

Vimoksalehi Lukoschek · Mark I. McCormick

Ontogeny of diet changes in a tropical benthic carnivorous fish, *Parupeneus barberinus* (Mullidae): relationship between foraging behaviour, habitat use, jaw size, and prey selection

Received: 28 January 2000 / Accepted: 12 December 2000 / Published online: 16 March 2001
© Springer-Verlag 2001

Abstract *Parupeneus barberinus* forages on benthic invertebrates using a wide range of foraging modes, including vigorous digging in the substratum, resulting in considerable disturbance to the benthos. Polychaetes were the most important prey item for all size classes, but fishes less than 120 mm total length consumed more small ostracods and nematodes than did larger fishes. Fishes greater than 120 mm total length consumed mostly bivalves, and fishes over 240 mm total length consumed mostly bivalves and crabs. A morphological examination of the feeding apparatus suggested that the size of important prey items consumed was determined by gape height and jaw width. Prey available to different size classes of fishes was determined by combining information on microhabitat use, foraging behaviours, and prey volumes in the substratum. Small fishes spent more time foraging on the reef flat and slope, compared with larger fishes that foraged mostly on the reef edge and base. In addition smaller fishes foraged mostly in the upper 2 cm of sediment, whereas larger fishes often foraged to depths of 10 cm. Selection ratios showed that different size classes of fishes selectively extracted different prey items from the substratum. Small fishes showed a preference for ostracods whereas large fishes selected for bivalves and crabs. Although polychaetes were the dominant prey item for all size classes, they were consistently selected against.

Introduction

Ontogenetic changes in dietary composition have been shown to be important for many fish species in temperate regions, in particular for benthic carnivores (Schmitt and Holbrook 1984a; Holbrook et al. 1985; McCormick 1998). Ontogenetic changes in dietary composition within a species may result in a greater similarity between species than between different size or age classes of the same species (Eggold and Motta 1992; Gillanders 1995). A range of factors may account for changes in either the taxonomic composition of diets or the size of prey items, or both, in different age or size classes of fish predators. These factors include habitat use, size-related morphological constraints, foraging behaviours, and feeding rates (Schmitt and Holbrook 1984a). Ontogenetic changes in these factors may function as adaptations that maximise energy intake, resulting in increased growth rates, whilst minimising the risk of predation (Grossman 1980; Brown 1985).

Potential interactions between habitat use, morphology, and foraging behaviours not only alter the suite and size of prey eaten by fishes, but they also change the availability of prey items to different age or size classes of fishes. Habitat use may vary on a number of spatial scales. On an intermediate scale there is a general trend for the smaller juveniles of many fish species to be found in shallower waters than adult conspecifics (Helfman 1978; Gillanders 1995; Green 1996). Likewise on a small scale, foraging habitat preferences, at the microhabitat level, may also change with age (Jones 1984; Schmitt and Holbrook 1984a; McCormick 1998). Size-related morphological changes are important in relation to many aspects of the feeding apparatus of fish. These include jaw length, gape height, and width (Schmitt and Holbrook 1984b; Luczkovich et al. 1995; Platell et al. 1998), inter-gill raker distances (Ibrahim and Huntingford 1988; MacNeill and Brandt 1990; McCormick 1998), and position and protrusibility of the mouth (Eggold and Motta 1992). Dietary changes or specialisations in

Communicated by G.F. Humphrey, Sydney

V. Lukoschek (✉) · M.I. McCormick
Department of Marine Biology,
James Cook University,
Townsville, Queensland 4811, Australia

E-mail: Vimoksalehi.Lukoschek@jcu.edu.au
Tel.: +61-07-47816941
Fax: +61-07-47814020

different size classes of fishes have been directly attributed to constraints related to ontogenetic changes in the relationships between morphological characters (Peterson and McIntyre 1998). However, size-related morphological changes in the efficiency with which a prey item is captured and consumed may also indirectly influence prey selection (Wainwright and Richard 1995).

Foraging behaviours and feeding rates may change considerably as fishes change in size and morphology (Schmitt and Holbrook 1984a; Luczkovich et al. 1995). However, while many studies have incorporated habitat and microhabitat use when assessing prey availability to predators (Jones 1984; Schmitt and Holbrook 1984a; McCormick 1998), most studies have not used detailed behavioural information to quantify ontogenetic changes in prey availability. Thus, conclusions regarding ontogenetic changes in selectivity of dietary items may be based on inaccurate assessments of prey availability.

The target of the present study, *Parupeneus barberinus* (Mullidae), is a benthic carnivore commonly found on fringing reefs throughout the Indo-Pacific region (Randall et al. 1997), including Lizard Island. *P. barberinus* is a diurnally foraging species that is potentially very important in structuring the soft sediment invertebrate community. Prey detection, on or below the substratum surface, is facilitated by the use of hyoid barbels bearing numerous sensory organs (Gosline 1984). A wide range of foraging modes are used to obtain prey, including vigorous digging in the substratum resulting in considerable disturbance to the benthos (Fricke 1975). Many fish species, in particular labrids, nemipterids, and other mullids, forage in association with *P. barberinus*. These fishes may benefit through the exposure of otherwise unavailable prey items, or by being attracted to areas of high prey abundance, or a combination of both. These associations amplify the potential impact that goatfish foraging may have on the mobile invertebrate assemblages.

This study investigated the ontogeny of diet changes of *P. barberinus*, at one location on the fringing back-reef of Lizard Island, northern Great Barrier Reef. Changes in the taxonomic composition of diets, and of prey availability, were investigated to determine ontogenetic changes in selectivity of prey items. Diet changes were examined in relation to changes in habitat and microhabitat use, foraging behaviour, and morphology.

Materials and methods

Study site and data collection

This study was conducted on a 1-km-long section of fringing reef on the leeward side of Lizard Island, a mid-shelf reef on the northern Great Barrier Reef (Fig. 1). At this location the reef flat (2–3 m deep) is approximately 50 m wide and consists primarily of larger granite boulders, coral, sand, and algae. The reef flat extends to the reef slope (45–70° to horizontal), comprised mostly of algae, dead coral, and sand, and to the reef edge, beyond which extends a level sandy reef base at 9–10 m water depth.

Ontogenetic changes in the foraging ecology and diet of *Parupeneus barberinus* were investigated in relation to fish size based on total lengths of fishes. As body size is related to age in fishes, it can be used as a correlate for age in ontogenetic studies (Schmitt and Holbrook 1984a). Although size is a continuous variable and attributes based on size probably change continuously throughout ontogeny, fishes were grouped into three size classes for analysis. The size classes were chosen based on a preliminary study that suggested that habitat use, foraging behaviour, and therefore possibly diet showed marked changes between each category. The categories used in all size-related analyses were: small: <120 mm total length; medium: 120–240 mm total length; and large: >240 mm total length. Behavioural observations of *P. barberinus* and sediment samples were collected at Turtle Reef from October 1998 to January 1999 between 0830 and 1730 hours.

Intermediate-scale distribution of *P. barberinus*

The depth-related size distribution of *P. barberinus* at the study location was examined using visual censuses. Fifty-metre strip transects were laid parallel to the reef crest (shallow) and the reef edge (deep) (eight replicates per habitat). Prior to censusing transects, 2–3 min were allowed to elapse, to ensure that disturbed fishes had returned to the sampling area. All *P. barberinus* within 5 m either side of the transect were counted and their total lengths estimated. Accuracy of size estimation was assessed by noting two points on the substratum directly behind a fish that corresponded to its length. The distance between these two points was then measured. Visually estimated sizes were found to be accurate to within 10–15% of those checked against the substratum. Due to the low numbers of *P. barberinus* sampled, results are presented as total numbers counted at each depth (per 4,000 m²), rather than mean numbers per transect. It was not possible to use chi-square homogeneity to test for differences between the frequency distribu-

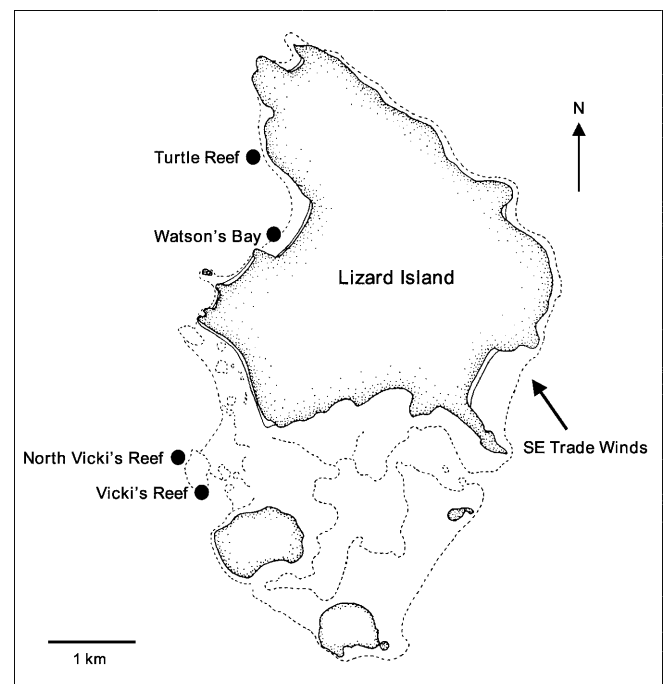


Fig. 1 Map of Lizard Island (14°40'S, 145°28'E) showing location of Turtle Reef, a sheltered back-reef that was the main study site. Also shown are Vicki's Reef, North Vicki's Reef, and Watson's Bay, also sheltered back-reefs, where some *Parupeneus barberinus* were collected for diet assessment

tions of the three size classes in the two habitats, as expected values were less than 5 in 67% of cells (Sokal and Rohlf 1987).

