Factors Affecting Fish Distribution in Coastal Habitats of the British Virgin Islands

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Abstract

Few studies of tropical fish communities compare fish distributions across the full range of near-shore tropical marine habitats. As a result, our understanding of tropical marine fish communities is often biased towards habitats preferred by researchers.

The distribution and habitat preferences of all 136 fish species occurring at 106 stations in three bays off Tortola in the British Virgin Islands were assessed. At a species level, habitat type was often the key factor influencing fish distribution. Of the 44 species occurring at more than 10 stations, 3 were sand specialists, 5 were strongly associated with mangroves, 7 were dependent on seagrass and algal beds and 14 were found only on the forereef. Eleven species were widely distributed both on the forereef and in bays, and 9 of them showed clear evidence of ontogenetic partitioning. The juveniles all preferred bay habitat types and moved onto the forereef as they approached sexual maturity.

At a community level, five distinct fish assemblages were found. The assemblage types were classified according to their distribution: 1) forereef, 2) reef flat, 3) non-mangrove associated seagrass, 4) mangrove associated seagrass and 5) eutrophic areas. Forereef stations were the most species-rich with 24 species per station while eutrophic stations had the most depauperate communities with only 4 species per station.

Variation in fish species richness at each station was largely explained by a simple habitat complexity index. It accounted for 70% of the variation in fish species richness and 21% of the variation in fish abundance. Rugosity and variety of growth forms were the most important predictors of species richness, but the height of the habitat architechture was the most useful predictor of fish abundance. Artificial reefs were constructed to test the effects of each habitat complexity variable experimentally. Increasing rugosity, variety of growth forms and percentage hard substrate increased the observed number of species but increasing the variety of hole-sizes, and height had no effect. The only complexity variable that had a significant effect on fish abundance was percentage hard substrate. In addition to the static substrate structure, long-spined sea urchins *Diadema antillarum* affected fish distribution because small fish shelter from predators in their spines. The urchins increase species richness and abundance in low complexity seagrass beds, but on artificial reefs, where shelter was not a limiting factor, the effect was less pronounced.

Organic pollution is another factor that negatively affects the fish community by reducing fish species richness and abundance. Poor water quality often alters the natural habitat, confounding observations, but fish species richness was reduced in polluted areas even when artificial reefs were used as habitat controls.

The applications of these findings to the management and conservation of fish in the British Virgin Islands are discussed.

For my parents, Lily and Vernon

Thank you for encouraging me to pursue the things that make me happy

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General Introduction

'How like fish we are ready, nay eager to seize upon whatever new thing some wind of circumstance shakes down upon the river of time! And how we rue our haste, finding the gilded morsel to contain a hook.'

ALDO LEOPOLD

A major component of tropical biodiversity is found in the marine habitat mosaics of shallow coastal areas (Ogden 1997). In these places mangroves, seagrass, sand, mudflats and algal beds dominate bays, while coral reefs, rubble areas or sandy patches occur in exposed areas that are washed by clean, nutrient-poor water from the open sea. Coral reefs have received particular attention because they form one sixth of the world's coastlines and they are the most biologically diverse marine ecosystems, but are being degraded by human activities and global warming (Brown 1997b, Roberts et al. 2002). Most of the world's tropical coastline is found in developing nations where fish are an important food source to many people and more than half of the 20 000-30 000 species of fish in the world are found in these areas (Cohen 1970). Fishes are ideal animals for ecological investigations because they are readily identified using field guides, they are species-rich and they occur in high densities. Additionally, warm tropical waters with high visibility are conducive to direct observations, unlike many other places that are often too cold and/or have very low visibility.

1.1 WHAT IS BIODIVERSITY?

Biodiversity is a measure of the total genetic and ecological diversity (Wilson 1988). Biodiversity consists of many different components nested in a hierarchy. These range from genetic variation within populations to genetic differences between geographically distinct populations or groups of species in assemblages and ecosystems so its quantification is very difficult (May 1994). The most common way to measure biodiversity is to count the number of species, although the term ‘biodiversity’ means much more than can be expressed by a straightforward number (Harper and Hawksworth 1994). Most aspects of biodiversity have been investigated in biomonitoring assessment programmes, paying attention to both the species composition, the trophic structure and ecological function of species (Franklin 1988, Noss 1990).

A useful classification system distinguishes between α, γ and β diversity. The total diversity of species within a community or habitat is α diversity. The species richness of a range of habitats in a defined geographical area is the γ diversity while β diversity is a measure of the rate and extent of change in species along a gradient from one habitat to another (Whittaker 1972, 1975).

Species richness is one of the most commonly used measures of species diversity. Total species richness, sometimes referred to as S_{max} or $S_{tot,}$ is the total number of species ocurring in a defined location or habitat. By plotting the number of species encountered against a measure of sampling effort the completeness of a species inventory or S_{max} can be assessed, because the curve should approach an asymptote when complete (Simberloff 1972). Because a complete census is seldom possible, a variety of non-parametric estimators have been proposed to estimate species richness. These include the first and second-order jackknife method (Quenoille 1949, Palmer 1991, Colwell and Coddington 1994), the bootstrap method (Efron 1981, Colwell and Coddington 1994) and the Chao estimator (Chao 1984).

Often, the observed species richness S_{obs} is used to directly compare stations that have been sampled with equal intensity (Krebs 1994). One problem arises when communities have different sample sizes—the larger sample might be expected to have more species. For example, if we compare a sample of 32 fish species from 2000 individuals with another sample of 21 species from 400 individuals, we do not know immediately which community would have the highest richness—but they can be directly compared by using rarefaction curves (Simberloff 1972, Heck et al. 1975). Rarefaction is a method that generates a curve by randomly selecting individuals from a pooled sum of samples, and not replacing them (Simberloff 1972, Heck et al. 1975, Tipper 1979, Coleman 1981).Next, the predicted species richness between different samples can be compared while correcting for differences in abundance.

Some biologists have combined species richness and abundance measures to form diversity indices but an explosion of different, yet mathematically similar indices confuse the literature, so much so that biological diversity was in danger of becoming a non-concept (Hulbert 1971). Species diversity indices are heavily dependant upon sample size and they don’t show species composition. As a result other more rational approaches, using rank-abundance plots for example, are becoming more popular (Noss 1990, Southwood and Henderson 2000).

We are currently experiencing very high rates of loss of biodiversity; they have been estimated at 100-1000 times the extinction rates pre-human levels (Pimm et al. 1995). Conservationists are alarmed by this loss and are actively engaged in activities designed to protect as much of the remaining diversity as possible. Reasons for conserving biodiversity are based on a value system that can be divided into five major categories:

i. *Direct value* – wild meat, fruit and medicine is a valuable resource, which contributes directly to the survival of many people, particularly in undeveloped countries. In tropical marine systems, fish and other marine products are the basis source of livelihood of tens of millions of people (Salvat 1992).

ii. *Option value* – some species that were apparently unimportant in the past have recently found commercial uses, and by conserving seemingly unimportant species we maintain their option value. For example, several species of giant clams are endangered as they have been overexploited for many years and cannot be harvested in a sustainable way. A few remaining individuals have been successfully used for brood stock in a lucrative aquaculture enterprise, which could then be used to help replenish natural populations (Birkeland 1997).

iii. *Indirect value* – the non-consumptive economic values of various ecosystem components such as coastal protection from storms, prevention of erosion and siltation by mangroves and reefs is difficult to calculate, but often taken for granted (White et al. 2000).

iv. *Amenity value* – the economic value of nature recreation and ecotourists is particularly important to small island economies such as the British Virgin Islands

(BVI). There are an estimated 15 million certified recreational divers worldwide that spend considerable amounts of money to see good reefs (Spalding et al. 2001). In 1997 over 10 million tourists visited the Great Barrier Reef, and the estimated value of this tourism was US$ 700 million (Spalding et al. 2001).

v. *Ethical value* – this is a largely aesthetic or spiritual concept to which no monetary value can be assigned; yet it is the prime motivation for an enormous amount of conservation work. It is very subjective and its importance is often underplayed (Wilson 1988).

1.2 COMMUNITIES AND ASSEMBLAGES

The word ‘community’ has many different connotations. In many ecological studies it refers to an arbitrary set of organisms in a particular place (Morin 1999). This means that a community may be defined at any relevant size, scale or level within a hierarchy of habitats (Begon et al. 1996). Elton (1927) has the following to say regarding animal communities:

> ‘One of the first things with which an ecologist has to deal is the fact that each different kind of habitat contains a characteristic set of animals. We call these animals associations, or better, animal communities, for we shall see later on that they are not mere assemblages of species living together, but form closely-knit communities or societies comparable to our own.’

Some ecologists maintain that it is virtually impossible to adequately define or delimit any entire natural community, as every single organism (including protists, algae, bacteria and viruses) and their interactions with each other would need to be accounted for in order to fully describe a community. Because few species have similar distributions, communities change gradually from place to place (Wilson 1991). This has lead to a debate on the very existence of communities, but the term is still used by many ecologists who give their own operational definitions (Palmer and White 1994, Morin 1999). The term **assemblage** describes any subset of a community with interesting properties and is usually a more appropriate term to use. An ecosystem consists of one or more communities together with their physical environment (Tansley 1935, Morin 1999). Changes in the physical environment will therefore affect the distribution of the animals, and as a result, changes in assemblage structure of various taxa have commonly been used to assess the impacts of disturbance in an environment (Noss 1990).

1.3 ECOLOGICAL VALUE OF DISTRIBUTION STUDIES

Bio-geographical studies describe relationships between the abundance of a species and their habitat, or to other species. Animal communities are frequently related to physicochemical and biotic variables. Quantitative description of habitats therefore, is essential in order to understand the processes affecting the animals living there. Recent developments in the field of Geographic Information Systems (GIS) have made computer-assisted mapping easier. Maps are therefore becoming increasingly popular tools for ecologists to use as a map is the best way to describe spatial phenomena (Johnston 1998). GIS modelling systems have been used to relate landscape structure to general community patterns and a wide variety of communities have been related to their physical environments using GIS. Some recent examples include bats (Jaberg and Guisan 2001), skylarks (Chamberlain et al. 1999), butterflies (Cowley et al. 2000), scale insects (Speight et al. 1998) and seagrass epiphytes (Frankovich and Fourqurean 1997).

The value of distributional studies can be categorised as follows:

i. Species distribution can be related to land use or environmental impacts. The effects of fishing usually cause strong changes in assemblages that can be revealed by distributional studies (Roberts 1995a, Russ and Alcala 1996, Russ 2002).

ii. Investigating the habitat preferences of a species can help to identify areas of conservation priority and these are reflected in distribution studies. One study of nurse sharks in the Florida keys showed that very shallow lagoon habitats were essential for nurse sharks, particularly those in breeding condition, and areas with high levels of human traffic either disrupted breeding activity or were avoided by the sharks altogether (Carrier and Pratt 1998). As a result, human access to these areas has been restricted during the shark's breeding season.

iii. We can only assess the relative importance of conserving a site if we have detailed knowledge of its fauna. If there was a detailed inventory of fish species distribution in the BVI, it would allow conservation planners to make informed decisions about which areas should be set aside as protected areas. Even a simple habitat assessment revealing which habitats have the highest species richness would aid conservation decision-making. A recent example would be a study demonstrating that certain species are dependent upon mangrove habitats. It was done by comparing the species composition of fish assemblages with increasing distance from mangrove areas (Nagelkerken et al. 2002).

iv. Information for future reference is documented by distributional studies, and it can be used to quantify species decline or for environmental impact assessments. One recent example in the Caribbean documents the decline in live hard coral cover in the Caribbean from about 50% to 10% over the 30 years (Gardner et al. 2003). Such gradual changes cannot be detected in short term studies and rely heavily on repeated surveys of hard coral cover and distribution over many years in a wide area. This paper drew considerable attention from the press and highlighted the need for serious marine conservation work in the Caribbean.

v. In addition to explaining ecological patterns at local scales, summaries of very large data sets can be very useful to identify global priority areas for conservation. One example of this is known as ‘biodiversity hotspots’ which maps areas with exceptional concentrations of endemic species and recommends that conservation planners should focus their efforts in these areas (Myers et al. 2000). A similar approach has been used for marine areas (Roberts et al. 2002). However, these large data set analyses are strongly dependent upon collections made at smaller scales and the availability of museum specimens. The lack of data, particularly in tropical areas often hinders these analyses (Knowlton 2001).

1.4 SPECIES RICHNESS AND HABITAT COMPLEXITY

No fewer than 25 competing hypotheses have resulted from the debate over mechanisms causing variation in plant and animal species richness in different parts of the world (Brown and Lomolino 1998). The most popular hypotheses state that variation in species richness is a consequence of differences in: (1) evolutionary time, (2) ecological time, (3) climatic stability, (4) climatic predictability (5) spatial heterogeneity, (6) productivity, (7) stability of primary production, (8) competition, (9) disturbance, (10) predation (Pianka 1967, May 1981, Begon et al. 1996, Brown and Lomolino 1998, Morin 1999). In spite of the contention over the mechanisms that may lead to spatial variation in species richness, a more limited set of variables have been used to predict species richness patterns, and the type of variable that can be used depends largely on the scale of the study.

At a *global level* (scales of thousands of kilometers) patterns in species richness can generally be predicted by examining climatic variables. Tropical areas with warm, wet and stable climates support the greatest number of species compared to temperate ones (Pianka 1967, Currie 1991, Morin 1999).

At *regional levels* (scales of tens and hundreds of kilometers) habitat heterogeneity, total habitat area (and connectivity) and net primary productivity are useful predictors of species richness in marine, freshwater and terrestrial ecosystems (Mac Arthur and Mac Arthur 1961, Molles 1978, Bellwood and Hughes 2001, Jaberg and Guisan 2001, Kerr et al. 2001). In tropical marine systems the direction of prevailing currents and potential up-stream sources of pelagic larvae are important (Ormond and Roberts 1997).

At *local levels* (scales less than ten of kilometers) regional-scale processes may be assumed to affect a local environment in a consistent way, yet there are often remarkable differences in species richness patterns over distances of a few meters, or even centimeters, depending on the body sizes and mobility of the taxonomic group involved. One factor, habitat complexity, is a very useful predictor of species richness at local scales in a number of different ecosystems. Different measures of habitat complexity have been related to species richness of birds (Mac Arthur and Mac Arthur 1961, Finch 1989, Telleria and Carrascal 1994), lizards (Pianka 1966, Pianka 1973), mammals (Dueser and Brown 1980, August 1983, Williams et al. 2002) insects (Southwood et al. 1979, Haslett 1997, Davidowitz and Rosenzweig 1998), aquatic invertebrates (Heck and Wetstone 1977, Gilinsky 1984), fish (Risk 1972, Gorman and Karr 1978, Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Gorham and Alevizon 1989, McClanahan 1994, Caley and St John 1996, Beukers and Jones 1997, Horan et al. 2000, Ferreira et al. 2001, Harding and Mann 2001), gastropods (Kohn 1967, Beck 2000) and even ostracods (Hull 1997). Disturbance events are another variable that may also affect local species richness (Connell 1978) and tropical marine examples include pollution and hurricanes (Lewis 1997).

1.5 TROPICAL COASTAL MARINE HABITATS

Near-shore tropical marine habitats throughout the world are under intense pressure from human activities and they have received much attention from fisheries biologists. The most threatened habitat types are:

Mangroves – there are 68 known species of mangrove trees in the world, the greatest diversity is found in the Indo-Pacific and their total area has been estimated at 18.15 million hectares (Semesi 1998). Mangrove areas have been reduced by 20 to 75% in many developing countries and they are one of the most threatened coastal habitats; they are cleared for land reclamation, harbour facilities, aquaculture or for wood (Kaly and Jones 1998). Their importance as habitats for juvenile fish (Morton 1990, Laegdsgaard and Johnson 1995) and shellfish (Marshall 1994, Turner et al. 1999) is well established, but not completely understood.

Seagrass – there are about 50 species of seagrass occurring in the world in both tropical and temperate regions, the greatest species richness being found in the Indo-Pacific (Hemminga and Duarte 2000). Seagrass beds enhance biodiversity in near-shore systems and they are habitats for seagrass specialists such as sea horses and they are nursery grounds for many juvenile fish e.g. (Baelede 1990, Coles et al. 1993, Rooker et al. 1998) and crustaceans (Edgar and Shaw 1995). They improve water quality, stabilise sediments and play an important role in nutrient and carbon cycling (Hemminga and Duarte 2000). Large-scale declines in seagrass areas have been reported throughout the world, because of eutrophication, siltation, organic loading of sediments, chemical pollution, mechanical damage from fishing, trawling and wasting disease (Hemminga and Duarte 2000).

Reefs – coral reefs are largely composed of the calcium carbonate skeletons of slow-growing hermatypic corals. Corals are small cnidarians that act as filter feeders that also rely on symbiotic algae called zooxanthellae for food. There are nearly 800 species of reef-building corals in the world (Spalding et al. 2001). Coral reefs are one of the most biologically diverse environments on earth and they harbour hundreds of thousands of different species ranging from algae to sponges, cnidarians, crustaceans, molluscs, echinoderms, bryozoans, tunicates, fish, reptiles and seabirds (Spalding et al. 2001). Such reefs can be found in over 100 countries but these are often economically impoverished and about half a billion people (8% of the world's global population) live within 100 km of a coral reef. Reefs are the mainstay of the economy of many small island nations, which derive economic benefits from reefs through fishing and tourism.

Coral reefs are declining worldwide because of increased mortality from hurricanes, coral bleaching, outbreaks of crown-of-thorns starfish *Acanthaster planci*, mass mortality of *Diadema antillarum* urchins in the Caribbean, eutrophication, sedimentation, oil pollution and coral mining (Brown 1997b, a, Bryant et al. 1998, Spalding et al. 2001). A recent study using several indicators of risk stated that 58% of the worlds reefs are potentially threatened by human activity, and outside the Pacific, 70% of all reefs are at risk (Bryant et al. 1998). The Caribbean has been especially hard-hit and the percent of live hard coral cover on these reefs has declined from 50% to 10% in the last 30 years (Gardner et al. 2003).

Other - Other tropical marine habitats are not considered threatened, and as a result have received little attention. They include algal beds, mud flats, sand bottoms, beaches, rocky bottoms and shores, as well as various man-made structures now common such as marinas and shipwrecks.

Despite well-known studies of fish in certain tropical habitats, only a few have included all the near-shore habitats that are naturally found in close proximity (Ogden 1997). This may be partly due to lack of standardised sampling methods across all habitats. The importance of ecosystem level approaches is emphasised by (Hemminga and Duarte 2000), who note that single habitat studies have overestimated the relative value of seagrasses as later studies revealed that juveniles using seagrass beds could also use alternative habitats.

1.6 FISH AS BIOINDICATORS

Animal communities have often been used to estimate the impact of a disturbance to the physical environment, According to Noss (1990), indicators should be:

i. Sufficiently sensitive to provide early warning of environmental problems.
ii. Distributed over a broad geographical area.
iii. Capable of providing continuous assessment over a wide range of stresses.
iv. Relatively independent of sample size.
v. Easy and cost effective to collect and study.
vi. Allow for differentiation between natural and man-made disturbance.
vii. Relevant to ecologically significant phenomena.

According to these criteria, fish in tropical marine habitats perfectly fulfil all of the requirements of a bioindicator assemblage, and any major disturbances to these systems will be manifested in the fish assemblage. Certain species respond differently to different conditions. In organically polluted streams for example, most aquatic invertebrates disappear but certain groups such as annelids (tubificidae) and dipteran larvae (chironomidae) are capable of surviving and they are known as indicator species (Wright et al. 1993). As a result, rapid assessment indices of water quality using benthic macroinvertebrate communities as indicators have become widespread in many parts of the world (e.g. Wright et al. 1993, Chessman 1995, Dallas 1997, Gratwicke 1998-1999).

Fish have also been included in some bioassessment protocols. These methods are sometimes referred to as a biological integrity indices and they measure flow, energy inputs, habitat structure, water quality, and biotic interactions (Karr 1981, 1990). Other studies have linked incidence of disease to pollution levels and have suggested that indicators of fish health can be used to assess the pollution loads of streams (Siligato and Bohmer 2001). These assemblage-wide studies have been mostly applied to freshwater scenarios, and tropical marine work has focussed on more specific fish assemblages and impacts.

Previous tropical marine work with fish as bioindicators includes the use of butterflyfish as indicators of live hard coral cover and reef habitat quality (Findley and Findley 1985). However, these would be unsuitable for use in the Caribbean as there are only three commonly encountered species of butterflyfish and they are much more speciose in the Indo-Pacific. Other taxa are known to be vulnerable to overfishing, they are: Serranidae, Lutjanidae, Lethrinidae, Mullidae, Labridae, Scaridae, Siganidae and Acanthuridae. They generally decrease in mean size, abundance and species richness in response to overfishing (Roberts 1995b, Russ and Alcala 1996, Wantiez et al. 1997, Russ and Alcala 1998).

1.7 INTRODUCTION TO THE STUDY SITE

The British Virgin Islands (BVI) is a self-governing overseas dependant territory of the United Kingdom and is an archipelago of more than forty islands, having a total land surface area of 150km^2 (Figure 1.1). The capital city is Road Town which is located on the south shore of the 61km^2 island of Tortola that is home to more than half of the 21 000 British Virgin Islanders (Anon 2003). The people on the islands are generally wealthy as the 2002 GDP estimate was US$ 16 000 per capita (Anon 2003). Tourism is the largest sector of the economy and over 350 000 tourists visited the country in 1998 accounting for 45% of the national income; offshore banking is the next largest source of revenue (Anon 2003).

The climate is warm and tropical. Water surface temperatures vary little from season to season, ranging from 25.5 °C in the winter to 28 °C in the summer. Hurricanes and tropical storms may occur between July and October (Spalding et al. 2001). Apart from the flat coral atoll of Anegada, the islands are steep-sided, volcanic formations and there are no permanent streams or rivers on any of the islands. The moderate tropical climate and clear waters of the BVI support a wide range of marine habitats, including some spectacular coral reefs. Over 530 of the 1500 species of fish found in the Caribbean have been recorded in the Virgin Islands (Froese and Pauly 2002). These reefs, with their diverse fishes are a prime attraction for many tourists.

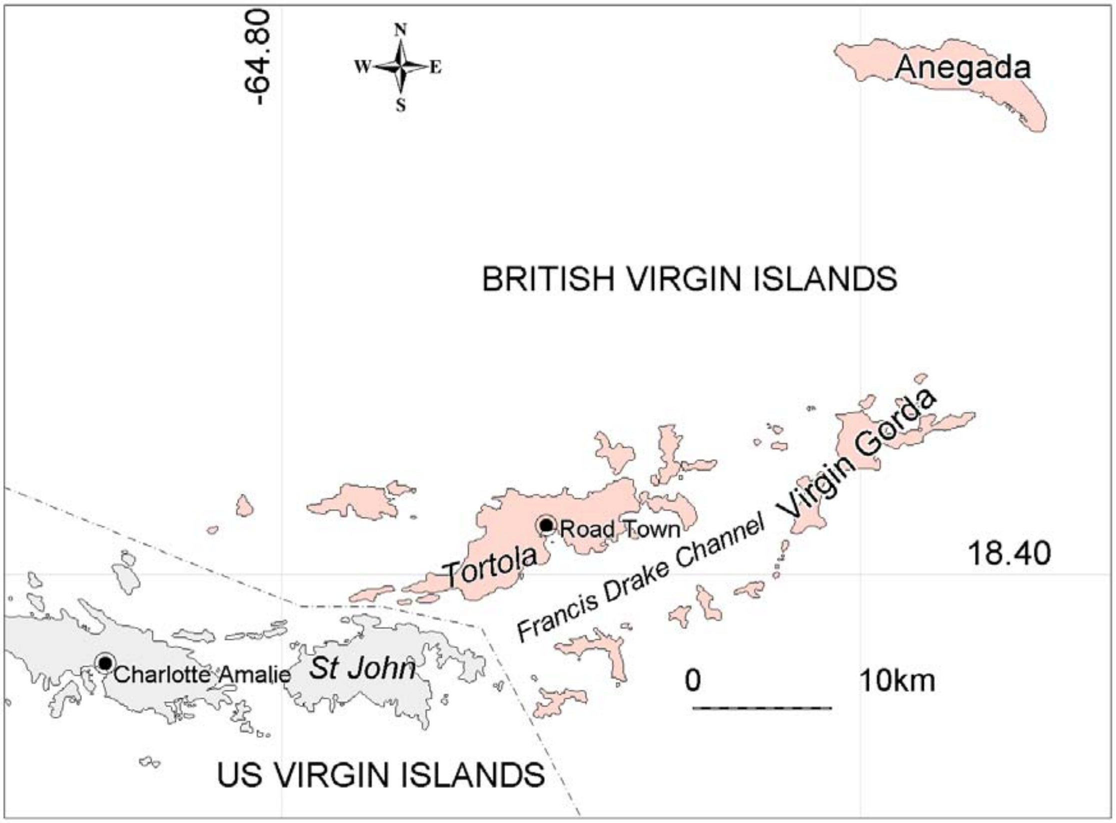

Fig 1.1 A map of the British Virgin Islands, an archipelago in the Caribbean, found east of Puerto Rico.

Marine conservation and research organisations

There are several private, volunteer and governmental organisations involved in conservation and research in the BVI. They generally work in cooperation with each other and form a powerful lobby in this small island nation.

The government department of Conservation and Fisheries has jurisdiction over all marine natural resources in the British Virgin Islands and is responsible for issuing research permits. This is a dynamic organisation and during the course of my fieldwork they ran several new initiatives and educational programmes.

The National Parks Trust is a non-governmental organisation responsible for managing, and enforcing fisheries regulations in national parks; at present the Wreck of the Rhone National Park is the only marine park. The Royal Mail Steamer R.M.S.Rhone is lying off Salt island where it sank in a hurricane 1867 and today, the wreck is one of the most famous wreck and dive sites in the Caribbean.

The H.Lavitty Stoutt Community College has a marine science programme and a new marine centre has recently been completed and dedicated to marine research. A memorandum of understanding has been agreed to promote research cooperation between the H. Lavity Stoutt Community College and the Oxford University Tropical Ecology and Entomology Research Group[1].

The Island Resource Foundation is an independent research organisation that has many regional collaboration projects and has an extensive library of local and unpublished documents. The Association of Reef Keepers is an organisation based in the BVI that coordinates Reef Check activities and it has a significant marine conservation awareness programme. The World Fish Centre (previously known as ICLARM) ran a

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[1] This thesis is one of the products of this agreement.

Caribbean marine protected areas project, part of which was based in the BVI. Their website www.fishbase.com has been a very useful source of information.

Fisheries regulations

The BVI has a comprehensive set of fisheries regulations designed to promote sustainable use of fisheries resources, although their enforcement is problematic. The following key regulations are well-publicised: a licence is required for all types of fishing in the BVI; use of spear guns is prohibited; detailed specifications (including minimum mesh sizes) are given for the design of fish traps and nets (Anon 2002). Fishing is prohibited in the following Marine Protected Areas: Horse Shoe Reef (Anegada), Hans Creek (Beef Island), South Sound (Salt Island), the Sound and Wedges Bay (Ginger Island), Big Reef (Peter Island), Green Cay (Jost van Dyke), Money Bay (Norman Island), Dead Chest and Guana Island (Anon 2002). There are only about 200 commercial fishermen in the BVI and their total catch in 1998 was estimated at 800 tonnes, but despite this, the impacts of commercial fishing are substantial and particularly affect groupers, snapper, lobster and conch (Oliver and Noordeloos 2002).

Eleven species of fish that are on the IUCN red list of threatened species (2002) are known to occur in the BVI, these are: queen trigger fish *Balistes vetula* Linnaeus 1758; marbled grouper *Dermatolepis inermis* Valenciennes1833; itajara *Epinephelus itajara* Lichtenstein 1822; Nassau grouper *Epinephelus striatus* (Bloch 1792); longsnout seahorse *Hippocampus reidi* Ginsberg 1933; hogfish *Lachnolaimus maximus* Walbaum 1792; mutton snapper *Lutjanus analis* Cuvier 1828; Cubera snapper *Lutjanus cyanopterus* Cuvier 1828; whale shark *Rhincodon typus* Smith 1828; rainbow parrotfish

Scarus guacamia Cuvier 1828 and bigeye tuna *Thunnus obesus* Lowe 1839 (Froese and Pauly 2002). There is a closed season on only 1 of these 11 threatened fish species, *E. striatus*, and it is between 30 November and 31 January. There is also a closed season on *E. guttatus* from 1 January – 31 March (Anon 2002).

Shallow marine habitats of Tortola

There are a variety of shallow-water marine habitats in the British Virgin Islands including:

Mangroves – the most abundant species of mangrove on Tortola is the red mangrove *Rhizophora mangle* L. (Fig 1.2) but white *Laguncularia racemosa* (L.) and black mangroves *Avicennia germinans* L. are also present (Overing 1997, Anon 2000). Red mangroves tend to grow in deeper water than the other two species and as a result, they are of direct value to fish as their submerged roots form extensive aquatic habitats (Fig 1.2). There are 4.5km^2 of mangroves in the British Virgin Islands (Spalding et al. 2001) but some are being destroyed, mainly for land reclamation and other development projects in various places on Tortola although some sites are being rehabilitated e.g. Nanny Cay Marina on the South West side of Tortola. Two large mangrove stands on the South East side of Tortola, namely Paraquita Bay and those at Bar Bay inlet, are being considered for designated as nature preserves (Overing 1997).

Fig 1.2 Variety of tropical marine habitats in the BVI contribute to the coastal mosaic: a) aerial view of Hodges Creek, Tortola, showing mangroves, seagrass and algal beds, sand and reef, b) seagrass bed foreground and mangrove roots growing adjacent to each other, c) rubble and sand, d) mangrove roots

Fig 1.2 (cont). Variety of tropical marine habitats in the BVI contribute to the coastal mosaic: e) bed of macroalgae, f) coral reef with gorgonians, g) boulders associated with land reclamation, h) pile of old bottles and other refuse.

Seagrass - There are three species of seagrass in the British Virgin Islands. The most abundant species is turtle grass *Thalassia testudinum* Banks & Soland which forms continuous beds (Fig 1.2) often interspersed by sandy patches, macroalgae the other seagrass species are manatee grass *Syringodium filiforme* Kuetz and shoal grass *Halodule wrightii* Asch. There are about 9.2 km^2 of seagrass off Tortola and its adjacent islands (Anon 2000). These seagrass beds grow in shallow, protected bays that are usually ideal mooring places for boats. The BVI has the highest density of charter yachts in the world (Spalding et al. 2001) and seagrass beds are being affected by anchor damage as well as dredging activities in marinas, although some more popular mooring places now have mooring balls installed. Organic pollution, like that found in Nanny Cay Marina may also be affecting seagrass beds because the reduced visibility and the increased sedimentation associated with organic pollution smother seagrass (Hemminga and Duarte 2000).

Coral reefs – 330km^2 of coral reefs surround the BVI covering more than twice the land surface area (Spalding et al. 2001). These reefs have been severely damaged by hurricanes in recent years, but the reefs also suffer from diseases and from bleaching most severely in 1998 (Oliver and Noordeloos 2002). Near the more heavily populated areas, increase in sedimentation, untreated sewage discharge and anchor damage from charter yachts have been noted as serious problems (Oliver and Noordeloos 2002).

Other – macroalgae beds, sand and mud flats, beaches, rubble and other artificial habitats such as shipwrecks, garbage and boulders associated with land reclamation projects form a significant, and often overlooked portion of the coastal habitat mosaic in the BVI (Fig 1.2). These robust habitats are generally not threatened and occur widely, they are homes to fish, and some of them have habitat specialists found nowhere else.

1.8 BASIS FOR THE RESEARCH

Most marine studies have treated the major marine habitats in complete isolation from each other, a factor lamented by (Ogden and Gladfelter 1983, Ogden 1997). This can seriously bias our understanding of ecosystems and cause problems when it comes to designing integrated coastal management plans. One example of this is that seagrass beds were once thought to be essential nursery areas for many fish species, but their importance has waned since recent studies have shown that these species can utilise alternate habitats as well (Hemminga and Duarte 2000). Recently more widespread surveys of habitats and their fish fauna have shown that different species may use several distinct coastal habitats at different stages of their life history (Nagelkerken et al. 2000a, Nagelkerken et al. 2000b, Nagelkerken et al. 2001). One of the reasons for this poor comparison of habitat types is that researchers generally use different survey techniques for different habitat types. While these techniques have been refined over years of extensive testing in environments that present very different logistical difficulties, they are ideal for testing hypotheses within, rather than across the different habitat types.

The recent papers examining distribution of fish assemblages in the Carribbean have generally examined fish at stations in bays and compared the fish assemblages between the habitat types (e.g. van der Velde et al. 1992, Sedberry and Carter 1993, Nagelkerken et al. 2000a, Nagelkerken et al. 2000c, Mateo and Tobias 2001, Adams and Ebersole 2002). However, few of these studies considered forereef fish assemblages, and a study including all the forereef and lagoon habitats would clearly provide a description with a wider range of validity than these previous studies.

Similarly, it is surprising how few studies compare habitats modified by human activity with unmodified habitats. My general impression from the literature is that any human impact in marine systems is detrimental to fish populations, unless it is in the form of artificial reefs, which can enhance local fish populations, or be detrimental to them, depending on your viewpoint (Bohnsack 1989, Hixon and Beets 1989, Heise and Bortone 1999). A simple description of the fish community throughout several marine bays with different levels and types of human activity might give some indication of the extent of human impacts on fish assemblages in similar bays elsewhere in the Caribbean, and provide a unique set of observations around which more specific hypotheses can be designed and tested.

There appears to be a strong effect of habitat complexity on fish populations and I feel that a clear look at the effects of complexity, regardless of habitat type or disturbance would be useful to ecologists. This is especially valid considering recent declines in live coral cover in the Caribbean (from 50% to 10% in the last 30 years) and the implications for localised effects on fish biodiversity are considerable (Gardner et al. 2003).

The marine resources of the BVI have not been extensively studied, and the distinct paucity of available literature is evident from the lack of references cited in this chapter. In contrast, the US Virgin Islands (USVI) has been extensively studied, and many of the processes occurring in this adjacent territory are assumed to be similar in the BVI. The brief account of the BVI's by Spalding et al (2000) in their world atlas of coral reefs appears to be the most in depth analysis of the state of BVI's marine resources in widely circulated published literature. The aim of this study is partly to increase our general understanding of BVI's marine resources, how they work and which factors strongly influence fish populations. This will advance our general understanding of reef ecology while simultaneously describing much-needed base-line data on the status of fish communities in the BVI.

Hopefully, by increasing our knowledge of the factors influencing general fish distribution patterns, we will be able to predict the effects of environmental changes such as destruction of mangroves, seagrass beds and coral reefs on fish populations. These trends and predictions are important sources of information to conservation biologists who need to design strategies to prevent further deterioration of valuable marine resources. In addition, basic systematic descriptions of habitat preferences, ontogenetic habitat use etc. are lacking for many Caribbean reef fish species. The author is part of an on-going collaborative research project known as Fish Base – www.fishbase.com that summarises the key biological information about every known fish species in the world. Results from this study will be made available to Fishbase so that other researchers may access the information.

1.9 THESIS OUTLINE

This thesis demonstrates the application of several key and sequential steps in the scientific method. Firstly, basic research topic is conceptualised and followed by an assessment of the best method to collect data whilst maximising precision and reducing bias. This is followed by an extensive observational survey describing apparent trends and correlations, as well as an assessment of some basic natural history of the fish species involved. These observations are used to identify important trends, which are the basis of hypothesis formation. The hypotheses are then tested experimentally in order to verify some of the suggested mechanisms affecting fish assemblage structure. Lastly, a small pilot study takes some of the main thesis findings and uses them in an applied way. The thesis does not give an account of many key things actually learned in the course of the project – such as budgeting, funds raising, networking with academics, governmental departments and the general public, crisis management, achieving goals in limited amounts of time on small budgets, recruitment of volunteers, when snorkelling is a better option than diving, how to mix cement, sew fish traps and many other things!

Chapter 2 reviews existing methods for surveying fish communities on coral reefs. As no existing method was appropriate for the purposes of this study, a new method was designed and piloted. In order to investigate how effective different sample sizes were at producing repeatable results, MDS plots were drawn of repeated measurements at each station for each sample. Next the cluster integrity for each sample was tested using a two-way ANOSIM analysis with the following null hypotheses *Ho 1-4:* There is no difference between samples grouped by station or grouped by sampling occasion. The data were described further using species accumulation curves and rank-abundance plots. These were interpreted together with MDS results in order to decide the best sampling protocol that would allow sufficient precision to distinguish between stations for environment-assemblage work and to sample most of the fish species in the in order to measure overall species richness.

Chapter 3 is an account of the broad trends, patterns and processes determining fish assemblage structure revealed by multivariate statistical methods. Stations were clustered using TWINSPAN analysis and the assemblages were described. Next, differences between assemblages were tested using the following null hypotheses:
Ho 1-3: There is no difference in species diversity/ number of species/ abundance between forereef, reef flat, seagrass, mangrove associated seagrass and eutrophic stations. This was followed by a CCA analysis and a Monte Carlo test in order to address the null hypothesis *Ho 4*: The ordination of stations and species is not affected by the measured habitat variables (i.e. they are randomly distributed).

Chapter 4 presents the fish distribution patterns of each species in the most abundant families. It describes the habitat preferences of the more abundant species using multiple regression models to test the hypotheses *Ho 1-48*: There is no linear relationship between of habitat composition and the abundance of species. Life history characteristics and ontogenetic habitat partitioning of the commoner species is also provided, and the following null hypotheses were tested: *Ho 49-61*: There is no difference in the length-frequency distributions of fishes between seaward reefs and lagoons. A full species list is presented and rare species are discussed in as much detail as the small sample sizes permit.

Chapter 5 deals with the issue of habitat complexity. While the previous two chapters consider habitat type and physicochemical variables, complexity was one of the most pronounced factors associated with local variations in fish species richness. The following hypotheses were tested: *Ho 1*: The ordination of stations and species is not influenced by the measured complexity variables (i.e. they are randomly distributed). *Ho 2-3*: There is no linear relationship between the measured complexity variables and number of fish species/ abundance. *Ho 4-5*: The complexity-abundance/number of species slopes do not differ in any of the 4 different habitat classes. In addition to discussing the results of this study, the issues involved in quantifying complexity are outlined, followed by a review of how habitat complexity affects fish communities around the world and other non-fish communities.

Chapter 6 presents the results of experiments testing five major hypotheses that were formed as a result of the habitat complexity observations: *Ho 1-3* Increasing rugosity of the substrate does not increase numbers of fish species/ abundance/ relative fish species richness calculated by rarefaction. *Ho 4-6*: Increasing reef height does not increase numbers of fish species/ abundance/ relative fish species richness calculated by rarefaction. *Ho 7-9*: Increasing variety of growth forms does not increase numbers of fish species/ abundance/ relative fish species richness calculated by rarefaction. *Ho 10-12*: Increasing variety of hole sizes does not increase numbers of fish species/ abundance/

relative fish species richness calculated by rarefaction. *Ho 13-15*: Increasing percentage hard substrate cover does not increase numbers of fish species/ abundance/ relative fish species richness calculated by rarefaction. It continues to test the effects of time of submersion of the artificial reefs as a covariable: *Ho 16-17*: There is no consistent variation in number of fish species or total fish abundance on the artificial reefs over the first 5 weeks of submersion. Finally, the effects of *Diadema* urchins on fish assemblages are investigated in and two-way ANOVA design experiment involving several artificial reefs. The null hypothesis tested is: *Ho 18-19*: The number of species/ total abundance of fishes at a site is unaffected by the habitat type or the presence of *Diadema antillarum.* This is followed by a discussion of the major components of habitat complexity, and how this information could be applied in other marine studies.

Chapter 7 is a small pilot study showing how fish communities in a polluted and an unpolluted bay can be compared if one removes the habitat effects by building small, inexpensive artificial reefs. In his simple experiment the following hypotheses are tested: *Ho 1-8*: There is no difference in number of fish species/ abundance/ diversity/ depth/ visibility/ dissolved oxygen/ phosphate/ nitrate between Nanny Cay and Soper's Hole. *Ho 9*: The ordination of stations and species is not influenced by the measured physicochemical variables (i.e. they are randomly distributed). Finally, *Ho 10-11*: the measured physicochemical variables are not linearly related to changes in fish species/ abundance on the artificial reefs. This chapter is illustrates one practical application of the habitat complexity findings.

Chapter 8 synthesises the general findings of the thesis, and relates them to our current theoretical understanding of fish community structure on reefs. It also examines the major marine conservation priorities in the BVI, and outlines suggestions about how current conservation efforts might be developed or improved. Lastly, a few suggestions are given to direct further research into potentially fruitful areas.

An adult slippery dick wrasse-*Halichoeres bivittatus*

2

Pilot Study and Sampling Design

> '*It is a mark of an instructed mind to rest assured with that degree of precision that the nature of the subject admits, and not to seek exactness when only an approximation of the truth is possible'*
>
> ARISTOTLE

2.1 INTRODUCTION

In ecological studies it is usually impossible to sample an entire population. As a result, we need to take several small samples of that population in order to make generalisations about it. Ecologists use many different methods and they all vary, depending on what they are trying to measure. Before a new method can be used with confidence, a pilot study should be undertaken to consider how well the samples portray the true population parameters. The aim of this chapter is to select and evaluate an appropriate method in order to map fish distributions in relation to habitat and physico-chemical variables over a fine scale in patchy habitats.

2.1.1 Precision

Precision measures how much results vary about the mean. More precise results have a smaller variance than less precise results. The greater the number of samples taken, the greater the precision will be, but precision only increases in proportion to the square root of the number of samples, so increasing effort will not proportionately increase the precision (Bibbey 1992, Greenwood 1996, Southwood and Henderson 2000). In order to investigate how this phenomenon applies to coral reef fishes, a cost-benefit analysis should be undertaken to investigate how intensive the sampling must be in order to obtain satisfactory results. A study with a few, but overly precise samples would have a smaller range of validity than a study that has a larger number of samples from different areas. However, if samples are not precise enough, it will be impossible to test hypotheses, as the variance would be so large that it is impossible to statistically differentiate between groups. There are several formulae for calculating the best number of samples in a study (Greenwood 1996, Southwood and Henderson 2000), but the decision is more commonly based on intuition and previous experience (Bibbey 1992).

2.1.2 Accuracy

Accuracy refers to how closely the sampled mean resembles the actual population mean. By sampling, we are trying to measure the population mean and the variance about it, so ecologists usually have no idea of how accurate their results really are (Bibbey 1992). Very precise results do not necessarily indicate a good study. The results could be inaccurate because of factors that skew the results in a particular direction, known as bias (Bibbey 1992). Bias in ecological projects is inevitable, but the best solution is to carefully design sampling protocols that try to anticipate and reduce sources of bias.

Some well-known sources of bias in animal community studies are:

i) *Observer* – different observers have different identification abilities.

ii) *Census method* – if methods and equipment are not properly standardised.

iii) *Effort and speed* – differences in enthusiasm between observers or from day to day.

iv) *Habitat* – animals are easier to detect in some habitats than others.

v) *Species* – some species are more conspicuous than others.

vi) *Density* – high densities of animals can swamp an observer, while low densities result in boredom.

vii) *Activity* – some species are more active (and therefore more conspicuous) in certain places.

viii) *Season* – both animal abundance and habitat characteristics may change seasonally.

ix) *Time of day* – animals vary in their activity levels throughout the day, while others are nocturnal.

x) *Weather* – extremes of weather like storms often result in uncharacteristic behaviour patterns in animals.

xi) *Artefacts* – the presence of observers may frighten away certain species or even attract others.

(Bibbey 1992).

2.1.3 Estimating fish abundance in tropical marine systems

Three main techniques are currently used to census fish in tropical marine systems: traps and nets, hook and line, and underwater observations. Hook and line techniques are unsuitable for monitoring entire fish communities because they are highly selective of large, predatory species; while traps and nets are species-selective and they require intensive labour in their manufacture, maintenance and deployment (Perrow et al. 1996). As a result, underwater visual census has been the most widely used method for assessment of tropical fish communities. The advantages of this technique are: it is inexpensive, non-destructive, and independent of the fishing technique. The fish are quickly accustomed to the presence of a diver allowing direct observation in their natural habitat (Perrow et al. 1996, Samoilys and Carlos 2000, Schmitt et al. 2002).While critics note that this method underestimates the abundance of nocturnally active, shy, small or cryptic species (Schmitt et al. 2002).

2.1.4 Visual census methods

There are three categories of underwater observation techniques: transects, roving diver methods and point counts. They have all been criticized for their high variability and low precision and power, but remain popular compared to the alternatives (Samoilys and Carlos 2000, Schmitt et al. 2002).

Transects are the most popular visual census method, the potential biases are well studied and the method is convenient when using SCUBA gear (Sale and Sharp 1983, Cheal and Thompson 1997, English et al. 1997, Schmitt et al. 2002). Transects are appropriate in areas with a uniform habitat and low population densities of the animal(s) being censused (Bibbey 1992), and transect surveys often examine large-bodied fishes of some commercial importance or particular interest such as groupers, angelfish, butterflyfish and parrotfish (e.g. (Roberts and Ormond 1987, Samoilys and Carlos 2000, Williams and Polunin 2001). Transects have also been used to compare fish communities between carefully selected areas of uniform habitat (e.g (McGehee 1994, Ohman and Rajasuriya 1998, Ferreira et al. 2001, Nagelkerken et al. 2001, Pet-Soede et al. 2001). Transects have distinct advantages when assessing abundance of large-bodied target species that occur in low densities but they are less satisfactory for assessing overall species richness and fish-habitat relationships in high-density fish communities of patchy marine habitats. While it is possible to select certain areas with a characteristic habitat type then to map them, this introduces bias from the researcher's choice of sampling location, and may lead to some habitat types being ignored or over-represented. If transects are placed randomly they will undoubtedly run over more than one habitat type, confounding fish-habitat analyses.

Roving diver techniques involve swimming randomly in a set area and recording all fish encountered and they have distinct advantages in rapid assessment of species composition (Pattengill-Semmens and Semmens 1998, Schmitt et al. 2002). This method is more effective at detecting rare species than transects, but is inappropriate for fine-scale fish and habitat distribution studies.

Point counts are the most suitable census techniques for use in heterogeneous habitats. Because habitat variables can be quantitatively recorded at each point and they are especially useful for investigating habitat effects on a community (Bibbey 1992). When using this method, particular attention should be paid to the selection and location of points, the number of visits, the duration of counts and the reduction of observer bias through training (Bibbey 1992). The most popular point count technique used is derived from a procedure originally described by Bohnsack and Bannerot (1986) (see examples in (Pattengill et al. 1997, Rosa and Moura 1997, Lindahl et al. 2001, Williams and Polunin 2001). The stationary diver method requires one diver to remain in the middle of an imaginary 7.5m radius cylinder about 4m above the reef. During an initial 5 minute time-period the diver records all fish species present and then instantaneous counts are made, in turn, of each species on the list (Bohnsack and Bannerot 1986).

The aim of this study is to assess the optimal survey design for monitoring fish assemblages in relation to their habitat and to achieve a comprehensive and precise sample, whist reducing potential sources of bias. As a result, application of the usual point-count methods would have some obvious weaknesses: (1) They would be difficult in shallow areas or places where visibility is low (as encountered in the various lagoon and back-reef habitats to be included in this survey). (2) The large size of the imaginary cylinder would make it difficult to count small, cryptic species that hide in structure. (3) The method gives a density estimate of fish, but does not account for disturbance by the observer. As a result, a new point-count survey method was designed to count fish for the purposes of mapping their fine-scale distributions and examining fish-habitat relations.

2.2 METHODS

2.2.1 Study location

Hodges Creek is a shallow, non-estuarine bay on the island of Tortola in the British Virgin Islands, Caribbean (Fig. 2.1). It is a mangrove-lined lagoon with a busy marina catering to the charter boat industry and the habitat is a mosaic of reef, seagrass, sand and macroalgae patches. Reef patches are largely composed of dead coralline boulders and some live finger coral *Porites* sp. Seagrass beds are dominated by turtlegrass *Thalassia testudinum* Banks & Soland with smaller patches of shoal grass *Halodule wrightii* Asch. while algal beds are mixed patches dominated by *Dictyota* sp., *Halimeda* spp. and *Penicillus* sp.

2.2.2 Observer Training

Both observers were trained thoroughly to reduce bias. During an intensive six-week period we surveyed shallow water habitats for at least three hours a day, identifying all fish species encountered. Characteristics of unidentified species were recorded and checked using field guides (Stokes 1980, Humann 1994, Lieske and Myers 2001). Particular attention was paid to small, cryptic species such as blennies and gobies. As a pre-emptive measure, fish that were difficult to identify were added to a list of ‘problem’ species and a standard protocol was established for them (see discussion).

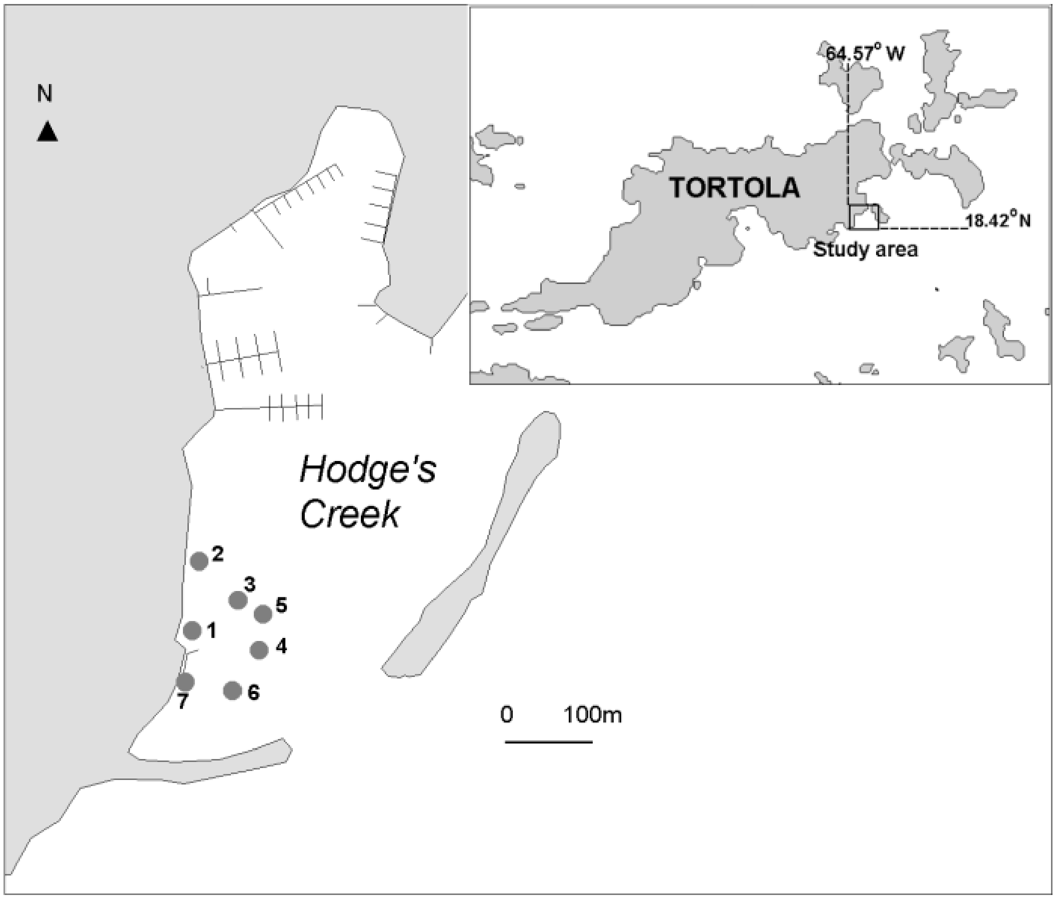


Fig 2.1 The location of the 7 preliminary sampling stations in Hodge's Creek. Station 1 = algal bed, station 2, 3, 5 = sand, station 4,6=seagrass, station 7 = reef & rubble.

2.2.3 Field Methods

Seven pilot stations were chosen in a variety of habitats, ranging in depth from about 50cm to 1.5m in Hodges Creek (Fig. 2.1). They were located by boat, using a Garmine Etrex GPS receiver. Marker floats were positioned about 30cm above the substrate so that they would not interfere with boat traffic. Station habitats were classified according to the predominant habitat type at each station. Station 1 was situated in an algal bed, stations 2, 3 and 5 were dominated by sand; stations 4 and 6 were in seagrass, while station 7 was mostly reef habitat.

Quadrat poles were made of ¼ inch PVC piping and measured 2.5m x 2.5m. If quadrats had been any larger, counting all fish would have proved difficult considering the low visibility and the high abundance of fish in some areas. Smaller quadrats would have resulted in smaller sample sizes and have reduced levels of precision.

At each station four quadrats were arranged around the station marker (Fig 2.2). Contiguous quadrats were avoided, as this would increase bias due to edge effects and risk of counting the same fish twice in different quadrats (Southwood and Henderson 2000). After a minute to allow fish to settle down, each quadrat was observed for five minutes. Five minutes was just long enough to detect all the fish at stations with high fish numbers, while longer times increased the risk of counting the same fish twice. The first four minutes were spent observing the quadrat from about a 1m distance. All fish in the quadrat, or moving through it, were identified and their lengths were recorded on an underwater slate. The last minute was spent actively searching for fishes hiding in structure, or camouflaged ones that were not detected previously. Stations were visited in

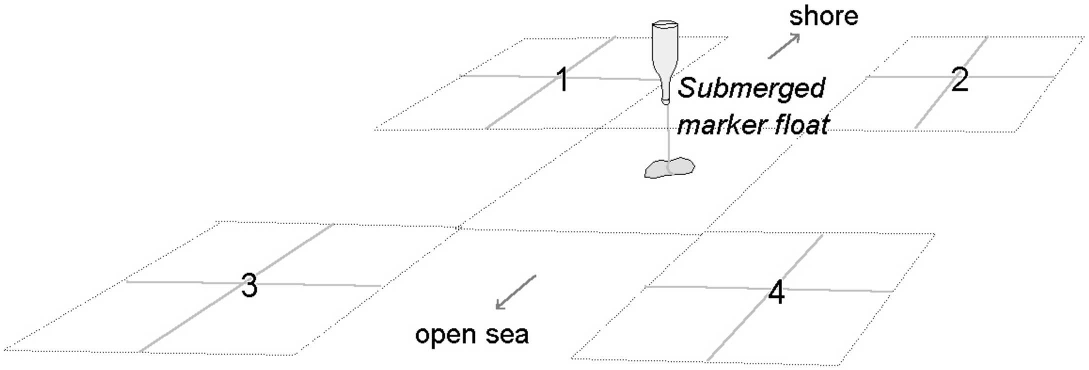


Fig 2.2 Sampling design—the orientation and layout of the 2.5m x 2.5m quadrats about the submerged float marking each station.

randomised order each day to control for possible time of day effects. Each station was visited 6 times every alternate day in June 2001.

2.2.4 Analysis

Large or small samples?

Would it be better to sample 1 quadrat at each station and sample more stations or to sample 4 quadrats at each station and sample fewer stations? The aim of the study is to find a sampling technique that can assess the characteristic fish assemblages in a limited area. In this patchy environment, samples that are too large would increase the number of microhabitats in the sample and hence reduce the ability of the method to detect habitat-related variations in the fish community. The differences between the sampling stations should also be pronounced enough so that *within* site variations in the fish assemblages caused by weather, tide and random variation are smaller than the *between* site variation.

A number of different multivariate methods are available to assess the similarity of stations (these are reviewed in Chapter 3). These stations had variable sample sizes with large numbers of zero-values, and non-normal distributions (even after data transformation) violating the assumptions of correlative approaches such as Principal Component Analysis (ter Braak 1986). Thus a non-metric Multidimensional Scaling (nMDS) analysis (Kruskal 1964) was undertaken for each of the sample sizes (one, two, three and four quadrats respectively) using PRIMER 5b, Plymouth Marine Laboratory, UK. Total abundances were square root transformed and a Bray-Curtis similarity matrix computed (Clarke and Ainsworth 1993). The final MDS plot ordinates the stations in two dimensional space and the Kruskal stress value is a measure of difference in rank order distance between sites in the original data and the in the ordination, thus it performs the same role as the Monte Carlo simulation applied to Canonical Correspondence Analysis. The following is a useful guide to interpretation of a 2 dimensional MDS output:

Stress = 0 the matrices compared are completely dissimilar (no shared species)

Stress <0.1 – a good ordination with little chance of misinterpretation.

Stress <0.2 – a potentially useful overall picture, but lacking in finer detail.

Stress 0.2-0.3 – potentially useful, may be improved by removal of rare species or some samples.

Stress >0.3 – points poorly sorted in the 2-D ordination space and should not be interpreted.

(Clarke and Ainsworth 1993, Clarke and Warwick 1994).

Next, a one-way ANOSIM (Clarke and Green 1988) permutation test was used to assess the significant differences between pre-defined groups of sample sites in the multidimensional analyses. For this analysis the stations were the groups of interest and the six sampling visits were the replicates. The hypothesis being tested was Ho: There is no difference in fish assemblages between stations. One advantage of this method is that even if the null hypothesis of no difference between groups is rejected, the ANOSIM R value can be examined to assess the degree of differences between the defined groups (Somerfield et al. 2002).

Since variance between stations and between sampling occasions (visits) is of interest, an auxiliary 2-way ANOSIM analysis was performed, the null hypothesis was Ho: There is no difference in the fish assemblages between stations or between visits.

How many visits per station?

