and nearby habitats. Unfortunately, those authors gave no estimates of variances associated with mean catch rates, precluding an unambiguous picture of the importance of mangrove habitats at their Western Australian study site. Perhaps the best evidence for the nursery-ground function in Australian mangroves comes from a study of habitat preferences of juvenile penaeid prawns (Staples *et al.,* 1985) in which immature banana prawns, *Penaeus merguiensis,* were found to be restricted to parts of estuaries which had a mangrove fringe. However, no study from the Indo-West Pacific region has systematically compared the densities and species compositions of entire fish and crustacean communities in mangroves and adjacent non-mangrove habitats. Given the rate of removal and non-fisheries exploitation of mangrove forest in this region (Saenger *et al.,* 1983), there is a pressing need for a clear understanding of the relationships between mangroves and juvenile fish and crustaceans.

In this paper we compare the daytime abundance and species composition of fish and crustaceans for mangroves and their adjacent nearshore habitats in tropical north-eastern Australia. We chose four estuarine mangrove systems and their adjacent habitats (seagrass or sandflats) for study. One site was sampled intensively to provide information on seasonal variation in densities and species composition among mangrove and seagrass habitats, whereas the fauna of the three remaining sites was sampled only twice during the study to allow (1) comparison between habitats for a number of sites, and (2) assessment of the variation in abundance and structure among mangrove habitats.

Materials and methods

Study sites

Mangrove and seagrass fauna were sampled approximately every 7 wk at Alligator Creek, Queensland, Australia (Fig. 1) for a period of 13 mo (February 1985–February 1986). This small estuary lies in an area of the dry tropics where the average annual rainfall is 1 215 mm. Forests of *Rhizophora stylosa, Ceriops tagal* and *Avicennia marina* dominate the mangrove vegetation of Alligator Creek, although a total of 17 species of mangroves has been recorded for the estuary (N. C. Duke, unpublished data). At low tide, the depths of water in the mainstream and smaller creeks draining the forest are 5 and 0.5 m, respectively. The maximum tidal range in this, and other estuaries studied, is ~3.5 m.

The seagrass sampling site was 1 km north-east of the mouth of the estuary on the extensive mudflats that are characteristic of this region of the coast. Four species of seagrasses, *Halophila ovalis, H. spinulosa, Halodule* sp. and *Cymadocea rotundata* form patchy meadows on the mudflats. Water depths over the seagrass sampling site ranged from 0 to 3 m, depending on the stage of the tide. Seasonal changes in water temperature, salinity and water clarity (Secchi disc depth) in the mainstream of the mangrove habitat and over the seagrass flats near Alligator Creek are shown in Fig. 2.

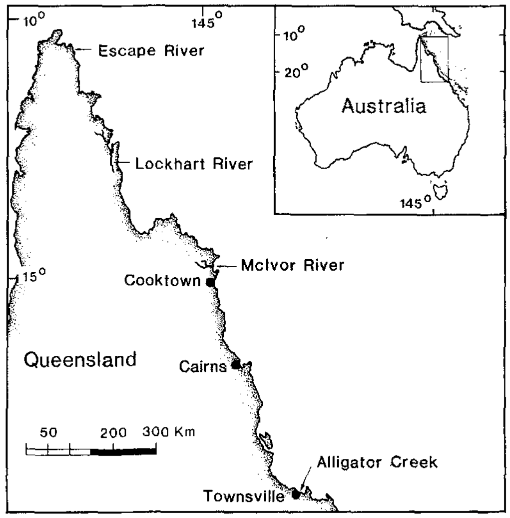

Fig. 1. Location of the four sampling sites (Alligator Creek, and the McIvor, Lockhart, and Escape Rivers in north-eastern Australia

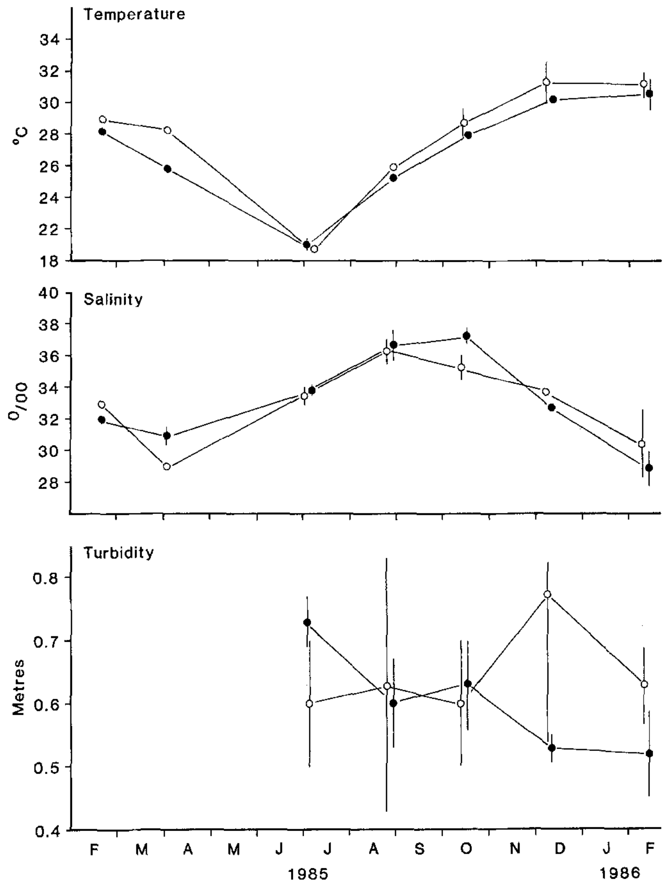

Fig. 2. Means (±1 SE) of water temperature, salinity and water clarity for mangrove (●) and seagrass (○) habitats at Alligator Creek during sampling period

Three other riverine mangrove systems and their neighbouring habitats on Cape York in far north Queensland (Fig. 1) were also sampled for nekton in the dry and wet seasons of 1985 and 1986, respectively (see "Sampling de-

Table 1. Ranges of physical parameters for sampling sites on Cape York, north Queensland, during dry (July, 1985)- and wet (January 1986)-season sampling periods

Site	Water temp. (°C)	Salinity (‰)	Water clarity (m)
McIvor River			
Dry season			
mangrove	22.1–25.8	8–15	0.65–1.20
sand	20.9–21.0	25–28	> 3.00
Wet season			
mangrove	27.0–28.5	15–27	0.65–2.00
sand	27.5–28.4	25–30	1.90–2.10
Lockhart River			
Dry season			
mangrove	23.2–25.2	31–32	1.10–1.30
seagrass	25.1–26.0	32	1.10–1.50
Wet season			
mangrove	26.8–29.2	8–24	0.30–0.90
seagrass	28.2–30.0	20–25	1.00–1.20
Escape River			
Dry season			
mangrove	24.2–24.8	32	1.10–1.30
sand	25.2–25.3	34	0.90–1.00
Wet season			
mangrove	26.0–27.2	12–26	0.40–0.50
sand	27.5–29.0	20–26	0.40–0.50

sign and data analysis" for details). The estuaries of the three rivers, the McIvor, Lockhart and Escape (Fig. 1) represent a gradient in terms of sediment characteristics. The percentage of sand in the sediment increases from the Lockhart through the Escape to the McIvor River. Alligator Creek sediments are similar to those of the Lockhart River. Sediments in the McIvor River are almost pure silica sand in places, with accumulations of organic muds occurring only in quiet river bends and behind sand bars. Ranges of water temperature, salinity and water clarity in all habitats of the three Cape York sites are listed in Table 1.