Foraging ecology

Focal animal behavioural observations were used to investigate aspects of the foraging ecology of *P. barberinus* (Martin and Bateson 1995). Observation periods of focal animals were terminated after 10 min, but sampling periods ranged from 2 to 10 min, as individuals were often lost before 10 min elapsed. At the commencement of each sampling period the total length of the fish was estimated and validated against the substratum using the method described above. For each fish the following information was recorded continuously throughout the sampling period: (1) general activity: mobile, foraging, or stationary. Since *P. barberinus* is rarely stationary this behaviour was not investigated further; (2) location in one of four reef zones: reef flat, reef slope, reef edge, or reef base; and (3) microhabitat association. Bite rates were recorded for 1- to 2-min intervals for a subset of fishes in each size class. During this time other behaviours were not recorded.

To obtain a detailed picture of the foraging patterns for each size class of *P. barberinus*, foraging behaviours were grouped into five categories:

1. *Feeding in water column*. Foraging in water column associated with extensive, rapid barbel movements. No contact with substratum.
2. *Skim surface*. Barbels in contact with the substratum. Prey obtained from surface of substratum. No penetration of substratum.
3. *Bite*. Foraged to a depth of 2 cm, resulting in small bite scars. Small amount of disturbance to substratum.
4. *Dig*. Foraged to depths of 2–6 cm, resulting in moderately sized bite scars. Moderate amount of disturbance to substratum.
5. *Shovel*. Foraged to depths greater than 6 cm, resulting in large bite scars. Large amount of disturbance to substratum.

Foraging depths were estimated by observing the depth to which fishes' snouts penetrated the substratum. Estimated foraging-depth categories were validated by periodically measuring the depth of feeding scars with a ruler and were found to be correct in 95% of cases.

Microhabitat associations were recorded to determine patterns of microhabitat use whilst foraging, and to assess foraging microhabitat preferences within the four reef zones. The substratum was classified into eight categories:

1. *Algal coral*. Macroalgae growing on dead scleractinian coral, coral rubble, and boulders.
2. *Sand patches*. Sand patches (< 30 cm diameter) between algae, soft and hard coral.
3. *Coarse sand*. Grains larger than a pinhead.
4. *Fine sand*. Grains smaller than a pinhead.
5. *Coarse rubble*. Diameter larger than fist size.
6. *Fine rubble*. Diameter smaller than fist size.
7. *Soft coral*. All soft corals.
8. *Hard coral*. All scleractinian corals, alive and dead. Most hard corals were dead and covered with turfing algae during this study.

These made up the majority of microhabitats available and included all microhabitats *P. barberinus* had been observed to use whilst foraging.

Altogether 78 individual fishes were observed for a total of 9 h 25 min. Observation effort was partitioned as follows into the size classes described above: 22 small individuals observed for 2 h 48 min; 28 medium individuals observed for 3 h 39 min; and 28 large individuals observed for 2 h 58 min. Bite rates were recorded for 36 fishes (12 from each size class) for a total of 61 min. Time budgets were generated for each size class by calculating the total time spent engaged in each type of behaviour (mobile and five types of foraging), associated with each microhabitat, in each reef zone. Total times were converted to proportions to enable comparisons

between the size classes and between resource use and availability. Although information regarding individual variability between fishes is lost using this method, combined time budgets were chosen because they provided a detailed picture of habitat use and foraging behaviour for each size class at the population level (Martin and Bateson 1995).

Microhabitat selectivity associated with benthic foraging

Microhabitat availability on the reef flat, reef slope, and reef edge was quantified by conducting benthic line-intercept transects in each reef zone (four replicate 20-m transects on the reef flat and edge; eight replicate 20-m transects on the reef slope). The presence of each microhabitat directly under the transect tape was recorded at 1-m intervals. Microhabitat selectivity was not investigated on the reef base, as there were only two microhabitats – coarse and fine sand.

The selection ratio E^* (Vanderploeg and Scavia 1979) was used to investigate the relationship between the relative availability of microhabitats and those used during benthic foraging. This electivity index was chosen as it is less sensitive to changes in relative availability of resources than most other selection ratios (Lechowicz 1982). Although traditionally used to examine selectivity in diets, it can also be used to explore habitat use. It measures the preferential use of each microhabitat by *P. barberinus* by comparing the proportional habitat use whilst foraging to the proportional availability in the environment. Values of E^* range from $E^* = 1$, indicating strong selection for a particular microhabitat, to $E^* = -1$, indicating strong avoidance of a microhabitat. E^* values around 0 indicate random use of a resource (Lechowicz 1982).

E^* was calculated separately for each size class of *P. barberinus* for the eight microhabitats in each reef zone, using the formula

$$E^* = [W_i - (1/n)] / [W_i + (1/n)]$$

where n is the number of resource types (microhabitats), and $W_i = (r_i/p_i) / \sum (r_i/p_i)$, where r_i = the proportion of the i th resource used and p_i = the proportion of the i th resource that is available (Vanderploeg and Scavia 1979).

Dietary analysis of *P. barberinus*

Parupeneus barberinus for dietary analysis were collected from four back-reefs at Lizard Island, namely Turtle Reef, Watson's Bay, Vicki's Reef, and North Vicki's Reef (Fig. 1), from October 1998 to January 1999. A total of 66 fishes were collected, evenly distributed across the three size classes. Most fishes (44) were collected at Turtle Reef. All collections were made between 0930 hours and 1700 hours by SCUBA, using either a speargun or a barrier net. Fishes were injected with 10% buffered formalin immediately upon capture to prevent further digestion of gut contents.

The alimentary tracts of fishes were dissected out in the laboratory and stored in 10% buffered formalin. The alimentary tract consisted of a short oesophagus leading to a small, highly muscular stomach with four pyloric caecae, and a medium length, thin-walled intestine. Gut content analysis was performed separately on the stomach and first half of the intestine. As intestinal contents comprised largely unrecognisable digested organic matter and sand, only stomach contents were analysed. Items were identified and classified into 28 categories, later pooled into ten broad taxonomic groups and a miscellaneous category. The categories were (1) Nematoda: all free-living nematode species; (2) Polychaeta: all polychaete species including worms and tubes; (3) Solemyidae: bivalves from the family Solemyidae, mostly one species, *Solemya veseliana*; (4) Tellinidae: tellinid bivalves, whether whole, partially crushed, or shell remains; (5) Bivalvia (other): bivalves from families other than Tellinidae and Solemyidae, including unidentifiable crushed bivalve remains; (6) Ostracoda: all ostracod species; (7) Pericarida: comprising Cumacea, Mysidacea, Tanaidacea, Isopoda, and Amphipoda; (8) Brachyura: all brachyuran crabs, including crab remains; (9) Eucarida: comprising Euphausiacea, Penaeidae, and Caridea; (10)

other crustacea: Copepoda, Stomatopoda, and unidentifiable crustacean remains; and (11) miscellaneous: comprising foraminifera, scaphopods, fish, egg cases, sipunculids, echiurans, cephalochordates, ophiuroids, chitons, and holothurians.

Percent volumetric abundance of each prey item, for medium and large fish, was obtained by running five random transects (using a 1-mm grid) through a Petri dish of dilute stomach contents and measuring the length of each prey item along the transect. As small fish had small stomach volumes, percent volumes were determined by counting the number of grid squares (1 mm²) directly beneath each prey item. The mean width of important prey items was estimated by measuring prey from five individuals of each size class. It was not possible to count individual prey items accurately, as crabs, bivalves, and polychaetes were often in pieces. Percent occurrence of each prey item was determined by counting the number of fishes' stomachs containing prey from each category.

Percent volume and percent occurrence of each prey category were used to determine the importance of dietary prey using Costello's graphical analysis. Important prey items were separated out from minor prey items by either percent volume, percent occurrence, or both (Costello 1990). The distribution of prey items on Costello's graph also indicates the predator's feeding strategy (Fig. 2) (Marshall and Elliott 1997).

Feeding selectivity

To determine feeding selectivity, samples of benthic prey were taken in the eight most important microhabitat-by-reef-zone combinations, determined by the proportion of time each size class spent foraging in each area. These were sand patch and coarse sand on the reef flat and slope, and coarse and fine sand on the reef edge and base. Sediment samples were collected by SCUBA using an air-lift suction sampler. This is a reliable quantitative method of sampling benthic invertebrates (Thommasin 1978). Within each microhabitat-by-reef-zone combination, replicate cores, delimited by a metal corer 35 cm in diameter, were collected into 1-mm mesh bags attached to the end of the PVC pipe of the suction sampler. Where possible, sediment samples were collected in three depth strata [0–2 cm (sample sizes = 1.92 m⁻³), 2–6 cm, and 6–10 cm (sample sizes = 3.84 m⁻³)], corresponding to the four benthic foraging categories. Sand patches and coarse sand on the reef slope and flat were generally not deeper than 6 cm, so only the first two depth layers were sampled. Five replicate core samples were taken of the sand patch and coarse sand microhabitats on the reef flat and slope, whereas ten replicate cores were taken of each of the fine and coarse sand microhabitats on the reef edge and base. Due to low numbers of invertebrates in each core, five replicate cores were combined for calculations of volumetric abundance. As this gave only one sample for coarse sand and sand patch, on the reef slope and flat, these microhabitats were combined for availability estimates.