Biodiversity studies need to ensure that most of the species present in a study area are collected, but it is often difficult to know if sampling effort in an area has been sufficient to collect all species (Heck et al. 1975). Species accumulation curves are an effective way to see if sampling has been sufficient, because as an area is sampled more intensively, fewer new species are encountered. In many ecological studies it is sufficient to collect 50-75% of the species at each station, particularly if a large number of stations are being examined (Heck et al. 1975). In this species-rich environment it was anticipated that most of the species would be rare, and just the commoner fishes would be useful in determining fish-habitat relationships. A sampling method that collected at least 50% of the S_{max} at any one station would be suitable for this study.

The species accumulation curves would not be expected to reach an asymptote over just 6 visits to the station, so the total species richness S_{max} was estimated using a non-parametric estimator of species richness, the Chao2 index for quantitative data (Cha0, 1987). In order to illustrate the typical species accumulation curve in comparison to the Chao 2 S_{max} for each station, a series of randomized iterations was performed (without replacement) to produce a mean accumulation over 50 cumulative samples. This was performed using EstimateS Freeware by Colwell, R. K. 1997-2000 and published at http://viceroy.eeb.uconn.edu/EstimateS. Next, the mean species accumulation for the 7 samples was plotted as a percentage of the Chao S_{max} values to show the proportion of the total species richness collected after each visit.

Rank-abundance plots were drawn in order to assess how many visits would be needed to encounter all of the more common species and to accurately assess their relative abundances. The data from increasing sampling effort (number of visits) was pooled and plotted on a logarithmic scale. These plots have two features, species richness and equitability or evenness (Taylor et al. 1976). The shape of the curve tells us the proportion of the species that are rare, and give some indication of the relative abundance of commoner species. Sampling effort for the commoner species will be considered adequate once the shape of the plots stabilises i.e. the ranking of the commoner species is consistent.

2.3 RESULTS

2.3.1 Observer Training

The observers soon became familiar with the fishes in the study area, and most could be identified immediately. The initial training also revealed certain groups of fish that were difficult to identify in the field.

Blenniidae (Blennies) - most blenny species were distinctive and easily identified, however, the most common blenny in the bay areas was the rosy blenny *Malacoctenus macropus* (Poey 1868), the mature males had a distinctive pink flush on their chins, but females and immature fish were difficult to distinguish from immature barfin blennies *Malacoctenus versicolor* (Poey 1876).

Clupeidae (Herrings, Sardines and Shads) - these were very difficult to identify by visual census using the available field guides and they difficult to count because they occurred in very large numbers.

Gerreidae (Mojarras) The genus *Eucinostomus* have various distinguishing features including pigment spots on the eye and the dorsal fin. These features, however, were variable and even after a serious attempt to come to grips with this group, identifications could not be made with conviction. The two most common species appeared to be bigeye mojarra *Eucinostomus havana* (Nichols 1912) and Jenny mojarra *Eucinostomus gula* Quoy & Gaimard 1824 although the following species may have also been present: mottled mojarra *Eucinostomus lefroyi* Goode 1874; and silver mojarra *Eucinostomus argenteus* Baird & Girard 1855.

Pomacentridae (Damselfishes) Juvenile damselfishes of longfin damselfish *Stegastes diencaeus* Jordan & Rutter 1897 and beaugregory *Stegastes leucostictus* Müller & Troschel 1848 were not easily distinguished from each other. The rest of the juvenile damselfish were easily separated in the field, but adults of *Stegastes leucostictus, Stegastes diencaeus,* dusky damselfish *Stegastes dorsopunicans* Poey, 1863 and cocoa damselfish *Stegastes variabilis* Castelnau, 1855 were indistinguishable.

Sparidae (Porgies and Seabreams) The genus *Calamus* were mostly smaller fish that were very difficult to separate using visual census characters outlined in the field guides. They were possibly saucereye porgy *Calamus calamus* Valenciennes, 1830, pluma porgy *Calamus penatula* Guichenot, 1868 or jolthead porgy *Calamus bajonado* Bloch & Schneider, 1801.

Scaridae (Parrotfishes) Juvenile parrotfishes of the genus *Scarus* could not be distinguished from each other. However initial phase and terminal phase adult fishes in were easily distinguished.

2.3.2 Effects of sample size and day-to-day variation

The MDS plots all had stress values ranging from 0.12 to 0.13 for the first two dimensions indicating that they were good ordinations with little chance of misinterpretation (Fig 2.3). The ANOSIM analysis indicated that at least one of the stations was significantly different from the rest in all designs (Fig 2.3). The Global R statistic indicated that increasing the sample size improved cluster integrity (Fig 2.3) and that the 4-quadrat design had the most distinctive clustering of all ($R = 0.93$, $p< 0.001$).

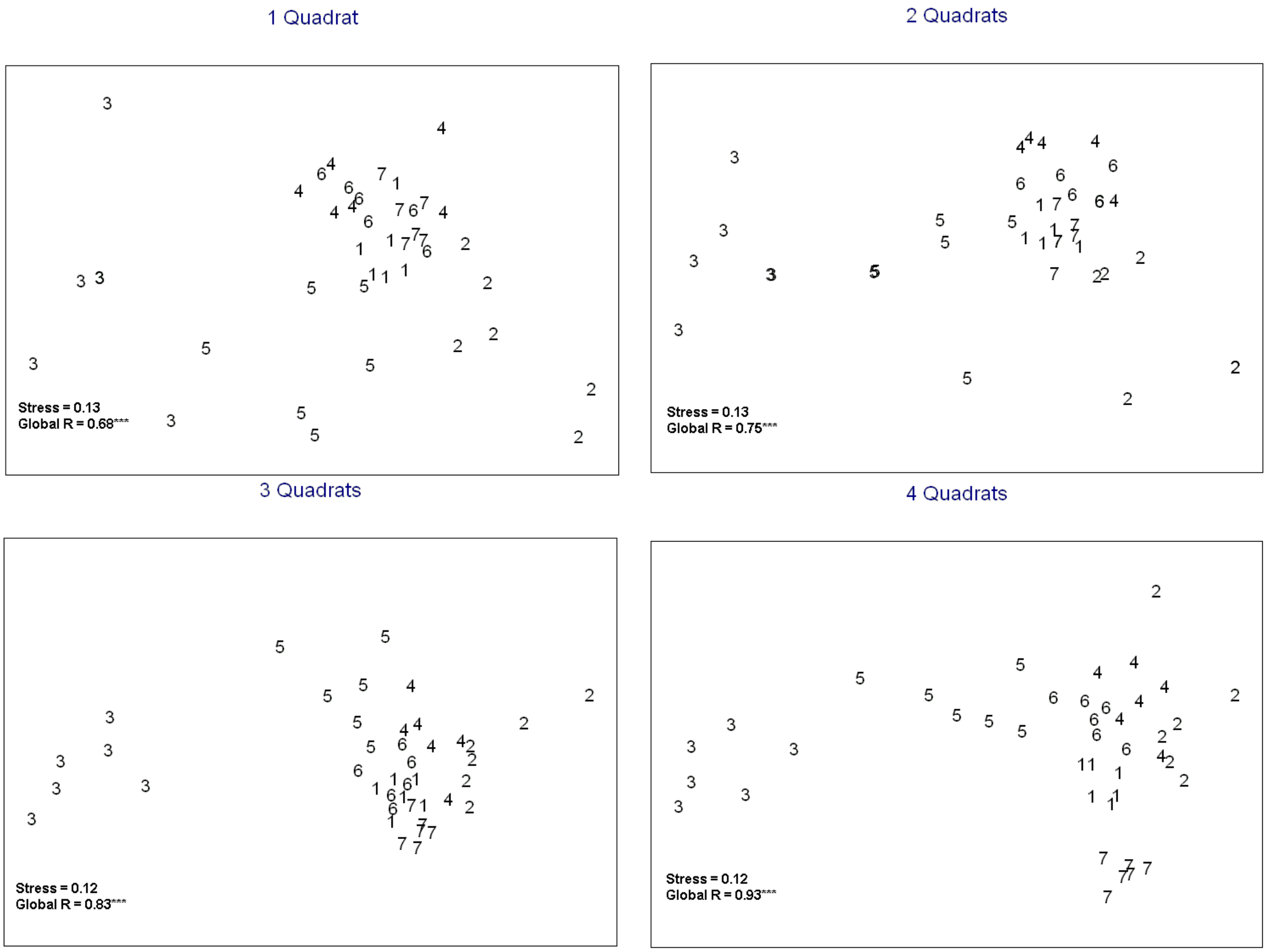


Fig 2.3 Non-Metric MDS plots of stations sampled on different days. A One-way ANOSIM analysis was run on data from each sample size to test for multivariate differences between assemblages at each station (1-7) over the course of six visits. *** indicates significant difference (p< 0.001) between fish assemblages at least one station.

The two-way ANOSIM test for the effects of sample site and sampling occasion (visit) showed that at least one station was significantly ($p < 0.001$) different from the rest using any design, while the clustering caused by daily variation in fish communities was only significant for the 2-quadrat design (Table 2.1). Thus, as sample size increases, the clustering of stations improves and becomes more repeatable, reducing the influence of day-to-day variation on fish assemblages.

It is clear from Fig 2.3 that there is some daily variation in fish assemblages at each station, even if it is not always statistically significant. Clearly, pooling data from 2 visits might reduce the potential bias from time of day, weather, tide or random variation and further increase the precision of measurement of fish assemblages. In order to investigate this, the data from the different sampling days were randomly paired with each other, reducing the number of repeated measurements from 6 to 3. Next, MDS and ANOSIM analyses were repeated on the pooled data (Fig 2.4) and this improved the site clustering and the clustering integrity, particularly for the 3 and 4 quadrat designs, which had Global R values of 0.98 and 0.94 respectively.

Table 2.1 Results of a two-way ANOSIM analysis testing for differences in fish assemblages between stations (n = 7) and visits (n = 6) for each sample size.

Design	**Factor**	**Global R**	**p**
1 quadrat	Station	0.68	0.001***
	Visit	-0.006	0.48ns
2 quadrats	Station	0.62	0.001***
	Visit	0.19	0.003**
3 quadrats	Station	0.69	0.001***
	Visit	0.08	0.10ns
4 quadrats	Station	0.72	0.001***
	Visit	-0.009	0.58ns

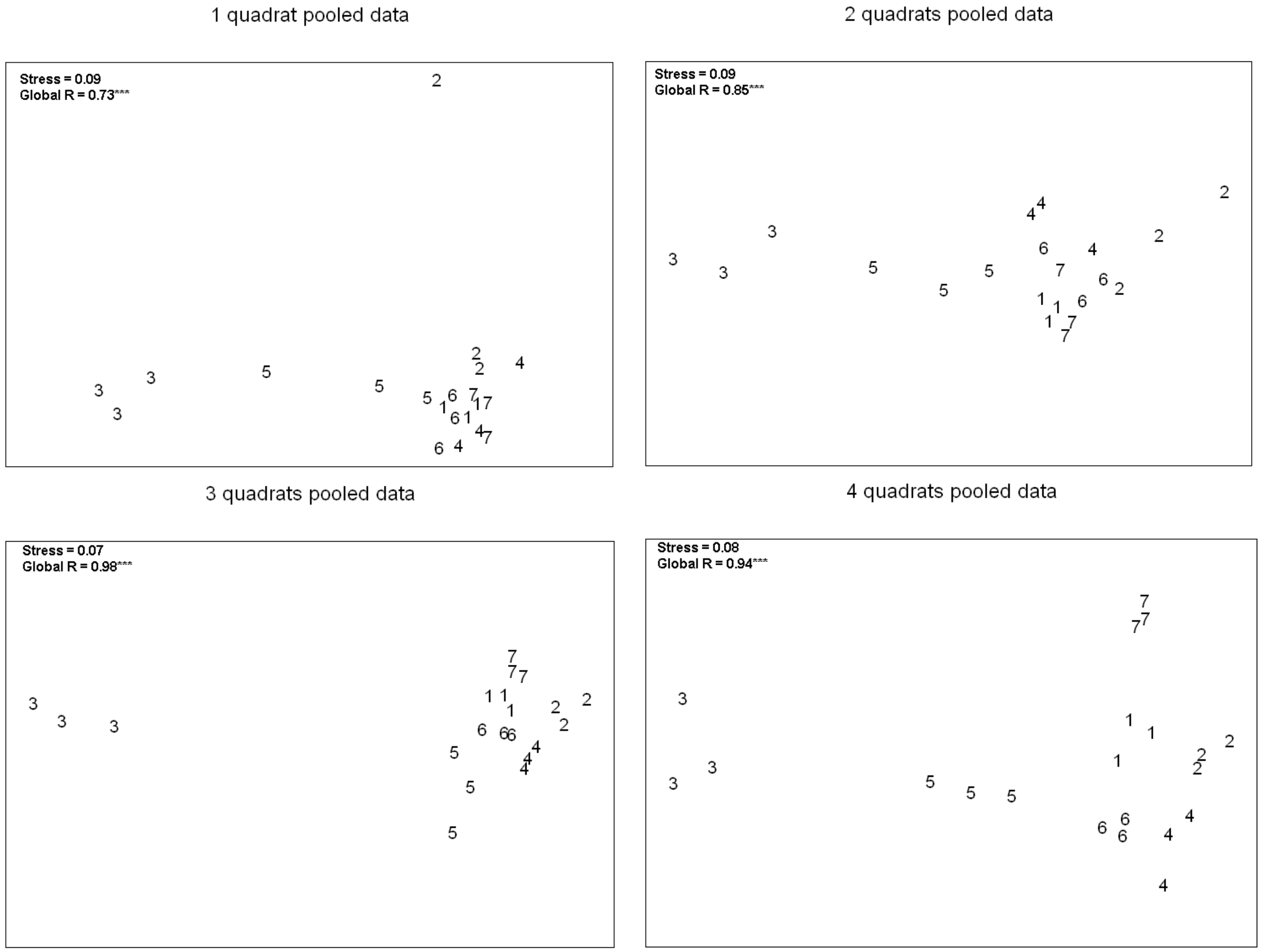


Fig 2.4 Non-Metric MDS plots of stations, each sample point used the pooled data from a randomized pair of visits. A One-way ANOSIM analysis was run on data from each sample size to test for multivariate differences between assemblages at each station (1-7) over the course of three samples (each using data from 2 visits). *** indicates significant difference ($p < 0.001$) between fish assemblages at least one station.

2.3.3 How many visits?

The ANOSIM and MDS analyses indicate that a sampling programme using 3 or 4 quadrats at each sampling site and visiting them twice gave the most precise measurements, however, they also indicate that sampling 3 or 4 quadrats once would have been adequate to characterise the fish assemblage at each station. Another factor for consideration is that it is desirable to assess the general fish biodiversity in the study area. The larger survey will include many samples (< 100) in several bays so a full assessment of the total species richness at each station S_{max} would be unnecessary. However, because the observed number of species S_{obs} at each station will be an important response variable in future discussions, it is important to assess roughly what proportion of the total species richness S_{obs} represents. The Chao 2 estimates of S_{max} are plotted against the observed species accumulation curve for each station (Fig 2.5). While the Chao S_{max} stabilised by the 6th sample in most cases, stations 6 and 3 did not level off, indicating that further samples are really required for a more accurate estimate of species richness at these stations. The overall species accumulation curve indicated that about 55% of the total species richness at each station is encountered in the first 2 sampling occasions, and then the rate of encounter of new species decelerates sharply (Fig 2.6).

The rank-abundance plot for the entire species compliment at all stations was remarkably stable in shape regardless of the total number of visits to each station. The common species all ranked very consistently, while the rare species were missed with lower sampling efforts (Fig. 2.7). Even so, in this limited sampling area, more than 80% of the total numbers of species encountered were found in the first 2 visits to the area.

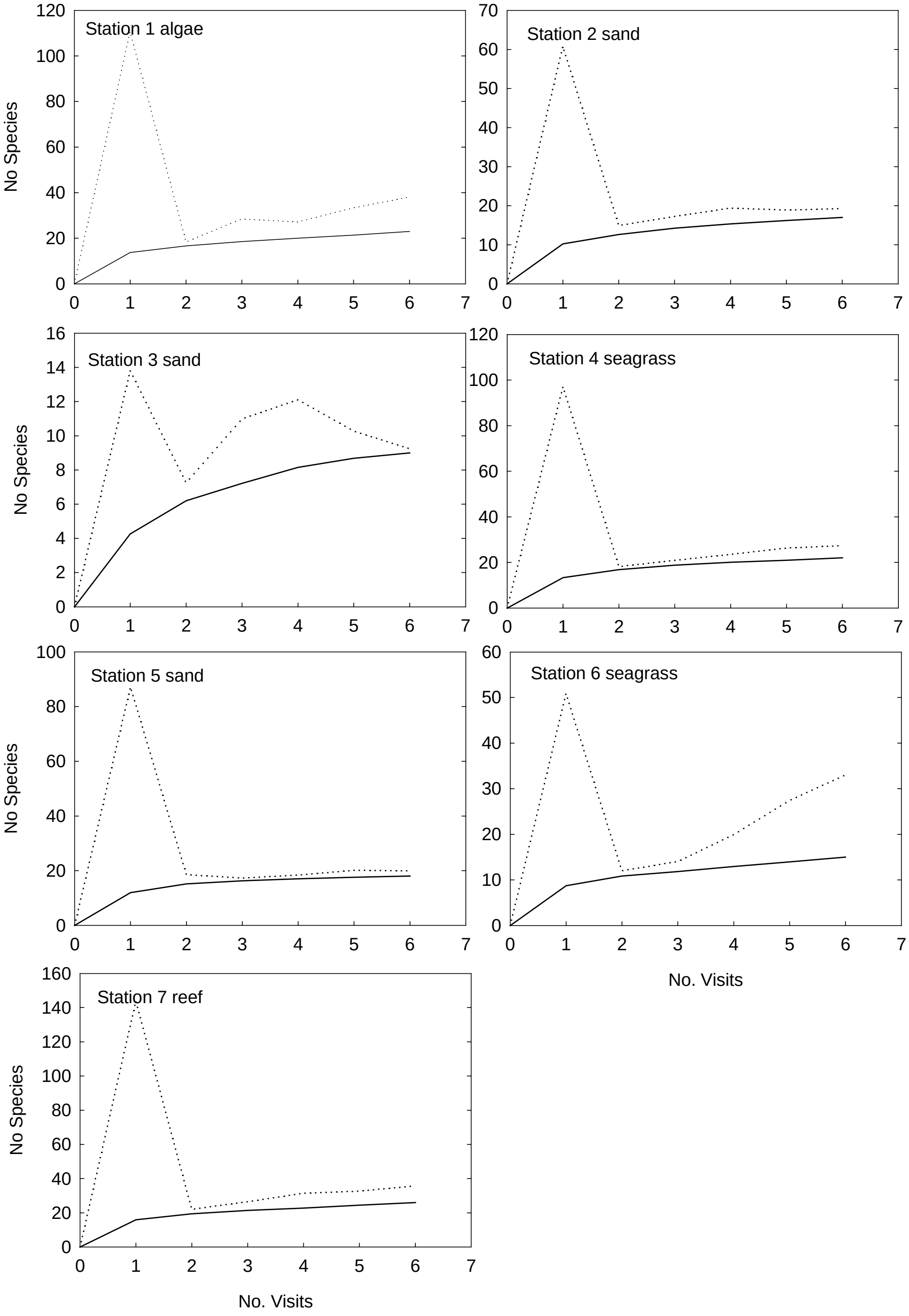


Fig 2.5 The accumulation curves for S_{obs} (solid) and Chao 2 estimate of S_{max} (dotted) with increasing sampling effort at each station. 50 randomised iterations were simulated using EstimateS software to illustrate the typical sampling curves at each station.

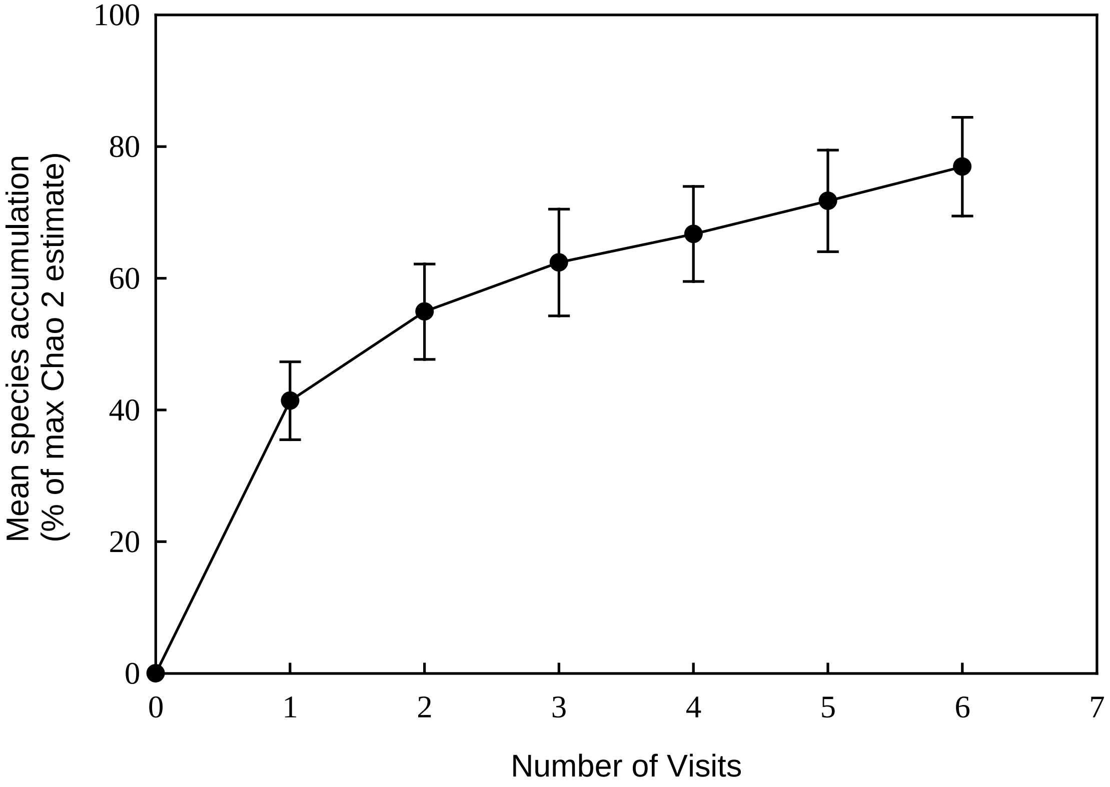


Fig 2.6 The mean (± SE) species accumulation curve for the pilot sample n=7 stations. The data are presented as a % of the extrapolated S_{max} using the final Chao2 species richness for each station (shown in Fig 2.5).

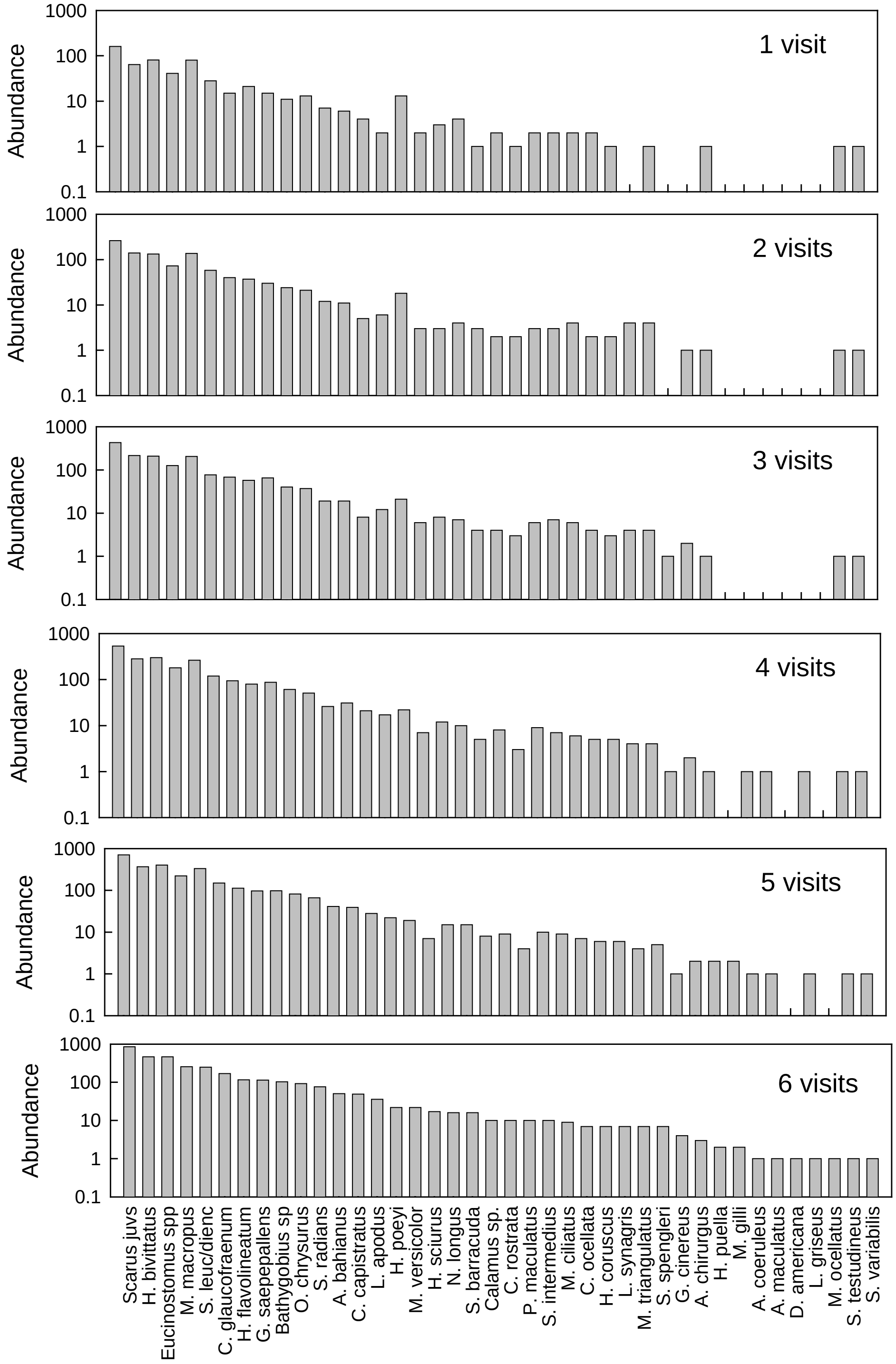


Fig 2.7 Rank-abundance plots of fish species pooled from all stations over the course of six visits, over 80% of all species were encountered by the second visit.

2.3.4 Cost

It was estimated that 1 quadrat could be sampled in about 7 minutes, while the cost of moving to a new station was about 30 additional minutes. Time was the major limiting factor in this study as other resources were readily available. No stations in the preliminary sampling required scuba equipment to sample, although in the main survey, the cost of tank rental and decompression considerations would become new factors to consider.

2.3 DISCUSSION

2.4.1 Observer training

All community studies have a few species that are difficult to identify in the field, but this should not discourage work on these communities. In fact, highlighting problem areas may lead to more vigorous attention to these groups by authors of field guides and taxonomic experts so that future studies may be improved. In order to maximise the taxonomic resolution of my field data, while being honest about which species I could distinguish in the field, I devised the following procedure for dealing with ‘problem’ fish species:

Blenniidae - the two species *Malacoctenus macropus* and *Malacoctenus versicolor* vary so much in their coloration that only mature male *M. macropus* are distinguishable from the rest, so the two species were lumped and called *M. macropus/versicolor*.

Clupeidae - the high densities of fish and the low taxonomic resolution meant that the best index of relative abundance would be simply to record presence or absence of clupeid schools in each quadrat on each sampling occasion, they were omitted from species diversity calculations.

Gerreidae - the difficulty in distinguishing members of the genus *Eucinostomus* meant that the only practical solution would be to identify them to genus level only; throughout this project and they were called *Eucinostomus* sp.

Pomacentridae - juvenile *Stegastes diencaeus* and *Stegastes leucostictus* were lumped and are referred to as *S. leucostictus/diencaeus*. Indistinguishable adults of of

Stegastes leucostictus, Stegastes diencaeus, Stegastes dorsopunicans and *Stegastes variabilis* are referred to as Stegastes spp.

Sparidae: Members of the genus Calamus were lumped and are called *Calamus* sp.

Scaridae: Juvenile *Scarus* sp. were identified to genus level only.

2.4.2 Effects of sample size and day-to-day variation

It was clear that larger samples produced more repeatable and distinctive clustering of data than small samples. This would be expected in any sampling programme because the precision of a measurement usually increases in rough proportion to the square root of sample size (Greenwood 1996, Southwood and Henderson 2000). Furthermore, the day-to-day variation had a significant effect on the two-quadrat design. This suggests that the daily variation in fish assemblages from sample sizes smaller than three quadrats are likely to be confounded by day-to-day variations in fish assemblages due to tide, weather or random variation. Samples larger than two quadrats, however, were less susceptible to this variation and were therefore more repeatable or precise. Therefore samples consisting of three or four quadrats would be the best option in the main study. In addition, the precision of samples could be further improved by pooling data from two visits to the station, but this would not be essential for a reasonable multivariate analysis of fish assemblages in a larger survey.

2.4.3 How many visits?

It appeared that just one visit would be adequate for a multivariate assessment of the fish assemblages at any one station, however, the mean species accumulation curve indicated that one visit to a station would only detect just over 40% of the total species richness at any one station. In species richness studies, it is usually desirable to collect at least 50% of the S_{max} even when a large number of samples is being collected in very diverse systems (Heck et al. 1975). Even though visiting stations twice would double the amount of sampling effort, (and the sampling costs) it would bring the species encounter rate up to about 54% of S_{max}, which would really be necessary in order to justify comparing the observed number of species at each station and for an overall assessment of fish diversity in the main survey. Doubling the sampling effort would also increase the precision of measurements and should reduce the bias due to tide, time of day or random variation.

Even in this small pilot sample, about 80% of the species encountered (overall) were encountered in the first two visits (Fig 2.7), and species encountered in subsequent were rare (often only 1 individual). Furthermore, the rank abundance plots for the commoner species were fairly stable and followed the log-normal distribution (Kempton and Taylor 1974), regardless of the number of visits. Thus sampling stations more than twice would probably not be worth the extra effort for the purposes of this study. This log-normal distribution is a widespread ecological phenomenon and a large number of the species are usually very rare in most ecological studies. As a result, it is often impossible to increase sampling effort enough to obtain samples large enough for statistical analyses of every species (Kempton and Taylor 1974, May 1975). This means that while rarer species are interesting from a biodiversity perspective, only the more abundant species will be of use in describing the ecological gradients and the final sampling design should cater to both concerns.

2.4.4 Optimal design

Optimal sampling design involves a trade off—balancing desired levels of accuracy and precision against the increasing costs associated with collecting more precise data. The initial choices about the range in sample sizes and the choice of underwater visual census methods were made in the light of practical considerations and from a review of the literature. The subsequent analyses suggest that at least 3 quadrats should be taken at each station and that each station should be visited at least twice. Thus the final recommended design is a point-sample cluster method using four quadrats at each station that are visited twice on different days at randomised times. This method allows sufficient resolution to distinguish between stations and to sample most of the fish species occurring there, while providing adequate sample sizes for environment-assemblage work.

On a more cautionary note, this method may assess fish assemblages fairly precisely, but it is still a visual census technique and is subject to the same criticisms as other visual census methods. There may be some bias introduced from observer presence which may frighten away some species e.g. bonefish (Humann 1994) and the abundance of nocturnally active, small or cryptic species such as cardinalfish may be underestimated (Schmitt et al. 2002). Because no other sampling techniques were used to validate the method I cannot judge to what extent these sources of bias skew the accuracy true population estimates. However, this method does not claim to accurately assess fish density or biomass and the results should be simply interpreted as an index of relative fish abundance that can be used to compare diurnal fish assemblages between stations and habitats.

A juvenile French angelfish *Pomacanthus paru*

3

Fish Assemblages and their Environment

> *‘The broad overlap and scattered centres of species populations along a gradient imply that most communities are intergraded continuously along environmental gradients, rather than forming distinct, clearly separated zones’*
>
> R.H WHITTAKER

3.1 INTRODUCTION

Synecology is the study of many species simultaneously in relation to environmental variables (Jongman et al. 1987) At complex levels of ecosystems and landscapes, it is very difficult to find evidence showing the relative importance of factors structuring species assemblages, or even more so, to prove these relationships experimentally. Some excellent studies in marine environments have linked environmental gradients to animal assemblages. For example, distributional studies on rocky shores have shown that invertebrates are strongly affected by tidal range and exposure (Stephenson and Stephenson 1949, Underwood 1973) as well as interspecific competition and habitat type (Fletcher and Underwood 1987). Estuarine studies have shown that depth and width of estuaries as well as turbidity levels are important factors structuring benthic invertebrate communities (Warwick et al. 1991). More recently synecological studies have focused on fish assemblages, relating them to factors such as habitat type (Rotherham and West 2002) and fishing pressure (Westera et al. 2003).

Synecological studies usually aim to identify broad trends and to describe assemblages in relation to the observed environmental variables using multivariate analysis (Digby and Kempton 1987, Jongman et al. 1987). Recent developments with refined statistical procedures (such as the Monte Carlo test) allow statistical tests of correlations observed in multivariate analyses (Leps and Smilauer 2003).

The aim of this chapter is to describe the basic patterns and processes related to fish assemblages by addressing the following questions:

1) Which sampling stations have the most similar fish assemblages and how are they distributed?
2) What are the characteristics of the major fish assemblages?
3) Which variables are the likely determinants of the variation in species composition between these assemblages?

3.1.1 Extracting patterns from continuous data

Many ecologists agree that species distributions lie on a complex population gradient in relation to a combination of all the environmental variables that define an organism's niche (Hutchinson 1957, Whittaker 1975). While it is accepted that communities usually vary in a continuous way, it is often easier to communicate these trends in the form of discrete categories. Without grouping data into sets with similar properties, it would be almost impossible to understand the processes that govern species composition.

Hierarchical classification methods have been widely used in vegetation studies, and they can readily be applied to animal communities. Hierarchical classification approaches dictate that that higher levels of organisation need to incorporate and constrain the behaviour of lower levels in the hierarchy (Noss 1990). The study of reefs over the years has lead to a well-used (and adapted) classification system that defines different reef zones with similar biotic assemblages they are: fore reef slope, reef crest, reef flat, lagoon and back reef slope (Sale 1991, Williams 1991, McGehee 1994). An increasing number of studies are using multivariate analyses to examine fish assemblages in habitats like mangroves and seagrass beds that are often found adjacent to reefs (van der Velde et al. 1992, Sedberry and Carter 1993, Nagelkerken et al. 2000a, Mateo and Tobias 2001). This ‘ecosystem’ approach has been advocated for some time (Ogden and Gladfelter 1983a, Ogden 1997) and these studies have revealed that different habitat types often occur as patchy mosaics gradually merging into one another. Processes occurring in one habitat type may also influence the fish assemblage in the adjacent areas; for example, the presence of mangroves in lagoons may influence the composition of fore reef fish assemblages (Nagelkerken et al. 2002, Nagelkerken and van der Velde 2002). Since observation is the first step in the scientific method, it was felt that a simple observational exercise mapping the fish community across all habitat types would reveal patterns of fish assemblage structure and that these could be used to generate hypotheses about fish distribution unbiased by preconceived ideas about fish habitat preference.

3.1.2 Multivariate approaches

Most studies of communities at landscape levels are descriptive field surveys. The datasets are bulky, complex and fraught with noise, redundancy, internal relations and outliers (Jongman et al. 1987). These surveys often include large numbers of species and environmental variables, making it impractical to perform a direct gradient analysis of every species and variable. A good way to expose the main factors structuring such datasets is by using multivariate analysis. Cluster analysis and ordination are two multivariate approaches can be used to compare the animal assemblage structure between samples:

Cluster analysis is an objective way to identify structure in data by dividing it into discrete but similar categories. Agglomerative methods start with single samples and then search for the most similar samples to make groups (Jongman et al. 1987). Divisive methods sort whole data sets into characteristic groups. One popular method is Two-Way Indicator Species Analysis (TWINSPAN). It indicates at each level in the hierarchy the species peculiar to each group (Jongman et al. 1987). TWINSPAN is preferable to other clustering methods as data are grouped in a hierarchy and species that are characteristic of those clusters (indicator species) are given at each division.

Ordination is a term applied to multivariate methods that arrange samples along axes according to their species composition (Jongman et al. 1987). Their output, ordination diagrams, arrange sites with similar species composition close together and dissimilar sites further apart. Additional interpretations and analyses can be made depending on the availability of environmental data (Jongman et al. 1987).

There are a number of different ordination methods available, including Bray and Curtis ordination, principal component analysis, correspondence analysis, detrended correspondence analysis, non-metric multidimensional scaling (NMDS), and canonical correspondence analysis (Kent and Coker 1992). These methods all have different advantages and disadvantages, but should produce broadly similar patterns in large, robust data sets. Marine ecologists have traditionally favored NMDS over the other (parametric) approaches because the method does not assume that the data are normally distributed or linearly related to environmental gradients, permitting data sets with large numbers of zero-values and rare species to be compared (Whittaker 1987, Clarke 1993). It is also less vulnerable to distortion resulting from strong gradients in beta diversity (Fasham 1977). While others have found little advantage of NMDS (Gauch 1982, Kent and Coker 1992) and criticize the fact that there is no objective criterion for determining the number of dimensions necessary to summarize sample variation (Austin 1985).

Canonical correspondence analysis (CCA) is a recently developed ordination technique that detects variations in assemblage composition, then undertakes an auxiliary analysis to identify and plot the environmental variables that correlate best to the ordination axes; these are displayed as a simple graphical plot of species sites and environmental vectors (ter Braak 1986). CCA incorporates a correlation and regression between environmental and species data in the ordination analysis. It assumes a Gaussian response curve to an environmental factor, and that the response curves are linear—which many real world data sets violate (Whittaker 1975, Kent and Coker 1992). These problems can be largely overcome by removing rarer species from the analysis and by appropriate transformation of data, but even so, critics argue that the inevitable violations of these assumptions cause distortion of the true relationships (Austin 1985). Despite these criticisms, parametric multivariate analysis is a good method for summarizing the relative composition of assemblages in relation to environmental variables. The general goal of attempting to describe and understand communities is far from any workable experimental design or data analysis algorithm because each station is to some degree unique; the broad characterisation of these samples according to the observed trends is a useful step in hypothesis formation (Gauch 1982).

3.1.3 Assemblages and indicator species

Often, there are so many possible environmental variables, most of which fluctuate strongly and/or remain unmeasured, that we are unsure exactly what the individual species are responding to. Species distribution patterns are indicative of the environmental gradients that form them. Species composition can therefore be a good indication of the environment even in the absence of environmental data (Digby and Kempton 1987).

Indicator species are a firmly entrenched tradition in ecological monitoring, and many designs focus on the ability to detect various kinds of anthropogenic disturbance to an environment (see review in Chapter 1). However, species assemblages that are indicative of certain environments also help us to understand how communities are arranged along natural environmental gradients, and they may give clues as to why assemblage structure varies from place to place. Understanding these key processes will help environmental managers to understand the effects of disturbance and to highlight the key areas for conservation priority.

3.1.4 Which environmental variables should be measured?

Many environmental variables could be measured in tropical marine habitats. However, with very real constraints on time, money and equipment, ecologists have to choose a limited set of variables that vary within the study area and that may directly (or indirectly) influence their communities in a biologically meaningful way.

Habitat type is one of the key variables influencing animal assemblages as the composition of these resource axes strongly influences fish assemblage composition (Kramer et al. 1997, Nagelkerken et al. 2000c). Assessing the changes in fish communities between different habitat types will provide environmental managers key information to predict the effects of habitat alteration on local fish communities, and to indicate which habitats are the most important from a conservation perspective. Habitats with high numbers of species, high proportions of rare, endemic fish or habitat specialists would be of particular interest when deciding upon conservation priority areas.

However, in these bays there are also a number of potential anthropogenic sources of eutrophication. Because nutrient supply (primarily in the form of nitrates and phosphates) is a major factor limiting primary producers in marine environments, nutrient enrichment in marine areas can dramatically alter the biological properties of marine ecosystems (Valiela 1995). Eutrophication is a form of disturbance in shallow marine environments that will change habitat characteristics, alter food webs and lead to a general decline in aquatic biodiversity, these effects are well known and many comprehensive reviews on the subject are available (Anon 1969, Wetzel 1975, Valiela 1995). Tropical marine waters that are not near river mouths are naturally nutrient-poor (oligotrophic). Nutrients in this system are a strongly limiting factor and producers sequester them as soon as they are released during the decay of plant or animal matter and therefore occur in almost undetectable concentrations (Valiela 1995). An assessment of the extent and degree of eutrophication gradients in the bays is likely to be an important factor that needs to be considered in this study. Good eutrophication indictors would be nutrient and visibility gradients. Low dissolved oxygen levels are often associated with eutrophication, but these measurements were not included as they are strongly dependent upon the time of day.

Many other factors are known to influence fish assemblage structure such as trophic interactions, recruitment and competition. Fish can also strongly influence the distribution of certain habitats such as macroalgae and seagrass (Ogden and Lobel 1978, Sale 1982, Hixon 1991, Sale 1991). However, the aim of this study is simply to provide a ‘snapshot’ of fish distribution patterns at a local scale over a wide range of habitats in order to determine the role of habitat type and water quality in structuring fish assemblages.

3.2 METHODS

3.2.1 Study area

One hundred and six stations were chosen in a semi-systematic way in Hodges Creek, Paraquita Bay and Brandywine Bay (Fig 3.1). These three bays were chosen because they encompass a wide variety of different habitats, and they are being rapidly modified by development, so the present study is a representative area that may provide useful historical data for future projects. The very large area covered and high number of samples mean that results from this study will be more widely applicable than other similar studies in the Caribbean at smaller scales (Sedberry and Carter 1993, Nagelkerken et al. 2000a, Mateo and Tobias 2001). While an even larger sample from more bays on different islands would have been desirable to increase the range of validity of this study, it was not feasible with limited time and resources.

The aim of the survey was to look at factors affecting fish distribution patterns, without any pre-conceived concepts about pristine or impacted habitats. If human activities are strongly influencing fish distribution patterns, this should be evident from the fish assemblages. Completely randomised sampling would have been ideal, but this was practically impossible because some areas were too shallow (less than 40cm deep) while others would have fallen in places such as main boat-traffic routes where it was unsafe to swim. This is a potential source of bias, but is compensated for by the large number of stations and range of habitat-types surveyed. Sites were selected by moving at least 30m in any direction from the nearest other sampling point and dropping a weighted float overboard, and marking the station using a Garmine Etrex GPS, then diving or snorkelling, depending on the depth, to sample the fish and environmental variables.

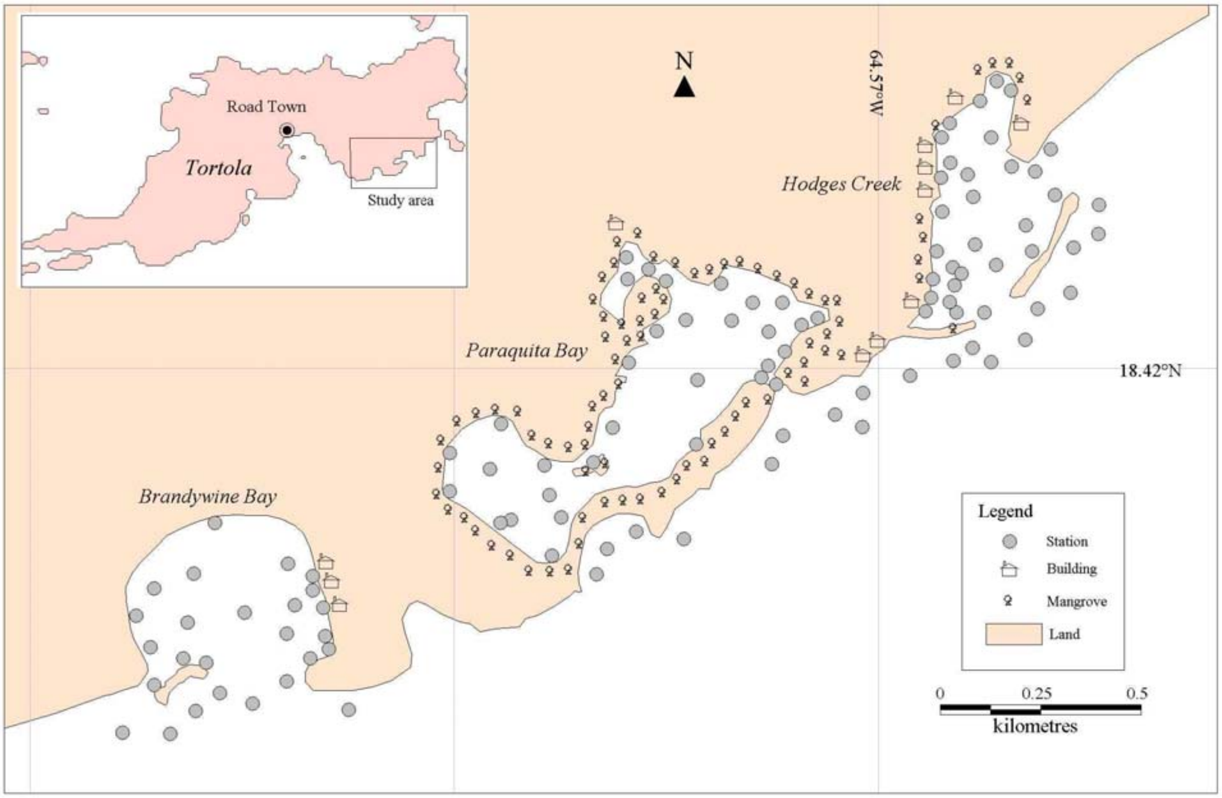


Fig 3.1 Study area, shoreline features and sampling stations in the three bays, Tortola, BVI.

3.2.2 Sampling fish

At each station four 2.5m x 2.5m quadrats were arranged about the submerged station marker and fish were allowed a minute to become accustomed to the presence of the quadrat and the observer. The next four minutes were spent observing the quadrat from a distance of 1m, identifying and estimating the lengths of each fish in the quadrat or moving through it. The last minute was spent actively searching for fish hiding in structure or camouflaged ones that were not detected previously. Stations were visited in randomised order to control for possible time-of-day effects; they were visited twice in total, the second sampling occasion being 2-4 weeks after the first. Samples were taken during the summer months of July, August and September 2001.

3.2.3 Sampling habitats

Habitat types were classified into the following categories: seagrass, calcareous macroalgae, fleshy macroalgae, sand or mud, mangrove roots, rocks, live hard coral, gorgonians, zooanthid mats, sponges and ‘other’. The level of discrimination between habitat classes has important repercussions in niche breadth studies depending on how selective the study animals are (Petraitis 1979). Certain habitat specialist species will select habitats at a more refined scale than this classification scheme. For example, juvenile *Microspathodon chrysurus* are known to favour firecorals (Tolimieri 1998), however, it was felt this was an appropriate level of discrimination considering that the objective of the study is to assess general fish assemblage properties over a wide range of habitats. On each occasion, the mean percentage cover was estimated in each quadrat and then all the data were used to calculate the mean percentage cover for the station.

3.2.4 Sampling physicochemical variables

Visibility - Visibility is a measure of light penetration. It was measured using a secchi disk attached to a measuring tape; one person held the black and white disk about 30cm below the water surface, while the other snorkelled away from the disk with one end of a measuring tape, looking back frequently. Visibility was the distance in meters at which the secchi disk disappeared.

Phosphates and nitrates were measured twice at each station using a Hach DR 850 Photospectrometer. Phosphate was detected using PhosVer 3 (USEPA) 0 – 2.5 mg/L range reagent and Nitrate was detected using a cadmium reduction, MR 0 – 5 mg/L range reagent. The Hach DR850 handbook procedure was followed.

Depth was recorded using a measuring tape. Variation in depth caused by tidal range is very small, with maximum changes in depth of 45cm on spring tides, so no measures were taken to correct depth readings to mean tide level.

3.2.5 Analysis

Data transformation to reduce the effects of extreme values - rare species that occurred in fewer than 10% of the sampling stations were removed from the analysis, this is a common practice with large data sets; otherwise rare species may unduly influence the grouping of stations (Jongman et al. 1987, Leps and Smilauer 2003). Data were square root transformed, this type of transformation reduces the effects of extremely abundant species that might unduly influence the result and this method can deal with zero values without biasing the data (Henderson 2003).

Cluster analysis – TWINSPAN (Hill, 1979) was used on presence/absence data for species at all stations using CAP software (Henderson and Seaby 2002a). This technique is usually carried out on the entire community, but rare species occurring at fewer than 8 stations were omitted so that the same species list could be used in a further ordination. TWINSPAN clusters were then plotted to illustrate the spatial distribution of similar fish communities on a map. Habitats were categorised simply by the variable covering the greatest percentage of the substrate at each station. The cluster analysis was then used to create a differentiated community table that summarises the properties of each node (Whittaker 1975). The Shannon-Wiener diversity index H' was chosen to give an estimate of species diversity for each node:

$$H' = - \Sigma\, pi \ln pi$$

where $pi = ni/\mathrm{N}$, where ni is the number of individuals of species i, and N is the total number of individuals in the sample (Mc Arthur 1955).

In order to illustrate the main differences between the TWINSPAN groups, a one way ANOVA was undertaken using SPSS v 12.0 to compare the mean number of species, abundance and Shannon-Weiner diversity. Each data set was tested for normality using a Kolmogorov-Smirnov and the Levene homogeneity of variance test using SPSS and was square root transformed if necessary.

Ordination – Canonical Correspondence Analysis (CCA) ter Braak (1986) was chosen because it ordinates the stations and species then relates them to environmental data. Fish abundance data were square root transformed and rare species occurring at fewer than 8 stations were removed, then analysed using ECOM (Henderson and Seaby 2002b). Plots are interpreted in the following way:

i) Arrows indicate environmental axes, obtained by extending the axes in both directions to either side of the plot.

ii) From each species point, drop a perpendicular to the axis and the result is a biplot that indicates in an approximate way the relative value of that species in relation to the environmental variable.

iii) The length of the arrow is a measure of the strength of correlation and hence the importance of that environmental variable in structuring the assemblages.

iv) Arrows pointing in similar directions have similar effects on the assemblage, but the longest arrow has the strongest effect.

(ter Braak 1986).

One environmental variable (rock) was strongly correlated with the other variables so the effects could not be separated out from each other. This is called multicolinearity and it makes the canonical coefficients unstable. The problem was solved by removing rock cover, thus retaining only one variable per set of strongly related environmental variables as stipulated by ter Braak (1986). A Monte Carlo randomization test (1000 permutations) was run using ECOM software to assess the probability of the observed pattern being due to chance (Crowley 1992).

3.3 RESULTS

3.3.1 Which stations have the most similar fish communities and how are they distributed?

The TWINSPAN cluster analysis of stations (Fig 3.2) split stations in to reef and non-reef areas. Indicator taxa for reef areas were adult damselfish *Stegastes* spp., blue tang, *Acanthurus coeruleus* Bloch & Schnieder, ocean surgeonfish *Acanthurus bahianus* Castelnau and bluehead wrasse *Thalassoma bifasciatum* (Bloch). Reefs were further split into reef flats (reefs that occur in bays) and fore reef areas that were deeper, well-developed reefs fringing the bays. Indicator taxa associated with fore reef zones were: stoplight parrotfish, *Sparisoma viride* (Bonnaterre), redfin parrotfish *Sparisoma rubripinne* (Valenciennes) and Bar jack *Caranx ruber* (Bloch).

Non-reef areas were classified into mangrove-associated areas with the following indicator species: yellowfin mojarra *Gerres cinereus* (Walbaum), and grey snapper *Lutjanus griseus* (Linnaeus), mangrove associated bay habitats were further split into eutrophic and non-eutrophic stations. Indicator species of non-mangrove associated clusters were: slippery dick *Halichoeres bivittatus* (Bloch), bridled goby *Coryphopterus glaucofraenum* Gill, and *Malacoctenus macropus/versicolor*.

The distribution of these assemblages (Fig 3.3) suggests spatial variation strongly influences fish assemblages. For example, the distinction between fore reef and reef flat stations is based on whether the reef habitats examined occur inside or outside the bays. Bays lined by mangroves had distinctive fish assemblages, showing that proximity to mangroves influenced non-reef fish assemblages more strongly than the actual substrate variables of non-reef habitats (Fig 3.3). Within the mangrove-associated

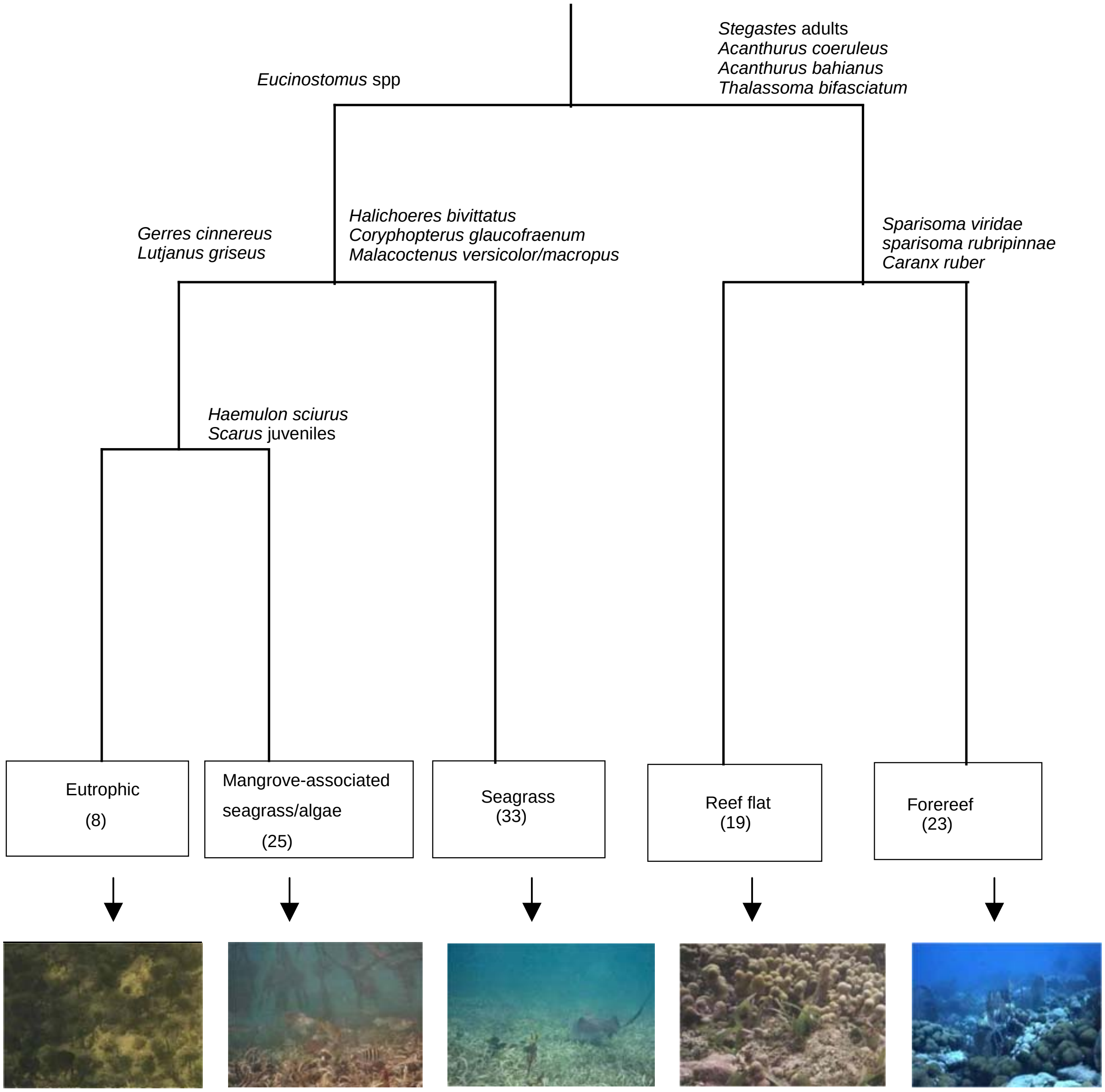


Fig 3.2 Twinspan species output showing 5 distinct fish assemblages, number of stations in each cluster shown in parentheses. TWINSPAN used presence/absence data with species occurring at fewer than 8 stations removed. Photos show habitat of one station in each cluster.

