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ORIGINAL PAPER

# Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs

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**Abstract** We surveyed fish distribution in three lagoons and adjacent forereefs in the British Virgin Islands recording about 28,000 fish from 40 families and 118 species. Canonical correspondence indicated that rock, sand, fleshy algae, gorgonians, mangroves and live hard coral were the most important habitat types influencing fish assemblage composition. About 47% of fishes occurring at more than 10 stations displayed evidence of ontogenetic partitioning between reefs and lagoons but post-settlement ontogenetic life history strategies were quite varied depending on the species. For example *Chaetodon striatus* juveniles occurred exclusively in lagoons and all sexually mature adults were found on reefs. Some differences were less pronounced as seen in *Halichoeres bivittatus* where individuals of all sizes occurred on reefs and lagoons, but when analysed it was found that reefs had larger individuals than lagoons. Some species, such as *Acanthurus bahianus*, were primarily reef species whose juveniles also used lagoon habitats while others, such as *Gerres cinereus*, were generally lagoon species whose adults occasionally moved onto reefs. Even with all this variation in life-history strategies, all the species that exhibited bay-reef partitioning used the lagoons as juveniles then moved onto reefs as adults and not vice versa, supporting the hypothesis that bays are important nursery areas for reef-dwelling fishes. These results show that a detailed review of the natural life-history strategies and habitat requirements are required before making further generalisations about the role of near-shore habitat types as nurseries for reef fishes. This is especially important given the rapid changes in tropical near-shore habitats around the world.

**Keywords** GIS · Length-frequency analysis · Canonical correspondence analysis · Caribbean · Mangrove · Seagrass

## Introduction

Many studies of fish habitat preferences in tropical lagoons illustrate their importance as nursery areas for juvenile reef fish (Parrish 1989; Robertson and Blaber 1992; Nagelkerken et al. 2000). However, there have been relatively few studies

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of non-estuarine lagoons in the Caribbean, e.g. (van der Velde et al. 1992; Sedberry and Carter 1993; Nagelkerken et al. 2000, Adams and Ebersole 2002). Only a few recent studies include a range of different non-estuarine lagoon habitats as well as the adjacent forereef in their methods (Lindquist and Gilligan 1986, Cocheret de la Moriniere et al. 2002, 2003).

These studies have greatly enhanced our understanding of the dynamics of Caribbean fish assemblages, but stations are often classified into pre-selected habitat groups, which in reality are a continuous, intergraded mosaic (Ogden and Gladfelter 1983, Ogden 1997). As a result, the importance of some habitats might be overemphasized while others, such as sand are commonly ignored. A simple descriptive approach using uniform methodology accompanied by a gradient analysis to examine the relative abundance of fishes across a range of widely distributed near-shore stations would be more informative of the overall effects of habitat variables on fish assemblages. Quantitative information about the habitat preferences is lacking for many fish species and a study of this nature would be a valuable resource to marine conservation managers who need to predict the impacts of habitat modification. This is particularly relevant today as increasing human impacts in marine environments are causing significant long-term habitat modification, and their effects on fish assemblages are difficult to ascertain (Brown 1997; Al et al. 1999; Edmunds 2002; Gardner et al. 2003; Underwood et al. 2003).

It is widely known that many reef fishes have different habitat requirements depending on their ontogenetic stage and that many juvenile fishes tend to use shallow bay habitats such as mangroves, seagrasses and backreefs then move onto reefs as adults (Nagelkerken et al. 2000a, b; 2001, 2002; Cocheret de la Moriniere et al. 2002). It has been hypothesized that the high density, diversity and abundance of fishes on reefs is due to the connectivity between reefs and bay habitats (Bardach 1959), or that these bay habitats serve as ''waiting rooms'' for recruitment to coral reefs (Parish 1989).

Recent studies in the Netherlands Antilles have shown that bay-reef recruitment is very important for certain commercially important species and these data have been used to formulate models that might be applicable more generally (Nagelkerken et al. 2000a, b, 2001, 2002; Cocheret de la Moriniere et al. 2002). Cocheret de la Moriniere et al. (2002) provided some important insight into the variety of different post-settlement lifecycle migrations ontogenetic migrations. Short distance migration occurs where fishes select habitats immediately adjacent to reefs, long distance migration occurs where juveniles select mangroves or seagrasses in bays and move onto reefs as adults while stepwise migration occurs where fish move progressively closer to the reef as they grow, using a succession of different habitats. However, the range of validity of this study has not yet been extended beyond the Netherlands Antilles, and there is a need to examine the phenomenon at other sites, as it is well known that nursery rules can vary geographically depending on the particular ecological setting (Beck et al. 2001).

While we have some excellent data for a few species, the non-commercially important species tend to be overlooked, and their ontogenetic habitat preferences are unknown, or available only in anecdotal references and field guides. Since nursery functions of habitats are often used to justify conservation prioritization, it is important that this phenomenon is also examined in commercially unimportant species, so that managers that have been entrusted to preserve the fish biodiversity in an area can make informed decisions taking into account the full complexity of multi-species systems. This important knowledge gap can only be filled by fairly descriptive studies that examine all fish species and use consistent sampling methods across habitats from a wide range of locations worldwide.

This study aims to address these issues by (i) mapping distributions of the common species across a range of different near-shore habitats; (ii) describing the patterns of ontogenetic partitioning of fish species in lagoon and forereef habitats and by testing for statistical differences in length-frequency distributions between fishes on bays and on reefs; and (iii) assessing the significant habitat variables affecting fish assemblage composition in the study area.

## Methods

### Study area

The study area is located on the South shore of Tortola, a 61 km$^2$ island in the British Virgin Islands in the Caribbean. The islands are steep-sided, volcanic formations with no perennial streams or rivers. The moderate tropical climate and clear waters of the Virgin Islands support a wide range of habitats including mangroves, seagrasses and coral reefs and over 530 of the 1,500 species of Caribbean fish have been recorded here (Froese and Pauly 2003). About 106 sampling stations were sampled in Hodges Creek, Paraquita Bay and Brandywine Bay (Fig. 1). There is no freshwater input other than rainwater. In fair weather, salinity ranges from 34 to 36 ppt, while tidal ranges do not vary much beyond 1–2 ft. Patches of mangroves, *Rhizophera mangle*, sand, seagrass, *Thalassia testudinum*, algal beds and coralline boulders form patchy mosaics inside the bays that are fringed by a spur-and-groove forereef. Lagoons are generally shallower, warmer and more protected from wave action than reefs and had fairly extensive and flat sandy bottoms, while reef substrates are more rugose and have more complex habitat types (Gratwicke and Speight 2005b).

### Sampling

About 79 lagoon stations and 27 reef stations were selected in a semi-systematic way by moving at least 30 m from the nearest other sampling point and dropping a weighted float overboard then marking the station's position with a Garmin Etrex GPS receiver. Fish and environmental variables were then recorded by diving or snorkeling depending on depth.

At each station, four 2.5 m × 2.5 m quadrats were sampled consecutively, making the total area sampled 25 m$^2$. The quadrat poles were made from 2.5 m PVC pipes that were marked at 5 cm intervals to assist with fish size estimates. They were not contiguous and were laid out on each of the four corners of an unsampled, 2.5 m × 2.5 m square with the station marker at its center. After laying each quadrat, the fish were allowed 1 minute to become accustomed to the

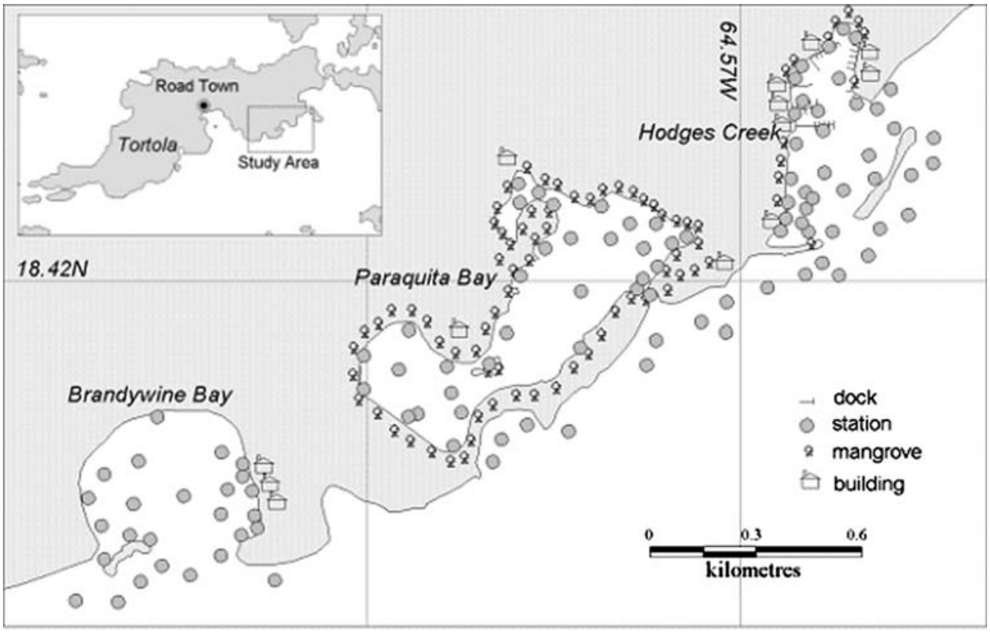

**Fig. 1** Study area, shoreline features and sampling stations in the three bays, Tortola, BVI

presence of the quadrat poles and the observer. Each quadrat was then observed for four minutes from a distance of about 1 m, counting and estimating the lengths of all fish in the quadrat or moving through it and care was taken not to disturb fishes in neighboring quadrats. A fifth minute was spent actively searching for fish hiding in structure or the camouflaged ones that were not detected previously. It is possible that some fish could have been counted twice if they swam the 2.5 m between quadrats during the sampling, but this was not a regular occurrence given the short sampling periods and distance between quadrats (B.G. personal observations). Stations were visited in randomized order to control for possible time-of-day effects and were visited twice, the second sampling occasion being 2–4 weeks after the first. This method was selected after extensive piloting of methods using different numbers of quadrats and different numbers of visits, and the regime used here was judged to have the best cost-benefit: precision ratio for a multi-species assemblage study in this area.[1] Samples were all recorded during the summer months of July, August and September 2001.