Rhizophora stylosa, R. apiculata and *Bruguiera gymnorrhiza* dominated the mangrove forests at the seaward end of the Lockhart and Escape estuaries where all mangrove sampling took place. *R. stylosa, Sonneratia alba, Avicennia marina* and *Ceriops tagal* were the dominant mangroves at the sampling sites within the McIvor estuary. Totals of 26, 31 and 31 species of mangroves have been recorded from the McIvor, Lockhart and Escape estuaries, respectively (N. C. Duke, unpublished data).

The major habitat type adjacent to the mangroves at Lockhart River was seagrass flat dominated by *Halophila ovalis* and *Halodule* spp. Open sand flats were the dominant habitat adjacent to mangrove forests at both the McIvor and Escape Rivers.

Field methods

A small pocket-seine net 6 m in length, 2 m deep and with 3 mm mesh throughout, was used to sample post-larval and juvenile fish in small, shallow mangrove creeks and similar water depths over seagrass beds. In the mangrove creeks, the net was dragged by two people for ten paces, closed-off and brought to the surface in mid-stream. The same procedure was followed over seagrass flats except that the net was dragged for twenty paces before closing.

A large seine-net, 30 m long, 1.5 m depth with 18 mm mesh throughout, was used to sample larger, more mobile fauna on mudbanks within the mangrove estuaries and over seagrass or sand banks. The net was set by hand in a semi-circle from the mangrove fringe, or the beach in the case of seagrass and other habitats, and then drawn onto the shore by two people. The net was used in water between 0.5 and 1.5 m deep. All samples with both seine nets were taken at or near low tide during the day. Samples from different habitats were taken within 2 h of each other at the Alligator Creek site, but this tight scheduling was not always possible for the more remote northern rivers, and habitats were sometimes sampled on different days.

Animals from each replicate netting were either preserved (10% formalin-seawater solution) or placed on ice in the field for later sorting in the laboratory. In the laboratory, all animals were identified, counted and species' groups were weighed.

Sampling design and data analysis

At the Alligator Creek site, both habitats were sampled with each net at about 7 wk intervals between February 1985 and February 1986. Usually three (and rarely four) replicate nettings with each net were performed in each habitat/time combination. All analyses of density data are based on the first three nettings taken in each habitat/time combination. Two-way analyses of variance (ANOVA) with habitats and times as fixed factors, were used to compare the equality of mean numbers of fish or crustaceans per netting. For small-seine nettings, catches were standardized to numbers of fish per 10-pace netting. Homogeneity of variance of cell means was tested using Cochran's test or the $F_{max.}$ test before ANOVAs were performed; raw data were transformed [$\log_{10}(x+1)$] where necessary.

For the three northern sites, sampling was possible on two days only at each site during each visit. Mangroves and their most common adjacent habitat (seagrass flats at Lockhart River; sand flats at the McIvor and Escape Rivers) were sampled with both nets ($n=3$ samples for each net/habitat combination). Three-way ANOVAs, with site (estuary), time of year and habitat as factors, were used to compare mean catch rates after appropriate transformations of the raw netting-data. Not all sites could be compared in one ANOVA because neither seagrass flats nor sandflats occurred in all sites. Hence, estuaries with seagrass flats nearby (Alligator Creek and Lockhart River) were analyzed separately from estuaries with adjacent sand flats (McIvor and Escape Rivers).

Analyses of the catch data for crustaceans were hampered by the extreme variability exhibited by the sergestid

Table 2. Catch of major fish species in mangrove, seagrass and sand habitats at all sites. Captured life-history stages are given for each species: A, adults; J, juveniles. Species of economic importance in Australia, *, and elsewhere in South East Asia, (*), are denoted. Numbers in parentheses over each column are number of nettings in each habitat-site combination

Species	Alligator Creek		McIvor River		Lockhart River		Escape River		Total		Life-history stage
	man-grove (44)	sea-grass (43)	man-grove (18)	sand (12)	man-grove (12)	sea-grass (13)	man-grove (12)	sand (12)	man-grove (86)	seagrass and sand (80)	
Priopridichthys gymnocephalus (Chandidae) (*)	13 943	42	1	0	70	0	867	0	14 881	42	A, J
Stolephorus indicus (Engraulidae) (*)	62	1 324	1 922	2	1	0	52	0	2 037	1 326	J
Leiognathus equulus (Leiognathidae) (*)	2 627	12	1	0	304	27	74	2	3 006	41	J
Ambassis buruensis (Chandidae) (*)	218	26	0	0	33	2	735	4	986	32	J
Leiognathus splendens (Leiognathidae) (*)	293	123	0	0	329	84	2	2	624	209	J
Pranesus eendrachtensis (Atherinidae)	33	2	0	0	201	0	496	3	730	5	A, J
Pseudomugil signifer (Pseudomugilidae)	681	2	0	0	0	0	0	0	681	2	A, J
Herklotsichthys castelnaui (Clupeidae) * (*)	50	1	0	0	538	0	1	0	589	1	J
Drombus ocyurus (Gobiidae)	479	44	0	0	1	45	1	0	481	89	A, J
Stolephorus bataviensis (Engraulidae) (*)	29	468	0	0	21	1	0	3	50	472	J
Pseudomugil inconspicuus (Pseudomugilidae)	0	0	0	0	0	0	429	0	429	0	A, J
Nematalosa come (Clupeidae) (*)	78	1	9	0	72	0	153	0	312	1	J
Gerres argyreus (Gerridae)	41	29	40	27	16	15	142	0	239	71	J
Chelanodon patoca (Tetradontidae)	257	12	14	0	0	0	0	3	271	15	J
Gazza minuta (Leiognathidae) (*)	118	9	0	0	133	0	7	1	258	10	J
Anodontostoma chacunda (Clupeidae) (*)	24	0	8	0	178	0	53	0	263	0	J
Acanthopagrus berda (Sparidae) *	231	3	0	0	6	0	6	0	243	3	J
Favonigobius sp. (Gobiidae)	4	43	145	1	1	44	1	0	151	88	A, J
Acentrogobius caninus (Gobiidae)	5	0	0	0	101	9	115	0	221	9	A, J
Thryssa hamiltoni (Engraulidae) * (*)	221	0	0	0	1	0	0	0	222	0	J
Leiognathus decorus (Leiognathidae) (*)	79	99	0	0	25	1	2	2	106	100	J
Liza subviridis (Mugilidae) * (*)	56	121	0	0	0	0	0	0	56	121	J
Sillago sihama (Sillaginidae) * (*)	68	21	39	1	0	1	1	40	108	63	J
Apogon ceramensis (Apogonidae)	0	0	0	0	0	0	154	1	154	1	A, J
Zenarchopterus buffonis (Hermiramphidae) * (*)	84	0	0	0	38	0	16	0	138	0	A, J
Secutor ruconius (Leiognathidae) (*)	32	37	0	0	7	13	0	42	39	92	J
Escualosa thoracata (Clupeidae) *	37	84	0	0	0	0	0	0	37	84	J
Drombus globiceps (Gobiidae)	34	16	1	0	4	0	58	0	97	16	A, J
Siganus guttatus (Siganidae) (*)	69	18	6	0	2	1	1	0	78	19	J
Arramphus sclerolepis (Hermiramphidiae) * (*)	7	53	0	0	0	26	0	10	7	89	A, J
Others	829 (73 spp.)	654 (91 spp.)	186 (27 spp.)	32 (12 spp.)	114 (27 spp.)	147 (26 spp.)	150 (25 spp.)	79 (26 spp.)	1 279 (103 spp.)	912 (123 spp.)	
Total	20 689	3 244	2 372	63	2 196	416	3 516	190	28 773	3 913	