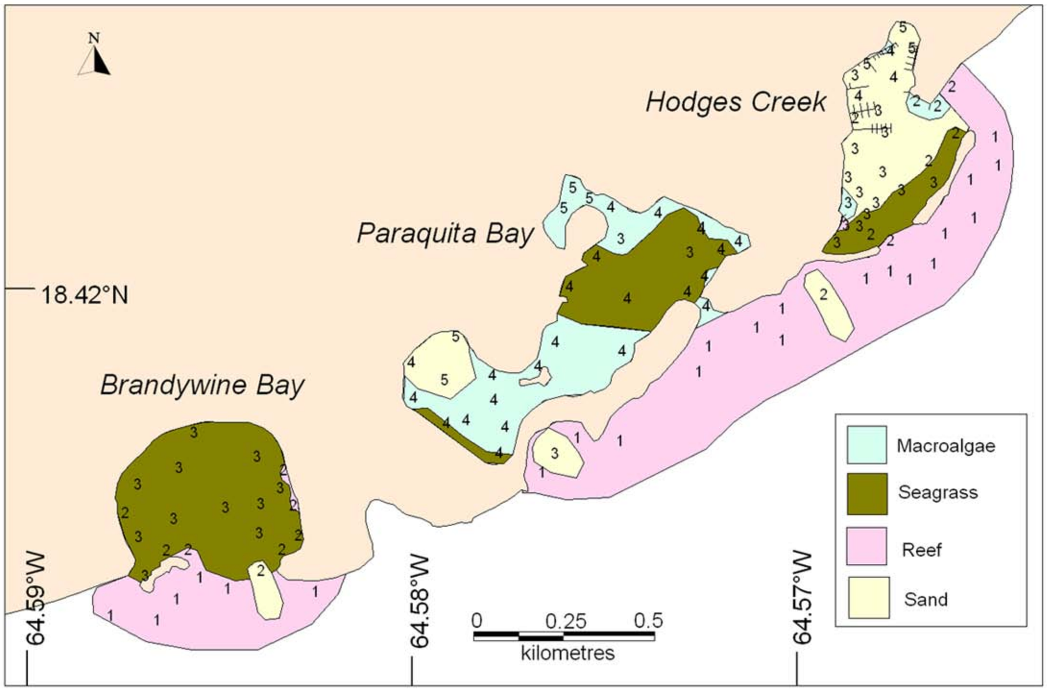


Fig 3.3 Twinspan groups plotted on map of dominant habitat types at each station. Clusters were: 1= fore reef, 2 = reef flat, 3 = seagrass 4 = mangrove-associated seagrass/algae 5 = eutrophic stations.

bays, a distinctive fish assemblage was observed in areas that were eutrophic due to pollutants from a busy marina (Hodges Creek) and an abattoir (Paraquita bay), although the eutrophication effects were spatially limited, probably because of rapid dilution of effluent.

3.3.2 What are the characteristics of the major fish assemblages?

Fish communities on the fore reef had the highest species richness with an average of 23 species per station and diversity with a mean *H'* of 2.3, fish were moderately abundant at these stations, while reef flat habitats had lower species richness and diversity with similar abundances (Fig 3.4, Table 3.1). Species diversity and richness was about half that of fore reefs for both mangrove-associated and non-mangrove associated seagrass beds, while eutrophic stations had very low mean species richness and diversity (Fig 3.4).

Fore reef assemblages – fishes occurring at more than half of the reef stations include abundant fishes: *Acanthurus bahianus, Acanthurus coeruleus, Halichoeres bivittatus, Scarus* juveniles, red band parrotfish *Sparisoma aurofrenatum* (Valenciennes) and *Thalassoma bifasciatum*; and less abundant fish: clown wrasse *Halichoeres maculipinna* (Muller & Trocschel), puddingwife *Halichoeres radiatus* (Linnaeus),

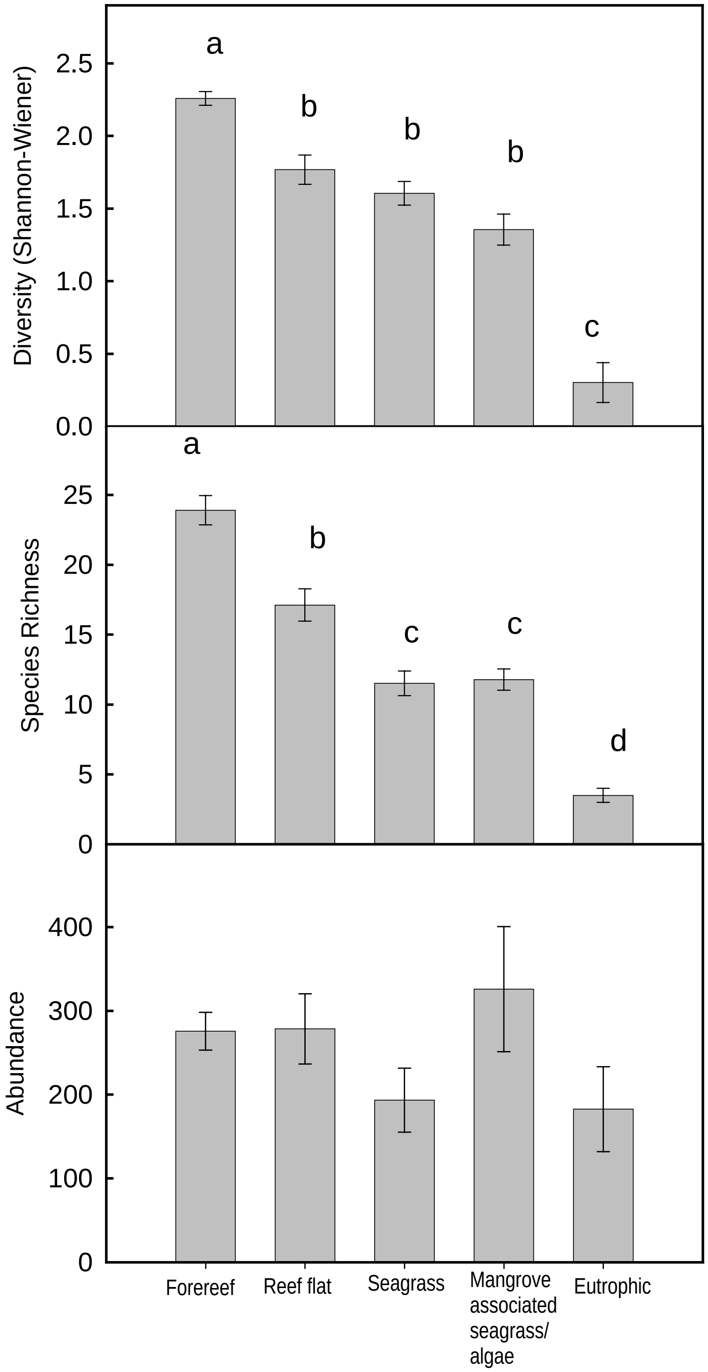


Fig 3.4 A comparison of means (one way ANOVA; df = 4, 99, 103) showing the variation in species diversity (F = 32.1, $p < 0.001$); species richness (F = 38.6, $p < 0.001$) and abundance (F= 2.3, p = 0.06) between the five TWINSPAN assemblages. Different letters above bars indicated significant differences at the 0.05 level (Tukey B test).

Table 3.1 A one-way ANOVA to compare the differences in a) Shannon-Wiener diversity, b) Observed Number of Species and c) Total fish abundance between the 5 Groups.

a) Shannon-Weiner = Group (Group is categorical)

	Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Shannon-Wiener	5.160	4	1.290	32.130	.000
Error	3.975	99	.040		
Total	9.134	103			

b) Species = Group (Group is categorical)

	Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Group	59.628	4	14.907	37.486	.000
Error	39.369	99	.398		
Total	98.998	103			

c) Abundance = Group (Group is categorical)

	Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Group	381	4	95	2.3	.060
Error	4023	99	40		
Total	4404	103			

longspine squirrelfish *Holocentrus rufus* (Walbaum), goldline blenny *Malacoctenus aurolineatus* Smith, saddled blenny *Malacoctenus triangulatus* Springer, yellowtail damselfish *Microspathodon chrysurus* Cuvier, redlip blenny *Ophioblennius atlanticus* (Valenciennes), *Scarus iseri/taeniopterus* adults, queen parrotfish *Scarus vetula* Bloch and Schneider, *Sparisoma rubripinne, Sparisoma viride* and dusky damselfish *Stegastes dorsopunicans* (Poey) (Table 3.2). These stations were on average 1m deeper than the others and visibility was 12.6m on average, which is nearly double that in bay habitats (Table 3.3). Fore reef habitat variables were quite distinctive, being dominated by rock, which formed nearly 70% of the substrate. Rocks were usually composed of dead and weathered coral, which was invariably covered in thin layers of microscopic algae, an important food source for grazing fish. Other characteristic fore reef habitat types were live hard coral, gorgonians, encrusting gorgonians, sponge and zooanthid mats.

Reef flat assemblages included both reef species: *Acanthurus coeruleus, Acanthurus bahianus, Halichoeres bivittatus, Scarus* juveniles, *Sparisoma aurofrenatum* and *Stegastes* adults; and bay species: French grunt *Haemulon flavolineatum* (Desmarest), *M. macropus/versicolor,* yellowtail snapper *Ocyurus chrysurus* (Bloch), bucktooth parrotfish *Sparisoma radians* (Valenciennes) and *S. diencaeus/leucostictus* juveniles (Table 3.2). Reef flat communities are thus an intermediate between reefs and bays and they were distributed in intermediate places (Fig 3.2). Reef flat stations differed from fore reef stations, as they were shallow, with lower visibility. The habitat was quite distinct, having less than a third of the rock cover of reefs that was mixed with about 50% seagrass and algae, they had half the live coral cover and no gorgonians (Table 3.3).

Table 3.2 Differentiated community table showing the mean abundance of characteristic species of each TWINSPAN cluster (occurring at >50% of stations in cluster). • = 1-10 ● = 11-100 ⬤ = 101-1000.

	Forereef	Reef flat	Seagrass	Mangrove-associated seagrass	Eutrophic
Gerres cinereus				•	•
Haemulon sciurus				•	
Lutjanus griseus				●	•
Sphyraena barracuda				•	
Eucinostomus spp.			●	●	⬤
Chaetodon capistratus		•			
Coryphopterus glaucofraenum			•		
Halichoeres poeyi		•	•		
Malacoctenus macropus/versicolor		•	•		
Halichoeres bivittatus	●	●	●	•	
Ocyurus chrysurus		•	●	●	
Scarus juvs	●	●	●	⬤	
Sparisoma radians		•	•	•	
Stegastes diencaeus/leucostictus juv	•	●	●	●	
Lutjanus apodus	•			•	
Haemulon flavolineatum		●			
Sparisoma aurofrenatum	●	•			
Acanthurus bahianus	●	•			
Stegastes spp	●	•			
Caranx ruber	•				
Acanthurus coeruleus	●	•			
Halichoeres maculipinna	•				
Halichoeres radiatus	•				
Holocentrus rufus	•				
Malacoctenus aurolineatum	•				
Malacoctenus triangulatus	•				
Microspathodon chrysurus	•				
Ophioblennius atlanticus	•				
Scarus iseri/taeniopterus	•				
Scarus vetula	•				
Sparisoma rubripinne	•				
Sparisoma viride	•				
Stegastes dorsopunicans	•				
Thalassoma bifasciatum	●	•			

Table 3.3 The means and standard errors of physicochemical variables measured for each TWINSPAN group.

	Forereef		Reef flat		Seagrass		Mangrove- associated seagrass		Eutrophic	
	Mean	se	mean	se	mean	se	mean	se	mean	se
NO3	>0.001	>0.001	0.011	0.005	0.009	0.003	0.006	0.003	0.021	0.009
P04	0.039	0.014	0.104	0.029	0.155	0.038	0.147	0.104	0.528	0.446
Depth (m)	2.46	0.25	1.28	0.24	1.58	0.18	1.60	0.17	1.59	0.36
Secchi (m)	12.64	0.77	6.81	0.48	6.16	0.30	6.14	0.40	3.30	0.97
Calcareous Macroalgae	4	0.90	11	2.97	6	0.96	12	2.98	0	0
Seagrass	0	0	30	5.74	43	5.74	20	4.93	0	0
Mangrove roots	0	0	0	0	0	0	4	1.29	0	0
Fleshy algae	4	1.13	7	2.10	10	2.91	32	3.47	30	12.80
Sand/mud	7	1.47	26	5.82	37	5.08	30	4.58	69	12.73
Rock	69	3.60	20	4.97	1	0.35	0	0	0	0
Zooanthid mat	2	0.84	1	0.99	0	0	0	0	0	0
Live hard coral	8	1.64	4	2.41	0	0	0	0	0	0
Gorgonian	3	0.67	0	0	0	0	0	0	0	0
Encrusting gorgonian	1	0.21	0	0	0	0	0	0	0	0
Rubble	3	1.41	2	0.95	2	1.25	0	0	0	0
Sponge	1	0.19	0	0	0	0	0	0	0	0

Non-mangrove associated seagrass and algal assemblages included: *Coryphopterus glaucofraenum*, blackear wrasse *Halichoeres poeyi* (Steindachner) and *Malacoctenus macropus/versicolor,* which occurred in over 50% of these stations, while *Halichoeres bivittatus, Ocyurus chrysurus*, *Scarus* juveniles, *Sparisoma radians* and *Stegastes diencaeus/leucostictus* juveniles occurred at over 50% of some reef stations as well (Table 3.2). They were shallow with moderate visibility and differed from reef flats, as there was almost no rock cover, but 60% of the substrate was composed of seagrass and algae. Physicochemical properties of mangrove-associated seagrass beds were similar to the other seagrass beds, the main difference being the absence of mangroves (Fig 3.3).

Mangrove associated seagrass and algal assemblages include: *Gerres cinereus*, bluestriped grunt *Haemulon sciurus* (Shaw), *Lutjanus griseus,* great barracuda *Sphyraena barracuda* (Walbaum) and mojarras *Eucinostomus* spp., occurring at more than 50% of only these stations. *Halichoeres bivittatus, Ocyurus chrysurus, Sparisoma radians* and *Stegastes leucostictus/leucostictus* were also common in non-mangrove associated bays, and are unlikely to be dependant upon mangroves (Table 3.2). *Scarus* juveniles were also common in both bay communities, but they were more abundant in mangrove-associated seagrass beds with an average count of 200 fish per station, but only 69 fish were present per non-mangrove-associated bay stations, suggesting that mangroves may be partially important to this taxon. The schoolmaster *Lutjanus apodus* (Walbaum) was common, occurring at more than 50% of both in reef and mangrove stations showing that both mangroves and fore reefs are important in their lifecycle. This distinct fish assemblage is found adjacent to mangrove stands that only make up 4% of habitat sampled (Table 3.3), so proximity to mangroves is likely to be one of the key variables determining the species composition of the assemblage (Fig 3.3).

Eutrophic assemblages - the only species that were common at polluted stations were *Gerres cinereus, Lutjanus griseus* and *Eucinostomus* spp (Table 3). *Eucinostomus* spp were abundant at polluted stations, with a mean of over 175 fish per station, they were also common in other bay habitats but they were not as abundant there. The eutrophic stations had high nitrate and phosphate levels and very low visibility, about half that in the rest of the bay. There was no seagrass, and about 30% of the sand/mud substrate was covered in macroalgae (Table 3.3).

3.3.3 Which variables strongly influence fish assemblages?

The main assemblages were all associated with particular distinctive habitat types. The TWINSPAN analyses and differentiated community table suggest that rock, live hard corals, gorgonians, presence of adjacent mangroves, seagrass, sand, visibility and nitrate and phosphate levels are all variables that influence assemblage composition. CCA analysis reveals a similar pattern, although rock cover was omitted because of multicolinearity problems (Fig 3.5 & 3.6). Of the remaining variables, visibility, sand, seagrass, live hard coral, gorgonians and fleshy macroalgae were the most important in explaining variation between stations (Fig 3.5 & 3.6). Visibility was highest at reef stations and lowest at eutrophic stations. Visibility is correlated to other habitat variables that are the more likely to be the causative factors explaining the observed differences in fish communities.

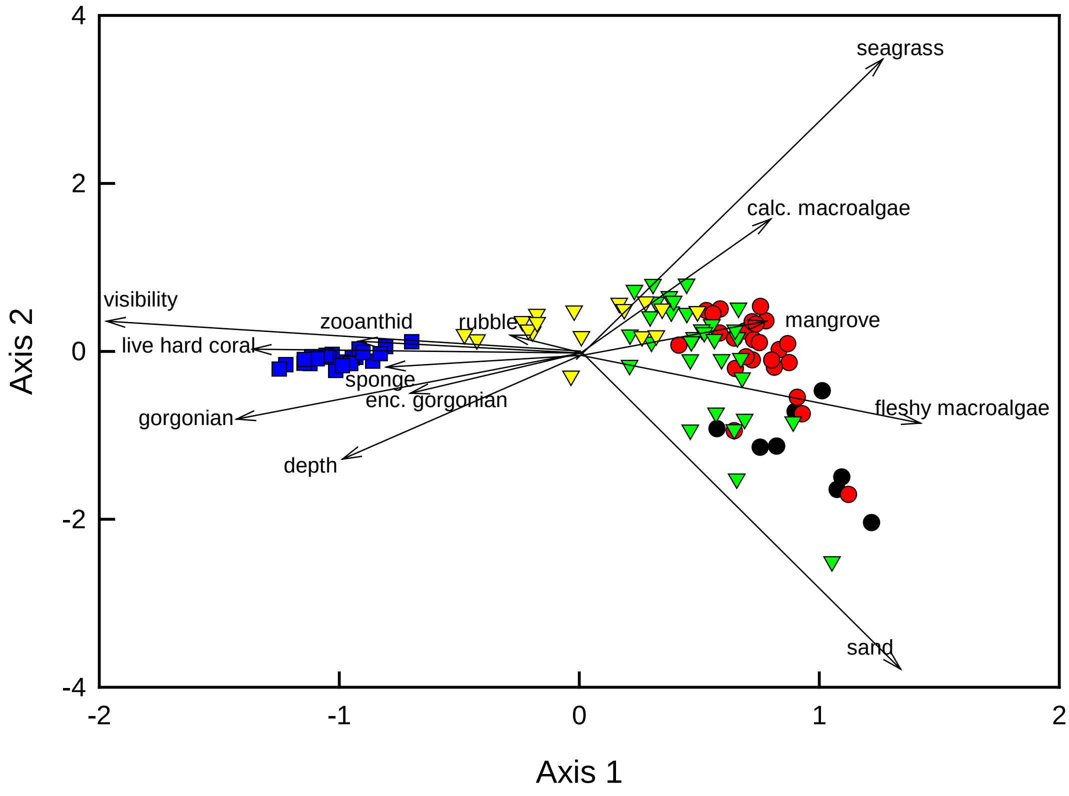


Fig 3.5 CCA plot of stations and environmental variables. TWIN SPAN clusters: ● Eutrophic; 🔴 Mangrove associated seagrass/algae; ▼ Seagrass; ▼ Reef flat; 🟦 Forereef. Eigenvalues: axis1, 0.53; axis 2, 0.15. *r* species-environment: axis1, 0.97; axis 2, 0.77. First 2 axes account for 26% of the variance. Monte Carlo test significant (p<0.001), 1000 permutations.

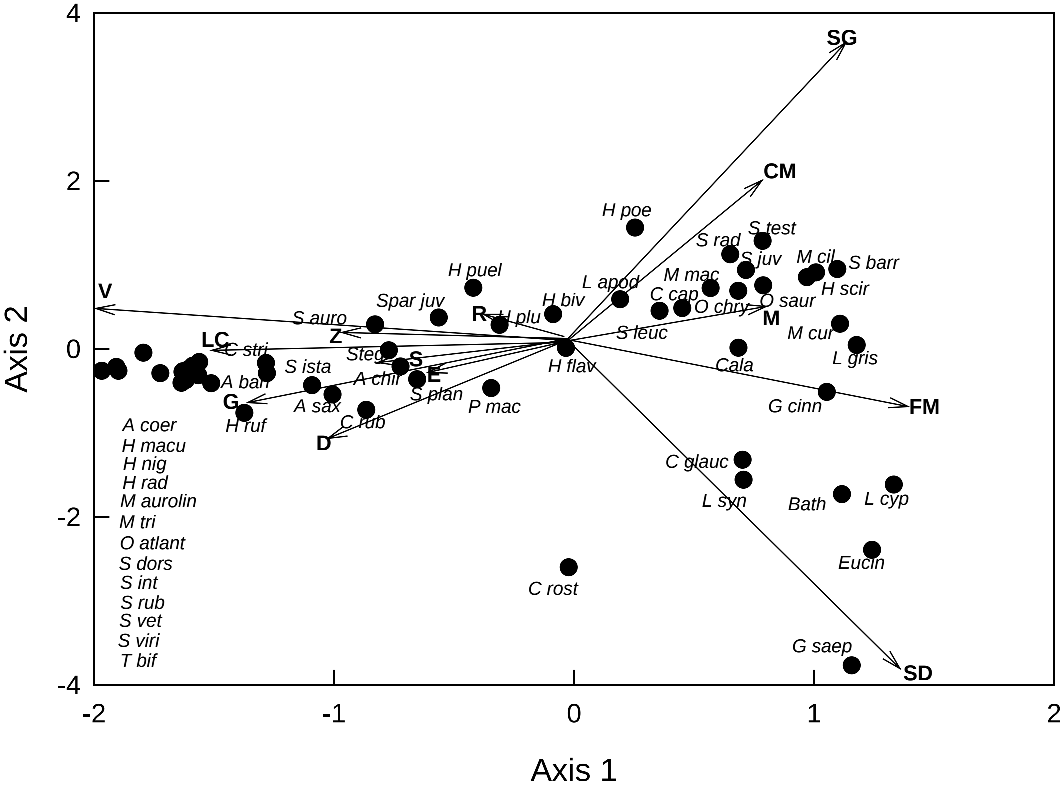


Fig 3.6 CCA plot of species and environmental variables. Environmental variables **SG** = seagrass, **CM** = calcareous macroalgae, **M** = mangrove, **FM** = fleshy macroalgae, **SD** = sand, **D** = depth, **E** = encrusting gorgonian, **G** = gorgonian, **S** = sponge, **LC** = live hard coral, **Z** = zooanthid, **V** = visibility, **R** = rubble. The initial letters of the following species are shown: *A. saxatilis, A. bahianus, A. chirugrus, A. coeruleus, Bathygobius* sp. *Calamus* sp. *C. rostrata, C. capistratus, C. striatus, C. glaucofraenum, Eucinostomus spp., G. cinereus, G. saepepallens, H. aurolineatum, H. flavolineatum, H. plumieri, H. sciurus, H. bivittatus, H. poeyi, H. maculipinna, H. radiatus, H. rufus, H. plumieri, H. puella, H. nigricans, L. cyprinoides, L. griseus, L. apodus, M. aurolineatus, M. ciliatus, M. curema, M. macropus/versicolor, M. triangulatus, M. chrysurus, O. atlanticus, O. chrysurus, O. saurus, P. maculatus, S. dorsopunicans, S. intermedius, Scarus juveniles, S. iserti/taeniopterus* (ads), *S. aurofrenatum, S. barracuda, S. radians, Scarus* juveniles, *S. planifrons, S. leucostictus/diencaeus* (juvs), *Stegastes adults, S. vetula, S. viride, S. rubripinne, S. testudineus, T. bifasciatum.* Eigenvalues: axis1, 0.53; axis 2, 0.15. *r* species-environment: axis1, 0.97; axis 2, 0.77. First 2 axes account for 26% of the variance. Monte Carlo test significant ($p<0.001$), 1000 permutations.

The strong apparent influence of visibility illustrates the importance of careful interpretation of CCA plots. The vectors (environmental variables) only imply association with certain stations or species and are not necessarily causative. The direct effect of mangroves in the CCA analysis was weak, even though TWINSPAN revealed that mangrove association was a very important factor. This would be expected, because only mangrove cover was measured, rather than the degree of mangrove-association of seagrass and algal beds. Nevertheless, the association is quite evident from Fig 3.3.

When the differentiated community table and the CCA plots were interpreted together, certain species emerged as likely habitat specialists: sand specialists were the dash goby *Gobionellus saepepallens* Gilbert and Randall, lane snapper *Lutjanus synagris* (Linnaeus) and *Coryphopterus glaucofraenum*; mangrove specialists included *Haemulon sciurus, Sphyraena barracuda, Lutjanus griseus* and *Gerres cinereus*. Seagrass and algal bed specialists were *Halichoeres poeyi, Sparisoma radians,* checkered puffer *Sphoeroides testudineus* (Linnaeus) and *Malacoctenus macropus/versicolor*. Fore reef specialists were *Acanthurus coeruleus, Halichoeres maculipinna,* black hamlet *Hypoplectrus nigricans* (Poey)*, Halichoeres radiatus, Malacoctenus aurolineatus, Malacoctenus triangulatus, Ophioblennius atlanticus, Stegastes dorsopunicans*, sand diver *Synodus intermedius* (Spix)*, Sparisoma rubripinne, Scarus vetula, Sparisoma viride* and *Thalassoma bifasciatum.*

The other species included in the analysis had more general requirements and they were common in a range of different TWINSPAN habitat clusters so they generally clustered towards the middle of the CCA plot (Fig 3.6).

3.4 DISCUSSION

3.4.1 Likely determinants of fish composition

The main factor grouping fish assemblages was whether they were in reef or non-reef habitats, and the two least-similar fish assemblages were fore reef and mangrove-associated seagrass stations. The dominant habitat variable distinguishing these stations was percent rock cover, which formed about 70% of the reef substrate, and none of the mangrove substrate (Table 3.3). Percentage rock cover is likely to directly influence fish communities because many fish species graze on the epilithic algae that grow on rock in all shallow, tropical marine environments (Carpenter 1986, Hixon and Brostoff 1996, Ferreira et al. 1998, Lawson et al. 1999). These algae are important nitrogen fixers in this oligotrophic environment and are the primary source of production on reefs (Klumpp and McKinnon 1989, Larkum 1999). In addition, rock acts as a stable substrate with a large surface area on which microscopic algae, macroalgae, live hard corals, gorgonians, encrusting gorgonians, sponges and other animals can grow. They cannot grow on sand, which is unstable and moves in turbulent environments with a grinding action that is not suitable for the settling and growth of algae (Hillebrand and Kahlert 2002), corals (Rogers 1990) or some types of invertebrate e.g. spiny lobsters (Booth 2001).

Because of the low levels of primary production associated with sand (Hillebrand and Kahlert 2002) and the lack of cover for non-burrowing fish and invertebrates, sand would support a low density of specialists. Sand specialists are camouflaged in an environment lacking cover and are adapted to foraging on the invertebrates living in the sand. Rocky areas, however, provide enough food and refuge to support many different species in high densities (Carpenter 1986). This phenomenon is widely recognised by aquatic biologists and has led managers to use artificial reefs to enhance fisheries production (Chou 1988, Bohnsack 1989, Sinis et al. 2000). Thus rock cover is likely to be one of the most important habitat variables structuring the fish assemblage in these bays.

Visibility was a physical variable that varied on a similar gradient to rock cover, and is a measure of the amount of light that can penetrate the water column. Not surprisingly, the reefs swept by nutrient-poor and phytoplankton-poor oceanic waters were the clearest, while shallow bays had low to moderate visibility with variable nitrate and phosphate levels. This may indicate why coral grows best in well-lit, low-sediment zones outside bays, but the direct effect of visibility on fish is probably slight. Evidence to support this hypothesis can be found in Fig 3.3 as seaward stations where sand was the dominant habitat type had similar fish to bays, even though the physicochemical properties of the water were similar to those of the neighbouring reef stations. Several other authors agree that fish distribution patterns are a direct function of substrate characteristics and are indirectly related to physicochemical variables (Risk 1972, Luckhurst and Luckhurst 1978, Gladfelter et al. 1980, Bell and Galzin 1984, Roberts and Ormond 1987, Nagelkerken et al. 2002).

Seagrass and macroalgal beds grow on sand and stabilise the substrate, increasing primary productivity directly and indirectly by supporting epiphytic algae and by providing cover for some fish species (Hemminga and Duarte 2000). Seagrass and macroalgal beds that were adjacent to mangrove areas had some characteristic fish species, highlighting the importance of mangroves in maintaining fish biodiversity (Fig 3.6).

Explanations for this interaction could be either: (1) The presence of the adjacent mangroves directly alters some environmental property of the adjacent seagrass/algal beds making them favourable to those fish species or (2) because mangroves are critical habitats at certain (usually juvenile) life-stages of some tropical Atlantic fish species which then move into adjacent seagrass beds (Yanez et al. 1993, Nagelkerken et al. 2001, Nagelkerken et al. 2002). Mangroves might be important to fishes, and in particular juvenile fish as they provide dense cover from predators. The mangrove roots also provide a stable surface that is covered in a distinctive epibiotic layer that may be an important food source for some fish species (Farnsworth and Ellison 1996).

Common symptoms of coastal eutrophication are: increased nitrate and phosphate loads, phytoplankton blooms, reduced light penetration, increased macro algal production in shallow areas, reduced dissolved oxygen levels, loss of seagrass habitats and changes in the fish assemblage (Granelli et al. 1990, Valiela 1995, Hemminga and Duarte 2000). The eutrophic areas in the study area had increased nitrates and phosphates, reduced visibility, reduced seagrass cover and increased macroalgae cover (Table 2). The fish assemblage at these stations exhibited reduced species diversity and richness but one taxon, *Eucinostomus* spp, increased in abundance at these stations and may be a good indicator taxon for eutrophication. However, it is impossible to tell without more replication and experimental controls, whether the observed deterioration in water quality is having a direct impact on the fish assemblage, or if is the observed change is a result of the characteristic sand/mud and algae habitats at these stations.

3.4.2 Habitat indicator species

While many species such as *Halichoeres bivittatus* had general habitat requirements, the following species were consistently associated with key habitat variables and they may be potential habitat indicator species:

Sand – *Gobionellus saepepallens, Lutjanus synagris* and *Coryphopterus glaucofraenum* are all pale-bodied species that are inconspicuous on a white sand background - an important adaptation to avoid predation in this open habitat type. Other authors have noted similar habitat preferences for these species (Humann 1994, Lieske and Myers 2001, Froese and Pauly 2003).

Mangroves – *Haemulon sciurus, Sphyraena barracuda, Lutjanus griseus* and *Gerres cinereus* were all associated with mangroves. While all of these species are known to occur on reefs as adults (Humann 1994), only *Lutjanus apodus* was abundant on both reefs and mangroves in this study. These results corroborate findings of Nagelkerken et al, (2002 a & b) working in Curacao, who note that *Lutjanus apodus, Haemulon sciurus, Scarus taeniopterus* and *Ocyurus chrysurus* are highly dependant upon mangroves and seagrass beds as nurseries for juvenile fish. They also suggest that *Lutjanus griseus, Sphyraena barracuda* and *Gerres cinereus* may be dependent on mangrove and seagrass nurseries. In this study, *Scarus* juveniles and *Ocyurus chrysurus* were found in bays without any mangroves, so they are unlikely to be highly dependant upon mangroves as Nagelkerken et al suggest. However, since *Scarus* juveniles were about 3 times as abundant in mangrove-associated compared to non-mangrove associated bays, they are probably partially mangrove dependent. Mangrove roots are probably key habitats because they provide shelter from predators (Farnsworth and Ellison 1996) 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). Small fish often aggregate around mangrove roots during the day in order to avoid predation (Nagelkerken et al. 2000b) and barracudas jacks and snappers patrol the mangrove margins to prey on these smaller fish (B. Gratwicke unpublished observations).

Seagrass and algal bed – *Halichoeres poeyi, Sparisoma radians, Sphaeroides testudineus* and *Malacoctenus macropus/versicolor* were usually only associated with seagrass and algal beds, supporting the observed habitat preferences noted by other authors (Humann 1994, Lieske and Myers 2001, Froese and Pauly 2003). These species are all small (less than 15cm) and camouflaged in seagrass, making them suited to a habitat that offers limited refuge from predators. Seagrass and algal beds have high productivity resulting from both growth of seagrass and the epiphytic algae growing on its leaves, this in turn supports crustaceans, gastropods and other invertebrates which are all potential sources of food for fish (Hemminga and Duarte 2000).

Fore reef – *Acanthurus coeruleus, Halichoeres maculipinna, Hypoplectrus nigricans, Halichoeres radians, Malacoctenus aurolineatus, Malacoctenus triangulatus, Ophioblennius atlanticus, Stegastes dorsopunicans, Synodus intermedius, Sparisoma rubripinne, Scarus vetula, Sparisoma viride* and *Thalassoma bifasciatum* were characteristic of fore reef stations, similar habitat preferences of these species are noted by other authors (Humann 1994, Lieske and Myers 2001, Froese and Pauly 2003). The rock-associated fish assemblages were species-rich and brightly colored compared to sand-associated fish, and similar patterns have been observed in the African Rift Valley Lakes (Danley and Kocher 2001). The structure of the reef provides cover from predators

(Hixon and Beets 1993, Caley and St John 1996), as well as food in the form of algae and invertebrates (Carpenter 1986). The abundance of fish at reef stations was also high. Because secure refuge places are readily available in these rocky habitats (unlike seagrass and sand habitats), non-piscivorous species such *Acanthurus coeruleus*, *Halichoeres maculipinna*, *Stegastes dorsopunicans*, *Sparisoma viride and Thalassoma bifasciatum* can probably afford to be brightly coloured in order to recognise conspecific mates/competitors in this high diversity environment with an abundance of refuge sites. The only piscivore in this group, *Synodus intermedius*, is cryptically coloured and waits on sand and rubble patches near reefs to ambush fish (DeLoach 1999).

The broad patterns of fish associations with each other and their environment have been discussed and appear to be broadly similar to results elsewhere in the Caribbean (Ogden and Gladfelter 1983b, Robertson et al. 1988, Hixon and Beets 1989, Mateo and Tobias 2001, Nagelkerken et al. 2001, Williams and Polunin 2001). Some species were common in several habitats and are apparently generalists. This could be either because they are true generalists or because different ontogenetic stages use different habitats. For example, *Ocyurus chrysurus* juveniles grow in seagrass nurseries and then move onto reefs as they mature (Froese and Pauly 2003). Rare species have not been considered in detail either, but these will both be examined in more detail in Chapter 4 dealing with autecology.

Adult stoplight parrotfish - *Sparisoma viride*

4

Fish Distribution Patterns and Ontogenetic Habitat Preferences

> *‘If the investigator was equipped with the sensory apparatus of* Gammarus *or* Plethodon *he would know that the supposedly suitable unoccupied sites were really quite unsuitable for any self respecting member of the genus in question.’*
>
> **G. E. HUTCHINSON**

4.1 INTRODUCTION

There are many excellent autecological studies of different Caribbean fishes and their habitat preferences, but they tend to feature species of commercial interest or attractive fishes such as butterfly fish. Our understanding of the processes structuring these coral reef assemblages are therefore somewhat biased. These biases might be reflected in conservation decision making, particularly if research activity focuses on a preferred, pre-selected habitat type. For example: seagrass beds were once thought to be very important nursery habitats for fish, but their exclusivity has faded over the years as a growing number of studies showing that many species can also use alternative habitats (Hemminga and Duarte 2000).

The aim of this chapter is to assess the γ diversity of fish, to provide a comprehensive species inventory, to provide distribution maps of the commoner species and to assess the degree of ontogenetic habitat partitioning by those species widely distributed in lagoons and on reefs.

The following questions will be addressed:

1) What is the total fish species richness within the study area, and has the survey effort been adequate?
2) What are the distribution patterns of each fish species and how do these relate to previous studies?
3) Which species exhibit a distinct ontogenetic partitioning of habitats, and if so, how do the habitat preferences of juveniles and adults differ?

4.1.1 Factors causing variations in fish distribution

Various factors may influence the distribution and abundance of animals from place to place and from time to time. Some species are strongly limited by the availability of resources such as food. For example, it is well known that damselfish on reefs strongly compete with each other for territory (a spatial resource) where they tend to algal gardens (a food resource) that they guard fiercely from conspecifics and other grazers (Robertson 1996, Gutierrez 1998, Bell and Kramer 2000, Bay et al. 2001). The availability of suitable substrate for an algal garden therefore controls the density of some damselfish species, and the other species in the vicinity. This is also broadly known as a bottom-up system because competition for limited food resources may affect other species at higher trophic levels in the food chain (Menge 1992).

Others imply that the distribution of predators and predator-free space are the most important factors affecting variation in the abundance of fish (these are top-down systems) (Hixon and Beets 1989, Hixon 1991, Carr and Hixon 1995), while variation in parasite loads and cleaning stations have been emphasised by others (Whiteman et al. 2002). All these mechanisms may affect fish assemblages simultaneously as different fish species respond differently to different resources.

4.1.2 Niche partitioning and spatial distribution

The first use of the term niche was in reference to the distribution of birds, stressing the spatial concept of the niche (Grinnell 1917). Elton (1927) defined a niche as the functional role and position of an organism in a community, emphasising its trophic relationships with other species, although later definitions have emphasized the effects of competition for resources (Pianka 1981). The term ‘niche breadth’ refers to the total range of resources used by an organism, meaning any environmental variable could be a resource axis, and the entire set of resources that could potentially be used is known as the ‘fundamental’ niche (Hutchinson 1957). If two niches overlap and the shared resource is in short supply there will be competition between the two overlapping species, but often factors such as high predation levels will reduce animal abundance to densities where competition does not occur (Pianka and Schall 1981). High predation levels on reefs are thought to be a major force affecting reef fish community structure and habitat selection (Hixon and Beets 1993, Carr and Hixon 1995). This may explain how fish that are mostly generalist feeders, with relatively unspecialised diets (Randall 1967) can coexist on a reef without competitive exclusion.

4.1.3 Habitat selection and species distribution

Species choose the places and habitats where they live depending upon the availability of a variety of different mechanism-linked resources such as predator-free space, food, nesting sites, etc (Kramer et al. 1997). Habitat selection is therefore a key process influencing the final distribution patterns of fish. If fish can select the habitats they live in and are able to access any habitat and freely share the available resources, then they will theoretically occupy the places of highest fitness benefit. Thus relative abundance should be positively correlated with intrinsic habitat quality (Kramer et al. 1997). The best quality habitat would be places with minimal predation risk and parasite loads and maximum food availability as well as favorable physicochemical conditions and a suitable adjacent habitat (Kramer et al. 1997, Morin 1999). A simple distribution map will not reveal the exact nature of species interactions, but it can reveal the extent to which an animal is selecting various habitats and their dependence on suitable adjacent habitat types, which is key information for resource managers. If a species distribution is strongly dependant on habitat, the relative abundance of species should be strongly correlated with the essential habitat variables. Species whose distributions are independent of habitat type i.e. they are generalists will be poorly correlated with habitat variables.

A basic quantitative assessment of optimal habitat requirements for many Caribbean reef fish species is unavailable, and we are largely dependant upon qualitative assessments by experts (Stokes 1980, Humann 1994, Randall 1996, Lieske and Myers 2001, Froese and Pauly 2003). This study will provide some objective information in a systematic way that might allow us to predict how fish communities might respond to changes in habitat.

4.1.4 Ontogenetic shifts in habitat use

The pattern of an animal's resource use that changes as it grows is known as the ontogenetic niche (Werner and Gilliam 1984). The change can be gradual as is seen in many fish species, or discrete such as when tadpoles metamorphose into frogs. An animal's feeding habits and its risk of predation is related to body size, therefore many species have extensive ontogenetic shifts in food and habitat use. Examples of ontogenetic niche change in fish are found in a great variety of species in both freshwater and marine environments (Stoner and Livingston 1984, Olson 1996, Appeldoorn et al. 1997, Ruzycki and Wurtsbaugh 1999). Knowing which habitats are important nursery areas for each fish species and a quantitative assessment of their dependence on those habitats will be an important resource for the management of commercial fish stocks and biological diversity in similar areas.

4.1.5 Seasonal changes and disturbance

Seasonal variation has a strong influence on fish abundance and distribution in many parts of the world (Kramer et al. 1997), but coral reefs only occur in warm, tropical climates with minor seasonal changes. Seasonal variation in fish species richness and abundance in the Caribbean is minor compared to other ecosystems (Sedberry and Carter 1993, Díaz-Ruiz et al. 1998). Temporal variation in reef habitats is usually caused by stochastic disturbance events such as hurricanes or coral bleaching (Bouchon et al. 1994, Brown 1997, Goreau 2000, McClanahan et al. 2001, Booth and Bereta 2002). Humans may also disturb habitats in a number of ways that might alter fish abundance and species richness (reviewed in Chapter 1).

Because there are a very large number of species in the study area, the results and discussion sections have been merged to make this chapter easier to read. In this way the results can be analysed and discussed briefly with immediate reference to distribution maps and length-frequency diagrams, preventing unnecessary repetition and cross referencing of figures. This will be followed by a summary of the key findings, and then a section on applications of these findings to marine managers.

4.2 METHODS

4.2.1 Sampling

Detailed sampling methods are given in Chapter 3 sections **3.2.1 – 3.2.2**. In addition to these methods, a comprehensive species checklist for the area was compiled by noting any unusual or rare fishes encountered while moving between stations or whilst swimming recreationally in the study area. While relative abundances were recorded during the survey, all species were subjectively categorised in the following way:

Rare fish were those that were encountered once or twice and never seen again in the study area. *Occasional* was used to describe fish that were either resident and could be seen in the same place from day to day, but occurred in very low numbers or fish that were encountered several times in the study area, but were not seen regularly. *Common* categorises fish perceived as characteristic of the area and which are frequently encountered in their respective habitats.

4.2.2 Analysis

Assessing γ diversity

It would be useful to assess the total species richness of the study area as a measure of the completeness of the species inventory. One method to estimate total species richness S_{max} uses a species accumulation curve (Simberloff 1972). The species accumulation curve can be irregular if samples are entered in a non-random order, so after randomising the order of the samples, a cumulative curve number of new species encountered in relation to the sampling effort is plotted. If a clear asymptote is reached, or can be extrapolated then it can be assumed that sampling effort was adequate.

An alternative simple but reliable non-parametric method that has been shown to be effective on fish communities is the Chao 2 index (Chao 1984) which can be calculated from the following formula:

$S_{max} = S_{obs} + (a^2/2b)$

Where a and b are the number of species represented by 1 and 2 individuals respectively and S_{obs} is the actual number of species observed (Chao 1984).

The estimate of total species richness in the study area was assessed using both methods, and this was compared to the total species list (from both sampling and recreational swimming) kept for the area in order to assess inventory completeness.

4.2.3 Fish-habitat correlations and distribution patterns

Fish habitat selectivity was assessed using a multiple linear regression for all of the 46 taxa occurring at more than 10 stations, and SPSS v 11.5 © software was used for the analysis. Multiple regression is an extension of linear regression because a response variable such as abundance can be a function of many environmental factors (Jongman et al. 1987). Multiple regression is, therefore, a useful form of direct gradient analysis that can assess which environmental factors explain significant amounts of the variation in abundance of a species (Jongman et al. 1987). This method has all the assumptions of a linear regression model that are well known in ecological literature and are reviewed extensively in Kent and Coker (1992):

a) Normally distributed data.

b) The data fit a linear model.

c) No spatial or temporal autocorrelation of data.

d) Lack of measurement error.

e) The standard error of residuals is evenly scattered about the mean.

f) In a multiple regression the predictor variables should not be collinear.

(Kent and Coker 1992)

Abundance values of a species commonly have skewed distributions, with many small values and a few extremely large ones resulting in a poisson distribution (Jongman et al. 1987). This skewed distributions violates the assumptions of the analysis (that data are normally distributed) and often have heterogeneous variance, which violates another assumption of the test (homogeneity of variances). One way to solve these problems is to transform the data using square root, log or inverse transformations, this often normalizes the data distribution and reduces the heterogeneity of variance (Grafen and Hails 2002). In this study, fish abundance data were examined for normality and square root transformed if necessary. Next, the data were analysed and the underlying distribution of regression residuals were examined in all the linear regressions to determine the legitimacy of the test and whether the transformation was appropriate (Jongman et al. 1987, Grafen and Hails 2002). Multicolinear environmental variables were removed and the remaining habitat variables were used as predictors in a multiple regression analysis of fish abundance. Only species occurring at 10 or more stations were used because smaller sample sizes are inadequate for this procedure (Jongman et al. 1987). In addition to the multiple regression results, the squared semi-partial (or part correlation) is presented. This is the proportion of (unique) variance accounted for by the habitat type, relative to the total variance in fish abundance (Anon 2003). Thus, the part correlation is a good indicator of the "practical relevance" of a predictor.

Because there were 46 taxa occurring at 10 or more stations, 46 similar null hypotheses were tested together. The fact that so many similar hypotheses are tested increases the probability of rejecting a null hypothesis that is true (Type I error). A Bonferroni adjustment (Bonferroni 1935) to the alpha (significance level) is required to correct for this problem. The desired alpha level (0.05) is divided by the number of similar hypotheses being tested (46 in this case). In this instance, there would be a chance of 0.90 (90 %) of finding one or more significant differences by chance alone in 46 tests. To correct for this the alpha level for each test would need to be lowered to 0.0011 in order to bring the overall alpha level back to 0.05.

Fish distribution maps were drawn by plotting relative abundance data for all species occurring at more than 10 stations on a base map of the area using MAPINFO Professional © software. Stations were categorised according to the dominant habitat type (i.e. the habitat type occupying the highest percentage cover relative to other habitats). These categories were plotted on a map using aerial photographs of the area (obtained from the Survey Department, Road Town, BVI) as references to assist with delineation of habitat boundaries.

4.2.4 Ontogenetic partitioning

Length-frequency histograms are a standard method for analysing size-differences and growth rates in fisheries studies (Jennings et al. 2001). A histogram of fish in each size category was plotted, using a moving average method (King 1995). Initial exploratory analysis of several species revealed that the size distribution of fishes in all sheltered lagoon habitats was similar, but it was different from the fish size distribution on all exposed forereef habitats outside the bays. Thus two lines were used on the length-frequency diagram–one that pooled all data of fish in bay habitats, and one used the pooled data from reefs outside bays. These length-frequency diagrams were only drawn for species occurring at more than 10 stations and that were widely distributed in lagoons and on the fore reef and were tested for significance using a Kolmogorov-Smirnov 2 sample test.

4.3 RESULTS AND DISCUSSION

4.3.1 Fish species richness

Forty-eight families and 136 species were recorded in the total species inventory (a combination of more than 28 000 fish recorded during the sampling and the other fish spotted during non-sampling periods) (Table 4.1). Three IUCN red-data list species, Nassau grouper *Epinephelus striatus* (Bloch 1792), hogfish *Lachnolaimus maximus* (Walbaum 1792) and mutton snapper *Lutjanus analis* (Cuvier 1828) occurred in the area but they were all rare (Table 4.1). It is worth noting here that most species recorded in this study are data deficient for IUCN red listing purposes, but a substantial IUCN revision of the Caribbean fish red lists will soon be available and many new additions to the list are likely to be made (M. L. Smith, pers. comm.).

The sampling effort was considered sufficient, because by the 80th sample, the species accumulation curve had reached an apparent asymptote of 118 species (Fig 4.1). Only 2 new species were encountered in the subsequent 20 samples, indicating that these additions were probably rare or vagrant species. The Chao estimate of S_{max} was 136 species, exactly the same number that were recorded in the total species inventory! It is therefore likely that most of the species that might be found in the study area using visual census methods were actually encountered. There is a small risk that this species richness estimate may be biased because no other census methods were used and a known weakness of visual census methods is that they tend to miss small cryptic or nocturnal species (Jennings et al. 2001).

Table 4.1 A list of the 136 species 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 of their rarity C = commonly encountered, O = occasional, R = rare, and notes on the observed habitat preferences of each species. Stations with '0' totals were present but did not enter the sampling quadrats.

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
	Apogon binotatus	0	0	P	R	Reef recess
	Apogon maculatus	0	0	H	O	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.
	Trachinotus goodei	0	0	H	R	Sandy, wave washed areas.
Carcharhinidae	*Carcharhinus limbatus*	0	0	H	O	Seaward reef, wary of divers.
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
Diodontidae	*Diodon holacanthus*	0	0	H	R	Reef flat
	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.

Table 4.1 Continued

Family	Species	Total	No Stations	Bays	Rarity	Observed habitats
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.
	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 docks.
Microdesmidae	*Ptereleotris helenae*	2	1	H	R	Deep sand.
Monocanthidae	*Aluterus scriptus*	0	0	H	R	Dock piling
	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.

Table 4.1 Continued

Family	**Species**	**Total**	**No Stations**	**Bays**	**Rarity**	**Observed habitats**
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	*Echidna catenata*	0	0	B	R	Reef recesses.
	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.
	Gymnothorax vicinus	0	0	H	O	Reef flat and seagrass areas.
Myliobatidae	*Aetobatus narinari*	0	0	B	R	Seagrass, occasionally leap clear of the water.
Ogcocephalidae	*Ogcocephalus nasutus*	0	0	H	R	Sand with sparse *Halodule wrightii*.
Ophichthidae	*Myrichthys breviceps*	0	0	H	R	Sandy seagrass.
	Myrichthys ocellatus	0	0	H	R	Reef flat with seagrass.
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.
Pempheridae	*Pempheris schomburgki*	2	1	B	O	Reef recesses.
Pomacanthidae	*Pomacanthus paru*	1	1	H	R	Juvenile on reef flat.
	Holacanthus ciliaris	0	0	B	R	Reef recesses.
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.
Rhincodontidae	*Ginglymostoma cirratum*	0	0	H	R	Reefs, wary of divers.
Scaridae	*Scarus* spp < 10cm	10245	76	BPH	C	Found in all habitats except sandy zones, particularly abundant in seagrass beds associated with mangroves.
	Scarus iseri/taeniopterus > 10cm	337	29	BPH	C	Seaward reef areas and structure in lagoons.
	Scarus vetula > 10cm	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.

Table 4.1 Continued

Family	**Species**	**Total**	**No Stations**	**Bays**	**Rarity**	**Observed habitats**
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.
Scorpaenidae	*Scorpaena plumieri*	0	0	H	R	Reef flat.
Serranidae	*Alphestes afer*	0	0	B	R	Seagrass with rocks.
	Cephalopholis fulva	1	1	P	R	Seaward reef
	Epinephelus adscensionis	3	3	PH	R	Seaward reef
	Epinephelus guttatus	9	6	BPH	O	Fore reef
	Epinephelus striatus	0	0	H	O	Reef flat
	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.
Syngnathidae	*Syngnathus caribbaeus*	0	0	H	R	Seagrass
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	**136**	**27 666**	**106**	**3**		

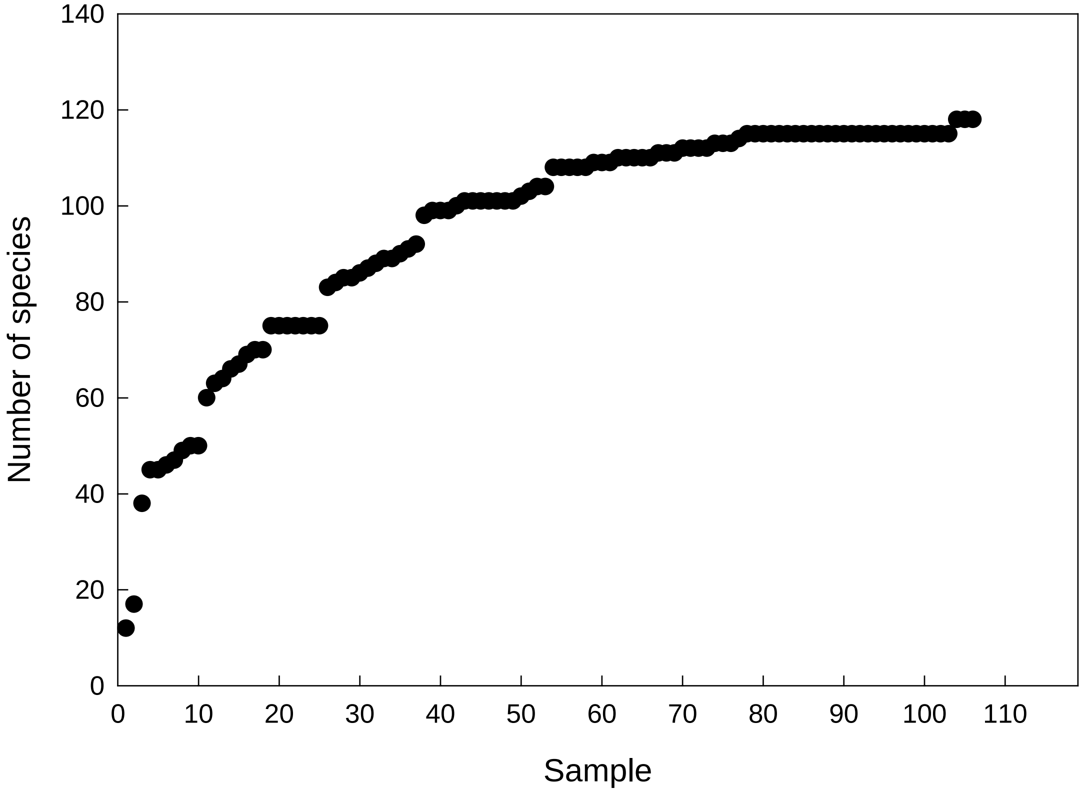


Fig 4.1 The iteratively randomised species accumulation curve for all 106 stations sampled in the area.

4.3.2 Fish-habitat correlations

The data were tested for multicolinearity using the ECOM software package. There was an appreciable level of multicolinearity (r^2 values of above 0.8) until either sand or rock was removed from the analysis (Table 4.2). Since sand can be considered the ‘default habitat type’ on which all other habitats are found, sand was usually excluded from the analysis unless there was an *à priori* reason for suspecting that sand was a preferred habitat type (*à priori* evidence was obtained using Table 4.1, and/or published literature). 100% sandy areas were usually characterised by very low species densities, in contrast to rocky areas that supported large numbers of species.

The degree of habitat specificity and the type of habitats favoured were different for each fish species, and these will be fully described in the individual species accounts. Habitat correlations are only presented for 44 out of the potential 136 species that occurred at 10 or more stations. Where ontogenetic partitioning of habitats was demonstrated (see section 4.3.3), the habitat preferences for both adult and juvenile fish are presented, sample-size permitting. The 44 species represent a sub-sample of the population and give important clues about which habitats contain the most habitat specialists. The percentage rock cover (usually in the form of dead coral) explained the bulk of the variance in abundance of 17 different taxa (40% of the total assessed) and may be considered one of the most important habitat variables influencing fish abundance and distribution. Upright gorgonians and live hard coral were the next most important variables, being significantly correlated with 10 and 7 species respectively (Table 4.3).

Table 4.2 Test for multicolinearity of habitat variables; an r^2 value of above 0.8 indicates appreciable multicolinearity (Henderson and Seaby 2002). Excluding either % cover sand or % cover rock solved multicolinearity problems. Generally % cover sand was excluded unless there was an a priori reason (i.e. observation from Table 4.1) suggesting that the species might prefer sand, in which case % cover rock was excluded instead.

Habitat Variables	All variables	Sand removed	Rock removed
Calcareous Macroalgae	0.98	0.08	0.15
Seagrass	0.99	0.40	0.45
Mangrove roots	0.87	0.11	0.10
Fleshy algae	0.99	0.41	0.33
Sand/mud	0.99		0.42
Rock and algal turf/film	0.99	0.49	
Zooanthid mat	0.78	0.42	0.43
Live hard coral	0.94	0.48	0.51
Gorgonian	0.76	0.31	0.33
Encrusting gorgonian	0.26	0.19	0.19
Rubble	0.94	0.06	0.07
Sponge	0.37	0.18	0.19

Table 4.3 The relationship between habitat variables and species abundance for fish occurring at more than 10 stations. Significance was tested at the 0.001 alpha level due to the Bonferroni adjustment. Only the significant (t test, $p < 0.001$) part correlations are indicated. CM = calcareous macroalgae, FA = fleshy algae, M = mangroves, SG = seagrass, S = sand, R = rock, Z = zooanthid, LHC = live hard coral, UG = upright gorgonian, EG = encrusting gorgonian, Ru = Rubble, Sp = Sponge.

Family	**Species**	**CM**	**FA**	**M**	**SG**	**S**	**R**	**Z**	**LHC**	**UG**	**EG**	**Ru**	**Sp**	**adj r^2**	**Sign**
Acanthuridae	*A. bahianus* adults						0.56							**0.75**	*****
	A. bahianus juveniles						0.34					0.59		**0.52**	
	A. coeruleus						0.47	-0.19	0.33					**0.77**	*****
Blenniidae	*O. atlanticus*						0.59							**0.72**	*****
Carangidae	*C. ruber*									0.23	0.26			**0.44**	*****
Chaetodontidae	*C. capistratus* juveniles													**0.16**	**ns**
Gerreidae	*Eucinostomus* spp.				0.38	0.44								**0.38**	*****
	G. cinereus juveniles			0.33										**0.26**	*****
Gobiidae	*C. glaucofraenum*	0.22				0.30								**0.08**	**ns**
	G. saepepallens					0.29								**0.06**	**ns**
	L. cyprinoides													**0.12**	**ns**
Haemulidae	*H. flavolineatum* adults									0.27				**0.31**	*****
	H. flavolineatum juveniles													**0.01**	**ns**
	H. plumieri													**0.03**	**ns**
	H. sciurus			0.30										**0.22**	*****
Holocentridae	*H. rufus*									0.29				**0.35**	*****
Labridae	*H. bivittatus* adults				0.26		0.53							**0.48**	*****
	H. bivittatus juveniles											0.30		**0.28**	*****
	H. maculipinna						0.49							**0.61**	*****
	H. poeyi		0.29											**0.13**	**ns**
	H. radiatus						0.43		0.21		0.19			**0.74**	*****
	T. bifasciatum						0.41		0.16	0.16			0.27	**0.87**	*****
Labrisomidae	*M. aurolineatum*						0.61							**0.58**	*****
	M. macropus/versicolor											0.27		**0.20**	*****
	M. triangulatus						0.26				0.38		0.31	**0.60**	*****
Lutjanidae	*L. apodus* adults			0.40					0.39	0.24				**0.40**	*****
	L. apodus juveniles			0.54										**0.37**	*****
	L. griseus		0.26											**0.27**	*****
	L. synagris													**0.03**	**ns**
	O. chrysurus juveniles				0.39									**0.30**	*****
Monocanthidae	*M. ciliatus*													**0.00**	**ns**
Mullidae	*P. maculatus*													**0.04**	**ns**
Pomacentridae	*A. saxatilis*									0.48				**0.44**	*****
	M. chrysurus						0.29	0.22						**0.62**	*****
	Stegastes spp adults						0.38							**0.56**	*****
	S. diencaeus/leucostictus juvs						0.33							**0.20**	*****
	S. dorsopunicans juvs						0.63							**0.58**	*****
	S. planifrons								0.35					**0.25**	*****
Scaridae	*Scarus* juvs	0.22	0.32											**0.15**	**ns**
	S. iseri/taeniopterus adults											0.47		**0.56**	*****
	S. vetula adults						0.48	-0.26	0.22					**0.54**	*****
	S. aurofrenatum adults						0.41			0.21	0.16			**0.75**	*****
	S. aurofrenatum juvs													**0.08**	**ns**
	S. radians		0.48											**0.36**	*****
	S. rubripinne adults						0.49			0.35				**0.74**	*****
	S. viride adults						0.30			0.32				**0.62**	*****
Serranidae	*H. puella*								0.36	0.31				**0.22**	*****
Sphyraenidae	*S. barracuda* juveniles			0.28										**0.18**	*****
Tot +ve correlations		**2**	**4**	**4**	**3**	**3**	**17**	**1**	**7**	**10**	**4**	**4**	**2**		

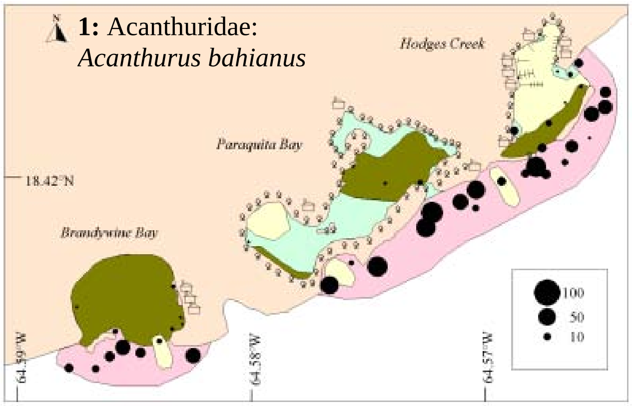
4.3.3 Accounts of species distribution and ontogenetic partitioning

The previous chapter gives an account of fish communities, their relationships with each other and their environment, but this approach sacrifices much of the information about rare species, and the unique biology of each species, including ontogenetic partitioning. This section groups the distribution maps for all species into a single main figure for ease of reference (Fig 4.2). A second figure assesses the degree of ontogenetic partitioning between protected lagoons and fore reef habitats of the more widely distributed species (Fig 4.3).