The total sum of fish counted in all four quadrats on both sampling occasions was used as a measure of relative abundance. Fish densities were not calculated because the count period lasted for 5 min and would hence overestimate instantaneous fish densities.

Habitat variables were: seagrass, calcareous algae, fleshy algae, mangrove, sand, rubble, rock, live hard coral, gorgonian, encrusting gorgonian, zooanthid, sponge or 'other'. At each sampling station the mean percentage cover was estimated by eye in each quadrat and then the data from all four quadrats on both sampling occasions were pooled.

## Analysis

A species accumulation curve was drawn to assess whether the sampling intensity was adequate for the three bays after iteratively randomizing the station order (Simberloff 1972). The relative abundance of the most common fish species (occurring at 10 or more of 106 stations) were mapped then grouped into one of the following categories: (1) taxa that could not be confidently identified to species level using the visual census method (these were omitted from further analyses); (2) predominantly lagoon species; (3) predominantly reef species; (4) species occurring in lagoons and on reefs.

Next, length-frequency diagrams were drawn for the species occurring both in lagoons and on reefs. The null hypothesis was that there is no difference in length-frequency distribution between the lagoon and forereef. It was tested using a non-parametric Kolmogorov–Smirnov independent samples test (Sokal and Rohlf 1990) using SPSS 12.0 software. The length at first sexual maturity quoted in FISHBASE (Froese and Pauly 2003) was marked on the length-frequency diagrams (where available) and species displaying significant ontogenetic bay-reef partitioning were split into sexually mature adults and juveniles for further analysis.

Habitat variables and fish species occurring at 10 or more stations were entered into a unimodal canonical correspondence analysis (CCA) (ter Braak 1986) using CANOCO version 4. The analysis of interspecies distances was undertaken using Hill's scaling and log-transformed species data with rare species downweighted to minimize their influence on the overall ordination. Environmental variables were selected using a manual forward selection of explanatory variables (this is a multivariate extension of the stepwise regression method). Variables were added to the model in order of the greatest contribution to total variation, but only if they were significant and did not cause any variance inflation factors exceeding 20 (Leps and Smilauer 2003).

Significance was determined at the $P < 0.05$ level using a Monte Carlo permutation test set at 499 permutations. Results were graphed as two-dimensional biplots of species and environmental variables in which arrows represent the direction of the environmental axis and the length of the arrow corresponds to the relative importance of that environmental variable (ter Braak 1986). To assess the influence of habitat gradients on fish

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[1] Gratwicke, B. 2004. Factors affecting the distribution of fishes in the British Virgin Islands. Unpublished DPhil Thesis, University of Oxford

assemblages, the analysis outlined above was performed three times: (1) on all 106 stations; (2) on all 79 lagoon stations and (3) on all 27 reef stations.

## Results

### Species richness

Nearly 28,000 fish from 40 families were recorded at 106 stations (Appendix A, Fig. 2). The most abundant fishes were *Scarus* juveniles < 10 cm, which made up almost 36% of the total numbers encountered, followed by *Eucinostomus* spp., *Halichoeres bivittatus* and *Thalassoma bifasciatum* (Appendix A). The most widespread species was *Halichoeres bivittatus*, occurring at 86 stations, followed by *Stegastes diencaeus/leucostictus* juveniles, *Scarus* juveniles, *Ocyurus chrysurus*, *Sparisoma radians*, *Eucinostomus* spp., *Malacoctenus macropus/versicolor* and *Stegastes* spp. adults (>50 stations each). By the 80th sample, the species accumulation curve flattened off at 118 indicating sufficient sampling effort (Fig. 2).

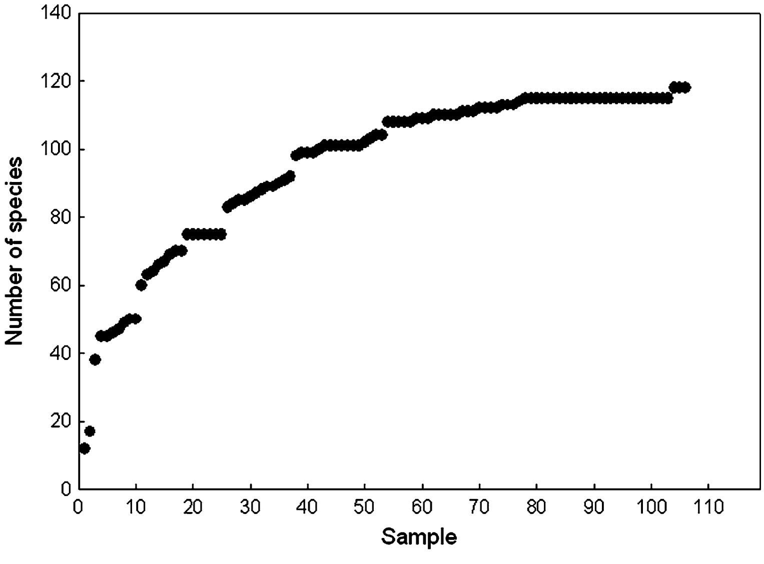
### Distribution and ontogenetic partitioning

Most of the species were too rarely encountered to include in any distributional and ontogenetic habitat preference analyses, but we noted the habitats in which they were recorded (Appendix A). Of the 43 species occurring at 10 or more stations, 7 could not be identified with certainty at all the life-history stages encountered. They were identified as far as possible to the lowest possible taxon or species-pairs (Fig. 3). About 17 of the remaining 36 species occurred both on the forereef and in the lagoon (Fig. 4). The rest of the species were either found predominantly in the bays (Fig. 5) or predominantly on the forereef (Fig. 6). No adults of *H. plumieri*, *H. sciurus* and *S. barracuda* were encountered even though adults were seen on the forereef at other times so the analyses for these three species should be considered representative only of the juveniles.

*Eucinostomus* spp., *Lutjanus griseus*, *Haemulon sciurus* and *Lophogobius cyprinoides* were common in mangrove-lined Hodges Creek and Paraquita Bay but were virtually absent from Brandywine Bay which lacks mangroves. Some fish, notably *Chaetodon capistratus*, *Coryphopterus glaucofraenum* and *Hypoplectrus puella* were found around the mouth of Paraquita Bay and there was no evidence of post-settlement migration deeper into the lagoon.

All species occurring in the lagoon and on the reef had significantly different length-frequency distributions between bays and reefs except

**Fig. 2** The iteratively randomised species accumulation curve for all 106 stations sampled in the area



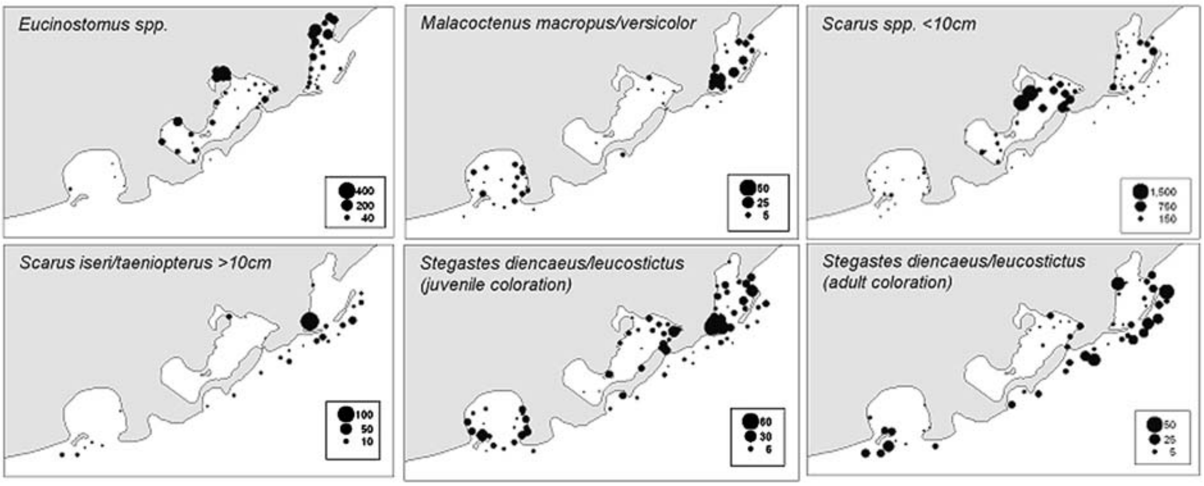


**Fig. 3** Distribution and relative abundance of taxa that could not be confidently identified to species level using the underwater visual census method

