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The Functional Value of Caribbean Coral Reef, Seagrass and Mangrove Habitats to Ecosystem Processes

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Caribbean coral reef habitats, seagrass beds and mangroves provide important goods and services both individually and through functional linkages. A range of anthropogenic factors are threatening the ecological and economic importance of these habitats and it is vital to understand how ecosystem processes vary across seascapes. A greater understanding of processes will facilitate further insight into the effects of disturbances and assist with assessing management options. Despite the need to study processes across whole seascapes, few spatially explicit ecosystem-scale assessments exist. We review the empirical literature to examine the role of different habitat types for a range of processes. The importance of each of 10 generic habitats to each process is defined as its "functional value" (none, low, medium or high), quantitatively derived from published data wherever possible and summarised in a single figure. This summary represents the first time the importance of habitats across an entire Caribbean seascape has been assessed for a range of processes. Furthermore, we review the susceptibility of each habitat to disturbances to investigate spatial patterns that might affect functional values.

Habitat types are considered at the scale discriminated by remotely sensed imagery and we envisage that functional values can be combined with habitat maps to provide spatially explicit information on processes across ecosystems. We provide examples of mapping the functional values of habitats for populations of three commercially important species. The resulting data layers were then used to generate seascape-scale assessments of "hot spots" of functional value that might be considered priorities for conservation. We also provide an example of how the literature reviewed here can be used to parameterise a habitat-specific model investigating reef resilience under different scenarios of herbivory. Finally, we use multidimensional scaling to provide a basic analysis of the overall functional roles of different habitats. The resulting ordination suggests that each habitat has a unique suite of functional values and, potentially, a distinct role within the ecosystem.

This review shows that further data are required for many habitat types and processes, particularly forereef and escarpment habitats on reefs and for *seagrass beds and mangroves. Furthermore, many data were collected prior to the regional mass mortality of Diadema and Acropora, and subsequent changes to benthic communities have, in many cases, altered a habitat's functional value, hindering the use of these data for parameterising maps and models. Similarly, few data exist on how functional values change when environmental parameters, such as water clarity, are altered by natural or anthropogenic influences or the effects of a habitat's spatial context within the seascape. Despite these limitations, sufficient data are available to construct maps and models to better understand tropical marine ecosystem processes and assist more effective mitigation of threats that alter habitats and their functional values.*

1. INTRODUCTION

Caribbean coral reef habitats, seagrass beds and mangrove stands provide many important ecosystem goods and services such as coastal defence, sediment production, primary production, fisheries and the maintenance of high species diversity (Moberg and Folke, 1999). Furthermore, all three systems often occur in close proximity and many physical and ecological processes transcend individual habitats. For example, estuarine mangroves trap riverine sediments (e.g., Ogden, 1997) that might otherwise discharge onto reefs and cause mortality through sedimentation (e.g., Torres *et al*., 2001). Ecological linkages among habitats include the migration of organisms on either an ontogenetic or a diurnal basis. Many snapper, grunts and parrotfish species, for example, undertake ontogenetic shifts in habitat use from seagrass beds or mangroves to their adult coral reef habitat (McFarland *et al*., 1985; Lindeman *et al*., 1998; Cocheret de la Morinière *et al*., 2002; Mumby *et al*., 2004a). Abiotic and ecological links frequently underpin key economic resources such as the Western Central Atlantic fishery for lobster (*Panulirus argus*), which was worth an estimated US$500 million in 1998 (Cochrane and Chakalall, 2001). The coastal zone also generates significant revenue from tourism (e.g., US$21 million annually in Bonaire, Birkeland, 1997), much of which is focused on shallow marine habitats.

The economic and ecological importance of tropical marine habitats is threatened by fundamental changes to their ecology, including increases in macroalgal cover and concomitant decreases in coral cover on reefs (e.g., Hughes, 1994; Gardner *et al*., 2003), reductions in the biomass of fish assemblages (e.g., Roberts, 1995) and species extinctions (e.g., Caribbean monk seal; Leboeuf *et al*., 1986). Changes to marine ecosystems in the Caribbean have been attributed to a suite of anthropogenic factors, including pollution, coastal development, overfishing, El Niño and introduced pathogens (e.g., Lessios *et al*., 1984; Tomascik and Sander, 1987; Richardson *et al*., 1998;

Landsea *et al*., 1999; Aronson and Precht, 2001; Jackson *et al*., 2001). Furthermore, the recovery rates of coral populations on reefs in the western Atlantic are lower than in the Indo-Pacific (Connell, 1997). Given the connectivity among tropical marine habitats, their great ecological and economic importance and the suite of threats to their health, it is important to understand how ecosystem processes function across whole seascapes. A better understanding of processes will illuminate the ecological and societal consequences of both natural and anthropogenic disturbances to the ecosystem. Furthermore, greater understanding of processes would enable the effects of potential management options, perhaps aimed at enhancing coral reef resilience, to be mapped, modelled and compared.

Understanding processes at the scale of seascapes is limited by the disparate nature of tropical marine research, with many studies focusing on a single reef zone or habitat. Here, we use the framework of processes described by Hatcher (1997a) to categorise available literature and assess the ‘‘functional value’’ of Caribbean marine habitats. Functional value indicates the importance of a particular habitat to a particular process. For example, we document that a seagrass bed has a higher (more important) functional contribution to primary production than, say, a sand flat. Wherever possible, we use direct measures of a process, but proxies were used where necessary. For example, the density of herbivores and piscivores was used as a proxy for secondary and tertiary production because few data are available to convert biomass to rates of production. This need to integrate static data on states with data on rates reflects the lack of empirical observations for many processes in many habitats. In addition to assigning functional values, we also assess the susceptibility of habitats to impacts from hurricanes, coral bleaching and disease. Because each of these disturbances is habitat specific, this analysis aims to indicate possible changes to the functional value of marine habitats.

Habitats represent an appropriate scale for reviewing functional values and susceptibility because, by definition, they are relatively homogeneous areas that might be expected to have a consistent contribution to a given process or response to a particular impact. Perhaps more importantly, the areal coverage, pattern and context of reef ecosystem habitats can now be mapped over a continuum of spatial scales using airborne and satellite remote sensing (e.g., Green *et al*., 1996). Access to spatial information on reef ecosystems is expanding rapidly, particularly through the proliferation of high-resolution satellite sensors (Mumby and Edwards, 2002). Costs of imagery acquisition have fallen and image handling is now easily accomplished on a desktop personal computer rather than a workstation. Resulting habitat maps subsequently provide a means of linking communities to their functional values at multiple scales across a seascape producing spatially explicit perspectives of ecosystem processes.

We review and summarise a diverse literature to provide a habitat-scale perspective of processes across seascapes and identify research gaps. Beyond providing a resource of literature, we anticipate that this review will foster the construction of large-scale static maps of reef ecosystem processes. Maps of processes, with each habitat recoded to represent its functional value, provide a very different perspective of a tropical marine seascape than a traditional habitat map. We use this concept to provide a putative management application (see Section 6.1) by showing how a computer algorithm, generating ‘‘windows’’ of a size equivalent to a putative marine reserve, highlights ‘‘hot spots’’ of functional value that could be considered priorities for conservation, particularly if combined with equivalent maps of susceptibility to impacts likely to reduce functional values. More sophisticated uses of maps of reef ecosystem functional values might include translating a single habitat map into several overlapping layers, each pertaining to a different process, and multiple layers could then be invoked to address particular ecological and management questions. For example, layers representing calcification, bioerosion and sediment production and settlement could be linked with bathymetry to model reef growth under different scenarios of sea-level change. Spatial representations of processes will also facilitate the creation of habitat-scale ecological models, which are gaining momentum worldwide (Atkinson and Grigg, 1984; Preece and Johnson, 1993; McClanahan, 1995; Kleypas *et al*., 1999b; Langmead and Sheppard, 2004; Wolanski *et al*., 2004; Wooldridge and Done, 2004; Mumby and Dytham, 2005) and an example of this application is also provided (see Section 6.2).

2. ASSIGNING FUNCTIONAL VALUES TO HABITAT TYPES

The term ‘‘habitat’’ means different things to different people; a sponge taxonomist, for example, may refer to smaller scale habitats than someone working with remotely sensed imagery. However, because this chapter aims to provide a framework for generating maps of processes, we focus on the level of habitat resolution achievable from high-resolution optical remote sensing. Remote sensing instruments differ widely in their spectral and spatial configuration, and these differences profoundly affect the types of habitat that can be discriminated (Mumby *et al*., 2004b). To highlight the general capabilities of remote sensing technologies to discriminate habitats and provide a guide to the spatial scale that we believe will be best suited to putative maps of ecosystem processes, at least in the near future, we present a systematic community and geomorphological classification proposed by Mumby and Harborne (1999) (Tables 1 and 2). The geomorphological label describes the habitat structure, whereas the benthic class indicates the biotic

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Table 1 Hierarchical classification scheme, and quantitative characteristics, for the geomorphological zones typically found on Caribbean coral reefs

First tier		Second tier	
Label	Characteristics	Label	Characteristics
Back reef			
Reef crest			
Spur and groove		Low relief spurs and grooves	Spurs <5 m in height
		High relief spurs and grooves	Spurs >5 m in height
Forereef	Reef with <45-degree slope		
Escarpment	Either reef or lagoon with >45-degree slope		
Patch reef		Dense patch reef	Aggregated coral colonies (living or dead) where colonies cover >70% of the benthos
		Diffuse patch reef	Dispersed coral colonies (living or dead) where colonies cover <30% of the benthos
Lagoon floor	Lagoon floor with <45-degree slope	Shallow lagoon floor	Depth <12 m
		Deep lagoon floor	Depth >12 m

Source: Redrawn from classification scheme developed by Mumby and Harborne (1999).

Table 2 Hierarchical classification scheme and quantitative characteristics for the benthic communities typically found on Caribbean coral reefs

First tier		Second tier	
Label	Characteristics	Label	Characteristics
Coral classes	>1% hard coral cover; relatively high rugosity	Branching corals	*Acropora* spp. visually dominate
		Sheet corals	*Agaricia* spp. visually dominate
		Ribbon and fire corals with green calcified algae	*Agaricia* tenuifolia visually dominant
		Montastraea reef	*Montastraea annularis* visually dominates
Algal dominated	>50% algal cover; 1% hard coral cover	Green algae	
		Fleshy brown algae and sparse gorgonians	~3 gorgonians m^{-2}
		Lobophora	Monospecific *Lobophora* beds
		Euchema and *Amphiroa*	Rare assemblage dominated by red algae with encrusting Sponges
Bare substratum dominated	Dominated by bare substratum; <1% hard coral; low rugosity	Bedrock/rubble and dense gorgonians	>3 gorgonians m^{-2} (usually >8 m^{-2}) and ~30% algal cover
		Bedrock/rubble and sparse gorgonians	~3 gorgonians m^{-2} and little algal cover
		Rubble and sparse algae	No gorgonians
		Sand with sparse algae	>90% sand
		Mud	
		Bedrock	No gorgonians
Seagrass dominated	>10% seagrass cover; low rugosity	Sparse seagrass	Standing crop 1–10 g m^{-2}; cover <30%
		Medium density seagrass	Standing crop 11–80 g m^{-2}; cover 30 ± 70%
		Dense seagrass	Standing crop >80 g m^{-2}; cover >70%
		Seagrass with distinct coral patches	Seagrass visually dominant, coral cover may reach 3%, gorgonians may be present

Source: Redrawn from classification scheme developed by Mumby and Harborne (1999).

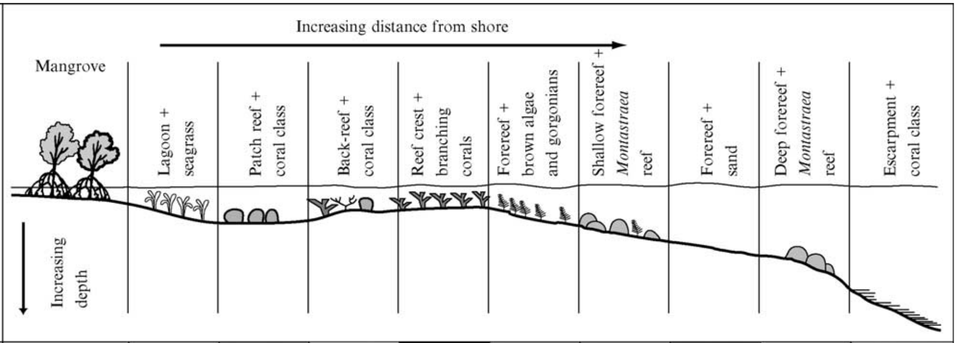
and abiotic composition of that structure, so each habitat has two descriptors (e.g., ‘‘reef crest + branching corals’’). Tables 1 and 2 also provide a context for those readers unfamiliar with the components of Caribbean tropical marine ecosystems. Furthermore, the labels used are by no means novel and represent synonyms derived from a huge body of literature devoted to describing and explaining the zonation of Caribbean coral reefs and the tables provide a general summary of reef zonation literature. The classification is not exhaustive and additional terms could be used (e.g., ‘‘transitional reefs,’’ in relatively marginal reefs such as those in Florida; Sullivan *et al*., 1994a). Similarly, there is a strong case for indicating whether stands of *Acropora palmata* are living or dead because populations have declined in much of the region (Sheppard *et al*., 1995).

Each of 10 generic habitat types, forming a schematic profile of a Caribbean marine ecosystem, is assigned a functional value for each process reviewed (Figure 1). Making such generalisations is fraught with difficulties because of, among other factors, the lack of data for many habitats, methodological differences, lack of specific habitat descriptions in empirical studies, the effects of marine reserves, biogeographical variations within the Caribbean and ecological changes over time (e.g., caused by *Diadema antillarum* mortality, coral bleaching and diseases and overfishing). Therefore, functional values of each habitat are simply placed into one of four semiquantitative categories (‘‘none,’’ ‘‘low,’’ ‘‘medium’’ or ‘‘high’’) to reflect the implicit problems. Assigning a functional value to each habitat is achieved using the relevant empirical data reviewed in the text and the rationale for each is made in a concluding paragraph at the end of each section. Wherever possible, such decisions are made using interpretation of quantitative data (e.g., rates of process X in habitat Y greater than the rate in habitat Z). Furthermore, where such data are available and reviewed in the text, they are also included in Figure 1 as a range of reported values for a given habitat. In cases in which the functional value is not clear (usually empirical data for a particular habitat were not found in the literature), a putative functional value is assigned based on circumstantial evidence or the authors’ observations.

3. FUNCTIONAL VALUES OF TROPICAL MARINE HABITATS

3.1. Modification of wave and current patterns

Waves and currents do not travel passively across a reef and are significantly modified by benthic habitats such that wave refraction and energy dissipation produce wave height and energy gradients (e.g., Sheppard, 1982; Sebens, 1997). Perhaps the most obvious example of energy dissipation



Ecosystem process (Section in text) (Units)	Mangrove	Lagoon + seagrass	Patch reef + coral class	Back-reef + coral class	Reef crest + branching corals	Forereef + brown algae and gorgonians	Shallow forereef + *Montastraea* reef	Forereef + sand	Deep forereef + *Montastraea* reef	Escarpment + coral class
Wave energy dissipation (3.1) (%)			?	?	72–97 (5)	?	45[a] (1)	?	?	?
Nitrogen fixation (3.2.1) (nmol N_2 g afdw^{-1} h^{-1})	?	?[b]	15.3 (1)	?	71.9 (1)	?	47.5 (1)	?	?	?
Gross community primary productivity (3.3.2) (g O_2 m^{-2} d^{-1})	?	2.9–3.2 (1)	5.4 (1)	62.0 (1)	15.7–44.0 (4)	?	5.4 (1)	<1.8 (1)	?	?
Density of *Sparisoma viride* (3.4.2) (Fish 100 m^{-2})	0.0–0.7 (3)	0.0–2.6 (6)	1.0–16.7 (4)	0.8–35.0 (4)	0.6–21.0 (6)	0.3–1.8 (3)	1.1–9.4 (9)	0.0 (1)	0.3–2.6 (7)	0–0.6 (2)
Density of Acanthuridae (3.4.3) (Fish 100 m^{-2})	0.4–1.7 (3)	0.1–1.4 (4)	11.7–65.3 (5)	18.0–97.5 (4)	9.8–51.4 (7)	?	2.0–19.3 (16)	0.0 (1)	0.5–4.5 (5)	1.0 (1)
Density of *Stegastes planifrons* (3.4.4) (Fish 100 m^{-2})	0.0–0.1 (4)	0.0–0.01 (4)	0.0–800.0 (4)	0.0–375.0 (3)	0.0 (1)	?	0.0–47.0 (5)	?	3.3–28.8 (4)	?
Density of *Diadema* (<1983) (3.4.5) (Individuals m^{-2})	?	0.0–2.8 (4)	6.7–72.8 (2)	0.1–3.9 (4)	2.4–25.8 (5)	0.5–4.5 (1)	3.5–18.0 (6)	0.0 (1)	0.1–1.7 (5)	?
Density of *Diadema* (>1983) (3.4.5) (Individuals m^{-2})[c]	<1	<1	<1	<1	<1	<1	<1	0	<1	0

Figure 1 (Continued)

Density of planktivores (3.5.1) (Fish 100 m^{-2})	0.0 (4)	0.0 (4)	?	?	?	?	18.3–128.9 (3)	?	90.1–138.3 (2)	?
Density of *Haemulon flavolineatum* (3.5.2) (Fish 100 m^{-2})	6.0–99.8 (5)	0.5–32.1 (6)	4.5–51.0 (2)	110–130 (1)	21.0 (1)	?	2.4–5.8 (4)	?	1.2–2.2 (3)	0.3 (1)
Density of *Epinephelus striatus* (3.5.3) (Fish 100 m^{-2})	0.0–212.0 (2)	0.0–? (2)	0.1–4.0 (2)	?	?	0.1–0.3 (1)	0.1–0.4 (1)	?	?	0.04 (1)
Density of *Panulirus argus* (3.6.1) (Individuals ha^{-1})	247.0–642.0 (1)	5.5–263.0 (4)	32.1–900.0 (3)	?	?	2.0–10.0 (2)	6.0–15.2 (2)	0.0 (1)	?	38.3 (1)
Density of *Strombus gigas* (3.6.2) (Individuals ha^{-1})	?	0–20000[d] (7)	11.7–15.8 (1)	0.0–111.0 (2)	?	24.0–31.0 (1)	?	2.0–310[e] (4)	?	?
Gross community calcification (3.7.2) (kg $CaCO_3$ m^{-2} yr^{-1})	?	0.1–0.2[f] (1)	?	3.5–3.8[d] (1)	1.5–10.0 (2)	?	1.6–10.3 (5)	0.9 (1)	1.9–4.7 (2)	0.3–1.0 (3)
Community bioerosion (3.8.2) (kg $CaCO_3$ m^{-2} yr^{-1})			?	?	?	?	≈0.4–3.3 (3)		?	?
Coral recruitment (3.9.2) (Juveniles m^{-2})	?	?	0.8–24.0 (1)	?	?	?	2.2–21.1 (4)		12.9 (1)	3.0–18.0 (3)
Scleractinian diversity (3.10.1) (Shannon diversity index)	?	?	1.56–2.09 (2)	0.35–1.62 (3)	0.01–1.4 (3)	0.48–1.36 (2)	0.75–2.20 (5)	?	1.54–2.12 (4)	1.26–1.81 (3)

[a] 45% dissipation of energy across a forereef (from a depth of 20 m to 5 m) but data not habitat specific.

[b] 0.03–140 mg N m^{-2} d^{-1}.

[c] At least seven studies have documented post-mortality densities of <1 individuals m^{-2} in a range of habitats.

[d] Aggregations of up to 295 juveniles m^{-2} documented.

[e] Aggregations of up to 2793 adults ha^{-1} documented.

[f] Net calcification rate measured by hydrochemical techniques.

across a reef is the creation of lagoons to the leeside of coral reefs that have suitably calm conditions for seagrass beds and mangroves (e.g., Moberg and Rönnbäck, 2003). Hubbard (1997) describes the feedback mechanism between the reef and oceanographic processes as a key feature of true reefs.

A significant proportion of oceanic water does not actually cross reefs but is deflected through passages (Hamner and Wolanski, 1988). Wave heights of water that does cross reefs are reduced, and data from Grand Cayman showed attenuation, from the shelf margin (at ∼22 m) to the forereef (at ∼8 m) to be 20% (causing wave-induced flow) and tidal current speeds were also reduced by 30% (Roberts *et al.*, 1977). In Puerto Rico, the height of waves generated by both trade and local winds decreased as they travelled across the forereef by 19.5% from a depth of 20 to 10 m and 26% from 20 to 5 m. There was a concomitant reduction in wave energy of 35% from 20 to 10 m and 45% from 20 to 5 m (Lugo-Fernández *et al.*, 1994). Roberts *et al.* (1977) also showed in Grand Cayman that strong rectilinear (reversing) tidal currents dominated the deep shelf margin, but these were transformed into weak directionally variable currents on the shallow terrace margin. Tidal current transformation was caused by frictional effects resulting from strong interactions between the water body and a topographically complex zone of coral spurs and sediment grooves. The change from tidal currents (shelf) to multidirectional flow (terrace) was associated with a 60–70% speed reduction, which further weakens towards the reef crest. The frictional interaction with the spurs and grooves further increased the roughness of the zone and established a feedback loop, so there was a change from current-dominated zones (>18 m) to wave-dominated zones (<18 m) and the crossover point represented a sediment reservoir.