Acanthuridae - Surgeonfishes

The relative abundance of all Acanthurids was strongly correlated with percentage rock cover (Table 4.3). One mechanism that might explain this pattern is the high availability of their food (algae) on rocky substrates. Epilithic algae are the major primary producers on reefs, but they are often very closely grazed and have small standing crops (Randall 1967, Reeson 1983). This explanation is supported by several other studies showing that food availability and competition with other algal grazers such as parrotfish and longspined sea urchins are the major factors limiting the distribution and abundance of surgeonfish (Hay and Taylor 1985, Carpenter 1986, Robertson 1991).

Adult ocean surgeonfish *Acanthurus bahianus* Castelnau 1855 were found exclusively on reefs, but juveniles were found both on reefs and in lagoons where they were associated with rock and rubble (Fig 4.2.1, Fig 4.3.1, Table 4.3). The shape of the length-frequency distributions suggest that lagoon habitats may be a significant source of recruitment to the adult population because the second year class of individuals living on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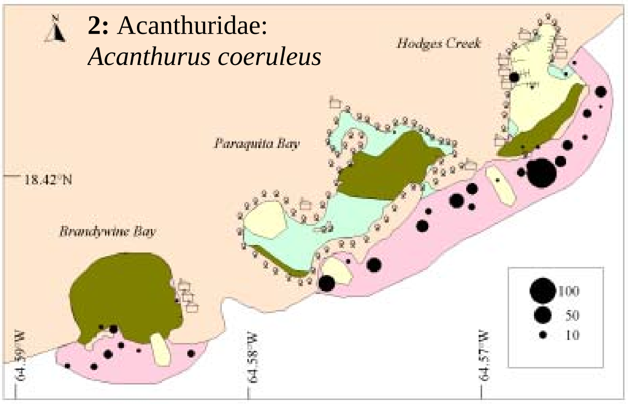
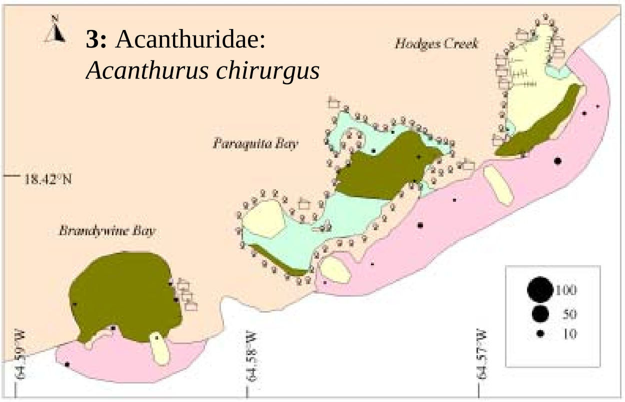
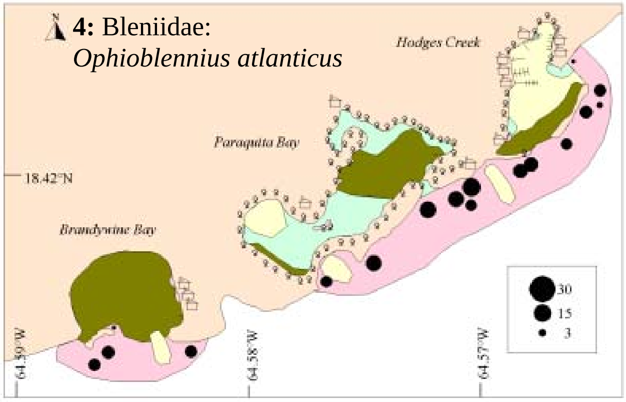
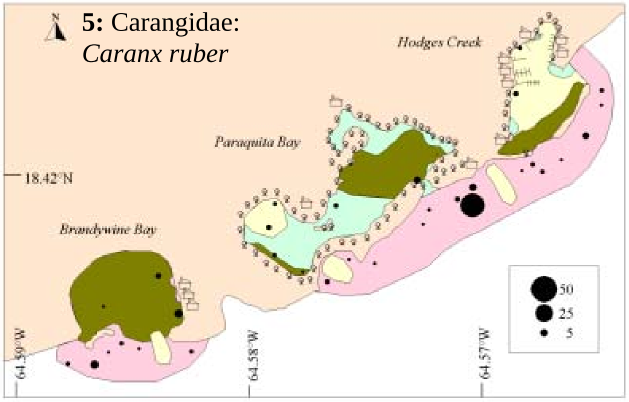
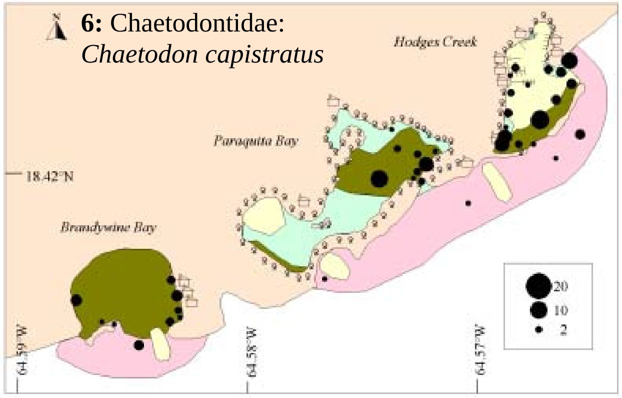
Acanthurus bahianus

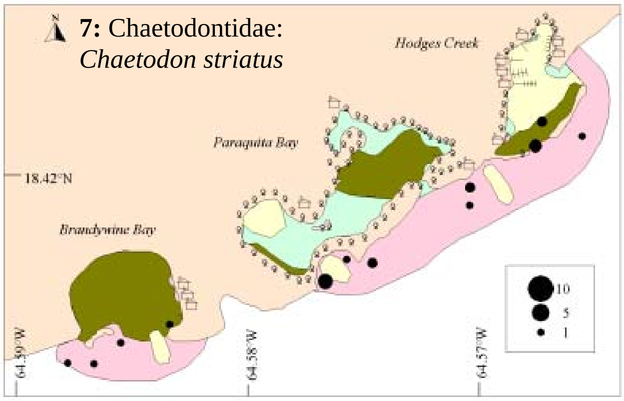

2: Acanthuridae:
Acanthurus coeruleus


3: Acanthuridae:
Acanthurus chirurgus


4: Bleniidae:
Ophioblennius atlanticus


5: Carangidae:
Caranx ruber


6: Chaetodontidae:
Chaetodon capistratus


7: Chaetodontidae:
Chaetodon striatus

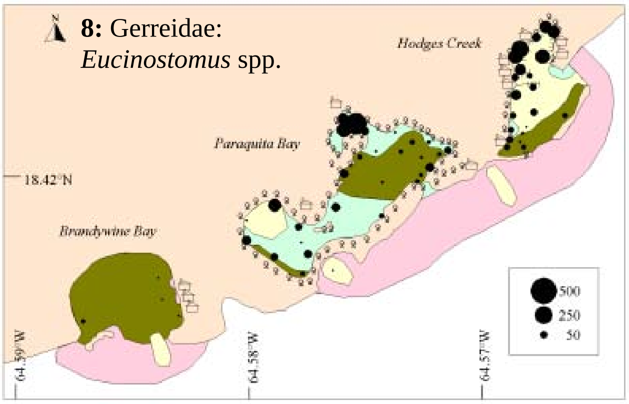
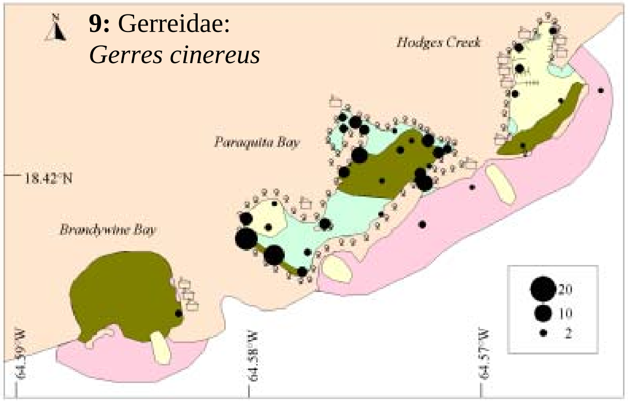
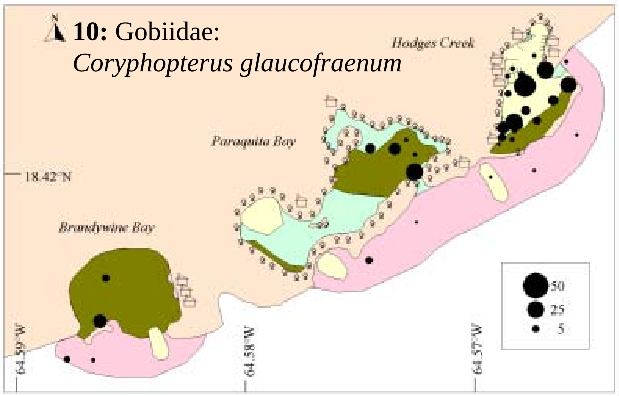
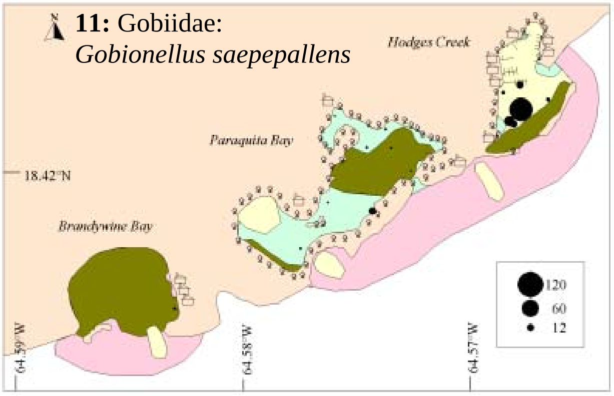
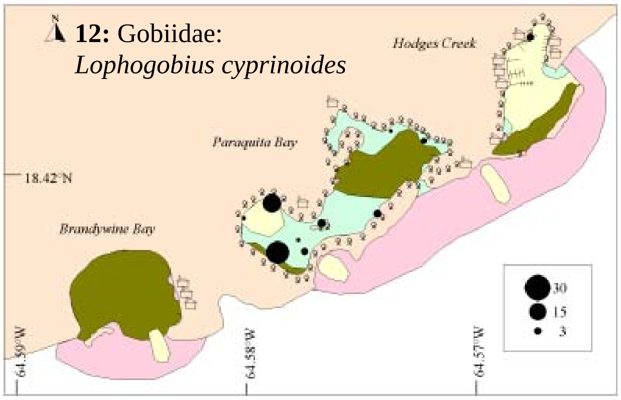

8: Gerreidae:
Eucinostomus spp.

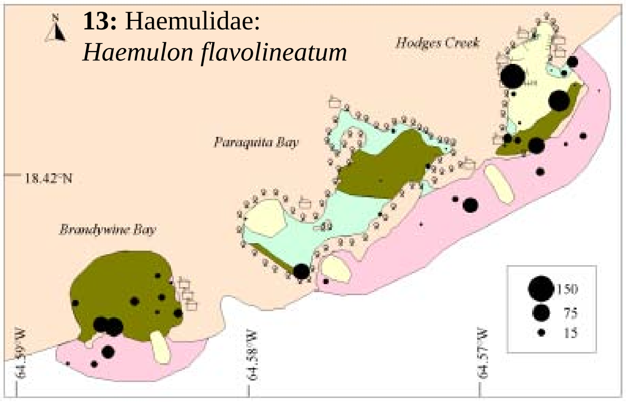
Fig 4.2.1-8 continued on next page…

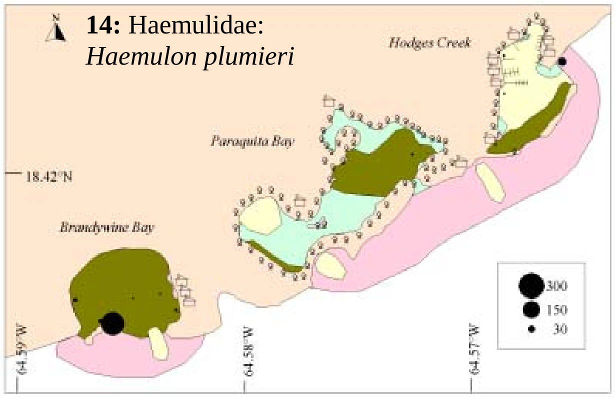

9: Gerreidae: *Gerres cinereus*

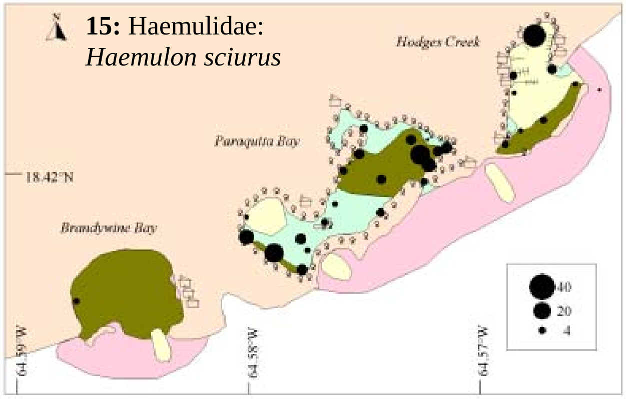

10: Gobiidae: *Coryphopterus glaucofraenum*


11: Gobiidae: *Gobionellus saepepallens*


12: Gobiidae: *Lophogobius cyprinoides*


13: Haemulidae: *Haemulon flavolineatum*


14: Haemulidae: *Haemulon plumieri*


15: Haemulidae: *Haemulon sciurus*

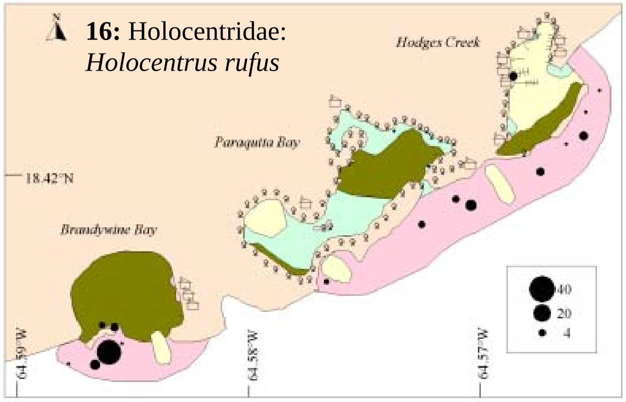

16: Holocentridae: *Holocentrus rufus*

Fig 4.2.9-16 continued from previous page…

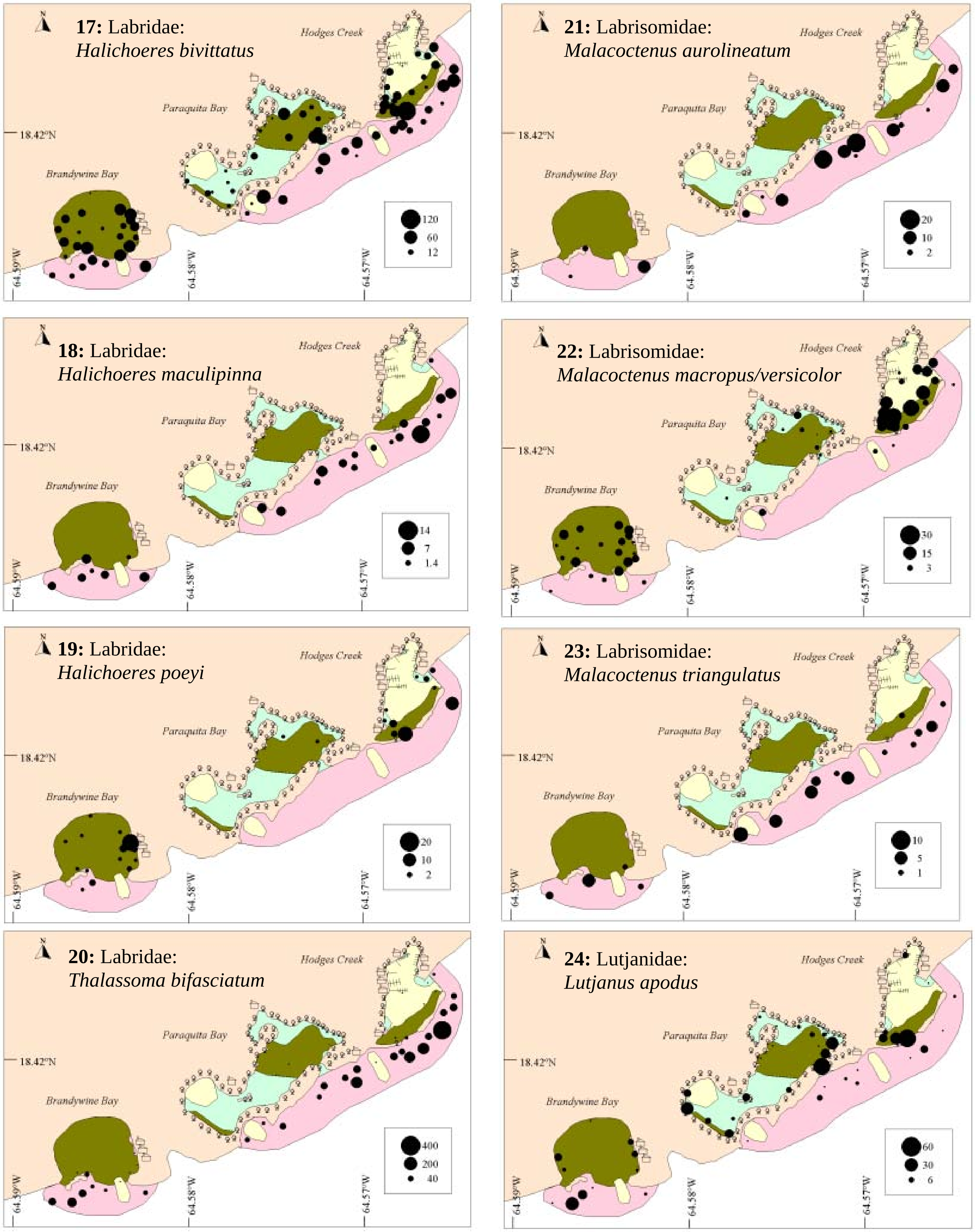


Fig 4.2.17-24 continued from previous page…

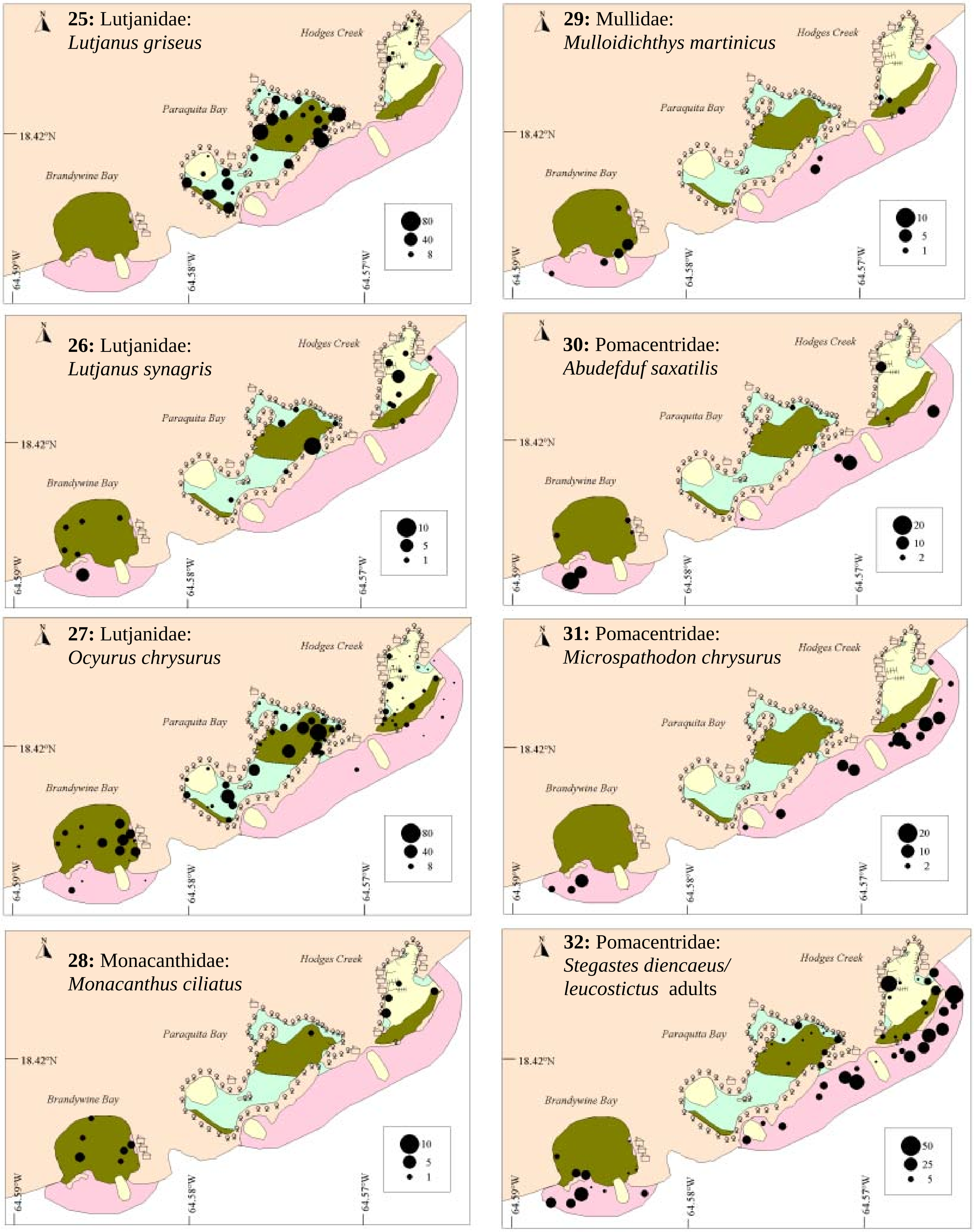
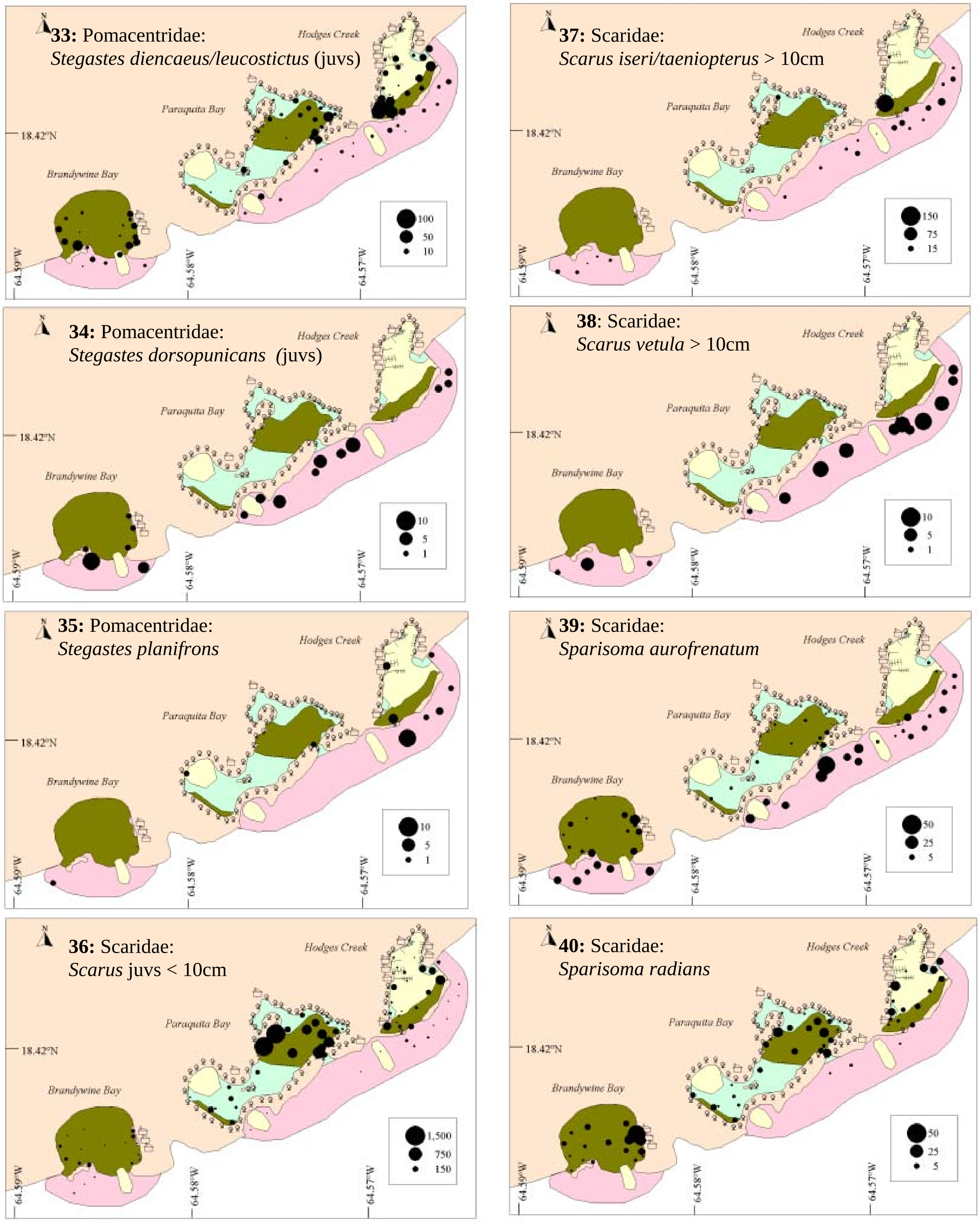


Fig 4.2.25-32 continued from previous page…



33: Pomacentridae: *Stegastes diencaeus/leucostictus* (juvs)

37: Scaridae: *Scarus iseri/taeniopterus* > 10cm

34: Pomacentridae: *Stegastes dorsopunicans* (juvs)

38: Scaridae: *Scarus vetula* > 10cm

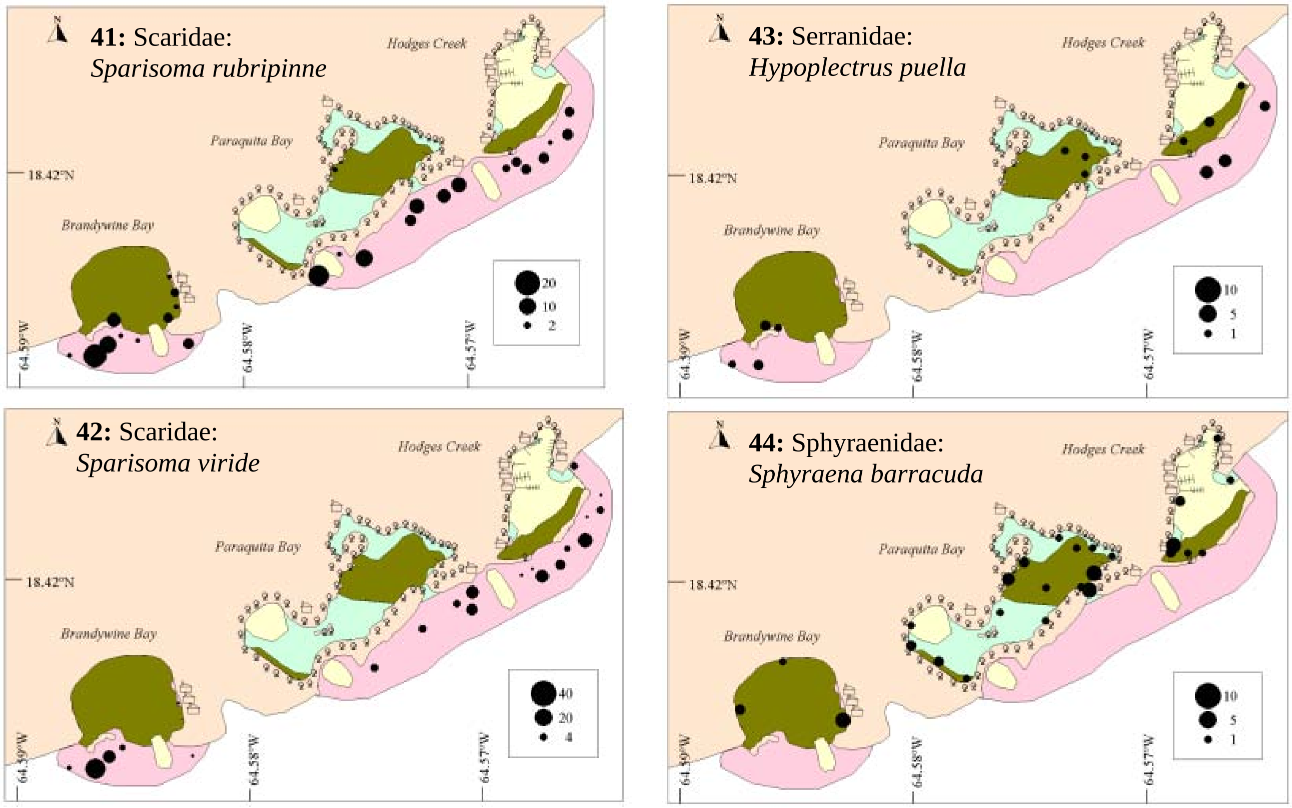
35: Pomacentridae: *Stegastes planifrons*

39: Scaridae: *Sparisoma aurofrenatum*

36: Scaridae: *Scarus* juvs < 10cm

40: Scaridae: *Sparisoma radians*

Fig 4.2.33-40 continued from previous page…



41: Scaridae: *Sparisoma rubripinne*

43: Serranidae: *Hypoplectrus puella*

42: Scaridae: *Sparisoma viride*

44: Sphyraenidae: *Sphyraena barracuda*

Fig 4.2.41-44 continued from previous page. Distribution patterns of fish occurring at > 10 stations in the study area, superimposed on basic habitat map. Dark green = seagrass, pale green = macroalgae, pale yellow = sand and pink = reef.

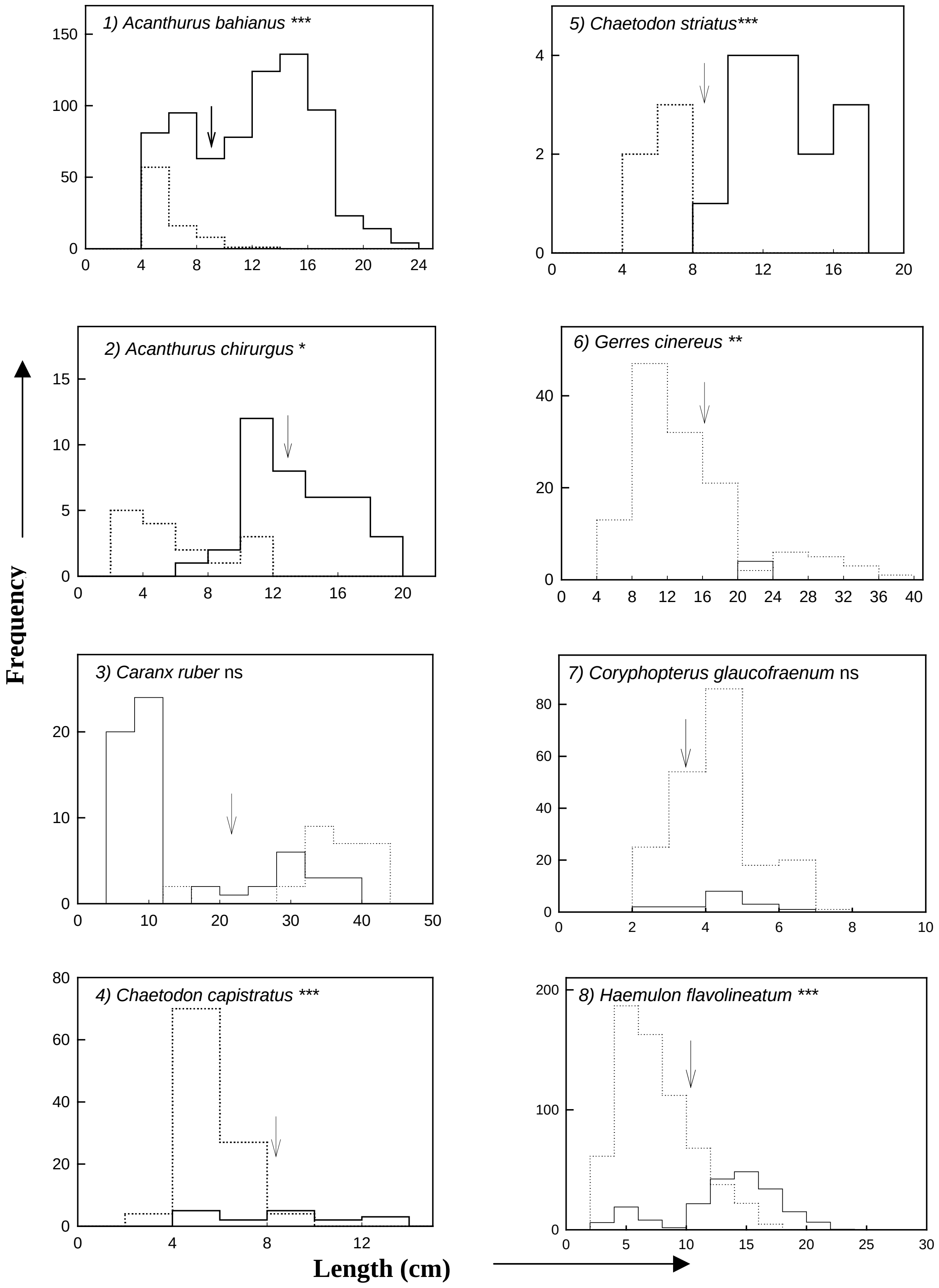


Figure 4.3 Continued on next page.

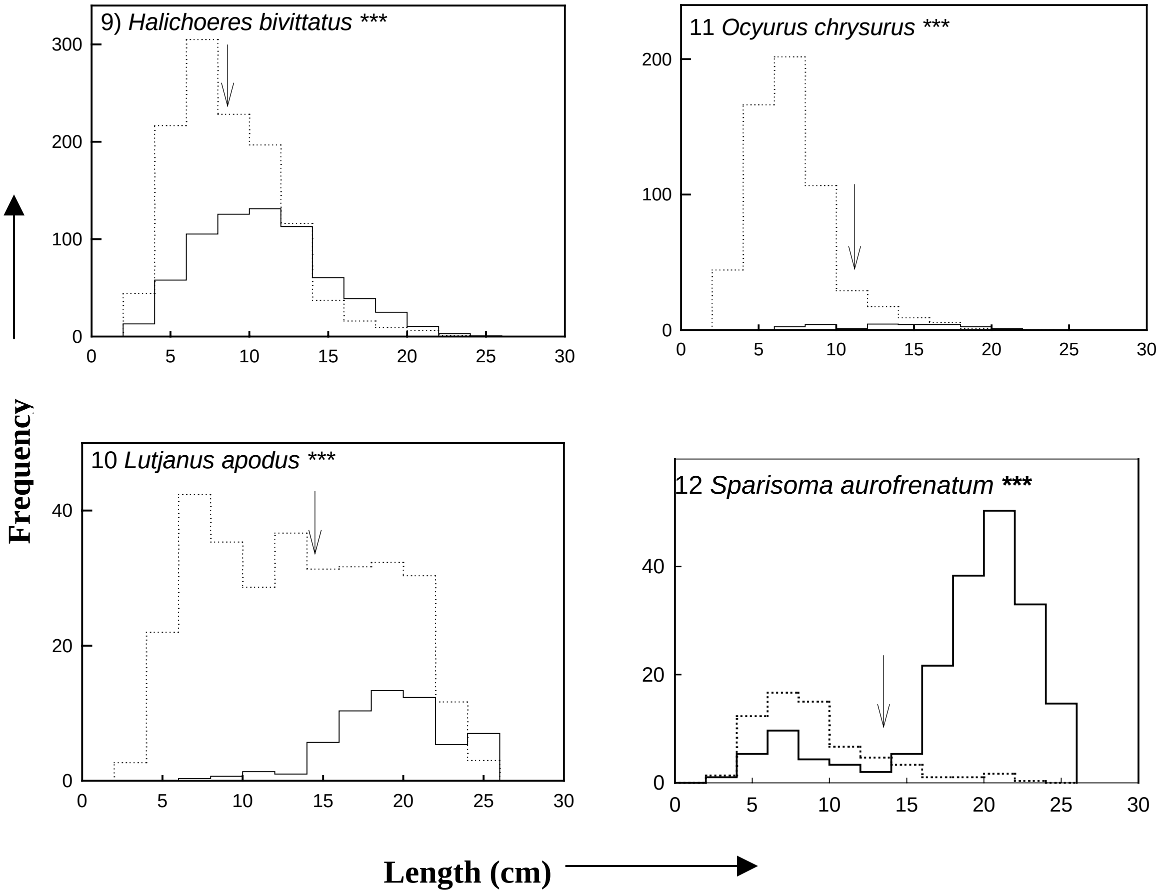


Figure 4.3 Length frequency distributions of fish in bays (dotted) vs forereef (solid). Arrows indicate size at first reproductive maturity as indicated in Fishbase. A Kruskall Wallace distributional test was used to compare the curves: ns p>0.05; * p<0.05; ** p<0.01; *** p<0.001.

the reef were 20% more abundant than the first year class (Fig 4.3.1). Similarly, workers in Barbados found that juvenile *A. bahianus* were most abundant in shallow reef flat and reef crest areas, while adults were most abundant in deeper seaward reef zones (Lawson et al. 1999). Larger fish become gregarious and on the reef they form large, multi-species groups and in these groups, they can successfully forage on high biomass algal turfs guarded by reef-dwelling damselfish (Foster 1985).

The blue tang surgeonfish *Acanthurus coeruleus* Bloch & Schneider 1801 is a reef specialist (Fig 4.2.2) and its juveniles were only occasionally encountered on reef flat areas. Studies in Barbados and Cozumel showed that yellow-coloured *A. coeruleus* preferred deeper reefs, while slightly larger blue individuals selected shallow back-reef areas in the lagoon (Díaz-Ruiz et al. 1998, Lawson et al. 1999). This pattern was not verified as fishes of all sizes were distributed almost exclusively on the seaward reef. One possible reason for the discrepancy might be the poor general development of the reef flat habitats in the bays studied. *Acanthurus coeruleus* is distinctly different from both *A. bahianus* and *A. chirurgus* as it has a thin-walled stomach and does not feed on much calcareous material (Reeson 1983). This physiological limitation may explain its specialised habitat preferences for the deeper fore reef consisting of rock and live hard coral while avoiding zooanthid mats in shallower zones (Table 4.3).

The doctorfish *Acanthurus chirugrus* (Bloch 1787) distribution was more sporadic than the other two *Acanthurus* species and when juvenile and adult data were separated neither class was abundant enough to perform statistical analyses of habitat preferences, but it was clear juveniles were more abundant in lagoons, and adults were more commonly encountered on reefs (Fig 4.3.2), suggesting ontogenetic use of habitat, as found in Curacao (Nagelkerken et al. 2000a). Several other studies indicate that it is the least specialised of the three species: For example doctorfish have has been collected from deep-water sponge bottoms and was the least habitat specific of the three species (Rocha et al. 2002), while in Curacao it was found in mangroves, seagrass beds and algal beds as well as reefs (Nagelkerken et al. 2000a).

Albulidae – Bonefishes

The bonefish *Albula vulpes* (Linnaeus 1758) was wary of divers, and hence may be underrepresented in the sample. Nevertheless, the sandy reef flat area adjacent to seagrass beds is considered a typical habitat for bonefish around the world where they feed on molluscs and crustaceans (Humann 1994, Mojica et al. 1995, Crabtree et al. 1998, Colborn et al. 2001).

Apogonidae – Cardinal fishes

Cardinal fishes are common reef fish seldom encountered by divers because they are nocturnal and hide in recesses during the day (Humann 1994). They are probably underrepresented in this study because, although all recesses in any quadrat were examined with scrutiny, these small fish may have hidden in small crevices completely out of view.

Dusky cardinal fishes *Phaeoptyx pigmentaria* (Poey 1860) were encountered at one deep reef station on the seaward reef (Table 4.1). They are known to prefer reefs and when they come out to forage at night, they are often associated with open basket stars *Astrophyton* (Humann 1994). Flame fish *Apogon maculatus* (Poey 1860) and barred cardinalfish *Apogon binotatus* (Poey 1867) were encountered in recesses on the forereef (Table 4.1). They are usually associated with any structures and recesses in lagoons or on reefs (Froese and Pauly 2003).

Aulostomidae -Trumpetfishes

Trumpetfish *Aulostomus maculatus* Valenciennes1837 are commonly encountered reef fishes in the Caribbean where they are important predators and they are strongly avoided by small fishes (Wolf 1986, Helfman 1989). They stalk their prey by swimming snout-down among branching gorgonians and tube sponges, using their similar colour and elongated body shape as camouflage (DeLoach 1999). This explains their observed habitat preference for gorgonians and sponges in this study (Table 4.1). A 10cm juvenile was encountered in seagrass, and could presumably use long seagrass blades as a form of camouflage in a similar way to the adults.

Belonidae – Needlefishes

Both the flat needlefish *Ablennes hians* (Valenciennes 1846) and hound needlefish *Tylosurus crocodilus* (Péron & Lesueur 1821) were observed in association with anchovy schools in lagoons where they feed on the surface. These observations are similar to those made by other workers (Humann 1994, Froese and Pauly 2003).

Blenniidae – Combtooth blennies

The redlip blenny *Ophioblennius atlanticus* (Valenciennes 1836) was found exclusively on the seaward reef where it favoured rocks, and was often located in shallow, turbulent areas (Table 4.3, Fig 4.2.4). Similar observations have been made elsewhere in the Caribbean, and it feeds on algae that grow on rocks in these habitats (Hunte and Cote 1989, Bath 1990, McGehee 1994).

Bothidae – Lefteye flounders

Platefish [aka Peacock flounder] *Bothus lunatus* (Linnaeus 1758) was primarily found in sandy patches where they rely on camouflage to ambush prey in the adjacent structurally complex habitats such as seagrasses or reefs, (Lieske and Myers 2001). It was found both in reefs and lagoons, showing a preference for sand or flat rocks. They are excellent at changing colour in response to the surface they are resting upon, and so they are unlikely to be strongly dependant upon habitat type, as long as the small fish that they prey on are available (Ramachandran et al. 1996).

Carangidae – Jacks and Pompanos

Jacks are schooling predators that are usually associated with reefs or open sea (Nelson 1994). They also move long distances, often in association with anchovy schools, indicating a pelagic lifestyle unconstrained by benthic habitat variables (Chapman and Kramer 2000). Only one blue runner *Caranx crysos* (Mitchill 1815) was encountered in Paraquita bay over an algal bed, and it is likely that it was a vagrant, or possibly a misidentification of an exceptionally dark bar jack. Horse-eye jack *Caranx latus* Agassiz 1831 juveniles and adults were commonly encountered around dock pilings in marinas, but they are also known to occur on the seaward reef (Humann 1994, Chapman and Kramer 2000, Froese and Pauly 2003). Bar jack *Caranx ruber* (Bloch,

1793) was also widely distributed on the seaward reef and in the lagoons, with no obvious habitat preferences (Fig 4.2.5). The apparent association with encrusting and upright gorgonians (Table 4.3) is probably an artifact because a large number of juveniles were seen in association with a large barracuda at one seaward reef station that by chance had high numbers of gorgonians (Fig 4.2.5). Length frequency distributions indicated there was no ontogenetic habitat partitioning, a pattern that might be expected from a pelagic fish. Leatherjack *Oligoplites saurus* (Bloch & Schneider 1801) were more strongly associated with habitat than the other jacks, as they were almost always encountered over seagrass beds (Table 4.1). It is known to be an estuarine-associated fish (Froese and Pauly 2003), although its encounter over a reef on one occasion indicates that they do roam more widely. Palometa *Trachinotus goodei* Jordan & Evermann 1896 was occasionally spotted on a wave-washed sandy shore, but is common in areas with clean sandy beaches, a habitat not found in the study area (Lieske and Myers 2001).

Carcharhinidae – Requiem sharks

Blacktip shark *Carcharhinus limbatus* (Müller & Henle 1839) was not recorded in any quadrats, probably because they occur in low numbers and are wary of divers. They were only fleetingly spotted on the seaward reef, but they are also known from lagoons (Blader 1986, Froese and Pauly 2003). These large, top predators are unlikely to be very habitat specific, and forage over a wide range of different habitats. It is possible that their wariness of divers has lead to an underestimate of their density, but in this type of community study, sporadic data from very large, very occasionally encountered species is of little use other than providing an historical record of its occurrence, which this study has done.

Chaenopsidae – Pike blennies, Tube Blennies and Flag Blennies

Holes in the sand containing the resident bluethroat pike blenny *Chaenopsis ocellata* Gill 1865 were found in two shallow, sandy stations in Hodges Creek with sparse seagrass *Halodule wrightii*, these observations are consistent with published accounts of this species (Humann 1994, Froese and Pauly 2003). The secretary blenny *Acanthemblemaria maria* Böhlke 1961 was encountered once in an empty tubeworm hole on a large dome-shaped coral, similar to observations by other authors (Humann 1994, Froese and Pauly 2003).

Chaetodontidae – Butterflyfishes

Both the foureye butterflyfish *Chaetodon capistratus* Linnaeus 1758 and the banded butterflyfish *Chaetodon striatus* Linnaeus 1758 provide striking examples of habitat partitioning as juveniles used the lagoons exclusively and moved onto seaward reefs as adults (Fig 4.2.6-7). This partitioning is documented elsewhere in the Caribbean where juveniles use a range of lagoon habitats, especially rocky structures, although no within-lagoon habitat seems to be favored in particular, then adults move onto the reef (Shulman 1985, Lindquist and Gilligan 1986, Nagelkerken et al. 2000a, Nagelkerken et al. 2001). Adults of both species are known to live on reef where they eat coral tissue, polychaetes and other invertebrates (Lasker 1985, Pitts 1991).

Clupeidae - Herrings, shads, sardines, menhadens

Anchovies generally occurred in very large schools, and could not be identified in the field so they were omitted from this survey. They are however an important source of food for many fishes, and transfer nutrients from pelagic to coastal systems. Larger predators such as tarpon and barracuda are often associated with these schools. The following anchovies are known to occur in the Virgin Islands: *Anchoa cayorum, Anchoa choerostoma*, *Anchoa colonensis, Anchoa cubana*, *Anchoa filifera, Anchoa lamprotaenia, Anchoa lyolepis*, *Anchovia clupeoides* and *Anchoviella perfasciata* (Froese and Pauly 2003). It is not known which of these species lived in the study area.

The larger, more distinctive redear herring *Harengula humeralis* (Cuvier 1829) was encountered twice in deep sandy-bottomed parts of Hodges Creek. It is known to be a habitat generalist occurring in lagoons and reefs and even in polluted areas where it feeds on planktonic crustaceans and fish (Ortaz et al. 1996, Lieske and Myers 2001, Froese and Pauly 2003).

Dasyatidae – Stingrays

Southern stingrays *Dasyatis americana* Hildebrand & Schroeder 1928 were occasionally encountered in lagoons with seagrass or sandy bottoms, but few were encountered in quadrats. Probably because of their large size, low relative abundance and their habit of burying themselves in the sand during the day (Lieske and Myers 2001).

Diodontidae – Porcupinefishes

Juveniles of these fish are never encountered in reef environments because they have a pelagic phase and settle as adults to preferred habitats, which are often in lagoons or reefs (Nelson 1994). It is worth noting here that one mass-recruitment of millions of 10-15cm longspined porcupine fish *Diodon holocanthus* Linnaeus, 1758 occurred in the BVI after this sampling period in August 2002 (pers. obs.) but both spot-fin porcupine fish *Diodon hysterix* Linnaeus, 1758 and *D. holocanthus* were rarely encountered in the survey of July, August and September 2001.

Gerreidae - Mojarras

The *Eucinostomus* spp. encountered were probably *E. gula* and *E. havana*, although *E. argenteus* and *E. lefroyi* are also known from the Virgin Islands (Froese and Pauly 2003). *Eucinostomus* spp. are generally found along sandy shores and in shallow lagoons with seagrass beds, while mangroves have also been noted as an important habitat for juveniles some species (Yanez et al. 1993, Motta et al. 1995, Branco et al. 1997, Chaves and Otto 1999, Pierce and Mahmoudi, Wilson and Meekan 2001, Froese and Pauly 2003). In this study, they were found exclusively in lagoons and occurred in higher numbers in mangrove-fringed areas and were significantly correlated with seagrass and sandy substrates (Fig 4.2.8, Table 4.3).

Eucinostomus spp. were also positively associated with nitrates, being more abundant in the low visibility, nitrate-rich areas, suggesting that they are tolerant of eutrophication, and therefore might be a useful indicator taxon in eutrophication studies (details given in Chapter 3). One factor that may contribute to its success is a flexible diet that ranges from one dominated by crustaceans in some areas to detritus and macroalgae in others (Branco et al. 1997).

Yellow fin mojarra *Gerres cinereus* (Walbaum 1792) occurred in a range of habitats (Fig 4.2.9)—a pattern verified by others (Lieske and Myers 2001), but the distribution maps imply a degree of association with mangrove-lined lagoons. Nagelkerken et al (2000a) note that juvenile *G. cinereus* are almost exclusively found in mangrove areas until the size of 12cm when they move onto the coral reef, among other habitats.

Gobiidae – Gobies

This was a large family, with a variety of different life-history patterns ranging from seaward reef specialists to mangrove specialists. Frillfin goby *Bathygobius soporator* (Valenciennes 1837) was encountered in very shallow stations with sand and rubble, displaying the same habitat preferences as described by others (Randall 1996, Froese and Pauly 2003). The bridled goby *Coryphopterus glaucofraenum* Gill 1863 was widely distributed (Fig 4.2.10), and was usually found on sandy patches near reefs, rock or seagrass but there was no ontogenetic partitioning of habitat (Fig 4.3.7). Other authors note a similar range in habitat preferences (Humann 1994, Forrester 1999, Lieske and Myers 2001). Sand and calcareous macroalgae were the most important habitat variables, although the overall multiple regression model was not significant (Table 4.3). The colon goby *Coryphopterus dicrus* Böhlke & Robins 1960 was encountered only on the seaward reef, although it is also known to live in shallow tide pools (Froese and Pauly 2003). The dash goby *Gobionellus saepepallens* Gilbert & Randall 1968 was encountered in lagoons with sand and seagrass (Fig 4.2.11), similar to habitat preferences observed by others (Humann 1994, Froese and Pauly 2003), but variations in abundance were not significantly related to habitat type. Both the sharknose goby *Gobiosoma evelynae* Böhlke & Robins 1968 and the orangesided goby *Gobiosoma dilepsis* (Robins & Böhlke 1964) were found on live hard corals on the seaward reef where they are known to be cleaner fish feeding on ectoparasites of larger fish (Froese and Pauly 2003). The crested goby *Lophogobius cyprinoides* (Pallas 1770) was associated with mangroves and fleshy algae beds where they were sometimes quite abundant (Fig 4.2.12); this species is a well-known estuarine fish, able to tolerate a wide range in salinities and is often associated with mangroves (Humann 1994, Froese and Pauly 2003). The orangespotted goby *Nes longus* (Nichols 1914) was occasionally encountered on sandy patches in lagoons, always in association with a shrimp, as it is elsewhere (Karplus 1992, Humann 1994).

Haemulidae – Grunts

Both adult and juvenile porkfish *Anisotremus virginicus* (Linnaeus 1758) are known to live on the seaward reefs (Böhlke and Chaplin 1993) an observation is verified by this study. Tomtate grunts *Haemulon aurolineatum* Cuvier, 1830 were not common in the area and only adults were encountered on the seaward reef in the actual survey. Juvenile *H. aurolineatum* are known to prefer seagrass and move onto the seaward reef when they mature (Yanez et al. 1993, Lieske and Myers 2001).

Both adult and juvenile Caesar grunts *Haemulon carbonarium* Poey 1860 were found on only the seaward reef. This is similar to previously recorded habitat types (Díaz-Ruiz et al. 1998, Lieske and Myers 2001). Smallmouth grunt *Haemulon* *chrysargyreum* Günther 1859 adults were encountered occasionally on the seaward reef but no juveniles were found in the survey. (Díaz-Ruiz et al. 1998) note that juveniles are known to live in seagrass beds and move onto seaward reefs as adults.

The French grunt *Haemulon flavolineatum* (Desmarest 1823) was the most abundant grunt in the study area (Table 4.3). Juveniles up to 10cm were found mostly in lagoons, although they did not exhibit strong habitat preferences in the lagoons while the adults, which were found mostly seaward reefs, were positively associated with upright gorgonians (Fig 4.3.8, Table 4.3). The small number of 5cm juveniles encountered on seaward reefs suggests that even though juveniles are more abundant in lagoons that they can use a wide range of habitats. These findings are similar to those of Nagelkerken et al (2000a, 2001, 2002) who note that juvenile *H. flavolineatum* live in a variety of lagoon habitat types but are not dependant upon any one in particular, and they move onto the seaward reef once they reach about 13cm.

Both adult and juvenile Spanish grunts *Haemulon macrostomum* Günther, 1859 were encountered on the seaward reef; they are known to live on reefs where they feed on crustaceans and urchins (Lieske and Myers 2001). Sailor's grunt *Haemulon parra* (Desmarest 1823) adults were found on the seaward reef, while the young were found in seagrass beds and mangroves, as they are elsewhere (Lieske and Myers 2001, Nagelkerken et al. 2001).

White grunts *Haemulon plumieri* (Lacepède 1801) were not significantly correlated with habitat type (Table 4.3). In Curacao, juveniles were found in a range of lagoon habitat types, while adults were found on reefs (Nagelkerken et al. 2000a). Juvenile *H. plumieri* <6cm feed during the day in a range of lagoon habitats while intermediate sizes (6-10cm) move onto seagrass beds at night where they feed on crustaceans and shelter on reefs by day, while larger adults live mainly on reefs (Meyer and Schultz 1985, Estrada 1986, Tulevech and Recksiek 1994, Nagelkerken et al. 2000b).

Juvenile bluestriped grunts *Haemulon sciurus* (Shaw 1803) were positively associated with mangroves, while larger adult fish were only found on the seaward reef. *H. sciurus* had the highest dependence on mangroves of all the grunts (Table 4.3, Fig 4.2.15). These observations corroborate other studies, which note that *H. sciurus* is highly dependant on mangroves as nursery areas, while larger adults are found on the reefs (Sedberry and Carter 1993, Nagelkerken et al. 2000a, Nagelkerken et al. 2001, Cocheret de la Moriniere et al. 2002, Nagelkerken et al. 2002).

Holocentridae – Squirrelfishes and Soldierfishes

This nocturnal family of fishes is often encountered under ledges and shelters during the day, and forage more widely on plankton and invertebrates at night (Nelson 1994). Both longspine squirrelfish *Holocentrus rufus* (Walbaum 1792) and squirrelfish *Holocentrus adscensionis* (Osbeck 1765) feed at night on reefs and seagrass beds, sheltering in any available structures by day (Froese and Pauly 2003). This explains the observed daytime distribution patterns in this study (Fig 4.2.16, Table 4.1). The reef squirrelfish *Holocentrus coruscus* Poey 1860 was only encountered in shallow, reef flat areas–its small size (13cm max) enabling it to live around small rocky patches. In other parts of the Caribbean it also occurs on the seaward reef (Lieske and Myers 2001). The dusky squirrelfish *Sargocentron vexillarium* (Poey 1860) was only found in very shallow, rocky, wave-washed seaward reef areas, although it supposedly favours shallow, sheltered reef flats and tidal pools (Lieske and Myers 2001). The blackbar soldierfish *Myripristis jacobus* Cuvier 1829 was found only in deeper seaward reef recesses, as it is elsewhere in the Caribbean, where it feeds on plankton above the reef at night (Humann 1994, Froese and Pauly 2003).