Percent volumetric abundances of prey items were obtained for each submicrohabitat (16 depth-by-microhabitat-by-reef-zone

combinations) using the displacement method (Hyslop 1980). To obtain accurate estimates of prey availability for each size class, the proportional volumes of each prey category in each submicrohabitat were weighted by an index. This index was calculated from the proportions of time each size class spent foraging in each submicrohabitat (skim and bite categories were combined to correspond to the 0- to 2-cm substratum layer). The resulting proportional volumes, of each prey category in each submicrohabitat, were summed and used for comparison with proportional volumetric abundances of dietary prey items.

The selection ratio (w_i) was used to examine which prey items each size class used more frequently than expected. This selection ratio was chosen as it is robust to the inclusion of common but rarely used resources, and it is possible to test statistically whether a resource is used in proportion to its availability (Manly et al. 1993). For each size class, selection ratios were calculated separately for seven food types using the formula

$$w_i = o_i/a_i$$

where o_i is the proportional volumetric abundance of the i th food item in a size class of *P. barberinus*, and a_i is the proportional volume of the i th food item available to that size class. Bonferroni corrected 95% confidence intervals (95% CI) were estimated for each selection ratio using the formula

$$Z\alpha_{/2k} \sqrt{o_i(1-o_i)/u_+a_i^2}$$

where $Z\alpha_{/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $\alpha_{/2k} = 0.05$, k = the number of food types, o_i is the proportional volumetric abundance of the i th food item in a size class of *P. barberinus*, u_+ is the number of food items used, and a_i is the proportional volume of each food item available to each size class. A food item was considered to be selected for when $w_i \pm 95\%$ CI was greater than 1, and selected against when $w_i \pm 95\%$ CI was less than 1 (Manly et al. 1993). As the total number of food items was not known, u_+ was estimated by counting the total number of whole prey items in the stomach of five fishes from each size class and multiplying the mean number of prey items per fish by the number of fishes sampled for each size class. As this underestimates u_+ , confidence intervals will be larger than if the total number of food items was known. The effect of this is to make the test more conservative. That is, it is more likely to find no selection for or against a food type (type II error). However, results for positive or negative selection become more reliable.

The presence of a prey item does not necessarily render it available to a predator (Johnson 1980). Gastropods and hermit crabs were not found in the stomachs of *P. barberinus*, although they made up a considerable proportion of benthic invertebrates in the substratum. These items were excluded, as including them as available resources would influence the selection ratios of all other categories considered (Johnson 1980). Selection ratios were not calculated for nematodes as they were not obtained in sediment samples. Nematodes were probably not retained by the 2-mm sieve used. The three bivalve categories (Table 1) were combined for calculations of selection ratios, because solemyid bivalves were not found in sediment samples. This may be because they were rare or had a clumped distribution and were therefore not obtained by the level of sampling in this study.

Morphology of the feeding apparatus

Gape height (mouth fully open), gape width (distance between angles of jaw with mouth closed), snout length (centre of eye to tip of jaw), and barbel length (attachment point to barbel tip), were measured on each fish prior to dissection. Gape height was measured as it was the largest measure of mouth gape, whereas gape width was measured as it was the smallest measure of gape and gave a good estimation of pharyngeal gape. Total length and weight were also recorded for each fish. Regression equations and correlation coefficients (r) were calculated for the relationships between total length and each of the four jaw characters. In each

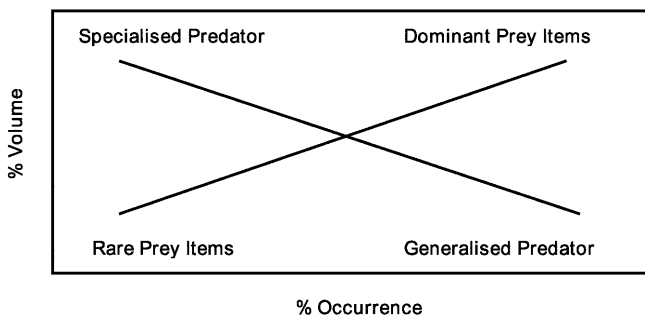


Fig. 2 Guide to interpretation of the Costello graphical method showing the important diagonals (after Costello 1990)

Table 1 Detailed taxonomic composition of stomach contents, given as mean percent volumetric abundance (\pm SE), for three size classes of *Parupeneus barberinus*

	< 120 mm		120–240 mm		> 240 mm	
	% Abundance	SE	% Abundance	SE	% Abundance	SE
Organic matter	45.7	4.1	29.3	2.9	20.7	2.3
Foraminifera	1.4	0.4	3.6	0.9	2.9	0.4
Nematoda	7.2	2.5	1.1	0.4	0.0	0.0
Polychaeta	18.9	3.9	25.6	2.7	30.0	3.2
Gastropoda	0.0	0.0	0.0	0.0	0.3	0.2
<i>Soleyma</i> spp.	0.0	0.0	5.7	2.5	4.0	1.1
Tellinidae	0.0	0.0	5.8	2.5	6.9	1.6
Bivalvia other	0.1	0.1	3.9	1.4	4.6	1.6
Scaphopoda	0.0	0.0	0.0	0.0	0.1	0.1
Ostracoda	8.2	2.9	3.4	1.2	0.4	0.3
Copepoda	0.6	0.4	0.0	0.0	0.0	0.0
Hoplocarida, Stomatopoda	0.0	0.0	0.0	0.0	0.1	0.1
Pericarida, Cumacea	0.3	0.3	0.3	0.3	0.3	0.3
Pericarida, Mysidacea	0.1	0.1	0.1	0.1	0.1	0.1
Peracarida, Tanaidacea	0.0	0.0	1.3	0.6	0.1	0.1
Peracarida, Isopoda	0.0	0.0	0.8	0.6	0.1	0.1
Peracarida, Amphipoda	2.0	0.9	2.0	0.7	1.9	0.8
Eucarida, Euphausiacea	0.0	0.0	0.2	0.2	0.0	0.0
Eucarida, Penaeidea	1.2	0.8	0.8	0.6	0.0	0.0
Eucarida, Caridea	5.3	2.8	4.9	2.3	1.4	0.6
Eucarida, Brachyura	0.0	0.0	3.2	1.2	20.1	4.1
Crustacea other	7.4	2.7	5.0	1.0	3.5	1.0
Sipuncula	0.6	0.4	0.9	0.5	0.5	0.3
Echiura	0.0	0.0	0.7	0.7	1.7	1.0
Ophiuroidea	0.0	0.0	0.0	0.0	0.6	0.4
Cephalochordate	0.0	0.0	1.8	1.8	0.0	0.0
Fish	0.2	0.2	0.2	0.2	0.0	0.0
Egg cases	0.9	0.9	0.0	0.0	0.0	0.0

case \log_{10} transformations of each morphological variable and total length were used to meet the assumptions of regression. The slopes of the regression equations estimate the scaling relationships between each morphological variable and total length, and the correlation coefficients measure the intensity of association between the two variables (Zar 1984).

Results

Intermediate scale distribution of *Parupeneus barberinus*

Overall, *Parupeneus barberinus* was more abundant in deeper water at the reef base than in shallow water on the reef flat (Fig. 3). The size class frequency distributions showed different patterns in the two habitats. In shallow water there were similar numbers of each size class, whereas in deeper water large fishes were at least 3 times more abundant than medium-sized fishes, and small fishes were completely absent (Fig. 3).

Small *P. barberinus* spent almost 60% of their time on the reef flat and approximately 20% on the reef slope and reef edge. They rarely ventured onto the reef base (Fig. 4). Fishes in the medium and large size classes spent most of their time (50%) on the reef edge. Large fishes spent more time on the reef base (almost 30%) than the reef slope (18%) or reef flat (5%). In contrast, medium-sized fishes spent larger proportions of time over the reef slope (>30%) and similar proportions of time over the reef flat and reef base (~10%) (Fig. 4).

Foraging ecology and habitat selectivity

Small *P. barberinus* spent more time foraging than travelling in all reef zones. Small fishes also spent proportionally more time foraging in the water column on the reef flat (21%), reef slope (29%), and reef edge (44%) than the other two size classes. Medium and large *P. barberinus* spent proportionally more time travelling than foraging in all reef zones except the reef base, where

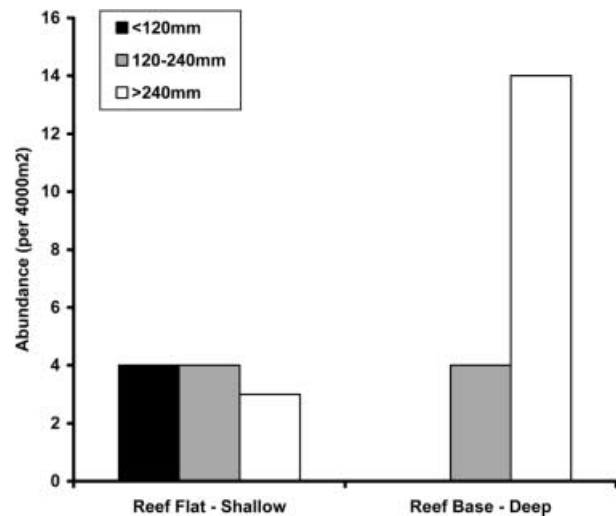


Fig. 3 Frequency distribution of three size classes of *Parupeneus barberinus* in shallow and deep habitats at Turtle Reef

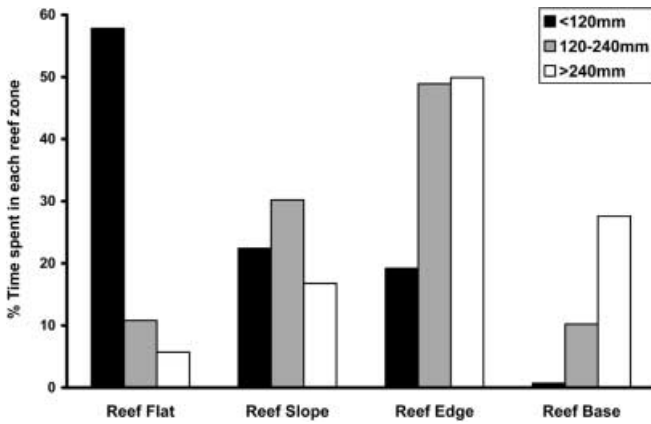


Fig. 4 Percent time spent in each reef zone by each of the three size classes of *Parupeneus barberinus* at Turtle Reef

both sizes classes spent proportionally more time foraging on the benthos (75% for medium and 60% for large fishes). Medium and large fishes also rarely foraged in the water column (<5% in all reef zones) (Fig. 5).