*Coryphopterus glaucofraenum*, *Caranx ruber* and *Hypoplectrus puella* (Fig. 7). While the basic pattern of ontogenetic partitioning in the remaining species was similar (juveniles tending towards lagoons and adults towards reefs), the life history strategies were slightly different for each species. The most extreme partitioning example was exhibited by *Chaetodon striatus*, where all juveniles occurred in lagoons and all sexually mature adults were on the reef. *Halichoeres bivittatus* juveniles and adults frequently occurred in both habitats but larger individuals favored the forereef more than lagoons (Fig. 7). Juvenile *Lutjanus apodus* and *Gerres cinereus* were found in lagoons, but sexually mature adults were observed in lagoons as well as reef habitats. *Acanthurus bahianus*, *Haemulon flavolineatum*, *Sparisoma aurofrenatum* and *Stegastes planifrons* juveniles were found in both lagoon and reef habitats while adults were all exclusively reef species. Overall, 47% of the species found in adequate numbers exhibited ontogenetic partitioning of habitats, indicating the extent and importance of this phenomenon.

## Habitat and fish assemblages

CCA analysis and Monte Carlo permutations identified rock, sand, fleshy algae, mangroves, gorgonians and live hard coral as the most significant habitat variables structuring the fish assemblages (in that order of importance), while seagrass, calcareous macroalgae, encrusting gorgonians, zooanthid mats, rubble, sponge and 'other' habitat variables had less marked effects on the fish assemblages. The overall CCA analysis strongly split bay habitat variables and species to the left and reef variables and species to the right (Fig. 8). This is unsurprising as they have markedly different compositions (Table 1). The first two CCA axes on the plot accounted for about 25% of the variation in species data, and 78% of the species–environment relations (Table 2). The large number of species on the plot, however, makes it cluttered and finer interpretation is difficult, but it is evident that juvenile stages are generally clustered to left (lagoons) and adult stages to the right (reefs).

In order to assess fish-habitat selectivity within lagoons and reefs the dataset was split into the 79 lagoon stations and the 27 reef stations. The same CCA procedure was run on each of the reduced datasets and all three plots were considered in the final interpretation. The most significant habitat variable accounting for the variation within lagoon fish assemblages was sand, fleshy algae, mangroves and rock. Overall, the first two axes accounted for 17% of the variation in species data and 76% of the species–environment relations (Table 3). On the reef, however, only sand, gorgonian and rock were significantly related to species composition.

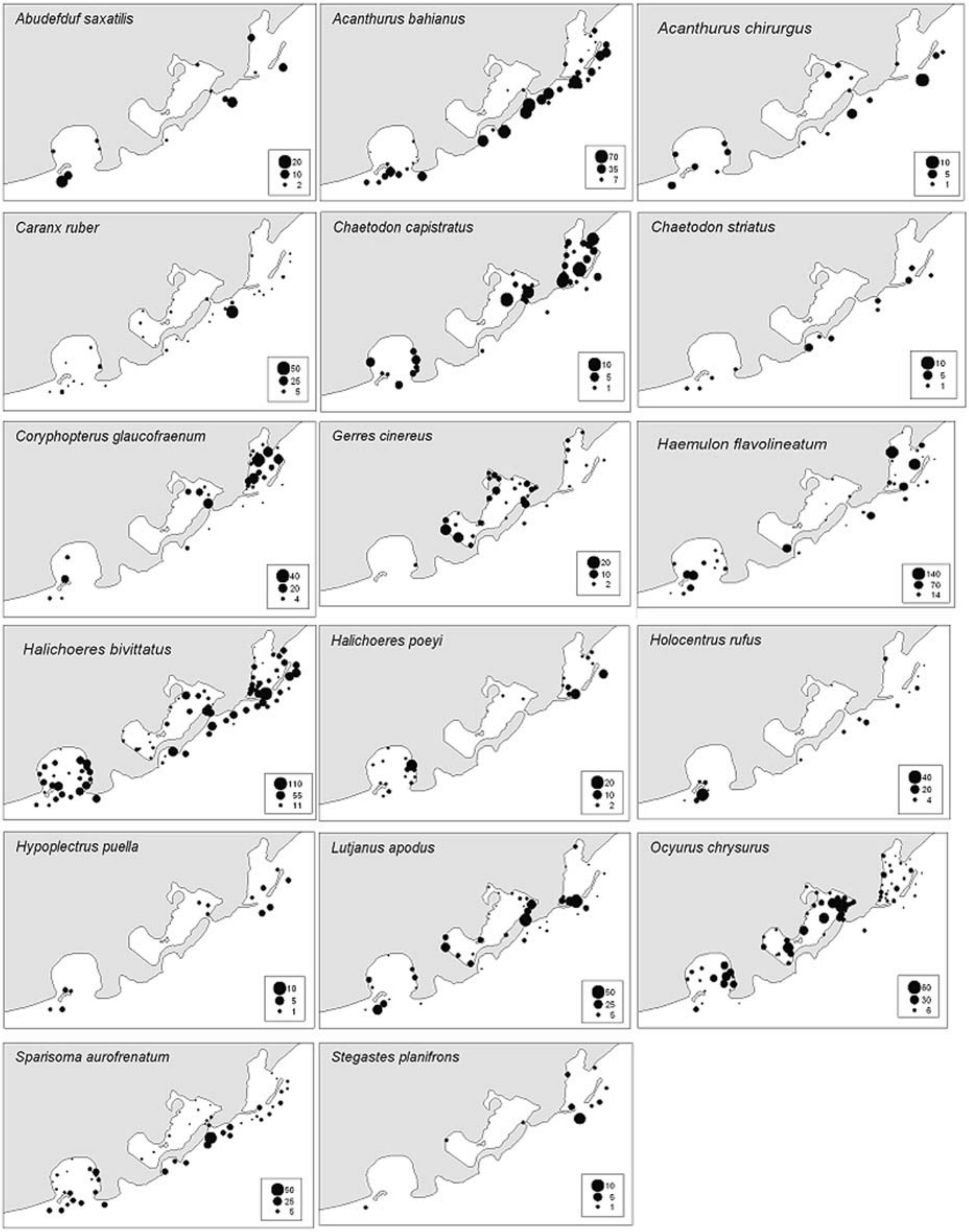


**Fig. 4** Distribution and relative abundance of species occurring both in lagoons and on the forereef

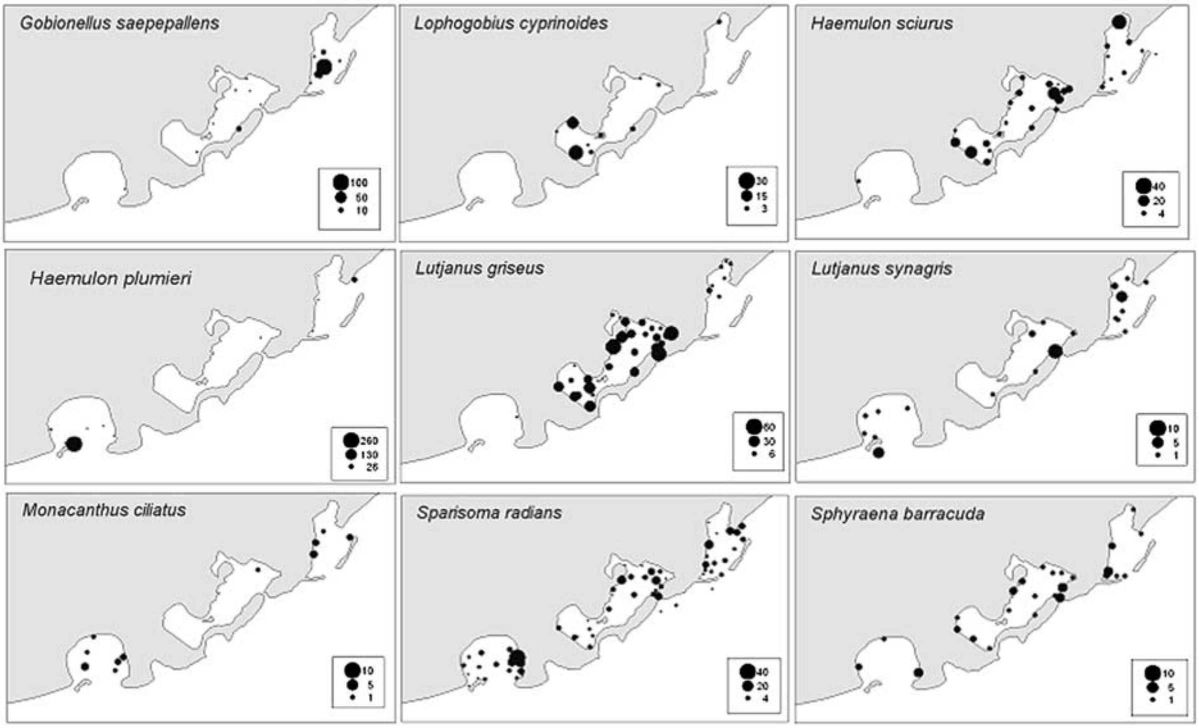


**Fig. 5** The distribution and relative abundance of species predominantly occurring in bays. Note that only juvenile *H. plumieri*, *H. sciurus* and *S. barracuda* were encountered in the study area, and the distribution of adults was not ascertained by this sampling programme although adults of these species were spotted on the reef at other times

Interestingly, in the overall analysis live hard coral was a significant predictor, albeit a weak one, but its effect was not significant in the forereef-only dataset, possibly due to the small number of forereef stations surveyed. The first two axes of the forereef-only dataset accounted for 33% of the variation in species data, and 93% of the species–environment relations.