Kyphosidae – Sea Chubs

The Bermuda sea chubb *Kyphosus sectator* (Linnaeus 1758) was encountered twice over the seaward reef. A study in St Lucia showed that they prefer reef habitats (Eristhee and Oxenford 2001), but they are also known to range widely over seagrass and rubble (Froese and Pauly 2003).

Labridae – Wrasses

The wrasses displayed a wide range of life-history strategies and habitat preferences. The slippery dick *Halichoeres bivittatus* (Bloch 1791) occurred in every habitat type and was the most widespread fish throughout the area; adults were positively associated with rock cover and seagrass, while juveniles favored rubble (Table 4.3, Fig 4.2.17). *Halichoeres bivittatus* was also the most abundant and widespread fish in a similar survey in the US Virgin Islands (Mateo and Tobias 2001). There was a slight shift in median size, more large fish being encountered on reefs than in lagoons (Fig 4.3), although the widespread occurrence of juveniles and adults in both zones is probably a result of some other process (such as higher predation rates, or competitive exclusion of smaller fish on reefs compared to the lagoons) rather than differing ontogenetic habitat preferences.

The yellowhead wrasse *Halichoeres garnoti* (Valenciennes 1839) was only distributed on seaward reefs with live hard coral cover. Juveniles were encountered in shallow and deep areas, while adults were generally only found at depths greater than 1.5m. These observations corroborate other studies that found them only in seaward reef habitats (Humann 1994, Lieske and Myers 2001, Froese and Pauly 2003).

The clown wrasse *Halichoeres maculipinna* (Müller & Troschel 1848) was found over rocky seaward reef and occasionally reef flat areas, being positively correlated with rock (Table 4.3, Fig 4.2.18) although juveniles are also known from sargassum beds (Froese and Pauly 2003).

The blackear wrasse *Halichoeres poeyi* (Steindachner 1867) was a seagrass specialist (Table 4.3) and was uncommon on reefs (Fig 4.2.19). The lack of structure as refuge sites in seagrass beds, mean that they are probably heavily reliant upon their green color for camouflage to avoid detection by predators.

The puddingwife wrasse *Halichoeres radiatus* (Linnaeus, 1758) was commonly encountered on the seaward reef, although adults were wary of divers (Table 4.1); juveniles are said to be more common on shallow reefs while adults can be found much deeper (Froese and Pauly 2003).

Hogfish *Lachnolaimus maximus* (Walbaum 1792) juveniles were discovered in low densities in Paraquita bay, a habitat that juvenile hogfish are known to prefer (Humann 1994), but adults prefer reefs and gorgonians in particular, although none were encountered (Froese and Pauly 2003). The fact that Paraquita bay is apparently a nursery area for this threatened species is particularly notable as Paraquita bay is being considered for designation as a protected area (N Eristhee, pers. com.).

Bluehead wrasse *Thalassoma bifasciatum* (Bloch 1791) were predominantly found on the seaward reef and had very specific habitat requirements. Habitat variables accounted for 87% of the variation in abundance. They favoured rocky areas with sponges, live hard corals and upright gorgonians while juveniles often swarmed around tall coral heads (Table 4.3, Fig 4.2.20). These tall coral heads often act as spawning sites for adults or as cleaning stations where juveniles wait to pluck ectoparasites from larger fish (Warner 1987, Johnson and Ruben 1988).

Labrisomidae – Labrisomid blennies

The palehead blenny *Labrisomus gobio* (Valenciennes 1836) was encountered once on the seaward reef, and is known from rubble and seagrass beds (Froese and Pauly 2003).

The goldline blenny *Malacoctenus aurolineatus* Smith 1957 was quite common on rocky reefs (Fig 4.2.21) and was positively correlated with rock cover (Table 4.3). It is also apparently associated with sea urchins (Lieske and Myers 2001).

The dusky blenny *Malacoctenus gilli* (Steindachner 1867) was only encountered on the seaward reef (Table 4.1) although they are known to occur in rubble and seagrass beds (Lieske and Myers 2001).

Female and immature rosy blennies *Malacoctenus macropus* (Poey 1868) and barfin blennies *Malacoctenus versicolor* (Poey 1876) were indistinguishable in the field so the two species have been lumped for the purposes of this study. *Malacoctenus macropus/versicolor* were significantly associated with rubble (Table 4.3). They are both known to occur in a wide variety of near shore habitats although *M. versicolor* apparently prefers sandy and rocky areas (Froese and Pauly 2003). In this study they were abundant in lagoons, but avoided the more sheltered parts of Paraquita bay (Fig 4.2.22).

The saddled blenny *Malacoctenus triangulatus* Springer 1959 was associated with encrusting gorgonians and rocks (Table 4.3). They were distributed entirely on the fore reef (Fig 4.2.23) and this supports other studies noting that they occur only on reefs or rocky areas where they are highly territorial (Draud et al. 1990).

Lutjanidae – Snappers

The mutton snapper *Lutjanus analis* (Cuvier 1828) was occasionally encountered in lagoons and on the seaward reef (Table 4.1). Other studies have found that juveniles favour seagrass and sandy habitats in lagoons while adults prefer reefs. It is a vulnerable redlist species and is thought to use mangroves as a nursery habitat (Nagelkerken et al. 2001, Froese and Pauly 2003).

Juvenile schoolmaster snappers *Lutjanus apodus* (Walbaum 1792) (2-22cm) were strongly associated with mangroves, while larger individuals (15-25cm) were found in shallow reef environments (Table 4.3, Figs 4.2.21 & 4.3.10). *Lutjanus apodus* are known to use mangroves as juveniles (<7cm), and as they grow, their dietary requirements shift from crustaceans to small fish, and they increasingly begin to roam onto reefs—presumably in search of small fish (Rooker 1995, Nagelkerken et al. 2000c, Cocheret de la Moriniere et al. 2002).

The grey snapper *Lutjanus griseus* (Linnaeus 1758) was also associated with algal beds adjacent to mangroves (Fig 4.2.25, Table 4.3). Juveniles are known to settle in mangroves and their adjacent seagrass/algal beds, while adults sometimes move out of lagoons onto to reefs (Nagelkerken et al. 2000c, Allman and Grimes 2002). In this study adults were occasionally spotted on reefs, but they were not common there, and no *L. griseus* were seen on reefs during sampling, although very large individuals were often seen in Paraquita bay, along with juveniles. Paraquita bay appears to be an area with an exceptional abundance of this commercially important species (Fig 4.2.25).

The dogsnapper *Lutjanus jocu* (Bloch & Schneider 1801) was encountered once in Paraquita bay, although it was also occasionally spotted on sandy patches on the seaward reef. Young are known to live in lagoons and estuaries, while adults live on the seaward reef (Froese and Pauly 2003).

Lanesnapper *Lutjanus synagris* (Linnaeus 1758) were found in sandy patches both in lagoons and seaward reefs (Fig 4.2.26). These observations corroborate other studies stating that they prefer sandy or sparsely vegetated seagrass areas and reefs (Mateo and Tobias 2001, Froese and Pauly 2003).

Juvenile yellowtail snapper *Ocyurus chrysurus* (Bloch 1791) were abundant in lagoons where they were significantly correlated with seagrass cover, while larger fish were found on seaward reefs suggesting ontogenetic partitioning of habitats (Table 4.3, Fig 4.2.27, Fig 4.3.11). Very similar observations have been recorded in other studies (Mateo and Tobias 2001, Nagelkerken et al. 2001). This study, however, does not support the hypothesis that mangroves are a key habitat for *O. chrysurus* (Nagelkerken et al. 2001, Nagelkerken et al. 2002) because the fish were abundant in Brandywine bay, which has no adjacent mangroves (Fig 4.2.27), instead, the key habitats for *O. chrysurus* were seagrass beds in lagoons (Table 4.3).

Microdesmidae – Wormfishes

The hovering goby *Ptereleotris helenae* (Randall 1967) was found in a sandy part of Hodges Creek near the docks (Table 4.1). This species is usually found on sand and rubble bottoms where it lives in 'U' shaped burrows (Froese and Pauly 2003).

Megalopidae – Tarpons

Tarpon *Megalops atlanticus* Valenciennes 1847 were encountered around docks in Hodges creek where they could often be seen chasing anchovy schools; they were also found on the seaward reef (Table 4.1). These fish can breath air and are often found in eutrophic, oxygen-poor lagoons and estuaries where they feed on anchovies (Chaverri 1994, Geiger et al. 2000, Froese and Pauly 2003). These conditions are similar to those around docks in Hodge's Creek (See Chapter 3 for physicochemical data).

Monocanthidae – Filefishes

Four filefishes were found in the study area in habitats that were all consistent with their respective published observations: fringed filefish *Monacanthus ciliatus* (Mitchill 1818) were characteristic of seagrass and algal beds; the scrawled filefish *Aluterus scriptus* (Osbeck 1765) was found around a dock piling in Hodges Creek; slender filefish *Monacanthus tuckeri* Bean 1906 was seen both in lagoons and on reefs while orangespotted filefish *Cantherhines pullus* (Ranzani 1842) was found only on reefs (Fig 4.2.28, Table 4.1 & 4.3). *Monacanthus ciliatus* is known to prefer seagrasses where they are omnivorous, while young are associated with sargassum; *A. scriptus* is known to prefer lagoons, but is also found on seaward reefs; *M. tuckeri* is known to prefer sandy bottoms and gorgonians while *C. pullus* is known to prefer seaward reefs with gorgonians, sponges and corals (Lieske and Myers 2001).

Mugilidae – Mullets

White mullet *Mugil cephalus* Valenciennes 1836 was a lagoon fish with both juvenile and adult fish being seen in Paraquita bay and Hodges creek (Table 4.1). These observations are consistent with its known preference for shallow, warm estuaries and brackish areas where they feed on algae, zooplankton and detritus (Sogard et al. 1989, Montano 1994, Blay 1995, Silva and Araujo 2000).

Mullidae – Goatfishes

Published observations of yellow goatfish *Mulloidichthys martinicus* (Cuvier 1829) and spotted goatfish *Pseudupeneus maculatus* (Bloch 1793) note their preference for sand/rubble areas in lagoons and on reefs, while juveniles prefer seagrass beds (Humann 1994, Lieske and Myers 2001). Similar observations were made in this study area, although there was not statistically significant correlation (Table 4.1, Fig 4.2.29).

Muraenidae – Moray Eels

Moray eels were only occasionally encountered, as they are generally active at night and hide in recesses during the day, making them quite difficult to see (Nelson 1994). It is likely that these are under-represented in the sample, and the small sample sizes mean that suggested habitat preferences are tentative at best. Chain moray *Echidna catenata* (Bloch 1795) and goldentailed moray *Gymnothorax miliaris* (Kaup 1856) were found on the seaward reef. Purplemouth moray *Gymnothorax vicinus* (Castelnau 1855) and spotted moray *Gymnothorax moringa* (Cuvier 1829) were found in reef flat habitats and *G. funebris* was encountered in all habitats. Despite the small sample sizes, the observed habitat types correspond remarkably well with published habitat preferences, although *G. vicinus* is said to prefer seaward reef areas to reef flat (Froese and Pauly 2003).

Myliobatidae – Eagle and Manta Rays

Spotted eagleray *Aetobatus narinari* (Castelnau 1855) were occasionally seen both in the water and leaping above the water surface of Brandywine bay (Table 4.1). They generally avoided divers; so none were counted in the sample quadrats, again showing that this sampling design is inappropriate for counting large-bodied fish that may be wary of divers. It is known to prefer sandy areas of coral reefs and seagrass patches where they feed on molluscs (Lieske and Myers 2001).

Ogcocephalidae – Batfishes

Shortnose batfish *Ogcocephalus nasutus* (Cuvier 1829) was found on one occasion crawling on a sandy bottom of Hodge’s Creek that had sparse *Halodule wrightii* (Table 4.1). It is known to prefer sand, mud or seagrass and rubble bottoms and ranges into very deep areas (200m +) (Froese and Pauly 2003).

Ophichthidae – Snakeels

Both goldspotted eel *Myrichthys ocellatus* (Lesueur 1825) and sharptail eel *Myrichthys breviceps* (Richardson 1848) were encountered in reef flat areas with seagrass and boulders in Hodge's Creek, but they were rare and were not sampled in any quadrats. They are also known to occur in seaward reef habitats (Lieske and Myers 2001).

Opistognathidae – Jawfishes

Yellowhead jawfish *Opistognathus aurifrons* (Jordan & Thompson 1905) were encountered on a patch of sand and rubble on the seaward side of Brandywine bay. They are known to prefer sandy areas (Lieske and Myers 2001).

Ostraciidae – Boxfishes

Buffalo trunkfish *Lactophrys trigonus* (Linnaeus 1758) was encountered once in Paraquita bay, over seagrass, while spotted trunkfish *Lactophrys triqueter* (Linnaeus, 1758) was found exclusively on the seaward reef. *Lactophrys trigonus* is a highly sought-after food fish but it was rarely encountered. In addition to sand and seagrass beds, it is known to use offshore reefs, while *L. triqueter* is found exclusively on reefs where it feeds on mollusks, crustaceans and tunicates (Humann 1994, Lieske and Myers 2001, Froese and Pauly 2003).

Pempheridae – Sweepers

Sweepers are nocturnal fish, and shelter under ledges during the day (Nelson 1994). The glassy sweeper *Pempheris schomburgki* Müller & Troschel 1848 was occasionally encountered in recesses on the seaward reef, an observation that is consistent with known habitat preferences (Humann 1994). They may have been underrepresented because of their nocturnal habit.

Pomacanthidae – Angelfishes

One juvenile French angelfish *Pomacanthus paru* (Bloch 1787) was found on the reef flat of Hodges creek, and an adult queen angelfish *Holocentrus ciliaris* (Linnaeus 1758) was encountered on the seaward reef of Brandywine bay. Other studies indicate that angelfish juveniles prefer shallow reef flat areas, while adults move onto the deeper seaward reef where they feed on sponges and algae (Lindquist and Gilligan 1986, Hourigan et al. 1989). These fish, along with some grouper species may have been negatively impacted by fishing activities (trap and spear fishing activities were observed in the study area), because they were quite common in similar habitats in a marine reserve off the nearby island of St John, USVI (pers obs.).

Pomacentridae – Damselfishes

Ten pomacentrid species were encountered in the study area. This diverse family includes members ranging from territorial herbivores, to omnivores and planktivores (Nelson 1994). Juvenile sergeant majors *Abudefduf saxatilis* (Linnaeus 1758) were found in shallow lagoon areas and tidal pools on the reef crest, while adults were encountered deeper on the seaward reef among gorgonians (Table 4.1, Fig 4.2.30). In addition to tidal pools, juvenile *A. saxatilis* are sometimes associated with sargassum, and adults prefer deeper reefs (Lieske and Myers 2001). Night sergeants *Abudefduf taurus* (Müller &

Troschel 1848) were less common than *A. saxatilis*, occasionally being encountered on shallow reef – they are known to prefer shallow surf zones where they consume zooanthus, other hydroids and algae (Lieske and Myers 2001).

Blue chromis *Chromis cyanea* (Poey 1860) were found at just two of the deeper seaward reef stations in large aggregations hovering over reefs. They are known to prefer deeper zones and feed on plankton above the reef, and their numbers are heavily reduced by predation (Hixon and Carr 1997, Lieske and Myers 2001). Brown chromis *Chromis multilineata* (Guichenot 1853) were more widespread in the study area, also being found on shallower reefs that *C. cyanea.*

Yellowtail damselfish *Microspathodon chrysurus* (Cuvier 1830) adults were found in shallow, rocky areas on the seaward reef with zooanthid mats (Table 4.1, Table 4.3, Fig 4.2.31), while juveniles preferred fire corals. *Microspathodon chrysurus* are known to be highly territorial, excluding conspecifics from their territory (including juveniles which prefer fire corals, a well-studied ontogenetic partitioning phenomena), and they are characteristic of shallow reef-fish assemblages (Robertson 1984, McGehee 1994).

The *Stegastes* species used a range of different habitats in the study area. They are strongly site-attached and territorial, defending algal gardens from other herbivores. Excellent studies have been done on microhabitat partitioning leading to different spatial distributions of these fish (McGehee 1995, Tolimieri 1998).

Longfin damselfish *Stegastes diencaeus* (Jordan & Rutter 1897) and beaugregory *Stegastes leucostictus* (Müller & Troschel 1848) were difficult to distinguish in the field, and they were lumped for the purposes of this study. The adult and juvenile colorations were markedly different; the yellow and blue juveniles changing to brown when they reached 5-8cm in length. The two categories were plotted on separate maps. The adult *Stegastes* spp. dominated seaward reef patches (Fig 4.2.32), while juvenile *S. diencaeus/leucostictus* dominated lagoons and reef flat areas (Fig 4.2.33) but the ontogenetic separation was less pronounced than in other families such as the butterflyfishes. Both adults and juveniles are known to occur in a wide range of shallow habitats and are particularly abundant in reef flat areas, where they favour hard rocks that provide substrates for growth of algal turfs and crevices for spawning sites. They are uncommon on deeper, flourishing reefs probably because there is less algal turf there (Itzkowitz 1991, Wellington 1992, McGehee 1994, Smith 1997, Froese and Pauly 2003).

Both juvenile and adult dusky damselfish *Stegastes dorsopunicans* (Poey 1863) only occurred in shallow, rocky areas particularly on the seaward reef (Fig 4.2.34). They are known to prefer rocky areas on shallow reefs (Robertson 1984, Williams 1991, McGehee 1995, Gutierrez 1998) and their numbers were strongly associated with rock cover (Table 4.3).

Bicolour damselfish *Stegastes partitus* (Poey 1868) were abundant on deeper seaward reef areas with a higher percentage live coral cover, although juveniles were occasionally encountered in reef flat habitats. Other studies have shown that smaller fish have higher survival rates in these rubble areas than deeper on the seaward reef where larger fish are often associated with *Montastrea annularis* (Nemeth 1997, Nemeth 1998).

Threespot damselfish *Stegastes planifrons* (Cuvier 1830) juveniles were occasionally encountered on the reef flat, but all adults were found on the seaward reef where they were positively associated with live hard coral (Table 4.3, Fig 4.2.35).

Elsewhere they are also considered characteristic of deeper reef slope stations with live coral where they guard algal lawns (Hinds and Ballantine 1987, McGehee 1994, Gutierrez 1998).

Priacanthidae – Bigeyes

The glasseye *Heteropriacanthus cruentatus* (Lacepède 1801) was occasionally found in reef recesses (Table 4.1). It is known to be nocturnal, and lives in seaward and lagoon reef habitats, sheltering under ledges by day (Froese and Pauly 2003).

Rhincodontidae – Nurse sharks

The nurse shark *Ginglymostoma cirratum* (Bonnaterre 1788) was spotted in deeper parts of the seaward reef. A carcass was also found dead on the reef crest, tangled in a seine net. Other known habitats include sand flats and mangroves (Carrier and Pratt 1998, Froese and Pauly 2003).

Scaridae – Parrotfishes

Even though terminal phase Striped parrotfish *Scarus iseri* (Bloch 1789) and princess parrotfish *Scarus taeniopterus* Desmarest 1831 were easily distinguished, the initial phase specimens (>10cm) were difficult to tell apart – as a result they were lumped into the same category. All *Scarus* juveniles less than 10cm were difficult to distinguish, and are simply referred to as *Scarus* juvs.

Scarus juveniles were the most abundant and widespread group of fishes in the study area, forming over 35% of the total number of fish counted. They were found on the seaward reef and in all three lagoons, but were strikingly more abundant in seagrass beds of Paraquita bay and Hodges Creek, lagoons that were lined with mangroves (Fig 4.2.36). These data support the hypothesis that *Scarus iseri* are to some extent dependant upon mangroves as nursery areas (Nagelkerken et al. 2001, Cocheret de la Moriniere et al. 2002, Nagelkerken et al. 2002). However, the identity of the *Scarus* juveniles on the reef and in Brandywine bay is uncertain, and possibly included *S. taeniopterus* or *S. vetula* juveniles, so the results must be interpreted with caution. *Scarus* juvenile numbers were correlated with the fleshy algae and calcareous algae that offer both food and cover to these small fish although the overall regression model was not significant (Table 4.3). Both the initial phase and terminal phase of *Scarus iseri /taeniopterus* were mostly found on the seaward reef (Fig 4.2.37). They were positively associated with areas of rubble, (Table 4.3) and they are known to be epilithic algal grazers in the pavement/rubble ‘halo’ around coral reefs (McAfee and Morgan 1996).

Queen parrotfish *Scarus vetula* Bloch & Schneider 1801 initial phase and terminal phase are known to prefer reefs where they are epilithic grazers, preferring flat surfaces (Bruggemann et al. 1994a) but no references discussing the habitat preferences of juveniles <10cm could be found and it is likely that they formed mixed schools with the other *Scarus* spp. *Scarus vetula* preferred deeper areas without zooanthid mats, but with rock and live hard coral (Table 4.3).

Redband parrotfish *Sparisoma aurofrenatum* (Valenciennes 1840) juveniles were mostly found in lagoon areas, but small numbers occupied seaward reef habitats and the had no significant habitat preferences, while adults preferred areas with rock cover and gorgonians (Table 4.3, Fig 4.3) similar to observations elsewhere (McAfee and Morgan 1996).

In contrast to the other parrotfishes, bucktooth parrotfish *Sparisoma radians* (Valenciennes 1840) juveniles and adults both lived exclusively in lagoons and they were strongly correlated with fleshy algae (Fig 4.2.40, Table 4.3). Other studies have shown that they favour lagoons where they are important seagrass grazers, and they are the only Caribbean parrotfish species that complete their entire lifecycle in seagrass-algae beds (Greenway 1995, Lieske and Myers 2001, Kirsch et al. 2002).

Redfin parrotfish *Sparisoma rubripinne* (Valenciennes, 1840) and stoplight parrotfish *Sparisoma viride* (Bonnaterre 1788) occurred primarily on reefs, (although juveniles were occasionally encountered seagrass habitats) (Fig 4.2.41-42). *Sparisoma viride* is a known reef specialist, foraging on algae that grow on dead coral (Bruggemann et al. 1994a, Bruggemann et al. 1994b, McAfee and Morgan 1996), while *S. rubripinne* is thought to prefer seagrasses, occurring only secondarily on reefs (Lieske and Myers 2001).and the discrepancy with the findings in this study clearly require further investigation.

Sciaenidae – Drums or croakers

The highhat *Equetus acuminatus* (Bloch & Schneider 1801) juveniles and adults were occasionally found in recesses, and they are found in lagoons with rough bottoms or under the eroded banks of seagrass beds (Humann 1994, Smith 1997, Lieske and Myers 2001). Similarly, spotted drum *Equetus punctatus* (Bloch & Schneider, 1801) was encountered in reef recesses – a habitat they are known to prefer (Humann 1994, Lieske and Myers 2001). The reef croaker *Odontoscion dentex* (Cuvier, 1830) was seen in reef recesses and in recesses among land reclamation boulders in Hodge's Creek. It is known to prefer caves and is secretive (Froese and Pauly 2003).

Scorpaenidae - Scorpion fishes

The spotted scorpionfish *Scorpaena plumieri* Bloch, 1789 was encountered once in a back-reef area of Hodge's Creek, but since it is highly cryptic, it is probably under-represented in the sample. This fish was also found in the seagrass-mangrove system in Mexico (Yanez et al. 1993), but is generally considered characteristic of shallow coral reef or rocky areas (Lieske and Myers 2001).

Serranidae – Seabasses, groupers and fairy basslets

Only two (out of the nine) serranid species living in the study area were categorised as common: the small seabasses, *Hypoplectrus puella* (Fig 4.2.43) and *Hypoplectrus nigricans*. The remaining species were rare or only occasionally encountered (Table 4.1).

The groupers are a well-studied subfamily of reef fish: rockhind *Epinephelus adscensionis* (Osbeck, 1765); red hind *Epenephelus guttatus* (Linnaeus, 1758), Nassau grouper *Epenephelus striatus* (Bloch, 1792) and the coney *Cephalopholus fulva* (Linnaeus, 1758) were all rarely or occasionally encountered on the seaward reef, apart from one small *E. striatus* on the reef flat (Table 4.1). Both juveniles and the adults are generally found on the seaward reef, although juvenile *E. striatus* are known to prefer algal covered reef flat areas (DeLoach 1999, Dahlgren and Eggleston 2000).

Groupers are a commercially important subfamily and they form spawning aggregations at certain times of the year that are usually targeted by fishermen (DeLoach 1999, Morris et al. 2000). Fishing activity in the BVI has probably reduced grouper numbers in a similar way to their observed decline in the neighbouring US territories of US Virgin Islands and Puerto Rico (DeLoach 1999). In 1970, *Epinephelus striatus* was noted as the fourth most common shallow-water fish landed in Puerto Rico, but now it is commercially extinct in Puerto Rico and the US Virgin Islands (DeLoach 1999). The fact that only one *E. striatus* specimen was seen outside the context of the sampling programme means that the densities are also very low in the study area (Table 4.1).

The mutton hamlet *Alphestes afer* (Bloch, 1793) is another grouper occurring in the study area. It was found in a pile of rocks near seagrass in Brandywine bay and it is known to frequent seagrass beds where it is well camouflaged (Froese and Pauly 2003).

The most abundant Serranid—the barred hamlet *Hypoplectrus puella* (Cuvier, 1828) was found in all lagoons and habitats, while the butter hamlet *Hypoplectrus unicolor* (Walbaum, 1792) was only occasionally encountered in back-reef habitats (Table 4.1).

The black hamlet *Hypoplectrus nigricans* (Poey, 1852) was common on the seaward reef. They are known to prefer shallow reefs where they are thought to mimic herbivorous adult damselfish so that they can approach their prey without arousing suspicion (DeLoach 1999, Lieske and Myers 2001).

The yellowtail hamlet *Hypoplectrus chlorurus* (Cuvier, 1828) was found once on the seaward reef in Brandywine bay and they are known to prefer coral-rich areas (Lieske and Myers 2001).

Sparidae – Porgies

The Western Atlantic seabream *Archosargus rhomboidalis* (Linnaeus, 1758) was encountered occasionally in Paraquita bay. They are known to prefer seagrass beds associated with mangroves, and venture occasionally onto reefs (Yanez et al. 1993, Lieske and Myers 2001).

Calamus spp. were most commonly seen over sandy areas or reefs but as the young fish could not be reliably identified in the field, they could have been a number of different species: jolthead porgy *Calamus bajonado*, saucereye porgy *Calamus calamus*, sheepshead porgy *Calamus penna* and pulma porgy *Calamus pennatula* are possible candidates as they occur in the neighbouring USVI.

Sphyraenidae – Barracudas

Great barracuda *Sphyraena barracuda* (Walbaum 1792) were encountered mostly in lagoons (Fig 4.2.44). Individuals 3-10cm lengths were often seen among mangrove roots, while larger specimens were found in all lagoons. This would explain the observed positive relationship between *S. barracuda* numbers and mangrove roots. A very large *S. barracuda* (1.5 m) was encountered on the seaward reef of Paraquita bay in association with many small *Caranx ruber*, but it did not swim into the quadrat. The dependence of juvenile *S. barracuda* on mangroves is quite well documented with larger fish moving into sheltered estuaries and then onto the seaward reef at about 45cm (Nagelkerken et al. 2000c, Lieske and Myers 2001, Nagelkerken et al. 2001, Froese and Pauly 2003).

Sygnathidae – Pipefishes

Caribbean pipefish *Syngnathus caribbaeus* Dawson, 1979 was found in the seagrass beds of Hodges creek. It prefers shallow weedy areas, and it may have been under-represented in the sampling programme as it is highly cryptic (Lieske and Myers 2001).

Synodontidae – Lizardfishes

The sand diver *Synodus intermedius* (Spix & Agassiz, 1829) prefers sandy patches between reefs (Böhlke and Chaplin 1993), a habitat that was also used in this study.

Tetraodontidae – Puffers

The bandtail puffer *Sphoeroides spengleri* (Bloch, 1785) was found in association with seagrasses a habitat that it is known to prefer (Humann 1994, Lieske and Myers 2001), while the checkered puffer *Sphoeroides testudineus* (Linnaeus, 1758) also ventured onto sand and rubble patches where it feeds on gastropods and other invertebrates (Yanez et al. 1993, Froese and Pauly 2003).

4.4 SUMMARY

4.4.1 Distribution patterns

More than 28 600 fish were recorded during the survey (Table 4.1). The most abundant taxon was *Scarus* spp juveniles <10cm, which made up almost 36% of the total number of fish encountered, followed by *Eucinostomus* spp. (mojarras), *Halichoeres bivittatus* and *Thalassoma bifasciatum* (counts all > 1000). The most widespread species was *Halichoeres bivittatus*, occurring at 86 stations, followed by *Stegastes diencaeus/leucostictus* juveniles, *Scarus* spp juveniles, *Ocyurus chrysurus, Sparisoma radians, Eucinostomus* spp, *Malacoctenus macropus/versicolor* and *Stegastes* spp. adults (>50 stations each). Distribution maps were plotted for all species occurring at 10 stations or more (Fig 4.2) while the field observations, as well as a subjective assessment of the rarity of fish encountered are given for species occurring at fewer than 10 stations (Table 4.1).

Of the more commonly encountered species *Acanthurus chirurgus, Haemulon plumieri, Halichoeres bivittatus, Lutjanus apodus, Lutjanus synagris, Mulloidichthys martinicus* and *Hypoplectrus puella* were distributed widely, in lagoons and on seaward reefs. Two species, *Monacanthus ciliatus* and were mostly in lagoon habitats, regardless of mangroves, while *Eucinostomus* spp., *Gobionellus saepepallens Haemulon sciurus, Lophogobius cyprinoides, Lutjanus griseus, Sphyraena barracuda* and *Scarus* spp. juveniles were most abundant in lagoons fringed with mangroves. *Chaetodon capistratus, Gerres cinereus, Coryphopterus glaucofraenum, Halichoeres poeyi, Malacoctenus macropus/versicolor, Ocyurus chrysurus, Stegastes diencaeus/leucostictus juveniles and*

Sparisoma radians were distributed mostly in lagoons with a small proportion of the population being encountered on the seaward reef.

Nine taxa, *Acanthurus bahianus, Chaetodon striatus, Caranx ruber, Holocentrus rufus, Abudefduf saxatilis, Stegastes* spp. adults*, Scarus iseri/taeniopterus* adults, *Sparisoma aurofrenatum* and *Sparisoma rubripinne* were located mostly on the seaward reef, with comparatively small numbers being found in lagoon habitats. Nine more taxa were found almost exclusively on the seaward reef: *Acanthurus coeruleus, Ophioblennius atlanticus, Halichoeres maculipinna, Thalassoma bifasciatum, Malacoctenus aurolineatum, Microspathodon chrysurus, Stegastes dorsopunicans, Scarus vetula* and *Sparisoma viride.*

Some fish species that live in lagoons and on reefs were distributed widely in the fairly open Brandywine and Hodges Creek bays, but in Paraquita Bay they were concentrated in the seagrass patch close to the small, single channel connecting this lagoon to the sea, known locally as the ‘cut’. This distribution pattern is likely to be a result of pelagic larval dispersal that depends on ocean currents to transport larvae. Species displaying this pattern were *Chaetodon capistratus, Coryphopterus glaucofraenum, Malacoctenus macropus/ versicolor, Stegastes diencaeus/leucostictus* juveniles and adults, and *Hypoplectrus puella*. These species are likely to be strongly site-attached after settlement as there is no evidence of their penetrating other areas of the lagoon that would be less affected by incoming currents generated from rising tides.

4.4.2 Habitat specialists and rare species

Six of the 44 species occurring at more than 10 stations (about 10%) had a distinct dependence upon seagrass beds with adjacent mangroves as nursery areas; they were Eucinostomus spp, *Gerres cinereus, Haemulon sciurus, Lutjanus griseus, Scarus* spp and *Sphyraena barracuda.* All of them apart from *Eucinostomus* spp. are commercially important fish species, highlighting the importance of maintaining and rehabilitating mangroves in order to enhance fisheries and preserving biological diversity. In addition, Paraquita Bay is a nursery habitat for *Lachnolaimus maximus*, an IUCN threatened species. All of these data support the planned designation of Paraquita Bay as a protected area.

Fourteen rare/unusual species were found only in Hodges Creek, which is suffering from the effects of eutrophication particularly near the marina (see chapter 3 for physicochemical details). Mitigation of these impacts should be a priority in order to preserve the rarer species in the study area, which include: *Chaenopsis ocellata, Labrisomus gobio, Ptereleotris helenae, Aluterus scriptus, Ogcocephalus nasutus, Myrichthys breviceps, Myrichthys ocellatus, Pomacanthus paru, Ginglymostoma cirratum, Scorpaena plumieri, Epinephelus striatus* (a red-data book species) and *Syngnathus caribbaeus.*

4.4.3 Ontogenetic partitioning

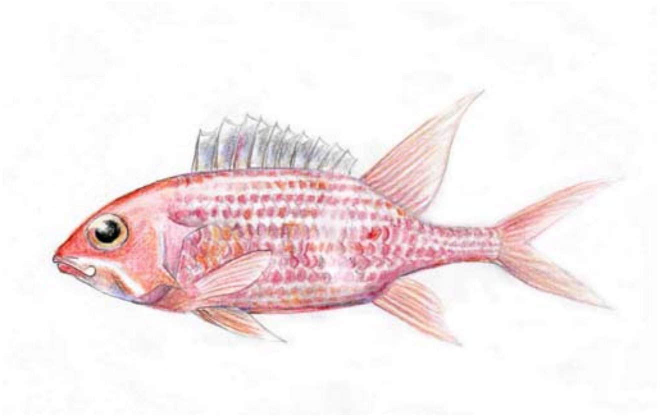
Caranx ruber and *Coryphopterus glaucofraenum* were the only species that lived on the seaward reef and in the lagoons, but did not show clear evidence of habitat partitioning.

Nine species, *Acanthurus bahianus, Acanthurus chirugrus, Chaetodon capistratus*, *Chaetodon striatus, Gerres cinereus, Haemulon flavolineatum, Lutjanus apodus, Ocyurus chrysurus* and *Sparisoma aurofrenatum* used the lagoons as nursery grounds for juveniles, while adults were found on reefs, displaying clear habitat partitioning (Fig 4.3). *Acanthurus bahianus* and *A. chirurgus* juveniles were not exclusively dependant upon lagoon habitats as nursery areas, but the shape of the length-frequency distributions suggests that the adult population on the reefs is strongly dependant upon the recruitment juveniles from non seaward reef habitats (Fig 4.3). The modal length for *H. bivittatus* in lagoons was 6-8cm compared with 10-12cm on the reef, implying a slight ontogenetic partitioning effect, larger fish preferring seaward reefs to lagoons.

Chaetodon capistratus juveniles (> 6cm) were exclusively found in lagoon habitats, and sexually mature adults (larger than 8cm) were exclusively found on the seaward reef; 6-8cm individuals were found in both habitats, suggesting that this was the size at which they left the nursery habitat.

Other species also displaying habitat partitioning effects were *Stegastes diencaeus/leucostictus* and *Scarus iseri/taeniopterus*, but identification difficulties with adult *Stegastes* spp. and juvenile *Scarus* spp. meant that juvenile and adult distributions were plotted on separate maps rather than length-frequency diagrams (Fig 4.2 32-37).

All of these observations suggest that the shallow, seagrass-sand-macroalgae mosaic of lagoons is more favorable to small fish while the sand-rock-coral mosaic on the seaward reef favours larger fish.



Longspine squirrelfish - *Holocentrus rufus*

5

Spatial Patterns of Fish Species Richness, Abundance and Habitat Complexity

> *'I have heard that a rock near the Bermudas, lying many miles out at sea, and at considerable depth was first discovered by the circumstance of fish being observed in the neighbourhood.'*
>
> CHARLES DARWIN

5.1 INTRODUCTION

Complexity may be defined as 'consisting of many different and connected parts' (Anon 1989). Therefore, an assessment of habitat complexity should attempt to quantify several different aspects of habitat structure and composition. Most fishermen know that the best place to find fish is around structure, such as a fallen log in a stream, a shipwreck or even artificial reefs. The first artificial reefs were built in Japan as early as the 1700's as fish aggregating devices (Meier et al. 1989).

According to the Hutchinsonian concept of a niche (Hutchinson 1957), more complex habitats will offer a greater variety of different resources such as shelter, nesting sites, food etc. to the animals living there. One would therefore expect more complex habitats to support a greater variety of species than less complex ones.

The aim if this chapter is to describe the spatial patterns of fish species richness, abundance and diversity in relation to habitat complexity across all stations by addressing the following questions:

1) Are fish species richness, diversity and abundance related to habitat complexity?
2) Is the complexity index independent of overall habitat type?
3) Which components of the habitat complexity index are most strongly correlated with changes in the fish assemblage?
4) What is the spatial variation in habitat complexity in the area?

5.1.1 Measuring complexity

Animal communities are usually delimited with reference to plants or environmental factors. The environment where an animal lives is often described using these habitat variables, either qualitatively or quantitatively. An example of a qualitative habitat classification for terrestrial systems is open-ground, field, scrub or woodland. Subcomponents form distinct layers, subsoil, topsoil, ground zone, low canopy, high canopy and air above the canopy (Elton and Miller 1954).

Because our definition of complexity includes several different interacting variables, a quantitative assessment of habitat complexity should include multiple observations. The assessments either refer to the physical structure (such as vegetation height and layering, substrate rugosity, refuge spaces), or to the composition of the habitat, such as, variety of growth forms or foliage types, plant species richness and variety of substrate particle sizes (mud, sand pebbles and boulders).

The quantification of various habitat complexity variables can be a very labour-intensive process, and obtaining precise data about the variation of many different structural features is beyond the scope of many ecological studies. A less expensive approach can be taken that gives a broad and approximate assessment of habitat complexity by using simple, subjective indices. Consultancy work often employs these methods because there is a premium on the amount of information returned whilst using limited resources—known more commonly as rapid bioassessment methods. They were originally devised for use in rivers (Barbour et al. 1999), but have spawned many conceptually similar indices.

5.1.2 Components of marine habitat complexity

Topographic complexity is one of the most frequently cited variables related to fish species diversity. (Risk 1972) working in the US Virgin Islands found that fish species diversity, but not abundance, was related to the topographic complexity. He measured complexity by draping a fine-linked chain over 1m transects. However, this took 5 hours underwater to assess a single 1m^2 quadrat! (Luckhurst and Luckhurst 1978) obtained similar results, using the term ‘rugosity’ to describe this aspect of complexity. Since then, rugosity has been positively correlated with reef fish diversity by many authors (e.g. (Sano et al. 1984, Roberts and Ormond 1987, McGehee 1994, Jennings et al. 1996, Beukers and Jones 1997, Chabanet et al. 1997, Ohman and Rajasuriya 1998).

Substratum diversity has been calculated in many different ways. One method is highly correlated to tropical marine fish species richness, but not to abundance. It involves calculating a diversity index from percentage cover of substratum variables based on the relative length of transect tape covering hard coral, soft corals, filamentous algae or coralline algal cover (Roberts and Ormond 1987). However, when Risk (1972) used a similar method he did not find a significant correlation, his seven substratum categories being sand, sponges, dead coral, and four species of coral. (Ohman and Rajasuriya 1998) found that the number of habitat variables (live hard corals of each genus, dead coral, coral rubble, other sessile invertebrates, algae, sand or sandstone) was correlated with fish species diversity (Shannon's index).

Refuge sites assessed by counting number of holes in the following size categories 1-5cm, 6-15cm, 16-30cm, 31-50cm and >50cm accounted for a significant proportion of total fish abundance, but the total number of holes was not significantly correlated with total fish species richness in a study by (Roberts and Ormond 1987). Luckhurst and Luckhurst (1978) assumed that an increase in the diversity of shelter sites would enhance species richness by increasing the refuge availability for a range of species of different body sizes. But other authors have suggested that an observed increase in species richness at stations with more holes is an artefact of the main effect—increasing fish abundance (Molles 1978, Caley and St John 1996). An excellent experimental study by Hixon and Beets (1993) found that the number of prey fish was influenced by the presence or absence of holes in artificial reefs, but that hole size and number of holes were less important.

Percentage live cover has been more controversial. On reefs, correlations have been found between the amount of live coral cover and fish species diversity indices and abundance (Carpenter et al. 1981, Bell and Galzin 1984, Sano et al. 1984); while other authors have found little or no correlation (Luckhurst and Luckhurst 1978, Mc Manus et al. 1981, Roberts and Ormond 1987). Seagrass cover has been positively correlated with fish species richness and abundance in numerous studies (Aliaume et al. 1990, Edgar and Shaw 1995, Hemminga and Duarte 2000).

Height or vertical relief has been positively correlated with the fish species richness and diversity in at least two studies (Luckhurst and Luckhurst 1978, Molles 1978).

Percentage hard substrate is a critical habitat variable in aquatic systems as it indicates the relative stability of substrates that algae, corals sponges etc. can grow on. Fish species richness has been significantly correlated with percentage hard substrate in a number of studies (Cohen et al. 1993, Guidetti 2000, Khalaf and Kochzius 2002).

In fact, most fish-habitat studies have made some assertion (either quantitative, qualitative or anecdotal) that habitat complexity influences fish diversity and or abundance. Most measures of habitat complexity are very time-consuming to measure, and are generally inapplicable over a range of habitats.

5.2 METHODS

5.2.1 Sampling

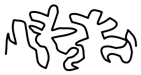
Detailed fish sampling methods are given in Chapter 3 sections **3.2.1 – 3.2.2**. In addition to these methods, a rapid-assessment habitat complexity index was designed. A self-explanatory Habitat Assessment Score (HAS) sheet was copied onto the back of an underwater slate (Table 5.1). On both occasions HAS variables in each of the four quadrats were recorded while the observer was waiting for fish to settle down after laying the quadrat poles. The mean HAS for each complexity category was calculated for each station and used in the analysis.

5.2.2 Analysis

The abundance data were square root transformed to normalize the data then tested for multicolinearity before running a Canonical Correspondance Analysis (CCA) (ter Braak 1986) on the fish and habitat complexity data using ECOM software (Henderson and Seaby 2002)(see full account of ordination methods **3.1.2**). Stations were categorised according to the dominant habitat type (i.e. the habitat type occupying the highest percentage cover relative to other habitat types).

A multiple regression model using complexity variables as predictors of fish species richness and abundance was carried out using SPSS v 11.5 software $^{©}$. An account of multiple regression methodology and rationale is given in section **4.2.3.**

Table 5.1 Habitat Assessment Score (HAS) sheet for near-shore coastal habitats, copied on to the back of an underwater slate. The HAS score for each category is assessed visually in each quadrat and recorded along with fish data.

	HAS SCORE				
	1	**2**	**3**	**4**	**5**
Rugosity (visual topographic estimate of the substrate in each quadrat)					
Variety of growth forms (stalked/ lobed/ filamentous/ ribbon-like/ massive/ branching/ cylindrical/ tube/ fan/ plate/ pinnate/ encrusting/ other)	< 2	3 & 4	5 & 6	7 & 8	9 -10
Height (visual estimate of average height of habitat architecture)	0-9cm	10-19cm	20-39cm	40-79cm	> 80cm
Refuge size categories (holes or gaps in habitat architecture or substrate in the following size categories: 1-5cm, 6-15cm, 16-30cm, 31-50cm & 50cm+)	0-1	2	3	4	5
Live cover (total % cover of living corals, mangrove roots, sea grass, macroalgae, sponges etc)	0-19	20-39	40-59	60-79	80-100
Hard substrate	0-19	20-39	40-59	60-79	80-100

In order to test the null hypothesis of there being no significant effect of habitat type on the slope of species number/ abundance, an ANalysis of CoVAriance (ANCOVA) was run using SPSS v 11.5 software ©. This tests for any differences in the complexity-response variable slopes. Number of species and total fish abundance were dependent variables, HAS score the fixed factor and habitat type a covariate.

The direct relationship between HAS and fish species richness and abundance was described using a scatter plot and linear regression. The spatial relationship between total HAS and species richness and abundance were investigated using MAPINFO GIS software © to produce interpolated maps. Fish distribution maps were drawn by plotting relative abundance data for all species occurring at more than 10 stations on a base map of the area using MAPINFO Professional © software.

5.3 RESULTS

5.3.1 CCA Analysis

Rugosity and percentage hard substrate were colinear ($r^2 = 0.84$) suggesting that areas with more hard substrate cover are also more topographically complex. This caused multicolinearity problems (see chapter **3.2.5**), so percentage hard substrate was excluded from the analysis. The CCA analysis showed that reef dominated stations were generally more rugose than sand, algae or seagrass. The seagrass and algae dominated stations had higher percentage live cover than sand or reef stations (Fig 5.1). Unsurprisingly, sandy stations were characterized by low rugosity; low vertical profiles; a lack of refuge; low percentage live cover and few growth forms (Fig 5.1). At least 19 species (about 35%) clearly favored rugose substrates of the forereef, they were: *Abudefduf saxatilis, Acanthurus bahianus, Acanthurus coeruleus, Chaetodon striatus, Halichoeres maculatus, Halichoeres radians, Holocentrus rufus, Hypoplectrus nigricans, Malacoctenus aurolineatus, Malacoctenus triangulatus, Microspathodon chrysurus, Ophioblennius atlanticus, Scarus iseri/taeniopterus, Scarus vetula, Stegastes dorsopunicans, Sparisoma rubripinne, Sparisoma viride, Synodus intermedius* and *Thalassoma bifasciatum* (Fig 5.2). Species apparently favoring places with a variety of refuge size categories and a variety of growth forms were *A. saxatilis, Haemulon flavolineatum, Hypoplectrus puella, Sparisoma* juveniles and *Stegastes planifrons* (Fig 5.2). A number of species were apparently associated with high percentages of live cover; they were *Gerres cinereus, Haemulon sciurus, Lutjanus griseus, Mugil curema, Ocyurus chrysurus, Sparisoma radians* and *Sphyraena barracuda* (Fig 5.2).

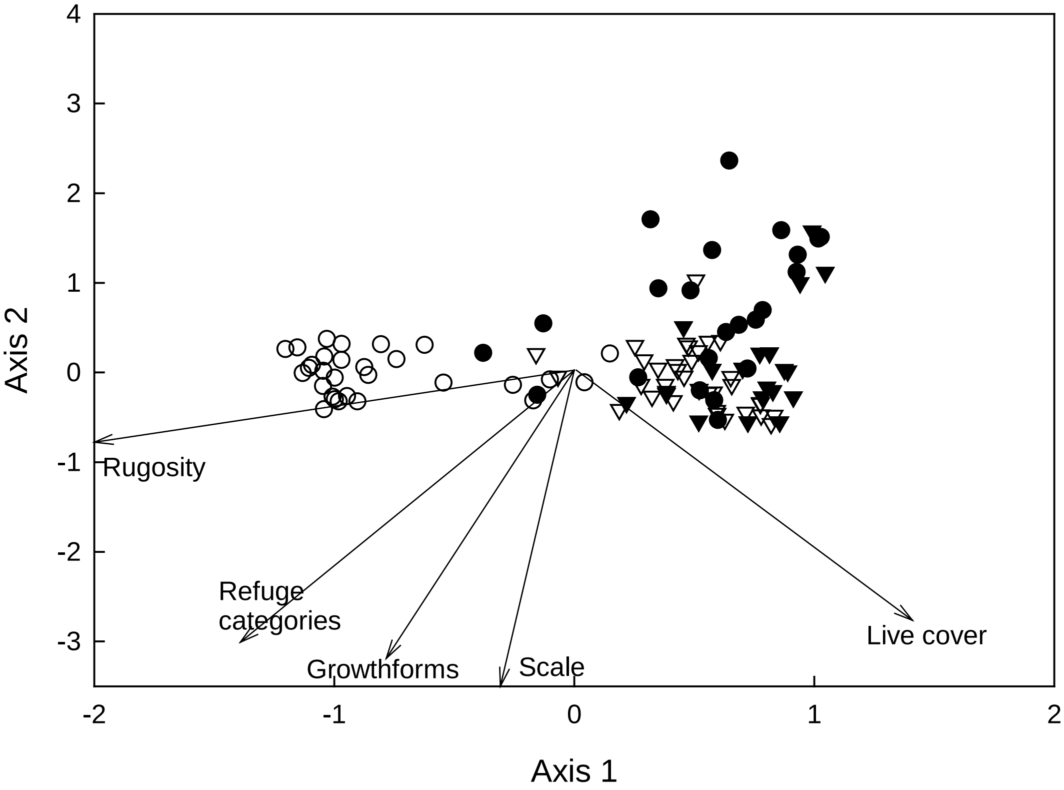


Fig 5.1 A CCA plot of habitat complexity variables and stations categorized by the main habitat variable present: ○ reef, ● sand, ▼ algae, ▽ seagrass. Eigenvalues: axis1, 0.45; axis 2, 0.12. *r* species-environment: axis1, 0.92; axis 2, 0.82. First 2 axes account for 21% of the variance. Monte Carlo test of all canonical axes significant ($p<0.01$), 1000 permutations.

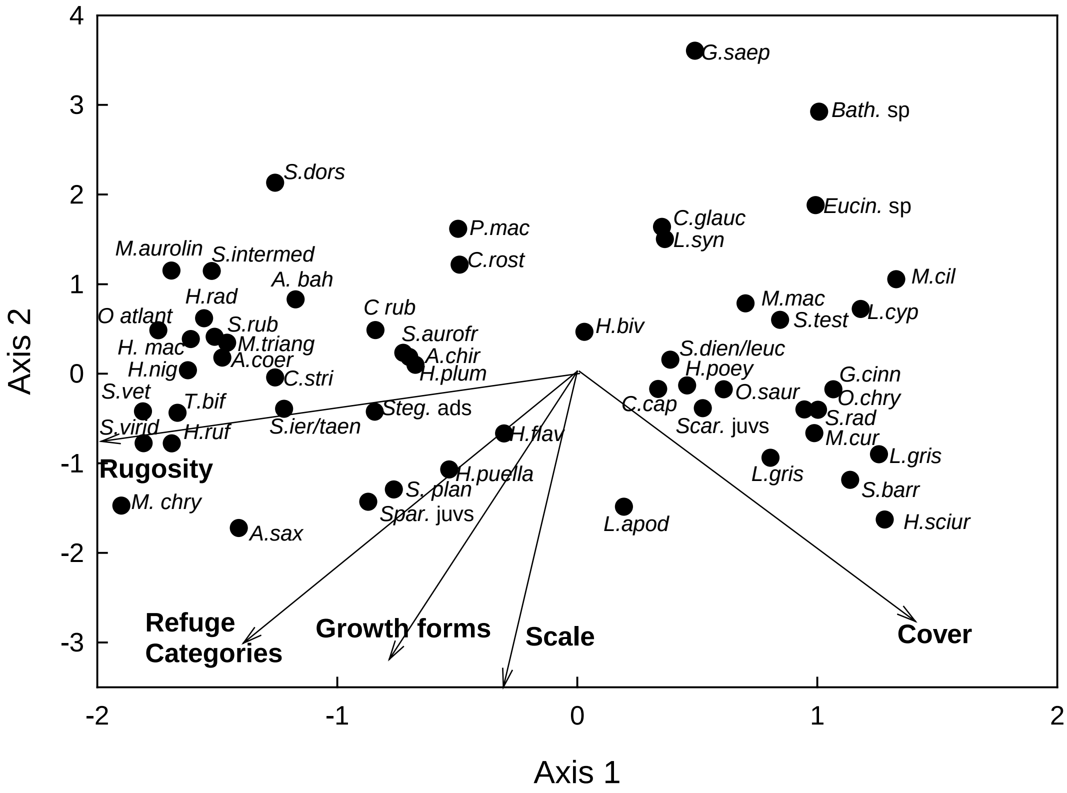


Fig 5.2 A CCA plot of habitat complexity variables and species. The initial letters of the following species are shown: *A. saxatilis, A. bahianus, A. chirurgus, A. coeruleus, Bathygobius* sp. *C. rostrata, C. capistratus, C. striatus, C. glaucofraenum, Eucinostomus spp., G. cinereus, G. saepepallens, H. aurolineatum, H. flavolineatum, H. plumieri, H. sciurus, H. bivittatus, H. poeyi, H. maculipinna, H. radiatus, H. rufus, H. plumieri, H. puella, H. nigricans, L. cyprinoides, L. griseus, L. apodus, M. aurolineatus, M. ciliatus, M. curema, M. macropus/versicolor, M. triangulatus, M. chrysurus, O. atlanticus, O. chrysurus, O. saurus, P. maculatus, S. dorsopunicans, S. intermedius, Scarus juveniles, S. iserti/taeniopterus* (ads), *S. aurofrenatum, S. barracuda, S. radians, Scarus* juveniles, *S. planifrons, S. leucostictus/diencaeus* (juvs), *Stegastes adults, S. vetula, S. viride, S. rubripinne, S. testudineus, T. bifasciatum.* Eigenvalues: axis1, 0.45; axis 2, 0.12. *r* species-environment: axis1, 0.92; axis 2, 0.82. First 2 axes account for 21% of the variance. Monte Carlo test of all canonical axes significant (p<0.01), 1000 permutations.

5.3.2 Multiple regression analysis

The combination of habitat complexity variables accounted for 71% of the variation in number of species but only 22% of the variation in total fish abundance (Tables 5.2 & 5.3). The two significant predictor variables of number of species were rugosity and variety of growth forms and they were positively correlated with number of species (Table 5.2). The only significant predictor variable of total fish abundance was scale, habitats with taller profiles tending to have more fish than shorter ones (Table 5.3).

5.3.3 Comparison across habitats

Sandy stations were generally less complex, and had fewer species than algal and seagrass beds, which in turn were less complex and species-rich than reefs (Fig 5.3). A similar, but less marked pattern was noted with overall fish abundance (Fig 5.3). An ANCOVA analysis indicated that the different habitats did not have significantly different complexity/species richness slopes (Table 5.4). This implies that differences complexity, rather than the attributes of particular habitat types were indeed responsible for the observed variations in number of fish species, and to a lesser extent, fish abundance.

Table 5.2a-c Multiple regression analysis of habitat complexity variables as predictors of number of fish species.

Model Summary (5.2a)

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	0.84(a)	0.71	0.69	4.08

a Predictors: (Constant), Cover , Refuge categories, Scale, Growth forms , Rugosity

ANOVA (5.2 b)

	Sum of Squares	df	Mean Square	F	Significance
Regression	4058	5	811	48.7	0.000(a)
Residual	1665	100	16		
Total	5724	105			

a Predictors: (Constant), Cover , Refuge categories, Scale, Growth forms , Rugosity
b Dependent Variable: Total no. species

Coefficients (5.2 c)

	Standardized Coefficients Beta	t	Significance	Part correlation
(Constant)		-1.72	0.088	
Rugosity	0.64	6.03	0.000	0.32
Growth forms	0.21	2.44	0.016	0.13
Scale	0.05	0.75	0.450	0.04
Refuge categories	0.09	0.90	0.370	0.04
Cover	0.03	0.33	0.736	0.01

a Dependent Variable: Total no. species

Table 5.3a-c Multiple regression analysis of habitat complexity variables as predictors of total fish abundance.