Most benthic foraging by small *P. barberinus* occurred in coarse sand in all reef zones (Fig. 6). This was disproportionate to the relative abundance of this microhabitat on the reef flat, slope, and edge, as indicated

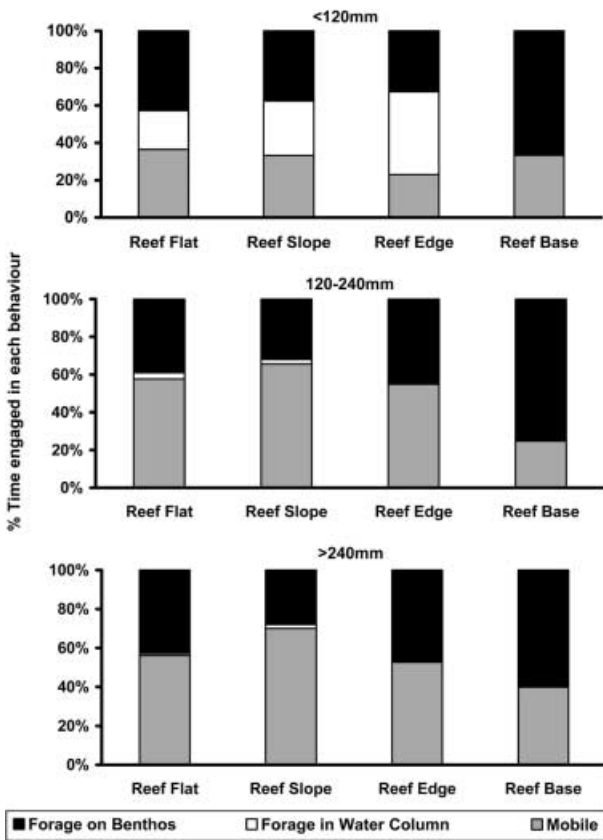


Fig. 5 Percent time spent mobile, foraging in water column, and foraging on the benthos by three size classes of *Parupeneus barberinus* at Turtle Reef

by E^* , which ranged from 0.567 to 0.752. Small fishes also selected sand patches on the reef flat (Fig. 6; Table 2). Medium and large size classes most strongly selected coarse sand while foraging in each reef zone, with the exception of large fishes on the reef flat ($E^* = 0$) (Table 2). Sand patches were selected for by medium and large size classes on the reef flat and slope. Sand patches were, however, more available than coarse sand on the reef slope and these two size classes spent the majority of their time foraging in sand patches in this reef zone (Fig. 6). Coarse rubble was selected for by medium-sized fishes on the reef flat, and fine rubble was selected for by large fishes on the reef edge (Table 2). Soft and hard corals were avoided by all size classes in all reef zones ($E^* = -1.00$).

Small *P. barberinus* foraged almost exclusively by skimming and biting in the surface substratum layer, although a very small proportion of the total benthic foraging time was spent digging in the 2- to 6-cm layer in sand patches on the reef flat (Table 3). Large fishes foraged in each of the three depth strata in both coarse

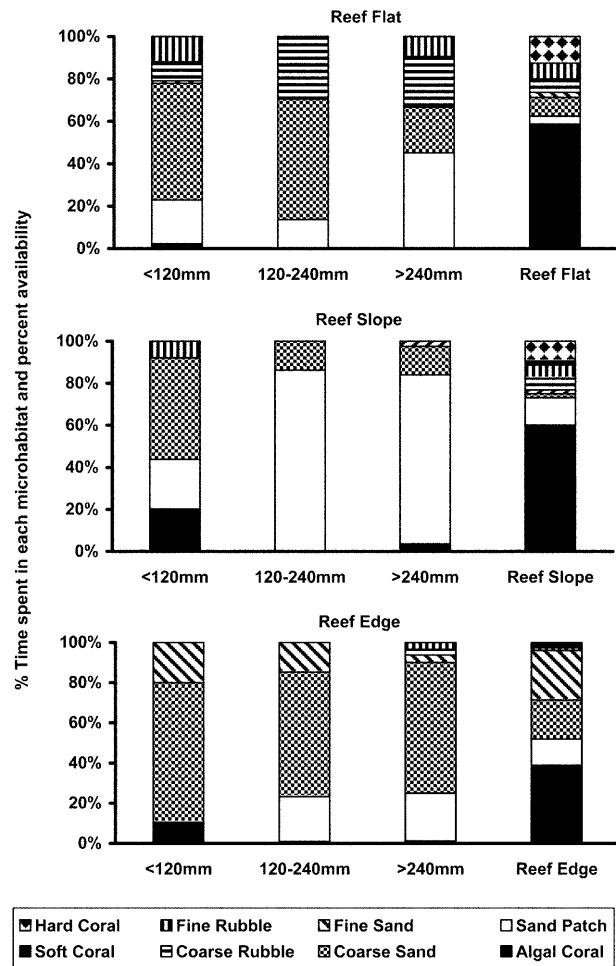


Fig. 6 Microhabitat use by three size classes of *Parupeneus barberinus* on reef flat, reef slope, and reef edge at Turtle Reef. Microhabitat availability in each reef zone shown in last bar of each graph

Table 2 Vanderploeg and Scania (E^*) selection ratios for microhabitats used by three size classes of *Parupeneus barberinus* in three reef zones during benthic foraging. All positive values of E^* are indicated in bold type. E^* values around 0 indicate random use. Selection for a microhabitat increases as values of E^* increase (maximum value is 1). Values of E^* over 0.3 are regarded as showing selectivity

Reef zone	Microhabitat	E^*		
		< 120 mm	120–240 mm	> 240 mm
Reef flat	Algal coral	-0.954	-1.000	-1.000
	Sand patch	0.520	0.325	0.663
	Coarse sand	0.567	0.555	0.000
	Fine sand	-0.568	-1.000	-1.000
	Coarse rubble	-1.000	0.435	0.217
	Fine rubble	-0.043	-1.000	-0.317
	Soft coral	-1.000	-1.000	-1.000
	Hard coral	-1.000	-1.000	-1.000
Reef slope	Algal coral	-0.831	-1.000	-0.935
	Sand patch	-0.337	0.581	0.537
	Coarse sand	0.752	0.617	0.594
	Fine sand	-1.000	-1.000	-0.166
	Coarse rubble	-1.000	-1.000	-1.000
	Fine rubble	-0.485	-1.000	-1.000
	Soft coral	-1.000	-1.000	-1.000
	Hard coral	-1.000	-1.000	-1.000
Reef edge	Algal coral	-0.362	-0.969	-0.939
	Sand patch	-1.000	0.013	0.292
	Coarse sand	0.720	0.310	0.538
	Fine sand	0.165	-0.474	-0.739
	Coarse rubble	-1.000	-1.000	-1.000
	Fine rubble	-1.000	-1.000	0.454
	Soft coral	-1.000	-1.000	-1.000
	Hard coral	-1.000	-1.000	-1.000

and fine sand on the reef base and reef edge, although they did not shovel in fine sand at the reef edge. Medium-sized fishes foraged in all depth strata of coarse sand

on the reef base and reef edge, but in sand patches on the reef slope they spent proportionally more time skimming the surface and biting. Overall, medium and large fishes

Table 3 Proportions of time *Parupeneus barberinus* spent using four types of foraging modes in each microhabitat-by-reef-zone combination for three size classes of fishes

Reef zone	Microhabitat	Depth	Time		
			< 120 mm	120–240 mm	> 240 mm
Reef flat	Sand patch	Skim	0.082		
		Bite	0.182		
		Dig	0.023		0.012
	Coarse sand	Skim	0.105		
		Bite	0.246	0.022	
		Dig		0.055	
Reef slope	Sand patch	Skim	0.055	0.076	
		Bite	0.034	0.127	0.036
		Dig		0.123	0.217
	Coarse sand	Skim	0.046		
		Bite	0.076	0.021	
		Dig			
Reef edge	Coarse sand	Skim	0.043	0.036	0.033
		Bite	0.080	0.074	0.082
		Dig		0.172	0.146
		Shovel		0.049	0.101
	Fine sand	Skim	0.013		
		Bite	0.019		0.013
		Dig		0.066	
		Shovel			
Reef base	Coarse sand	Skim			0.083
		Bite	0.011	0.019	0.059
		Dig		0.079	0.070
		Shovel		0.018	0.064
	Fine sand	Skim			0.016
		Bite		0.032	
		Dig		0.032	0.048
		Shovel			0.021

spent the majority of time digging in the 2- to 6-cm layer in most microhabitat-by-reef-zone combinations where they foraged (Table 3).

Foraging rates tended to decrease with increased fish size (ANOVA of regression: $F = 4.301$, $df = 1$, $P = 0.046$) (Fig. 7). More specifically, small fishes tended to feed consistently at higher rates, 1.1–1.6 bites per second, whilst medium and large size classes showed more variability in foraging rates. These ranged between 0.6 and 1.67 bites per second for medium-sized fishes and between 0.41 and 1.49 bites per second for large fishes.