The lagoons acted as nursery areas for many fish species that selected mangroves and macroalgae (e.g. *Lutjanus apodus*, *Haemulon sciurus* juveniles, *Sphyraena barracuda* juveniles, *Gerres cinereus* juveniles, *Lophogobius cyprinoides* and *Lutjanus griseus*, Fig. 9a). *Haemulon flavolineatum* juveniles, *Haemulon plumieri* juveniles, *Halichoeres poeyi* juveniles, *Halichoeres bivittatus*, *Acanthurus bahianus* juveniles, *Chaetodon capistratus* juveniles, *Sparisoma aurofrenatum* juveniles and *Thalassoma bifasciatum* preferred rocky areas within lagoons while the sand-dwelling species were usually inconspicuous, pale-colored fish such as *Coryphopterus glaucofraenum* and *Gobionellus saepepallens* or larger predators such as *Caranx ruber* and *Lutjanus synagris* (Fig. 9a).

On the forereef (Fig. 9b), only three species were clearly associated with rocks: *Ophioblennius atlanticus*, *Malacoctenus aurolineatum* and *Stegastes dorsopunicans*. Species that favored sandier areas on the forereef were: *Halichoeres bivittatus*, *Acanthurus bahianus* juveniles, *Sparisoma aurofrenatum* juveniles and *Halichoeres maculipinna* (Table 3). Gorgonians covered about 3% of the forereef stations and *Holocentrus rufus* adults, *Caranx ruber*, *Sparisoma viride*, and *Microspathodon chrysurus* favored gorgonians. The remaining forereef species had more general habitat preferences, and their numbers were probably related to factors other than the measured habitat variables.

Figure 9 indicates that the species mostly associated with sand in lagoons were different from those associated with sand on the forereef. More importantly, for the species that were observed in both habitat types at the same life history stage (e.g. *Halichoeres bivittatus*, *Sparisoma*

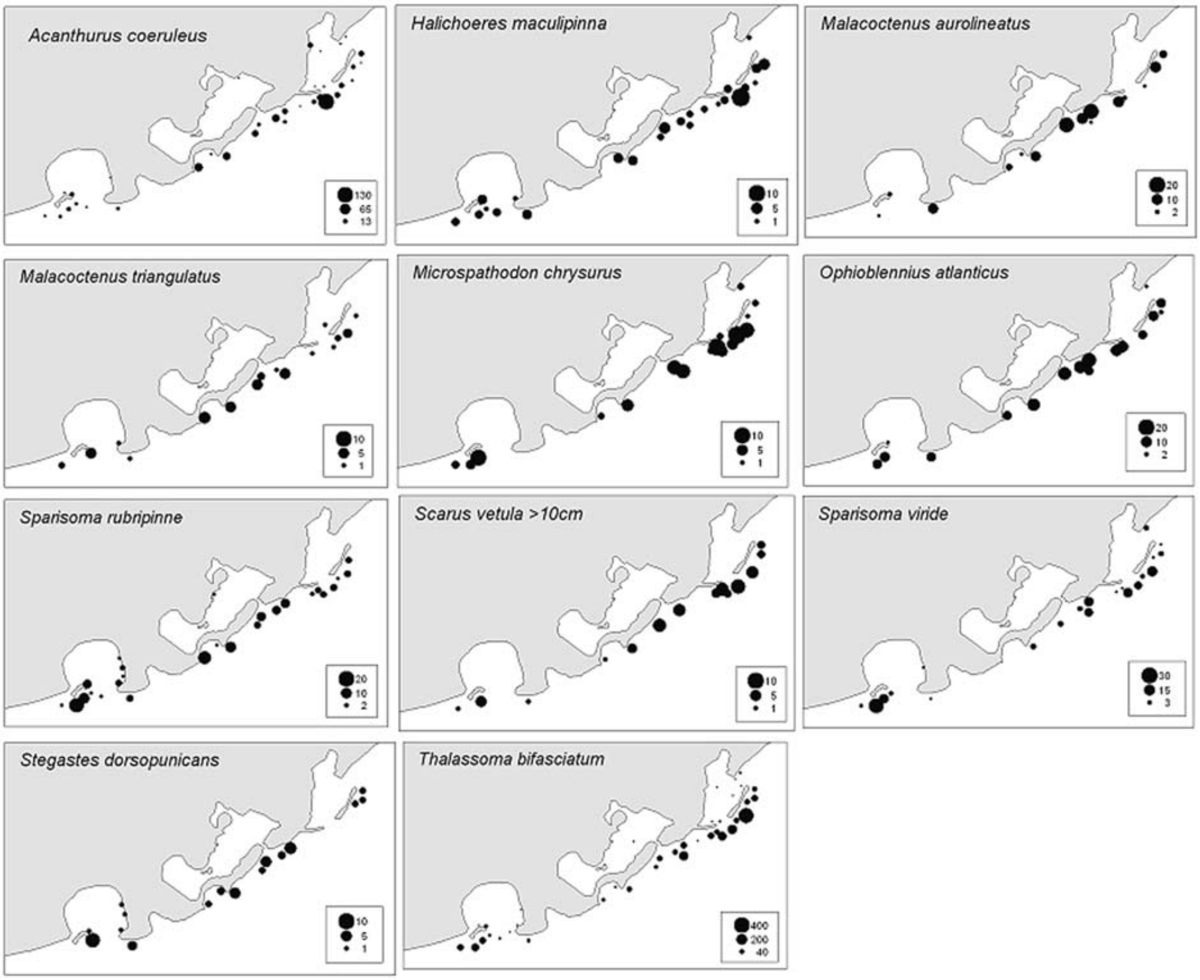


**Fig. 6** Distribution and relative abundance of species occurring predominantly on the forereef

*aurofrenatum*, *Lutjanus apodus* and *Acanthurus bahianus*), there were obvious differences in habitat associations between bays and reefs. For example, *S. aurofrenatum* juveniles on the forereef were strongly influenced by sand, while in lagoons, they were strongly associated with rock.