Water movement is altered significantly as it flows across the forereef, but the reef crest also has a vital role in the hydrodynamics of a reef ecosystem. For example, Suhayda and Roberts (1977) studied water movement across the reef crest and showed that wave height and period were typically reduced by ∼50% and that this varied with water depth. Roberts *et al.* (1992) reviewed four studies and indicated that wave energy decay between the

Figure 1 Functional values of habitats for ecosystem processes across a schematic profile of a Caribbean tropical marine seascape, derived from empirical literature reviewed in the text. Black, dark grey, light grey and no shading indicate high, medium, low and no functional values, respectively. Figures represent range of published values. The number of studies (some of which may contribute more than one value) used to derive the ranges are in parentheses. ? indicates a putative class, but quantitative data have not been found in the literature. The two sets of functional values for the density of Diadema antillarum refer to the mass mortality of the urchin in 1983. The shallow Montastraea reef is regarded as being at a depth of ∼5–12 m and the deep Montastraea reef ∼12–20 m. The mangrove habitat includes creeks.

forereef and lagoon in the Caribbean ranged from 72 to 97%. Lugo-Fernández *et al.* (1994) showed that wave heights decrease by an average of 82% across the reef crest, with a simultaneous 97% energy loss, and this leads to the formation of strong across-reef currents capable of moving coarse sediment. If the crest is at or above the water level, it becomes a ''high-pass'' filter controlled by wave overtopping (water carried over the crest top). Conversely, if the crest is deeper than 1 m, it functions as a ''low-pass'' filter controlled by wave dissipating mechanisms. Suhayda and Roberts (1977) highlighted that wave-driven currents flowed onshore continuously over the reef crest and had the greatest velocity at low tide when wave breaking was most intense. The hydrological functioning of many reef crest zones currently found on Caribbean reefs is likely to have been significantly altered following the dramatic reduction in *Acropora* populations because of white band disease (see Section 5.3), but few data are available.

Across an entire reef there is a characteristic gradient from high-velocity flow in shallow zones, induced by waves, to unidirectional or directionally variable currents of lower velocity in the deeper reef and lagoonal habitats (Sebens, 1997). The exact characteristics of water flow across the depth gradient can be modified by reef topography. Spur and groove zones are particularly important because strong on-shelf flow can be entrapped and advected up deep grooves at the shelf margin, and subsequently over the reef crest, and these areas typically have high levels of turbulence (Roberts *et al.*, 1977). Under particular conditions of reef topography and significant wave action, it is also possible that water levels on the outer edge of reef flats may be raised (''set up'') by up to 20% of the incident wave height above the mean water level just seaward of the reef (Tait, 1972). Such wave setup can significantly affect circulation and can drive flow into lagoonal areas and out through reef channels.

3.1.1. Habitat functional values (Figure 1)

Reef crests clearly have a high functional value for dissipating wave energy (72–97%). Wave energy is also dissipated across the forereef (45% from a depth of 20–5 m; Lugo-Fernández *et al.*, 1994), but there appear to be no data on the role of different habitats, so each is assigned a putative medium functional value. Currents dominate water flow along the shelf margin (Roberts *et al.*, 1977), so in the absence of quantitative data, the escarpment is proposed as having a low functional value. Data are also scarce for the back reef and patch reef, but some wave energy crosses the reef crest and the rugosity of these habitats presumably dissipates some of the remaining energy (low functional values). Seagrass beds and mangroves require calm conditions (Moberg and Rönnbäck, 2003) and are assigned no functional value.

3.2. Biogeochemical cycling

Section 3.3 (Primary productivity) focuses on carbon cycling (the ‘‘currency’’ of community biogeochemistry, Kinsey, 1985), and here, we consider how different reef ecosystem habitats are involved in nutrient (primarily nitrogen) cycling. The process of nitrogen cycling on reefs is described by D’Elia and Wiebe (1990) and Downing *et al.* (1999), but neither contains information on how the component pathways (e.g., ammonification and nitrification) vary between habitats. Indeed, it is clear from the literature that there is very little spatially explicit data on nutrient cycling, and available data are generally restricted to soft-sediment habitats or shallow Indo-Pacific reefs. For example, lagoons are likely to be areas of high denitrification (loss of fixed nitrogen) because there is a low redox potential close to the surface of the sediments and a large input of organic matter to lagoonal sediments (D’Elia and Wiebe, 1990). Because of the lack of data, we limit our discussion of habitat functional values in reef biogeochemistry to nitrogen fixation.

3.2.1. Nitrogen fixation

Like other aspects of reef biogeochemistry, much of the research on nitrogen fixation has been undertaken in the Indo-Pacific and on a limited number of habitats (e.g., Wiebe *et al*., 1975), but it is possible to discern general trends. Nitrogen fixation is a function of the abundance of nitrogen fixing biota, particularly cyanobacteria (Adey and Steneck, 1985) and their hydrodynamical environment. The hydrodynamic regimen is important because nitrogen fixation is generally positively correlated with water-flow speed (Williams and Carpenter, 1998 and references therein). Shallow reef areas, therefore, provide an optimal environment for nitrogen fixation. D’Elia and Wiebe (1990) list the sites of major nitrogen fixation as windward forereef and ‘‘spur and groove’’ zones, particularly those with extensive algal turfs. The presence of *Diadema* can also increase chlorophyll-specific acetylene reduction (a measure of nitrogen fixation) in shallow water, although fixation only supported <2% of the nitrogen required by an algal turf community in St. Croix (Williams and Carpenter, 1997).

In shallow (<6 m) water in the Bahamas, Goldner (1980) examined nitrogen fixation rates by epiphytic cyanobacteria (e.g., found on seagrasses and macroalgae) and epilithic cyanobacteria (e.g., found on rock, sand and coral rubble). Nitrogen fixation rates were firstly found to be most active on intertidal beach rock (423.0 nmol N_2 g ash-free dry weight^{-1} [afdw^{-1}] h^{-1}), *Thalassia* (173.9 nmol N_2 g afdw^{-1} h^{-1}) and the macroalga *Acanthrophora* (145.4 nmol N_2 g afdw^{-1} h^{-1}). Secondly, rates varied between habitats and were 71.9 nmol N_2 g afdw^{-1} h^{-1} in an *A. palmata* zone, 47.5 nmol

N_2 g $afdw^{-1}$ h^{-1} on a forereef and 15.3 nmol N_2 g $afdw^{-1}$ h^{-1} on a small patch reef. Goldner (1980) then suggested that nitrogen fixation rates may be correlated with surface area of the substratum; patch reefs had lower nitrogen fixation rates than the reef crest and had a smaller surface area available for algal colonisation. Goldner (1980) further concluded that the highly variable fixation rates probably reflected the patchy distribution of cyanobacteria. The patchy distribution of cyanobacteria is partly caused by spatial patterns of herbivore densities (see Section 3.4). Damselfishes have particularly important effects on cyanobacterial cover, and Brawley and Adey (1977) showed that Caribbean damselfishes increase cyanobacteria abundance in the turf algae within their territories by reducing grazing pressure. Data from the Great Barrier Reef (Sammarco, 1983) suggest that nitrogen fixation is positively correlated to fish grazing (higher outside damselfish territories), but it is unclear whether this is a systematic difference between regions or reflects a complex interaction between cyanobacteria and damselfishes that varies between species and habitats.

Nitrogen fixation in seagrass beds is accomplished by bacteria in the sediment around roots, known as the *rhizosphere*, and epiphytes on the leaves and stems, known as the *phyllosphere*. Nitrogen fixation rates in seagrass beds are sufficient to frequently make phosphorus the limiting nutrient (Fourqurean *et al.*, 1992). There has been some debate on the relative contributions of fixation by the rhizosphere and phyllosphere, and there is significant variation in results between sites and the effect of nitrogen fixation on primary productivity (summarised by Welsh, 2000). However, empirical evidence indicates that in the absence of significant nutrient inputs, both the phyllosphere and the rhizosphere are important sites of nitrogen fixation in *Thalassia* communities (Goering and Parker, 1972; Capone *et al.*, 1979). Rates of nitrogen fixation in the Caribbean vary from 0.03 to 140 mg N m^{-2} d^{-1} in six studies using a variety of techniques (summarised by Welsh, 2000). Variations in fixation rates across seagrass beds of different densities appear to have received little attention, but the close relationship between photosynthetic activity of plants and bacterial fixation in the rhizosphere indicates that fixation is likely to be tightly correlated to seagrass biomass. In mangrove stands, there seems to be some nitrogen fixing by root associated bacteria, but tidal influx is likely to be a more important source of nutrients (Hogarth, 1999).

3.2.2. Habitat functional values (Figure 1)

There are few habitat-specific data measuring nitrogen fixation using comparable techniques. However, seagrass beds and reef crests appear to have optimal conditions (high functional values) for nitrogen fixation because of the combined effects of the rhizosphere and phyllosphere (0.03–140 mg N m^{-2} d^{-1}) and high water movement and rugosity (71.9 nmol N_2 g $afdw^{-1}$ h^{-1}) in shallow water, respectively. Other available data indicate medium functional values for shallow *Montastraea* reefs (47.5 nmol N_2 g $afdw^{-1}$ h^{-1}) and low functional values for patch reefs (15.3 nmol N_2 g $afdw^{-1}$ h^{-1}). Nitrogen fixation appears to be correlated to surface area (Goldner, 1980), so we assign a low functional value for gorgonian-dominated habitats. Fixation rates are likely to be low on deep *Montastraea* reefs and escarpments because of decreased light levels, and we have assigned low functional values. Though supporting depauperate benthic communities, sand habitats are likely to have some cyanobacteria present and are assessed as having a low functional value. Back reefs presumably have lower fixation rates than reef crests because of differences in hydrodynamical conditions and available surface area and thus are assigned medium functional values. Mangroves appear to have a low functional value with limited nitrogen fixing on prop roots (Hogarth, 1999).

3.3. Primary production

3.3.1. Physical and biotic controls of primary production and key photosynthesising taxa

Photosynthesis is a fundamentally important process in reef systems, as it uses light energy to create organic material. Measurements of gas fluxes, such as the production of oxygen, can be used to estimate the rate of photosynthesis, which can be converted into primary productivity and expressed as mass of organic matter per unit area per unit time (e.g., Hatcher, 1988). As is discussed, patterns of primary productivity vary significantly across reef habitat and zones depending on the components of their communities. In addition to variations caused by benthic communities, there are overarching spatial controls on primary productivity, the most obvious of which is light availability (reviewed by Larkum, 1983; Hatcher, 1990). Gross primary productivity decreases with increasing depth on a forereef as light and photosynthetic area decrease. However, the relationship between productivity and changing depth is complicated by photoadaption, grazing, self-shading, topographical complexity, stability of the reef surface and disturbance regimens (de Ruyter van Steveninck and Breeman, 1981; Barnes and Devereux, 1984; Hatcher, 1997b).

Along with investigating the effects of light, the apparent paradox of relatively low nutrient levels in tropical waters and high primary productivity has led to considerable research. While scarcity of nutrients has great potential for limiting photosynthesis, the link between nutrient concentrations and primary productivity is highly complex. A series of case studies of anthropogenic input of additional nutrients has provided variable results and detailed predictions are difficult (see, for example, Connor and Adey, 1977; Lapointe and O'Connell, 1989; Larned, 1998; Hughes *et al.*, 1999). Furthermore, few of these data are habitat specific and further interpretation is outside the scope of this review. In addition to physical controls, spatial variation in grazing pressure is an important controlling factor of primary productivity (see Section 3.4). However, linking grazing pressure to primary productivity is complicated by feedbacks caused by the evolution of defence mechanisms and intraspecific and interspecific feeding selectivity, which have significant effects on the algal community structure present in a given area (Hatcher, 1988).

Calculating community primary productivity for a particular habitat from organism productivity is complex because of methodological difficulties such as calculating surface area in rugose environments, differing spatial and temporal scales of measurement and the inclusion or exclusion of heterotrophic respiration (Hatcher, 1988). However, because of the lack of community-scale data on primary productivity, we provide a brief overview of the primary productivity rates of major benthic taxa that can be used to calculate values for whole habitats (e.g., Wanders, 1976b; Rogers and Salesky, 1981). Much of the research on primary productivity has focused on the coral–algal symbiosis to the detriment of work on algae, seagrass and phytoplankton (Hatcher, 1988). Despite a bias towards coral research, it is clear that algal communities are a major source of reef primary production (e.g., Lewis, 1977) and there is a pattern between the functional groups. Generally there is a negative relationship between resources dedicated to herbivore resistance and those dedicated to primary productivity. Therefore, highly grazed sheet and filamentous algae are generally more productive than fleshy and coarse branched species, which have some protection from grazing, which are in turn more productive than lightly grazed, but heavily protected, calcareous and coralline species (Littler *et al.*, 1983b; Littler and Littler, 1984; Morrissey, 1985). For example, net photosynthetic rates in Belize were 6.28 mg C g organic dry weight^{-1} h^{-1} for sheet algae, 5.48 for coarsely branched species and 0.16 for crustose species (Littler *et al.*, 1987). Rates for turf algae were relatively low (1.67 mg C g organic dry weight^{-1} h^{-1}), possibly because of the compact configuration and particulate matter content of the species studied. On a shallow reef in Bonaire, rates were 61.44 μg O_2 cm^{-2} h^{-1} for crustose corallines and 72.87 μg O_2 cm^{-2} h^{-1} for sparse turfs (van Rooij *et al.*, 1998). A more dramatic difference between functional forms was demonstrated in Curaçao where annual productivity rates were 350 g gross of organic C m^{-2} for crustose Corallinaceae (0.02 mg O_2 cm^{-2} h^{-1}) and 710 g C m^{-2} (0.05 mg O_2 cm^{-2} h^{-1}) for algal turfs (Vooren, 1981).

Filamentous (turf) algae are a particularly important component of the epilithic algal community because they exploit the high surface area that the complex topography of a reef provides. Indeed, Adey and Steneck (1985) suggest that shallow reef productivity corresponds with the distribution and abundance of turf algae. Constant grazing keeps turf algae in an exponential growth phase and turfs have a higher surface to volume ratio than macroalgae (Littler and Littler, 1984; Hatcher, 1997b). In shallow water, high primary productivities by turf algae are maintained despite extremely high light intensities and exposure to ultraviolet (UV) because they have a high saturating light intensity and there is an apparent lack of photoinhibition (Vooren, 1981; Carpenter, 1985a). Adey and Goertemiller (1987) refer to algal turfs as "master producers" and use harvesting techniques to give production rates up to 14 g (dry) m^{-2} d^{-1}, which decline with increasing depth. Rogers and Salesky (1981) give net productivity rates of 0.23–0.93 g O_2 m^{-2} h^{-1} (gross productivities of 0.76–0.89 g O_2 m^{-2} h^{-1} for a limited number of samples) for algal turf communities in St. Croix and compare these to values of 0.30–0.64 g O_2 m^{-2} h^{-1} on a Curaçao reef crest (Wanders, 1976b).

Macroalgae, such as *Acanthophora*, *Halimeda*, *Padina*, *Penicillus* and *Sargassum* are also important primary producers (e.g., Hillis-Colinvaux, 1980; Rogers and Salesky, 1981; Hatcher, 1988). High densities of herbivores limit macroalgal growth, but algae are particularly abundant when grazing pressure is reduced, such as in deeper water or following *Diadema* urchin mass mortality (Hatcher, 1997b). Adey *et al.* (1977) discuss bank barrier reefs in Martinique where corals have been replaced on the reef crests by dense stands of fleshy algae, particularly *Sargassum*, forming a "fleshy algal pavement." Macroalgal reef crests are highly productive, demonstrated by the primary productivity on Martinique being twice that of the back reef at St. Croix because macroalgal standing crop was 20–30 times higher than the filamentous algae in St. Croix, which more than counteracted for filamentous algae being 10–20 times more productive per unit weight. Adey *et al.* (1977) documented similar formations on Grenada and S. Lucia and suggested that these reefs are characterised by high turbidity and lack large-scale porosity, meaning that they do not have large populations of grazing *Diadema* and parrotfishes. Rogers and Salesky (1981) give net productivity rates of 1.16–8.98 g O_2 m^{-2} h^{-1} (gross productivity of 2 g O_2 m^{-2} h^{-1} for one sample) for macroscopic algal communities in St. Croix. The gross productivity of *Sargassum platycarpum* and two species of *Dictyota* were recorded as 6.0–15.6 g O_2 m^{-2} d^{-1} (net productivities 3.1–10.3 g O_2 m^{-2} d^{-1}) on a Curaçao reef crest (Wanders, 1976a).

The coral–algal symbiosis has high rates of primary productivity because, for example, zooxanthellae densities and coral growth forms are able to change with decreasing light intensities (reviewed by Hatcher, 1988;

Muller-Parker and D'Elia, 1997) and research has facilitated the production of detailed energy budgets for particular species (Edmunds and Spencer Davies, 1986). As for many algal studies, research on the primary productivity of corals has been predominantly in shallow water and Rogers and Salesky (1981) give net productivity rates of 0.15–0.54 g O_2 m^{-2} h^{-1} (gross productivity of 0.52–0.76 g O_2 m^{-2} h^{-1} for three samples) for *A. palmata* in St. Croix and show how these values are similar to previous data in the Caribbean. Production rates for six species of coral ranged from 33.06–782.51 kcal m^{-2} yr^{-1} in Barbados (Lewis, 1981). Coral productivity can vary intraspecifically between habitats and *A. palmata* net primary productivity was highest in a shallow forereef (0.5–1.0 m, 0.44 g O_2 m^{-2} h^{-1}), intermediate in a back reef (0.36 g O_2 m^{-2} h^{-1}) and lowest in the deep forereef (8–10 m, 0.28 g O_2 m^{-2} h^{-1}) where there was less light (Gladfelter and Monahan, 1977). Such intraspecific, and indeed interspecific, changes have been linked to zooxanthellae types within corals; Diekmann *et al.* (2002) showed that *Montastraea annularis* and *Acropora cervicornis* had strong habitat-related correlations between zooxanthellae type and depth. In contrast, there was no correlation between *Madracis* zooxanthellae and depth, so this species has a generalist zooxanthellae–coral association, which is equally successful over a range of habitats.

3.3.2. Community primary productivity

The importance of organic production on reefs has led to a large number of studies using a variety of techniques and addressing a range of research topics. These studies of primary productivity have allowed a succession of authors to propose standard empirical values for coral reef zones. For example, Kinsey (1983) suggested that shallow unperturbed Pacific reef systems have four or five "modes" of metabolic performance, particularly "coral/algal," "algal pavement" and "sand/rubble" with community gross photosynthesis rates of 20, 5 and 1 g C m^{-2} d^{-1}, respectively (see also Kinsey, 1985, for more examples). The concept of modes of metabolic performance was extended by Hatcher (1988, 1990), who presented a figure summarising, from the available literature, primary productivity for entire reefs plus six reef zones and seven major benthic taxa contributing to reef productivity. Although the work of Kinsey (1985) and Hatcher (1988, 1990), summarising productivity rates across standardised habitats, epitomises the approach taken by this chapter, most of the empirical studies they cited were from the Indo-Pacific and their extrapolation to Caribbean reefs is difficult and are not used here to assign functional values. Indeed, there are further difficulties comparing Caribbean primary productivity rates before and after the mass mortality of *Diadema antillarum* (discussed in more detail in Section 3.4).

Data from St. Croix clearly show the decrease in net productivity of algal turf communities over the course of a few months (37% per unit area from 0.68 to 0.43 g O_2 m^{-2} d^{-1}) because of the decrease in grazing and ammonium from *Diadema* excretion (Carpenter, 1988; Williams and Carpenter, 1988).

Although absolute values of primary productivity are difficult to transfer between regions because of differences in community composition, the general trends are likely to be universal because of the overarching control of photosynthesis by light and its attenuation with increasing depth and they are supported by some Caribbean empirical data. Perhaps clearest of these trends is the high productivity of back reefs because of the large surface area, high light intensities and the steady flux of nutrients (reviewed by Hatcher, 1997b). In St. Croix, three back reefs (depth <0.9 m) and three shallow forereefs (<6.3 m) differed significantly in their mean gross primary production (62.0 g O_2 m^{-2} d^{-1} vs 15.7) and net primary production (36.5 g O_2 m^{-2} d^{-1} vs 8.9) (Adey and Steneck, 1985). Adey and Steneck (1985) also showed that algal turfs were the major producers in each zone and attributed differences in productivity to lower surface areas, less water movement and higher coral cover in the forereef sites. Data from St. Croix also highlighted intersite differences in back reef productivity linked to geological age; turf algae was most abundant on a reef with intermediate age because of the high surface area provided by dead colonies of the rugose coral *A. palmata* in comparison to younger sites with either abundant living *A. palmata* or older sites with limited surface area. The values for the back reef were higher than the rates (27 g O_2 m^{-2} d^{-1}) for a shallow *A. palmata*–dominated (45% cover) reef crest (Rogers and Salesky, 1981). For a different shallow water habitat (algal ridges) in St. Croix, Connor and Adey (1977) provided similarly high productivity rates (gross production 64.8–121.5 g O_2 m^{-2} d^{-1}). Elsewhere in the Caribbean, equivalent gross production rates were reported for both a shallow *A. palmata* reef and a *Sargassum*-dominated plateau (41.4 and 28.0 g O_2 m^{-2} d^{-1}, respectively) in Curaçao (Wanders, 1976a,b). In a rare study on a shallow (3–4 m) reef dominated by *Montastraea* rather than *A. palmata*, Rogers (1979) obtained gross productivity rates in Puerto Rico of 5.4 g O_2 m^{-2} d^{-1} and contrasted the results with the higher rates (20–44 g O_2 m^{-2} d^{-1}) reported by Odum (1959), also in Puerto Rico, which were in shallower areas with lower coral cover (more algae).