prawn *Acetes sibogae*. Although this was the most abundant species in the total catch from all sites and habitats (see Table 3), it occurred in only 69 and 56% of small-seine nettings at Alligator Creek and the other sites, respectively. The means and ranges of the coefficient of variation for catches of *A. sibogae* in mangroves and seagrass at Alligator Creek were 111% (79 to 137) and 135% (86 to 173), respectively. Given these levels of temporal and spatial variability, data for *A. sibogae* were removed from the data set for total crustaceans during analyses of mean total crustacean densities and comparisons of crustacean species composition. Data for *A. sibogae* were analyzed separately.

All comparisons of species composition were made using an agglomerative, hierarchical classification technique. Bray-Curtis similarity coefficients (Bray and Curtis, 1957) were calculated between all groups used in a comparison, the two most similar groups were fused to form a cluster, and the process was repeated using Burr's incremental sums-of-squares strategy (Burr, 1970). Species lists for each habitat/time combination used in the analyses were obtained by pooling data from the three small and three large seine nettings.

Statistical comparisons of mean catches for individual species were often not necessary, because many fish and crustacean species were captured almost exclusively in one habitat. For those species represented by large numbers in mangrove and other habitats, heterogeneity chi-square tests were used on data pooled within months, to compare densities across habitats. For the chi-square tests, months with total catches less than 10 were excluded from the analyses.

Results

Total catches, all sites

Two hundred and three species of fish and 47 species of crustaceans were captured during the entire sampling program. Mangrove habitats yielded 133 fish species, with ten species making up more than 85% of the total catch (Table 2). The perchlet *Priopridichthys gymnocephalus* was by far the most abundant mangrove fish-species. Nettings over seagrass and sand habitats adjacent to mangroves yielded 159 fish species, with the top ten species accounting for 68% of the catch. Nineteen of the top 30 species captured were represented entirely by juveniles (Table 2). Only 8 of the top 30 fish species from all habitats are important commercial, bait or sport fishes in Australia. However 18 of the top 30 fish are harvested species elsewhere in South-East Asia.

Four prawn species, *Acetes sibogae, Penaeus merguiensis, Metapenaeus ensis* and *Leander tenuicornis* accounted for more than 99% of the total mangrove crustacean catch (total of 30 species) (Table 3). Seven species, *A. sibogae, M. ensis, Alpheus richardsoni, Periclimenes andamanensis, P. obscurus, Latreutes pygmaeus* and *L. porcinus* accounted for a similar proportion of the seagrass and sand catches. The sergestid *Acetes sibogae* was by far the numerical dominant in both habitats. Only three crustaceans, the commercially important penaeids *Penaeus merguiensis, P. semisulcatus* and *M. ensis* were represented entirely by juvenile individuals.

Habitat comparisons: Alligator Creek

Throughout the sampling period, daytime densities of postlarval and small juvenile fish captured with the small seine-net were significantly higher in mangroves than over seagrass flats (Fig. 3, Table 4). Mangroves harboured between four and ten times the total number of fish found over the seagrass habitat. Fish densities also exhibited seasonal changes in both habitats, with maximum and minimum densities occurring in austral summer (December–April) and winter (July–August), respectively (Fig. 3, Table 4).

The pattern of abundance across habitats changed with time for more mature fish captured with the large seine-net (Fig. 3), as evidenced by the highly significant habitat × time interaction of the ANOVA (Table 4). Fish were more abundant in mangroves in five of the seven sampling periods, but catches in mangroves and seagrass were similar in August and December (Fig. 3).

Crustaceans captured with the small seine-net (caridean and penaeid prawns and portunid crabs) were more abundant in the mangrove habitat throughout most of the year, except July (Fig. 4, Table 4). Large seine-net catches of crustaceans (mainly penaeid prawns and portunid crabs) showed seasonal changes in the pattern of densities across habitats (Fig. 4) as evidenced by the highly significant interaction term of the ANOVA (Table 4). These larger crustaceans were more abundant in the mangroves, except in April 1985 and February 1986 (Fig. 4).

Classification analyses of the Alligator Creek fish catches revealed the presence of distinct mangrove and seagrass faunas throughout the 13 mo of sampling (Fig. 5). The mangrove fishes also clustered into two further groups, a summer group (February 1985, 1986; December, April, 1985) and a winter group (July, August, October, 1985). The seagrass fish fauna changed throughout the year, forming two major clusters, one from samples taken early in the sampling period (February, April, July, 1985) and one from all subsequent samples (Fig. 5).

Crustacean catches (without *Acetes sibogae*) also clustered into distinct mangrove and seagrass faunas (Fig. 5). With the exception of the February 1986 crustaceans, mangrove crustaceans clustered into summer and winter groups (Fig. 5). Seagrass crustaceans split into two groups, one containing only the April and July, 1985 catches.

Habitat comparisons: all sites

Analysis of the fish-catch data from small-seine nettings in the two sites with seagrass beds adjacent to mangroves (Al-

Table 3. Catch of major crustacean species in mangrove, seagrass and sand habitats at all sites. Captured life-history stages are given for each species; A, adults; J, juveniles. Species of economic importance in Australia, *, and elsewhere in South East Asia, (*), are denoted. Numbers over each column are number of nettings in each habitat-site combination