Model Summary (5.3a)

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	0.47(a)	0.22	0.18	5.91

a Predictors: (Constant), Cover , Refuge categories, Scale, Growth forms , Rugosity

ANOVA (5.3b)

	Sum of Squares	df	Mean Square	F	Sig.
Regression	974	5	194	5.57	0.000(a)
Residual	3497	100	34		
Total	4472	105			

a Predictors: (Constant), Cover , Refuge categories, Scale, Growth forms , Rugosity
b Dependent Variable: Sqrt total no. fish

Coefficients (5.3c)

	Standardized Coefficients Beta	t	Significance	Part correlation
(Constant)		1.675	.097	
Rugosity	.260	1.483	.141	.131
Growth forms	-.124	-.861	.391	-.076
Scale	.271	2.176	.032	.192
Refuge categories	.154	.922	.359	.082
Cover	.164	1.133	.260	.100

a Dependent Variable: Sqrt total no. fish

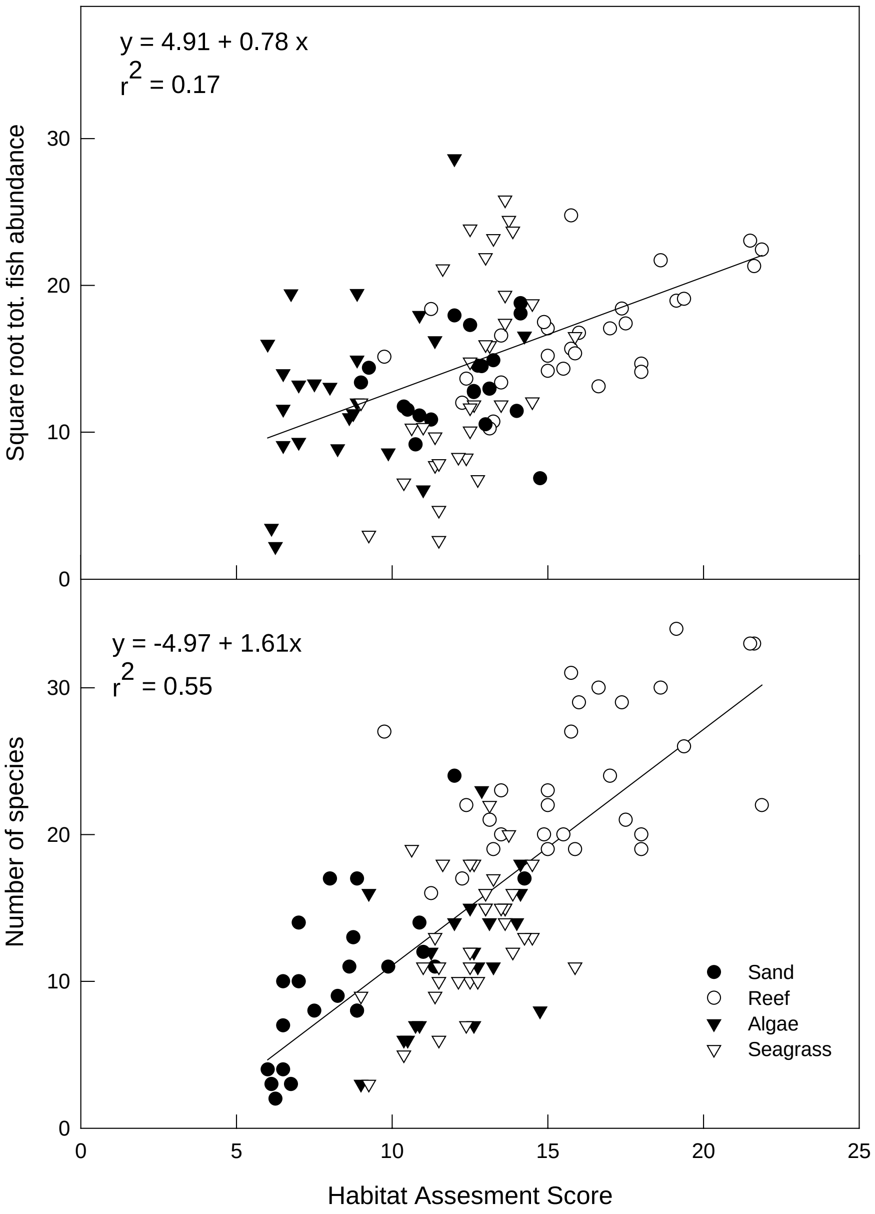


Fig 5.3 The relationship between the total HAS and species richness and abundance. The direct correlations are illustrated, but the multiple regression models account for 22% and 71% of the variation in fish abundance and number of species respectively (Table 5.2 and 5.3).

Table 5.4 ANCOVA analysis testing for differences in HAS (fixed factor) and habitat type (covariate) for a) total no of species and b) abundance.

a) Species = HAS + Habitat (where HAS is a fixed variable and Habitat is a covariable)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	5189.582(a)	66	78.630	5.022	.000
Intercept	2028.649	1	2028.649	129.570	.000
Habitat	9.831	1	9.831	.628	.433
HAS	4923.025	65	75.739	4.837	.000
Error	579.303	37	15.657		
Total	29712.000	104			
Corrected Total	5768.885	103			

a R Squared = .900 (Adjusted R Squared = .720)

b) Abundance = HAS + Habitat (where HAS is a fixed variable and Habitat is a covariable)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	2311.261(a)	66	35.019	1.399	.135
Intercept	1409.691	1	1409.691	56.304	.000
Habitat	1.935	1	1.935	.077	.783
HAS	2293.566	65	35.286	1.409	.130
Error	926.370	37	25.037		
Total	25458.250	104			
Corrected Total	3237.631	103			

a R Squared = .714 (Adjusted R Squared = .203)

5.3.4 Map of spatial variation in habitat complexity, species richness and abundance

The maps of habitat complexity, number of species and abundance (Fig 5.4) show that forereef areas are generally more complex than bay habitats, and these patterns are closely mirrored by variation in numbers of species. A similar, but less marked, pattern is evident with total fish abundance. Closer examination reveals patches outside bays with low complexity and species richness, while certain areas inside bays are both complex and species-rich, illustrating the patchiness of these habitats and the need for a single method that can be used to compare them. The total fish abundance at two stations in Paraquita bay was exceptionally high (Fig 5.4). This was connected to an exceptional recruitment of thousands of juvenile parrotfish that might ordinarily have been less abundant at these stations. One final interesting pattern to note is that the number of species immediately surrounding the mouth of Paraquita bay, which is entirely cut off from the ocean except by this small gap is slightly higher than might be expected judging from the habitat complexity index.

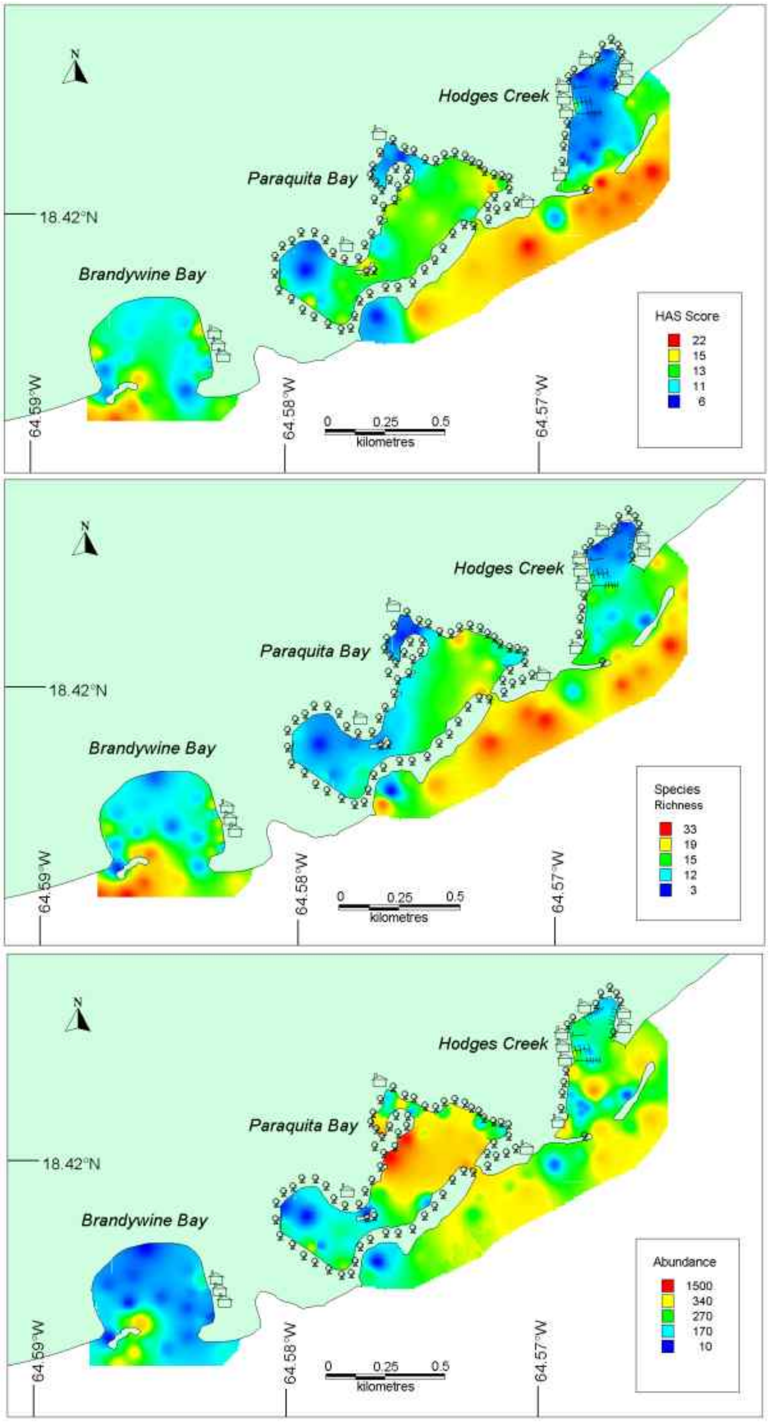


Fig 5.4 A map of habitat complexity index, species richness and abundance, interpolated using MAPINFO software from 106 stations in the sample area.

5.4 DISCUSSION

Overall, habitat complexity was an excellent predictor accounting for 71% of the variation in fish species richness in a variety of different habitats. This result may not be surprising, since many other fish diversity studies have come up with similar findings in many different parts of the world (Risk 1972, Gorman and Karr 1978, Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Gorham and Alevizon 1989, McClanahan 1994, Caley and St John 1996, Beukers and Jones 1997, Horan et al. 2000, Ferreira et al. 2001, Harding and Mann 2001). This study is the first time that a comprehensive list of different complexity variables has been examined simultaneously across a range of different marine habitats, and it has proven to be very effective at predicting fish species richness. The method is also a simple rapid assessment approach that is much more user-friendly than previous methods, taking just 1 minute per quadrat compared to Risk 1972 who spent 5 hours underwater assessing a single quadrat! Only 21% of the variation in fish abundance could be accounted for by this index, but it may be useful to take this potential source of variation into account in future fisheries models.

5.4.1 HAS variables

Rugosity and **percentage hard substrate** were multicolinear. While both variables are biologically important in shallow tropical marine areas, they are not entirely independent as rock is the principal hard substrate in a marine environment, and it is both hard and rugose. Rocky substrates are stable with large surface areas on which microscopic algae, macroalgae, live hard corals, gorgonians, encrusting gorgonians, sponges and other animals can live. It is biologically important because many fish species graze on the epilithic algae (Carpenter 1986, Hixon and Brostoff 1996, Lawson et al. 1999, Ferreira et al. 2001). These algae are important nitrogen fixers (Larkum 1999) and are the primary source of production on reefs (Klumpp and McKinnon 1989). They cannot grow on sand, which is unstable and moves in turbulent environments with a grinding action that is not suitable for the settling and growth of algae (Hillebrand and Kahlert 2002), corals (Rogers 1990) or some invertebrates such as lobsters (Booth 2001). Rugose substrates may also offer more cover from predators, or nesting sites that would make them attractive to some species. At least 35% of the fish species analysed were strongly positively correlated with rugosity, making this the most significant variable explaining variation in number of fish species in the multiple regression model where its standardised correlation coefficient was 0.64.

Variety of growth forms was the second most important habitat complexity variable for predicting number of fish species with a correlation coefficient of 0.21. The variety of growth forms is an indication of the variety of different types of substrate and will be an indication of the variety of niches available. A variety of growth forms may result in increased species richness by providing camouflage to some fish. For example, trumpetfish *Aulostomus maculatus* are dependent on cylindrical sponges and branching gorgonians for camouflage to stalk their prey (DeLoach 1999). Others use certain habitat types for protection e.g. juvenile yellowtail damselfish *Microspathodon chrysurus* are strongly associated with blade-like firecorals (Robertson 1984). The variety of growth forms will be indicative of a greater range of possible food niches. One example of a food specialist is the bucktooth parrotfish *Sparisoma radians* that feeds on ribbon-like seagrasses (Greenway 1995, Kirsch et al. 2002). Other studies examining the diversity of growth forms have used a variety of methods, a factor that has lead to confusion and contradictory results. At least two studies indicate positive correlations between fish species richness and coral species richness or substratum diversity indices (Roberts and Ormond 1987, Ohman and Rajasuriya 1998). Another study found no correlation between coral species richness and fish species richness (Luckhurst and Luckhurst 1978) and Risk (1972) found no correlation between fish species richness and substrate diversity. The assessment of variety of growth forms is an attractive method because it is a simple, direct measure of the diversity of living substrata but does not require expertise in benthic plant and invertebrate taxonomy, and should be used together with rugosity estimates in future research.

Scale was not a significant predictor of number of species in the multiple regression model, but it was, however, a significant variable explaining variation in fish abundance and had a correlation coefficient of 0.27. Taller habitats do not necessarily increase the variety of hiding places, or potential kinds of food, but they will usually have larger relative substrate surface areas than shorter habitat types. In nutrient-poor tropical marine systems, reefs with higher surface areas would have higher levels of substrate-linked productivity and might therefore support more fish, or they may simply have more places for fish to hide in.

Increasing the variety of **Refuge size categories** would theoretically enhance species richness by increasing the refuge availability to a range of species with different body sizes (Luckhurst and Luckhurst 1978). Other authors suggest that any observed increase in species richness at stations with more holes is an artefact of the main effect–increasing fish abundance (Molles 1978, Caley and St John 1996). The methods in this study were chosen based on protocol established by Roberts and Ormond (1987) who found that the variety of hole-categories accounted for a significant proportion of total fish abundance, but the total number of holes was not significantly correlated with total fish species richness. In this study, however, other variables were more important predictors of fish abundance and number of species.

Percent live cover was not a significant predictor variable for fish species richness or abundance, it is probably because some habitats with low fish species diversity, such as seagrass and algal beds, had very high percentage of live cover. Certain species that favor these habitats were however correlated with percentage live cover (Fig 5.2). The ratio of live coral cover on reefs and the percentage cover of seagrass may be useful fish species diversity predictors *within* habitat types (Carpenter et al. 1981, Bell and Galzin 1984, Sano et al. 1984, Aliaume et al. 1990, Edgar and Shaw 1995, Hemminga and Duarte 2000), but the relationship breaks down when applied *between* habitat types.

5.4.2 Spatial patterns of species richness, abundance and overall habitat complexity

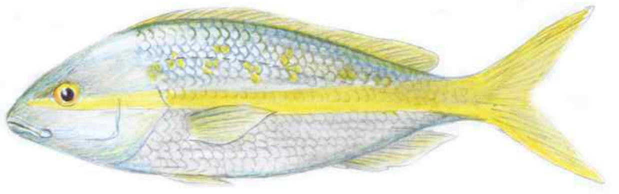
Reef areas are generally more complex habitats than seagrass and algal beds and these are more complex than sand. The more complex habitats supported more fish and more species than seagrass or sand, a pattern noted by others (Sedberry and Carter 1993, Nagelkerken et al. 2000, Mateo and Tobias 2001). This is, however, the first attempt to quantify habitat complexity variables and relate them to fish species richness across a number of habitats. The index performs well, accounting for both within habitat and between habitat differences in complexity. Forereef areas tend to be the most complex with high species richness, but the spatial variation in habitat complexity is patchy (Fig 5.3), reflecting the mosaic of different habitat types. Bay habitats on the other hand are less complex with lower species richness and abundance. The mouth of Paraquita bay had more species than one might expect in relation to the complexity. (Nagelkerken et al. 2000) noted a similar pattern around the mouth of an enclosed bay in Curaçao. This is probably related to large volumes of water entering the bay through one restricted opening. As the tide rises and pelagic juveniles of reef fish enter Paraquita bay, they will probably settle onto the first suitable substrate they encounter, resulting in higher species richness and abundance around the mouth of the bay. One part of Paraquita bay had exceptional numbers of schooling juvenile parrotfish. While seagrass habitats are known to support very high numbers of juvenile parrotfish (Nagelkerken et al. 2000), this exceptionally large number of fish was probably related to a recent recruitment pulse of pelagic juveniles settling in this thick, shallow seagrass bed where predators could be avoided.

5.4.3 Potential Applications

The fact that many complexity variables are useful predictors of fish community properties means that these results do have some immediate implications in the field of tropical marine research. For example, comparing fish species richness inside and outside marine reserves should take into account differences in habitat complexity. In a review of 25 studies of marine reserve design, only 5 attempted to factor habitat variables out of reserve/fished comparisons (Russ 2002). The present method is a substantial advance in this field and could easily be applied elsewhere.

Similarly the effects of environmental impacts such as sedimentation and eutrophication on fish communities cannot be directly assessed unless habitat-type controls (such as artificial reefs) are used to detect effects. Disturbance events such as hurricanes, coral bleaching, and crown of thorns outbreaks that degrade habitat structure will probably lead to predictable reductions in local reef fish diversity. On a similar vein, one might expect artificial reefs and shipwrecks on a sandy bottom to increase local fish species diversity and abundance.

It is recommended that any future adaptations of this rapid assessment method comparing different habitat types should discard the live cover category, and pay particular attention to the possible colinear relationship between rugosity and hard substrate. A comparative study in another biogeographic region would be useful to extend the range of validity of these data, which were only collected in one very localised area.



Yellowtail snapper – *Ocyurus chrysurus*

6

Experiments Testing the Effects of Habitat Complexity, Time and Sea Urchins on Fish Assemblages.

> *'But any child could tell you that fish like to live in those little plastic castles!'*
>
> ANDREW EVANS

6.1 INTRODUCTION

The previous chapter describes factors that are correlated with fish species richness. This is an essential step in hypothesis formation but experimental tests of each hypothesis are required to compare each complexity variable separately. This chapter explores the effects of three factors on fish communities:

1 Habitat complexity

The following hypotheses are tested:

a) Increasing rugosity increases fish species richness/abundance.
b) Increasing height increases fish species richness/abundance.
c) Increased variety of growth forms increases fish species richness/abundance.
d) Increased variety of hole sizes increases fish species richness/abundance.
e) Increased percentage hard substrate increases fish species richness/abundance.

2. Time

The weekly fish communities on the reefs is described and examined for any evidence of fish succession patterns on newly installed artificial reefs.

3. Urchins

I also tested the hypothesis that long-spined sea urchins *Diadema antillarium* increase the number of fish/species by providing shelter in low-complexity environments.

6.1.1 Habitat complexity

Habitat complexity is a useful predictor of variation in species richness at local scales for many different animal species (Mac Arthur and Mac Arthur 1961, Pianka 1966, Southwood et al. 1979, Roberts and Ormond 1987). However, quantifying habitat complexity is a difficult concept that often involves some measure of both the physical structure and the composition of habitat, and not all of the variables will have an equal weight in determining the species richness and or abundance (see chapter 5).

Many fish-habitat studies have demonstrated correlations between some measurement of habitat complexity and fish species richness (Risk 1972, Gorman and Karr 1978, Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Gorham and Alevizon 1989, McClanahan 1994, Caley and St John 1996, Beukers and Jones 1997, Horan et al. 2000, Ferreira et al. 2001, Harding 2003). These studies are complimented by artificial reef experiments that manipulate habitat in order to assess their effect on fish communities. Most studies simply document increases in fish species richness and/or abundance around artificial reefs using the surrounding habitats as controls e.g. (Diamant et al. 1986, Bortone et al. 1988, Santos and Monteiro 1998, Heise and Bortone 1999, Freitas and Petere 2001). Others compare the effectiveness of different reef designs. For example, when fish aggregating devices (usually streamers or flags) are attached to artificial benthic reefs, they attract more fish than other artificial reef designs (Beets 1989, Gorham and Alevizon 1989). Increasing the size and hence the volume of artificial reefs can also increase the abundance and species richness of fish, but this is a non-linear effect (Borntrager and Farrell 1992). Reefs with taller vertical profiles attract more fish than shorter ones (Molles 1978, Kellison and Sedberry 1998, Rilov and Benayahu 2002). And finally, increasing the variety of hole sizes and/or the number of holes in an artificial reef usually increases fish species richness and abundance (Hixon and Beets 1993, Ody and Harmelin 1994, Caley and St John 1996, Kellison and Sedberry 1998) .

While these independent studies have been very informative, a more systematic approach simultaneously examining all complexity variables would indicate which of these factors is the most important. The results of this experiment may also yield clues about the potential mechanisms structuring fish communities at local scales.

6.2.2 Time

Settling plants, algae and animals can readily change the structure of artificial reefs. This is known as the fouling community, which is often an added attraction on shipwrecks. These communities are particularly spectacular in the tropics because they often include corals. Algal colonisation is usually very rapid as diatoms and bacteria colonise new hard surfaces within 24hrs and algal sporelings attach within the first week, although grazing fish keep the epiphytic algal layer closely cropped (Baily-Brock 1989).

Sessile animals such as corals and bryozoans take much longer times to settle and grow successfully.

It may take years for a well-developed fouling community to accumulate on artificial reefs, but fish often colonise the structures within hours of immersion (Baily-Brock 1989). More work needs to be done in this field to determine whether the observed accumulation of benthic algae and animals always has the same end-point and therefore represents a predictable succession pattern or not. (Shulman 1985)who worked in the US Virgin islands found that the number of fish species at new reef sites increased for the first 6 days and then species numbers began to stabilise. The fish community on an artificial reef may eventually become saturated with species. However, this is not regarded as a stable-climax community because there is usually a high species-turnover and fish numbers are variable depending on stochastic processes, predation and the recruitment of pelagic larvae (Sutherland 1974, Sale 1977, Doherty 1991, Hixon 1991).

6.2.3 Urchins

In addition to the inert substrates, sessile plants, algae and macroinvertebrates that contribute to habitat complexity, other animals may provide habitats. For example, some fish are associated with particular animals for food, shelter or protection from predators e.g. the pearlfish *Carapus bermudensis* that shelters in the anus of sea cucumbers during the day and forages in seagrass beds at night, or the remora *Remora remora* that attaches to large free-swimming fishes such as sharks (Humann 1994).

Many different species of fish have been observed sheltering in the spines of long-spined sea urchins *Diadema antilliarum* (Randall et al. 1964), similar observations have been made elsewhere (e.g. Magnus 1967, Hartney and Grorud, 2002) and this phenomenon may explain some of the variation in fish species richness unaccounted for in the habitat complexity study.

6.2.4 The need for an experimental approach

Initial observations indicated that variety of growth forms and percent hard substrate/rugosity were the most important complexity variables explaining variation in fish species richness. The variety of hole-sizes and the height of the habitat were the most useful variables explaining variation in fish abundance (Chapter 5). These variables were often correlated with each other, making it difficult to determine exactly which ones affected fish species richness and abundance. It was necessary to devise a systematic experiment that simultaneously tested each of the complexity variables using artificial reefs as appropriate controls. Artificial reefs are also ideal for experimentally testing the effects of other variables highlighted by field observation, such as the effects of urchins.

6.2 METHODS

6.2.1 Study area

Artificial reefs were positioned in 5 different stations situated in sparse seagrass on the south shore of Tortola (Fig 6.1). The reefs were situated in areas unfrequented by tourists and with no obvious sources of disturbance e on the fish community apart from occasional Antillean fish traps set by local fishermen. Turtlegrass *Thalassia testudinum* covered about 60% of the substrate and the most abundant macroinvertebrates were short-spined urchins known as sea eggs *Tripneustes ventricosus* and long-spined sea urchins *Diadema antillarum*. Small octopi *Octopus vulgaris* and spiny lobsters *Panulirus argus* were the most commonly encountered macroinvetebrates on the artificial reefs.

6.2.2 Habitat complexity

The localities were varying distances from other habitats such as coral reefs and mangroves that may have acted as potential sources of fish recruits to the artificial reefs. This factor was accounted for in the analysis by treating the 5 different localities as blocks in a randomised block-design ANOVA.

> ‘[A randomized block design ANOVA is] a type of two-way ANOVA (usually without replication) especially common in agricultural research, but also with applications in other biological field and laboratory experiments.’
> (Sokal and Rohlf 1990) p 346.

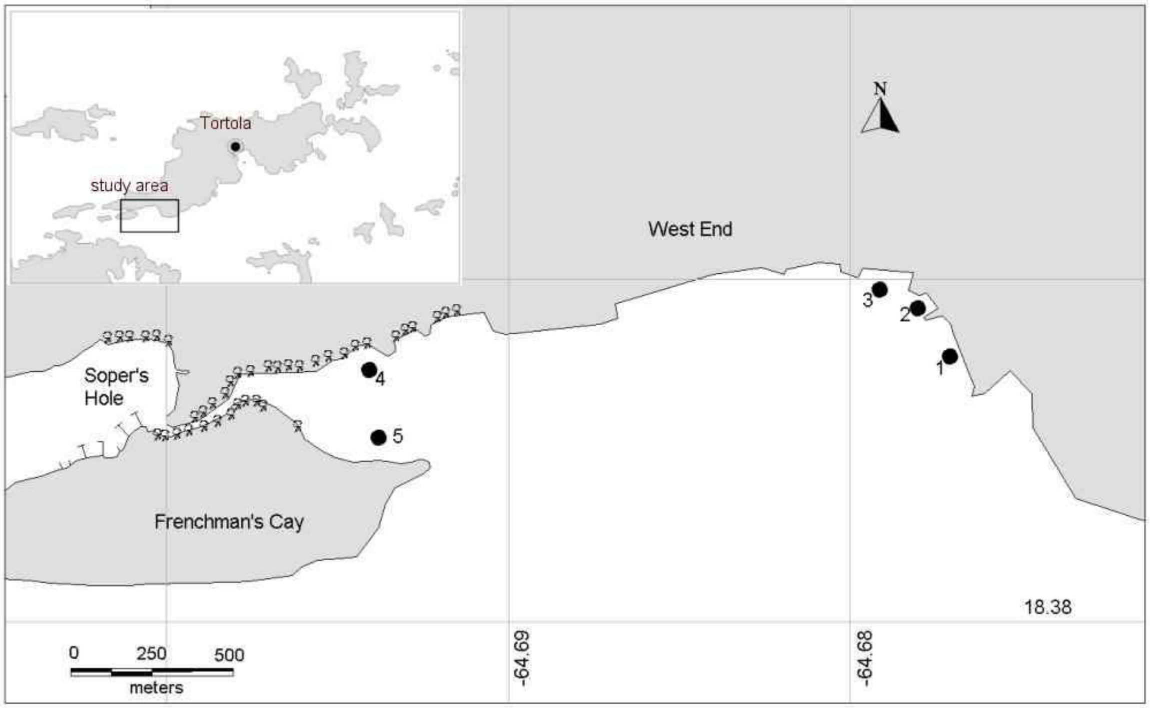


Fig 6.1 The location of the 5 sites where each of the 15 experimental reefs were located off Tortola, an island in the British Virgin Islands.

Fifteen treatments were established at each of the 5 stations to test various complexity hypotheses:

a) Increasing rugosity increases fish species richness/abundance

A flat $1m^2$ concrete reef served as the control, it was constructed using a $1m^2$ wooden base made from wooden planks which was covered with a 3cm layer of concrete. The first treatment consisted of six concrete blocks, 40cm x 20 cm x 15cm in size, without holes, arranged on a $1m^2$ concrete base. The second treatment increased the rugosity using 12 blocks in six stacks that were each 2 blocks high (Fig 6.2). The hypothesis predicts that the flat control reef will have fewer fish/species with 1 block-high ‘wrinkles’ and these in turn should have fewer fish/species reefs with 2-block high ‘wrinkles’.

b) Taller reefs have higher fish species richness/abundance than short reefs

The short reef was constructed using six concrete blocks, without holes, measuring 40cm x 20cm x 20cm. They were arranged tightly together in a single layer. The tall reef was built using eighteen concrete blocks. They were arranged in a similar way, but piled 3 blocks high (Fig 6.3). The hypothesis predicts that the taller reef would have more fish/species than the shorter reef.

c) Increased variety of growth forms increases fish species richness/ abundance

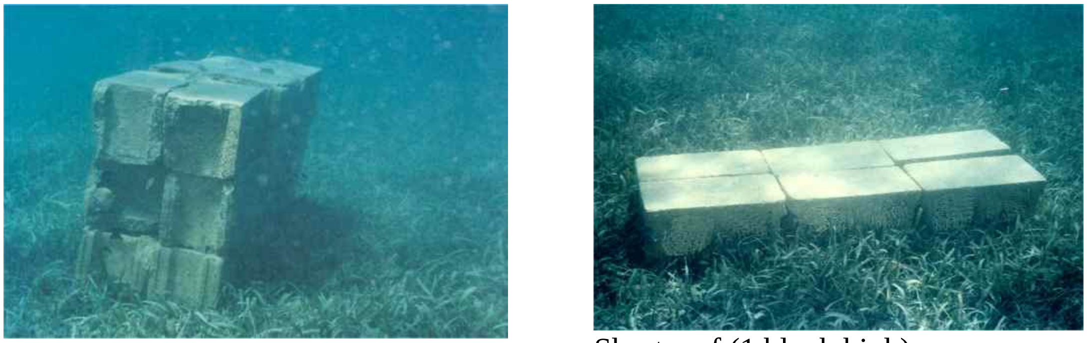
A flat, $1m^2$ concrete reef with no growth forms served as the control in this experiment. The first treatment (1 growth form) was made from a similar concrete base with only one type of growth form embedded into the concrete base. Each of the 5 replicates had a

Flat (control)

1 block high

2 blocks high

Fig 6.2 Experimental units used to test the effect of rugosity on fish species richness and abundance. Concrete platforms are 1m^2 and each reef was replicated once at each of the 5 stations.



Tall reef (3 blocks high)

Short reef (1 block high)

Fig 6.3 Experimental units used to test the effect of vertical profile on fish species richness and abundance; concrete blocks measure 20x20x40cm. Each unit was replicated once at each of the 5 stations.

different type of growth form embedded in it. One reef had 10 glass bottles (cylinder); one reef had 10 plastic bottles with the bottoms sawn off (tube); one had 10 small tree branches (branching); one with 10 upright tiles (plate-like) and one with 10 canvas strips (filamentous). The second treatment (5 growth forms) used two of each of these growth forms in each replicate (Fig 6.4). Some might argue that the single growth form reefs are not true replicates as each of the 5 units differs from each other. For the purposes of testing this hypothesis what is important is that there is only one kind of growth form present, and the actual type of growth form is irrelevant to the hypothesis. The reason that each of the replicates had one growth form selected from the 5-growth form design was because if each of these growth forms was not represented in the one-growth form design, one especially important kind of growth form in the 5-growth form design might bias the results. The hypothesis predicts that flat reefs with no growth forms will have fewer fish/species than the reefs with 1 type of growth form, and these in turn should have fewer fish/ species than the reefs with 5 different types of growth forms.

d) Increased variety of hole sizes increases fish species richness/abundance

Six concrete blocks, without holes, measuring 40cm x 20cm x 20cm were arranged tightly together in one layer as the control (no holes). A similar arrangement of blocks with large, 13cm x 13cm holes, was the first treatment (large holes), and a similar arrangement of blocks with 4cm x 8 cm holes was the second treatment (small holes). A reef consisting of both small and large holes was the final treatment (Fig 6.5).

There were fewer holes per unit volume in the large-holed structures (12) than in ones with mixed-hole sizes (24). In turn, these had fewer holes than the small-holed (36)

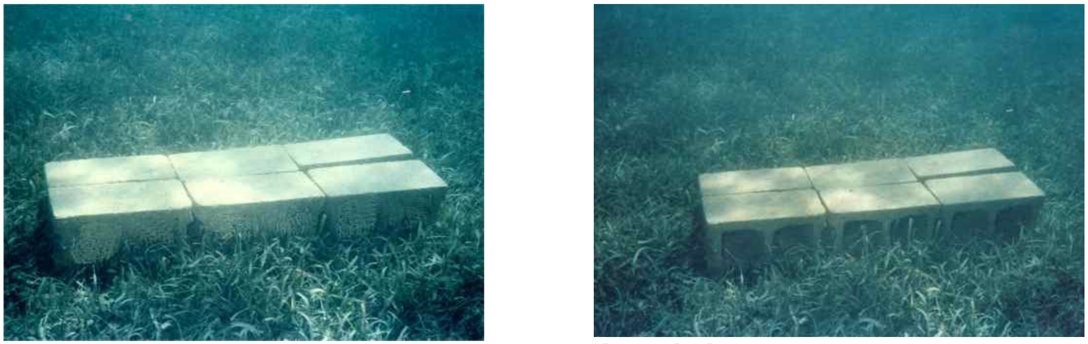
0 growth forms (control)

1 growth form (plate)

1 growth form (cylinder)

5 growth forms (cylinder, branch, plate, ribbon & tube)

Fig 6.4 Experimental units used to test the effect of variety of growth forms on fish species richness and abundance; concrete platforms are 1m^2. All treatments were replicated once at each of the 5 stations.



no holes (control)

large holes

small holes

small and large holes

Fig 6.5 Experimental units used to test the effect of variety of hole sizes on fish species richness and abundance. Large holes are 13cm x 13cm and small holes are 4x8 cm.

structures. It is worth noting here that Hixon and Beets (1993) found that number of holes was only a limiting factor for fishes on artificial reefs with fewer than 12 holes but not for reefs with more than 12 holes. The purpose of this experiment was to test the effect of variety of hole sizes, keeping the volume of the artificial reef constant. The hypothesis predicts: i) That the reef with no holes will have fewer fish/species than all the other reefs with holes; ii) There will be no difference in fish/species between the small-holed reefs and the large-holed reefs; iii) The small and large-holed reefs will have more species than any other design.

e) Increased percent hard substrate increases fish species richness/abundance

The control, 0% hard substrate plots were selected from bare sandy patches occurring in the seagrass beds at each of the respective stations. Plots $1m^2$ were marked in the sand as permanent plots using steel pegs. Fifty percent hard substrate treatments were created in sandy areas by covering 50% of the substrate with 20cmx 20cm terracotta tiles. The $1m^2$ flat concrete reefs served as the 100% hard substrate treatment. In order to assess the relative effects of percentage hard substrate compared to the surrounding habitat type, a $1m^2$ plot of seagrass was also examined. The hypothesis predicts that the soft substrate will have fewer fish/species than the 50% hard substrate, which in turn will have fewer fish/species than the 100% hard substrate. The hypothesis would also technically predict that the seagrass plot should have the same number of fish/species as the sand plot, but because of the growth forms hypothesis one would actually expect the seagrass plot to have more fish/species than the sand plot.

The different treatments were positioned at least 10m from their nearest neighbor in a randomised order at each of the 5 stations. Water depth varied between 1 and 5m and mean visibility was 10m. Reefs were left for at least 1 week so that a fish population could become established on each of the reefs/plots. All fish spotted hiding in, under or located within 30cm of each reef were counted once weekly for a period of 5 weeks in the months of July and August 2002.

6.2.3 Presence of sea urchins increases numbers of fish/species by providing shelter in low-complexity environments

Ten rock reefs (high complexity environments) were built consisting of 1m^2 mounds of 10-20cm diameter rocks piled to a height of about 40cm. They ranged between 1 and 3m depth at stations 1 and 2. Five reefs were left bare, but the remaining 5 reefs each had 10 *Diadema antillarum* placed on them and they were left for a period of 1 week during which reefs were checked daily and urchin numbers were replenished if any had emigrated. After one week fish were counted for a period of 5 minutes. In surrounding seagrass beds (low-complexity environments), 1m^2 quadrats were laid on daytime urchin aggregations (ranging from 6-11 individuals) and fish were counted and then compared with an adjacent seagrass quadrat (5m away) that did not have any urchins. The hypothesis predicts that if shelter were the limiting factor that in the low complexity seagrass beds, that presence of urchins would increase numbers of fish/species. On high-complexity reefs, however, where shelter is less of a limiting factor there would be less difference between numbers of fish/species on reefs with and without urchins.

6.2.4 Analysis

1. Complexity

The data from all sampling occasions was pooled and the total number of fish species and total abundance of fish counted over the 5-sample period was calculated for each reef/plot. While sampling effort was constant over all experimental units, the total sample size varied. One problem when comparing samples of different sizes is that larger samples would be expected by mere chance alone to have more species than smaller samples (Simberloff 1972, Caley and St John 1996). The species richness of samples of different sizes can be made comparable through a process called rarefaction. Rarefaction curves use the expected number of species drawn from random sub-samples of each sample (Simberloff 1972). Thus, rarefaction curves were calculated for each sample in each experiment and compared at the abundance level of the reef with the smallest total number of fish using Biodiversity Pro Software © Natural History Museum and Scottish Association for Marine Science.

Data were tested for normality using a Kolmogorov-Smirnov and homogeneity of variance using the Levene test and appropriately transformed if necessary. Each hypothesis (1-5) was analysed in turn using a two-way ANOVA and a Tukey test to account for significant differences in the response variables (total fish abundance, observed number of species and expected number of species with constant sample size (rarefied)) using (SPSS v11.5 $^{©}$ software).

2. Time

The hypothesis that fish species richness and abundance changed from week to week was tested using an ANCOVA analysis testing for the overall effects of reef (fixed factor) and time (covariate) using SPSS v11.5 © software. A species accumulation curve over the 5-week period was drawn to investigate any stabilisation of the fish community during the sampling period.

3. Urchins

The hypothesis that presence of sea urchins affected fish species richness and abundance on each habitat type was tested using a two-way ANOVA (SPSS v11.5 © software).

6.3 RESULTS

A total of 60 fish species were encountered on all 65 reefs/ plots during the 5-week sampling period. Fish were rapidly attracted to the new structures, for example, during the construction of one rocky artificial reef on a sandy substrate with no visible fish present in the vicinity, 7 different species had been attracted to the site within 20 minutes (pers. obs)! Many of the fish attracted to the reefs were juvenile fish, particularly white grunts *Haemulon plumieri*, tomtates *Haemulon aurolineatum,* yellowtail snappers, *Ocyurus chrysurus* and juvenile parrotfish *Scarus* spp. These small, numerically dominant fish sheltered near the artificial reefs from roving predators such as the jacks *Caranx ruber* and *Caranx latus*. After the first week, reefs were covered in an algal film, but the fouling community did not develop substantially during the 5-week sampling programme—probably because of high grazing pressure from juvenile parrotfish and surgeonfish (pers. obs).

6.3.1 Complexity variables

a) Increasing rugosity increases fish species richness/abundance

Fish abundance was not significantly affected by changes in rugosity, but there were significant differences in fish abundance between bays (Fig 6.6, Table 6.1). Rugose reefs had significantly higher observed and expected numbers of species than the flat reefs, but there was no significant difference between reefs with 2-block-high stacks and the less rugose 1-block stacks (Fig 6.6, Table 6.1). Therefore increasing rugosity does not necessarily increase fish species richness proportionally. There were no significant differences in observed or expected number of species between bays (Table 6.1).

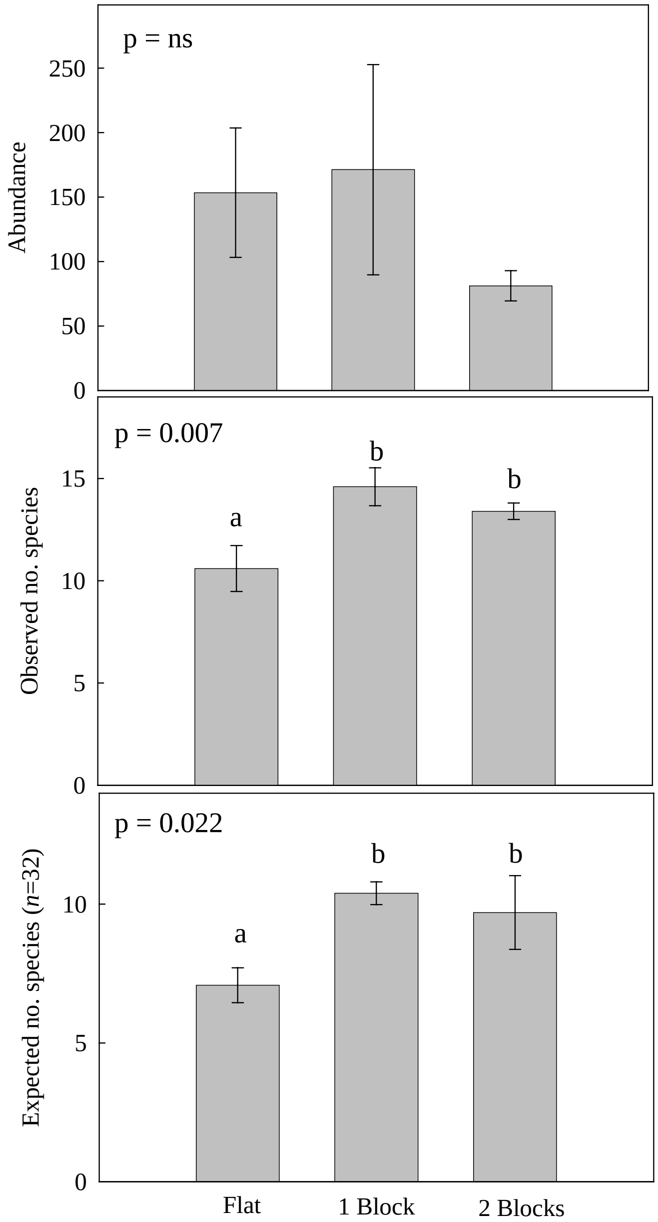


Fig 6.6 The effects of rugosity. Shown are the means ±SE of each response variable. The p values for significant differences are shown (full ANOVA tables overleaf). There is no significant difference between means with identical letters (*post hoc* Tukey Test).

Table 6.1 RBD ANOVA testing the main effects of rugosity (treatment) and bay (block) on a) abundance, b) observed number of species and c) expected number of species calculated by rarefaction to smallest sample (n = 32).

a) Abundance = Rugosity + Bay (Rugosity and Bay are categorical)

Source	Type II Sum of Squares	df	Mean Square	F	Sig.
Model	1950.5(*)	7	278.6	28.4	.000
Rugosity	26.6	2	13.3	1.3	.310
Bay	177.0	4	44.2	4.5	.034
Error	78.4	8	9.8		
Total	2029.0	15			

* R Squared = .961 (Adjusted R Squared = .928)

b) Species = Rugosity + Bay (Rugosity and Bay are categorical)

Source	Type II Sum of Squares	df	Mean Square	F	Sig.
Model	2553.8(*)	7	364.8	169.688	.000
Rugosity	42.1	2	21.0	9.798	.007
Bay	28.4	4	7.1	3.302	.071
Error	17.2	8	2.1		
Total	2571.0	15			

* R Squared = .993 (Adjusted R Squared = .987)

c) Expected no species (Rarefaction, *n* 32) = Rugosity + Bay (Rugosity and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1289.2(*)	7	184.1	77.8	.000
Rugosity	30.4	2	15.2	6.4	.022
Bay	27.5	4	6.8	2.9	.093
Error	18.9	8	2.3		
Total	1308.1	15			

* R Squared = .986 (Adjusted R Squared = .973)

b) Taller reefs have higher fish species richness/abundance than short reefs

There was no significant effect of reef height on fish abundance, observed number of species of expected number of species (Fig 6.7, Table 6.2), but abundance was significantly affected by bay (Table 6.2).

c) Increased variety of growth forms increases fish species richness/abundance

There was no significant effect of rugosity on the total number of fish on each reef; instead, the actual bay was a better predictor of variation in fish abundance (Fig. 6.8, Table 6.3). The observed number of species on reefs with 5 growth forms was significantly higher than the 0 growth forms model (Fig 6.8, Table 6.3). While the variety of growth forms was not a significant predictor of variation in the expected species richness, the observed trend was consistent with the hypothesis—increasing variety of growth forms was associated with increased species richness (Fig 6.8, Table 6.3).

d) Increased variety of hole sizes increases fish species richness/abundance

The results of this experiment were not conclusive. The small-holed reef had significantly higher numbers of fish (about 270) than all the other designs (Fig 6.9, Table 6.4). The observed number of species, however, was not significantly different between reefs without holes, small holes only, or large holes only. The only two treatments that were in fact significantly different were the large-holed treatment that had significantly fewer fish species (12) than the mixed-hole treatment (16 species). While the differences in species richness calculated by rarefaction were not significantly different, the final pattern was consistent with the hypothesis—small and large-holed reefs were more

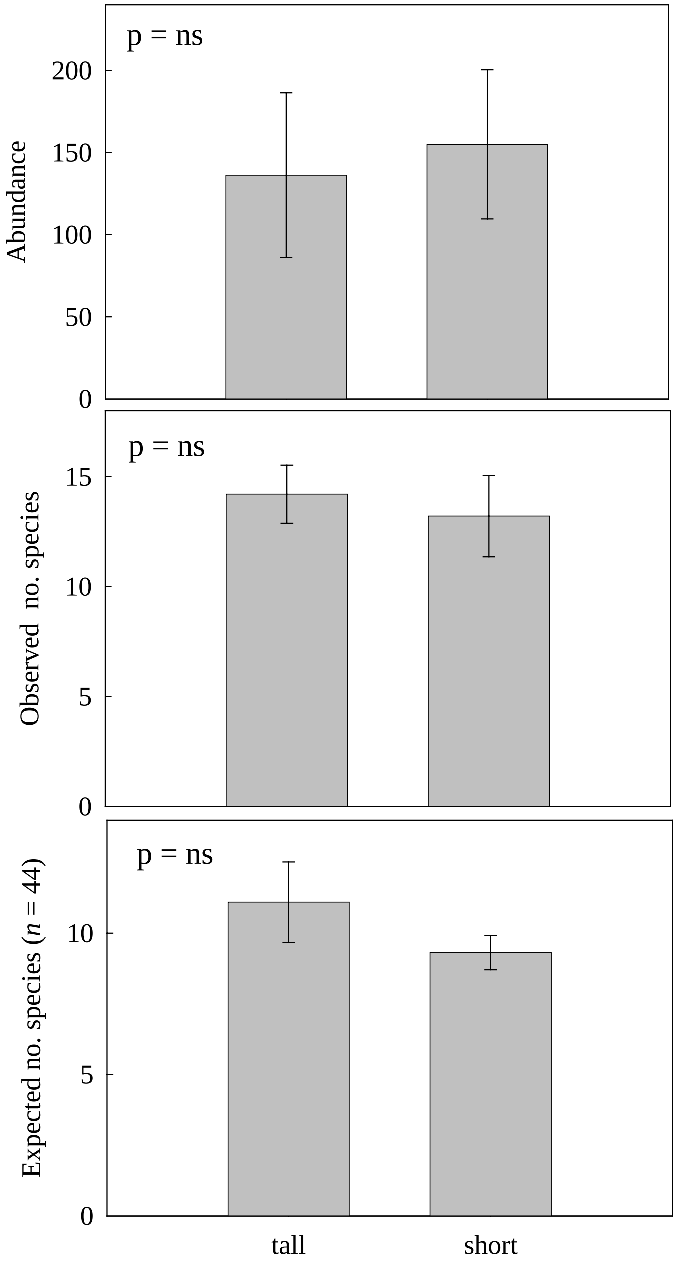


Fig 6.7 The effects of vertical profile for tall reefs (60cm high) and short reefs (20cm high). Shown are the means and SE for each response variable. Data were analysed using a 2-way ANOVA (tables overleaf).

Table 6.2 RBD ANOVA testing the main effects of height (treatment) and bay (block) on a) abundance, b) observed number of species and c) expected number of species calculated by rarefaction to smallest sample (n = 44).

a) Abundance = Height + Bay (Bay and Height are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	297045.6(*)	6	49507.600	26.839	.003
Bay	84168.4	4	21042.100	11.407	.018
Height	883.6	1	883.600	.479	.527
Error	7378.4	4	1844.600		
Total	304424.0	10			

* R Squared = .976 (Adjusted R Squared = .939)

b) Species = Height + Bay (Bay and Height are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1912.0(*)	6	318.6	17.953	.007
Bay	32.6	4	8.1	.459	.765
Height	2.5	1	2.5	.141	.726
Error	71.0	4	17.7		
Total	1983.0	10			

* R Squared = .964 (Adjusted R Squared = .910)

c) Expected no. species (Rarefaction, *n*44) = Height + Bay (Bay and Height are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1063.1(*)	6	177.192	20.778	.006
Bay	13.9	4	3.495	.410	.796
Height	7.9	1	7.957	.933	.389
Error	34.1	4	8.528		
Total	1097.2	10			

* R Squared = .969 (Adjusted R Squared = .922)

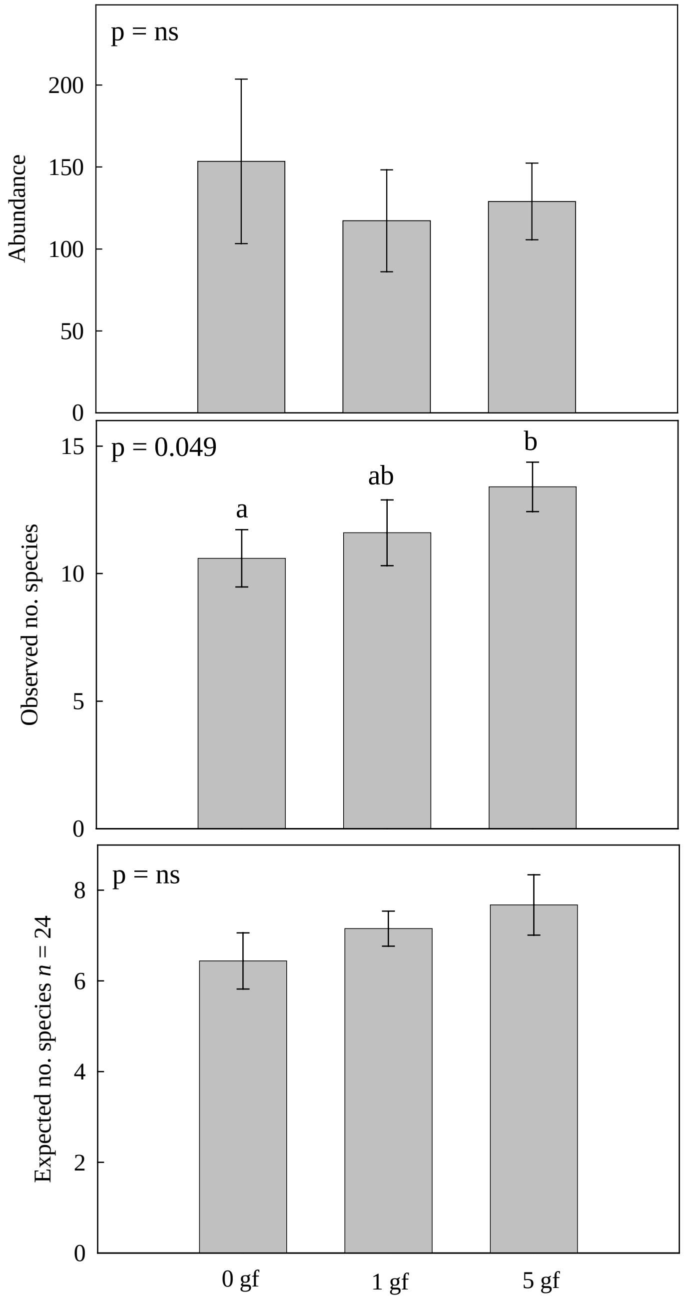


Fig 6.8 The effects of growth forms (gf). Shown are the means ± SE of each response variable. Data were analysed using a 2-way ANOVA (tables overleaf). There is no significant difference between means with identical letters (*post hoc* Tukey Test).

Table 6.3 RBD ANOVA testing the main effects of growth forms (treatment) and bay (block) on a) abundance, b) observed number of species and c) expected number of species calculated by rarefaction to smallest sample (n = 24).

a) Abundance = Growth Form + Bay (Growth Form and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	332514.7(*)	7	47502.1	20.1	.000
Growth forms	3384.4	2	1692.2	.7	.516
Bay	62196.9	4	15549.2	6.6	.012
Error	18834.2	8	2354.2		
Total	351349.0	15			

* R Squared = .946 (Adjusted R Squared = .899)

b) Species = Growth Form + Bay (Growth Form and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	2188.1(*)	7	312.5	139.9	.000
Growth forms	20.1	2	10.0	4.5	.049
Bay	55.7	4	13.9	6.2	.014
Error	17.8	8	2.2		
Total	2206.0	15			

* R Squared = .992 (Adjusted R Squared = .985)

c) Expected no. species (Rarefaction, *n*24) = Growth Form + Bay (Growth Form and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	765.9(*)	7	109.4	75.0	.000
Growth forms	3.8	2	1.9	1.3	.320
Bay	7.8	4	1.9	1.3	.335
Error	11.6	8	1.4		
Total	777.6	15			

* R Squared = .985 (Adjusted R Squared = .972)

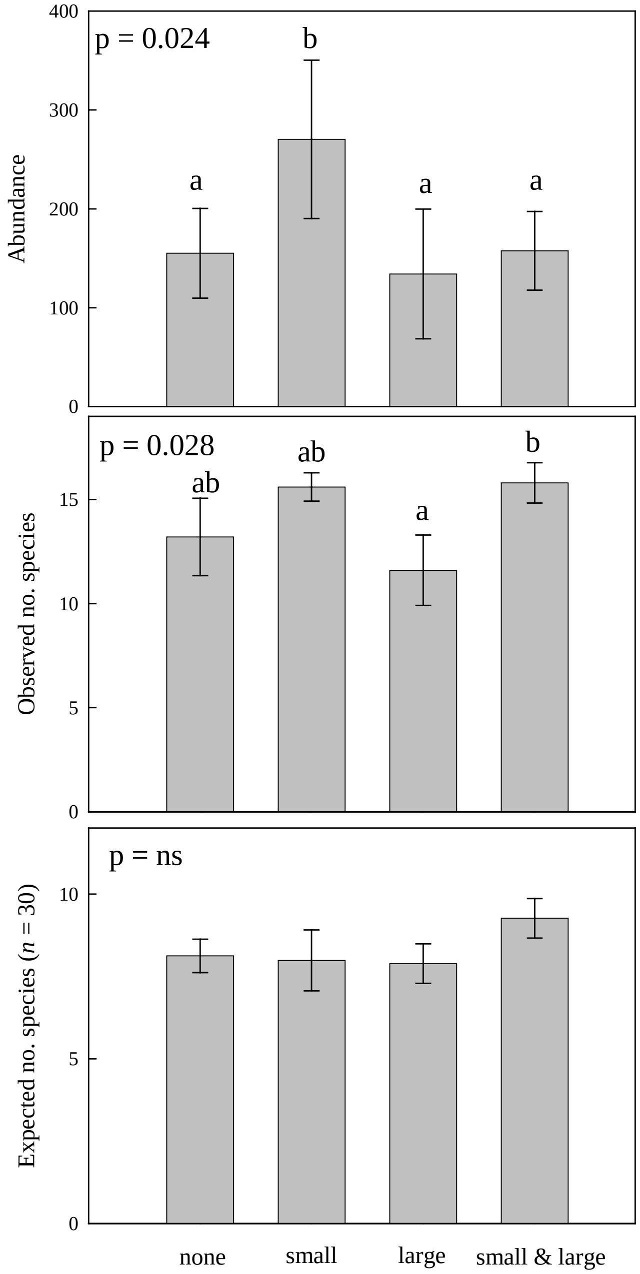


Fig 6.9 The effects of hole size. Shown are the means and SE of each response variable. Data were analysed using a 2-way ANOVA (tables overleaf). There is no significant difference between means with identical letters (*post hoc* Tukey Test).

Table 6.4 RBD ANOVA testing the effects of hole size (treatment) and bay (black) on a) abundance, b) observed number of species and c) expected number of species calculated by rarefaction to smallest sample (n = 30).

a) Abundance = Holes + Bay (Holes and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	935689.3(*)	8	116961.1	27.9	.000
Holes	56924.5	3	18974.8	4.5	.024
Bay	236870.3	4	59217.5	14.1	.000
Error	50225.7	12	4185.4		
Total	985915.0	20			

* R Squared = .949 (Adjusted R Squared = .915)

b) Species = Holes + Bay (Holes and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	4106.7(*)	8	513.3	109.4	.000
Holes	60.9	3	20.3	4.3	.028
Bay	97.7	4	24.4	5.2	.011
Error	56.3	12	4.6		
Total	4163.0	20			

* R Squared = .986 (Adjusted R Squared = .977)

c) Expected no. species (Rarefied *n*30) = = Holes + Bay (Holes and Bay are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1401.7(*)	8	175.2	90.9	.000
Holes	6.1	3	2.0	1.0	.401
Bay	13.5	4	3.3	1.7	.203
Error	23.1	12	1.9		
Total	1424.8	20			

* R Squared = .984 (Adjusted R Squared = .973)

species-rich than the others, however it is not significant at the α = 5% level because there is a 20% probability that this observed relationship is due to chance (Table 6.4).

e) Increased percent hard substrate increases fish species richness/abundance

There was a distinct increase in fish species richness with increasing percentage hard substrate (Fig 6.10, Table 6.5). However the sample sizes were so small for some of the sand, seagrass and 50% hard substrate treatments that rarefaction curves could not be calculated for expected numbers of species. Interestingly, the 1m^2 seagrass quadrat that technically has 0% hard substrate, but is more stable than sand because seagrass roots hold it together, had a similar number of fish to the 50% hard substrate treatment.

6.3.2 Temporal variation

Several new fish species were encountered every week and the species accumulation curve did not approach an asymptote over the course of this study (Fig 6.11). However, the mean of about 6 species of fish per reef did not change significantly over the 5 weeks (Fig 6.11, Table 6.6) indicating a stabilisation in number of fish species richness in spite of a constant change in the component species. The abundance of fish did change significantly over time, but it did not increase steadily to a plateau, as might be expected if fish were simply colonising unoccupied substrate until carrying capacity is approached. Instead, the numbers increased consistently until week 4 and then declined (Fig 6.11).