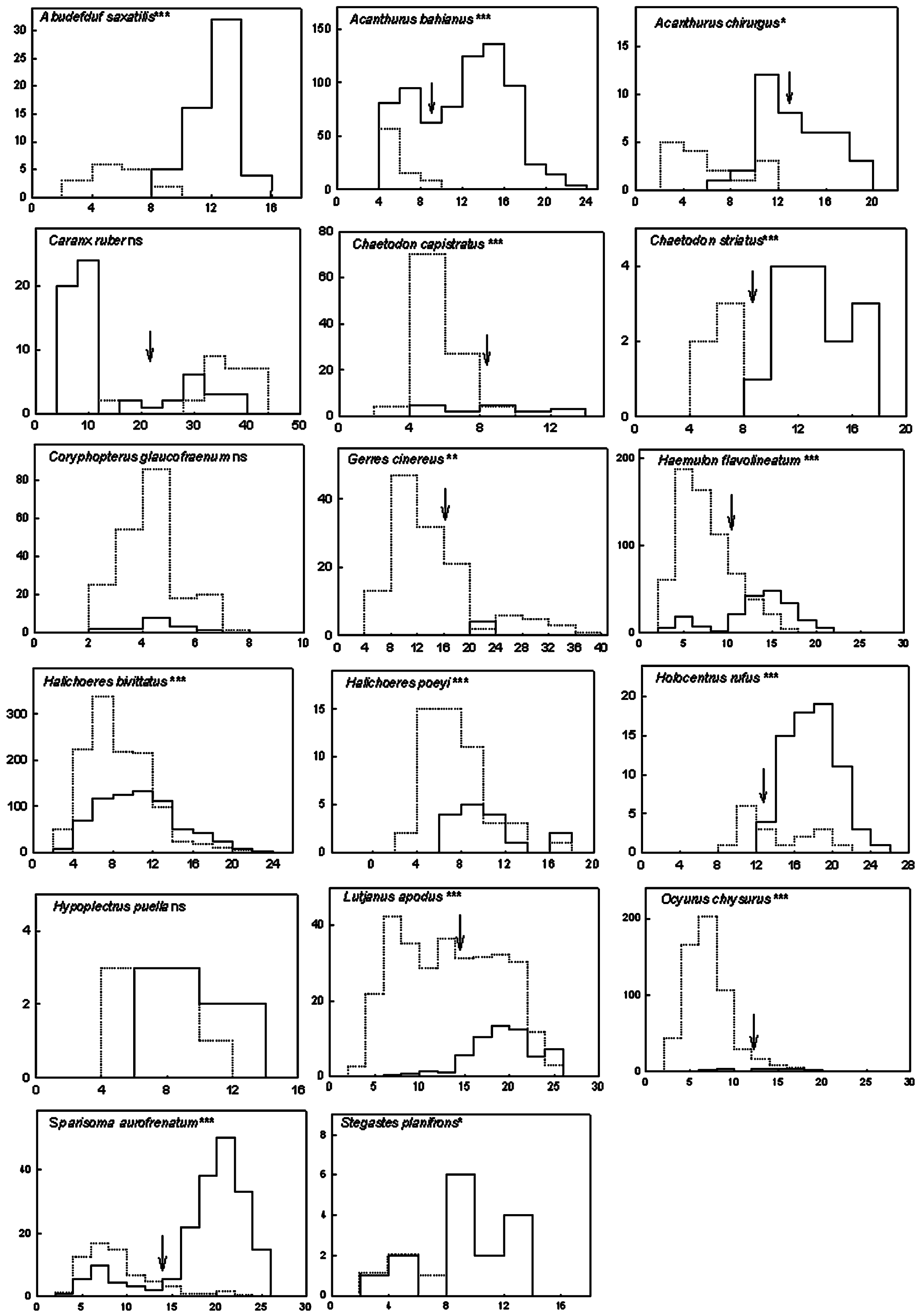
## Discussion

### General distribution patterns

The two mangrove-lined bays were the exclusive homes of mangrove-associated fish species *Lutjanus griseus*, *Haemulon sciurus* and *Lophogobius cyprinoides*, similar to findings elsewhere (Humann 1994; Chaves and Otto 1999; Nagelkerken et al. 2000). Other species such as *Lutjanus apodus* and *Sphyraena barracuda* juveniles were predominantly found in the mangrove-lined lagoons and have been noted as mangrove-dependent (Nagelkerken et al. 2000a, b) but their occurrence in Brandywine Bay, which lacked mangroves, is indicative of their ability to inhabit mangrove-free areas (albeit in lower numbers). Some of the mangrove-associations recorded at an island scale (Nagelkerken et al. 2002) may therefore also be applicable at the scale of individual lagoons.

### Habitat correlations

The apparent habitat preferences of the fishes in the overall plot (Fig. 8) do not tally particularly


Abudefduf saxatilis***
Acanthurus bahianus***
Acanthurus chirurgus*
Caranx ruber ns
Chaetodon capistratus ***
Chaetodon striatus***
Coryphopterus glaucofraenum ns
Gerres cinereus **
Haemulon flavolineatum ***
Halichoeres bivittatus ***
Halichoeres poeyi***
Holocentrus rufus ***
Hypoplectrus puella ns
Lutjanus apodus ***
Ocyurus chrysurus ***
Sparisoma aurofrenatum***
Stegastes planifrons*

◀**Fig. 7** The length-frequency distributions of fishes occurring in lagoons (dotted line) and on reefs (solid line). A Kolmogorov–Smirnov $z$ tests for differences ns = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. The arrow indicates size at first reproductive maturity if available in FISHBASE (Frose and Pauly 2003)

well with the individual lagoon and reef analyses (Fig. 9). This is because the reefs and lagoons have distinctive habitat composition, and different habitats may be limiting factors in each. For example, *Acanthurus bahianus* juvenile abundances are correlated with rock cover in the overall analysis and in lagoons but the forereef-only analysis suggests they preferred sandy stations, probably because rock was more of a limiting factor in lagoons than on reefs.

Any habitat correlations with relative fish abundance are not necessarily causative and it is well established that other mechanisms such as predation, food availability, recruitment, space, competition and disease are likely to be the main factors regulating fish populations in any given place (Hay and Taylor 1985; Shulman 1985; Carr and Hixon 1995; Robertson 1996; Hixon and Carr 1997; Kramer et al. 1997; Bay et al. 2001; Mora et al. 2003). Nevertheless, habitat type is an important variable that is inextricably linked with factors like predation risk and food availability, thus many species select habitats where they will be able to optimize their chances of growth, survival and reproduction (Kramer et al. 1997; Dahlgren and Eggleston 2000).

Rock cover was one of the most important habitat variables influencing the fish assemblages. Rocky areas provide food and refuge from predators that are major factors affecting community structure (Hixon and Beets 1989, Hixon 1991) and thus support many different species in high densities (Carpenter 1986). The rocky areas were characterized by high fish densities and species richness that varied depending the habitat complexity (Gratwicke and Speight 2005b). On the forereef where rock cover and structure was abundant (Table 1) rock-specialists such as *Ophioblennius atlanticus*, *Malacoctenus aurolineatum* and *Stegastes dorsopunicans* were characteristic while in lagoons with limited stable substrate and cover *Halichoeres bivittatus*, *Haemulon plumieri*, *Thalassoma bifasciatum* and juveniles of *Haemulon flavolineatum*, *Chaetodon capistratus*, *Sparisoma aurofrenatum*, *Halichoeres poeyi* and *Acanthurus bahianus* were clustered around the rocky areas (Fig. 9).

Because of the relatively low levels of primary production associated with sand (Hillebrand and Kahlert 2002) and the lack of cover for non-burrowing fish and invertebrates, sand assemblages tended to be characterized by sand specialists that are usually pale and inconspicuous e.g. *Gobionellus saepepallens*, *Coryphopterus glaucofraenum* and *Eucinostomus* spp. or they burrow (e.g. *Nes longus*). Roving predators, such as jacks, were also spotted in these areas, presumably searching for prey fishes straying from cover.

Mangroves are recognised as key habitats for juvenile fishes in many parts of the world (Pinto and Punchihewa 1996; Chaves and Otto 1999; Laegdsgaard and Johnson 2001, Cocheret de la Moriniere et al. 2002) and the findings that *Lutjanus apodus*, *Lutjanus griseus*, *Haemulon sciurus* juveniles, *Sphyraena barracuda* juveniles, *Gerres cinereus* juveniles, *Lophogobius cyprinoides* and *Mugil curema* are associated with mangroves supports the findings of other authors (Humann 1994, Nagelkerken et al. 2000, Cocheret de la Moriniere et al. 2002). Mangrove roots are probably key habitats because they provide shelter from predators and support a diverse assemblage of epiphytic algae and invertebrates, providing an array of potential food sources for both predators and grazers (Farnsworth and Ellison 1996).

Gorgonians were more abundant on deeper reefs and the general effects of gorgonians may be partly correlated with well-established depth-zonation patterns on reefs (McGehee 1994). Some species may, however, have a distinct preference for upright gorgonains for food, e.g. *Chaetodon striatus* (Lasker 1985) while long, slender trumpetfish, *Aulostomus maculatus*, are attracted to gorgonians for camouflage where they wait among the fronds to ambush small fish (DeLoach 1999).

Live hard coral (LHC) had a weak influence on the overall dataset that was not detected in the reef-only analysis, making determination of its influence difficult and inconclusive. This may be partly due to the lack of live hard coral cover in

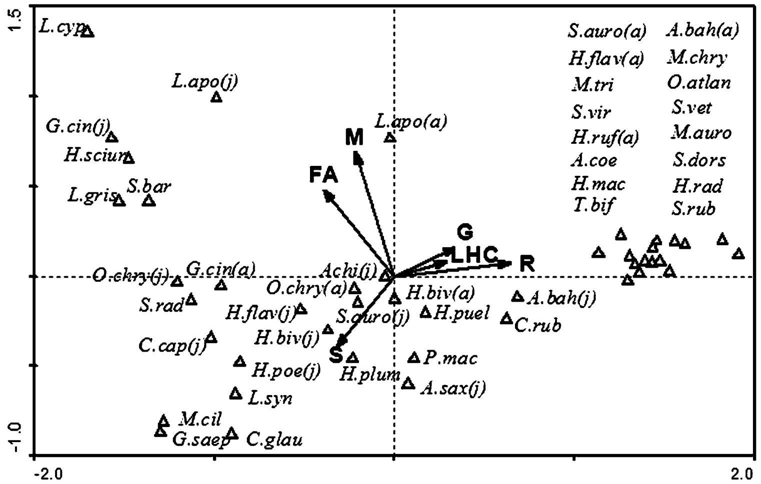


**Fig. 8** CCA analysis of species occurring at more than 10 stations and significant ($P < 0.05$) environmental variables were selected using the Monte Carlo permutation FA = fleshy algae, M = mangrove, G = gorgonian, LHC = live hard coral, R = rock, S = sand. Abbreviations of the following species are given: *A. bahianus*, *A. chirurgus*, *A. coeruleus*, *A. saxatilis*, *C. capistratus*, *C. glaucofraenum*, *C. ruber*, *G. cinereus*, *G. saepepallens*, *H. bivittatus*, *H. flavolineatum*, *H. maculipinna*, *H. plumieri*, *H. poeyi*, *H. puella*, *H. radiatus*, *H. rufus*, *H. sciurus*, *L. apodus*, *L. cyprinoides*, *L. griseus*, *L. synagris*, *M. aurolineatus*, *M. chrysurus*, *M. ciliatus*, *M. triangulatus*, *O. atlanticus*, *O. chrysurus*, *P. maculatus*, *S. aurofrenatum*, *S. barracuda*, *S. dorsopunicans*, *S. radians*, *S. rubripinne*, *S. vetula*, *S. viride*, *T. bifasciatum*. Ontogenetic stage is indicated as (*j*) juvenile, and (*a*) adult where necessary. Taxa that could not be confidently identified at all stages of their live history using under water visual census methods were omitted from analysis

the study area. Other studies, notably from the Pacific, have highlighted the importance of live coral on certain fish assemblages (Carpenter et al. 1981; Bell and Galzin 1984; Sano et al. 1984) while others report none (Sale and Dybdahl 1975; Luckhurst and Luckhurst 1978; Roberts and Ormond 1987) and in some instances it seems that habitat structure may be a more important variable than live cover (Gratwicke and Speight 2005a, b).