Species	Alligator Creek		McIvor River		Lockhart River		Escape River		Total		Life-history stage
	man-grove (44)	sea-grass (43)	man-grove (18)	sand (12)	man-grove (12)	sea-grass (13)	man-grove (12)	sand (12)	man-grove (86)	seagrass and sand (80)	
Acetes sibogae (Sergestidae) (*)	37 492	61 721	3	0	9 165	348	3 150	15 164	49 810	77 233	A, J
Penaeus merguiensis (Penaeidae) * (*)	6 014	45	1	0	367	0	0	0	6 382	45	J
Metapenaeus ensis (Penaeidae) *	1 222	475	135	5	20	20	110	42	1 487	542	J
Alpheus richardsoni (Alpheidae)	10	757	0	0	2	1	1	0	13	758	A, J
Periclimenes andamanensis (Palaemonidae)	80	680	0	0	0	1	0	0	80	681	A, J
Periclimenes obscurus (Palaemonidae)	23	493	0	0	0	0	0	0	23	493	A, J
Leander tenuicornis (Palaemonidae)	473	0	0	0	1	0	31	0	505	0	A, J
Latreutes pygmaeus (Hippolytidae)	1	330	0	0	0	0	0	0	1	330	A, J
Latreutes porcinus (Hippolytidae)	3	265	0	0	0	0	0	0	3	265	A, J
Latreutes sp. (Hippolytidae)	1	190	0	0	0	0	0	0	1	190	A, J
Matuta lunaris (Calattidae)	0	140	0	1	0	0	0	3	0	144	A, J
Portunus pelagicus (Portunidae) * (*)	17	112	0	0	0	0	1	4	18	116	A, J
Penaeus semisulcatus (Penaeidae) * (*)	0	115	0	1	0	15	1	0	1	131	J
Palaemon serenus (Palaemonidae)	11	0	0	0	8	0	32	0	51	0	A, J
Macrobrachium sp. (Palaemonidae)	27	1	0	0	0	0	0	0	27	1	A, J
Others	122 (16 spp.)	118 (22 spp.)	4 (2 spp.)	1 (1 sp.)	12 (5 ssp.)	3 (2 spp.)	2 (2 spp.)	4 (2 spp.)	140 (16 spp.)	126 (25 spp.)	
Total	45 496	65 442	143	8	9 575	388	3 328	15 217	58 542	81 055	

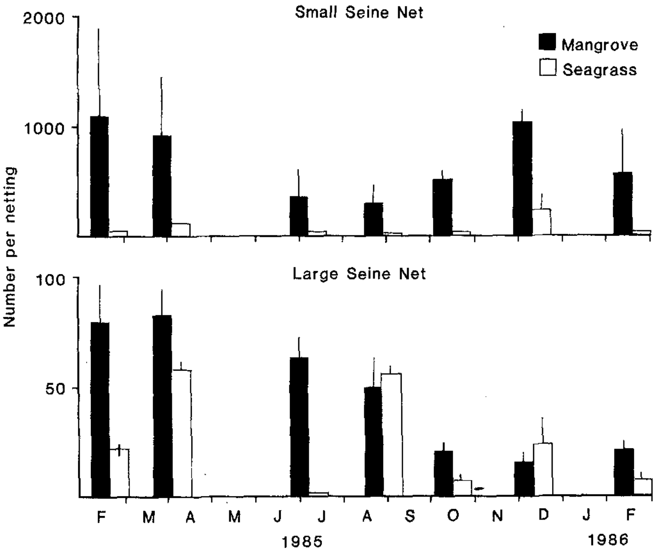

Fig. 3. Mean (±1 SE) numbers of fish per netting for both net tpyes in mangrove and seagrass habitats at Alligator Creek during sampling period

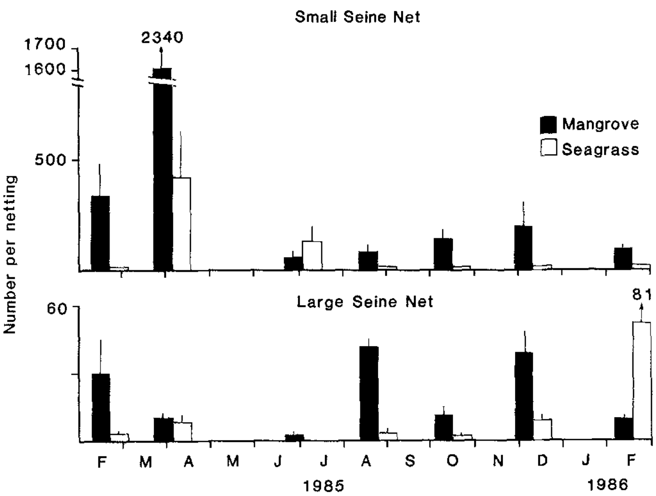

Fig. 4. Mean (±1 SE) numbers of crustaceans per netting for both net types in mangrove and seagrass habitats at Alligator Creek during sampling period

Table 4. Summary of two-way ANOVAs testing for similarity in mean total abundances of fish and crustaceans per netting across habitats (mangrove, seagrass) and time (seven dates) at Alligator Creek. Results for the two seine nets are presented separately. NS: not significant at $P=0.05$; *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$

Net and variate	Source of variation		
	Habitat	Time	Interaction
Small seine net			
Σ fish per netting	***	*	NS
Σ crustaceans per netting	***	***	***
Large seine net			
Σ fish per netting	***	***	***
Σ crustaceans per netting	***	***	***

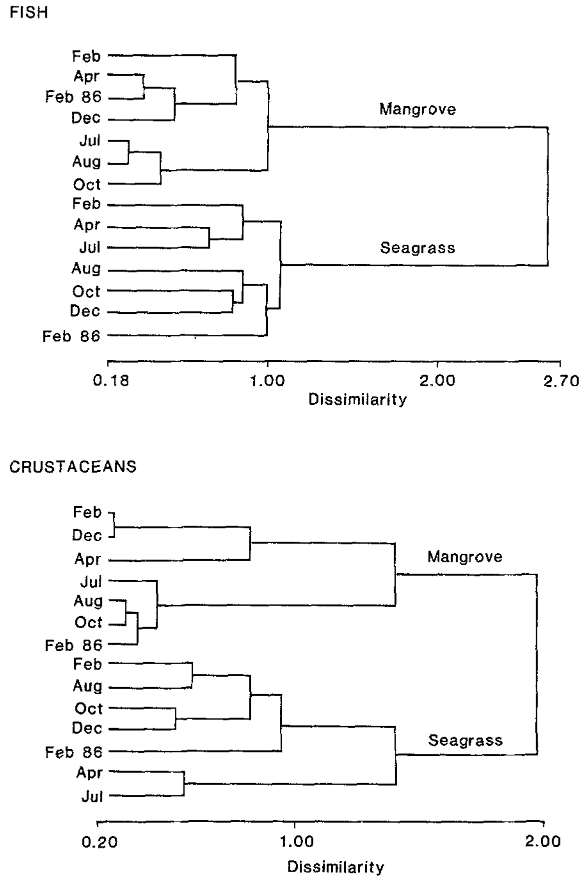

Fig. 5. Dendrograms from classification analyses of the 14 habitat/date records of fish and crustacean species abundance at Alligator Creek

ligator Creek and Lockhart River) revealed that fish were significantly more abundant in mangroves in both estuaries, and this pattern was similar in both seasons (Fig. 6, Table 5). Similar analyses of data from the McIvor and Escape Rivers indicated that numbers of fish per netting varied significantly between both habitat (mangroves or sandflats) and site (Fig. 6, Table 5). The significant habitat × time interaction in the analysis (Table 5) resulted from the substantial seasonal difference in mean catches in the McIvor River mangrove habitat.