Diet assessment

There was considerable similarity in the gross taxonomic composition of the diets for each of the three size classes of *P. barberinus*. However, there were also marked shifts in the proportional volumetric contributions for some taxonomic groups (Fig. 8). Polychaetes dominated in the diets across the three size classes, accounting for 18.9%, 25.6%, and 30% of the volumetric abundance in the small, medium, and large size classes, respectively. Crabs dominated the diets of large fishes, making up 20.1% of stomach contents, but accounted for only 3.2% and <1% of the stomach contents of medium and small fishes, respectively. Tellinid, solemyid, and other bivalves made up 3.9–6.9% of the stomach contents of the two larger size classes but were almost completely absent in the stomachs of small fishes. By contrast nematodes and ostracods accounted for 7.2% and 8.2% of the stomach contents of small fishes but were absent or only made up a small proportion of the stomach contents in medium and large *P. barberinus*. The proportional volumetric abundances of eucaridean, pericaridean, and other crustaceans were similar across the three size classes. The eucarids comprised mostly caridean prawns, whilst the pericarids comprised mostly amphipods, in all

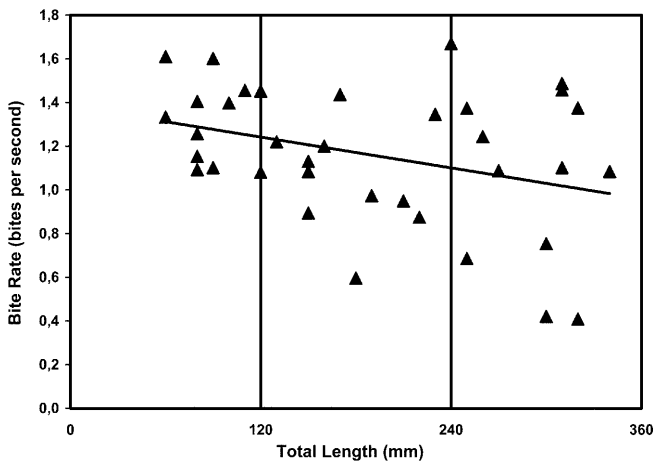


Fig. 7 Bite rates for three size classes of *Parupeneus barberinus* at Turtle Reef

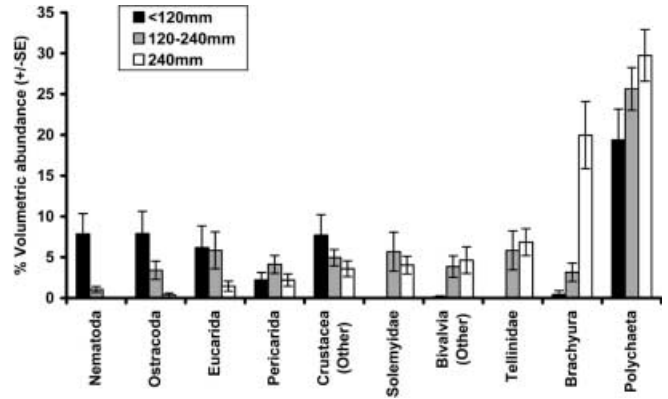


Fig. 8 Percent volumetric abundance (\pm SE) of prey items in stomachs of three size classes of *Parupeneus barberinus* at Lizard Island

three size classes (see Table 1 for detailed taxonomic breakdown of prey items). None of the stomachs examined were completely empty; the stomachs of two of the smallest fishes, however, contained very few prey items.

Costello’s graph of the importance of prey items showed similar patterns (Fig. 9). Polychaetes were the

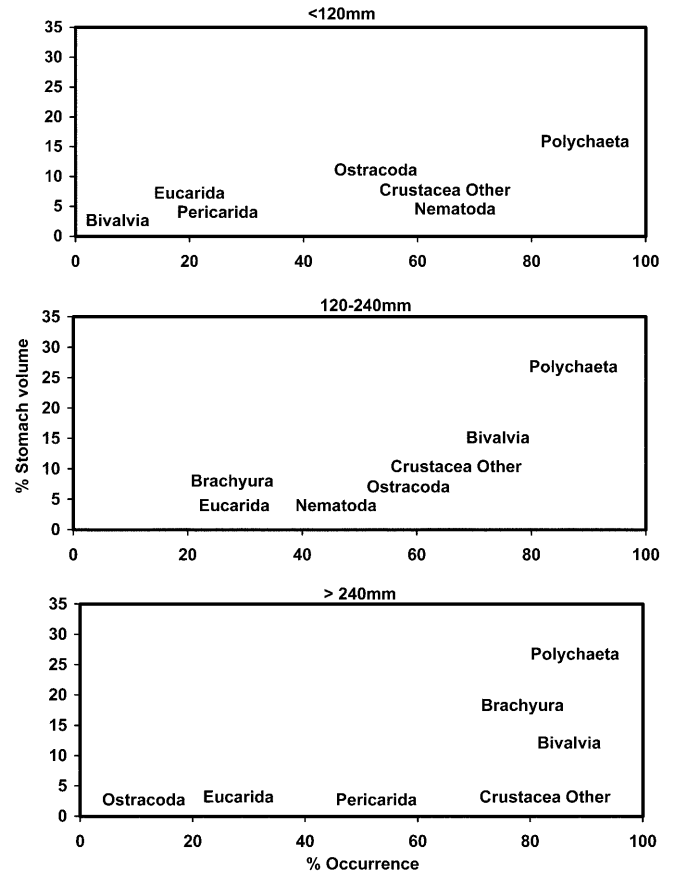


Fig. 9 Costello’s graphs showing importance of prey items based on percent volumetric abundance and percent occurrence of prey items in three size classes of *Parupeneus barberinus*

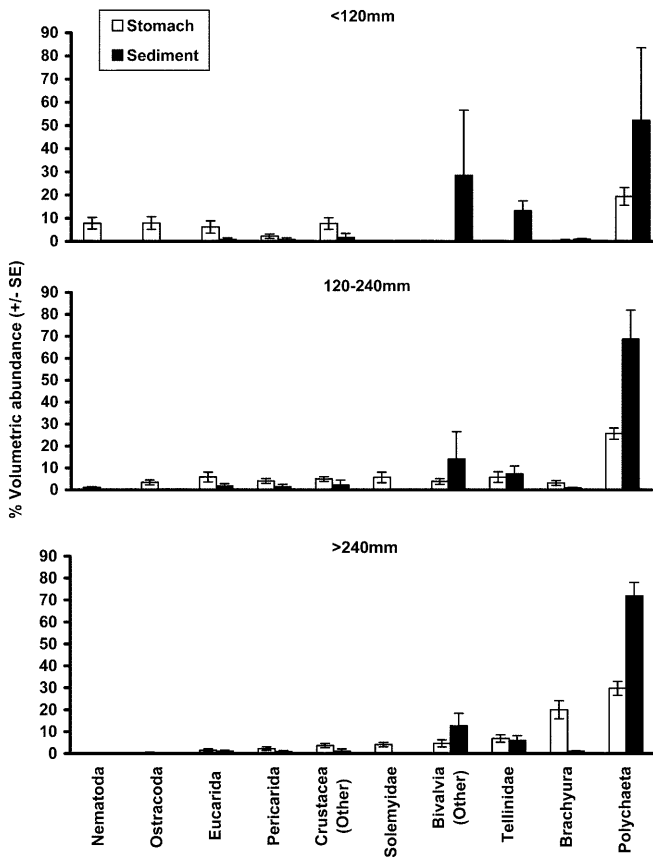


Fig. 10 Percent volumetric abundance of prey items in stomachs of three size classes of *Parupeneus barberinus*, and available to each size class at Turtle Reef

most important prey item in terms of both percent volumetric abundance and occurrence. They were found in the stomachs of 80–90% of fishes across all size classes. Crabs and bivalves were important in the diets of large *P. barberinus* based on both percent abundance and occurrence, whereas nematodes and ostracods were important in the diets of small fishes. Ostracods and

nematodes were also important in the middle size class due to their high percent occurrence. Bivalves were also important in the middle size class due to both their percent occurrence and abundance. Other crustacea were important in each of the three size classes based mostly on percent occurrence (Fig. 9).

Feeding selectivity

The taxonomic composition of benthic invertebrates sampled in the 16 submicrohabitats was similar to that found in the stomachs of *P. barberinus*. Benthic invertebrates were numerically sparse and constituted very low volumes in the substratum due to their small size (Tables 4, 5, 6). Gastropods or polychaetes had the highest volumetric abundance in the surface layer of all microhabitats, except the reef base, where bivalves were most abundant. Polychaetes were most abundant in all other submicrohabitats, except the 2- to 6-cm layer on the reef slope where gastropods were most abundant. Hermit crabs were comparatively abundant in sand on the reef slope and flat, and in the upper layer of fine and coarse sand on the reef edge. Bivalves were most abundant in coarse and fine sand on the reef base. Faunal abundance decreased with depth in all reef zones except the reef base, where polychaete abundance increased with depth. Fauna in foraging microhabitats on the reef flat comprised solely polychaetes, molluscs, and hermit crabs (Tables 4, 5, 6).

Selection ratios showed that each size class of *P. barberinus* selected certain prey items from the substratum whereas other prey items were avoided. Moreover, whereas some prey items were consistently selected against by all size classes, other prey items were selected for by one of the size classes yet avoided by others (Table 7).