Seagrass, sponge, zooanthid, rubble and other habitats had no strong influence on the fish assemblage. Seagrass is known to be a key habitat for certain fish species such as *Sparisoma radians* (Kirsch et al. 2002), and is apparently an important nursery habitat for juvenile fish (Parrish 1989; Nagelkerken et al. 2001), but the influence of other habitat variables on fish assemblages was more important in these three bays. Others have also noted that the fish fauna in tropical marine

**Table 1** A comparison of overall habitat composition of the forereef and lagoon stations

| Habitat | Lagoon (*n* = 79) | | Reef (*n*=27) | |
|---|---|---|---|---|
| | Mean % | SD | Mean % | SD |
| Calcareous algae | 9.3 | 11.6 | 3.9 | 4.5 |
| Seagrass | 31.2 | 29.7 | 0.2 | 0.6 |
| Mangrove | 1.5 | 4.4 | 0.0 | 0.0 |
| Fleshy algae | 19.2 | 20.2 | 3.3 | 4.7 |
| Sand | 33.5 | 27.4 | 15.7 | 23.1 |
| Rock | 3.5 | 11.6 | 60.3 | 23.5 |
| Zooanthid | 0.0 | 0.0 | 2.3 | 4.5 |
| Live hard coral | 0.3 | 1.7 | 7.9 | 9.5 |
| Gorgonian | 0.0 | 0.0 | 3.0 | 4.2 |
| Encrusting gorgonian | 0.0 | 0.0 | 0.3 | 0.8 |
| Rubble | 0.9 | 4.9 | 2.7 | 5.8 |
| Sponge | 0.1 | 0.3 | 0.9 | 1.9 |
| Other | 0.4 | 1.6 | 0.0 | 0.0 |

**Table 2** Summary of the CCA analysis on all 106 stations, using the six significant explanatory variables

| Canonical axes | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Total inertia |
|---|---|---|---|---|---|
| Eigenvalues | 0.549 | 0.128 | 0.100 | 0.056 | 2.724 |
| Species–environment correlations | 0.959 | 0.681 | 0.666 | 0.735 | |
| Cumulative % of variance | | | | | |
| Species data | 20.2 | 24.9 | 28.5 | 30.6 | |
| Species-environment relation | 63.0 | 77.7 | 89.3 | 95.6 | |
| Sum of all eigenvalues | | | | | 2.724 |
| Sum of all canonical eigenvalues | | | | | 0.871 |

seagrass beds is strongly influenced by their proximity to other habitat types (Pollard 1984; Hemminga and Duarte 2000).

It has been shown on small, fixed habitat types that species composition can vary considerably due to the priority effects of competitors and predators (Shulman et al. 1983). In this study some species were closely associated with particular habitats types, but the priority effects of competition were not examined. When looking at the scale of bays and lagoons (kilometers), species assemblages were both distinctive and predictable depending on the habitat type (Figs. 8, 9), but at the scale of stations (2.5 m) individual species interactions may have been be more important.

The fact that rocks and mangroves were the most important lagoon habitats for juvenile fish indicates that mangrove restoration and construction of small artificial rocky reefs might be effective ways to mitigate habitat destruction in marinas where natural habitats have been extensively modified. This may increase overall species and abundance in degraded habitat types, but the fact that different species have very different habitat requirements means that the only way to maintain regional biodiversity is to protect and maintain the health and diversity all natural habitat types.

## Ontogenetic partitioning

In order to fully comprehend the potential impacts of the habitat modification on fish populations in the Caribbean, we need detailed descriptive studies of key habitat requirements of fishes at all stages in their lifecycle (Atwood et al.

**Table 3** Summary of the CCA analysis on (a) the lagoon stations and (b) the forereef stations using the significant habitat variables

| Canonical axes | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Total inertia |
|---|---|---|---|---|---|
| *(a) Lagoon* | | | | | |
| Eigenvalues | 0.190 | 0.166 | 0.076 | 0.034 | 2.096 |
| Species–environment correlations | 0.744 | 0.770 | 0.695 | 0.551 | |
| Cumulative % of variance | | | | | |
| Species data | 9.1 | 17.0 | 20.6 | 22.2 | |
| Species–environment relation | 40.8 | 76.4 | 92.6 | 100.0 | |
| Sum of all eigenvalues | | | | | 2.096 |
| Sum of all canonical eigenvalues | | | | | 0.466 |
| *(b) Forereef* | | | | | |
| Eigenvalues | 0.091 | 0.061 | 0.011 | 0.061 | 0.462 |
| Species–environment correlations | 0.875 | 0.844 | 0.668 | 0.000 | |
| Cumulative % of variance | | | | | |
| Species data | 19.7 | 32.9 | 35.3 | 48.5 | |
| Species–environment relation | 55.8 | 93.1 | 100.0 | 0.0 | |
| Sum of all eigenvalues | | | | | 0.462 |
| Sum of all canonical eigenvalues | | | | | 0.163 |

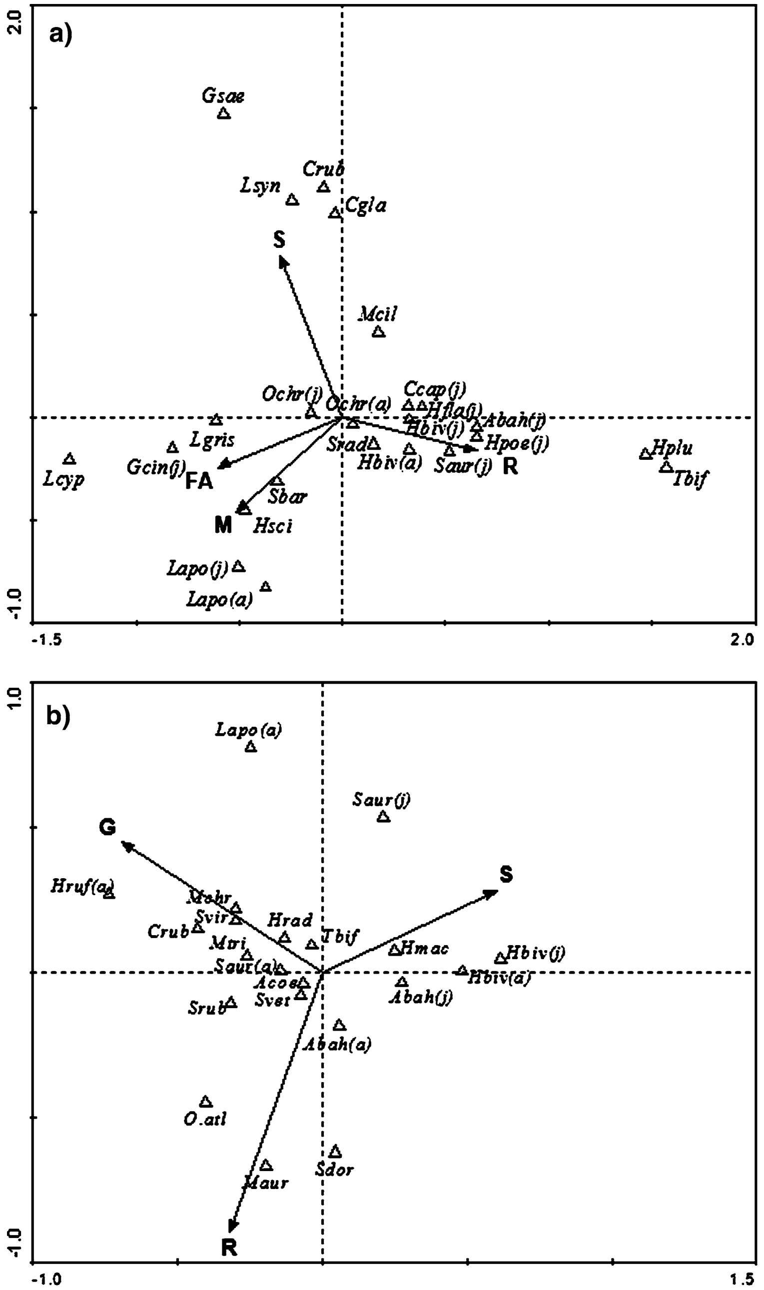


**Fig. 9** CCA analysis of (**a**) lagoon and (**b**) forereef fish occurring at more than 10 stations. Redundant environmental variables were eliminated using a Monte Carlo test of significance in a manual forward selection procedure. Habitat variables and species names given in Fig. 8

1992, Edmunds 2002, Gardner et al. 2003, Miller et al. 2003). Studies of single biotopes and life stages can create a biased impression of how marine systems function. For example, seagrass beds were once assumed to be essential nursery areas for many fishes, however recent studies have shown that most species can utilize alternate habitats (Hemminga and Duarte 2000). This still does not give any impression of the relative importance of seagrass, thus nursery habitats should really be defined as "A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur'' (Beck et al. 2001).