Large-seine nettings yielded more fish in mangrove habitats in Alligator Creek and Lockhart River, while overall the Lockhart site had greater densities of fish during both seasons (Fig. 6, Table 5). Seasonal differences in relative catches occurred in mangroves and seagrass at both sites (habitat × time interaction, Table 5). Analysis of large-seine netting data from the McIvor and Escape Rivers indicated that while mangrove habitats harboured more fish than sand flats in all site/time combinations, overall the Excape River had greater fish densities (Fig. 6, Table 5). There were also seasonal differences in relative catches in mangrove and sand habitats at both sites (habitat × time interaction, Table 5). In addition, dry-season nettings, with both nets, over different substrates (mud vs sand) within the McIvor River mangrove habitat revealed that mud

Table 5. Summary of three-way ANOVAs comparing catches in different habitats for different sites and seasons (see "Materials and methods – Sampling design and data analysis"). Results for the two seine nets are presented separately. There were insufficient data for analyses of crustaceans captured by large-seine net. NS: not significant at $P=0.05$; *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$

Taxa (net) and sites	Source of variation						
	Site (S)	Time (T)	Habitat (H)	Interactions			
				S×T	S×H	T×H	S×T×H
Fish (small seine)							
Alligator Creek and Lockhart River	NS	NS	***	NS	NS	NS	NS
McIvor and Escape Rivers	**	NS	***	NS	NS	**	NS
Fish (large seine)							
Alligator Creek and Lockhart River	***	NS	***	NS	NS	**	NS
McIvor and Escape Rivers	*	NS	***	NS	NS	**	NS
Crustaceans (small seine)							
Alligator Creek and Lockhart River	***	*	***	***	NS	*	NS
McIvor and Escape Rivers	***	*	***	***	NS	*	NS

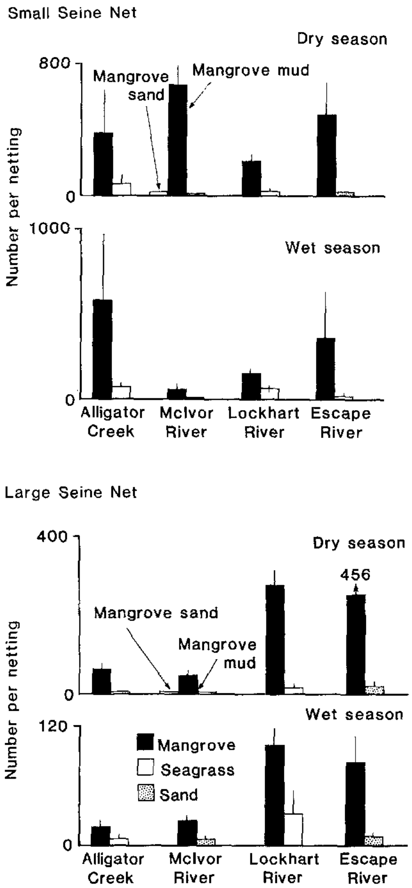

Fig. 6. Mean (±1 SE) numbers of fish per netting for both net types in mangrove and other habitats at four sites during two seasons. Note substantial differences between nettings over different substrates within the McIvor mangrove habitat in the dry season

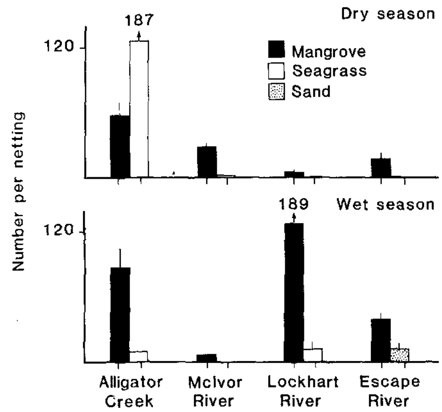

Fig. 7. Mean (±1 SE) numbers of crustaceans per small-seine netting in mangrove and other habitats at four sites during two seasons

areas harbour significantly (Student's t-tests, $P<0.001$) more fish (Fig. 6).

A dramatic increase in catches of crustaceans in the small seine occurred at Lockhart River during the wet season (site×time interaction, Table 5 and Fig. 7), and the relative abundance of crustaceans in mangroves and seagrass changed with season (habitat×time interaction, Table 5 and Fig. 7). Analysis of small-seine crustacean-catches from the McIvor and Escape Rivers indicated a significant seasonal shift in densities across habitats, with densities in the Escape lowest and highest in the dry and wet seasons, respectively (Fig. 7, Table 5). There were also changes in the relative abundances of crustaceans in mangroves and sand with season (habitat×time interaction; Table 5 and Fig. 7).

Among all four estuarine mangrove sites along the coast, there were significant differences in the catches for both fish and crustaceans (Table 6). The ranking of catches among estuaries changed with season for fish captured with the small seine-net (significant site×season interaction, Table 6) due mainly to the dramatic change in fish densities with season in the McIvor River (Fig. 6). However, more than 90% of the number of fish captured in the McIvor mangroves in July were anchovies, *Stolephorus* spp., which move readily between mangrove and other habitats in large schools (see below: "Single-species comparisons"). Removal of all *Stolephorus* spp. catch-data

Table 6. Summary of two-way ANOVAs comparing catches among the four mangrove estuaries during two seasons. NS: not significant at $P = 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.005$. There were insufficient data for analyses of crustaceans captured by large-seine net. Results for the two seine nets are presented separately

Net and variate	Source of variation		
	Site (Si)	Season (Se)	Interaction (Si × Se)
Small seine-net			
Σ fish per netting	NS	NS	*
Σ fish per netting (without *Stolephorus* spp.)	***	NS	NS
Σ crustaceans per netting	**	**	***
Large seine-net			
Σ fish per netting	***	*	NS

from the analysis of small-seine fish-data revealed that there were significant differences in catches of all other fish among sites, and that this pattern was consistent over time (Table 6). Alligator Creek and Escape River mangrove samples consistently had greater numbers of fish than those from Lockhart River, while the McIvor site always ranked lowest (Student-Newman-Keuls test). By contrast, in both seasons larger fish were more abundant in the Lockhart and Escape Rivers than in the other two estuaries, while more fish were captured during the dry season in all estuaries (Table 6, Fig. 6).

The relative abundance of mangrove-crustaceans among estuaries changed with time (Table 6, Fig. 7). In the dry season, greatest and smallest catches were recorded in Alligator Creek and Lockhart River, respectively. In the wet season, Alligator Creek and Lockhart River ranked highest, while lowest catches were recorded in the McIvor River.

Single-species comparisons

Of the ten most abundant fish species in all catches (which together made up 74% of the total catch), seven species, *Priopridichthys gymnocephalus, Leiognathus equulus, Ambassis buruensis, Pranesus eendrachtensis, Pseudomugil signifer, P. inconspicuus* and *Herklotsichthys castlenaui* were restricted almost entirely to mangroves at all sites (Table 2). The goby *Drombus ocyurus* was captured in greatest numbers in mangroves at Alligator Creek, but the reverse was true at Lockhart River. At Alligator Creek *Stolephorus indicus* was present in greatest numbers over seagrass flats in all months except October 1985 (chi-square tests). However the pooled data from the other three sites shows that *S. indicus* was found almost exclusively in the mangrove habitat. These data suggest that *S. indicus* moves readily between mangrove and adjacent habitats. For most months and sites (3 out of 4 comparisons), *Leiognathus splendens* was most abundant in the mangrove habitat.