Studies of primary productivity on forereefs are remarkably rare in the Caribbean, and indeed elsewhere (Hatcher, 1988), because of sampling difficulties using traditional flow respirometry. The new "Submersible Habitat for Analysing Reef Quality" (SHARQ) (Yates and Halley, 2003) may provide an important tool for measuring a range of community metabolism parameters from a range of habitats. Currently, SHARQ has only been used in the Caribbean (Florida) on patch reefs, dense and sparse seagrass and sand. Patch reef data indicated that gross production is 5.4 g O_2 m^{-2} d^{-1} and sand production was 1.8 g O_2 m^{-2} d^{-1} (Yates and Halley, 2003). The latter value supports previous research that has shown that carbonate sands have limited topographical complexity and a depauperate benthic community but have productive microalgae in their top layer (Dahl, 1973; Kinsey, 1985; Hatcher, 1988) and can occupy vast areas, so their contribution to the primary productivity of whole systems may be important.

Seagrass beds frequently contribute large portions of the primary production of coastal ecosystems (e.g., Thayer *et al*., 1984; Fourqurean *et al*., 1992) and *Thalassia testudinum* has long been recognised as one of the most productive of all plants (e.g., Odum, 1956; Westlake, 1963). The high productivity of seagrasses is supplemented by a range of other taxa in seagrass beds, particularly epiphytic algae, benthic microalgae and macroalgae and phytoplankton (e.g., Bach, 1979). Seagrass habitats are routinely described in terms of the density or biomass of plants and there are clear data showing that leaf productivity of *T. testudinum* is closely and positively correlated to leaf standing crop and the relationship is consistent over a range of sediment types and water depths (Zieman *et al*., 1989). In addition to leaf production, a high proportion of the productivity of whole *T. testudinum* plants is accounted for by the rhizomes (e.g., 35% in a subtropical lagoon; Kaldy and Dunton, 2000). There is some evidence that the two most abundant Caribbean seagrasses (*T. testudinum* and *Syringodium filiforme*) have similar specific productivity (Barber and Behrens, 1985). Normally productivity of seagrass decreases with depth as light is attenuated (e.g., Kaldy and Dunton, 2000), but in south Florida, Fourqurean *et al.* (2001) reported the opposite relationship. The increasing productivity with depth was attributed to buffering against temperature extremes and the turbidity of nearshore shallow waters. Van Tussenbroek (1995) showed that *Thalassia testudinum* in a lagoon was more productive than in a back reef environment, probably because of nutrient availability. Seagrass productivity also exhibits a strong seasonal signal (e.g., Fourqurean *et al*., 2001).

In addition to the range of factors that cause intrahabitat variations in productivity, methodological differences in calculating the productivity of seagrass limit comparisons to reef habitats. Many studies, because of complex problems using gas-exchange methods with vascular hydrophytes (Zieman, 1975), measure *Thalassia testudinum* using a variety of leaf-marking techniques with results usually expressed as g (dry weight) m^{-2} d^{-1} for "aboveground" productivity. Areal productivity varies significantly across the Caribbean, as shown by CARICOMP (1997b) who provides values for 14 sites ranging from 0.8 (Bahamas) to 7.5 g m^{-2} d^{-1} (Mexico). A series of studies across a variety of spatial and temporal scales and across gradients of depth and water conditions in Florida give values ranging from 0.3 to 4.0 (Zieman, 1975; Bach, 1979; Zieman *et al*., 1989; Tomasko and Lapointe, 1991; Fourqurean *et al*., 2001) with comparable data available from Belize (0.5–1.3 g m^{-2} d^{-1}) (Tomasko and Lapointe, 1991) and Mexico (0.88–1.46 g m^{-2} d^{-1}) (van Tussenbroek, 1995). Yates and Halley (2003) convert the data of Fourqurean *et al.* (2001) to provide a range of net primary productivity values of 0.05–3.52 g O_2 m^{-2} d^{-1}. Perhaps the best data comparable to values presented for coral habitats are from use of the SHARQ in Florida, which generated gross productivity values for dense and sparse seagrass beds (2.9 and 3.2 g O_2 m^{-2} d^{-1}, respectively) in Florida (Yates and Halley, 2003). Using smaller benthic chambers, higher values of 3.82–4.96 g C m^{-2} d^{-1} were recorded in the Bahamas along with a net primary productivity rate for epiphytes of 5.22 g C kg^{-1} d^{-1} (Koch and Madden, 2001).

Comparing mangrove primary production with reef habitats is particularly difficult because of methodological difficulties of measuring rates for mangroves themselves along with the algal and seagrass production on the sea floor and prop roots that maximise productivity in mangal systems (Hogarth, 1999). The metabolism of mangrove trees displays considerable variation at both local and regional scales, primarily because of environmental control (by tides, climate and seawater composition) (Gattuso *et al.*, 1998). Wiebe *et al.* (1997c) provide litterfall data for seven sites across the Caribbean with values ranging from ~0.5 to 9.5 g m^{-2} d^{-1} with significant seasonal variation. Lugo and Snedaker (1974) reviewed published studies from Florida and Puerto Rico using carbon dioxide–exchange techniques, which give gross primary productivity rates of 5.3–13.9 g C m^{-2} d^{-1} and give some evidence that rates of photosynthesis and respiration vary between species and zones of mangrove forests. For example, an area of red mangrove (*Rhizophora mangle*) leaf has a higher net primary productivity than an equivalent area of black mangrove (*Avicennia germinans*) leaf in the adjacent zone and individuals displaced from their normal zone had a lower productivity than individuals characteristic of that zone. One of the few studies considering prop-root algae gives a net primary productivity rate of 8.54 g C kg^{-1} d^{-1} (Koch and Madden, 2001).

Yates and Halley (2003) provide gross production-to-respiration ratios (P:R) of 0.80, 0.90, 1.08 and 0.85 for patch reefs, sand areas, sparse seagrass beds and dense seagrass beds, respectively. P:R ratios are important because they indicate whether a reef, zone or benthic component is autotrophic ($P:R > 1$) or heterotrophic ($P:R < 1$). As expected from the limited number of productivity studies in the Caribbean, there are few P:R values available in the literature. Koch and Madden (2001) recorded P:R values of 1.6 and 1.7 for mangroves and seagrass beds, respectively. Lewis (1977) reviews previous studies to give P:R values of 0.8–1.4 for *Thalassia* beds in Florida and Puerto Rico. Rogers (1979) gives a P:R of 0.7 for a shallow *Montastraea* reef and data in Adey and Steneck (1985) allow calculation of values of 0.98 and 1.01 for their forereef and back reef sites, respectively. Shallow reefs in

Puerto Rico are reported as having a P:R of 1.1 (Odum *et al.*, 1959). The available data correspond to values in reviews dominated by Indo-Pacific studies (Hatcher, 1988), which give P:R values ranging from 0.5–5.5 (fore-reef), 1.0–4.0 (reef crest), 0.7–3.2 (back reef) and 0.7–1.4 (patch reef) and indicate ratios typically >1 in high energy zones, especially those with algal turf (organic sources), and <1 in lower energy zones (organic sinks). The spatial variation of autotrophic and heterotrophic zones is an interaction of factors such as light, water movement aiding nutrient uptake and grazing. Hatcher (1997b) states that in shallower habitats, gross productivity is high enough to offset respiration so that P:R is >1 and organic matter is exported downstream by wave pumping, by gravity down the slope to deeper water, laterally by advection or by feeding of pelagic consumers. Therefore, reef structure (e.g., proportion of shallow habitats) is a major determinant of net production. Furthermore, there is some evidence that the P:R of 1, with a variation of only ′0.1, proposed for a ‘‘standard’’ Pacific reef flat and a ratio for a whole reef ecosystem very close to 1 (Kinsey, 1983, 1985), may also be true in the Caribbean.

3.3.3. Habitat functional values (Figure 1)

High functional values are assigned to habitats with rates of gross primary productivity >15 g O_2 m^{-2} d^{-1} (back reefs and reef crests). Medium functional values are given to habitats with rates of gross primary productivity between 5 and 15 g O_2 m^{-2} d^{-1} (shallow *Montastraea* reefs and patch reefs). The abundance of productive brown macroalgae in relatively shallow water but, with low rugosity and grazing pressure, indicates that gorgonian-dominated forereefs are also likely to fall in the 5–15 g O_2 m^{-2} d^{-1} range (medium functional value). Similarly, there are no data for deeper *Montastraea* reefs or escarpments, so they are assigned low functional values (i.e., <5 g O_2 m^{-2} d^{-1}) because of the attenuation of light with increasing depth. Sand has a low functional value (1.8 g O_2 m^{-2} d^{-1}), although this rate is likely to be an overestimate of the sand habitat in Figure 1, as it was generated in shallow water (Yates and Halley, 2003). Yates and Halley (2003) also provide data for seagrass beds, which indicates that they may have a low functional value (2.9–3.2 g O_2 m^{-2} d^{-1}), but because of the limited data, problems with gas-exchange techniques, evidence of higher rates elsewhere (Koch and Madden, 2001) and the known seasonal variations, we assign a medium functional value. Comparable rates of gross primary productivity for mangrove stands are not available, but the combination of mangrove trees along with the algal and seagrass production on the sea floor and prop roots indicates that rates would be at least 5–15 g O_2 m^{-2} d^{-1} (medium functional value).

3.4. Secondary production

3.4.1. Overall patterns of herbivore densities and their effects

Herbivory, the grazing of primary producers, is a vital process in trophic energy flow on a coral reef (e.g., Lubchenco and Gaines, 1981). Inevitably, secondary productivity is inextricably linked to primary productivity because high levels of primary productivity are necessary to support an abundant herbivore community. Conversely, high grazing pressure is an important causal agent of the zonation of primary producers (Ogden, 1976; Hay, 1981a; Hay *et al*., 1983; Littler *et al*., 1983a, 1987; Hay, 1985). Section 3.3 has reviewed the observed patterns of primary productivity across a seascape, and this section aims to document one of the key factors that determine these patterns. Initially, we discuss the overarching pattern of density of herbivores across a reef ecosystem then provide details of the distributions of the four most important taxa of the Caribbean macroherbivore community: Scaridae, Acanthuridae, Pomacentridae and *D. antillarum* (e.g., Ogden, 1976). Herbivore density is used as a proxy for secondary production because calculations of production also require parameters such as production/biomass and consumption/biomass ratios, which are scarce for reef ecosystem fishes (van Rooij *et al*., 1998) and variations between habitat types are unclear. Microherbivores (e.g., amphipods), though important grazers in reef communities (Carpenter, 1997), are not included in this chapter because their habitat preferences are not well studied. Larger herbivores (e.g., turtles and manatee) have an important influence in seagrass beds on the plants, other associated grazers and fauna and chemical and decompositional processes occurring within a meadow (Ogden *et al*., 1983; Thayer *et al*., 1984). However, they are omitted here because of the lack of data and the effects of overharvesting, which has reduced their ecological role in reef ecosystems (e.g., Jackson, 1997). Grazing by herbivores is an important component in reef bioerosion, but this is treated separately in Section 3.8.

Variation in the density of herbivores across tropical seascapes and the patterns has been linked to a few key factors such as topography, proximity to nearby shelter, predator abundance, density of territorial competitors and local availability of food resources (Lewis and Wainwright, 1985). For fishes, grazing is mainly inversely related to tidal exposure and wave action and positively correlated with the availability of shelter from predators (Hixon, 1997). Therefore, the density of herbivorous fishes is highest on shallow, rugose sections of the reef and lowest in areas that are deep, topographically simple or where water movement interferes with feeding (Hay, 1981b). Densities of *Diadema* are also higher in shallower reef areas and *Diadema* generally accentuates patterns of fish grazing (decreasing with increasing depth with the exception of very shallow turbulent water). Not surprisingly, such a strong trend has been supported by herbivory assays and a *Thalassia* bioassay showed that feeding, predominantly by fishes, in shallow (1–10 m) zones was significantly higher than deep (30–40 m) reefs or very shallow flats (Hay and Goertemiller, 1983). A similar assay showed *Thalassia* loss on a reef flat and sand plain to be very low relative to that of a shallow reef slope and that across the reef slope, herbivory decreased linearly with depth and was highest in the most topographically complex habitats (Hay *et al*., 1983). Therefore, grazing was highest in an *Acropora* and ledge habitat, lowest on a sandy slope and intermediate in a *Porites*, massive coral and gorgonian-dominated habitat. Lewis and Wainwright (1985) and Littler *et al.* (1987) showed that the order of herbivory, from lowest to highest rates, was seagrass bed (too shallow for fishes, limited shelter), lower forereef, outer ridge (both too deep for many herbivores), upper forereef and then the rubble and carbonate pavement of the back reef (shallow with plenty of shelter and fast algal growth rates).

The relative importance of fish grazing compared to urchin grazing on the distribution of algae is equivocal. Hay *et al.* (1983) showed that herbivorous fishes accounted for 97% of grazing during the day and 90% of the total, while urchins accounted for only 9% of the total. In contrast, Foster (1987) used caging experiments to show that the effect of fishes on grazing of fleshy algal turfs on shallow moderately exposed reef flat habitats was limited compared to *Diadema*. Hay (1984) suggested that studies stressing the importance of urchins were usually on overfished reefs and fishes are the most abundant grazers on ‘‘natural’’ reefs (see also Horn, 1989). The balance between grazing by fishes and *Diadema* and the ecology of Caribbean reefs were fundamentally altered in the early 1980s by the mass mortality of the urchin because of a waterborne pathogen (e.g., Lessios, 1988). The mass mortality of *Diadema* and its effects on benthic communities are discussed in more detail in the subsequent section dedicated to *Diadema*, but it is appropriate to highlight here the interactive effect on fish communities. The loss of *Diadema* on many reefs increased populations and led to the spatial redistributions of fishes because of previous exploitative competition, but the changes rarely maintained grazing pressure at premortality levels, especially in areas with high fishing pressure. For example, in St. Croix fish grazing intensity increased by 380% 1 wk after the mass mortality of *Diadema* (Carpenter, 1985b). In the longer term Carpenter (1990a) showed that fishes were three times more abundant in the back reef and shallow (2 m) forereef, two times more abundant on the middepth (5 m) forereef and four times more abundant on the deep (10 m) reef. The additional fishes were mainly juvenile parrotfishes except in the shallow forereef where they were generally surgeonfishes. Overall, however, grazing intensity only increased in three of the four zones (not in the shallow forereef). The degree of change in grazing intensity was dependent on initial conditions, the change of fish populations and which fish taxa were affected (e.g., surgeonfishes appear to respond differently to changes in algal abundance). Further data specifically for surgeonfishes showed that *Acanthurus chirurgus* and *A. coeruleus* increased their population sizes, but *A. bahianus* did not (Robertson, 1991), possibly because it is much less reliant than the other two species on habitats (i.e., those on the reef) that had been most affected by *Diadema*. As fishes are less systematic grazers than urchins, increases in fish abundance could not compensate for the loss of *Diadema* and algal cover increased in cover and biomass in St. Croix (Carpenter, 1990a). Similarly, after *Diadema* mass mortality, Morrison (1988) showed on an area of shallow reef that despite increases in fish grazing, abundances of erect and filamentous algae increased and abundances of corallines decreased, but *Diadema* mortality had little effect on the deeper reef. *Diadema* having a major role on shallow reefs but only a minor role relative to fishes in deeper communities is particularly important and is discussed in more detail in subsequent sections.

3.4.2. Scaridae distributions

Parrotfishes are extremely important herbivores on coral reefs and commonly predominate in slightly deeper areas (>5 m) than surgeonfishes (e.g., Lewis and Wainwright, 1985). Most adult parrotfishes decrease in density with increasing depth (van Rooij *et al*., 1996a) and significantly influence algal cover in different habitats because of differential grazing pressures (Lewis, 1985; Lewis and Wainwright, 1985; Horn, 1989). Species that crop or scrape algae from corals can also alter coral distributions. The effect of parrotfish grazing on coral distributions was demonstrated by Littler *et al.* (1989) who showed that zonal patterns of *Porites astreoides* and *Porites porites* forma *furcata* in a back reef were strongly associated with parrotfish feeding intensity. Like all herbivores, parrotfish distributions are reliant on factors such as proximity to nearby shelter, food resources and biological interactions. Habitat rugosity is, therefore, a key variable determining parrotfish densities because it affects the number of available shelters and type of food resources available. By extension, topography has an important effect on social behaviour because parrotfish behaviour can be adaptive with changing density (see van Rooij *et al*., 1996b for an example). Parrotfish distributions can generally be grouped by feeding modes as species feeding by ‘‘sucking’’ are most abundant over sand in back reefs and lagoons, while ‘‘croppers’’ and ‘‘scrapers’’ are more abundant in shallow reef areas (Horn, 1989). However, there has been extensive research to document more specific interspecific habitat preferences of the Caribbean Scaridae. Because there are a relatively large number of species of parrotfishes in the Caribbean, the habitat preferences of perhaps the most studied species (*Sparisoma viride*) is described in detail here and data for other species are summarised elsewhere (Table 3). *Sp. viride* is also one of the most abundant herbivores in reef ecosystems, accounting for 22–31% of total herbivore biomass in Bonaire (Bruggemann *et al*., 1996; van Rooij *et al*., 1998), where its biology has been studied in detail (Bruggemann *et al*., 1994a,b,c; van Rooij *et al*., 1995a,b, 1996a,b,c; van Rooij and Videler, 1996, 1997).

Tolimieri *et al*. (1998) studied recruitment rates to forereefs in the Virgin Islands and reported rates of ~0–4 recruits 60 m^{-2} and further showed that rates were higher in the back reef (~3.5–8 recruits 60 m^{-2}) compared to the reef crest (~0.5–2.0 recruits 60 m^{-2}) or reef base (~0.5–1.0 recruits 60 m^{-2}) (Tolimieri, 1998b). *Sp. viride* juveniles commonly use a variety of nursery areas, particularly shallow reefal zones such as seagrass beds, the back reef, patch reefs, reef crest and *Acropora cervicornis* and ''dropoff'' zones from 4 to 12 m (Hanley, 1984; van Rooij *et al*., 1996a; Overholtzer and Motta, 1999; Nagelkerken *et al*., 2000c). Nagelkerken *et al*. (2000c) stated that seagrass beds were the most important biotope for juvenile *Sp. viride* in Bonaire (density 26.1 fish 1000 m^{-2}) and the reef from 3 to 5 m was also important. However, *S.. viride* was absent from seagrass beds in Panama, Curaçao, St. Croix and south Florida (Weinstein and Heck, 1979; Thayer *et al*., 1987; Nagelkerken *et al*., 2000a; Mateo and Tobias, 2004) and rare in the Bahamas (Newman and Gruber, 2002). *Sp. viride* is rarely seen in mangrove stands: a density of 1.4 fish 1000 m^{-2} in Bonaire (Nagelkerken *et al*., 2000c), 0.7 fish 100 m^{-2} in Curaçao (Nagelkerken and van der Velde, 2002), no individuals seen in south Florida (Thayer *et al*., 1987), only one individual in mangroves in Biscayne Bay (Serafy *et al*., 2003) and one fish in mangroves among a total of >65,000 fish in the Bahamas (Newman and Gruber, 2002).

Van Rooij *et al*. (1996a) surveyed five reef habitats in Bonaire, and densities of juvenile *Sp. viride*, interpolated from their graphs, were ~40, 125, 400, 380 and 150 fish ha^{-1} for the shore zone, *A. palmata* zone, *A. cervicornis* zone, drop off and upper reef slope, respectively. However, juvenile densities varied significantly around the island, particularly in shallow water with maxima of ~3,500, 2,100 and 1,500 fish ha^{-1} for the shore zone, *A. palmata* zone and *A. cervicornis* zone, respectively at one site because of intrahabitat variations in benthic communities (van Rooij *et al*., 1996b). Similarly, lower values were recorded at another site (~60 and 25 fish ha^{-1} for the *A. palmata* zone and upper reef slope, respectively). A density of ~25 juvenile fish ha^{-1} was given for a gorgonian-dominated zone. In Mexico, the density of *Sp. viride* juveniles on a series of forereefs (12 m) depth was 1.7 fish 100 m^{-2} (González-Salas *et al*., 2003). Within nursery areas there are intrahabitat patterns of preferred microhabitats as

Table 3 Habitat preferences of selected Caribbean Scaridae[a]

Species	Juveniles	Adults
All species	Use nursery areas, particularly lagoonal seagrass beds, patch reefs, back-reef areas and *Acropora cervicornis* zones (4–6 m) before moving to deeper parts of the reef (e.g., van Rooij *et al*., 1996a; Nagelkerken *et al*., 2000c); *Scarus* spp. are relatively dominant in *Acropora palmata* zones from 2 to 4 m (van Rooij *et al*., 1996a)	
Scarus guacamaia	Has a functional dependency on mangroves (Mumby *et al*., 2004a)	Prefers reefs (Gygi, 1975; Nagelkerken and van der Velde, 2002)
Scarus iserti	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002) and seagrass beds and mangroves (Nagelkerken and van der Velde, 2002)	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002); includes patch-reef halos in its foraging (Overholtzer and Motta, 1999); associates with forereef Porites rubble and live colonies (Tolimieri, 1998c); strongly correlated with substrate rugosity (Mumby and Wabnitz, 2002); may aggregate in foraging groups generally in 1–3 m of water over a bottom of coral rubble, sandy sediment and scattered coral heads (Ogden and Buckman, 1973); migrates diurnally from shallow feeding areas to deeper nocturnal resting areas (Ogden and Buckman, 1973)
Scarus vetula	Found on shallow (2 m) reef habitats (Nagelkerken and van der Velde, 2002)	Associates with forereef *Porites* and *Acropora* rubble (Tolimieri, 1998c); preferred sleeping areas are near reef slopes with dense coral cover, particularly *Acropora cervicornis* (Dubin and Baker, 1982)

(Continued)

Table 3 (Continued)

Species	Juveniles	Adults
Sparisoma aurofrenatum	Use the back reef and patch reefs (Adams and Ebersole, 2002) and forereefs (5–15 m) (Nagelkerken and van der Velde, 2002)	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002); includes areas of *Thalassia* in foraging (Overholtzer and Motta, 1999); associates with forereef *Porites* rubble (Tolimieri, 1998c); more abundant in deeper habitats (Lewis and Wainwright, 1985)
Sparisoma chrysopterum	Favours mangroves (Nagelkerken and van der Velde, 2002)	Found on patch reefs (McAfee and Morgan, 1996); more abundant in shallower habitats (Lewis and Wainwright, 1985; Nagelkerken and van der Velde, 2002).
Sparisoma radians	Almost exclusively associated with dense stands of seagrass and macroalgae (Ogden, 1976; Lobel and Ogden, 1981)	
Sparisoma rubripinne	Favours shallow (2 m) forereefs (Nagelkerken and van der Velde, 2002)	Associates with forereef *Porites* rubble (Tolimieri, 1998c); uses seagrass and reef crests (McAfee and Morgan, 1996) and shallow forereefs (Nagelkerken and van der Velde, 2002)

shown by Tolimieri (1998a) in a shallow (from 3 to 6 m to emergent) back reef, containing patch reefs, in the U.S. Virgin Islands. Tolimieri (1998a) showed that recruitment rates were higher to colonies of live and dead *P. porites* compared to *M. annularis*, but there was no evidence of microhabitat choice at settlement (i.e., caused by differential mortality or movement or both). Furthermore, recruits settled in higher numbers on patch reefs with conspecifics, persistence was greater at higher recruit densities and the presence of damselfishes had no effect on settlement but did reduce recruitment. The data led Tolimieri (1998a) to conclude that both presettlement and postsettlement processes can alter recruitment patterns of *Sp. viride* from initial settlement patterns. Tolimieri (1998b) showed that within a site, recruitment was correlated with the percentage cover of *P. porites* and at a larger scale, the cover of *P. porites* at 10 sites on three islands explained 66–81% of the variation in recruits in 3 of 4 yr. Contemporary adult abundance was correlated with mean recruitment at the scale of sites and islands, so microhabitat characters that affect recruitment may influence adult abundance at large spatial scales (Tolimieri, 1998b).