Polychaetes were the most important food items for all size classes; however, selection ratios showed that all size classes ate fewer polychaetes than expected from their availability in the substratum (Table 7). This was

Table 4 Volumetric abundances (\pm SE) of prey items for each depth-by-microhabitat-by-reef-zone combination at Turtle Reef: reef flat and reef slope. Volumes in cm^3 per $2,500 \text{ cm}^3$

	Reef flat				Reef slope			
	Coarse sand and sand patch				Coarse sand and sand patch			
	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE
Nematoda								
Polychaeta	1.079	1.079	0.810	0.270	1.835	1.187	0.621	0.297
Bivalvia	0.216	0.184	0.129	0.046	0.884	0.852	0.229	0.213
Gastropoda	1.529	0.159	0.749	0.039	1.892	0.952	0.715	0.240
Ostracoda								
Pericarida					0.024	0.024	0.018	0.006
Eucarida					0.040	0.006	0.021	0.002
Anomura	0.584	0.407	0.380	0.204	0.794	0.605	0.507	0.304
Brachyura								
Other Crustacea					0.238	0.238	0.059	0.059

Table 5 Volumetric abundances (\pm SE) of prey items for each depth-by-microhabitat-by-reef-zone combination at Turtle Reef: reef edge. Volumes in cm^3 per $2,500 \text{ cm}^3$

	Coarse sand						Fine sand					
	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE
	0–2		2–6		6–10		0–2		2–6		6–10	
Nematoda												
Polychaeta	0.756	0.108	0.648	0.108	0.486	0.000	1.295	0.216	0.702	0.162	0.702	0.054
Bivalvia	0.134	0.134	0.339	0.339	0.294	0.000	0.450	0.227	0.083	0.058	0.013	0.013
Gastropoda	1.376	0.126	0.197	0.074	0.282	0.112	0.800	0.198	0.222	0.125	0.159	0.022
Ostracoda	0.005	0.005					0.003	0.003				
Pericarida	0.033	0.033									0.006	0.006
Eucarida	0.033	0.033	0.006	0.006	0.006	0.000	0.006	0.006			0.012	0.005
Anomura	0.363	0.022	0.003	0.003	0.056	0.062	0.358	0.257				
Brachyura	0.088	0.044	0.005	0.005			0.044	0.044				
Other Crustacea	0.050	0.050	0.000	0.000			0.088	0.088	0.022	0.022		

Table 6 Volumetric abundances (\pm SE) of prey items for each depth-by-microhabitat-by-reef-zone combination at Turtle Reef: reef base. Volumes in cm^3 per 2500 cm^3

	Coarse sand						Fine sand					
	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE	Depth (cm)	SE
	0–2		2–6		6–10		0–2		2–6		6–10	
Nematoda												
Polychaeta	1.583	0.504	2.105	0.486	2.717	0.126	2.591	1.079	1.241	0.270	3.238	1.403
Bivalvia	3.650	0.272	0.781	0.357	0.166	0.032	2.715	1.643	0.676	0.298	0.283	0.124
Gastropoda	2.142	0.138	0.506	0.001	0.072	0.031	2.251	0.001	0.563	0.063	0.026	0.024
Ostracoda	0.008	0.003					0.003	0.003				
Pericarida	0.016	0.008	0.007	0.002			0.031	0.031	0.016	0.016		
Eucarida	0.055	0.004	0.004	0.002			0.063	0.050				
Anomura	0.143	0.069										
Brachyura	0.094	0.000			0.019	0.003			0.022	0.022		
Other Crustacea	0.016	0.016	0.007	0.007	0.004	0.004	0.150	0.150			0.025	0.025

Table 7 Selection ratios (w) and Bonferroni corrected 95% confidence intervals (95% CIs) for seven prey categories for three size classes of *Parupeneus barberinus* at Turtle Reef. If 95% CIs encompass zero then prey are consumed randomly. Selection ratios \pm 95% CIs greater than 1 indicate selection for prey, whereas values less than 1 indicate selection against prey

	< 120 mm		120–240 mm		> 240 mm	
	w	95% CI	w	95% CI	w	95% CI
Polychaeta	0.371	0.115	0.373	0.084	0.414	0.074
Bivalvia	0.002	0.012	0.688	0.213	0.833	0.227
Ostracoda	100.016	52.043	48.245	34.017	6.131	11.754
Pericarida	2.823	2.856	2.806	1.793	2.461	1.909
Eucarida	7.313	4.340	3.475	1.846	1.386	1.331
Other Crustacea	4.448	2.346	2.192	1.272	3.428	2.068
Brachyura	0.458	1.046	3.540	2.596	19.806	4.617

because of the high availability of polychaetes to all size classes (Fig. 10). Their availability increased as *P. barberinus* increased in size, along with their proportional contribution to the fishes' diets.

The availability of bivalves to *P. barberinus*, due to habitat and microhabitat selection, decreased as fishes increased in size, even though bivalves became increasingly important in the diets of fishes with increased size. The proportional availability of bivalves was larger in the substratum than their proportional abundance in

fishes' stomachs for all size classes (Fig. 10), but bivalves were only selected against by small and medium-sized fishes (Table 7).

The proportional availability of ostracods, eucaridean, pericaridean, and other crustaceans and crabs was similarly small for all size classes of *P. barberinus* (Fig. 10). Selection ratios showed that small and medium-sized fishes ate more ostracods, eucaridean, and other crustaceans than expected from their availability in the substratum. By contrast, large fishes selected

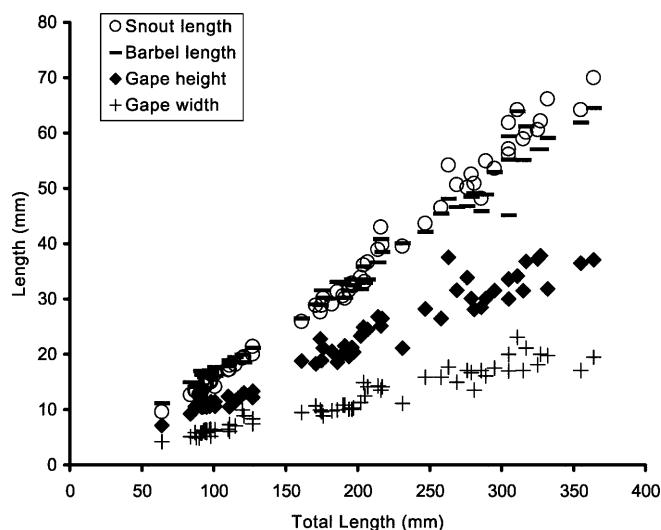


Fig. 11 Relationships between gape height, gape width, snout length, and barbel length with total length of *Parupeneus barberinus*, at Turtle Reef

strongly for brachyuran crabs, and to a lesser extent for other crustaceans (Table 7).

Solemyid bivalves accounted for 5.7% and 4.0% of the volumetric abundances of prey items for medium and large *P. barberinus*, respectively (Table 8). Solemyid bivalves comprised one genus, *Solemya*. Examination of the raw data showed that solemyids were found in the stomachs of fishes collected from all four reefs, including 17 fishes from Turtle Reef, but they were not found in sediment samples. Although it was not possible to calculate selection ratios for solemyids, due to their absence in the sediment, there appears to be strong selectivity for this prey item by medium and large fishes.

Morphology, prey size, and foraging behaviour

All four morphological characters increased in size as the total length of fishes increased (Fig. 11). Correlation coefficients showed high correlations between total length and each of the four morphological variables (Table 9). Scaling exponents for gape height and width were very similar (Table 9); gape height was consistently larger than gape width across the full size range of *P. barberinus* investigated. Snout and barbel lengths

Table 9 Correlation coefficients, slopes (\pm SE), and intercepts (\pm SE) of regressions of \log_{10} -transformed data of each of four morphological variables against \log_{10} -transformed total length for *Parupeneus barberinus*

Morphological variable	Correlation coefficient (r)	Scaling exponent	y -intercept
Gape height	0.985	0.967 ± 0.022	-0.881 ± 0.049
Gape width	0.974	0.940 ± 0.027	-1.086 ± 0.062
Barbel length	0.994	1.027 ± 0.014	-0.826 ± 0.031
Snout length	0.997	1.178 ± 0.012	-1.172 ± 0.027

were similar for all fishes, although in small fishes barbel length tended to be larger than snout length, whereas in larger fishes this trend was reversed. This trend is reflected in the scaling exponents (Fig. 11; Table 9).

Small fishes had gape heights less than 13 mm and widths less than 9.9 mm (Fig. 11). Polychaetes eaten by small fishes tended to be smaller (mean width 0.67 ± 0.05 mm) than those eaten by medium-sized fishes (mean width 1.91 ± 0.33 mm) and large fishes (mean width 2.33 ± 0.32 mm). Other prey items of the small size class, such as ostracods, nematodes, egg cases, and crustaceans were generally less than 2 mm wide (mean width of ostracods 0.15 ± 0.01 mm). Maximum snout length was 19.45 mm for small fishes, and the longest barbels were 19.9 mm (Fig. 11). Small fishes foraged almost exclusively in the upper 2 cm of the substratum using skim and bite behaviours and spent considerable proportions of time foraging in the water column (Table 3; Fig. 5).

Maximum gape height and width for medium-sized *P. barberinus* was 26.8 mm and 14.9 mm, respectively (Fig. 11). Larger prey items, such as bivalves (mean width 3.10 ± 0.20 mm), were more important in the diets of medium-sized fishes than small prey items, such as ostracods and nematodes (Fig. 9). Maximum snout length was 42.9 mm in this size class, and maximum barbel length was 40.8 mm (Fig. 11). Almost 53% of benthic foraging by medium-sized fishes consisted of digging in the 2- to 6-cm layer of the substratum, while less than 7% consisted of shoveling in the deeper substratum layer (Table 3).