Of the 15 dominant crustaceans, in all catches nine were restricted almost entirely to seagrass or sand habitats, and most of these were captured only at Alligator Creek. These included the commercially important *Portunus pelagicus* and *Penaeus semisulcatus* and a group of small caridean prawns (Table 3). Four species, the commercially important *P. merguiensis* and three small paelmonid prawns, were captured almost entirely in mangrove habitats at Alligator Creek and Lockhart River (Table 3). Only two species, the sergestid prawn *Acetes sibogae* and the commercially important *Metapenaeus ensis*, were captured in large numbers in all habitats at most sites.

At Alligator Creek, *Acetes sibogae* was most abundant in mangroves in all months except February 1986, when a massive catch (total of 60 895) was recorded from the seagrass habitat (chi-square tests). In the other estuaries, significantly more *A. sibogae* were captured over seagrass or sand habitats in both seasons. *Metapenaeus ensis* was most abundant in mangroves at Alligator Creek and in the other rivers in all but one month.

Discussion

Community structure

Mangrove fishes from Alligator Creek, Lockhart River and Escape River were dominated by the families Chandidae, Leiognathidae, Engraulidae, Atherinidae, Gobiidae, Clupeidae and Pseudomugilidae, typical of tropical mangrove systems elsewhere in the Indo-West Pacific region (Chua, 1973; Blaber, 1980; Krishnamurthy and Prince Jeyaseelan, 1981; Collette, 1983; but see Blaber *et al.*, 1985). There was often replacement of species by congeners or confamilials at different sites. For instance *Pseudomugil signifer*, an important member of the Alligator Creek mangrove fauna was replaced by *P. inconspicuus* in the Escape River (Table 2). Similar replacements were observed for members of the Gobiidae and Chandidae. However the mangrove fish fauna of the McIvor River was markedly different to that of the other sites, with only three families, Engraulidae, Gerridae and Gobiidae represented in large numbers (Table 2).

Apart from the sergestid *Acetes sibogae*, which was patchily distributed and abundant in all habitats, at Alligator Creek small resident caridean prawns of the families Alpheidae, Palemonidae and Hippolytidae were the dominant members of the seagrass crustacean fauna, as has been observed for seagrass systems elsewhere in Australia (Wadley, 1978; Young and Wadley, 1979; Howard, 1984). The mangrove crustaceans were dominated by juvenile penaeids, *Penaeus merguiensis* and *Metapenaeus ensis*, and small, resident Palaemonidae which are abundant in mangroves elsewhere in Australia (Staples, 1979; Staples *et al.*, 1985).

Factors responsible for differences between habitats

In addition to differences in community structure among habitats, the present study revealed that during the daytime post-larval and small juvenile fish and crustaceans (captured with the small seine-net) were significantly more abundant in mangroves than in all other habitats used for comparison. The only exception to this pattern was the July catches of crustaceans at the Alligator Creek site.

Why should mangrove habitats harbour different faunas and have greater densities of fish and crustaceans than nearby (~ 1 km) sites? Three factors have previously been cited as important determinants of the inshore distribution patterns of juvenile fish and crustaceans: (1) differences in physical factors between habitats; (2) differences in structural heterogeneity and thus the intensity of predation between habitats; and (3) differences in productivity and food availability between habitats.

Blaber and Blaber (1980) argued that water clarity has a major influence on habitat choice by juvenile fish in inshore waters, with turbid water providing greater protection from potential predators. It is unlikely that differences in water clarity influenced habitat choice by fish or crustaceans at Alligator Creek or the more northern sites, because in general, turbidity differed little between mangrove and other nearby habitats. However, water clarity may be important in explaining variation in densities on larger scales (i.e., among estuaries, see below: "Factors responsible for differences between mangrove sites"). It has also been suggested that low salinities may act as cues which guide juvenile prawns and fish to inshore nursery grounds (e.g. Hughes, 1969; Young and Carpenter, 1977). In the present study, there were no consistent patterns of salinity differences between habitats. Yet greatest densities of small fish and crustaceans were usually recorded in mangrove habitats at all sites. It seems unlikely, therefore, that differences in salinities influenced between-habitat differences in densities at each site.

The final choice of nursery sites within nearshore areas may depend on factors such as habitat structure and protection from predation (Heck and Orth, 1980) or levels of production and food availability (Odum and Heald, 1975). There is a growing number of experimental tests of the refuge value of seagrass and saltmarsh vegetation for small invertebrates (see Kneib, 1984; Orth *et al.*, 1984), but to date there has been only one study on the role of structure provided by intertidal macrophytes (saltmarsh and mangrove forests) in mediating predation on macrocrustaceans or fish. In laboratory experiments which compared rates of predation on juvenile *Penaeus aztecus* with different densities of simulated *Spartina* stems, Minello and Zimmerman (1983) showed that marsh-grass structure reduced predation rates on prawns by two of the four predatory fish which were common in nearby marshes. Similar laboratory and field experiments are needed in which mangrove prop-root densities are manipulated to alter the refuge structure available to juvenile fish, before we are able to say with certainty whether shelter from predation provided by mangrove prop roots, knee roots and overhanging branches is responsible for the greater density of juvenile nekton using mangrove habitats in Queensland.

Mangrove habitats have long been considered major feeding sites for juvenile fish and crustaceans because of the production of large quantities of detrital material (Odum and Heald, 1975). However, the food value of mangrove and other refractory detritus has recently come under question (e.g. Tenore *et al.*, 1982), and it may be that the complex food chains which are now believed to operate in mangrove systems (Odum *et al.*, 1982; Robertson, 1987) decrease the energy available to higher consumers in the system (e.g. Boesch and Turner, 1984). At present it is not possible to say whether juvenile fish and crustaceans occur in greater densities in mangrove habitats because they are sites of greater food abundance. However, work in progress on zooplankton standing stocks in all habitats at Alligator Creek (Dixon and Robertson, 1986; A. Robertson, unpublished data) will be used for future tests of the trophic dependence of zooplankton-feeding juvenile fish on mangrove forests.

It must be made clear at this point that our results on the densities of seagrass fauna refer only to beds dominated by species of *Halophila* and *Halodule*. Meadows of these species, although common, are short and sparse, thus providing poor cover for fish and macrocrustaceans. It is likely that the dense, relatively tall meadows of other seagrasses which occur in other parts of northern Australia (e.g. species of *Cymodocea* and *Enhalus*) harbor greater fish densities.

Factors responsible for differences between mangrove sites

Mangroves vary in their value as habitats for fish and crustaceans, as evidenced by the significant differences in the densities of both faunal groups among the four estuaries sampled in the present study. Factors responsible for between-site differences in densities fall into two categories: those operating outside mangrove habitats and those intrinsic to mangroves. The influence of offshore processes on the density of mangrove nekton is well illustrated by studies on the population dynamics of the banana prawn *Penaeus merguiensis* in the Gulf of Carpentaria in northern Australia. Between-year and between-site differences in the densities of offshore breeding stocks of *P. merguiensis* are responsible for variation in larval densities (Crocos and Kerr, 1983). Seasonal and spatial differences in current patterns coupled with the vertical migratory behaviour of the larvae result in different advection patterns of larvae (Rothlisberg, 1982; Rothlisberg *et al.*, 1983) and cause significant between-site and between-season differences in the number of post-larvae and juveniles found in mangrove habitats around the Gulf (Staples, 1979).