Our study illustrates nursery effects at two different levels. Juveniles of some species clearly preferred lagoon habitats to reefs (Figure 8) but were not associated with any particular habitats within the lagoons, while others were more specialized and were closely associated with particular habitat types within lagoons. The ontogenetic partitioning was observed in many different families including: Pomacentridae, Chaetodontidae, Acanthuridae, Gerreidae, Haemulidae, Lutjanidae, Labridae, Holocentridae, and Scaridae and similar results have been found in other places (Stoner and Livingston 1984, Lindquist and Gilligan 1986, Rooker 1995, Gutierrez 1998, Nagelkerken et al. 2000, Adams and Ebersole 2002, Cocheret de la Moriniere et al. 2002). The actual species life-history patterns varied markedly within each family, resulting in some advanced resource partitioning. For example, *Sparisoma radians* was found only in lagoons throughout its life cycle, juvenile *S. aurofrenatum* were found in both lagoons and reefs while *S. rubripinne* was found only on reefs throughout its lifecycle (Figs. 4–7). This broad range in habitat requirements even among very closely related species may point to their evolutionary origins. For example, envision an ancestral fish that used both lagoons and reef habitats. If an event such as a change in sea level isolated the lagoons from the forereef, this would provide two isolated and very distinctive environments with different evolutionary pressures: a seagrass and algae-filled lagoon and an unconnected forereef, potentially giving rise to two new species adapted to those environments.

Other authors have shown that intermediate fish sizes may have different habitat preference from juveniles and sexually mature adults (Appeldoorn et al. 1997, Nagelkerken et al. 2000, Cocheret de la Moriniere et al. 2002), thus the lagoon-reef classification presented here is an over-simplification. However, the value of this very broad, multi-species study is that it is one of few systematic analyses of ontogenetic partitioning patterns that also includes commercially unimportant species and it gives us one of the first real glimpses at the widespread importance of lagoon-reef habitat partitioning from a biodiversity perspective. The fact that 47% of the fishes examined displayed significant lagoon-reef partitioning indicates the extensive nature of the phenomenon, but the detailed species accounts show the huge variety of different life-history strategies employed by each species. A review paper of similar studies will be required to place this in a regional or global context, but the necessary descriptive studies are mostly lacking, especially for species that are not commercially important.

Our results indicate that fish assemblages vary continuously in relation to simple habitat variables and these are particularly apparent when ontogenetic factors are taken into account. While many studies are beginning to address ontogenetic questions in relation to reef fish communities, there is a considerable knowledge gap in the ontogenetic life-history patterns of many Caribbean reef fish species and this study provides new insights for several species. The fact that some species appear to have incremental ontogenetic transitions from habitat type to habitat type means that fish assemblage composition may depend not only on the type of habitat available, but on the contiguity and dispersion of adjacent habitat types too.

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**Appendix** A list of species from 40 families encountered in the three bays, including the total counts for each species, the number of stations and the bays B = Brandywine, P = Paraquita, H = Hodges Creek. A subjective assessment (B.G.) of their occurrence in the sampling area C = commonly encountered, O = occasional, R = rare, and notes on the observed habitat preferences of each species

| Family | Species | Total | No. Stations | Bays | Rarity | Observed habitats |
|---|---|---|---|---|---|---|
| Acanthuridae | *Acanthurus bahianus* | 828 | 43 | BPH | C | Seaward reef, back-reef and seagrass |
| | *Acanthurus coeruleus* | 536 | 34 | BPH | C | Seaward reef |
| | *Acanthurus chirurgus* | 47 | 18 | BPH | C | Seaward reef, reef flat, seagrass, sand |
| Albulidae | *Albula vulpes* | 2 | 1 | H | O | Seagrass and sand, wary of divers |
| Apogonidae | *Phaeoptyx pigmentaria* | 3 | 1 | P | R | Reef recess |
| Aulostomidae | *Aulostomus maculatus* | 15 | 6 | BPH | C | Seaward reef with gorgonians, one juvenile in seagrass |
| Belonidae | *Ablennes hians* | 5 | 3 | BH | O | Lagoon areas with anchovies |
| | *Tylosurus crocodilus* | 1 | 1 | B | O | Lagoons with anchovy shoals |
| Blenniidae | *Ophioblennius atlanticus* | 145 | 17 | BPH | C | Shallow, rocky seaward reef |
| Bothidae | *Bothus lunatus* | 2 | 2 | PH | O | Sandy patches lagoons and seaward reef |
| Carangidae | *Caranx crysos* | 1 | 1 | P | R | Algal bed |
| | *Caranx latus* | 17 | 6 | PH | C | Lagoon dock pilings |
| | *Caranx ruber* | 114 | 32 | BPH | C | Mostly seaward reef, sometimes in lagoons, juveniles in large shoals associated with sharks or barracudas |
| | *Oligoplites saurus* | 38 | 9 | BP | C | Seagrass, occasionally on reef |
| Chaenopsidae | *Acanthemblemaria maria* | 2 | 1 | B | R | Hole in live dome-shaped coral |
| | *Chaenopsis ocellata* | 4 | 2 | H | R | Sandy with sparse *Halodule wrightii* |
| Chaetodontidae | *Chaetodon capistratus* | 125 | 38 | BPH | C | Juveniles in reef flat and seagrass, adults on seaward reef |
| | *Chaetodon striatus* | 20 | 12 | BPH | C | Juveniles in reef flat and seagrass, adults on seaward reef |
| Clupeidae | *Harengula humeralis* | 4 | 2 | H | O | Sandy lagoon |
| Dasyatidae | *Dasyatis americana* | 1 | 1 | P | O | Sand and seagrass |
| | *Diodon hystrix* | 1 | 1 | H | O | Reef recess |
| Gerreidae | *Eucinostomus* spp. | 3192 | 54 | BPH | C | Mangroves, sand and macroalgae, abundant in eutrophic areas |
| | *Gerres cinereus* | 133 | 36 | BPH | C | Juveniles in mangroves and seagrass, adults also on reef |
| Gobiidae | *Bathygobius soporator* | 36 | 9 | BH | C | Very shallow sandy-rubble pools in the surf zone |
| | Coryphopterus glaucofraenum | 273 | 34 | BPH | C | Sandy areas, usually adjacent to rock in the lagoons and on the seaward reef |
| | *Coryphopterus dicrus* | 30 | 4 | BH | C | Sandy areas on the seaward reef |
| | *Gobionellus saepepallens* | 182 | 16 | BPH | C | Sand-seagrass lagoon areas |
| | *Gobiosoma evelynae* | 8 | 5 | BP | C | Live, massive coral domes |
| | *Gobiosoma dilepis* | 3 | 1 | B | R | Live, massive coral dome |
| | *Lophogobius cyprinoides* | 60 | 10 | PH | C | Mangroves and associated algal beds |
| | *Nes longus* | 16 | 6 | PH | C | Sand, associated with burrowing decapods |
| Haemulidae | *Anisotremus virginicus* | 2 | 2 | BH | O | Seaward reef |
| | *Haemulon aurolineatus* | 4 | 1 | P | O | Adults on the reef, juveniles in seagrass |
| | *Haemulon carbonarium* | 17 | 2 | BP | O | Adults and juveniles on seaward reef |
| | *Haemulon chrysargyreum* | 15 | 2 | BH | O | Adults on seaward reef |
| | *Haemulon flavolineatum* | 914 | 41 | BPH | C | Adults on the seaward reef or land-reclamation rocks in lagoons, juveniles in seagrass, mangrove or reef flat zones |
| | *Haemulon macrostoma* | 10 | 3 | BP | O | Adults and juveniles on seaward reef |
| | *Haemulon parra* | 9 | 6 | BP | O | Adults on the seaward reef, juveniles in mangrove-seagrass |