Intermediate or midphase *Sp. viride* are commonly seen in shallow back reefs and reef crests (Hanley, 1984). In Bonaire, sexually inactive male intermediate or midphase *Sp. viride* were restricted to shallow areas because terminal phase adults held territories deeper than 3 m where food resources were greater (van Rooij *et al*., 1996c). Within their reefal habitat, adult *Sp. viride* have specific food preferences that influence the quality of a territory (Bruggemann *et al*., 1994a). In contrast to intermediate phase fish, territorial terminal phase adults increase in physical condition with increasing depth because in deeper areas they have a lower reproductive effort, reduced territory defence and an increased availability of high yield grazing patches (van Rooij *et al*., 1995a). In addition to forereefs, terminal phase adults can also be found in a range of shallow habitats including reef crests (Hanley, 1984) and in Bermuda prefer agitated water near exposed reefs and shorelines (Gygi, 1975). A survey across the Belize Barrier Reef gave densities of 3, 11, 7, 2 and 3 intermediate and terminal phase fish 400 m^{-2} for back reef, high relief spur and groove, low relief spur and groove, the inner reef slope and outer ridge, respectively (Lewis and Wainwright, 1985). Further data for a mixed community back reef in Belize showed densities of *Sp. viride* varied from 2.8 to 9.7 fish 400 m^{-2} during a 12-mo period, which contrasted with their absence at three macroalgal-dominated sites (Lewis, 1986). Van Rooij *et al*. (1996a) surveyed five habitats in Bonaire and densities of adult *Sp. viride*, interpolated from their graphs, were $\sim$600, $\sim$250, $\sim$200, $\sim$125 and $\sim$50 fish ha^{-1} for the shore zone, *A. palmata* zone, *A. cervicornis* zone, drop off and upper reef slope, respectively, which were similar to those found at two other sites (van Rooij *et al*., 1996b). Also in Bonaire, mean densities on four forereef sites (0–3, 3–5, 10–15 and 20–25) were 11.1, 34.6, 11.4 and 6.3 fish 1000 m^{-2} (Nagelkerken *et al.*, 2000c). On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 2.7, 2.3, 2.6 and 1.9 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). Mean densities for back reef/reef crest, shallow (2 m), middepth (5 m) and deep (10 m) forereef sites in St. Croix before and after the mass mortality of *Diadema* were 18.9, 37.8, 41.9 and 23.2 fish 310 m^{-2} (Carpenter, 1990a). Densities on a series of reef crest and forereef sites (8–12 m) in the Bahamas were 4.7 and 1.6 fish 100 m^{-2}, respectively (Kramer *et al.*, 2003), 12.8 on reef crests and 9.4 on forereef sites in St. Vincent (Deschamps *et al.*, 2003), 1.3 fish 100 m^{-2} on forereef sites in Cuba (Claro and Ramos, 2003) and 1.1–2.7 fish 100 m^{-2} on forereef sites in the Windward Netherlands Antilles (Klomp and Kooistra, 2003). The mean density of *Sp. viride* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 0.14 fish 40 m^{-2} (Schmitt *et al.*, 2002). Terminal phase adults avoid carbonate platforms in gorgonian zones and sandy bottoms and seagrass beds with limited shelter (Gygi, 1975; Hanley, 1984; Bruggemann *et al.*, 1994b). Data from Belize found densities of $\sim$4.5 200 m^{-2} for *Sp. viride* on a topographically complex *Montastraea* reef compared to $\sim$0.5 200 m^{-2} for a gorgonian-dominated terrace (Mumby and Wabnitz, 2002). On a pavement with dense gorgonians in Bonaire, a density of $\sim$175 fish ha^{-1} was reported (van Rooij *et al.*, 1996b). Densities of 13 fish 500 m^{-2} were recorded along the edge between a deep reef slope ($\sim$15–20 m) and algal plain (Barlow, 1975). On the sides of sheltered patch reefs in Panama, mean *Sp. viride* densities were $\sim$5–10 fish 60 m^{-2} compared to $\sim$0 60 m^{-2} on surrounding seagrass beds (McAfee and Morgan, 1996). Similarly, densities were shown to be low in *Thalassia* beds and a sand channel in Belize (densities of all Scarids 0.5 and 0.0 400 m^{-2}) (Lewis and Wainwright, 1985). On a coral–algal patch reef in Bermuda, densities were 0.96 fish 100 m^{-2} (Gygi, 1975), 6.4 fish 100 m^{-2} on patch reefs in St. Croix (Mateo and Tobias, 2004) and 2.8 fish 100 m^{-2} for a patch reef in Costa Rica (Fonseca and Gamboa, 2003). Adults were absent below a depth of 22 m in Bonaire (van Rooij *et al.*, 1998).

*3.4.3. Habitat functional values (*Sparisoma viride*; Figure 1)*

Forereef sand channels (all Scarids absent; Lewis and Wainwright, 1985) appear to have no functional value. Assigning functional values for other habitats is confused by wide ranges in densities caused by biogeographical and intrahabitat substrate variations and data presented for various life phases, but we define low functional values where densities are generally <1 fish 100 m^{-2} (mangroves, seagrass beds and escarpments). Functional values are medium where values are generally 1–2 fish 100 m^{-2} (gorgonian-dominated pavements and deep *Montastraea* reefs) and high where densities are generally >2 fish 100 m^{-2} (patch reefs, back reefs, reef crests and shallow *Montastraea* reefs). Documented ranges (Figure 1) are for juveniles and adults only and do not include recruits, but it appears that back reefs are particularly important for *Sp. viride* recruitment (Tolimieri, 1998b).

3.4.4. Acanthuridae distributions

There are three species of surgeonfish in the Caribbean (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*), which occur as individuals or large highly aggregated mixed-species schools (Reinthal and Lewis, 1986; Lawson *et al*., 1999). Surgeonfishes are generally more common in shallower habitats (<5 m) than parrotfishes, but a similar combination of factors including topography, proximity to nearby shelter, predator abundance, density of territorial competitors and local availability of food resources dictates interspecific abundances and distributions (Bardach, 1958; Foster, 1985; Lewis and Wainwright, 1985). For example, Robertson (1991) showed that ~50% of adult *A. bahianus* on a patch reef were found feeding in sand and seagrass, while *A. coeruleus* rarely left the reefs and only ~15% of *A. chirurgus* were seen away from the reef. Predation is a particularly important factor structuring populations, and *A. chirurgus* and *A. bahianus* settlement in Panama was low at the edge of patch reefs, intermediate in the grazed halo and highest in dense seagrass because of predation rates (Sweatman and Robertson, 1994). Risk (1998) showed that the settlement of *A. bahianus* was increased in the presence of conspecifics and decreased in the presence of *Stegastes leucostictus*. Such interactions with conspecifics and other species may play an important role in ontogenetic habitat shifts (postsettlement persistence).

Like many fish species, juvenile surgeonfishes use shallow nursery areas before an ontogenetic shift into slightly deeper water (van Rooij *et al*., 1996a; Nagelkerken *et al*., 2000c). While such ontogenetic shifts are relatively easy on continuous areas of reef, adults of all three species relocate between isolated patch reefs and substantially alter the size and composition of populations so that postsettlement mortality or relocation overrides the effects of settlement patterns (Robertson, 1988). In a study in Bonaire, Nagelkerken *et al.* (2000c) showed that seagrass beds were most important for *A. chirurgus*, shallow reef areas were used by *A. bahianus* and *A. coeruleus* used a variety of biotopes including mangrove roots, seagrass beds and four depth zones from 0 to 20 m on the reef. On Curaçao, *A. chirurgus* mean densities in mangroves and seagrass beds were 0.7 and 0.6 fish 100 m^{-2}, while the other two species were absent (Nagelkerken and van der Velde, 2002). A single fish was seen in 60 m^2 of mangrove in Florida (Serafy *et al*., 2003). The presence of surgeonfishes in mangroves and seagrass beds has also been shown in Florida, the Bahamas and Panama (Weinstein and Heck, 1979; Thayer *et al.*, 1987; Newman and Gruber, 2002). In Barbados, Lawson *et al.* (1999) showed that the density of small and large juvenile *A. bahianus* was highest in the back reef and declined in the reef crest and was lowest in a spur-and-groove habitat. Newly settled *A. coeruleus* were only found on the reef crest and in the spur-and-groove zone, but larger juveniles were more common in the back reef. On isolated patch reefs in Panama, Robertson (1988) documented that the settlement habitat of *A. bahianus* and *A. chirurgus* was the reef–seagrass interface (<3 m) with scattered corals and patches of bare rock. The settlement habitat for *A. coeruleus* was the outer shallow periphery of patch reefs (10 m wide, <2 m deep) plus areas in the emergent centres that consisted of rock substrate with sparse corals. Adams and Ebersole (2002) showed the importance of lagoonal patch reefs and rubble areas, as opposed to other lagoon habitats (seagrass, algal plain and sand), as nurseries for *Acanthurus* spp. in St. Croix but stated that these areas were used in preference to the back reef. In Barbados, Sponaugle and Cowen (1996) showed that the settlement pattern of *A. bahianus* was modified by postsettlement processes (e.g., habitat selection) of juveniles and this was more important than larval supply. There was some evidence that the postsettlement processes were linked to a preference for shallow depths, lower abundances of algal turf, less rock cover and lower rugosity and hence juveniles were usually found on shallow sand-rubble regions (Sponaugle and Cowen, 1996).

The density of all acanthurid species are grouped in many studies or can be calculated from reported values for each species. For example, across the Belize Barrier Reef, acanthurid density was 0.4, 50.5, 42.2, 31.5, 2.8, 0 and 2.0 fish 400 m^{-2} in a *Thalassia* bed, back reef, high relief spur and groove zone, low relief spur and groove zone, inner reef slope, sand channel and outer ridge, respectively (Lewis and Wainwright, 1985). In a back reef/reef crest site and three forereef sites (depths of 2, 5 and 10 m) in St. Croix, densities were 35.4, 349.3, 97.8 and 24.6 fish 310 m^{-2} (Carpenter, 1990a). Nagelkerken *et al.* (2000c) give densities in Bonaire as 13.6, 3.6, 102.4, 41.2, 13.9 and 9.7 fish 1000 m^{-2} in a seagrass bed, mangroves and four reef habitats (0–3, 3–5, 10–15 and 20–25), respectively. On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 22.1, 6.7, 6.3 and 2.4 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). In a study of back reef habitats in Belize, adult density was 12.8 fish 100 m^{-2} in a mixed community compared to 0–2.4 fish 100 m^{-2} for macroalgal-dominated sites (Lewis, 1986). Juvenile densities at the same sites were 5.2 fish 100 m^{-2} (mixed community) and 1–12.1 fish 100 m^{-2} (macroalgal dominated). Also in Belize, a forereef at 12 m had a density of acanthurids of 0.9–1.6 25 m^{-2} (Williams *et al.*, 2001) and the density in a high relief spur-and-groove zone was 637.9 fish ha^{-1} (Reinthal and Lewis, 1986). The mean density of acanthurids in four deep (15–20 m) forereef sites in southeastern Hispaniola was 1.78 fish 40 m^{-2} (Schmitt *et al*., 2002). Densities on patch reefs in St. Croix were ~7 fish 60 m^{-2} and ~3 fish 150 m^{-2} on a shallow *A. palmata*/*Millepora* reef in St. Thomas (Hay and Taylor, 1985). Lawson *et al*. (1999) did not survey *A. chirurgus* in Barbados, but densities for *A. bahianus* and *A. coeruleus* combined were 23.6, 4.9 and 1.6 fish 50 m^{-2} in back reef, reef crest and spur-and-groove habitats, respectively. Similarly, *A. chirurgus* was not surveyed in a shore zone, *A. palmata* zone, *A. cervicornis* zone, dropoff and upper reef slope in Bonaire, but densities for the other two species combined were ~9,750, ~1,000, ~250, ~1,000 and ~50 fish ha^{-1}, respectively (van Rooij *et al*., 1996a). Densities of *A. bahianus* and *A. chirurgus* on patch reefs and seagrass beds in St. Croix were 65.3 and 0.3 fish 100 m^{-2}, respectively (Mateo and Tobias, 2004). The mass mortality of *Diadema* affected surgeonfish populations, and in Panama, densities of *A. coeruleus* and *A. chirurgus* increased by 160–250%, but no changes were seen for *A. bahianus* (Robertson, 1991). Densities were also clearly affected by marine reserves in Barbados (Rakitin and Kramer, 1996) but not the Netherlands Antilles or Belize (Polunin and Roberts, 1993).

AGRRA surveys, conducted across the Caribbean from 1997 to 2000 (Kramer, 2003), counted acanthurids as an indicator of herbivory and represent an extensive database of densities on reef crests and shallow (generally 8–15 m) forereefs. All the following studies used the AGRRA protocol, but only fish counts collected using belt transects in specific habitats are included to ensure comparability with other studies. In Andros (Bahamas), densities varied from 9.9 to 12.7 on the reef crest and 4.0–4.7 fish 100 m^{-2} on the forereef (Kramer *et al*., 2003). In Costa Rica, densities were 2.5 on a carbonate bank, 20.0 on a patch reef, 25.0 in a spur-and-groove zone and 3.2 fish 100 m^{-2} on a forereef platform (Fonseca and Gamboa, 2003). On forereef spurs in Cuba densities were 2.2–4.5 fish 100 m^{-2} (Claro and Ramos, 2003), 3.9–5.7 fish 100 m^{-2} on forereefs in Mexico (Núñez-Lara *et al*., 2003), 11.1 fish 100 m^{-2} on fringing reefs in Curaçao (Bruckner and Bruckner, 2003) and 19.3 fish 100 m^{-2} in the Windward Netherlands Antilles (Klomp and Kooistra, 2003). In St. Vincent, densities were 12.0 on reef crests and 2.0 on the forereef sites (Deschamps *et al*., 2003) and in the Turks and Caicos were 15.0 on patch reefs and 5.2–5.4 fish 100 m^{-2} on fringing reefs (Hoshino *et al*., 2003). In reef crest sites in Venezuela, the mean density was 29.7 fish 100 m^{-2} and 11.0 fish 100 m^{-2} on fringing reefs (Posada *et al*., 2003). The density on a series of fringing reefs in the Virgin Islands was 18.2 fish 100 m^{-2} (Nemeth *et al*., 2003). In Abaco (Bahamas), densities were 27.8 and 51.4 fish 100 m^{-2} in a back reef and reef crest, respectively, and 7.7 and 8.6 fish 100 m^{-2} on fringing reefs in Belize and Bonaire, respectively (Kramer and Bischof, 2003).

3.4.5. Habitat functional values (Figure 1)

Forereef sand channels appear to have no functional value for surgeonfishes (Lewis and Wainwright, 1985). We define low functional values as densities generally <2, medium functional value as 2–10 and high functional value as >10 fish 100 m^{-2}. Therefore, we assign low functional values to mangroves, seagrass beds, deep *Montastraea* reefs and escarpments, medium functional value to shallow *Montastraea* reefs and high functional values to patch reefs, back reefs and reef crests. There are few data for gorgonian-dominated forereefs, but because of the lack of topographical complexity, we assign this habitat a low functional value.

3.4.6. Pomacentridae distributions

Nonplanktivorous damselfishes are a conspicuous component of the benthic reef fish community and defend small contiguous territories against intruding fishes (e.g., Randall, 1967; Itzkowitz, 1977b; Hay, 1981b). Territorial defence is so strong that surgeonfish and parrotfish density may be inversely related to damselfish density (Lewis and Wainwright, 1985). Damselfishes have a vital role within the ecology of a reef because of their abundance and territoriality. Importantly within the context of this review, damselfishes have specific habitat preferences so that their effects have significant spatial variation across a seascape. The effects of damselfishes are caused by the distinct biotic patches within damselfish territories having functional differences to benthic communities outside territories (Hay, 1985). Horn (1989) reviews the research on damselfishes and shows that fishes affect (1) coral recruitment, growth and bioerosion; (2) local microfaunal abundance; (3) nitrogen fixation by cyanobacteria and (4) algal abundance and local diversity. Algal mats within territories appear to inhibit settlement of corals by encouraging filamentous algae (e.g., Lobel, 1980). Conversely, there are data from the Great Barrier Reef showing coral recruits can be increased compared to nonterritory areas (e.g., Sammarco and Carleton, 1981), but it is not clear whether this represents a regional difference or reflects subtle variations between species or habitats. External bioerosion in damselfish territories generally decreases because there is less grazing and predation by fishes (Sammarco *et al*., 1986), but internal bioerosion is unchanged (Sammarco *et al*., 1987) or significantly increased (Risk and Sammarco, 1982). Damselfishes can significantly affect algal communities because many studies show biomass, and potentially productivity, is higher inside their territories (reviewed by Horn, 1989). The effects of damselfishes on algal biomass and diversity were investigated in a study by Brawley and Adey (1977) in Jamaica where outside damselfish territories on the Jamaican lower reef terrace (22 m) areas were heavily grazed, and there were only small quantities of noncrustose algae. In comparison, in the damselfish territories, there were many algal turf species covering an *A. cervicornis* framework and *Lobophora*. It was concluded that only calcified encrusting algae would be on the terrace if damselfishes were absent and that damselfishes significantly influence the dynamics of some reefs by increasing the abundance of turf algae and hence reef productivity. Effects were even more profound on the reef flat (0–2.5 m) because reef flat damselfish territories were contiguous, and therefore, the algal community across the whole zone had been altered (Brawley and Adey, 1977). Increases in algal diversity inside *Stegastes planifrons* territories (compared to outside) were also demonstrated on a back reef in Puerto Rico (Hinds and Ballantine, 1987). In contrast, other data show that damselfish species may increase the density of vegetation but not the species composition (de Ruyter van Steveninck, 1984). The effect of damselfishes on algal diversity is such that damselfishes are sometimes labelled *keystone species* of shallow reef areas (Hixon and Brostoff, 1983). Since there are a relatively large number of species of damselfishes in the Caribbean, the habitat preferences of perhaps the most studied species (*S. planifrons*) is described in detail here and patterns for other species are summarised elsewhere (Table 4).

S. planifrons is either absent from mangrove, lagoonal sand and seagrass habitats (Weinstein and Heck, 1979; Thayer *et al*., 1987; Adams and Ebersole, 2002; Newman and Gruber, 2002; Serafy *et al*., 2003) or in very low densities (0.1 and 0.01 fish 100 m^{-2} in mangroves and seagrass, respectively, in Curaçao; Nagelkerken *et al*., 2000a) and prefers to recruit to coral heads (Booth and Beretta, 1994). For example, *S. planifrons* recruited exclusively to living coral on patch reefs in Panama at a rate of $\sim$1.5 m^{-2} (Gutiérrez, 1998) and at two fringing reef sites (depths of 4.5–10 m and 12.7–13.3 m) in the U.S. Virgin Islands was 1.72 recruits 25 m^{-2} and 0.83 25 m^{-2}, respectively (Booth and Beretta, 1994). The relationship between *S. planifrons* and coral substrata has also been investigated by Tolimieri (1995) in the U.S. Virgin Islands, where densities of settlers on patch reefs ranged from 0 to $\sim$8 m^{-2}. At a scale of 0.25 m^{2}, patch reefs consisting of *M. annularis* had higher numbers of settlers, caused by a microhabitat choice during settlement, but these small-scale recruitment patterns did not scale up to explain large-scale variations between sites. Recruitment rates on forereefs (6–10 m) throughout the Virgin Islands were from 0 to $\sim$1.75 fish 30 m^{-2} (Tolimieri *et al*., 1998). Itzkowitz (1977a) also indicated that juvenile *S. planifrons* were particularly associated with *Montastraea* corals.