Large *P. barberinus* had maximum gape heights and widths of 37.8 mm and 23.1 mm, respectively (Fig. 11). Diets of large fishes comprised mostly large prey items, such as crabs (mean width 5.19 ± 0.50 mm) and bivalves (mean width 4.52 ± 0.31 mm) (Fig. 8). The diets

Table 8 Comparison between percent volumetric abundances (\pm SE) of bivalves from the families Solemyidae, Tellinidae, and other bivalve families combined

	< 120 mm		120–240 mm				> 240 mm					
	Stomach		Sediment		Stomach		Sediment		Stomach		Sediment	
	% vol	SE	% vol	SE	% vol	SE	% vol	SE	% vol	SE	% vol	SE
Solemyidae	0	0	0	0	5.7	2.5	0	0	4	1.1	0	0
Tellinidae	0	0	13.3	4.3	5.8	2.5	7.2	3.6	6.9	1.6	9.3	3.4
Other	0.1	0.1	28.5	28	3.9	1.4	13.8	12	4.6	1.6	19.7	8.9

of large fishes also included large echiuran worms not eaten by small fishes (Table 1). Maximum snout length was 69.9 mm and barbel length reached a maximum of 64.5 mm (Fig. 11). Almost 18% of benthic foraging time of large fishes was devoted to shovelling in the 6- to 10-cm substratum layer, whereas 47.6% was spent digging in the middle layer (Table 3).

Discussion

Ontogenetic changes in diet and prey item selectivity were demonstrated across the three size classes of *Parupeneus barberinus* investigated in this study. These ontogenetic changes were driven by a hierarchy of processes acting on different spatial scales. Broad-scale distribution and abundance patterns across reef zones, selectivity of foraging microhabitats within reef zones, and behavioural constraints associated with morphological limitations interact to determine both the diets and the actual availability of prey items in the substratum, for each size class of *P. barberinus*. Selection for or against food items is determined by these differences between resource use and availability. However, fish behaviours and diets are also influenced by other factors.

All fishes need to balance their susceptibility to predation with their need to obtain food for survival. Smaller juveniles tend to be more vulnerable to predation than larger adults yet also have higher energy requirements (Brown 1985). Size-related differences in foraging behaviour and spatial distribution of *P. barberinus* may be the result of an interaction between these factors. Small fishes probably minimise the risk of predation by remaining mobile while foraging, either in the water column or on the surface of the substratum, rather than stopping to penetrate the substratum. Likewise the reef flat may provide a refuge from predation for small fishes, which rarely ventured onto the open reef base. Juvenile damselfish have been shown to experience lower levels of predation amongst topographically complex habitats compared with open habitats (Beukers 1996). By contrast, large fishes were mostly stationary whilst foraging and spent most of their time on the reef edge and the open reef base. This depth-related size distribution pattern is common amongst fishes (Helfman 1978), as is the pattern of juveniles being in closer proximity to sheltered habitats than are larger adults (Jones 1984).

Smaller fishes spent more time foraging than large fishes in each reef zone, presumably to obtain their required energy levels. Their feeding rates were also less variable and generally higher than those of larger fishes. Brown (1985) found that juvenile centracids, *Micropterus salmoides*, *Ambloplites rupestris*, and *Lepomis gibbosus*, spent more time feeding in the early part of their lives compared with later; however, this was not true for the temperate wrasse, *Pseudolabrus celidotus* (Jones 1984). Fish foraging rates have also been found to decrease with increased fish size (Jones 1984; McCormick 1998),

although this pattern is not always clear (Choat and Clements 1993).

Foraging microhabitat selectivity was demonstrated for all three size classes of *Parupeneus barberinus*, but there was no distinct ontogenetic change in microhabitat preference. There were also no clear associations between the choice of foraged microhabitats by *P. barberinus* and prey availability in the substratum. Jones (1984) similarly found no association between prey availability and microhabitat selection for the juvenile *Pseudolabrus celidotus* in New Zealand. By contrast, the surfperch, *Embiotoca jacksoni*, concentrated its feeding efforts on turf that had the highest prey densities (Schmitt and Holbrook 1984a). However, the differences in these results may be scale dependent to some extent. For example, if sand had been considered a single microhabitat and compared with other available microhabitats at our study location, a relationship between microhabitat use and prey availability would probably have emerged. In addition, the patchy distribution and extremely low densities of invertebrates at the study location probably resulted in poor relative abundance estimates of the invertebrate fauna.

Changes in size of the feeding apparatus have also been associated with changes in foraging behaviour and microhabitat use, thus altering the range of exploitable prey items (Stoner and Livingston 1984; Wainwright 1988; McCormick 1998). Mouth gape has been shown to be an important determinant of prey size (Peterson and McIntyre 1998). The pharyngeal gape, which is usually narrower than the mouth gape, is thought to be an even more important determinant of prey size (Peterson and McIntyre 1998) except in fishes that crush their prey with the pharyngeal jaw apparatus (Wainwright and Richard 1995). However, although increased gape height and width were associated with increased size of the most important prey items for *Parupeneus barberinus*, the maximum size of prey consumed was not constrained by either mouth gape or pharyngeal gape in this species. It is possible, however, that the ability to handle larger prey items was reduced in smaller fishes, thus making it more efficient to select smaller prey items (Wainwright and Richard 1995).

The wide range of unique foraging behaviours of *P. barberinus* and other Mullidae can be directly attributed to a number of morphological specialisations in this family (Gosline 1984). The hyoid barbels of mullids are long, strong, highly mobile, and able to detect prey items in the substratum. More importantly, mullids can raise or lower the barbels while maintaining a horizontal position in the water column. This enables them to search for food over large expanses of unprotected sediment yet maintain a position that enables the rapid acceleration necessary to escape from predators (Gosline 1984). Elongation of the preorbital region of the head allows mullids to dig in the substratum to gain access to prey items. This feature is most pronounced in the genus *Parupeneus*, which has a considerably extended snout compared with other mullid genera (Gosline 1984).

Depths at which *P. barberinus* foraged increased as the size of the feeding apparatus increased. Eggold and Motta (1992) similarly found that small mullet did not dig into the substratum whilst foraging, whereas larger mullet did. Sweatman (1996) found that foraging depth rarely exceeded snout length (50–70 mm) for *Lethrinus nebulosus*. As the increased size of all four morphological variables was highly correlated with increased body size in *P. barberinus*, it is difficult to identify the morphological variables that determined the depths at which fishes foraged in the substratum. However, as each size class rarely foraged deeper than either their barbel or snout lengths, foraging depth is most likely to be associated with these morphological variables. Fishes may not be able to detect prey at depths greater than their barbel lengths whilst probing for food in the substratum. At the same time fishes are unlikely to forage to depths greater than their snout lengths, as this would bring their eyes below the sediment surface and decrease their ability to detect predators.

Overall the two larger size classes of *P. barberinus* spent most of their benthic foraging time digging deeply into the substratum, whereas small fishes tended to concentrate their foraging efforts in the surface layers. In the marine environment, deeper sediment layers tend to have lower prey abundances than the surface layers (Birtles and Arnold 1983). This was also true in this study, especially with respect to the most important prey items for *P. barberinus*. It is possible, however, that some prey items from the surface sediment layer were consumed by larger fishes whilst foraging in deeper layers of the substratum.

This study is unique in its attempt to obtain a reliable estimate of the prey that is 'available' to a particular size class of fish, by incorporating information regarding microhabitat use and prey abundance in the substratum. This should provide the most accurate assessment of ontogenetic changes in prey selectivity by *P. barberinus*. The prey available to particular size classes did not differ markedly, although polychaete availability increased and bivalve availability decreased as fishes increased in size. Certain prey items were consistently selected for or against by all size classes. Consumption of polychaetes was lower than expected from their availability for all three size classes, whereas eucarids and other crustaceans were consumed more than expected from their availability. Pericarids were consumed in proportion to their availability by all three size classes. There were, however, ontogenetic changes in selectivity for or against ostracods, bivalves, and brachyuran crabs. These food items also differed most in their relative importance across the three size classes.

Most mullids feed primarily on polychaetes and crustacea; however, considerable differences have been found in the diets of different species (Hobson 1974; Platell et al. 1998). Diets also differ for the same species at different locations, and between size classes of a species at the same location (Sorden 1981). In the Gulf of Aqaba the most important prey of *P. barberinus* were

crustacea (Wahbeh and Ajian 1985), whereas at our study location they were polychaetes. However, if all crustacean groups are combined, crustaceans also become the most important prey item for small fishes at Turtle Reef (Table 3). In spite of this, crustacea made up smaller proportions of the diets of *P. barberinus* at our study location than in the Gulf of Aqaba for all size classes (Wahbeh and Ajian 1985). Polychaetes were the second most important prey item for *P. barberinus* in the Gulf of Aqaba. This difference in the most important prey item may be related to differences in the relative abundance of crustaceans and polychaetes in the substratum between the two locations; however, this information is lacking for the Gulf of Aqaba.

One of the most important ontogenetic changes in the diet of *P. barberinus* at our study location was between different groups within the crustacea. Smaller fishes tended to eat small ostracods whereas larger fishes ate larger crabs. Although ontogenetic changes were investigated in *P. barberinus* from the Gulf of Aqaba, this level of detail was not obtained (Wahbeh and Ajian 1985). However, crabs increased in importance for the mullid *Upeneus lineatus* with increased size, though not for the smaller congeneric *Upeneus stotti* (Platell et al. 1998). Interestingly, although bivalves became an increasingly important component of the diets of the larger size classes of *P. barberinus* at Turtle Reef, in the Gulf of Aqaba fishes of all size classes almost completely avoided bivalves (Wahbeh and Ajian 1985). Again this may have been due to differences in availability.