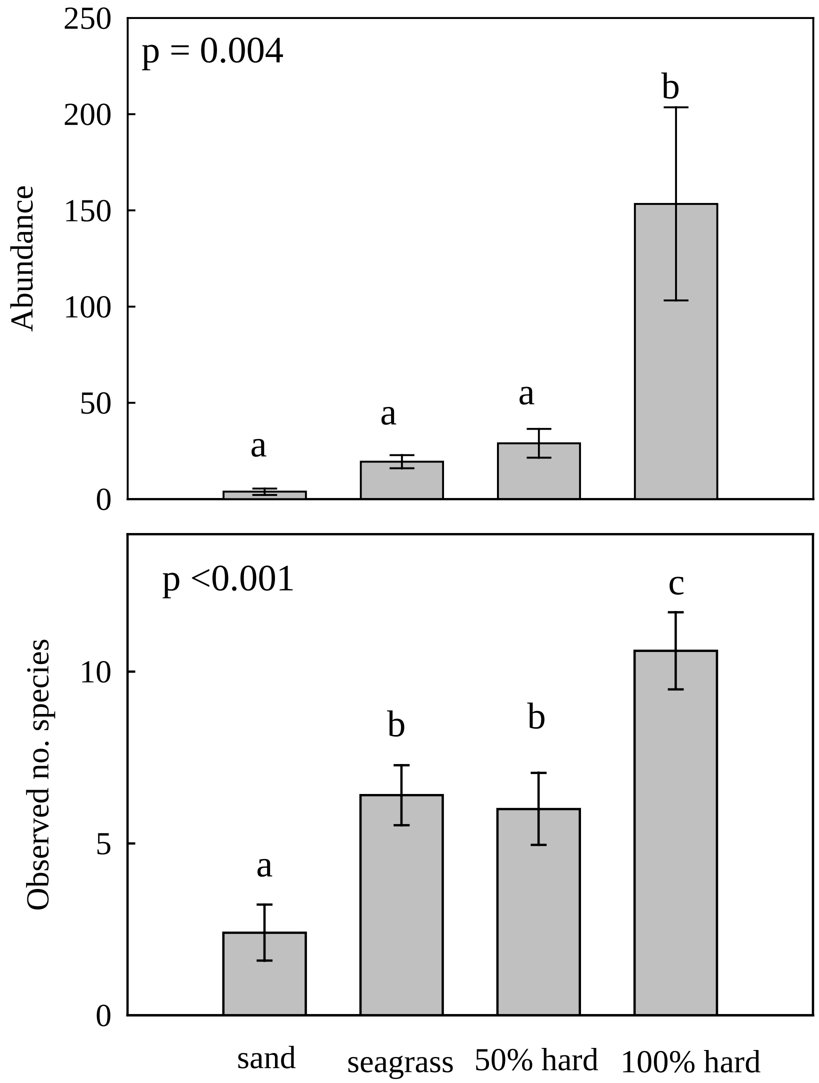


Fig 6.10 The effects of hard substrate. Shown are the means and SE of fish species richness and abundance for each treatment. Data were analysed using a 1 way ANOVA and a post hoc Least Significant Difference (LSD) test. There is no significant difference between means with identical letters.

Table 6.5 RBD ANOVA testing the effects of percentage hard substrate and bay on a) abundance, b) observed number of species note: expected number of species calculated by rarefaction could not be calculated as smallest sample was 0.

a) Abundance = Substrate + Bay (Substrate and Bay are categorical variables)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	139781.1(*)	8	17472.6	5.8	.003
Substrate	70977.6	3	23659.2	7.9	.004
Bay	15964.3	4	3991.0	1.3	.313
Error	35858.9	12	2988.2		
Total	175640.0	20			

* R Squared = .796 (Adjusted R Squared = .660)

b) Species = Substrate + Bay (Substrate and Bay are categorical variables)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1020.200(*)	8	127.525	49.685	.000
Substrate	168.950	3	56.317	21.942	.000
Bay	44.800	4	11.200	4.364	.021
Error	30.800	12	2.567		
Total	1051.000	20			

* R Squared = .971 (Adjusted R Squared = .951)

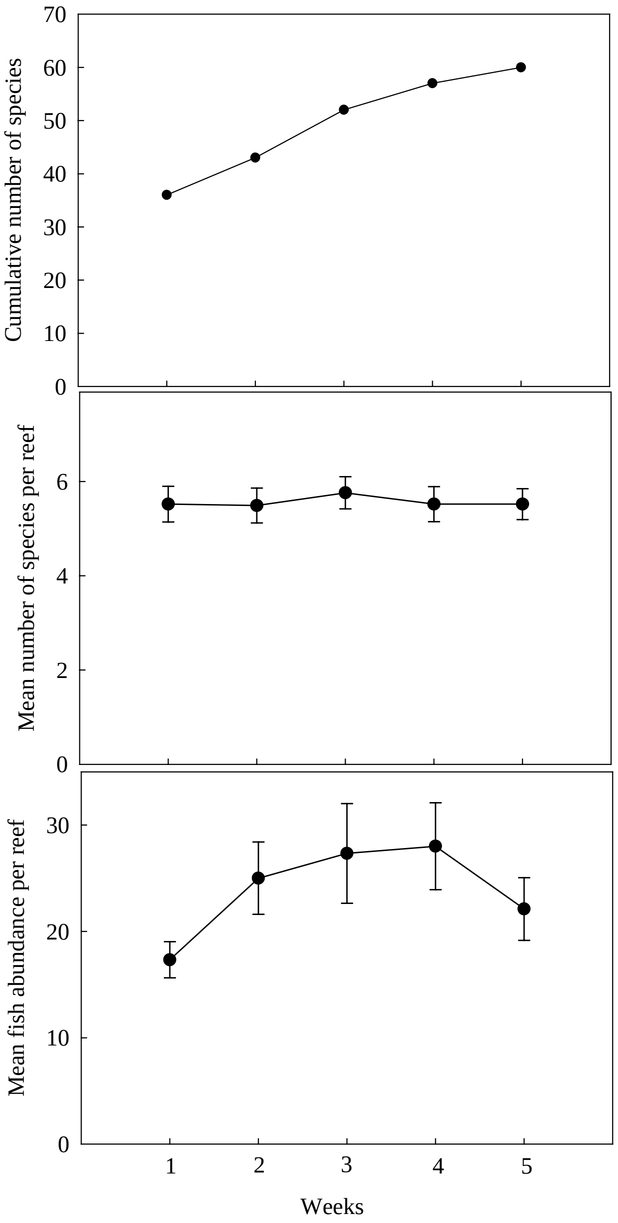


Fig 6.11 Species accumulation curve for all 65 reefs/plots over a period of 5 weeks (top). The effect of time, plotted ± SE on fish species richness (middle) and abundance (bottom) were tested using and ANCOVA analysis with time as a covariate, there were no significant differences in number of species or number of fish with week (see full ANCOVA tables overleaf).

Table 6.6 ANCOVA analysis to test the effect of reef (fixed factor) and the effect of time (covariate) and on a) observed number of species and b) abundance.

a) Species = Reef + Time (Reef is categorical, time is continuous)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	12202.2(a)	66	184.8	73.5	.000
Reef	3957.7	65	60.8	24.2	.000
Week	.006	1	.006	.002	.961
Error	650.7	259	2.5		
Total	12853.0	325			

* R Squared = .949 (Adjusted R Squared = .936)

b) Abundance = Reef + Time (Reef is categorical, time is continuous)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	361868.7(*)	66	5482.8	16.3	.000
Reef	198229.3	65	3049.6	9.1	.000
Week	1019.3	1	1019.3	3.0	.082
Error	86702.2	259	334.7		
Total	448571.0	325			

* R Squared = .807 (Adjusted R Squared = .757)

There were several different patterns in fish numbers with time. The first group of fish were: juvenile yellow-tail snapper *Ocyurus chrysurus*, slippery dick *Halichoeres bivittatus,* ocean surgeonfish *Acanthurus bahianus,* four-eye butterfly fish *Chaetodon capistratus*, lane snapper *Lutjanus synagris* and bucktooth parrotfish *Sparisoma radians.* They colonised the reefs immediately in high numbers, but their numbers declined as new species arrived (Table 6.7). The second group was comprised of juvenile grunts, *Haemulon aurolineatum* and *Haemulon plumieri* which occurred in very high numbers on the reefs and the recruitment pulse of these fish is largely responsible for the overall pattern in fish abundance on the reefs in Fig 6.15. They started in low numbers and increased to peaks in week 3 and 4 then began to decline. The third group of fish increased in number over time and includes the damselfish *Stegastes leucostictus* and all three of the macroinvertebrates, spiny lobster *Panulirus argus,* common octopus *Octopus vulgaris* and long-spined sea-urchins *Diadema antilliarum*. The remaining species had inconsistent variations in abundance and/or occurred in low numbers (Table 6.7).

Table 6.7 The fish species encountered on all 65 experimental reefs over the first 5 weeks of sampling.

	Week 1	Week 2	Week 3	Week 4	Week 5
Acanthuridae					
Acanthurus bahianus	70	50	30	22	11
Acanthurus chirugrus	2	3	2	2	6
Acanthurus coeruleus	7	6	8	6	4
Apogonidae					
Apogon maculatus	1	3	4	2	2
Aulostomidae					
Aulostomus maculatus	0	2	0	1	5
Belonidae					
Tylosurus crocodilus	0	0	1	2	0
Blenniidae					
Parablennius marmoreus	2	5	2	2	0
Bothidae					
Bothus lunatus	0	4	6	4	2
Carangidae					
Caranx latus	0	0	2	0	0
Caranx ruber	4	6	12	1	5
Chaetodontidae					
Chaetodon capistratus	54	40	37	44	46
Chaetodon striatus	0	1	0	0	0
Diodontidae					
Diodon holocanthus	0	0	0	2	4
Gerreidae					
Gerres cinereus	0	0	2	0	0
Gobiidae					
Coryphopterus dicrus	0	0	1	1	1
Coryphopterus glaucofraenum	10	14	20	29	13
Gobionellus saepepallens	1	0	0	0	0
Gnatholepis thomsoni	0	0	0	1	0
Nes longus	0	1	0	0	1
Haemulidae					
Haemulon aurolineatum	0	141	545	382	210
Haemulon carbonarium	0	1	0	0	0
Haemulon flavolineatum	32	7	11	31	28
Haemulon macrostomum	0	0	0	0	2
Haemulon melanurum	0	0	0	0	1
Haemulon parra	0	0	2	1	0
Haemulon plumieri	154	542	435	628	470
Holocentridae					
Holocentrus adscensionis	1	0	1	0	0
Holocentrus coruscus	2	0	1	2	0
Holocentrus rufus	0	0	2	0	2
Labridae					
Halichoeres bivittatus	148	100	89	73	88
Halichoeres poeyi	34	33	25	23	31
Halichoeres radiatus	3	7	0	0	0
Thalassoma bifasciatum	4	8	10	11	7
Labrisomidae					
Malacoctenus gilli	0	0	0	1	0
Malacoctenus macropus/versicolor	22	22	22	24	25
Malacoctenus triangulatus	0	0	0	0	1

Table 6.7 cont. The fish species encountered on all experimental reefs over the first few weeks of sampling.

	Week 1	**Week 2**	**Week 3**	**Week 4**	**Week 5**
Lutjanidae					
Lutjanus synagris	15	11	5	10	8
Ocyurus chrysurus	286	314	197	210	167
Monocanthidae					
Cantherhines pullus	3	2	0	0	3
Monacanthus ciliatus	1	0	1	2	0
Monacanthus tuckeri	0	0	2	1	0
Mullidae					
Mulloidichthys martinicus	2	2	0	0	1
Pseudupeneus maculatus	15	2	2	2	0
Muraenidae					
Gymnothorax vicinus	2	1	5	2	3
Ophichthidae					
Myrichthys ocellatus	0	0	1	0	0
Ostraciidae					
Lactophrys trigonus	0	0	0	1	0
Pomacentridae					
Stegastes leucostictus	28	25	27	45	33
Stegastes partitus	0	0	0	1	1
Scaridae					
Sparisoma aurofrenatum	4	2	8	6	3
Scarus spp < 10cm	96	164	164	158	160
Sparisoma radians	84	63	49	49	54
Sparisoma rubripinne	0	0	3	0	0
Sparisoma viride	1	3	3	5	6
Serranidae					
Alphestes afer	11	13	16	11	14
Hypoplectrus puella	23	27	18	21	16
Hypoplectrus unicolor	2	0	0	0	0
Sparidae					
Calamus calamus	1	0	0	0	0
Synodontidae					
Synodus intermedius	1	0	2	2	0
Tetraodontidae					
Canthigaster rostrata	1	2	2	0	2
Sphoeroides spengleri	0	1	1	0	0
No species	**36**	**36**	**42**	**40**	**37**
No fish	**1127**	**1628**	**1776**	**1821**	**1436**
Echinodermata					
Diadema antilliarum	0	3	23	13	28
Mollusca					
Octopus vulgaris	0	4	3	7	8
Crustacea					
Panulirus argus	0	2	2	2	4

6.3.3 Urchins

Diadema antillarum did significantly affect the diurnal fish community largely by providing shelter for small fish. A total of 56 different fish species were encountered in this experiment, and the most common fish species encountered sheltering among the urchins spines were *Haemulon* spp. *Ocyurus chrysurus, Chaetodon capistratus, Halichoeres bivittatus* and *Acanthurus bahianus.* The presence of urchins had a much stronger effect of fish species richness and abundance in the low-complexity seagrass beds than on high-complexity reefs (Fig 6.12). Fish abundance in seagrass was increased more than six fold when *Diadema* were present, but on artificial reefs fish urchins doubled fish numbers. Number of fish species almost doubled in seagrass quadrats with urchins, but the difference was less pronounced on reefs with or without *Diadema.*

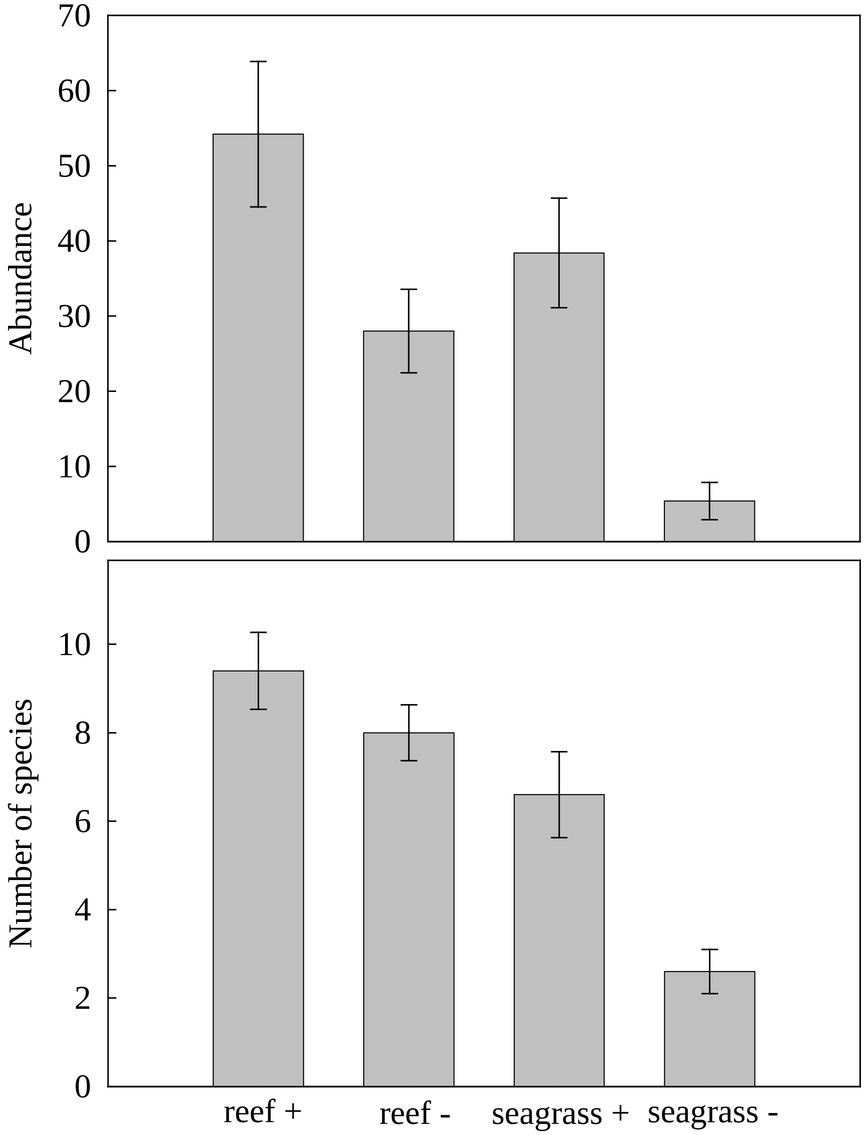


Fig 6.12 A comparison of the differences in fish species richness and abundance on reefs and seagrass plots with urchins (+) compared to those without urchins (-). Both urchins and habitat significantly affected abundance and number of species, see two-way ANOVA results overleaf.

Table 6.8 A Two-way ANOVA testing for the effects of habitat and presence of urchins on a) abundance of fish and b) number of fish species.

a) Abundance = Habitat + Urchins (Habitat and Urchins are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	26069.0(*)	3	8689.6	39.5	.000
Habitat	1843.2	1	1843.2	8.3	.010
Urchins	4380.8	1	4380.8	19.9	.000
Error	3739.0	17	219.9		
Total	29808.0	20			

* R Squared = .875 (Adjusted R Squared = .852)

b) Species = Habitat + Urchins (Habitat and Urchins are categorical)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Model	1004.9(*)	3	334.9	101.6	.000
Habitat	84.0	1	84.0	25.4	.000
Urchins	36.4	1	36.4	11.0	.004
Error	56.0	17	3.2		
Total	1061.0	20			

* R Squared = .947 (Adjusted R Squared = .938)

6.4 DISCUSSSION

This study has demonstrated that more complex habitats generally do support more species than less complex habitats, and the mechanisms responsible for causing this pattern are habitat selection based on the availability of numerous resources such as food, shelter, nesting sites etc. These resources are generally more abundant in more complex habitats than less complex ones. A summary of the effects of all the hypotheses tested on fish species richness and abundance is given in Table 6.3.

6.4.1 Complexity variables

a) Rugosity—many field studies describe positive correlations between fish species richness and substrate rugosity (Risk 1972, Luckhurst and Luckhurst 1978). This is usually measured using a finely-linked chain draped over the substrate and is a ratio of actual distance over the substrate surface in relation to the linear distance (Luckhurst and Luckhurst 1978). The results of this experiment illustrate that presence of ‘wrinkles’ on the substrate do increase number of fish species (both observed and expected), but that 40cm-high ‘wrinkles’ do not increase number of species more than 20cm-high ‘wrinkles’. The traditional method of using a finely linked chain draped over the substrate would have given much higher rugosity values for the 40cm-high treatment than for the 20cm-high treatment, but this was not reflected in the fish species richness. The presence of structure on the flat substrate probably reduced the ability of roving predators such as barjacks *Caranx ruber* to detect prey, even though this experimental treatment did not provide any holes that would have excluded them. However if the experiment were repeated varying the number of ‘wrinkles’- rather than their height—one might expect some correlation between the number of ‘wrinkles’ and fish species richness because more complicated matrices would offer more protection than less complicated ones.

b) Vertical profile—there were no significant differences in abundance or observed or expected number of species between 20cm high reefs and 60cm high reefs. However, several other studies document the effect of increasing vertical profile of the substrate and increased species richness or abundance (Molles 1978, Kellison and Sedberry 1998, Rilov and Benayahu 2002). In addition, taller reefs are likely to have larger stable surface areas than shorter ones (Dahl 1973) and may also be more conspicuous in the water column, and hence are more effective at aggregating pelagic fish and larvae. This is the principle behind fish aggregating devices (FADs). The vertical height of jetty pillars in the Red Sea was correlated with fish species richness and abundance but they ranged 1-20m (Rilov and Benayahu 1998). These discrepancies in results may be explained by one of the following reasons: a) Vertical profile does have an important effect on the fish community of a reef, but the differences in height tested in this experiment were not sufficient to detect a significant effect or b) The sample sizes (n = 5) were not sufficient to statistically distinguish weak observed differences between the reefs (Fig 6.7); or c) The height differences detected in the other studies were due to some other variable such as increased refuge availability on taller reefs, and this was incidentally correlated with the vertical profile of the reef.

c) Growth forms—assessing the variety of growth forms present in a quadrat is a rough assessment of the habitat heterogeneity in that area; it can be used in a range of different habitat types without having to identify individual algae sponges or corals. Even though the growth forms used in this experiment did not offer a range of different potential food resources (as might have been the case if the growth forms were alive), the mere presence of a variety of different shapes was enough to significantly increase the observed numbers of species on the artificial reefs. Natural history based observations on the reefs may give us clues about the different mechanisms involved. For example, small grunts *Haemulon* spp used the filamentous canvas strips to hide from predators while damselfish *Stegastes leucostictus* preferred the hollow cups as nesting sites and the trumpetfish *Aulostomus maculatus* preferred branching growth forms because it stalks its prey using the branches to camouflage its long, thin body (pers. obs). While no other studies have related fish species richness to the variety of growth forms *per se*, the fish species richness has been correlated with an index of the diversity of substratum variables (Roberts and Ormond 1987) and to the number of different habitat categories (Ohman and Rajasuriya 1998). There was also a clear trend of an increasing expected number of species with increasing variety of growth forms it was not significant, the statistical significance of the observed trend might be improved if larger numbers of experimental reefs were used or larger fish samples were obtained.

d) Hole sizes—while the mixed design had a greater number of species than any other design, the number of species was not significantly larger than the small-hole only design or even the no-hole design. The hypothesis that a greater variety of holes might increase the fish abundance was rejected because only the number of small holes had any effect. While the results may not have proved the initial hypotheses, they still offer valuable insight into the possible mechanisms structuring fish communities.

The small-holed reefs had many more fish than the other reefs. This is probably because they excluded larger predatory fish better than the reefs that had large holes, and the reef without holes. This would create a larger refuge space from predators that could support a greater number of fish, explaining the observed pattern. These findings are similar to those of other authors who claim that any observed increase in species richness at stations with more holes is an artefact of the main effect—increasing fish abundance (Molles 1978, Caley and St John 1996). The rarefied (expected) species richness results remove any of these abundance effects and the fact that there were no significant differences between the treatments supports their claim. However, the reef design with a variety of hole sizes did have an average of about two more species than any of the other designs and the significance of this trend might improve if the sample sizes were increased, and should be investigated further.

e) Percent hard substrate – more fish and more fish species were associated with increasingly stable substrates. Dahl, (1973) notes

> ‘In the fluid environment of the sea a fixed point of attachment is one of the scarcest and most desirable of resources, particularly in the photic zone.’

Fish species richness has been also been correlated with percentage hard substrate in the Red Sea (Khalaf and Kochzius 2002). Hard substrates are often covered in thin film of periphyton that are an important food resource to grazing animals, and are a significant contribution to the total primary production in these marine systems. Theoretically, increasing the total hard surface area of a reef will increase its net productivity and hence increase the total number of fish explaining the observed pattern. Presence of seagrass in a quadrat might have a similar effect because the seagrass leaves offer a stable surface for periphyton growth, as well as cover from predators (albeit limited in these sparse seagrass beds). The artificial reefs did have a thin film of periphyton, which was evident even after their first week in the water, however, the six week duration of the experiment was not sufficient to develop the lush epilithic fouling community that is often evident on natural reefs or on old ship wrecks, and the effect may have been even stronger if the reefs had been submerged for longer periods of time.

6.4.2 Variability over time

Ocyurus chrysurus, *Halichoeres bivittatus*, *Acanthurus bahianus*, *Chaetodon capistratus*, *Lutjanus synagris* and *Sparisoma radians* initially colonised the reef in high numbers and then declined as other fishes became more abundant. All of these species are present in low densities in seagrass beds (refer to chapters 3 and 4), and they probably migrated from surrounding seagrass beds to the hard structures for refuge. As other species colonised the reefs either from recruitment of pelagic larvae e.g. *Haemulon* species or as adults that presumably migrated from adjacent reefs e.g. *Aulostomus maculatus* and *Gymnothorax vicinus,* the numbers of the initial colonists declined possibly as a result of competition and/or predation.

Number of species on the artificial reefs did not fluctuate significantly over short time-intervals and it is therefore a good indicator of the habitat type even in a reef-fish community with considerable species turnover. A similar study in US Virgin Islands showed that number of fish species increased on newly built artificial reefs for the first 6 days and then stabilised (Shulman 1985). This initial colonisation period in this study was missed because reefs were left to acclimatise for 1 week after construction before sampling commenced.

Fish abundance is a poor indicator of habitat type because it had such high variability compared to observed number of species. Different fish species changed in abundance, probably for a variety of reasons. However, the overall peak in fish abundance was largely due to a recruitment event of *Haemulon* species. The decline was presumably due to their mortality from reef-associated predators such as purplemouth moray *Gymnothorax vicinus,* mutton hamlet *Alphestes afer,* peacock flounder *Bothus lunatus,* lizardfish *Synodus intermedius* or the roving predators bar jack *Caranx ruber,* horse-eye jacks *Caranx latus* and crocodilefish *Tylosurus crocadylus* (Table 6.2). Shulman (1985) also noted that very large recruitment pulses of grunts strongly influenced fish abundance so she treated the *Haemulon* spp data separately. Patterns of recruitment are thought to have a strong influence on coral reef fish communities and keep them in a state of non-equilibrium. The high species turnover and failure of fishes to reach a carrying capacity on these artificial reefs support this recruitment-limited hypothesis (Sutherland 1974, Sale 1977, Doherty 1991).

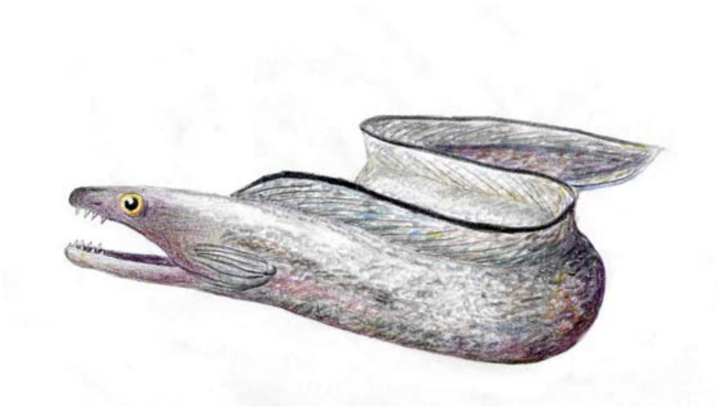
6.4.3 Urchins

Most previous studies on *Diadema antilliarum* examine the competitive grazing interactions between urchins and herbivorous fish (Randall 1965, Foster 1985, Hay and Taylor 1985, Carpenter 1986, 1990, Robertson 1991). *Diadema* are found in all habitats and tend to aggregate during the day in groups or in sheltered locations and feed on algae in the open at night (DeLoach 1992). These data indicate that the urchins contribute to the complexity of the area they inhabit. A number of different species of juvenile fish sheltered in their spines, an effect that was most pronounced in seagrass beds where shelter is a limiting factor, but was less pronounced on reefs where there were alternative types of refuge.

6.4.4 Management applications

The building of artificial reefs is a common fisheries management tactic used to increase fisheries production in most parts of the world in both freshwater and marine environments e.g. (Chou 1988, Gregg 1995, Minton and Heath 1998, Sinis et al. 2000, Freitas and Petere 2001, Lok et al. 2002). Artificial reefs have a range of potential management uses since their first documented accounts in Japan in the late 1700's (Meier et al. 1989). They have been used as dive attractions (often in the form of accidental or deliberate ship wrecks); anti-trawling devices (Lok et al. 2002); to increase fish and lobster stocks in fishing areas (Walker et al. 2002); as a tool for the rehabilitation of natural reefs (Clark and Edwards 1999); to increase primary production in an oligotrophic system (Guiral et al. 1993); to increase fish recruitment to an area (Beets 1989) or to increase local biodiversity.

These findings may contribute to the understanding of optimal artificial reef design. If the aim of a particular artificial reef programme is to increase local fish biodiversity, then optimal artificial reef design should: a) offer a stable substrate in regions where this is unavailable, b) have a rugose surface with a large number of small refuge holes, and c) have a variety of different ‘growth forms’ attached. Providing there is a suitable stable substrate, the growth forms are likely to grow naturally in the form of a fouling community, given sufficient time.



Purplemouth moray – *Gymnothorax vicinus*

7

A Comparison of Fish Assemblages and Water Quality in Two Marinas

‘Filthy water cannot be washed.’

WEST AFRICAN PROVERB

7.1 INTRODUCTION

In Chapter 3, it was apparent that eutrophic stations with poor water quality had low species richness and abundance. One fish taxon, the mojarras *Eucinostomus* spp. was apparently tolerant of the effects of eutrophication and thrived in these areas. Because the survey had no experimental component, it was difficult to determine whether water quality directly affected the fish community, or whether it reduced the habitat complexity and therefore had an indirect effect on the fish. This small, applied study will compare the fish communities in 2 marinas with different water quality using artificial reefs as habitat controls. It will also serve as a preliminary assessment of the potential use of marine fish as biotic indicators of pollution.

7.1.1 Eutrophication

Eutrophication is the ‘excessive enrichment of waters with nutrients and the associated adverse biological effects’ (EEA 1994). This widespread problem in tropical marine environments is usually associated with discharge of untreated sewage. Common symptoms are increased nitrate and phosphate levels, increased macroalgal production in shallow areas, reduced dissolved oxygen, loss of seagrass and coral habitats and changes in the fish community (Hallock and Schlager 1986, Granelli et al. 1990, Valiela 1995, Hemminga and Duarte 2000). Eutrophication has altered many tropical marine habitats in different parts of the world (Hallock and Schlager 1986, Naim 1993, Bjork et al. 1995, Al et al. 1999, Hughes et al. 1999), and it is difficult to determine whether the associated change in the fish community occur because of the altered habitat type or because of the poor water quality.

7.1.2 Bioasessment of water quality

Animal communities can be used to estimate the impact of a disturbance to the physical environment, animal bioindicators should be: (1) sufficiently sensitive to disturbance, (2) widely distributed (3) capable of living in a wide range of condtitions (4) relatively independent of sample size, (5) easy and cost effective to study, (6) allow for differentiation between natural and man-made disturbance and (7) relevant to ecologically significant phenomena (Noss 1990).

Certain species respond differently to different conditions. For example; in severely organically polluted streams, most aquatic invertebrates disappear, but certain groups proliferate such as tubificid oligochaetes and chironimid larvae that are capable of surviving in low oxygen conditions because they contain haemoglobin (Wright et al. 1993). Rapid assessment indices of stream water quality, that score benthic macroinvertebrates on their known sensitivity to organic pollution are used to assess the ecological health of many streams around the world (Wright et al. 1993, Chessman 1995, Dallas 1997, Gratwicke 1998-1999). Fish have also been included in some bioassessment protocols and these methods are sometimes referred to as biological integrity indices (Larkin and Northcote 1969, Karr 1981, 1990a, Karr 1990b, Hughes et al. 1998). These indices compare fish assemblage structure at a number of unimpacted reference sites and impacted sites that have been assessed using number of independent physical measures of riparian and water quality (Hughes et al. 1998). Fish in tropical marine habitats perfectly fulfill all of the requirements of a bioindicator assemblage, and any major disturbances to these systems should be manifested in the fish community. Coralliverous Chaetodontid species have been used as an indicator taxon to assess the health of coral reefs in the Indo-Pacific, but they are poor habitat indicators in the Caribbean as there are only three species (Bell and Galzin 1984, Findley and Findley 1985, Lewis 1997). A number of other families are particularly vulnerable to commercial fishing such as Serranidae, Lutjanidae, Lethrinidae, Mullidae, Labridae, Scaridae, Siganidae and Acanthuridae, they generally decrease in mean size, abundance and species richness in response to overfishing (Roberts 1995, Russ and Alcala 1996, Wantiez et al. 1997, Russ and Alcala 1998). Despite the extensive use of fish as bioindicators in marine systems, the effects of pollution have largely focused on benthic invertebrates and algae (Naim 1993) or molluscs (Kan et al. 1997, Negri et al. 2002) and little is known about the response of tropical marine fish assemblages to eutrophication.

7.1.3 Marine eutrophication

In open marine systems, effluent is rapidly diluted and pollutant concentrations are variable. Nutrient enrichment associated with discharge of wastewater will result in symptoms of eutrophication that decline sharply along a dilution gradient. One might expect fish to respond to these environmental gradients, but the effects of water quality can only be deduced if the habitat is similar across the entire pollution gradient. This is rarely found in practice, but habitat bias can be eliminated using artificial reefs as habitat controls.

7.2. METHODS

7.2.1 Study location

Two marinas with high volumes of charter yacht traffic were chosen on the west end of Tortola (Fig 7.1). Nanny Cay has berths for 180 yachts or motor cruisers. It is a shallow bay with two small channels to allow water flow through the quiet backwaters of the bay (Fig 7.1), although the amount of freshwater entering the bay is limited and probably depends on the tide and prevailing currents. The bay is lined with mangroves on one side, and the substrate consists of mud covered in macroalgae, but becomes sandier towards the mouth of the bay. Substantial housing and shopping complexes line either side of the bay, and at least one bank-side complex discharges waste water directly into the bay.

Soper's Hole has 150 berths and is comparable in size to Nanny Cay; it is lined with mangroves on one side (Fig 7.1) and has a sandy substrate with some muddy areas. Macroalgae and seagrass are present in sparse patches around the marina. A deep channel between the island and the mainland allows clean water to flow into the bay. The volume of water moving through this channel was not calculated, but judging from the swift currents at certain times of the day, the volume of fresh water moving through this channel was higher than both channels through Nanny Cay. Several shopping complexes and housing developments line the bay, but no obvious wastewater discharges into the bay were visible.

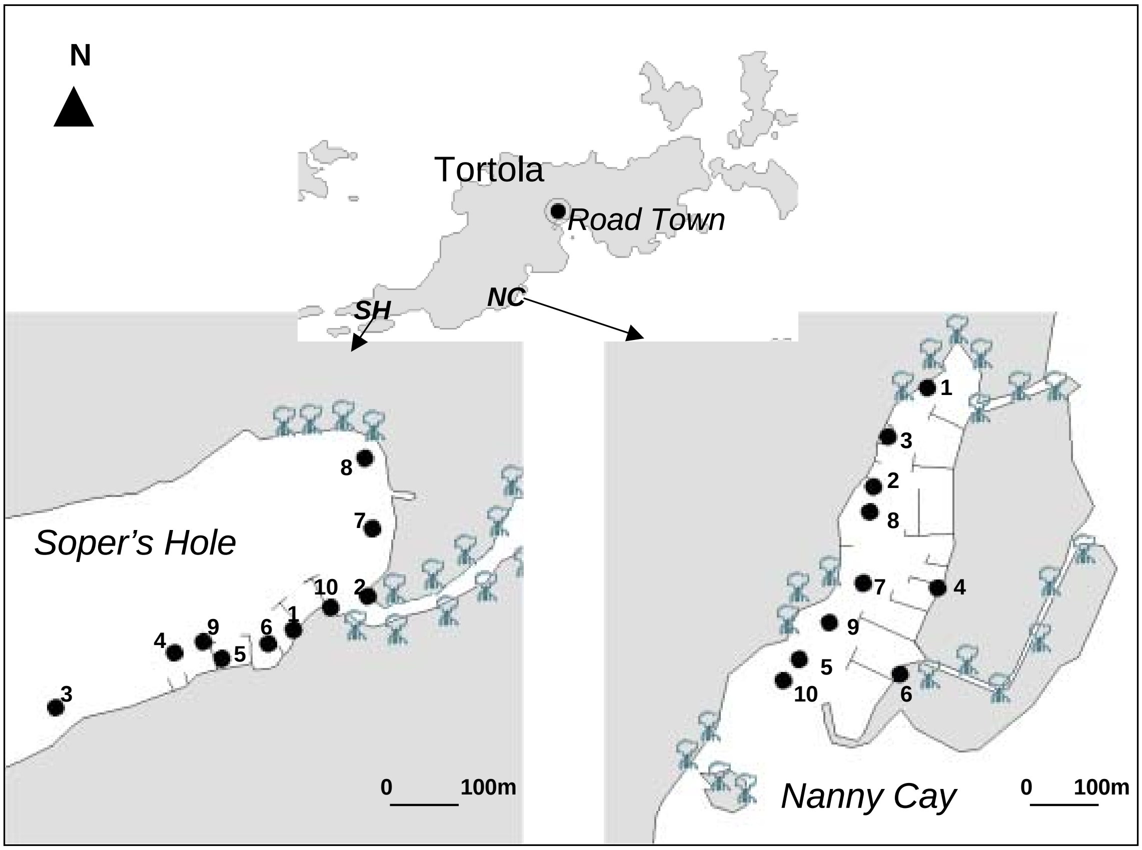


Fig 7.1 The location of twenty artificial reefs in the two marinas Nanny Cay (NC) and Soper's Hole (SH) on Tortola; an island between the Atlantic Ocean and the Caribbean Sea, west of Puerto Rico.

7.2.2 Artificial reefs

Artificial reefs were built by gathering large pebbles and rocks from the shoreline, ranging roughly between 10 and 20cm diameter, then transporting them to a station and arranging them on the substrate to form a 1m x 1m square-based mound, about 40cm high. In a very short period of time (less than a day in most instances), these reefs aggregated a large number and variety of fish. Ten artificial reefs were built in each bay ranging from the more sheltered backwaters to the mouth of the bay. They were left for one week prior to monitoring.

7.2.3 Sampling methods

Stations were visited once every week for three weeks in August 2002. All fish on the reef were identified and counted during a five-minute observation period. Depth was measured using a fibreglass measuring tape. Temperature was measured using a waterproof digital thermometer. Turbidity was measured using a secchi disc attached to a measuring tape. One person would hold the disc about 30cm below the water surface, while the other swam away from the disc with the tape, measuring the distance at which the disc was no longer visible. Phosphate and nitrate concentrations were measured using a Hach DR 850 photo spectrometer, and low-range reagents using methods described in the user manual. Dissolved oxygen (DO) levels in eutrophic systems are highly variable depending of the time of day due to photosynthesis by algae. DO levels were therefore measured within the first hour after sunrise each day using a portable HANNA H1-9142 dissolved oxygen meter.

7.2.4 Data analyses

Differences between the mean number of fish, number species, Shannon-Weiner diversity, depth, visibility, Dissolved Oxygen, phosphate and nitrate in each bay were tested using a two-sample t test. Because 8 simultaneous comparisons were employed, the corrected p value was calculated using the Bonferroni correction for multiple comparisons.

The similarity of fish assemblages across stations was assessed using Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979) which is a form of divisive cluster analysis that indicates at each level in the hierarchy the species peculiar to each group (Jongman et al. 1987). TWINSPAN is preferable to other clustering methods as data are grouped in a hierarchy and indicator species are given at each division, using CAP software package (Henderson and Seaby 2002a). Data were square root transformed since this type of transformation reduces the effects of extremely abundant species that might unduly influence the ordination technique and the method can deal with zero values without biasing the data (Henderson 2003).

Canonical Correspondence Analysis (CCA) in the software application ECOM (Henderson and Seaby 2002b) was used to ordinate stations, and rare species (occurring at fewer than 3 stations) were removed. A Monte Carlo test with 499 randomisations was run to test for the probability of the observed pattern being due to chance. Canonical Correspondence Analysis detects variations in a community composition, then undertakes an auxiliary analysis to identify and plot the environmental variables that correlate best to the ordination axes and displays these as a simple graphical plot of species sites and environmental vectors (ter Braak 1986). As a result it is preferable to other ordination methods, but can only be used if a large number of environmental variables have been measured. The relationship between water quality variables and fish species richness and abundance was analysed using multiple regression analysis.

7.3 RESULTS

7.3.1 Characteristics of the two bays

Nanny Cay displayed characteristic symptoms of eutrophication: low visibility, high phosphate and nitrate concentrations and low dissolved oxygen levels. Soper’s Hole, however, was comparatively unpolluted (Fig. 7.2). Fish communities in Nanny Cay Marina were characterised by having a lower species richness and abundance than in Soper’s Hole (Fig. 7.2).

7.3.2 TWINSPAN analysis

The TWINSPAN cluster analysis separated the reefs from the two stations quite distinctly (Fig. 7.3). The Mojarras, *Eucinostomus* spp, more abundant in the polluted Nanny Cay stations and hence are a TWINSPAN indicator species for these sites. The barjack *Caranx ruber*, redband parrotfish *Sparisoma aurofrenatum* and bridled goby *Coryphopterus glaucofraenum* were the indicator species for the unpolluted Soper’s Hole stations (Fig 7.3). The TWINSPAN community differentiation table shows that 24 species were unique to Soper’s Hole, while only four species, were unique to Nanny Cay. Three of these, smooth trunkfish *Lactophrys triqueter*, dusky damselfish *Stegastes dorsopunicans* and horse-eye jack *Caranx latus*, were rare - only being encountered once, while the schoolmaster *Lutjanus apodus* was encountered at 5 different Nanny Cay stations (Table 7.1).

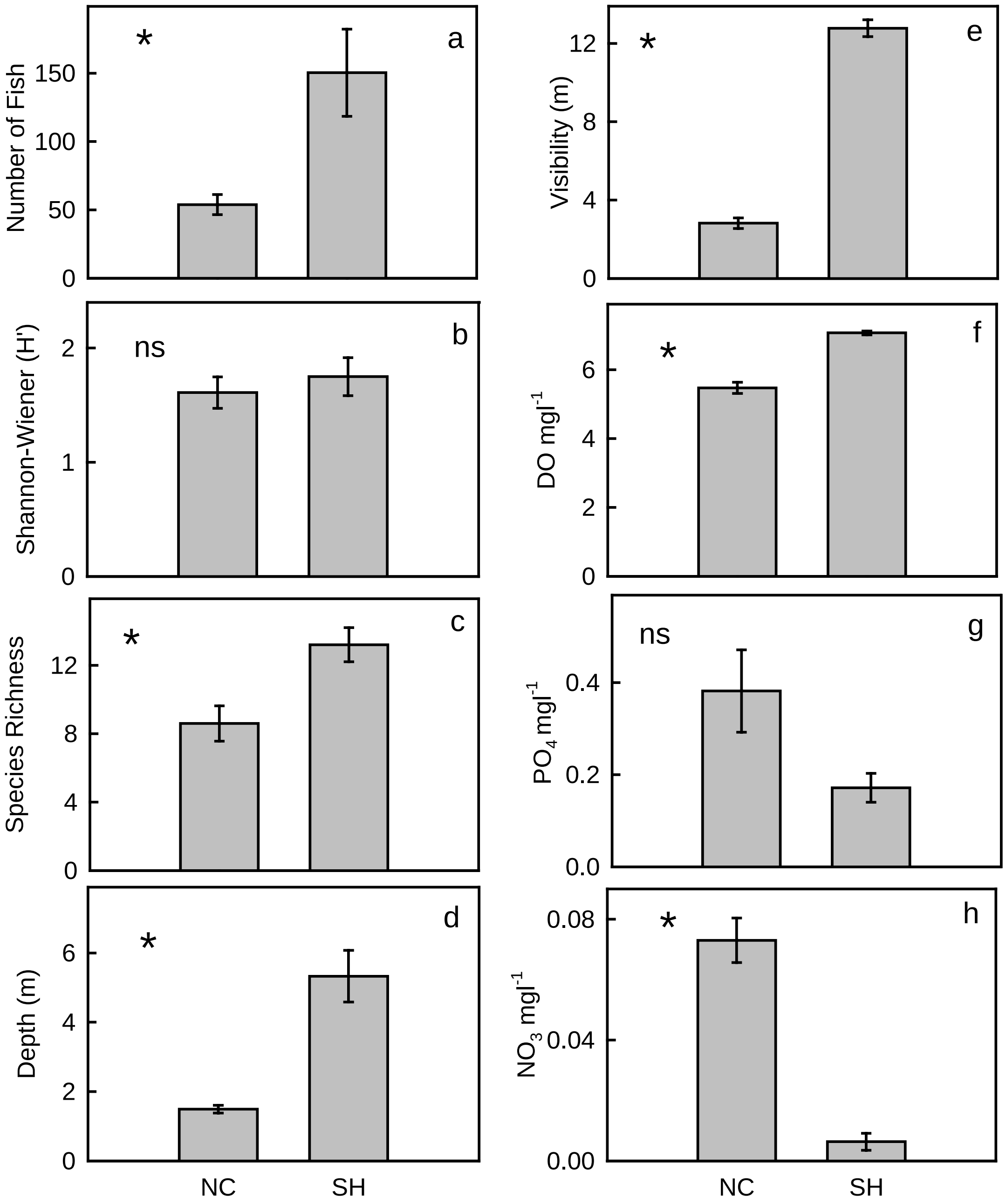


Fig 7.2 A comparison of the mean ± SE biological and physicochemical variables in Nanny Cay (NC) and Soper's Hole (SH). Differences were tested using a two sample t test, * = significant difference at Bonferroni corrected p = 0.00625 critical p value.

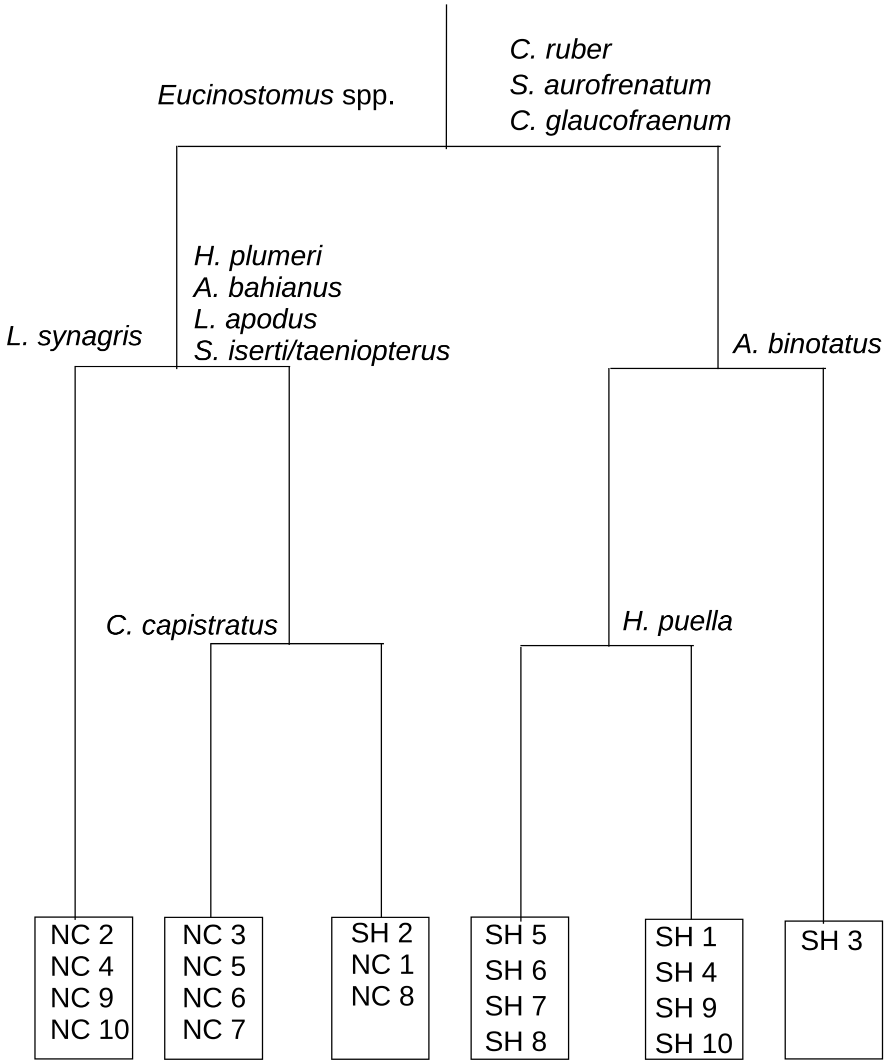


Fig. 7.3 A TWINSPAN cluster analysis of stations, grouping the eutrophic Nanny Cay (NC) stations to the left and the comparatively unpolluted Soper's Hole (SH) stations to the right. The analysis was done on square root abundance data for all species with a maximum of 5 indicators per division and 6 levels of division. Species indicate the fish common to their respective station clusters.

Table 7.1 Community differentiation table of species counted on the three sampling occasions, arranged in order of Twinspan analysis of species output. Numbers refer to TWINSPAN species output cluster. Symbols refer to the mean abundance of that species on a logarithmic scale: · ≤ 1, • = 1-10, ● = 10-100.

		SH1	SH2	SH3	SH4	SH5	SH6	SH7	SH8	SH9	SH10	NC1	NC2	NC3	NC4	NC5	NC6	NC7	NC8	NC9	NC10
1	*B. lunatus*								·												
1	*C. personatus*								·												
1	*H. aurolineatum*					●		•	•	·											
1	*S. planifrons*						·														
1	*S. spengleri*							·													
1	*S. variabilis*						·														
1	*S. vetula*						·														
2	*A. chirugrus*									·											
2	*A. coeruleus*	•			·					·											
2	*C. calamus*	·									·										
2	*C. glaucofraenum*	•	·	·	•	•	•		•	•	•										
2	*C. rostrata*	·																			
2	*C. ruber*				·	•	·		·	·	•										
2	*G. cinnereus*	·																			
2	*H. chlorurus*									·											
2	*M. martinicus*									•	·										
2	*P. maculatus*	•				·				·	•										
2	*S. aurofrenatum*	•			·	•	·	·	•	·											
2	*S. viridae*	·																			
2	*T. bifasciatum*				·																
3	*A. binotatus*			·																	
3	*C. parrae*			·																	
3	*H. puella*	·	·	·	·					·	·										
3	*P. paru*			·																	
4	*A. bahianus*	·		•	•	·	•		•	•	•	•		·		•	·				
4	*L. synagris*	•	•	●		·	●	•	•	·	•		·		·			·		·	•
4	*S. radians*		•				·	·		·	·						·				
5	*C. capistratus*	·			·		•	•		•	•		•	•	•	•	·	·			
5	*H. bivittatus*	•	•		•	•	•	•	·	•	•	·			·	·	·	·			·
5	*O. chrysurus*	•	•	●	•	•	•	•	•	•	•	·		·	•		·	·	·	•	·
6	*S. ista*	•	•				•	•	•	·		•		•		•	•	•	•		●
6	*S. leucostictus*	·	·			·	·		·	·				·	·	•	•	·	•		
7	*H. flavolineatum*		·			•		●	•	·		•	·	•	•	•	•	•		•	·
7	*L. griseus*						·		·			·	•	·	·		•		•	•	
7	*S. fuscus*																			·	
7	*S. testudinum*		·					·				·									
8	*Eucinostomus* spp.		•								•	•		·	·		•	•	•	•	
8	*H. plumeri*	·	·	•								·				·	•				
9	*A. saxatilis*															·					
9	*C. latus*																·				
9	*G. funebris*											·							·		
9	*H. poeyi*											·									
9	*H. sciurus*											•									
9	*L. apodus*											·		·		·	·	•			
9	*L. cyprinoides*													·							
9	*L. triqueter*															·					
9	*M. macropus*		·														·		·		

7.3.3 Canonical correspondence analysis

The CCA analysis distinctly separated Nanny Cay and Soper's Hole stations (Fig 7.4). The Nanny Cay stations were associated with high temperature, phosphates and nitrates and low dissolved oxygen and depth. Three species, grey snapper *Lutjanus griseus*, *Lutjanus apodus* and *Eucinostomus* spp. favoured these conditions (Fig 7.4). *Caranx ruber,* tomtate grunt *Haemulon aurolineatum*, spotted goatfish *Pseudupeneus maculatus,* redband parrotfish *Sparisoma aurofrenatum,* barred hamlet *Hypoplectrus puella*, *Coryphopterus glaucofraenum* and blue tang *Acanthurus coeruleus* were associated with deeper, cooler, high dissolved oxygen and low phosphate and nitrate water (Fig 7.4).

7.3.4 Multiple regression using water quality variables

At both stations there are water quality gradients some stations having poorer water quality and others having better water quality (Fig 7.4). A multiple regression model using the measured physicochemical water quality variables (but excluding visibility because of multicolinearity problems) accounted for 48% of the observed variation in fish species richness but did not explain a significant proportion of the variation in fish abundance (Table 7.2). In the multiple regression model, nitrate concentration was the best predictor of fish species richness, followed by phosphate concentration (Table 7.2).

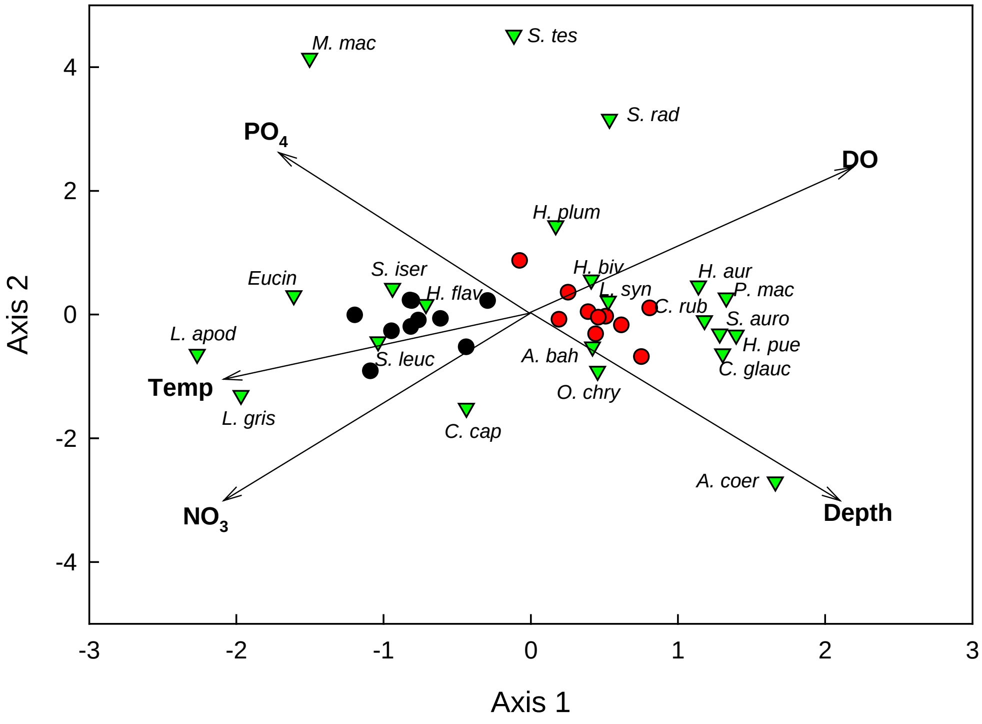


Fig. 7.4 Canonical Correspondance analysis of stations and species ● = Soper's Hole 🔴 = Nanny Cay stations ▼ = species. The initials of the following taxa are used as species labels: *Acanthurus bahianus, Acanthurus coeruleus, Caranx ruber, Chaetodon capistratus, Coryphopterus glaucofraenum, Eucinostomus spp. Haemulon aurolineatum, Haemulon flavolineatum, Haemulon plumieri, Halichoeres bivittatus, Hypoplectrus puella, Lutjanus apodus, Lutjanus griseus, Lutjanus synagris, Ocyurus chrysurus, Pseudupeneus maculatus, Scarus iserti/taeniopterus, Sparisoma aurofrenatum, Sparisoma radians, Stegastes leucostictus/diencius*. Eigen values: axis 1, 0.36, axis 2, 0.06. First 2 axes account for 27% of the variance. Monte Carlo test significant (p = 0.03), 499 permutations.

Table 7.2 A multiple regression analysis of water physicochemical variables and a) fish species richness and b) abundance.

a) Coefficients: Number of species

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	Sig.
1	(Constant)	4.256	8.861		.480	.638
	Nitrate	-59.726	26.256	-.583	-2.275	.038
	Phosphate	6.775	3.096	.402	2.188	.045
	Dissolved Oxygen	1.134	1.351	.260	.839	.414
	Depth	.010	.394	.006	.025	.980

a) ANOVA (Adj $r^2 = 0.48$)

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	172.655	4	43.164	5.434	.007(a)
	Residual	119.145	15	7.943		
	Total	291.800	19			

a Predictors: (Constant), Depth, Phosphate, Nitrate, Dissolved Oxygen
b Dependent Variable: Number of species

b) Coefficients Number of fish (sqrt transformed)

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	Sig.
1	(Constant)	-2.772	9.869		-.281	.783
	Nitrate	-24.743	29.244	-.257	-.846	.411
	Phosphate	.183	3.448	.012	.053	.958
	Dissolved Oxygen	2.197	1.504	.536	1.460	.165
	Depth	-.182	.439	-.126	-.414	.685

b) ANOVA (Adj $r^2 = 0.27$)

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	110.378	4	27.595	2.800	.064(a)
	Residual	147.809	15	9.854		
	Total	258.187	19			

a Predictors: (Constant), Depth, Phosphate, Nitrate, Dissolved Oxygen
b Dependent Variable: Number of fish (sqrt transformed)

7.4 DISCUSSION

7.4.1 Experimental design

This chapter should be viewed as a preliminary investigation into the potential use of marine fish as bioindicators. It is, as suggested in the title, simply a comparison between an obviously eutrophic marina and one that is comparatively clean.

The two marinas had quite distinct fish assemblages. There are many possible reasons for these differences other than eutrophication; these are connected to the fact that only two marinas were examined limiting the range of validity of the results to the two bays concerned. The results from these kinds of experiments must be interpreted with caution, for example, Soper's Hole is deeper, fish living in the bay may be recruited from different places, and the habitats adjacent to the artificial reefs may have been slightly different in each bay. A more thorough experimental design should have included a large number of unpolluted bays and polluted ones in the analysis (there is no true control in this design). However, such a large-scale project is logistically difficult and would require sampling additional polluted bays in other countries.

7.4.2 Water quality gradients

The water quality in each bay varied on a continuous gradient from more polluted areas near sewage outlets and/or with high boat traffic to less polluted areas, and species richness was negatively influenced by nitrate concentration. The artificial reefs in the most polluted areas had the lowest fish species richness and abundance—as might be expected from a strongly eutrophic system (Deegan et al. 2002).

Because nutrients are often a factor limiting primary production in aquatic environments, increasing the nutrient budget of aquatic systems through mild eutrophication can lead to an increase in overall algal productivity that may cascade up the food chain and cause an increase in fish productivity (Larkin and Northcote 1969, Hulot et al. 2000). In severely eutrophic systems, decay of nutrient-rich pollutants have a very high biological oxygen demand leading to diel fluctuations in DO, and elevated carbon dioxide levels that may make fish avoid heavily eutrophied zones (Larkin and Northcote 1969). The adverse effects of other chemicals that are also associated with severe eutrophication, such as ammonia, may adversely affect fish, deterring them from strongly eutrophic areas. As fish respond to a number of different variables, they will be useful indicator taxa in eutrophication studies (Larkin and Northcote 1969).