An ontogenetic habitat shift of *S. planifrons* has been highlighted by Ebersole (1985) who showed that juvenile fish inhabited back reef areas of

Table 4 Habitat preferences of selected Caribbean Pomacentridae

Species	Juveniles	Adults
Microspathodon chrysurus	Rare on back reefs and commonly found on shallow forereefs in association with live and dead *Acropora* and *Millepora* (Itzkowitz, 1977a; Williams, 1991; Tolimieri, 1998c)	
Stegastes diencaeus	May firstly be attracted to the presence of conspecifics and secondly adopt a position adjacent to a live coral or *Acropora* rubble in preference to sand (Foster, 1985; Robertson, 1996; Tolimieri, 1998c); favours shallow (2–15 m) forereefs (Nagelkerken and van der Velde, 2002)	
Stegastes dorsopunicans	In back reefs, which have a lower biomass of turf algae than required by adults (Foster, 1985); settlers predominate on reef crests with a rocky substratum (Gutiérrez, 1998); favour shallow (2 m) forereefs (Nagelkerken and van der Velde, 2002)	Generally found in *Acropora palmata*/*Acropora* rubble habitats with a high biomass of preferred algal turf (Foster, 1985; Tolimieri, 1998c).
Stegastes leucostictus	Settles preferentially in shallow water (1–2 m depth) and almost exclusively in calm back reef areas (Shulman, 1984; Ebersole, 1985; McGehee, 1995; Robertson, 1996); areas of *A. palmata* are avoided (Ebersole, 1985)	Territories are in areas of living (all types) and dead corals (particularly *Porites* rubble) of ~1 m^2 (Ebersole, 1985; Wellington, 1992; Tolimieri, 1998c) or more generally "small rubble and sand" or "low-profile rubble" (Itzkowitz, 1977a; Williams, 1991); may favour mangrove habitats (Nagelkerken and van der Velde, 2002)

Stegastes partitus	Recruit to back reefs but settle at similar densities on both the back reef and forereef in coral-rubble habitats, particularly *Montastraea annularis* and *Porites* rubble (Sponaugle and Cowen, 1996; Nemeth, 1997; Tolimieri, 1998c)	Adults are more abundant on the forereef (Nemeth, 1997), particularly between 5 and 15 m (Nagelkerken and van der Velde, 2002); differential mortality rates, which are higher in back reefs compared to forereefs, can explain apparent preferences for forereefs (e.g., McGehee, 1995)
Stegastes variabilis	Found in water deeper than 10 m because of habitat selection at settlement (Wellington, 1992; Robertson, 1996); possibly because of the lower levels of competition in deeper water, has no clear microhabitat associations, although it requires areas of living and dead corals and can have large territories up to 14 m^2 (Wellington, 1992; McGehee, 1995)	

sand with scattered corals in a narrow depth band (1.5–3.7 m), but adults were found on the main reef and other areas dominated by acroporids. The ontogenetic habitat shift means that adult *S. planifrons* are common on shallow forereef areas (e.g., McGehee, 1995; Gutiérrez, 1998) but are only found on branching or creviced coral heads, such as *Porites* and *Montastraea*, with relatively complex internal structure (Ebersole, 1985) and *Acropora* rubble (Tolimieri, 1998c). In a comparison between back reefs and shallow forereefs in Puerto Rico, *S. planifrons* was more abundant in the forereef (0.47 vs 0.05 individuals m^{-2}; McGehee, 1994). Lirman (1994) has documented a link between *S. planifrons* and *Agaricia tenuifolia* in Honduras and shown that adult fish prefer living foliose heads on the main reef, whereas juveniles favour dead foliose colonies in the lagoon (back reef). Lirman (1994) indicated that juveniles seem to settle onto adult territories until they are too large and then move to the lagoon before shifting back out onto the reef. *S. planifrons* actively defend their territories against conspecifics so ontogenetic shifts reduce competition for space between adults and juveniles. Densities of recruits were also correlated with the density of conspecific adults in the U.S. Virgin Islands (Booth and Beretta, 1994).

Acropora and *Porites* rubble are important microhabitats in back reefs (Tolimieri, 1998c) along with pure stands of *A. palmata* and *Agaricia agaricites* (Robertson *et al*., 1981; Ebersole, 1985) and *Millepora* (Williams, 1991). In Jamaican back reefs, densities of *S. planifrons* were negatively correlated with patch size of *A. cervicornis*, indicating intraspecific territorial spacing on larger patches (Williams, 1978). The link between *S. planifrons* abundances and *A. cervicornis* patches can be further complicated by the pattern of patches and in Jamaica Itzkowitz (1977b) showed that colonies $<1\ \text{m}^2$ had to be within 6 m of a larger colony to be inhabited. Densities in *A. cervicornis* patches in Jamaican back reefs were 0–2.0 fish m^{-2} (Itzkowitz, 1977b) and $\sim$1.5–3.75 fish m^{-3} (Williams, 1978). There is evidence that female *S. planifrons* in particular favour *M. annularis* heads for territory sites (Williams, 1978). In Panama, *S. planifrons* has a "refuge" habitat (virtually only species found and mainly adults) of *Agaricia* at 1.5–10 m on the sides of patch reefs with densities across whole patch reefs of 0.1–1.5 m^{-2} (Robertson, 1996) but can reach 2.89 m^{-2} on patch reefs dominated by *Agaricia* (Robertson *et al*., 1981). One of the few studies of the density of *S. planifrons* in a range of habitats was undertaken in Bonaire (van Rooij *et al*., 1996a) and densities in a shore zone, *A. palmata* zone, *A. cervicornis* zone, dropoff and upper reef slopes were $\sim$0, $\sim$0, $\sim$2,000, $\sim$3,500 and $\sim$1,000 fish ha^{-1}, respectively. On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 1.0, 12.2, 26.0 and 28.8 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). The mean density of *S. planifrons* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 1.3 fish 40 m^{-2} (Schmitt *et al*., 2002).

*3.4.7. Habitat functional values (*Stegastes planifrons*; Figure 1)*

S. planifrons clearly favours habitats with corals and is either absent or at very low densities of $\leq$0.1 fish 100 m^{-2} in seagrass beds and mangroves, so these habitats have no functional value. Sand beds are also assigned no functional value because of the lack of coral cover, although data are absent. A single survey of an *A. palmata* reef crest indicated *S. planifrons* was absent (van Rooij *et al*., 1996a), but because of the presence of coral heads in this habitat, it is likely to support individuals elsewhere and is assigned a low functional value. Patch reef and back reef habitats are obviously important sites for recruits and juveniles (e.g., Tolimieri, 1995) and with densities often $>$50 fish 100 m^{-2} (high functional values). Forereef *Montastraea* habitats are a preferred habitat of adult *S. planifrons*, with densities commonly 1–50 fish 100 m^{-2} (medium functional values). Data are scarce for gorgonian-dominated habitats and escarpments, but the low coral cover and low primary productivity in these habitats, respectively, indicate that their functional values are probably low.

3.4.8. Diadema antillarum *distribution*

D. antillarum inhabits a range of habitats, particularly rock, coral reef, mangrove roots, seagrass beds and sand (Randall *et al*., 1964). *Diadema* has intermediate abundances in very shallow water, because excessive wave action affects grazing rates (Foster, 1987) but intertidal densities can be high (Bauer, 1980). On forereefs, densities are highest from 2 to 10 m ($\sim$15 m^{-2} in heavily fished reefs in Jamaica) and then decrease with increasing depth, and *Diadema* is effectively absent from $<$20–25 m (e.g., Ogden and Lobel, 1978; Liddell and Ohlhorst, 1986; Morrison, 1988; Jackson, 1991). *Diadema* densities are also correlated with habitat structural complexity and cover of algal-covered, dead coral substratum (Weil *et al*., 1984). Density patterns may also vary temporally; in Panama, *Diadema* declined or disappeared from reef flats during seasons of repeated subaerial exposures, but recolonised the habitat during periods of higher water levels (Cubit *et al*., 1986). Within shallow areas, *Diadema* is strongly correlated with changes in structural heterogeneity (Lewis and Wainwright, 1985) but is found across coral reefs along with sandy areas and *Thalassia* beds (Lessios, 1991). Structural heterogeneity is also important for juvenile *Diadema* as individuals recruit into small crevices in the reef, but this process is further dependent on low algal biomass (Bak, 1985).

Reflecting these general trends, an extensive study throughout the West Indian Marine Province found densities of 2.4–25.8 m^{-2} for different types of reef crests (excepting one anomalous site in Tobago with a density of

0.04 m^{-2} and $\geq$7.8 when *A. palmata* was common), 0.5–4.5 m^{-2} for gorgonian-dominated habitats, 9.8 m^{-2} for shallow ($<$7 m) *Montastraea* reefs and 0.1–1.7 for deep ($>$10 m) *Montastraea* reefs (Bauer, 1980). In Venezuela, mean densities were 2.74 m^{-2} in the inner reef flat (back reef), 3.10 m^{-2} on the outer reef flat (reef crest), 5.6 m^{-2} on the reef front and 0.67 m^{-2} on the deep forereef (Weil *et al.*, 1984). Across the Belize Barrier Reef, densities were 0.13 m^{-2} in the back reef, 4.31 m^{-2} in a high relief spur and groove zone, 0.05 m^{-2} in a low relief spur and groove zone, 0.14 m^{-2} on the inner reef slope and 0.69 m^{-2} on the outer ridge (Lewis and Wainwright, 1985). In a back reef/reef crest site and three forereef sites (depths of 2, 5 and 10 m) in St. Croix, densities were 6.4, 13.4, 9.0 and 5.8 m^{-2} (Carpenter, 1990a). Hughes *et al.* (1987) reviewed a series of Jamaican studies to give densities of 3.9 m^{-2} for a back reef site, 8.1–11.7 for shallow ($<$10 m) forereefs and 3.5–12.2 m^{-2} for deep ($>$10 m) forereefs and 0.7 m^{-2} for a site at 20 m. High densities of 33.5–72.8 m^{-2} have been recorded for Jamaican patch reefs (Sammarco, 1982). Further data for Jamaica gave densities of 3.1–3.4, 8.1–9.1 and 13.6–18.0 individuals m^{-2} for the back reef, shallow forereef (3 m) and deeper forereef (10 m), respectively (Steneck and Dethier, 1994), and *Diadema* densities of 5.8–15.8 m^{-2} were recorded on a Jamaican reef crest (Morrison, 1988). Bak *et al.* (1984) give densities on the deep (9–36) reef slope in Curaçao as 0.26–0.73 m^{-2}, which contrasted with values of $\sim$12 m^{-2} for an *A. palmata* and shallow forereef zones (Bak and van Eys, 1975). Densities on patch reefs in St. Croix were 6.7–12.0 m^{-2} (Ogden *et al.*, 1973; Hay and Taylor, 1985). *Diadema* are absent from sand channels on the forereef (Lewis and Wainwright, 1985) and densities in seagrass beds vary from 1.2–2.8 m^{-2} in the Florida Keys (Randall *et al.*, 1964; Bauer, 1976, 1980) to being absent in Belize (Lewis and Wainwright, 1985).

The abundance of *Diadema* in shallow water exacerbates the influence of herbivory by parrotfishes, surgeonfishes and damselfishes on benthic communities, adding to the significant differential effects of herbivores across the seascape. There is extensive research on the effect of *Diadema* on algal communities, but much of the work is small scale (e.g., on patch reefs) and often on overfished areas (Hay, 1984). For example, *Diadema* grazed $\sim$20% of the monthly net benthic primary production of a fringing coral reef in Barbados (Hawkins and Lewis, 1982). *Diadema* has a strong preference for algal turf, and in enclosure experiments, algal species richness and algal community primary production were maximised at intermediate *Diadema* densities (Carpenter, 1981). In addition to the effects on reefs, *Diadema* grazing is a major factor in establishing sandy "halos" around patch reefs (Ogden *et al.*, 1973). Although *Diadema* has a strong preference for algal turf, the seasonal reduction of this food source can result in the use of alternatives, particularly live coral (Carpenter, 1981). *Diadema* has a further effect on coral community structure in shallow water because of the interaction between algae and coral recruits (Sammarco, 1980).

Much of the work on the ecology of *Diadema* is on relatively natural reefs, but as previously mentioned, the abundance of *Diadema* was dramatically reduced in the early 1980s by a mass mortality caused by a waterborne pathogen (for a review of the spread of the disease, see Lessios *et al*., 1984). There is also evidence of another smaller mortality event in 1990/91 in the Florida Keys (Forcucci, 1994), leading to densities no greater than 0.05 m^{-2} (Chiappone *et al*., 2002a). Densities elsewhere were also $<1\ \mathrm{m}^{-2}$, even in shallow water (Bak *et al*., 1984; Hunte *et al*., 1986; Liddell and Ohlhorst, 1986; Carpenter, 1988; Levitan, 1988; Moses and Bonem, 2001). Since the premortality distribution of *Diadema* varied significantly across Caribbean reefs, it was inevitable that mass mortality should have differential effects across habitats with the most significant effects in the upper 10 m. Carpenter (1990b) studied the patterns of effects across different zones, namely the back reef, reef crest, shallow (<2 m), middepth (<5 m) and deep (10 m) forereefs. Prior to mortality, *Diadema* densities were highest in the shallow forereef and decreased with depth, so at 10 m, densities were the same as the back reef and reef crest. Mass mortality reduced densities over all zones by 95–99%. *Diadema* mortality had the effect of increasing algal biomass by 319, 439, 305 and 22% in back reef, shallow forereef, middepth forereef and deep forereef, respectively (i.e., the effect was less dramatic in deeper water). Algal productivity per unit area initially decreased by 37% in the back reef, then increased with increasing biomass. At 2 m, productivity decreased initially but, unlike the back reef, did not subsequently increase. There were no significant changes in productivity at 5 and 10 m. Productivity per unit biomass also decreased at all sites except 10 m and was clearly correlated with the previous densities of *Diadema*. Although the shallow zones were more productive than premortality values, the additional algal biomass was not available to herbivores. The increased, but unavailable, algal biomass led to an increase of algal detritus in the back reef and lagoon as algae died and were dislodged, leading to a fundamental change in the functioning of these communities (Carpenter, 1990b). In Jamaica, the mean effect of *Diadema* mortality on benthic coral communities was an algal abundance increase of 95% and a coral cover decrease by up to 60% of original levels (Hughes *et al*., 1987). Hughes *et al.* (1987) showed that reduction of coral cover was especially apparent in shallow water, in part because deeper corals are more resistant to overgrowth.

The potential recovery of *Diadema* to reestablish the spatial variations in densities that were apparent premortality remains enigmatic. Following mass mortality, there has been only limited recovery of *Diadema* populations, despite the apparently vacant niche. Low recovery rates could be caused by low fertilisation success, lack of suitable substrates for recruitment, postsettlement mortality and interspecific competition (summarised by Chiappone *et al.*, 2002b). However, a study by Edmunds and Carpenter (2001) on the north coast of Jamaica found evidence of a recovery of *Diadema* on shallow forereefs (densities $\sim 5\ \mathrm{m}^{-2}$). The increased densities of *Diadema* have reduced macroalgal cover and increased the density of juvenile corals. Whether such a recovery of *Diadema*, and the potential to increase coral cover, will occur in other parts of the Caribbean is an important issue for future research.

*3.4.9. Habitat functional values (*Diadema antillarum*; Figure 10)*

Diadema appear to be absent from forereef sand channels (Lewis and Wainwright, 1985) and escarpments (e.g., Morrison, 1988), so these habitats appear to have no functional value. Although *Diadema* are recorded as occurring among mangrove roots (Randall *et al.*, 1964), there are no quantitative data on their density and this habitat is assigned a putative low functional value. There is significant intrahabitat variation in natural densities in the remaining habitats, but we assign a low functional value to habitats where densities are generally $<1\ \mathrm{m}^{-2}$ (deep *Montastraea* reef), medium function value to habitats where densities are generally 1–5 m^{-2} (seagrass beds, back reefs and gorgonian-dominated forereefs) and high functional value to habitats where densities are generally $>5\ \mathrm{m}^{-2}$ (patch reefs, reef crests and shallow *Montastraea* reefs). The effect of the mass mortality was to reduce densities of *Diadema* to $<1\ \mathrm{m}^{-2}$, so we present a second set of functional values for post-1983 habitats where each is reduced to a low functional value, although higher values have been recorded in certain areas (Edmunds and Carpenter, 2001).

3.5. Tertiary production

Tertiary producers in a coral reef ecosystem encompass a wide range of taxa, but for the purposes of this chapter, our discussion is limited to the dominant group, fishes. As for secondary production, we use tertiary producer densities as a proxy for tertiary production; the differences between habitat types of key variables to convert biomass to production are unclear. Since there is a high diversity of predators, this section provides an overview of the densities of tertiary producers in different habitat types and, with the exception of specific examples, does not include the habitat preferences of all individual species, as was possible for secondary producers. Furthermore, although the interactions between densities of primary and secondary producers have been well studied, the effects of varying densities of tertiary producers on secondary producers are less clear. Although tertiary consumers also feed on one another (e.g., Hobson, 1991), *tertiary producers* is used here as a generic term for species not feeding on primary producers.

3.5.1. Planktivores

The diverse assemblage of planktivores present on reefs can be classified as "tertiary producers" because most feed on zooplankton (reviewed by Hobson, 1991), which are most abundant along reef edges adjacent to deep water (Hobson and Chess, 1978, 1986). Caribbean diurnal planktivores, such as *Chromis cyanea* and *Clepticus parrae*, were most abundant in deeper zones (terraces and deep lagoonal patch reefs) in the San Andres Providencia archipelago where there is a high availability of prey (Mejia and Garzon-Ferreira, 2000). Similarly, Alevizon *et al.* (1985) reported dramatically higher abundances of both *C. cyanea* and *Chromis multilineata* in two forereef habitats compared to the reef crest and back reef patch reefs in the Bahamas. In Curaçao, mean densities of *C. cyanea* were 0.1, 4.8, 76.5 and 65.3 fish 100 m^{-2} on four forereef sites (2, 5, 10 and 15 m, respectively) (Nagelkerken and van der Velde, 2002). At the same sites, densities of *C. multilineata* were 3.6, 13.4, 48.5 and 14.0 fish 100 m^{-2} and densities of *C. parrae* were 0.6, 0.1, 3.9 and 10.8 fish 100 m^{-2}. The mean densities of *C. cyanea*, *C. multilineata* and *C. parrae* in four deep (15–20 m) forereef sites in southeastern Hispaniola were 36.4, 16.7 and 2.2 fish 40 m^{-2}, respectively (Schmitt *et al*., 2002). *Chromis* spp. and *C. parrae* were found on patch reefs and in back reefs but comprised <3% of the individuals in these habitats (Adams and Ebersole, 2002). *Chromis* spp. and *C. parrae* are not found in mangroves and seagrass beds (Weinstein and Heck, 1979; Thayer *et al*., 1987; Nagelkerken and van der Velde, 2002; Newman and Gruber, 2002; Serafy *et al*., 2003).

Smaller individuals of planktivorous species are often more widely distributed because of the high predation pressure on deeper reefs, and if shelter is limited at the reef edge, even the larger individuals found in this habitat may have migrated from other areas to feed (Hobson, 1991). In Mexico, the mean densities of juvenile *C. cyanea* and *C. parrae* on a series of forereefs (12 m) depth were 26.1 and 17.5 fish 100 m^{-2}, respectively (González-Salas *et al*., 2003). Available shelter at the reef edge is dependant on the type of benthic community and rugose: coral-rich habitats provide better shelter than habitats with low coral cover. For example, *C. cyanea* is typically found in aggregations (<100) centred on a prominent coral (de Boer, 1978). In addition to shelter requirements, on the Great Barrier Reef large, stationary aggregations of planktivores have been documented where water movement brings abundant food to the reef edge (Thresher, 1983), and this seems likely to be true in the Caribbean. Therefore, densities of planktivores along a reef edge will be patchy because of both variations of water movement and changes of benthic community.

3.5.2. Habitat functional values (Figure 1)

There are few habitat-specific data for densities of planktivores, but it is clear that the highest densities (>90 fish 100 m^{-2}) are found in deeper *Montastraea* reefs and presumably, although data are particularly scarce, escarpment habitats (high functional values). Densities on shallower *Montastraea* reefs are generally lower (18.3–128.9 fish 100 m^{-2}), and this habitat is assigned a medium functional value. All the other reef habitats (patch reefs, back reefs, reef crests and gorgonian-dominated forereefs) have some shelter and will be inhabited by planktivores, but food availability is limited by the distance to deepwater (low functional values). Mangroves, seagrass beds and sand have no functional value.

3.5.3. Invertivores

Fish predation on benthic invertebrates is reviewed by Jones *et al.* (1991), and there appears to be considerable spatial variation in both the densities and the effects of invertivores, but data are limited despite between 27 and 56% of some fish communities being benthic invertebrate predators. The potential effects of invertivores on invertebrate populations was highlighted by Keller (1983) in Jamaica where fish predators influence the population dynamics of the urchins *Tripneustes ventricosus* and *Lytechinus variegatus* in seagrass beds. Corallivorous fishes represent a discrete group of benthic invertivores that are worthy of special mention as they might be expected to vary spatially between habitats in accordance with coral cover. Despite efforts to link butterflyfish (Chaetodontidae) abundances with coral cover (e.g., Findley and Findley, 2001), there are few obligate corallivores in the Caribbean and this link is less clear than might be expected. However, *Chaetodontidae* species do tend to be most abundant on shallow forereefs, where coral cover is highest (e.g., Findley and Findley, 2001).