It is probable that similar temporal and spatial variation in recruitment processes influenced the patterns of abundance of small crustaceans among estuaries in the present study. A dramatic increase in the mean abundance of juvenile banana prawns *Penaeus merguiensis* in the

Lockhart River was responsible for the observed greater total catches of crustaceans in that river during the wet season. Few *P. merguiensis* were ever captured in the Escape River, but large numbers of very small *Metapenaeus ensis* were responsible for the increase in the wet-season mean-total catches at that site. At the most southern site, Alligator Creek, *M. ensis* was abundant in the dry season but rare in the wet season (own unpublished data), while the reverse was true for *P. merguiensis,* which recruited heavily during the summer wet months (own unpublished data). The results was that mean total catches of crustaceans remained constant with time. Mean total catches of crustaceans in the McIvor River fell during the wet season, indicating a failure of recruitment at that site.

Because we lack detailed information on large-scale variation in recruitment patterns of most of the juvenile fish captured in the present study, it is difficult to speculate on whether offshore processes influenced the observed between-site variation in fish abundance. However, the fish data revealed some intriguing patterns. For instance, in both seasons small-seine catches in Alligator Creek and Escape River yielded more fish than those from the Lockhart River, while the McIvor River always had the lowest mean catches (based on analysis of the data without *Stolephorus* spp.). However, larger fish were always more abundant in the Lockhart and Escape Rivers.

One likely hypothesis which explains the low catches of large fish in Alligator Creek and McIvor River could be that low mangrove primary production in these estuaries is reflected in lowered carrying capacities of higher consumers. The very sandy sediments in the McIvor River contain low concentrations of phosphorus, which has a strong negative influence on mangrove primary production (Boto and Wellington, 1983; Boto *et al.,* 1984; Boto, personal communication). Some of the lowest potential net primary-production estimates (*sensu* Bunt *et al.,* 1979) for forests on Cape York in north-eastern Australia have been made at the McIvor River (K. G. Boto, personal communication). Large catches of fish in the McIvor were recorded only in areas of the river which accumulated organic-rich sediments, which presumably are richer feeding grounds for fish. Alligator Creek differs from the more northern sites in having only a fringe of mangrove forest and extensive high intertidal clay pans, owing to the low annual rainfall at that site. A small ratio of forest area to area of water would result in a lower potential input of mangrove detritus to the waterways.

The above hypothesis does not, however, account for the relatively high abundance of juvenile fish (small-seine nettings) in mangroves at Alligator Creek. One possible explanation for this pattern is that predation pressure on juvenile fish in Alligator Creek is lower than at other sites. Alligator Creek is a popular sports-fishing site less than 10 km from Townsville, the largest city in north Queensland. Consistent removal of large piscivorous fish species by anglers may have resulted in greater survivorship of small prey fish, such as those captured with the small seine-net.

It appears unlikely that variation in water clarity among mangrove habitats explains the observed differences in fish densities, as has been suggested by other work in Australia (Blaber, 1980; Blaber *et al.,* 1985). There was a broad overlap in water clarity values across all sites in the present study and very clear water, such as that observed in parts of north-western Australia (Blaber *et al.,* 1985), was never observed.

Mangroves as nursery sites

Are mangrove swamps major nursery sites for important commercial or sport fish and crustaceans in northeastern Australia? The results of this study have shown clearly that the mangrove habitat was a major nursery site for juveniles of the banana prawn *Penaeus merguiensis,* one of the most important commercial species of prawn in Australia (Rothlisberg *et al.,* 1985). Previous studies on the habitat preferences of young *P. merguiensis* in the Gulf of Carpentaria in northern Australia have also shown that post-larvae and juveniles are restricted to mangrove habitats (e.g. Staples *et al.,* 1985). In addition, in the present study, 8 out of 9 cross-habitat comparisons showed that juveniles of the prawn *Metapenaeus ensis* were significantly more abundant in mangrove habitats. By contrast, *M. ensis* was found to be evenly distributed across mangrove and seagrass habitats in the Gulf of Carpentaria (Staples *et al.,* 1985).

In contrast to the situation for juvenile prawns, mangroves in north Queensland do not appear to be major nursery sites for the juveniles of fish species considered to be of commercial importance in Australia. Among the top 30 fish species captured, 11 resident species (those represented by adults and juveniles) made up at least 65% of the total number of fish captured in the mangroves. Of the remaining 19 species, which were represented entirely by juveniles, only three species, the clupeid *Herklotsichthys castelnaui,* the engraulid *Thryssa hamiltoni* and the sparid *Acanthopagrus berda,* were found in significantly greater numbers in mangroves and were of any economic importance in Australia (the first two as baitfish, the other as a sport fish).

Viewed in a less parochial fashion, however, data from the present study indicate that mangroves are probably very important nursey sites for commercially exploited fishes elsewhere in South-East Asia. Adults of the family Leiognathidae (pony fish) are the most abundant fishes in several South-East Asian trawl fisheries (Pauly, 1979), and the present study has revealed that juveniles of two of the most heavily exploited pony fish species, *Leiognathus equulus* and *L. splendens,* are mangrove-dependent as juveniles. This suggests that the large-scale modification of mangrove swamps occurring elsewhere in South-East Asia may have significant effects on offshore fish catches.

Many of the small fish which dominated mangrove catches in this study are important prey species for higher consumers. For instance four of the top five fish species captured in the present study together make up 65% of the diet of the commercially important giant perch or barramundi, *Lates calcarifer,* in north Queensland mangrove swamps (A. I. Robertson, unpublished data). The value of mangrove habitats to fish is thus not limited to a nursery-ground function.

Acknowledgements. P. Dixon, R. Klein, K. Osborne, P. Raffles, and T. Smith helped with the field collections, often under trying conditions. P. Christopherson, P. Dixon and M. Rajagopalan helped with analyses of the catch. W. Ellery, J. Hardman and P. Raffles helped with ship-time organization. D. Hoese identified members of the family Gobiidae. C. Mundy helped with data reduction and D. Williams, K. Boto, A. Dartnall and B. Chalker provided useful criticisms of earlier drafts of the manuscript.