**Appendix** continued

| Family | Species | Total | No. Stations | Bays | Rarity | Observed habitats |
|---|---|---|---|---|---|---|
| | *Haemulon plumieri* | 340 | 11 | BPH | C | Adults on seaward reef, juveniles in back-reef |
| | *Haemulon sciurus* | 233 | 31 | BPH | C | Adults encountered on the seaward reef, juveniles in mangrove-seagrass areas |
| Holocentridae | *Holocentrus adscensionis* | 13 | 6 | BPH | C | Recesses on reef and in lagoons |
| | *Holocentrus coruscus* | 4 | 3 | PH | O | Back-reef recesses |
| | *Holocentrus rufus* | 95 | 18 | BPH | C | Recesses on reef and in lagoons |
| | *Sargocentron vexillarium* | 3 | 2 | BP | O | Shallow, rocky seaward reef |
| | *Myripristis jacobus* | 47 | 7 | BPH | C | Seaward reef recesses |
| Kyphosidae | *Kyphosus sectator* | 6 | 2 | B | O | Spotted occasionally on the seaward reef |
| Labridae | Halichoeres bivittatus | 2044 | 86 | BPH | C | A true habitat generalist that could be found anywhere |
| | *Halichoeres garnoti* | 24 | 4 | BH | C | Only found on seaward reef, usually with high live-coral cover |
| | *Halichoeres maculipinna* | 76 | 24 | BPH | C | Found in rocky seaward reef areas |
| | *Halichoeres poeyi* | 76 | 27 | BPH | C | Found in seagrass beds |
| | *Halichoeres radiatus* | 53 | 24 | BPH | C | Found in seagrass beds |
| | *Lachnolaimus maximus* | 1 | 1 | P | O | Juveniles in seagrass and algae bed |
| | *Thalassoma bifasciatum* | 1973 | 37 | BPH | C | Seaward reef, large aggregations of juveniles around tall coral heads |
| Labrisomidae | *Labrisomus gobio* | 1 | 1 | H | R | Reef |
| | *Malacoctenus aurolineatum* | 101 | 15 | BPH | C | Rocky reef with sponges |
| | *Malacoctenus gilli* | 6 | 3 | PH | C | Rubble near live coral on the seaward reef |
| | *Malacoctenus macropus/versicolor* | 307 | 52 | BPH | C | Shallow reef flat, rubble and seagrass-algae zones |
| | *Malacoctenus triangulatus* | 44 | 16 | BPH | C | Seaward reef with rock, encrusting gorgonians and sponges |
| Lutjanidae | *Lutjanus analis* | 5 | 5 | P | O | Sand, seagrass or reefs |
| | *Lutjanus apodus* | 406 | 47 | BPH | C | Juveniles associated with mangroves, adults also on reefs |
| | *Lutjanus griseus* | 604 | 38 | BPH | C | Juveniles associated with mangroves, adults also on reefs |
| | *Lutjanus jocu* | 1 | 1 | P | O | Sandy patches, seagrass or reefs |
| | *Lutjanus synagris* | 37 | 20 | BPH | C | Juveniles associated with sandy zones, seagrass and lagoons, adults also on reefs |
| | *Ocyurus chrysurus* | 710 | 72 | BPH | C | Juveniles found in seagrass, particularly abundant if fringed by mangroves, adults on reefs |
| Megalopidae | *Megalops atlanticus* | 3 | 3 | H | O | Occasionally on reefs, but most commonly in association with anchovy schools around dock |
| Microdesmidae | *Ptereleotris helenae* | 2 | 1 | H | R | Deep sand |
| Monocanthidae | *Cantherhines pullus* | 8 | 6 | BPH | C | Seaward reef |
| | *Monacanthus ciliatus* | 19 | 11 | BPH | C | Seagrass and algal beds |
| | *Monacanthus tuckeri* | 8 | 6 | BH | C | Reefs with gorgonians and seagrass |
| Mugilidae | *Mugil curema* | 50 | 8 | PH | C | All lagoon areas |
| Mullidae | *Mulloidichthys martinicus* | 30 | 6 | PH | C | Sandy lagoon areas, rubble and on reefs |
| | *Pseudupeneus maculatus* | 20 | 11 | BPH | C | Sandy lagoon areas, rubble and on reefs |
| Muraenidae | *Gymnothorax funebris* | 2 | 2 | BP | O | Reef recesses and seagrass and mangroves |
| | *Gymnothorax miliaris* | 1 | 1 | H | O | Reef recesses |
| | *Gymnothorax moringa* | 3 | 2 | BP | O | Reef flat areas |
| Opistognathidae | *Opistognathus aurifrons* | 2 | 1 | B | R | Sand patch on seaward side of lagoon |
| Ostraciidae | *Lactophrys trigonus* | 1 | 1 | P | R | Seagrass |
| | *Lactophrys triqueter* | 1 | 1 | P | O | Seaward reef |

**Appendix** continued

| Family | Species | Total | No. Stations | Bays | Rarity | Observed habitats |
|---|---|---|---|---|---|---|
| Pempheridae | *Pempheris schomburgki* | 2 | 1 | B | O | Reef recesses |
| Pomacanthidae | *Pomacanthus paru* | 1 | 1 | H | R | Juvenile on reef flat |
| Pomacentridae | *Abudefduf saxatilis* | 69 | 13 | BPH | C | Juveniles shallow reef crest, adults reef |
| | *Abudefduf taurus* | 4 | 1 | P | O | Shallow reef |
| | *Chromis cyanea* | 41 | 2 | H | O | Large schools, deep seaward reef with live hard coral |
| | *Chromis multilineata* | 52 | 4 | BPH | C | Schools above reef |
| | *Microspathodon chrysurus* | 92 | 17 | BPH | C | Shallow reef with zooanthid, juveniles with fire coral |
| | *Stegastes diencaeus/ leucostictus ads* | 505 | 52 | BPH | C | Shallow, rocky reef |
| | *Stegastes diencaeus/ leucostictus* juvs | 861 | 79 | BPH | C | Most abundant in seagrass, mangrove, and reef flat areas, also found on seaward reef |
| | *Stegastes dorsopunicans* | 48 | 16 | BPH | C | Seaward reef with rock and algal cover |
| | *Stegastes partitus* | 18 | 7 | PH | C | Deeper seaward reef with high live coral cover, juveniles also on reef flat |
| | Stegastes planifrons | 21 | 10 | BPH | C | Deeper seaward reef with high live coral cover, juveniles also on reef flat |
| | *Stegastes variabilis* | 6 | 5 | BPH | C | On seaward reef, reef flat and seagrass |
| Priacanthidae | *Heteropriacanthus cruentatus* | 6 | 3 | PH | O | Reef recesses |
| Scaridae | *Scarus* spp < 10 cm | 10,245 | 76 | BPH | C | Found in all habitats except sandy zones, particularly abundant in seagrass beds associated with mangroves |
| | Scarus iseri/taeniopterus > 10 cm | 337 | 29 | BPH | C | Seaward reef areas and structure in lagoons |
| | *Scarus vetula* > 10 cm | 59 | 14 | BPH | C | Seaward reef areas |
| | *Sparisoma aurofrenatum* | 328 | 52 | BPH | C | Seaward reef areas, juveniles also in seagrass and back-reef zones |
| | *Sparisoma radians* | 333 | 60 | BPH | C | Mostly restricted to seagrass and algal beds |
| | *Sparisoma rubripinne* | 130 | 26 | BPH | C | Seaward reef zones |
| Scaridae | *Sparisoma viride* | 130 | 21 | BPH | C | Seaward reef areas, juveniles also in back-reef zones |
| Sciaenidae | *Equetus acuminatus* | 9 | 4 | BP | O | In recesses of seaward reef |
| | *Equetus punctatus* | 6 | 3 | PH | R | Recesses in reef areas |
| | *Odontoscion dentex* | 5 | 1 | H | O | Reef recesses and structure in lagoons |
| Serranidae | *Cephalopholis fulva* | 1 | 1 | P | R | Seaward reef |
| | *Epinephelus adscensionis* | 3 | 3 | PH | R | Seaward reef |
| | *Epinephelus guttatus* | 9 | 6 | BPH | O | Fore reef |
| | *Hypoplectrus chlorurus* | 1 | 1 | B | O | Seaward reef |
| | *Hypoplectrus puella* | 21 | 13 | BPH | C | Seaward reef, back-reef and seagrass |
| | *Hypoplectrus unicolor* | 3 | 2 | H | O | Back-reef |
| | *Hypoplectrus nigricans* | 12 | 8 | BPH | C | Seaward reef |
| Sparidae | *Archosargus rhomboidalis* | 21 | 3 | P | O | Seagrass and algal beds |
| | *Calamus* sp. | 22 | 9 | BPH | C | Seaward reef, seagrass and sand |
| Sphyraenidae | *Sphyraena barracuda* | 46 | 26 | BPH | C | Juveniles among mangroves, while large individuals on seaward reef and in lagoons |
| Synodontidae | *Synodus intermedius* | 9 | 8 | BPH | C | Sandy patches among the seaward reef |
| Tetraodontidae | *Canthigaster rostrata* | 16 | 8 | BH | C | Seagrass and reef |
| | *Sphoeroides spengleri* | 6 | 3 | PH | O | Seagrass |
| | *Sphoeroides testudineus* | 11 | 9 | BPH | C | Seagrass, sand and rubble |
| Total | 118 | 27,666 | 106 | 3 | | |

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