Major families of invertivores on reefs include Labridae, Holocentridae and Balistidae, but we focus on the habitat preferences of the Haemulidae (grunts) because they are arguably the best studied and have some fisheries importance. Grunts make ontogenetic migrations between habitats because of changes of diet and habitat requirements for reproduction, and Appeldoorn *et al.* (1997) showed a general inshore to offshore ontogenetic migration for *Haemulon plumieri* in Puerto Rico and the Bahamas. Small juvenile *H. plumieri* were among *Thalassia* and small coral colonies then migrated to patches of *A. cervicornis* in seagrass beds and sheltered reef edges near *Thalassia*. Subadults preferred reefs, high relief back reefs or areas with moderate surge and sand with gorgonians. Adult *H. plumieri* were usually solitary either on forereefs or, if inshore, on a reef–sand interface.

Grunts use a range of nursery habitats but show interspecific variations in habitat preferences (Nagelkerken *et al*., 2000c). Seagrass beds are important for juvenile *Haemulon flavolineatum* and *H. sciurus* and shallow reefs for *H. chrysargyreum*. Shulman and Ogden (1987) showed that 95% of *H. flavolineatum* settled onto sand and in seagrass beds and then migrated to nearby reefs and the remaining 5% settled directly onto reef structures. Some grunts may use lagoon patch reefs and rubble areas as nurseries in preference to the back reef and other lagoon habitats (Nagelkerken *et al*., 2000c; Adams and Ebersole, 2002). If lagoonal habitats such as seagrass beds are scarce, higher densities of grunts settle directly onto reefs (Tupper and Juanes, 1999). Lindeman *et al.* (1998) provides a detailed discussion of grunt settlement patterns within Biscayne Bay, Florida. Mangroves are also important nursery habitats for grunts (Thayer *et al*., 1987; Newman and Gruber, 2002). The role of mangroves for grunts was clearly demonstrated in Belize by Mumby *et al.* (2004a) who showed that in reef systems (e.g., atolls) where mangroves were present, Haemulidae biomasses on patch reefs, shallow forereefs and *Montastraea* reefs increased by 478%, 240% and 40%, respectively, compared to systems where mangrove was absent. Habitat preferences of adult grunts are less well studied than those of the juveniles, but Gaut and Munro (1983) provide an excellent summary table of the characteristic habitats of 14 species of Haemulidae. Although adult grunts have preferred diurnal habitats, they also undertake nocturnal migrations to lagoonal feeding areas, particularly seagrass beds (Ogden and Zieman, 1977). This functional link between habitats is discussed in more detail in Section 4.1.

To assign habitat functional values for invertivores, we review published densities of *H. flavolineatum* as a representative species of the Haemulidae. In Curaçao, juvenile densities were 82.7–99.8 and 15.1–32.1 fish 100 m^{-2} in mangroves and seagrass beds, respectively, with significant decreases in density at night (Nagelkerken *et al*., 2000a,b; Cocheret de la Morinière *et al*., 2002; Nagelkerken and van der Velde, 2002). The decreased densities in the seagrass at night (1.4 fish 100 m^{-2}) reflected juveniles, which are susceptible to predation, seeking shelter and censuses only counting larger nocturnally migrating individuals (Nagelkerken *et al*., 2000b). Densities of 0–21 fish 500 m^{-2} were given for surveys in seagrass beds at night in St. Croix (Ogden and Zieman, 1977). On the adjacent island of Bonaire, densities in mangroves and seagrass beds were 59.9 and 115.3 fish 1000 m^{-2}, with seagrass cited as the most important biotope for juveniles (Nagelkerken *et al*., 2000c).

Where mangroves were scarce (St. Croix), juvenile *H. flavolineatum* recruited to seagrass beds and back reefs and peak densities in back reefs were 1.1–1.3 fish m^{-2} (Shulman and Ogden, 1987). In St. Croix, densities on seagrass beds and patch reefs were 0.5 and 51.0 fish 100 m^{-2}, respectively (Mateo and Tobias, 2004) and 4.5 fish 100 m^{-2} for a patch reef in Costa Rica (Fonseca and Gamboa, 2003). Densities on a series of reef crest sites in the Bahamas were 21.0 fish 100 m^{-2}, respectively (Kramer *et al.*, 2003). Densities on the forereef in Curaçao were 0.5, 4.0, 2.7 and 2.2 fish 100 m^{-2} at 2, 5, 10 and 15 m, respectively (Nagelkerken and van der Velde, 2002). Densities on the forereef in Bonaire were 52.4, 37.4, 12.4 and 2.9 fish 1000 m^{-2} at 0–3, 3–5, 10–15 and 20–25 m, respectively (Nagelkerken *et al.*, 2000c). The mean density of *H. flavolineatum* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 0.71 fish 40 m^{-2} (Schmitt *et al.*, 2002) and 5.5 fish 100 m^{-2} on shallower (8–12 m) forereef sites in Cuba (Claro and Ramos, 2003). Densities of *H. flavolineatum* ($>$15 cm) were 0.13–0.4 (back reef) and 2.92–5.8 (crest spurs) fish 240 m^{-2} and 9.7–23.17 fish ($>$5 cm) 400 m^{-2} on shallow fringing reefs in Barbados with no significant difference inside and outside a marine reserve (Rakitin and Kramer, 1996; Chapman and Kramer, 1999). There was also no significant difference in abundances inside and outside a reserve in Belize, but abundance, mean length and biomass of *H. flavolineatum* were higher inside a reserve in Saba (Polunin and Roberts, 1993).

*3.5.4. Habitat functional values (*Haemulon flavolineatum*; Figure 1)*

Mangroves, seagrass beds, patch reefs, back reefs and reef crests appear key habitats for *H. flavolineatum*, particularly as nursery habitats, with densities generally $>$5 fish 100 m^{-2} and are assigned high functional values. Seagrass beds are also important nocturnal feeding areas for adult grunts (Ogden and Zieman, 1977). Densities on forereefs (shallow and deep *Montastraea* reefs) are generally 1–5 fish 100 m^{-2} and are assigned medium functional values. Escarpments are assigned a low functional value as densities appear to be $<$1 fish 100 m^{-2}. There are few data for gorgonian-dominated forereefs, but the low topographical complexity indicates that this habitat may have a low functional value. Sand channels, with no structural relief, are likely to have no functional value.

3.5.5. Piscivores

Piscivores are a diverse group that can comprise up to 53% of the species in an area (Hixon, 1991). There are few available data suggesting overall patterns of piscivore densities across a reef profile and there has been little systematic work demonstrating predation rates across mangrove, lagoon and reef habitats. Even across the reef itself, such empirical data are scarce compared to the information available on herbivory and its consequent effects on algal zonation. However, the habitat preferences of individual species are well studied, and we initially present a detailed discussion of the habitat requirements of the commercially important *Epinephelus striatus* (Nassau grouper). The review of *E. striatus* is followed by a more general discussion of the habitat preferences of other serranids and lutjanids. The detail provided for *E. striatus* reflects (1) the amount of empirical data available in the literature and (2) the research interest in constructing spatially explicit population models to aid conservation of remaining stocks of this species.

A significant proportion of the work on *E. striatus* juveniles and their ontogenetic shifts has been conducted in the central Bahamas and further research is needed to refine the characteristics of key habitats and assess variations in habitat preferences across the Caribbean region. Eggleston (1995) showed that recently settled fish resided, generally solitarily, within coral clumps (especially *Porites* spp.), which are covered by macroalgae (especially *Laurencia*) in off-reef tidal creek systems and lagoons (mean density 0.37–2.12 fish m^{-2} with a maximum of 8 m^{-2}) and absent in seagrass. *Laurencia* cover was, therefore, positively correlated with postsettlement grouper density, but algal displacement volume, numbers of holes, ledges and sponges were not significant determinant factors. Densities of juvenile *E. striatus* in macroalgal-dominated tidal creeks are an order of magnitude higher than any other habitat (Eggleston, 1995; Dahlgren and Eggleston, 2001), but other substrata (e.g., seagrass or corals without macroalgae) are utilised, particularly in areas that lack expansive macroalgal meadows. Hence, Colin *et al.* (1997) record recently settled *E. striatus* on artificial substrates (cement blocks and conch shells), natural reefs and rubble mounds protected by the sand tilefish (*Malacanthus plumieri*).

Larger juveniles tend to reside outside or adjacent to algal-covered coral clumps and, like smaller juveniles, are mostly solitary (88%), and densities were 0–0.06 m^{-2} (Eggleston, 1995). The ontogenetic shift from algal clumps seems to occur when the advantages of the higher growth rates, which are possible outside *Laurencia* clumps, outweigh the need to avoid predators (Dahlgren and Eggleston, 2000, 2001). Predation rates increase with decreasing size, so small juveniles must remain within the algal-covered coral clumps. When *E. striatus* juveniles are large enough (typically 120–150 mm), they tend to exhibit an ontogenetic habitat shift from patches of macroalgae and *Porites* spp. to patch reef habitats (Eggleston, 1995). On patch reefs, *E. striatus* (like all serranids) exhibit high site fidelity to territories (e.g., Eggleston *et al.*, 1997). Territories within a patch reef environment may span several patches and groupers have been observed moving freely from reef to reef but exhibit homing tendencies to their territory (Bardach, 1958; Beets and Hixon, 1994). There is also evidence on artificial and natural patch reefs ($\sim$0.04 fish m^{-2}) in the U.S. Virgin Islands that larger individuals were found on reefs with larger shelter holes (Beets and Hixon, 1994).

It has long been recognised that groupers move into deeper water as they mature and adult *E. striatus* are widely dispersed on coral rich forereefs (e.g., Bardach, 1958). Adults are highly sedentary living among the benthic community in holes, caves and crevices (Eggleston, 1995; Chiappone *et al.*, 2000). Although groupers are seen in a variety of habitats in the 1–300 m depth range (Chiappone *et al.*, 2000), dependence on specific habitat characteristics appears relatively strong. Habitat dependence occurs because groupers commonly feed by ambushing prey and are more dependent on hard substrate habitat with suitable shelter than other predators such as lutjanids (Parrish, 1987; Sluka *et al.*, 2001). Therefore, existing research has more commonly linked *E. striatus* densities to high or moderate topographical relief (Sluka and Sullivan, 1996; Sluka *et al.*, 1996b, 1997). In the heavily fished Florida Keys, mean densities were 0.045 fish 100 m^{-2} on patch reefs, 0.04 100 m^{-2} in a high-relief spur-and-groove zone, 0.01–0.02 100 m^{-2} in a low-relief spur-and-groove zone and 0.04 100 m^{-2} in a deep (20–30 m) forereef slope (Sluka *et al.*, 1998, 2001). Densities in the Bahamas were $\sim$0.2–0.4, $\sim$0.1–0.25 and $\sim$0.1–0.35 fish 100 m^{-2} on channel reefs, windward hard-bottoms and fringing reefs, with higher densities inside a marine reserve (Sluka *et al.*, 1996a). Sluka *et al.* (1997) also clearly showed the effect of the same marine reserve on *E. striatus* with a biomass inside a park of 574 g 100 m^{-2} compared to 118–156 g 100 m^{-2} outside.

Reproductively active *E. striatus* have specific habitat requirements for transient mass spawning events, but they are poorly understood. Mass spawning sites have commonly been seen near continental shelf breaks or the edges of insular shelves (Colin *et al.*, 1997; Domeier and Colin, 1997). Further work is required to refine the location of specific spawning sites based on requirements such as available migration routes and oceanographic currents that transport larvae to optimal settlement conditions (e.g., Colin *et al.*, 1997). Fish have been documented to migrate at least 220 km (Bolden, 2000), so the functional value of particular spawning sites must be very high. The mean number of *E. striatus* at an aggregation site in Little Cayman was 400–5200 individuals (Whaylen *et al.*, 2004).

E. striatus shows a pattern typical of many larger serranids of an ontogenetic shift from lagoonal nursery grounds to deeper forereef areas as adults. Density patterns are different for the smaller groupers, *Epinephelus cruentatus*, *E. fulvus*, *E. guttatus* and *E. adscensionis*. *E. cruentatus* prefers channel reefs (Sluka *et al.*, 1996b), particularly areas with high relief. High coral cover provides high topographical relief, and *E. cruentatus* densities are correlated with coral cover, especially that of *M. annularis* and *Agaricia*. *E. cruentatus* juveniles are found at all depths but have a highly variable distribution (Luckhurst and Luckhurst, 1977; Nagelkerken, 1977; Sluka *et al*., 1994). *E. fulvus* prefers patch reefs surrounded by sandy shoals and seagrass beds (Sluka *et al*., 1994) and low-relief windward hard-bottom sites (Sluka *et al*., 1996b). *E. guttatus* also favours windward hard-bottom sites. In the Leeward and Windward Islands, *E. fulvus* and *E. guttatus* are very abundant on sandy bottoms with isolated coral patches (Nagelkerken, 1981). *E. adscensionis* was most abundant on fringing reefs in the Bahamas compared to channel reefs or windward hard-bottom areas (Sluka *et al*., 1996b).

Adult lutjanids generally have a weaker habitat dependence than serranids because they lead less sedentary lives and are less reliant on an ambush strategy, which requires specific habitat characteristics (Parrish, 1987). Like serranids, juvenile snappers have specific lagoonal nursery habitat requirements. Nursery habitats are generally in shallower water than adults, and readers are referred to Lindeman *et al.* (1998) for a detailed analysis of the habitat preferences of newly settled lutjanids. Almost all adult and juvenile snappers associate strongly with either a hard-bottom area or a habitat with some structural relief such as tidal creeks and mangroves (Parrish, 1987; Thayer *et al*., 1987; Newman and Gruber, 2002). Indeed, the absence of mangroves as a nursery habitat reduces the biomass of adult snapper seen on adjoining reefs (Mumby *et al*., 2004a). Specifically, *Lutjanus analis* are frequently associated with seagrass beds near inlets and patch reefs (Mueller *et al*., 1994). *L. apodus* juveniles are found among mangrove prop-roots, tide pools and shallow lagoonal areas, small adults are common in *A. palmata* areas and larger individuals are found in both mangrove and coral reef habitats (Rooker, 1995; Nagelkerken *et al*., 2000c). Juveniles of *Lutjanus mahogoni* and *L. griseus* are found in seagrass beds in bays, mangroves or in shallow water along the shore, larger individuals are commonly near stands of *A. palmata* and escarpments while adults are found in deeper zones (Nagelkerken *et al*., 2000c; Nagelkerken and van der Velde, 2002). However, newly settled stages of *L. griseus* are not found on hard-bottom communities (Lindeman *et al*., 1998). Lirman (1999) showed that in Florida and the U.S. Virgin Islands, areas of *a. palmata* had higher abundance of snappers than areas without this coral, which provides high topographical relief. In contrast to many other snappers, *Ocyurus chrysurus* is perhaps least constrained in its feeding environment, as it forages freely throughout much of the water column for plankton and small fishes (Parrish, 1987). Juvenile *O. chrysurus* (<8 cm) are particularly common and relatively sedentary in seagrass beds in bays and stony, sandy areas close to shore (Watson *et al*., 2002) and mangroves (Nagelkerken and van der Velde, 2002). Adults are mainly in more rugose areas closer to escarpments (Watson *et al*., 2002).

*3.5.6. Habitat functional values (*Epinephelus striatus*; Figure 1)*

Assigning functional values based on the density of *E. striatus* is complicated by the effects of fishing and marine reserves and the lack of systematic density assessments across seascapes. However, macroalgal tidal creek systems appear to be the most important settlement areas for *E. striatus* with densities up to 212 fish 100 m^{-2} (Eggleston, 1995) and are assigned a high functional value for mangroves. Though less important than tidal creeks in the Bahamas, seagrass beds also function as settlement areas, particularly in areas without *Laurencia* clumps in tidal creeks, and are given a medium functional value. Patch reefs are an important habitat during ontogenetic migration (Eggleston, 1995), although densities vary significantly and are assessed as having a high functional value. Densities on forereef habitats vary from 0.1 to 0.35 fish 100 m^{-2} and are assigned a medium functional value (gorgonian-dominated forereefs and shallow and deep *Montastraea* habitats). A single published density for an escarpment was <0.1 fish 100 m^{-2}, but this habitat is often important for mass spawning (Domeier and Colin, 1997) and thus is assigned a medium functional value. Few studies discuss the use of back reefs and reef crests, but the offshore ontogenetic migration indicates that individuals may use these habitats and they are given putative low functional values. Sand channels, with no structural relief, are likely to have no functional value.

3.6. Densities of *Panulirus argus* and *Strombus Gigas*

Panulirus argus (Caribbean spiny lobster) and *Strombus gigas* (queen conch) are two of the most important fishery species in the Caribbean (Birkeland, 1997; Cochrane and Chakalall, 2001). The high commercial demand for the two species and the need to conserve remaining stocks have led to considerable research interest in mapping their distributions and constructing population dynamics models, so we include a detailed review of their habitat preferences. *P. argus* feeds mainly on benthic autotrophs, gastropods and bivalves, and *S. gigas* feeds on detritus, benthic autotrophs and polychaetes (Opitz, 1996), so they are discussed here separately from secondary and tertiary producers.

3.6.1. Panulirus argus

P. argus larvae have a well-documented series of pelagic stages (Butler *et al.*, 2001). As soon as *P. argus* larvae move inshore to settle, they begin a complex spatial interaction with the seascape. Firstly, planktonic larvae must avoid predation, which is highest over coral reefs but lower near shore (Acosta and Butler, 1999). Subsequent predation on benthic settlers is also higher on the reef than in vegetated habitats in a lagoon and bay. To minimise predation, postlarval *P. argus* exhibit several behavioural traits, such as migration during the darkest lunar phase, use of surface waters to move across the reef and settlement in vegetated habitat (Acosta and Butler, 1999). Settlement preferences have also been seen in the Bahamas where surveys showed that there were mainly juveniles and preadults on seagrass beds with no individuals on unvegetated areas (Smith and van Nierop, 1986). Further work in the Bahamas demonstrated that some nursery habitats always had higher settlement than others because of wind-induced along-shore transport (Eggleston *et al*., 1998b). In addition to along-shore transport, other biological and physical factors such as postlarval patchiness and coastal upwelling were important. Further, there was a general decline in settlement rates from more seaward nursery sites to more inshore sites. The seaward-inshore decrease in settlement rates was caused by the dilution of larvae, as incoming water mixed with water on the banks, and the ever decreasing abundance of larvae still available to settle (Eggleston *et al*., 1998b). Large-scale patterns between sites >50 km apart were also affected by regional variation in hydrodynamic transport.

P. argus phyllosome larvae are released from eggs hatched on the seaward fringes of coral reefs before preferentially settling in nursery habitats (Stockhausen *et al*., 2000). Hence, the hydrodynamic link between adult populations and benthic settlers is very important. Lipcius *et al.* (1997) suggested that postlarval supply is probably decoupled from adult abundance by physical transport and that adult abundance is likely to be decoupled from postlarval supply by the effects of varying habitat quality upon survival (mean density of adults at four sites, encompassing a range of habitats was 0–150 ha^{-1}). Lipcius *et al.* (1997) then showed that in the Bahamas, the decoupling can generate sinks and sources of postlarvae. Hence, one site was a sink because adult abundance was the lowest even though it had the highest postlarval supply, but little nursery habitat compared to three other sites (sources), which had higher adult abundances despite lower postlarval supply.

Within vegetated nursery areas, postlarval *P. argus* appear to seek clumps of algae as a settlement habitat and as a residence for early benthic phase juveniles. In the Florida Keys, and potentially many other parts of the Caribbean, the favoured alga tends to be patches of the highly branched *Laurencia*, which provide refuge and an abundant, diverse prey fauna (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986). In contrast, within an unproductive Mexican lagoon with low-standing crop of *Laurencia*, density and distribution of early benthic phase juveniles (146–263 ha^{-1}) were related to patches of *Lobophora* (Briones-Fourzán and Lozano-Álvarez, 2001).

Seagrass biomass does not significantly influence juvenile survival (Lipcius *et al*., 1998; Briones-Fourzán and Lozano-Álvarez, 2001). The role of algal patches in reducing predation has facilitated the development of a habitat-survival function (HSF) for algal-stage juveniles (Lipcius *et al*., 1998). An HSF model's survival changes with habitat structure and encompasses all characteristics of the habitat within three elements: the absolute abundance of elements, relative abundance of elements and the scale of area or volume used to measure elements (McCoy and Bell, 1991), which in this case is plant biomass. The HSF for *P. argus* was hyperbolic for algal biomass and even modest increases in habitat structure significantly enhanced *P. argus* survival, especially at low-to-moderate levels of habitat structure, which should theoretically be avoided by juveniles (Lipcius *et al*., 1998). The HSF is supported by empirical data, and Butler *et al.* (1997) concluded that recruitment in Florida was tightly linked to a nursery habitat that is heterogeneous and ephemeral, and predictions of adult populations need to be coupled with information on the spatial and temporal changes in nursery habitat structure.