Literature cited

Austin, H. M.: A study of the ichthyofauna of the mangroves of western Puerto Rico during December, 1967–August, 1968. Caribb. J. Sci. *11,* 27–39 (1971)

Bell, J. D., D. A. Pollard, J. J. Burchmore, B. C. Pease and M. J. Middleton: Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Aust. J. mar. Freshwat. Res. *35,* 33–46 (1984)

Blaber, S. J. M.: Fish of the Trinity Inlet system of North Queensland with notes on the ecology of tropical Indo-Pacific estuaries. Aust. J. mar. Freshwat. Res. *31,* 137–146 (1980)

Blaber, S. J. M. and T. G. Blaber: Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. *17,* 143–162 (1980)

Blaber, S. J. M., J. W. Young and M. C. Dunning: Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of North-western Australia. Aust. J. mar. Freshwat. Res. *36,* 257–266 (1985)

Boesch, D. F. and R. E. Turner: Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries *7,* 460–468 (1984)

Boto, K. (G.), J. S. Bunt and J. T. Wellington: Variations in mangrove forest productivity in northern Australia and Papua New Guinea. Estuar., cstl Shelf Sci. *19,* 321–329 (1984)

Boto, K. G. and J. T. Wellington: Phosphorus and nitrogen nutritional status of a northern Australian mangrove forests. Mar. Ecol. Prog. Ser. *11,* 63–69 (1983)

Bray, J. R. and J. T. Curtis: An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. *27,* 325–349 (1957)

Bunt, J. S., K. G. Boto and G. Boto: A survey method for estimating potential levels of mangrove forest primary production. Mar. Biol. *52,* 123–128 (1979)

Burr, E. J.: Cluster sorting with mixed character types: fusion strategies. Aust. Comput. J. *1,* 98–103 (1970)

Chua Thia-Eng: An ecological study of the Ponggol estuary in Singapore: Hydrobiologia *43,* 505–533 (1973)

Collette, B. B.: Mangrove fishes of New Guinea. *In:* Biology and ecology of mangroves, pp 91–102. Ed. by H. T. Teas. The Hague: Dr. W. Junk 1983

Crocos, P. J. and J. D. Kerr: 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 (1983)

Dixon, P. and A. I. Robertson: A compact, self-contained zooplankton pump for use in shallow coastal habitats: design and performance compared to net samples. Mar. Ecol. Prog. Ser. *32,* 97–100 (1986)

Heck, K. L. and R. J. Orth: Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay – decapod crustaceans. Estuaries *3,* 289–295 (1980)

Howard, R. K.: The trophic ecology of caridean shrimps in an eelgrass community. Aquat. Bot. *18,* 155–174 (1984)

Hughes, D. A.: Responses of salinity change as a tidal transport mechanism of the pink shrimp *Penaeus duroarum.* Biol. Bull. mar. Biol. Lab., Woods Hole *153,* 505–526 (1969)

Kneib, R. T.: Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries *7,* 392–412 (1984)

Krishnamurthy, K. and M. J. Prince Jeyaseelan: The early life history of fishes from Pichavaran mangrove ecosystem of India. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer *178,* 416–423 (1981)

Lindall, W. N., J. R. Hall, W. A. Fable and L. A. Collins: A survey of fishes and commercial invertebrates of the shore and estuarine zone between Cape Romano and Cape Sable, Florida, 62 pp. Springfield, Va.: National Marine Fisheries Service, U.S. Department of Commerce 1973. (PB-235 215 NTIS)

Minello, T. J. and R. J. Zimmerman: Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. J. exp. mar. Biol. Ecol. *72,* 211–231 (1983)

Odum, W. E. and E. J. Heald: The detritus-based food web of an estuarine mangrove community. *In:* Estuarine research, pp 265–286. Ed. by L. E. Cronin. New York: Academic Press, Inc. 1975

Odum, W. E., C. C. McIvor and T. J. Smith, III: The ecology of the mangroves of south Florida: a community profile, 144 pp. Washington, D.C.: U.S. Fish and Wildlife Service, Office of Biological Services 1982. (FWS/OBS-81-24)

Orth, R. J., K. L. Heck, Jr. and J. van Montfrans: Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries *7,* 339–350 (1984)

Pauly, D.: Theory and management of tropical multispecies stocks: a review with emphasis on the Southeast Asian demersal fisheries. Stud. Rev. int. Cent. Living aquat. Resour. Mgmt, Manila *1,* 1–35 (1979)

Robertson, A. I.: The determination of trophic relationships in mangrove-dominated systems: areas of darkness. *In:* Mangrove ecosystems of Asia and the Pacific: status, exploitation and management, pp 292–304. Ed. by C. D. Field and A. J. Darnall. Townsville: AIMS and Australian Committee for Mangrove Research 1987

Rothlisberg, P. C.: Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia. Fish. Bull. U.S. *80,* 541–554 (1982)

Rothlisberg, P. C., J. A. Church and A. M. G. Forbes: Modelling the advection of vertically migrating shrimp larvae. J. mar. Res. *41,* 511–538 (1983)

Rothlisberg, P. C., D. J. Staples and P. J. Crocos: A review of the life history of the banana prawn, *Penaeus merguiensis,* in the Gulf of Carpentaria. *In:* Second Australian National Prawn Seminar, pp 125–136. Ed. by P. C. Rothlisberg, B. J. Hill and D. J. Staples. Cleveland: NPS2 (1985)

Saenger, P., E. J. Hegerl and J. D. S. Davie: Global status of mangrove ecosystems. Environmentalist *3* (Suppl. 3), 1–88 (1983)

Staples, D. J.: Seasonal migration patterns of postlarval and juvenile banana prawns, *Penaeus merguiensis* de Man, in the major rivers of the Gulf of Carpentaria, Australia. Aust. J. mar. Freshwat. Res. *30,* 143–157 (1979)

Staples, D. J.: Ecology of juvenile and adolescent banana prawns, *Penaeus merguiensis* in a mangrove estuary and adjacent offshore area of the Gulf of Carpentaria. I. Immigration and settlement of postlarvae. Aust. J. mar. Freshwat. Res. *31,* 635–652 (1980 a)

Staples, D. J.: Ecology of juvenile and adolescent banana prawns, *Penaeus merguiensis,* in a mangrove estuary and adjacent offshore area of the Gulf of Carpentaria. II. Emigration, population structure and growth of juveniles. Aust. J. mar. Freshwat. Res. *31,* 653–665 (1980 b)

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

Tenore, K. R., L. Cammen, S. E. G. Findlay and N. Phillips: Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? J. mar. Res. *40,* 473–490 (1982)

Wadley, V. A.: A checklist and illustrated key to the epibenthic shrimps (Decapoda: Natantia) of Moreton Bay, Queensland. Rep. Div. Fish. Oceanogr. C.S.I.R.O. Aust. *99,* 1–24 (1978)

Yanez-Arancibia, A., F. A. Linares and J. W. Cay, Jr.: Fish community structure and function in Termines lagoon, a tropical estuary in the southern Gulf of Mexico. *In:* Estuarine perspectives, pp 465–482. Ed. by V. S. Kennedy. New York: Academic Press 1980

Young P. C. and S. M. Carpenter: Recruitment of postlarval penaeid prawns to nursery areas in Moreton Bay, Queensland. Aust. J. mar. Freshwat. Res. *28,* 745–773 (1977)

Young, P. C. and V. W. Wadley: Distribution of shallow-water epibenthic macrofauna in Moreton Bay, Queensland, Australia. Mar. Biol. *53,* 83–97 (1979)

Date of final manuscript acceptance: May 18, 1987.
Communicated by G. F. Humphrey, Sydney