7.4.3 Indicator species

Some fish are more tolerant of eutrophication than others (Larkin and Northcote 1969, Wetzel 1975). *Eucinostomus* spp., along with *Lutjanus griseus* and *Lutjanus apodus* were quite tolerant of eutrophic conditions. These species were correlated with warm, shallow, high phosphate, low dissolved oxygen water (Fig 7.4). These data support similar observations on *Eucinostomus* spp and *L. griseus* in Hodges creek and Paraquita bay (Chapter 3). In these bays, the abundance of mojarras was an order of magnitude higher at stations that had symptoms of chronic eutrophication, making *Eucinostomus* a clear indicator of eutrophication. All four of the ‘tolerant’ taxa are mangrove-associated fish (Chaves and Otto 1999, Nagelkerken et al. 2002) and might therefore be pre-adapted to eutrophic environments that would be found in places where mangrove-derived detritus is decomposing. These species may therefore be considered tolerant of eutrophication effects, while other more sensitive clean-water species, including *Caranx ruber*, *Sparisoma aurofrenatum* and *Coryphopterus glaucofraenum* would either disappear or only be present in very low numbers, resulting in reduced species richness.

7.4.4 Potential viability of a biotic water quality index using fish

These preliminary results are a promising indication that fish assemblages on artificial reefs could be used as biotic indicators of marine pollution. More extensive replication of this study would be required to design a firm biomonitoring protocol. An assessment of the apparent sensitivity of a large number of species would be required before an accurate biomonitoring index could be designed to cover a wide geographical area.

The main value of these indicator species would be to provide a simple, user-friendly way to assess the ecological health of a marine bays, without the use of extensive water chemistry data that are often highly variable depending upon the time of day or tidal phase and the activities of the polluter. Once problem areas are identified, by the presence of pollution tolerant species and the absence of the intolerant ones, a more detailed assessments using more sophisticated chemical analyses over a prolonged time period would indicate the likely source and extent of the problem.

Mojarra – *Eucinostomus* sp.

8

General Discussion and Conclusion

> *"Would you tell me, please, which way I ought to go from here?"*
> *"That depends a good deal on where you want to get to," said the Cat.*
> *"I don't much care where --" said Alice.*
> *"Then it doesn't matter which way you go," said the Cat.*
> *"--so long as I get somewhere," Alice added as an explanation.*
> *"Oh, you're sure to do that," said the Cat, "if you only walk long enough."*
>
> LEWIS CARROLL

8.1 SUMMARY

This project started with the simple idea to explain the patterns of fish distribution in a diverse and species-rich environment. It began with a literature review, introducing the main concepts that are used throughout, and was followed by an appraisal of the traditional fish census methods. Once the best method for the research was chosen, an extensive data set was collected. This was used to determine five basic types of fish assemblage with similar composition. When distributions were examined at a species-level, some fish were apparently habitat-specialists while others had more general habitat requirements. Most of the fish species that were distributed throughout the study area showed patterns of ontogenetic partitioning—juveniles used bay habitats and moved onto reefs as they approached sexual maturity. When looking at the community as a whole, more species were clearly found in more complex habitats. A simple habitat complexity index accounted most of the variation in fish species richness. The various hypotheses formed from these observations were tested experimentally using artificial reefs and finally, a potential application was piloted, by looking at the effects of water quality using simple, inexpensive artificial reefs as habitat controls.

8.2 MAIN DISCOVERIES

8.2.1 Fish species inventory and range extensions

During the course of the study, the FISHBASE species list for the British Virgin Islands (BVI) was improved, with 27 new species being recorded for the territory and 5 new species for the Virgin Islands including the US Virgin Islands (Table 8.1). This reflects in part how limited the work on fish communities has been in the BVI. For example the commonest fish in the study site the slippery dick wrasse, *Halichoeres bivittatus* was not present on the BVI list. This is likely to be due to the fact that it is not commercially important and has not been paid much attention during previous studies. In contrast, the US Virgin Islands (USVI) fish species list is much more comprehensive because they have been intensively studied by many prominent fish biologists (e.g. Hixon, Beets, Randall and Risk). Because of their close proximity one would expect the USVI list to be similar to the British Virgin Islands list. The five species that don't appear on either the USVI list or the BVI list are the species of the most interest because their presence in this study may be considered true range-extensions (Table 8.1). They are: redlip blenny *Ophioblennius atlanticus*, long spine porcupine fish *Diodon holocanthus*, dash goby *Gobionellus saepepallens*, orange sided goby *Elecatinus dilepis* and the crested goby *Lophogobius cyprinoides*.

Table 8.1 Species missing from the FISHBASE species list for the British Virgin Islands, compared with the US Virgin Islands list (June 2003). 27 new fish species were recorded for the BVI and 5 new species for the Virgin Islands as a region. (*note that the author has submitted these additions to FISHBASE to be updated in July 2003 as part of ongoing collaboration)

Family	Scientific name	Common name	Author	USVI list
Aulostomidae	*Aulostomus maculatus*	Trumpetfish	Valenciennes, 1837	✓
Blenniidae	*Ophioblennius atlanticus*	[Redlip blenny]	(Valenciennes, 1836)	✗
Chaetodontidae	*Chaetodon capistratus*	Foureye butterflyfish	Linnaeus, 1758	✓
Dasyatidae	*Dasyatis americana*	Southern stingray	Hildebrand & Schroeder, 1928	✓
Diodontidae	*Diodon holacanthus*	Long-spine porcupinefish	Linnaeus, 1758	✗
Gerreidae	*Gerres cinereus*	Yellow fin mojarra	(Walbaum, 1792)	✓
Gobiidae	*Gnatholepis thompsoni*	Goldspot goby	Jordan, 1904	✓
Gobiidae	*Gobionellus saepepallens*	Dash goby	Gilbert & Randall, 1968	✗
Gobiidae	*Elacatinus dilepis*	Orangesided goby	(Robins & Böhlke, 1964)	✗
Gobiidae	*Gobiosoma evelynae*	Sharknose goby	Böhlke & Robins, 1968	✓
Gobiidae	*Lophogobius cyprinoides*	Crested goby	(Pallas, 1770)	✗
Holocentridae	*Holocentrus adscensionis*	Squirrelfish	(Osbeck, 1765)	✓
Holocentridae	*Holocentrus coruscus*	Reef squirrelfish	Poey, 1860	✓
Holocentridae	*Myripristis jacobus*	Blackbar soldierfish	Cuvier, 1829	✓
Labridae	*Halichoeres bivittatus*	Slippery dick	(Bloch, 1791)	✓
Muraenidae	*Gymnothorax funebris*	Green moray	Ranzani, 1840	✓
Muraenidae	*Gymnothorax moringa*	Spotted moray	(Cuvier, 1829)	✓
Muraenidae	*Gymnothorax vicinus*	Purplemouth moray	(Castelnau, 1855)	✓
Ophichthidae	*Myrichthys breviceps*	Sharptail eel	(Richardson, 1848)	✓
Ophichthidae	*Myrichthys ocellatus*	Goldspotted eel	(Lesueur, 1825)	✓
Pomacentridae	*Abudefduf saxatilis*	Sergeant major	(Linnaeus, 1758)	✓
Pomacentridae	*Chromis multilineata*	Brown chromis	(Guichenot, 1853)	✓
Rhincodontidae	*Ginglymostoma cirratum*	Nurse shark	(Bonnaterre, 1788)	✓
Sciaenidae	*Equetus acuminatus*	High-hat	(Bloch & Schneider, 1801)	✓
Sciaenidae	*Equetus punctatus*	Spotted drum	(Bloch & Schneider, 1801)	✓
Scorpaenidae	*Scorpaena plumieri*	Spotted scorpionfish	Bloch, 1789	✓
Tetraodontidae	*Sphoeroides spengleri*	Bandtail puffer	(Bloch, 1785)	✓

8.2.2 Fish assemblages

Simultaneous studies of a combination of near shore habitats have long been called for (Ogden and Gladfelter 1983, Parish 1989, Ogden 1997), but comparative studies have often been hampered by the use of different sampling methods in different habitat types and a preferential bias to studying coral reefs. More recently, comparative studies of several habitats using similar methods have become more common (Sedberry and Carter 1993, Nagelkerken et al. 2000, Mateo and Tobias 2001). The point-count visual census methods used in this study will be useful to future workers wishing to compare different habitats. In addition to improving the fish species inventory, many (of the previously anecdotal) fish habitat preferences have been verified in a quantitative manner.

The habitat preferences of more abundant species have been established and will be of use to fisheries managers and ecologists. For example some species are dependant upon mangroves during at least some stage of their life history (Chapters 3 & 4). These include: bluestriped grunt *Haemulon sciurus* (juveniles), grey snapper *Lutjanus griseus* (juveniles and adults), schoolmaster snapper *Lutjanus apodus* (juveniles and adults), yellowfin mojarra *Gerres cinereus* (juveniles), great barracuda *Sphyraena barracuda* (juveniles), unidentified parrotfish *Scarus* sp. (juveniles), crested goby *Lophogobius cyprinoides* (juveniles and adults) as well as beaugregory and longfin damselfish *Stegastes diencaeus/leucostictus* (juveniles). Six of these species are commercially important. This information can be used by managers to assess the likely effects of mangrove clearance or planting on the fish community at any site.

Seagrass is another habitat of concern to marine managers because it is vulnerable to degradation from dredging, pollution and anchor damage. Certain fish species were strongly dependent upon seagrass and algal beds during at least some stage of their life history. They include: Mojarras *Eucinostomus spp* (juveniles and adults), grey snapper, *Lutjanus griseus*, yellowtail snapper *Ocyurus chrysurus* (juveniles), bucktooth parrotfish *Sparisoma radians* (adults and juveniles) and blackear wrasse *Halichoeres poeyi* (juveniles and adults). It is probable that degradation of seagrass beds will be detrimental to these fish species.

Live hard coral is becoming increasingly threatened at a global level. In the British Virgin Islands, main threats include blackband disease, coral bleaching and hurricane damage while organic pollution, sedimentation and anchor damage are serious problems near heavily populated areas (Spalding et al. 2001). The fish species that have strong positive correlations with live hard coral cover are the most likely to be impacted by its loss. They include: blue tang surgeonfish *Acanthurus coeruleus,* doctorfish *Acanthurus chirugrus,* puddingwife wrasse *Halichoeres radiatus,* bluehead wrasse *Stegastes planifrons,* queen parrotfish *Scarus vetula* and the barred hamlet *Hypoplectrus puella.*

Bear in mind that about 60% of the fish species found in the study area were too rare to statistically describe their habitat preferences. Therefore, the effects of habitat loss can be roughly predicted for fewer than half of the fish species highlighting the need to use the precautionary principle in these diverse environments. Habitats may also interact with each other. For example, seagrass beds appear to support higher numbers and more fish species when there are adjacent mangroves present (Chapter 3). Many reef fish may use bay habitats as nursery areas, so the impacts of water pollution in a bay may have many indirect effects on the reef community, even if pollutants are diluted to very low concentrations by the time they reach the fore reef.

8.2.3 Habitat complexity and number of fish species

This project is the first attempt to quantify the habitat complexity for a range of different marine habitat types and to compare them. The rapid assessment approach was very user-friendly and the recorded numbers could be used to mentally reconstruct the habitat structure, ranging from the most complex situations to the least complex ones. The index accounted for about 70% of the variation in number of fish species but only 21% of the variation in fish abundance (Chapter 5). Experimental manipulation of the variables showed that rugosity, variety of growth forms; percentage hard substrate and the number of small holes are all important habitat complexity variables significantly affecting number of species, species richness or abundance (Chapter 6).

In addition to the static substrate structure, the presence of longspined sea urchins *Diadema antillarum* significantly increases fish species richness and abundance in seagrass habitats where cover is limiting, probably because their spines provide refuge for juvenile fish. However, this effect is less pronounced on reefs where there are alternative sources of cover (Chapter 6). In polluted situations, poor water quality acts as a disturbance on the fish community, reducing species richness and abundance on habitat controls (artificial reefs) (Chapter 7).

The fish community on artificial reefs may have a stable number of species over time, but the actual species composition changes, resulting in considerable species turnover. It is not clear whether this is a successional change or simply stochastic variation. Fish abundance on reefs is less predictable and depends not only on the reef structure but also on shoaling habits, juvenile recruitment pulses and predators amongst other things.

8.3 IMPLICATIONS

8.3.1 Processes structuring fish communities

Much attention has been focused on the debate about how high numbers of fish species on reefs can coexist. The arguments fall into two camps. The first camp believes that fish communities are **deterministic**, and will eventually form a predictable community in the form of a climax community. They imply that in order to coexist sympatrically in a limited system each fish species must have a different fundamental niche. If species share a niche (in the sense of Hutchinson's n-dimensional hypervolume), then the less competitive species should be driven to extinction through interspecific competition (Gauze 1934). Therefore all species on a reef must have a fundamentally different niche, even if we have not quantified it. They imply that it is only a matter of time before we will tease apart the mechanisms structuring the community, and that the composition of a fish community at a given site is generally predictable with respect to the prevailing environmental conditions. In more formal terms, the competition hypothesis states that competition (usually for limited food and habitat resources) is the predominant interactive force determining the abundance and local diversity of fishes (Ebersole 1980, Anderson et al. 1981, Gladfelter and Johnson 1983, Williams and Polunin 2001).

The second camp suggests that reef fish populations seldom reach carrying capacity and are density independent **stochastic** processes that form unpredictable communities. Many species can coexist in these communities without competitive displacement because they seldom reach densities where severe competition will occur. Proponents of this hypothesis argue that reef fish have surprisingly generalist and opportunistic diets, and therefore have high levels of dietary overlap. If these populations were allowed to approach carrying capacity, competitive displacement for food resources would reduce the number of species that could coexist. At least two mechanisms that might lead to this scenario have been suggested. The **recruitment-limited hypothesis** states that recruitment rates are very low due to high mortality in the planktonic stages and that adult distributions are a result of largely unpredictable (stochastic) settlement events of pelagic larvae (Sale and Dybdahl 1975, Doherty 1981, Sale and Douglas 1984, Doherty 1991). The **predation hypothesis** states that fish populations will not reach carrying capacity because post-settlement mortality due to piscivory is so high that resource-limitation due to competition is unlikely (Hixon 1991, Caley and St John 1996).

My artificial reef study (Chapter 6) is similar to many other artificial reef studies that found no stable climax community on experimental units (Sale and Dybdahl 1975, Shulman et al. 1983, Caley and St John 1996). Species abundance and composition changed continuously in an unpredictable way and particular reef designs did not attract unique species assemblages suggesting that the communities on these reefs were stochastically controlled and density-independent.

However, the fact that the observed number of fish species was strongly affected by habitat complexity and that a very approximate rapid assessment index of this complexity could explain more than 70% of the variation in observed species richness suggests a more deterministic community structure. The recruitment-limited hypothesis may explain the apparently stochastic variation in fish species composition while the predation hypothesis would explain why higher numbers of fish exist in more complex habitats with greater refuge availability. If these are the primary mechanisms structuring fish communities, then the total number of richness on the different reefs should be directly proportional to abundance, as implied by (Caley and St John 1996), but this was disproved by the rarefaction curves for the rugosity experiment in my study (Chapter 6). I suspect that scaling issues may come into play here. The small survey samples and the small sizes of experimental units (both temporally and spatially) in relation to the home ranges of some reef fish species would have higher levels of intrinsic variation than larger ones, giving the false appearance of stochasticity. If the survey of fish (Chapter 3&4) is repeated in a few years time, without any obvious intervening disturbance, I would expect the species richness, composition, and even the relative proportions of fish in the sample to be approximately the same. This would show that fish communities in near-shore habitats are ultimately predictable and hence deterministically structured on a large scale.

This project has illustrated that every fish species is different in some way (Chapter 3). Habitat preferences range from generalists to specialists, some species even use different habitats at different stages of their life history. Different fish need different resources for a variety of reasons including camouflage, nesting, feeding and refuge. Fish body sizes span several orders of magnitude and their territories range from tens of centimeters to tens of kilometers. Even breeding strategies and seasons vary tremendously between species. Faced with this diversity it seems likely that more complex habitats would offer a greater variety of niche spaces than less complex ones and therefore higher numbers of species should coexist in more complex environments. Take the damselfish *Stegastes leucostictus* as just one example: it happily coexists with some non-grazing fish species but fiercely defends its algal gardens from other grazers (Draud et al. 1990).

In conclusion, it appears that the high fish species diversity on reefs is maintained through a combination of both the habitat structure and many ecological processes such as recruitment, predation, disease, intraspecific and interspecific competition, all of which operate in varying degrees depending upon the species involved and their location. Because of the complex nature of species interactions in these highly diverse systems it is unlikely, even if we could calculate the extent of niche overlap and levels of competition between species that we would be able to predict the exact species composition of an unknown site beyond assessing the availability of preferred habitat types.

8.3.2 Habitat complexity predicts species richness at small scales

The increase in species richness with increasing habitat complexity has been part of mainstream ecological theory since Mac Arthur's work on bird species richness in 1961. The review (Chapter 5) of subsequent work in this field describes a similar relationship in many different taxa ranging from fish, mammals and beetles to ostracods and this might therefore be a generally applicable ecological assembly rule. The Hutchinsonian concept of the niche, as an *n* dimensional hypervolume predicts that a quadrat with many different habitats can support more species than a quadrat with only one habitat type. This is because some species are adapted to specialise in certain habitats. A quadrat with many habitat types has more exploitable resource axes and therefore has more available 'niche space'. Diversity of habitat types has been used to predict species richness in many taxa e.g. butterflies (Kerr et al. 2001), fish (Guégan et al.

1998) and rodents (Cramer and Willig 2002), but they do not account for the variation in species richness caused by differences in habitat complexity.

Why, for example, should an artificial reef made from blocks with many small holes support more species than one without holes? They are both similar habitat types differing only in complexity. Alternatively, why will an area of seagrass contain fewer species than an equivalent area containing only boulders? After all, both habitats have their own specialist species; for example, the bucktooth parrotfish *Sparisoma radians* specialise in seagrass habitats while other species e.g. the dusky damselfish *Stegastes dorsopunicans* are rock specialists (Chapter 4). Might it be because more species specialise in complex habitat-types than in less complex ones? The multiple regression analysis of habitat preferences indicated that this might be the case as 3 species were significantly associated with sand, 8 species with seagrass and algal beds and 17 with rock! It is likely that more complex habitats have a greater variety of other resource axes—such as camouflage availability, nesting sites, refuge space or food—and this larger niche space will therefore accommodate new species.

If this hypothesis is correct, it could be used to predict the variation in species richness in localised areas; for example the variation in fish species richness between a tall coral head with an adjacent patch of rubble (this is the α diversity). However it is not known what implications this might have when assessing γ diversity (total species richness of a range of many habitats in a single geographical locality). The literature suggests that the number of different habitat types and their total areas, as well as the rates of change in species between habitat types are likely to be more important γ diversity predictors than habitat complexity.

8.3.3 The production versus attraction debate on artificial reefs

Most reef biologists have some opinion regarding this widely published albeit academic debate. It is generally acknowledged that any kind of artificial structure placed in the sea (or even in freshwater lakes) will be conspicuous by the large number of fish that are attracted to it. This knowledge dates back to the late 1700’s when Japanese fishermen built artificial reefs to increase the local abundance of fish (Meier et al. 1989). Two basic views exist (Pickering and Whitmarsh 1997).

The first school of thought states that artificial reefs do not increase fish production in an area; they simply aggregate fish that were present in low densities into localised high-density situations. Construction of artificial reefs is therefore potentially destructive as it exploits a natural behavioural trait of fish in order to increase the rate at which they can be caught and removed from the system (Bohnsack 1989).

The second school of thought maintains that artificial reefs are very productive habitats and that fish production is increased on the reef due to increased food availability and refuge from predators. Artificial reefs will therefore increase both the productivity and the total number of fish in an area without necessarily being detrimental to the fish populations in surrounding habitats (Alevizon and Gorham 1989, Ambrose and Anderson 1990). Artificial reefs would therefore be beneficial to fishermen and have minimal environmental impact, provided they are carefully designed and located in suitable sandy areas. Whilst proponents of this view encourage artificial reef construction they usually suggest a prior environmental impact assessment to prevent the construction of artificial reefs in a situation that may be detrimental to the environment. Impacts should be carefully considered to prevent the haphazard dumping of man-made-junk such as old ships, cars or oil platforms and using the apparently ‘environmentally friendly’ excuse that they are providing valuable habitats for fish and increasing fisheries production in the area (Brock 1989, Gorham and Alevizon 1989, Rountree 1989).

While this project provides no empirical data to settle the debate, it provides a theoretical framework that might shed some useful light on the matter. If an artificial reef is constructed in a sandy habitat, then this will increase the total hard surface area for benthic primary production and it will offer refuge from predators, nesting sites and other variables (resource axes) that were not previously available. This increases the total niche space available for fish and will therefore allow more species to coexist. The artificial reef will undoubtedly increase the productivity, but the extent to which the artificial reef production supports its fish community naturally depends on the feeding and roaming habits of the fish species involved. I would therefore argue that artificial reefs are beneficial in terms of fish biodiversity and in fisheries production. Their use should be encouraged, provided the reef construction sites are carefully chosen sandy areas and the potential impacts assessed. Critics might argue that sand-specialist fishes (such as those listed in Chapter 4) might be negatively impacted. This may be true in local terms, but sand is not a habitat type considered to be in short supply. In marine habitats it tends to be the default habitat type, i.e. what’s left after the destruction of seagrass beds, mangroves or coral reefs. Carefully planned artificial reefs not only provide a host of beneficial effects reviewed in Chapter 6 but also provide valuable experimental research opportunities that enhance our understanding of how marine systems function.

8.4 POTENTIAL APPLICATIONS

8.4.1 Predicting the effects of habitat modification on fish assemblages

The fish distribution studies of (Chapters 2, 3 and 4) offer new methods that can be used to survey fish populations elsewhere by other researchers to compare many different habitats using a uniform methodology. Additionally, the assessment of the habitat requirements of all the fish species found in the study area could immediately be used to predict fish community changes in the event of habitat modification, such as mangrove rehabilitation.

8.4.2 Use of rapid habitat complexity assessment indices

Because this rapid habitat assessment index was so strongly related to local variations in species richness, I hope that similar assessment methods will be used in other fish community studies and perhaps even in other ecological disciplines.

In addition to accounting for spatial variation in species richness the habitat complexity index offers a potentially user-friendly way to select areas of conservation priority such as marine reserves. If the best quality habitats can be identified they can be preserved and hence the maximum biodiversity can be protected in a minimal geographical area.

Many biologists try to make inferences about the effects of disturbance on the communities. A typical example that comes to mind is a study investigating the effects of fishing. If fish species richness in a reserve with highly complex habitats (selected on the basis of habitat quality) is compared with non-reserve areas (that happen to be less complex), then conclusions about species richness are confounded by habitat complexity. The use of a habitat complexity index would offer a way to account for this variation and to compare the sites. Alternatively, one could construct habitat controls – such as the artificial reefs in Chapter 7. In this way, species richness of different areas can be compared without worrying about the potentially confounding issues of complexity.

The habitat complexity hypothesis predicts that any factor that might reduce habitat complexity (such as death and bioerosion of hard corals after bleaching episodes) will result in a corresponding reduction in fish species richness. Marine managers should strive, wherever possible, to prevent degradation of naturally complex habitats.

8.4.3 Optimal artificial reef design

One potentially applied aspect of the research suggests ways in which artificial reefs might be designed to support the maximum number of species. Artificial reef should a) provide stable substrate in typically sandy regions where this is unavailable, b) have a rugose surface with a large number of small refuge holes, and c) have a variety of different ‘growth forms’ attached to it. In the long term, the last point could be disregarded because providing there is a suitable stable substrate, the growth forms are likely to grow naturally in the form of a fouling community.

8.5 A BRIEF ACCOUNT OF THE MAIN ENVIRONMENTAL ISSUES AFFECTING MARINE SYSTEMS IN THE BVI

This section is based largely on opinions I have formed during by stay in the British Virgin Islands. I am aware that most of the issues I outline are being dealt with by the Conservation and Fisheries Department in their coastal management strategy. This section aims to provide a brief overview of the issues to those unfamiliar with the BVI, and to suggest some original ideas that might stimulate the debate on problem solving. I wish to both commend and support the environmental efforts made by the Conservation and Fisheries Department, the National Parks Trust, the Community College and various private associations such as the Association of Reef Keepers, the Island Resources Foundation and the Charter Boat Association for their efforts to maintain and improve the quality of coastal habitats in the BVI.

8.5.1 Problems linked to climate change

A problem that has dominated much of the recent environmental press is the phenomenon of global warming linked to greenhouse gasses (IPCC 1990, Wilcocks 2002). Global warming may affect tropical marine environments in two ways. Firstly the elevated sea surface temperatures above 33 °C have been reported to stress corals to a point where they expel symbiotic zooxanthellae, this is also known as bleaching, and this may lead to the death of corals (Bruno et al. 2001, Nadaoka et al. 2001, Podesta and Glynn 2001, Ralph et al. 2001). Other authors warn that the mass bleaching event observed around the world that have been widely attributed to high sea surface temperatures linked to an El Niño Southern Oscillation cannot be attributed solely to sea surface temperature change (Atwood et al. 1992, Huppert and Stone 1998, Winter et al. 1998). Even though the 2001/2002 field seasons were not El Niño years, several incidents of bleaching were observed, albeit scattered in small pockets and mostly linked to *Acropora* species (B. Gratwicke pers. obs).

Another effect of global warming linked to the elevation of sea surface temperatures is the predicted increase in hurricane frequency (Leatherman 1994, Michener et al. 1997). These storms can, and have recently caused considerable damage to shallow water coral reefs in the BVI, which has experienced two particularly damaging hurricanes Hugo (1986) and Marylin (1995) recently (IRF 2003). However, there is a large degree of uncertainty in predicting future weather patterns and these assessments need to be viewed cautiously (Lively 1996).

While the predictability of climate change and its knock-on effects may be disputed, it is no excuse for complacency, especially for small island nations like the BVI. The BVI should be concerned about the possible effects of climate change, and need to join other small island states that have formed a lobbying group for the reduction of carbon emissions on the globe. However, the BVI is highly dependant upon fossil fuels for the generation of electricity, transport and desalination of seawater. It would be hypocritical for the BVIslanders to criticize other nations for their carbon emissions without taking a close look at their own lifestyles. One obvious example of this is the lack of public transport on Tortola and the extremely high density of vehicles there. If an inexpensive and efficient public transport system were created, and the number of private vehicles on the island more strongly regulated by the government, then it could be used as an example to larger countries, such as the USA that do have very large total carbon emissions. Many other initiatives at a government could be investigated for example, promoting alternative sources of power and educational programmes.

8.5.2 Pollution

Several areas in the BVI suffer from eutrophication; two cases (Hodge's Creek and Nanny Cay) have been highlighted in this thesis although these are certainly not the only examples. Both bays have elevated nutrient levels and display symptoms of eutrophication. I would suggest an adaptive management approach to solve the problem (Fig 8.1). The waste-disposal mechanisms of the adjacent businesses and/or residential areas should be investigated to establish the exact source and nature of the pollutants. Those people responsible for the pollution should be encouraged to implement appropriate mitigating measures as soon as possible. The party(ies) responsible for causing the environmental degradation should be encouraged to hire an independent consultant to periodically assess the levels of recovery. I suspect that the two problem areas mentioned above are primarily land-based sources of pollution, but the BVI has one of the highest charter-boat densities in the world and this has raised concern about the levels of organic waste discharged in near-shore marine areas (Spalding et al. 2001). This problem clearly needs further investigation.

I would support the creation of a broad-scale, pro-active water pollution-monitoring programme by the appropriate governmental department. A monitoring group could help to identify problem areas and to devise appropriate mitigating measures. In this way the vulnerable shallow water marine habitats of the British Virgin Islands will be

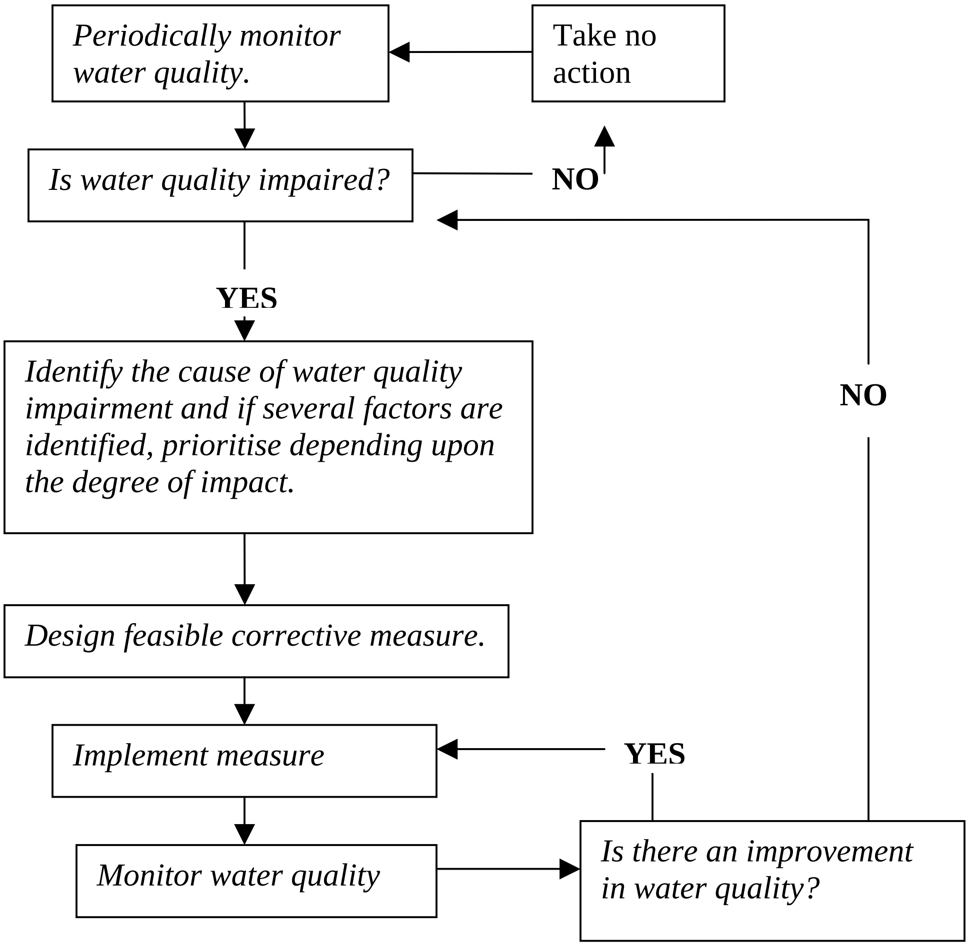


Fig 8.1 Adaptive management flow chart for water quality management.

spared from the unnecessary degradation that has occurred in many other parts of the world (Brown 1997, Spalding et al. 2001).

8.5.3 Habitat modification

The Conservation and Fisheries Department appears to have drawn serious attention to many habitat modification issues at both public and government levels. Continued pressure for thorough environmental impact assessments (EIA's) of all future development projects as well as an on-site environmental monitoring and adaptive management programme would have my full support.

Siltation appears to be an issue of concern, because of the building of road embankments and other coastal developments that cut into the very steep hills. During rainstorms, runoff flows down these embankments and it generally flows directly into the sea with very high silt loads that are deposited on coral reefs, e.g. Brewer's Bay. Sediment is known to be detrimental to corals and is a severe problem in the US Virgin Islands (Hubbard et al. 1987). Severe siltation that damages coral reefs would reduce reef complexity and have detrimental knock-on effects on the fish community.

'Land reclamation' involves dumping large quantities of earth and rubble onto shallow marine habitats and it appears to be a popular way to acquire relatively inexpensive flat land in the BVI. Several land reclamation projects were in progress on Tortola during my stay 2001-2002. Land reclamation is a sensitive issue and any land reclamation that does take place is subject to scrutiny from both the public and conservation officials. Very effective methods have been devised to reduce siltation problems associated with creating these new patches of land, but reclaimed areas cover valuable marine habitats such as mangroves, seagrass beds and coral reefs.

The best solution to this problem is to discourage land reclamation outright—but this is not always realistic. On the basis of my research, I would recommend that any developer 'reclaiming' land should be encouraged to replace the habitats destroyed by the reclamation project. This could involve creation of new artificial reef areas (using large rocks) situated at a site selected by conservation officials, which would be a sandy-bottomed area adjacent to the reclamation project. An artificial reef would provide shelter for fishes displaced by the reclamation and offer stable surfaces for corals and other benthic organisms to settle and grow. The planting of mangrove trees around newly reclaimed land areas would help to both stabilise the new area, reducing the risk of damage to the landfill site during storms and would simultaneously enhance fish stocks.

Mangrove clearing is a particularly sensitive issue in the BVI at the moment and efforts to prevent further destruction of this extremely valuable habitat has (hopefully) been brought under control by the Conservation and Fisheries Department. I strongly support efforts to gain protected status for the remaining mangrove stands such as those in Paraquita Bay and Fat Hogs bay (Overing 1997). There is an ongoing mangrove rehabilitation programme on the island to replace mangroves. It may be worthwhile approaching various landowners historically responsible for the death and or clearing of mangroves (e.g. at Pockwood Pond) and encouraging them to assist in mangrove rehabilitation efforts.

Dredging is often necessary to make marinas deep enough for safe boat traffic, and has been implemented in many places in the BVI. This usually leads to the destruction of seagrass beds, and may cause siltation problems on near-by reefs. The deep areas often have poor rates of water exchange leading to the accumulation of pollutants often associated with development. Flow-through channels increasing rates of water exchange such as at Soper’s hole are not always feasible, in which case there must be particularly rigorous control of nutrient inputs to these areas.

Anchor damage is another potential source of habitat damage—a 1987 survey of 186 boats in the USVI revealed that 32% were anchored in seagrasses and 14% in coral communities. About 40% of the anchors in coral and 58% in seagrass beds caused damage (Rogers et al. 1988). It can be assumed that similar levels were found in the BVI, but since then considerable effort has been made by the BVI National Parks Trust to provide mooring balls at popular spots for boaters to use instead of anchors. Both the Conservation and Fisheries Department and the Charter Boat Association have embarked on education campaigns to teach boaters to avoid anchoring in seagrass beds or on reefs. A similar study to Rogers (1988) might help to assess the effectiveness of this campaign.

Diver damage is likely to be a problem in the BVI because much of the tourist activity in the BVI revolves around diving. While these effects have not been assessed, it is likely that sites with high volumes of diver traffic could be damaged as they have elsewhere (Hawkins and Roberts 1994, Harriott et al. 1997, Rouphael and Inglis 2002, Zakai and Chadwick 2002). It is in the best interests of all stakeholders to prevent damage to reefs by divers. Most dive-tour operators educate people to avoid contact with live coral and to control their buoyancy, but this is not foolproof. One possible mitigating measure, apart from education, or direct regulation of the traffic at popular dive sites, would be to create artificial reefs with appeal to divers—such as a ‘shipwreck’.

Conservation authorities in consultation with dive companies could carefully position the artificial reefs in a sandy area at a suitable depth and spatial location for divers. If mooring balls are provided and its location is well publicised this may reduce traffic (and hopefully reef damage!) to other popular itineraries. The presence of a stable substrate would allow the development of a natural fouling community, including corals and provide suitable habitat for fish in areas currently devoid of cover.

8.5.4 Overfishing

As with many other countries, one of the major problems regarding overfishing is not so much devising rules that might solve the problem, but enforcing them. The FAO fisheries statistics for the BVI suggest a sharp decline in fish landings has occurred in recent years see Fig. 8.2. These declines could be due to declining fish stocks, declining numbers of fishermen or simply erroneous data returns (Spalding's 1998 estimate is 800 tonnes compared to an estimate of 42 tonnes from FAO). This thesis gives some anecdotal evidence for the possible decline in Nassau Grouper numbers (Chapter 3) and regardless of the questionable accuracy of the FAO statistics, the combined impact of artisanal fishermen and illegal spearfishermen should not be underestimated. In the USVI grunts, porgies, groupers, snappers, goatfishes, and boxfishes are particularly vulnerable to fishing pressure (Beets 1996).

The BVI has a comprehensive set of fisheries regulations (briefly reviewed in Chapter 1). However, 11 species of fish that are on the IUCN redlist of threatened species are known to occur in the BVI, these are: *Balistes vetula, Dermatolepis inermis, Epinephelus itajahara, Epinephelus striatus, Hippocampus reidi, Lachnoliamus* *maximus, Lutjanus analis, Lutjanus cyanopterus, Rhincodon typus, Scarus guacamia* and *Thunnus obesus* (Froese and Pauly 2003). There is a closed season on only 1 of these 11 threatened fish species, Nassau grouper *Epenephelus striatus* and it is between 30 November and 31 January, and there is also a closed season on the red hind *Epenephelus guttatus* from 1 January – 31 March (Anon 2002). In addition to enforcing existing fisheries regulations, I recommend that all eleven redlist species be protected entirely by law, with no open season. Local fishermen should be taught how to identify and handle these species should they be caught accidentally.

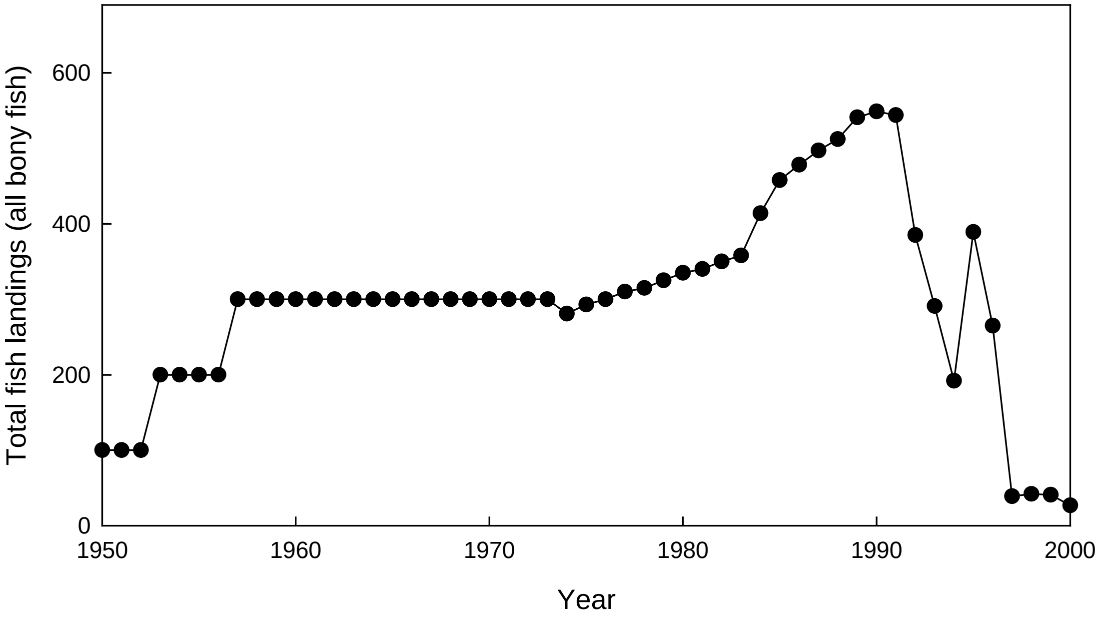


Fig 8.2 FAO fishery statistics for the British Virgin Islands source: (FAO 2003).

8.6 FURTHER RESEARCH

The ideas presented in this thesis could be further explored in an almost infinite number of ways, but I shall pick three areas that in my own opinion should yield fruitful results that would substantially advance our knowledge in this field.

8.6.1 Fish distributions on a larger scale

Several excellent studies have examined marine fish species richness at global levels (Findley and Findley 2001, Roberts et al. 2002)and numerous small-scale studies of tropical marine fish species richness exist. There is, however, a distinct paucity of information at intermediate regional scales and the few studies that have been made have been very rewarding (Roberts et al. 1992, Nagelkerken et al. 2002). Given the increasing attention given to spatial scaling effects by ecologists e.g. (Ritchie and Olff 1999) a regional-scale analysis of fish distribution patterns in the BVI would advance our understanding of the general processes affecting species richness at different scales (Acosta and Robertson 2002). Island biogeography theory has become a central and much-applied principle in terrestrial ecology (Gustafson and Gardner 1996, Boecklen 1997, Dennis and Shreeve 1997, Brown and Lomolino 2000) although the applications in marine systems are poorly understood. Because islands are essentially natural experiments a comprehensive, large-scale database of fish in the Virgin Islands would allow us to test a number of hypotheses that we can only speculate about at present. For example: are adult populations of bluestriped grunt *Haemulon sciurus* limited to islands with mangroves that act as nurseries to their juveniles?

A large and thorough set of fish distribution maps such as those created by birdwatchers could be designed. Naturally, such a large project would require excellent planning and organization, but could be potentially achieved by a small network of volunteers, using the Internet to network and to receive submissions in the same way as Birdlife International Bird Atlas projects around the world. (Note: the author has kept species lists for over 40 different locations in the BVI during the course of his recreational diving that could be added to such a data base if it is ever created).

8.6.2 Baseline monitoring programme of environmental change

The survey data could be used as a baseline study in order to monitor environmental changes in the future. If even a small number of the 2001 sampling stations could be repeated periodically, it would improve our understanding of the long-term processes affecting shallow marine habitats. A baseline dataset is a very valuable resource especially considering the recent disturbance events in the region ranging from hurricanes and coral bleaching to mass mortality of *Diadema* as well as the potential for environmental degradation due to pollution and habitat modification. Continued monitoring in the area is highly recommended.

8.6.3 Index of biotic integrity using fish as bioindicators

Biotic indices of water quality have many advantages over traditional chemical analysis (Table 8.2). I would like to see a standard protocol created that uses shallow water marine fish communities on simple artificial reefs being used as bioindicators in order to assess water quality throughout the Caribbean. Chapter 7 outlines the potential

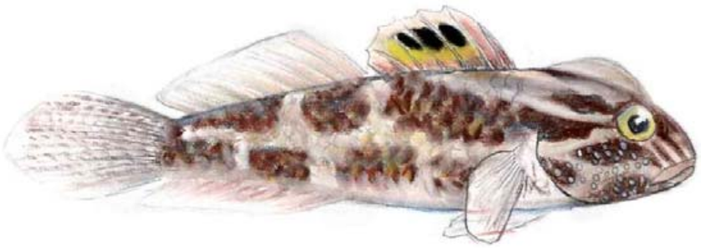
Table 8.2 A comparison of a biotic index compared to chemical analysis as a tool for monitoring water quality. (Karr 1991, Resh et al. 1995, Chutter 1998, Gratwicke 1998, Barbour et al. 1999).

Biomonitoring	**Chemical analysis**
Broad range, will detect all forms of pollution	Very specific, each contaminant must be tested for specifically
Moderately sensitive	Very sensitive
In pollution episodes, the biota will contain the only clues as to what has happened, long after polluted water has been diluted or swept away.	Results reflect instantaneous condition of the water which may be misleading
Shows the effects of pollution on the community in a very simple index that is easy to interpret and communicate back to the public.	Results can be difficult to interpret
Inexpensive, appropriate technology that requires some experience in identifying fish. Basic chemical tests (pH, Dissolved Oxygen, Visibility etc. should be carried out on site)	Expensive, endless numbers of contaminants to test for can make costs prohibitive.
Ecological health of the system can be determined	No information about the health of the river can be obtained.

for monitoring water quality changes using fish as bioindicators. With more detailed surveys, fish could be categorized according to their relative sensitivity to pollution. Artificial reefs constructed in polluted bays could be compared with communities at unpolluted reference sites, creating a standard protocol for biotic water quality assessment similar to methods used throughout the United States.

8.7 FINAL THOUGHTS

It has been a great privilege for me to work on this diverse and awe-inspiring topic. Many important ecological thinkers have devoted considerable time to the subject of coral reefs, one of the most biologically diverse habitats on the planet, and yet we understand them only superficially. I now understand why Charles Darwin talks so enthusiastically about coral reefs on the Voyage of the Beagle—it is difficult to be dry and scientific about a topic that simply needs so many adjectives to communicate the spiritual aspects of the experience! I hope that others may use my small contribution to the subject to promote a greater understanding of how these systems work and to conserve them for future generations. Words simply cannot describe the joy of snorkeling in gin-clear waters above a colourful reef, teeming with fish, and catching one’s first glimpse of a juvenile yellow-tail damselfish—a small, blue, sparkling jewel—darting between the orange blades of fire coral.



Crested goby - *Lophogobius cyprinoides*

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List of all fish encountered in the BVI

Species	**Author**	**Common Name**	**Family**
Ablennes hians	(Valenciennes, 1846)	Flat needlefish	Belonidae
Abudefduf saxatilis	(Linnaeus, 1758)	Sergeant major	Pomacentridae
Abudefduf taurus	(Müller & Troschel, 1848)	Night sergeant	Pomacentridae
Acanthemblemaria maria	Böhlke, 1961	Secretary blenny	Chaenopsidae
Acanthurus bahianus	Castelnau, 1855	Ocean surgeon	Acanthuridae
Acanthurus chirurgus	(Bloch, 1787)	Doctorfish	Acanthuridae
Acanthurus coeruleus	Bloch & Schneider, 1801	Blue tang surgeonfish	Acanthuridae
Aetobatus narinari	(Euphrasen, 1790)	Spotted eagle ray	Myliobatidae
Albula vulpes	(Linnaeus, 1758)	Bonefish	Albulidae
Aluterus scriptus	(Osbeck, 1765)	Scrawled filefish	Monocanthidae
Alphestes afer	(Bloch, 1793)	Mutton hamlet	Serranidae
Anisotremus virginicus	(Linnaeus, 1758)	Porkfish	Haemulidae
Apogon binotatus	(Poey, 1867)	Barred cardinalfish	Apogonidae
Apogon maculatus	(Poey, 1860)	Flamefish	Apogonidae
Archosargus rhomboidalis	(Linnaeus, 1758)	Western Atlantic seabream	Sparidae
Aulostomus maculatus	Valenciennes, 1837	Trumpetfish	Aulostomidae
Bathygobius soporator	(Valenciennes, 1837)	Frillfin goby	Gobiidae
Bothus lunatus	(Linnaeus, 1758)	Plate fish	Bothidae
Calamus spp.			Sparidae
Cantherhines pullus	(Ranzani, 1842)	Orangespotted filefish	Monocanthidae
Canthigaster rostrata	(Bloch, 1786)	Sharpnose puffer	Tetraodontidae
Caranx crysos	(Mitchill, 1815)	Blue runner	Carangidae
Caranx latus	Agassiz, 1831	Horse-eye jack	Carangidae
Caranx ruber	(Bloch, 1793)	Bar jack	Carangidae
Carcharhinus limbatus	(Müller & Henle, 1839)	Blacktip shark	Carcharhinidae
Chaenopsis ocellata	Gill, 1865	Bluethroat pikeblenny	Chaenopsidae
Chaetodon capistratus	Linnaeus, 1758	Foureye butterflyfish	Chaetodontidae
Chaetodon striatus	Linnaeus, 1758	Banded butterflyfish	Chaetodontidae
Chromis cyanea	(Poey, 1860)	Blue chromis	Pomacentridae
Chromis multilineata	(Guichenot, 1853)	Brown chromis	Pomacentridae
Coryphopterus dicrus	Böhlke & Robins, 1960	Colon goby	Gobiidae
Coryphopterus glaucofraenum	Gill, 1863	Bridled goby	Gobiidae
Dasyatis americana	Hildebrand & Schroeder, 1928	Southern stingray	Dasyatidae
Diodon holacanthus	Linnaeus, 1758	Long-spine porcupinefish	Diodontidae
Diodon hystrix	Linnaeus, 1758	Spot-fin porcupinefish	Diodontidae
Echidna catenata	(Bloch, 1795)	Chain moray	Muraenidae
Epinephelus adscensionis	(Osbeck, 1765)	Rock hind	Serranidae
Cephalopholis fulva	(Linnaeus, 1758)	Coney	Serranidae
Epinephelus guttatus	(Linnaeus, 1758)	Red hind	Serranidae
Epinephelus striatus	(Bloch, 1792)	Nassau grouper	Serranidae
Equetus acuminatus	(Bloch & Schneider, 1801)	High-hat	Sciaenidae

Species	**Author**	**Common Name**	**Family**
Equetus punctatus	(Bloch & Schneider, 1801)	Spotted drum	Sciaenidae
Eucinostomus spp.			Gerreidae
Gerres cinereus	(Walbaum, 1792)	Yellow fin mojarra	Gerreidae
Ginglymostoma cirratum	(Bonnaterre, 1788)	Nurse shark	Rhincodontidae
Gnatholepis thompsoni	Jordan, 1904	Goldspot goby	Gobiidae
Gobionellus saepepallens	Gilbert & Randall, 1968	Dash goby	Gobiidae
Elacatinus dilepis	(Robins & Böhlke, 1964)	Orangesided goby	Gobiidae
Gobiosoma evelynae	Böhlke & Robins, 1968	Sharknose goby	Gobiidae
Gymnothorax funebris	Ranzani, 1840	Green moray	Muraenidae
Gymnothorax miliaris	(Kaup, 1856)	Goldentail moray	Muraenidae
Gymnothorax moringa	(Cuvier, 1829)	Spotted moray	Muraenidae
Gymnothorax vicinus	(Castelnau, 1855)	Purplemouth moray	Muraenidae
Haemulon aurolineatum	Cuvier, 1830	Tomtate grunt	Haemulidae
Haemulon carbonarium	Poey, 1860	Caesar grunt	Haemulidae
Haemulon chrysargyreum	Günther, 1859	Smallmouth grunt	Haemulidae
Haemulon flavolineatum	(Desmarest, 1823)	French grunt	Haemulidae
Haemulon macrostoma	Günther, 1859	Spanish grunt	Haemulidae
Haemulon melanurum	(Linnaeus, 1758)	Cottonwick grunt	Haemulidae
Haemulon parra	(Desmarest, 1823)	Sailor's grunt	Haemulidae
Haemulon plumieri	(Lacepède, 1801)	Grunt	Haemulidae
Haemulon sciurus	(Shaw, 1803)	Bluestriped grunt	Haemulidae
Halichoeres bivittatus	(Bloch, 1791)	Slippery dick	Labridae
Halichoeres garnoti	(Valenciennes, 1839)	Yellowhead wrasse	Labridae
Halichoeres maculipinna	(Müller & Troschel, 1848)	Clown wrasse	Labridae
Halichoeres poeyi	(Steindachner, 1867)	Blackear wrasse	Labridae
Halichoeres radiatus	(Linnaeus, 1758)	Puddingwife wrasse	Labridae
Harengula humeralis	(Cuvier, 1829)	Redear herring	Clupeidae
Heteropriacanthus cruentatus	(Lacepède, 1801)	Glasseye	Priacanthidae
Holacanthus ciliaris	(Linnaeus, 1758)	Queen angelfish	Pomacanthidae
Holocentrus adscensionis	(Osbeck, 1765)	Squirrelfish	Holocentridae
Holocentrus coruscus	Poey, 1860	Reef squirrelfish	Holocentridae
Holocentrus rufus	(Walbaum, 1792)	Longspine squirrelfish	Holocentridae
Sargocentron vexillarium	(Poey, 1860)	Dusky squirrelfish	Holocentridae
Hypoplectrus chlorurus	(Cuvier, 1828)	Yellowtail hamlet	Serranidae
Hypoplectrus nigricans	(Poey, 1852)	Black hamlet	Serranidae
Hypoplectrus puella	(Cuvier, 1828)	Barred hamlet	Serranidae
Hypoplectrus unicolor	(Walbaum, 1792)	Butter hamlet	Serranidae
Kyphosus sectator	(Linnaeus, 1758)	Bermuda sea chub	Kyphosidae
Labrisomus gobio	(Valenciennes, 1836)	Palehead blenny	Labrisomidae
Lachnolaimus maximus	(Walbaum, 1792)	Hogfish	Labridae
Lactophrys trigonus	(Linnaeus, 1758)	Buffalo trunkfish	Ostraciidae
Lactophrys triqueter	(Linnaeus, 1758)	Smooth trunkfish	Ostraciidae
Lophogobius cyprinoides	(Pallas, 1770)	Crested goby	Gobiidae

Species	**Author**	**Common Name**	**Family**
Lutjanus analis	(Cuvier, 1828)	Mutton snapper	Lutjanidae
Lutjanus apodus	(Walbaum, 1792)	Schoolmaster snapper	Lutjanidae
Lutjanus griseus	(Linnaeus, 1758)	Grey snapper	Lutjanidae
Lutjanus jocu	(Bloch & Schneider, 1801)	Dog snapper	Lutjanidae
Lutjanus synagris	(Linnaeus, 1758)	Lane snapper	Lutjanidae
Malacoctenus aurolineatus	Smith, 1957	Goldline blenny	Labrisomidae
Malacoctenus gilli	(Steindachner, 1867)	Dusky blenny	Labrisomidae
Malacoctenus macropus	(Poey, 1868)	Rosy blenny	Labrisomidae
Malacoctenus versicolor	(Poey, 1876)	Barfin blenny	Labrisomidae
Malacoctenus triangulatus	Springer, 1959	Saddled blenny	Labrisomidae
Megalops atlanticus	Valenciennes, 1847	Tarpon	Megalopidae
Microspathodon chrysurus	(Cuvier, 1830)	Yellowtail damselfish	Pomacentridae
Monacanthus ciliatus	(Mitchill, 1818)	Fringed filefish	Monocanthidae
Monacanthus tuckeri	Bean, 1906	Slender filefish	Monocanthidae
Mugil curema	Valenciennes, 1836	White mullet	Mugilidae
Mulloidichthys martinicus	(Cuvier, 1829)	Yellow goatfish	Mullidae
Myrichthys breviceps	(Richardson, 1848)	Sharptail eel	Ophichthidae
Myrichthys ocellatus	(Lesueur, 1825)	Goldspotted eel	Ophichthidae
Myripristis jacobus	Cuvier, 1829	Blackbar soldierfish	Holocentridae
Nes longus	(Nichols, 1914)	Orangespotted goby	Gobiidae
Ocyurus chrysurus	(Bloch, 1791)	Yellowtail snapper	Lutjanidae
Odontoscion dentex	(Cuvier, 1830)	Reef croaker	Sciaenidae
Ogcocephalus nasutus	(Cuvier, 1829)	Shortnose batfish	Ogcocephalidae
Oligoplites saurus	(Bloch & Schneider, 1801)	Leatherjack	Carangidae
Ophioblennius atlanticus	(Valenciennes, 1836)	[Redlip blenny]	Blenniidae
Opistognathus aurifrons	(Jordan & Thompson, 1905)	Yellowhead jawfish	Opistognathidae
Parablennius marmoreus	(Poey, 1876)	Seaweed blenny	Blenniidae
Paraclinus fasciatus	(Steindachner, 1876)	Banded blenny	Labrisomidae
Pempheris schomburgki	Müller & Troschel, 1848	Glassy sweeper	Pempheridae
Phaeoptyx pigmentaria	(Poey, 1860)	Dusky cardinalfish	Apogonidae
Pomacanthus paru	(Bloch, 1787)	French angelfish	Pomacanthidae
Pseudupeneus maculatus	(Bloch, 1793)	Spotted goatfish	Mullidae
Ptereleotris helenae	(Randall, 1967)	Hovering goby	Microdesmidae
Scarus iseri	(Bloch, 1789)	Striped parrotfish	Scaridae
Scarus taeniopterus	Desmarest, 1831	Princess parrotfish	Scaridae
Scarus vetula	Bloch & Schneider, 1801	Queen parrotfish	Scaridae
Scorpaena plumieri	Bloch, 1789	Spotted scorpionfish	Scorpaenidae
Sparisoma aurofrenatum	(Valenciennes, 1840)	Redband parrotfish	Scaridae
Sparisoma radians	(Valenciennes, 1840)	Bucktooth parrotfish	Scaridae
Sparisoma rubripinne	(Valenciennes, 1840)	Redfin parrotfish	Scaridae
Sparisoma viride	(Bonnaterre, 1788)	Stoplight parrotfish	Scaridae
Sphoeroides spengleri	(Bloch, 1785)	Bandtail puffer	Tetraodontidae
Sphoeroides testudineus	(Linnaeus, 1758)	Checkered puffer	Tetraodontidae

Species	**Author**	**Common Name**	**Family**
Sphyraena barracuda	(Walbaum, 1792)	Great barracuda	Sphyraenidae
Stegastes diencaeus	(Jordan & Rutter, 1897)	Longfin damselfish	Pomacentridae
Stegastes leucostictus	(Müller & Troschel, 1848)	Beaugregory	Pomacentridae
Stegastes dorsopunicans	(Poey, 1863)	Dusky damselfish	Pomacentridae
Stegastes partitus	(Poey, 1868)	Bicolor damselfish	Pomacentridae
Stegastes planifrons	(Cuvier, 1830)	Threespot damselfish	Pomacentridae
Stegastes variabilis	(Castelnau, 1855)	Cocoa damselfish	Pomacentridae
Syngnathus caribbaeus	Dawson, 1979	Caribbean pipefish	Syngnathidae
Synodus intermedius	(Spix & Agassiz, 1829)	Sand diver	Synodontidae
Thalassoma bifasciatum	(Bloch, 1791)	Bluehead	Labridae
Trachinotus goodei	Jordan & Evermann, 1896	Palometa	Carangidae
Tylosurus crocodilus crocodilus	(Péron & Lesueur, 1821)	Hound needlefish	Belonidae