After algal-stage juvenile *P. argus* outgrow their algal refugia, they dwell in small crevices provided by sponges, gorgonians, coralline algae, seagrass, patch reef and rock-rubble habitats (Lipcius *et al*., 1998; Acosta and Robertson, 2003). The mean densities of juveniles on patch reefs inside and outside a marine reserve in Belize were 55.9 and 32.1 ha^{-1}, respectively (Acosta and Robertson, 2003). The change to a ''postalgal'' juvenile occurs when individuals attain a partial size refuge from predation (typically 16–25 mm carapace length) and are able to forage relatively safely at night (Smith and Herrnkind, 1992). The shift from algal dwelling to crevice sheltering could potentially be a bottleneck for *P. argus* populations (Childress and Herrnkind, 1994). At two sites in the Florida Keys, densities of mainly postalgal juveniles were found to be generally highest in channels (0.0247–0.0642 m^{-2}), followed by hard-bottom habitats ($\sim$0.04 m^{-2}) and patch reefs ($\sim$0.01–0.09 m^{-2}), but they were rarely in seagrass (0.001 m^{-2}) and never in mangrove prop-roots, and densities in all habitats were reduced by a 2-d fishing miniseason (Eggleston and Dahlgren, 2001). The mean densities of juveniles in shallow Florida hard-bottom habitats were $\sim$454 ha^{-1} (Forcucci *et al*., 1994), 278 ha^{-1} (Marx and Herrnkind, 1985) and 0–18 400 m^{-2} (Childress and Herrnkind, 1997). Eggleston and Dahlgren (2001) showed that postalgal juvenile density was related to the density and volume of large sponges in channel habitats because they provided abundant refugia and a possible corridor for migrating juveniles. The relationship with sponges in channels was dramatically demonstrated when cyanobacterial blooms caused sponge mortalities in $\sim$20% of the Florida Keys' nursery (Butler *et al*., 1995; Herrnkind *et al*., 1997). The reduction in available sponge microhabitats led to *P. argus* using alternative shelters, such as coral heads and solution holes. Overall, there was a relatively low effect on *P. argus* densities because of continued production in a larger unaffected nursery region and a fortuitously high postlarval supply. It was suggested that the latter was unlikely to remain until the sponges had recovered.

Many regions of the Caribbean have seagrass and patch reef areas, instead of the extensive hard-bottom areas with large sponges and solution holes present in Florida. Acosta and Butler (1997) suggest that mangroves may play a larger role in the life history of *P. argus* because of the areal coverage of seagrass beds in these regions. Their work in Belize showed that juveniles to subadults sheltered among mangrove prop roots, in undercut peat banks and under corals near islands. Although juvenile and subadult *P. argus* preferred large stony corals, the use of mangrove roots and peat banks increased when coral density was low. Furthermore, population sizes were higher near mangrove islands surrounded by shallow seagrass beds compared to those isolated by deeper water. Similarly, further research demonstrated that *P. argus* was more abundant, with a higher proportion of juveniles, in mangrove islands or large coral patch reefs surrounded by seagrass compared to areas surrounded by sand and rubble (Acosta, 1999). The work of Acosta and Butler (1997) and Acosta (1999) clearly show that vegetated areas may function as movement corridors for juveniles.

Subadults move to dens provided by patch reefs, boulders and undercut limestone ledges and seagrass banks (Lipcius *et al*., 1998; Stockhausen *et al*., 2000). Adults may migrate seaward to a depth of $\sim$100 m but are found in a range of sheltered habitats including reefs, rocky bottoms, rock or coral outcrops, undercuts along seagrass blowouts and sponge and gorgonian aggregations associated with reefs (Kanciruk, 1980; Smith and van Nierop, 1986; Cox *et al*., 1997; Stockhausen *et al*., 2000; Eggleston and Dahlgren, 2001). Mean densities of adult lobsters in marine reserve in Belize was 45.7–91.2 ha^{-1} on a patch reef, 38.3 ha^{-1} on a reef wall and 15.2 ha^{-1} on the forereef at 5–7 m (Acosta and Robertson, 2003). *P. argus* forages opportunistically throughout its home range, feeding in rocky areas, grass and algal flats and favours areas with a diversity of habitat types (Lipcius *et al*., 1997; Acosta and Robertson, 2003). In Florida, adult *P. argus* were seen at night emerging from dens on a spur-and-groove forereef to forage on the reef flat in sand (10.6 ha^{-1}), *Thalassia* beds (18.1–38.6 ha^{-1} but only 5.4 ha^{-1} for *Syringodium*) and rubble (54.3 ha^{-1}) habitats (Cox *et al*., 1997). Foraging *P. argus* adults were most common in an extensive rubble ridge because this habitat had abundant and accessible prey. Fishing pressure disrupts natural distribution patterns, and Acosta and Robertson (2003) showed that, outside marine reserves (where mean densities across three habitats were 8.2 ha^{-1} compared to 32.1 ha^{-1} inside the reserve), adult *P. argus* were predominantly on the deep lightly fished reef wall. Similarly, on offshore reefs in the Florida Keys, densities were significantly reduced, from initial values of

$\sim$0.003–0.02 m^{-2}, after a 2-d fishing miniseason (Eggleston and Dahlgren, 2001). Densities of *P. argus* across four habitats (reef, gorgonian-dominated pavements, *Thalassia* beds and barren sediments) in the Bahamas were 1.8, 2.9, 1.65 and 0 individuals 3,000 m^{-2} (Smith and van Nierop, 1986).

The presence of appropriate diurnal dens is particularly important for explaining interhabitat and intrahabitat variations of subadult and adult *P. argus* densities. Den availability is linked to habitat topography, which might be expected to be highest in *Montastraea* reef habitats, but few data are available, especially for adults. Dens provide protection from predators, but the relationship is complex and variations are caused by a suite of factors, particularly predation risk and aggregation with conspecifics. The relationship between the presence of dens, predators and conspecifics was examined by Eggleston and Lipcius (1992). These authors demonstrated that when conspecific density was low and predation risk was low, *P. argus* used shelters whose dimensions scaled to their own size (i.e., they were the best ''fit''). In contrast when conspecific density was high and predator density was low, large shelters with the highest potential for gregariousness were used. When conspecific and predator density was high, there was gregarious habitation in smaller shelters. Finally, when conspecific density was low and predation risk was high, smaller shelters were used by individuals. Similarly, Eggleston *et al.* (1997) showed that predator pressure and the size of shelters jointly explained the observed distribution and abundance of *P. argus* on patch reefs. Predator avoidance may also explain, at least in part, the single file chains or ''queues'' of adults autumnally migrating from shallow to deep water (Herrnkind and Cummings, 1964; Kanciruk and Herrnkind, 1978). Marx and Herrnkind (1985) suggest that aggregation may also depend on the local distribution of food. The change of density during aggregation in a hard-bottom (6–8 m depth) ''pathway'' site prior to migration in Bimini was from 2–10 lobsters ha^{-1} to hundreds in the available crevices (Kanciruk and Herrnkind, 1978).

*3.6.2. Habitat functional values (*Panulirus argus*; Figure 1)*

Laurencia in seagrass beds and mangrove channels is commonly a preferred settlement habitat for *P. argus* (juvenile densities 10–642 ha^{-1}), so they are assigned a high functional value. Seagrass banks may also be used by subadults and as a foraging habitat for adults with densities of 5.5–38.6 ha^{-1}. Similarly, mangroves may be important to subadults in some areas (Acosta and Butler, 1997). Shallow hard-bottom areas are important for juveniles in some areas (particularly Florida), but this habitat is not represented in our schematic profile (Figure 1). Patch reefs are used by postalgal animals (10–263 individuals ha^{-1}) and adults (5.5–38.6 individuals ha^{-1}) and are given a high functional value. Adults appear to use a range of hard-bottom habitats (2–15.2 individuals ha^{-1}; there are few data from deeper *Montastraea* reefs), so each is assigned a medium functional value. In an unfished population, mean density of *P. argus* was higher on the escarpment than the forereef (38.6 ha^{-1}; Acosta and Robertson, 2003) and is assigned a high functional value. Sand may have a low functional value as a foraging habitat (Cox *et al*., 1997). Few studies give densities for reef crests and back reefs, but the offshore ontogenetic migration indicates that individuals may use these habitats and they are putatively given low functional values.

3.6.3. Strombus gigas

S. gigas juveniles use nursery habitats that range from shallow sand and coral-rubble reef flats to moderate-density seagrass (Randall, 1964; Davis and Stoner, 1994; Stoner *et al*., 1996b). After ~1 yr, infaunal *S. gigas* emerge from the sediment and feed epibenthically on algae and detritus (Randall, 1964). *S. gigas* nurseries contain important metamorphosis cues for the planktotrophic larvae and laboratory work has shown that the alga *Batophora oerstedii* induces the highest proportion of metamorphosis (Davis and Stoner, 1994). Davis and Stoner (1994) found other cues to be sediment, *Thalassia* blades and detritus, but there was a low response to *Laurencia*. Similarly, in the Bahamas, *Batophora oerstedii* was the dominant alga in nurseries and its abundance provided the best index of habitat quality (Hanisak, 1992). Highest growth rates occurred when *S. gigas* was feeding on *Batophora*, which indicates why nurseries more frequently contain this alga compared to *Laurencia* and seagrass detritus, although epiphytes are the actual metamorphic cue rather than the macrophytes themselves (Davis and Stoner, 1994).

Metamorphic cues appear to vary across the Caribbean region. In the Turks and Caicos Islands, *Laurencia* was among the most effective metamorphosis inducers of farmed larvae, along with the *Thalassia* epiphyte *Foslielalla* sp. and *Batophora* (Boettcher and Targett, 1996). Laboratory work found no metamorphic response to seagrass, but high rates of metamorphosis on a substratum of complex physical and biotic structures such as the calcareous red algae *Neogoniolithon*, *Dasycladus* and the matrix of algae and sediment attached to rock (Stoner *et al*., 1996b). In the Florida Keys, *S. gigas* is commonly found on hard-bottoms because seagrass is long, dense and silty and inhibits juvenile movement (Stoner *et al*., 1996b). Therefore, the presence of epiphytes and appropriate macroalgae is more important in the Florida Keys. Irrespective of the exact metamorphic cue, it is important that juvenile *S. gigas* find a nursery area of high algal productivity to ensure good growth and survival (Stoner, 1989). Indeed *S. gigas* densities in nursery habitats may be limited by food abundance (Stoner, 1989). Davis and Stoner (1994) showed that metamorphosis was higher for *Thalassia* test detritus from nursery grounds compared to test detritus from outside nursery areas because it varies in composition and quality. Stoner *et al.* (1996b) suggest that detritus from nursery areas has a unique bacterial and algal film that leads to higher growth rates of *S. gigas* and that nursery areas have high algal recruitment.

Medium-density seagrass beds are commonly preferred habitats for juvenile *S. gigas* because there is a lower predation risk than sandy areas or sparse seagrass areas (Ray and Stoner, 1995). Mortality rates are also higher in dense seagrass than medium-density seagrass because high seagrass biomass can hamper locomotion and there are often more predators (Ray and Stoner, 1994). Ray and Stoner (1995) concluded that postsettlement mortality is high in all habitats and that predation is the most important mechanism influencing *S. gigas* distribution. *S. gigas* also aggregate to reduce predation pressure and groups of ~100,000 juveniles have been seen (Iversen *et al.*, 1986; Stoner and Ray, 1993; Ray and Stoner, 1994; Stoner and Lally, 1994; Ray-Culp *et al.*, 1999). *S. gigas* may also reduce predation pressure by behavioural patterns such as concentrating in shallow waters (<1 m) and burying (Iversen *et al.*, 1986). Densities of juvenile conch in seagrass beds in the Bahamas were 0–2.0 individuals m^{-2} (Stoner, 1989; Ray and Stoner, 1994, 1995; Stoner *et al.*, 1995, 1996a) but can aggregate at densities of 2.5–295 m^{-2} (Stoner and Lally, 1994). Within a marine reserve in the Turks and Caicos Islands, algal plains were an important habitat for juvenile *S. gigas* (483 ha^{-1}) and densities were greater than seagrass beds (179 ha^{-1}), sand plain (232 ha^{-1}) and gorgonian/sponge plain (21 ha^{-1}) (Béné and Tewfik, 2003). Densities outside the reserve were not significantly lower (331, 497, 85 and 24 ha^{-1}, respectively).

On the Great Bahama Bank, most of the juveniles were found in aggregations in seagrass beds at a water depth between 1.5 and 4.0 m, which constituted only 1.5% of the available area (Stoner *et al.*, 1996a). Such research has important consequences for management because only specific parts of seagrass beds are important nursery areas (Stoner *et al.*, 1995). Only the most persistent aggregations could be predicted on the basis of preferred seagrass biomass, but important nurseries were always located in tidal channels, which supplied clear, oligotrophic water (Stoner *et al.*, 1996a). Nurseries in tidal channels are subject to flushing with oceanic water on every tide, and although this could cause preferable temperatures, a more likely hypothesis was the role of indirect effects such as larval transport and recruitment or the effects on benthic productivity. Therefore, the boundaries of *S. gigas* nursery habitats are set by precise combinations of physical and biological factors, but the exact locations of aggregations shift from year to year (Stoner *et al*., 1996a). In a review of *S. gigas* nursery habitats, Stoner (2003) further stresses the need to combine traditional habitat definitions with the "dynamic features and ecological processes that provide a functional space for subject species."

Adult *S. gigas* tend to prefer deeper water compared to juveniles and are found to at least 70 m, but rarely $>$30 m. Adults ontogenetically migrate from nursery habitats to denser seagrass areas, tidal channels and gorgonian-rich plains and can also be found on gravel and coral rubble (Randall, 1964; Appeldoorn and Rolke, 1996; Stoner *et al*., 1996a). *S. gigas* may also migrate seasonally. In the Turks and Caicos Islands, individuals preferred a *Syringodium* bed parallel to the shore during the summer then shifted offshore, beyond the seagrass beds, to sparse algae and sand habitats during the winter (Hesse, 1979). Densities of juvenile and adult conch in the Turks and Caicos Islands, measured using transect across a series of habitats, was 9.48 100 m^{-2}. Habitat-specific data inside a marine reserve in the Turks and Caicos Islands gave densities of 833, 410, 78 and 3 adults ha^{-1} for algal plains, seagrass beds, sand plain and gorgonian/sponge plain, respectively (Béné and Tewfik, 2003). Fishing significantly reduced densities outside the reserve (86, 24, 28 and 7 ha^{-1}, respectively). In back reefs (1–10 m) in the Florida Keys, adult densities were 13.4–111 ha^{-1} and conch favoured this habitat over adjacent seagrass beds (Glazer and Kidney, 2004). In a survey in a range of habitats from the back reef to shore across Belize, densities of *S. gigas* were 0–45.2 ha^{-1} (hard-bottom habitats), 8.7–46.1 ha^{-1} (seagrass), 8.1–13.3 ha^{-1} (sand) and 11.7–15.8 ha^{-1} (patch reefs) (Appeldoorn and Rolke, 1996).

Although density is thought to generally decrease with increasing depth, deep populations could be sustaining shallow highly exploited fisheries (Stoner and Sandt, 1992). The unfished population described by Stoner and Sandt (1992) occurred at 18 m in the Bahamas, had a relatively constant density and included few juveniles. Density was highest on sandy areas in July as a result of immigration from surrounding winter hard-ground feeding areas and subsequent emigration. The sandy areas may be best for egg laying because sand sticks to the eggs and acts as camouflage and a physical deterrent (Randall, 1964). A preference for a sand habitat by reproducing *S. gigas* adults has also been documented in back reefs in the Florida Keys (Glazer and Kidney, 2004). The close proximity of feeding and reproductive habitats may be an important characteristic of an optimal spawning site in deeper water (Stoner and Sandt, 1992). Mean densities, over 4 yr, for the various habitats were 0.77, 3.62, 3.05 and 0.06 individuals 100 m^{-2} for the reef front, rubble field, mounds and sand transects, respectively (Stoner and Sandt, 1992). Stoner and Ray-Culp (2000) have shown that per capita rates of population growth become negative at low population densities ("Allee effect") in *S. gigas* populations when adults cannot find reproductive mates. Mating in a bare-sand habitat (depth of 10–20 m) in the Bahamas never occurred when density was <56 animals ha^{-1} and spawning never occurred at <48 animals ha^{-1} (range of densities 2–2,793 ha^{-1}, with highest densities inside a marine park).

*3.6.4. Habitat functional values (*Strombus gigas*; Figure 1)*

Assigning functional values to habitats for *S. gigas* densities is complicated by the effects of ontogenetic shifts, marine reserves, juvenile aggregations and the limited number of biotopes studied. However, seagrass beds are a key habitat for both juvenile and adult *S. gigas*, with densities of 0–20,000 ha^{-1} and juvenile aggregations of up to 295 individuals m^{-2} (high functional value). Algal plains are also important for juveniles and adults (Béné and Tewfik, 2003), but this habitat is not represented in our schematic profile (Figure 1). Densities of 0–50 animals (generally adults) ha^{-1} have been documented for patch reefs, back reefs and gorgonian plains, and these habitats are assigned medium functional values. Densities for sand plains vary widely (2–310 ha^{-1}), but they are important sites for reproduction with aggregations up to 2,793 individuals ha^{-1} and so are assigned a high functional value (Stoner and Ray-Culp, 2000). Mangal systems contain some seagrass and sand beds in creeks, so they are assigned a low functional value. Reef crests have received limited attention in the literature, but the turbulence at reef crests limits the presence of coral-rubble and sand, so this habitat might be expected to have a low functional value. *Montastraea* reefs are not explicitly considered in the literature but do tend to contain small areas of sand and coral rubble, so it is assigned a low functional value. *S. gigas* adults are rarely found >30 m, so escarpments appear to have no functional value.

3.7. Calcification and reef growth

In tropical marine ecosystems, biological calcium carbonate production (calcification) is the metabolic process with the largest "end product" and is dominated by contributions from corals, coralline red algae and calcareous green algae (Smith, 1983). Community calcification rates are used to assign functional values to habitats (Figure 1), but because of the limited amount of data, we first briefly review the calcification rates of individual taxa, which can be used to calculate community rates based on their areal cover (Chave *et al.*, 1972; Hubbard *et al.*, 1990). We also review patterns of interior framework building, but functional values are not assigned because of the lack of quantitative data.

3.7.1. Calcification rates of individual taxa

There are a range of calcifying taxa in tropical marine ecosystems including calcareous algae, foraminifera, molluscs, echinoderms and bryozoans, but scleractinians have received the most research attention. Coral calcification and growth rates are not strictly synonymous because the former measures an increase in mass while the latter is generally based on linear extension. Conversion of growth rates to mass of $CaCO_3$ must be adjusted for density and shape of the organism (Stearn *et al*., 1977; Hubbard *et al*., 1990 provide example calculations). However, calcification and growth are grouped together here, as the difference is relatively minor in the context of assessing the spatial pattern of coral calcification across a reef. Overall, depth, light, turbidity and sedimentation rate are the major controls of coral growth and calcification rates, although the slope of the substratum and rates of heterotrophy may also be important (Gladfelter and Monahan, 1977; Foster, 1980; Hubbard and Scaturo, 1985; Tomascik and Sander, 1985). Depth is a particularly important variable because it represents the combined effects of light, water movement and sometimes temperature and salinity (Buddemeier and Kinzie, 1976). The effects of light (depth in combination with turbidity) are important because a coral's metabolism relies on photosynthetic zooxanthellae (e.g., Muller-Parker and D'Elia, 1997), although the mechanistic link between zooxanthellae and photosynthetically enhanced calcification is still unclear and growth rates also vary with coral morphology (Fagerstrom, 1987; Jackson, 1991). The relationship between depth and growth rate is rarely linear, and generally within the upper 10–15 m of a reef, growth is dependent on the species present and other local environmental factors, such as sedimentation. Below 10–15 m, growth rate generally declines dramatically with increasing depth (Buddemeier and Kinzie, 1976). There may be a smaller effect of photoinhibition in very shallow water, so the highest growth rates are often a short distance below the surface (Huston, 1985b).

Many forereef habitats are dominated by the major reef-builder *M. annularis* and the correlation between growth rate and depth has been well documented for this species. For example, in Curaçao, growth was found to be light saturated to a depth of 15 m (8–16 mm yr^{-1}), then decreased rapidly (2–3 mm yr^{-1} at a depth of 30 m) (Bosscher and Meesters, 1993). In St. Croix, Hubbard and Scaturo (1985) showed that *M. annularis* growth rates could be grouped into those $<$12 m (0.7–0.9 cm yr^{-1}) and those $>$18–20 m (0.2 cm yr^{-1}). Hubbard and Scaturo (1985) suggested that the change represented a "light compensation depth"; at all depths shallower than 12 m, maximum growth rates can be sustained and are suboptimal below $\sim$18 m. However, patterns of growth rates with changing light intensities are not consistent between species. Huston (1985b) demonstrated that like *M. annularis*, growth rates decreased with depth (from 1 to 30 m) for *Porites astreoides*, *Colpophyllia natans* and *Siderastrea siderea*, but rates for *Montastraea cavernosa* were highest in the middle of its depth range and did not change with depth for *A. agaricites*. Growth rates for *Diploria labyrinthiformis*, *Colpophyllia natans*, *Montastraea cavernosa*, *P. astreoides*, *S. siderea* and *Stephanocoenia* were 0.15–0.45 cm yr^{-1} in St. Croix (Hubbard and Scaturo, 1985). Also in St. Croix, rates of 3.0–3.5 mm yr^{-1} (*P. astreoides*), 71 mm yr^{-1} (*C. cervicornis*), 59–82 mm yr^{-1} (*A. prolifera*) and 47–99 mm yr^{-1} (*A. palmata*) were reported by Gladfelter *et al*. (1978). Hubbard *et al*. (1990) use growth rates and coral cover data to give gross carbonate production rates by corals in a reef system in St. Croix as being 0–5.78 kg m^{-2} yr^{-1} (mean for entire shelf was 1.13 kg m^{-2} yr^{-1}). Coral $CaCO_3$ production for individual habitats in St. Croix were 0.9, 2.3, 3.8, 0.6 and 0.8 kg m^{-2} yr^{-1} for hardground, shallow reef, coral gardens, sand flat and slope and deep reef, respectively (Sadd, 1984).