Bivalves in the diets of *P. barberinus* at our study location consisted mostly of juveniles or species with thin shells, such as tellinids and solemyids. In particular the genus *Solemya* had very thin shells (Reid 1998). Solemyid bivalves are unusual in that they tend to avoid clean sand and typically live in U-shaped burrows in fine silty anoxic sediments in shallow water. This allows them access to both oxygenated and anoxic environments necessary for normal respiration and their sulphide-oxidising metabolism (Reid 1998). Most of the substratum consisted of clean sand, and this too was the most important foraging microhabitat for *P. barberinus*. It is likely that solemyid bivalves were clumped together in small pockets of habitat suitable for their metabolic requirements and therefore not obtained in sediment samples. They were, however, collected in a much more intensive sampling program conducted at Turtle Reef by the authors the following year, and *P. barberinus* is obviously able to locate them. By contrast gastropods were almost completely avoided in both locations. Mullids generally avoid gastropods and this may be because they have a tendency to secrete toxic chemicals and are well protected by their strong shells (Palmer 1979). In addition mullids lack crushing dentition and a pharyngeal mill and are thereby restricted to eating crustaceans and soft-bodied invertebrates (Hiatt and Strasburg 1960).

Polychaetes were the most important prey item for *P. barberinus* in the current study; however, because of

their comparatively high availability to *P. barberinus*, they were found to be selected against by all size classes. Polychaetes were also the most important prey item for *Mulloidichthys flavolineatus* at Midway Islands, Hawaii, and the most abundant taxon in sediment samples (Sorden 1981). Numerical densities of polychaetes were 10–100 times higher at Midway Islands than at Turtle Reef. In spite of this, *M. flavolineatus* at Midway Islands consumed more polychaetes than expected from their availability in the substratum. In fact Sorden (1981) found that, at the level of family, some polychaetes were selected for and others were selected against.

Although ontogenetic changes in composition and selectivity of dietary prey items have been investigated for a wide range of fish species (Munro 1976; McCormick 1995; Platell et al. 1998), very few studies to date have been carried out on tropical fishes. This study has demonstrated ontogenetic changes in habitat use and foraging behaviour for the tropical mullid *P. barberinus*. These factors are linked to, and interact with, size-related morphological constraints and the need to maximise energy intake while minimising the risk of predation, resulting in ontogenetic changes in selectivity and composition of dietary prey items. In addition, this study is unique in its attempts to interpret ontogenetic changes in the composition and selectivity of prey items of a species in terms of habitat selection at a range of spatial scales, detailed feeding behaviour, and morphology. Similar studies are now required on a variety of important tropical benthic carnivorous fishes.

Acknowledgements This research was funded through an Australian Research Council small grant to M.I. McCormick. Logistic and laboratory support was provided by James Cook University Marine Biology Department and Lizard Island Research Station. We thank C. Dudgeon, A. Hoey, E. Vytopil, J. Peach, J. Ackerman, and J. Kritzer for assistance with data collection and C. Arango, P. Arnold, D. Barton, O. Bellwood, J. Collins, J. Cruz, F. Hoedt, and W. Robbins for assistance with identification of invertebrates. We thank D. Bellwood and J. Caley for advice and critical comments.

References

- Beukers JS (1996) The relative roles of recruitment and post-recruitment processes in the regulation of a coral reef damselfish. PhD thesis. James Cook University, Townsville, Australia
- Birtles A, Arnold P (1983) Between the reefs: some patterns of soft substrate epibenthos on the central Great Barrier Reef shelf. In: Baker JT, Carter RM, Sammarco PW, Stark KP (eds) Proceedings of the Inaugural Great Barrier Reef Conference, Townsville 1983. James Cook University Press, Townsville, Australia, pp 159–163
- Brown JA (1985) The adaptive significance of behavioural ontogeny in some centrarchid fishes. *Environ Biol Fishes* 13:25–34
- Choat JH, Clements KD (1993) Daily feeding rates in herbivorous labroid fishes. *Mar Biol* 117:205–211
- Costello MJ (1990) Predator feeding strategy and prey importance: a new graphical analysis. *J Fish Biol* 36:261–263
- Eggold BT, Motta PJ (1992) Ontogenetic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*. *Environ Biol Fishes* 34:139–158
- Fricke HW (1975) The role of behaviour in marine symbiotic animals. In: Jennings DH, Lee DJ (eds) Symbiosis. (Symposia of the Society for Experimental Biology 29) Cambridge University Press, Cambridge, pp 581–594
- Gillanders BM (1995) Feeding ecology of the temperate marine fish *Achoerodus viridis* (Labridae): size, seasonal and site-specific differences. *Mar Freshw Res* 46:1009–1020
- Gosline WA (1984) Structure, function and ecology in the goatfishes (family Mullidae). *Pac Sci* 38:312–323
- Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (family Labridae). *Mar Ecol Prog Ser* 133:1–11
- Grossman GD (1980) Ecological aspects of ontogenetic shifts in prey size utilisations in the bay goby (Pisces: Gobiidae). *Oecologia* 47:233–238
- Helfman GS (1978) Patterns of community structure in fishes: summary and overview. *Environ Biol Fishes* 3:129–148
- Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol Monogr* 30:65–127
- Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish Bull* 72:915–1031
- Holbrook SJ, Schmitt RJ, Coyer JA (1985) Age-related dietary patterns of sympatric adult surfperch. *Copeia* 1985:986–994
- Hyslop EJ (1980) Stomach contents analysis – a review of methods and their application. *Fish Soc Br Isles* 1980:411–429
- Ibrahim AA, Huntingford FA (1988) Foraging efficiency in relation to within-species variation in morphology in three-spined sticklebacks, *Gasterosteus aculeatus*. *J Fish Biol* 33:823–824
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Jones GP (1984) The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Environ Biol Fishes* 10:43–58
- Lechowicz MJ (1982) The sampling characteristics of electivity indices. *Oecologia* 52:22–30
- Luczkovich JJ, Norton SF, Gilmore RGJ (1995) The influence of oral anatomy on prey selection during the ontogeny of two percid fishes, *Lagodon rhomboides* and *Centropomus undecimalis*. *Environ Biol Fishes* 44:79–95
- MacNeill DB, Brandt SB (1990) Ontogenetic shifts in gill-raker morphology and predicted prey capture efficiency of the Alewife, *Alosa pseudoharengus*. *Copeia* 1990:164–171
- Manly BJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman & Hall, London
- Marshall S, Elliott M (1997) A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. *J Fish Biol* 51:526–545
- Martin P, Bateson P (1995) Measuring behaviour: an introductory guide, 2nd edn. Cambridge University Press, Cambridge
- McCormick MI (1995) Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Mar Biol* 121:627–637
- McCormick MI (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar Biol* 132:9–20
- Munro JL (1976) Aspects of the biology and ecology of Caribbean reef fishes: Mullidae (goatfishes). *J Fish Biol* 9:79–97
- Palmer AR (1979) Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 3:697–713
- Peterson CC, McIntyre P (1998) Ontogenetic diet shifts in *Roeboides affinis* with morphological comparisons. *Environ Biol Fishes* 53:105–110
- Platell ME, Potter IC, Clarke KR (1998) Do the habitats, mouth morphology and diets of the mullids *Upeneichthys stotti* and *U. lineatus* in coastal waters of south-western Australia differ? *J Fish Biol* 52:398–418

- Randall JE, Allen GR, Steene RC (1997) Fishes of the Great Barrier Reef and Coral Sea. Crawford House, Bathurst, Australia
- Reid RGB (1998) Class bivalvia. In: Beesley PL, Ross GJB, Wells A (eds) Mollusca: the southern synthesis. Fauna of Australia, part A, vol 5. CSIRO, Melbourne, pp 235–247
- Schmitt RJ, Holbrook SJ (1984a) Ontogeny of prey selection by black surfperch *Embiotoca jacksoni* (Pisces: Embiotocidae): the roles of fish morphology, foraging behaviour, and patch selection. *Mar Ecol Prog Ser* 18:225–239
- Schmitt RJ, Holbrook SJ (1984b) Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia* 1984:6–12
- Sokal RR, Rohlf FJ (1987) Introduction to biostatistics. Freeman, New York
- Sorden CT (1981) Food specialization by *Mulloidichthys flavolineatus* (Mullidae) at Midway Islands. In: Cailliet GM, Simenstad CA (eds) Gutshop: fish food habit studies. Washington Sea Grant Publication, Seattle, pp 228–231
- Stoner AW, Livingston RJ (1984) Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1984:174–187
- Sweatman H (1996) Impact of tourist pontoons on fish assemblages on the Great Barrier Reef. CRC Reef Research Centre, James Cook University, Townsville, Australia
- Thommasin B (1978) Soft-bottom communities. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. (Monographs on oceanographic methodology, 5) UNESCO, Paris, pp 263–298
- Vanderploeg HA, Scavia D (1979) Two electivity indices for feeding with special reference to zooplankton grazing. *J Fish Res Bd Can* 36:362–365
- Wahbeh MI, Ajian A (1985) The food and feeding habits of the goatfish, *Parupeneus barberinus* (Lacepede), from Aqaba, Jordan. *J Fish Biol* 27:147–154
- Wainwright PC (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* 69:635–645
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environ Biol Fishes* 44:97–113
- Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall, Englewood Cliffs, N.J.