Calcifying algae can be divided into three groups (coccolithophores, aragonite depositing and calcite depositing) based on the location, organisation and nature of their deposits (Borowitzka, 1983). Coccolithophores are predominantly midoceanic species, so their contribution to reefal budgets is low. There is great interspecific and intraspecific variation in calcification rates, linked to environmental and physiological conditions during measurement and the techniques used, but calcification rates for the aragonite-depositing green and brown algae are generally higher than those for calcite-depositing coralline reds (Borowitzka, 1983). Crustose (lithothamnioid) coralline algae also have a functional role different from that of green and brown algae. Crustose coralline algae have long been recognised to have an important role in consolidating reef frameworks (Howe, 1912), whereas calcifying species of green and brown algae tend to generate sediment (Hillis-Colinvaux, 1980), a proportion of which is then bound into the reef structure. Red coralline algal biomass is generally highest in the turbulent shallows and lowest at 40 m because of patterns of grazing pressure (e.g., Liddell and Ohlhorst, 1987; Steneck, 1997) but are found on solid substrata intertidally and subtidally to 268 m (Littler and Littler, 1984). Although coralline algae grow more vigorously in the shallows, weight accretion is greater in deeper reef areas because there is a reduced grazing pressure (Bak, 1976). Calcification rates of coralline algae are difficult to measure because of the confounding effects of herbivory, but in St. Croix rates of growth were estimated at ~0.03 mm yr^{-1} leading to gross carbonate production rates of 0.02 kg m^{-2} yr^{-1} (Hubbard *et al*., 1990). Rates were higher (growth 0.9–2.3 mm yr^{-1}) in a further study in St. Croix (Adey and Vassar, 1975) and in Barbados where growth rate was 2 mm yr^{-1}, with a potential calcification rate (if cover was 100%) of 0.167–2.378 kg m^{-2} yr^{-1} and actual productivity (using percentage cover data from the reef) of 0.025–0.95 kg m^{-2} yr^{-1} (Stearn *et al*., 1977).

Calcifying green and brown algae are most common in habitats with light grazing pressure, a pattern that has been significantly altered by overfishing, the mass mortality of *Diadema* and anthropogenic nutrient inputs. The increase of macroalgal biomass on Caribbean reefs has affected the distribution of calcareous plants and they are now found in almost every habitat type. Before the increase of macroalgae, Hillis-Colinvaux (1980) provided a detailed description of *Halimeda* abundances across a Jamaican reef and showed percentage cover to be linked to the availability of hard substrates free of other biota and grazing pressure. In addition, Hillis-Colinvaux (1980) and Littler and Littler (1984) showed that the ability to produce attachment sites allows dense patches of calcifying Chlorophyta, such as *Halimeda*, to grow on protected shallow areas with soft bottoms, often in association with seagrass, and on deeper reef slopes. Calcifying Phaeophyta, such as *Padina*, are common on the reef flat but also subtidally to moderate depths (Littler and Littler, 1984). Rates of calcification for calcareous macroalgae can reach ~2,400 g $CaCO_3$ m^{-2} yr^{-1} in the Bahamas and Panama (Freile *et al*., 1995; Freile and Hillis, 1997).

3.7.2. Community calcification rates

Community calcification rates are highest in shallow (<10 m) areas because calcification and primary productivity are generally positively correlated (Smith and Buddemeier, 1992; Gattuso *et al*., 1999). Within shallow zones, calcification is affected by community composition but is highest for areas of continuous coral, lower for algal pavement and lowest for sand and rubble (Done *et al*., 1996; Gattuso *et al*., 1998). However, for example, calcification in a given habitat decreases with an increasing percentage cover of fleshy algae. From a literature review, Smith and Kinsey (1976) proposed two common calcification rates for shallow reef communities; 4 kg $CaCO_3$ m^{-2} yr^{-1} for seaward areas and 0.8 kg $CaCO_3$ m^{-2} yr^{-1} for protected areas because of variations in water motion. They suggested that the ‘‘standard’’ rates are insensitive to coral versus coralline algal dominance. Smith (1983) suggested that 90–95% of coral reef areas calcifies at the lower rate and 5–10% calcifies at the higher rate and extended the concept by introducing a higher rate of 10 kg $CaCO_3$ m^{-2} yr^{-1} (see also Smith, 1981; Kinsey, 1985). Smith (1983) indicated that 1–2% of reef areas may calcify at the highest rate, while 4–8% and 90–95% calcify at the 4 and 0.8 kg $CaCO_3$ m^{-2} yr^{-1} rates, respectively. Such figures are ‘‘net calcification,’’ measured by decreases in alkalinity, and measure net precipitation minus dissolution, and these hydrochemical methods are restricted to very shallow areas (Vecsei, 2001). Much of the data summarised by Smith and Kinsey (1976) were from Pacific reefs but were proposed as appropriate global standards, although extrapolation to the Caribbean is equivocal and there will be considerable spatiotemporal variation and dependence on environmental conditions. Kinsey (1981) reflects on the comparison between Pacific and Atlantic growth rates and states that differences are more of a function of discrimination of zones for study (finer in the Atlantic) than any fundamental difference in the communities' calcification rates, but functional values in this review are assigned using only Caribbean data. Kinsey (1981) also assessed calcification rates in Jamaica and gives values of 3.5–3.8 kg $CaCO_3$ m^{-2} yr^{-1} for the back reef and 6.1–8.0 kg $CaCO_3$ m^{-2} yr^{-1} on an *A. palmata*–dominated reef crest.

Further data from Caribbean reefs are available but are often calculated by ''biological estimate'' (or ''gross production'' or ''census-based'') techniques. Biological estimates are generated by combining calcified standing crop of each component in a benthic community and its growth or turnover, but this is tedious unless an area is dominated by a few organisms (Chave *et al.*, 1972; Smith, 1983). The methodological difference from the ''net calcification'' values provided by Smith and Kinsey (1976) is important because the biological estimate approach gives higher values of calcification rates. Chave *et al.* (1972) generated data, using hypothetical community assemblages, for shallow sand flats (0.4 kg $CaCO_3$ m^{-2} yr^{-1}), coral mounds on sand (10 kg), algal ridges (9 kg) and complete coral coverage on outer slopes (60 kg). Using actual data on community composition, Stearn *et al.* (1977) provide a value of 15 kg $CaCO_3$ planimetric m^{-2} yr^{-1} (9 kg $CaCO_3$ m^{-2} of reef surface yr^{-1}) on a fringing reef (<10 m) in Barbados (calculated from production of corals and red coralline algae). The rates for a Jamaican forereef terrace (0–20 m) and for a forereef slope (20–60 m) were, respectively, 4.6 kg $CaCO_3$ m^{-2} yr^{-1} and 0.6 kg $CaCO_3$ m^{-2} yr^{-1} (Land, 1979). In St. Croix, calcification rates for five habitats were 1.2, 3.1, 5.0, 0.85 and 1.0 $CaCO_3$ kg $CaCO_3$ m^{-2} yr^{-1} for hardground, shallow reef (depth of 5–8 m), coral gardens, sand flat and slope (6–20 m) and deep reef (20–32 m), respectively (Sadd, 1984). Incorporating more detail on spatial variability and geological history, a reef-wide average (from the beach to a depth of 40 m) for the same site was calculated as 1.21 kg $CaCO_3$ m^{-2} yr^{-1} but up to 5.78 kg $CaCO_3$ m^{-2} yr^{-1} at some survey sites (Hubbard *et al.*, 1990). A rate of $\sim$3.1 kg $CaCO_3$ m^{-2} yr^{-1} was calculated for a forereef (5–10 m) in Curaçao (Bak *et al.*, 1984).

Vecsei (2001) modified the biological estimate approach to deduce regional assessments of forereef carbonate production using averaged coral cover, coral extension and density data. Values for very shallow forereefs with a dense ramose coral (*Acropora*) framework in the Caribbean (mainly for the period 1960–1990) were $\sim$10 kg $CaCO_3$ m^{-2} yr^{-1}. In contrast, shallow biodetrital (low proportion of framework and high rubble and sediment content) forereefs such as in St. Croix produce only $\sim$1.5 kg

$CaCO_3$ m^{-2} yr^{-1}. Furthermore, Vecsei (2001) showed that production rates decrease exponentially with depth. For framework reefs (e.g., Jamaica, Bonaire and Curaçao) values for all community types were 10.1–17.3 kg $CaCO_3$ m^{-2} yr^{-1} at 0–10 m, 4.5–8.1 kg at 10–20 m and 0.8–3.0 kg at 30–40 m. On biodetrital reefs, production drops from 1.5 kg $CaCO_3$ m^{-2} yr^{-1} at 0–20 m to 0.1–0.8 kg at 20–40 m. Vecsei (2004) advanced the concept of regional assessments and gave values, for both framework and biodetrital reefs with explicit treatment of algal production, of 1.6–10.3 (0–10 m), 1.9–4.7 (10–20 m), 0.8–1.0 (20–30 m) and 0.3 kg $CaCO_3$ m^{-2} yr^{-1} (30–40 m), and these values are used in preference to the 2001 data when considering functional values.

Data for calcification rates in soft-sediment habitats are limited, but carbonate shelves have received some attention. Data for the Great Bahama Bank, using equilibrium thermodynamics, showed how rates were 4–5 kg $CaCO_3$ m^{-2} yr^{-1} on the bank margins and $\sim$0 kg $CaCO_3$ m^{-2} yr^{-1} in the shallowest, innermost areas (Demicco and Hardie, 2002). The new "Submersible Habitat for Analysing Reef Quality" (SHARQ), developed by Yates and Halley (2003), is an excellent tool for assessing community calcification (and dissolution) rates in a range of habitats but calculates net rates using hydrochemical methods, which are difficult to compare with the gross rates for reef habitats. Mean net daily calcification in Florida was highest on patch reefs (1.14 g $CaCO_3$ m^{-2}) and lowest in dense seagrass beds (0.25 g $CaCO_3$ m^{-2}). Calcification rates in sparse seagrass beds and on a single sandy area were approximately equivalent (0.44 and 0.41 g $CaCO_3$ m^{-2}, respectively).

3.7.3. Habitat functional values (Figure 1)

Community calcification rates appear highest in reef crests and shallow *Montastraea* reefs, with values generally >5 kg $CaCO_3$ m^{-2} yr^{-1} (high functional values). However, the abundance of *Acropora* has been reduced by white band disease (see Section 5.3) and consequently calcification rates, and the functional value, of reef crests may be lower than values in the published literature. Rates for back reefs and deep *Montastraea* reefs are generally 1–5 kg $CaCO_3$ m^{-2} yr^{-1} and are assigned medium functional values. A single value of 0.4 kg $CaCO_3$ m^{-2} yr^{-1} is available for patch reefs (Yates and Halley, 2003) but was measured using hydrochemical techniques, and we assume gross production rates would be higher (potentially 1–5 kg $CaCO_3$ m^{-2} yr^{-1}) and it is assigned a medium functional value. Rates in sand and escarpment habitats are generally <1 kg $CaCO_3$ m^{-2} yr^{-1} and they are given low functional values. There are few data for gorgonian-dominated habitats, but the abundance of octocorals and fleshy algae and low coral cover indicates that they have a low functional value. Similarly, mangroves and seagrass beds are given a low functional value because of the presence of calcified algae and occasional colonies of *Manicina* and *Porites*. The only published (net) calcification rate for seagrass beds (0.09–0.16 kg $CaCO_3$ m^{-2} yr^{-1}) is consistent with this assessment (Yates and Halley, 2003). Carbonate shelves are also important sites for calcification (Demicco and Hardie, 2002) but are not represented in our schematic profile (Figure 1).

3.7.4. Reef interior framework building

Calcification is a key process of reef growth and is a component of construction, which Fagerstrom (1987) lists as one of five interacting processes of reef development along with binding, sediment deposition and transportation and destruction. The five processes produce a recently dead semiconsolidated reef mass, which is then converted into lithified reef limestone by diagenesis. All of the processes described by Fagerstrom (1987) vary between reef habitats, but the focus in this section is on construction and binding because the spatial variation in sediment transport and deposition and destruction (bioerosion) are reviewed in the next section (Section 3.8). Reef construction in a habitat is not solely dependent on calcification rates because reef development is influenced by the type of framework in a given area, which in turn depends on the net balance of light, wave, sediment and exposure stresses (Chappell, 1980). In addition to calcification rates, reef growth is also affected by antecedent topography, sea-level changes and subsidence, which are likely to be complex and variable across a continental shelf (Davies, 1983; Hubbard, 1997). Davies (1983) also lists turbidity, temperature and water chemistry as affecting Holocene reef growth, but the link between all these variables and reef framework construction at the scale of habitats is poorly understood.

Coring work (e.g., Hubbard, 1997) showed that, at least on certain reefs, the correlation between coral communities and the interior frameworks of reefs is less than previously thought. The majority of cores in some habitats show out-of-place coral debris mixed with loose sediment and other carbonate debris. The abundance of out-of-place coral debris in the interior framework of a habitat is particularly apparent on biodetrital reefs such as those studied by Hubbard *et al.* (1986) in St. Croix. Biodetrital reef frameworks consist mainly of coral rubble tossed onto the shelf by hurricanes. Within a reef, there is evidence of variation in the general pattern of framework retention. Deeper slower accreting reefs may have higher proportions of retention, though still >35%, of "original" corals, than shallower areas (Hubbard, 1997). Furthermore, more exposed reefs have higher proportions of framework retention than sheltered ones, possibly because they have more robust coral growth.

In Jamaica, Perry (1999) examined framework preservation in back reef, forereef, forereef terrace and deep forereef habitats. Back reefs had limited framework development and extensive framework alteration because of grazing and boring ($<5\%$ of *in situ* framework preservation and 95% sediment and rubble). Deeper (30 m) forereefs also had limited framework preservation ($\sim 20\%$) because of high rates of bioerosion, particularly by sponges, and slower calcification rates and increased skeletal densities. On shallower forereefs and terraces (<12 m), $\sim 50\%$ of the relatively abundant and fast-growing corals had been preserved *in situ*. Massive and lobate corals, such as *M. annularis*, are particularly likely to be preserved *in situ*, despite their susceptibility to macroboring (Perry, 1998a). Furthermore, rubble from the many corals broken by storms were rapidly encrusted and cemented within shallower zones (Perry, 1999). Rasser and Riegl (2002) reported that rubble cementation was highest in intertidal and supratidal zones, back reefs, reef-flats and shallow forereef rubble accumulations. Diagenetic cementation is primarily correlated with rapid seawater pumping through the framework leading to precipitation of magnesium calcite and aragonite crystals. The process of cementation is often seen to be particularly important in shallow water sites. Coralline algae, and other organisms, can rigidly bind rubble but appear less important than diagenetic cementation and may be restricted to specific zones, such as shallow forereef environments where coralline algae are abundant. Overall, rubble binding into interior reef frameworks was demonstrated to vary significantly between habitat types. Rubble binding was highest on forereefs with low sloping angles because rubble can accumulate and there are high rates of diagenetic cementation and frequent coralline algal binding. In deeper sites and framework cavities, microbially driven cementation is also important (Camoin *et al*., 1999).

The work of Rasser and Riegl (2002) supports the suggestions of Macintyre (1997) that the importance of coralline algae cover in the buildup of modern reefs is less than previously thought. Sponges may play a role in reef framework consolidation (Goreau and Goreau, 1973) and their abundance varies between habitats. Goreau and Goreau (1973) suggested that in Jamaica, *Millepora* and lithothamnoid algae were important cementers in the exposed surf zone and reef flat, but this was mainly achieved by coralline red algae and the foraminifera *Gypsina* in the forereef. Within taxa, there is further interspecific variation in the pattern of diagenesis. Constantz (1985) showed the species most susceptible to diagenesis are those with the narrowest (e.g., *Acropora*) and most loosely arranged (e.g., *Porites* and *Agaricia*) aragonite fibres. *Montastraea* and *Diploria* are less susceptible, so habitats dominated by *Acropora* may exhibit faster rates of diagenetic cementation than those characterised by *Montastraea*.

3.8. Bioerosion and sediment transport

Calcified organisms and structures on a reef are broken down in part by bioerosion to produce a proportion of the carbonate sediments that fill interstitial framework spaces during reef accretion. Three key processes determining the composition of the internal fabric of a reef are the type and intensity of bioerosion and net rate of sediment transport and settlement (Fagerstrom, 1987; Hubbard, 1997). In St. Croix, Hubbard *et al.* (1990) showed that nearly 55% of the carbonate production on a reef was reduced to sediment by bioerosion each year, and Bruggemann *et al.* (1996) stated that variation in bioerosion rates is as important as calcium carbonate production in shaping the physical and biological features of a reef. However, with increasing degradation of reef communities by anthropogenic impacts, some habitats may be dominated by bioerosion (Done *et al.*, 1996; Glynn, 1997), potentially weakening corals, reducing topographical complexity and assisting asexual fragmentation. This section focuses on carbonate sediment production by bioerosion and the spatial patterns of sediment settlement and movement across a reef seascape. Functional values are presented only for bioerosion because of the lack of habitat-specific quantitative data for the latter. Physical damage also creates carbonate sediment but is a function of wave energy, and these patterns are discussed in Sections 3.1 and 5.1. Mechanical erosion may be negligible other than during heavy storms (Scoffin *et al.*, 1980).

3.8.1. Major bioeroding taxa

There are few habitat-specific data on rates of community bioerosion (incorporating all taxa for a particular habitat), so we provide a brief review of the major bioeroding taxa, as densities and erosion rates can be combined to estimate total $CaCO_3$ destruction (e.g., Scoffin *et al.*, 1980). Many taxa are bioeroders (Risk and MacGeachy, 1978; Glynn, 1997), although research on the spatial distributions and rates and controls of erosion of some taxa is limited. Perry (1998a) provides one of the few comprehensive assessments across a Caribbean reef of invertebrate macroboring communities and the amount of reef framework they remove. Perry (1998a) showed that sponges were the dominant macroborers on forereef sites, whereas sipunculans and polychaetes were only important at back reef, lagoon and shallow forereef sites in Jamaica. Bivalves were important within back reef and lagoon patch reef habitats. Overall, macroboring was highest in the back reef and deep (>20 m) forereef habitats.

Boring siliceous sponges are frequently cited as a significant component of bioerosion (e.g., Scoffin *et al.*, 1980; Perry, 1998a). In Bermuda, Gygi (1975) showed that boring by *Cliona* may have had up to 100 times greater effect than grazing by the parrotfish *Sp. viride*. Indeed, Davies (1983) and Wilkinson (1983) suggest that sponges may be the primary eroders in some reef environments, and their proportional contribution has presumably increased since the mass mortality of *Diadema*. The rate of bioerosion by sponges was 24.9×10^6 g yr^{-1} (although this also includes minor contributions by bivalves, barnacles and worms) for a fringing reef in Barbados (Scoffin *et al.*, 1980), which is converted to 180 g CaCO$_3$ m^{-2} yr^{-1} by Glynn (1997). Further data for sponge bioerosion rates include 256 g^{-3} kg CaCO$_3$ m^{-2} yr^{-1} in Bermuda (Rützler, 1975) and 0.19–3.29 kg CaCO$_3$ m^{-2} yr^{-1} in St. Croix with a correlation to carbonate production (Moore and Shedd, 1977).

The percentage cover of boring sponges varies spatially and in Jamaica ranges between 0 and 32% of the benthos. Sponge cover is negatively correlated with depth, possibly because of the lack of turbulence-induced mechanical damage to hard substrata (Liddell and Ohlhorst, 1987). Bioerosion rates vary, depending on skeletal density, with dense species (e.g., *M. annularis*) more bored, and the percentage of dead skeletal surface available for recruitment by borers (Highsmith *et al.*, 1983). The density of borers may also be promoted by grazers providing suitable substrata, which is a key factor affecting bioerosion by sponges (reviewed by Wilkinson, 1983). Substratum availability, combined with nutrient availability, mechanical stimuli, high light intensity and strong currents in shallow areas (Rützler, 1975), leads to a positive correlation between high rates of coral growth and sponge bioerosion. However, the effects of sponge bioerosion may be more obvious in deeper water because of the lower calcification rates of coral (Wilkinson, 1983; Fagerstrom, 1987). Furthermore, sponge bioerosion may be reduced in areas with very high water velocities. In a comparison of shallow habitats, Holmes (2000) found that *Cliona* abundance in the rubble component of the back reef supported significantly fewer invasions than that of the reef crest and forereef zones of Barbados' fringing reefs. In Barbados, the back reef zone is a zone of heavy wave action (Lewis, 1960) and the scour and high sedimentation possibly lead to an inhospitable environment for sponges, which require considerable amounts of energy to clear blocked canals (Reiswig, 1971).

In addition to boring species, a major component of bioerosion in most habitats is grazing by herbivorous fishes and sea urchins (Bruggemann *et al.*, 1996). Consequently, bioerosion varies significantly across a reef because the density of herbivores decreases with increasing depth. For example, the rate of bioerosion by herbivorous fishes is highest in the shallows and decreases with depth (Ogden, 1977; Bruggemann *et al.*, 1996). Since the patterns of density of key bioeroders, namely parrotfishes and the urchin *D. antillarum*, are documented in detail elsewhere (Section 3.4), they are not repeated here. Generally, the erosion of calcium carbonate and reworking of sand by *Diadema* during grazing on algae and corals is much higher than that attributable to fishes (reviewed by Bak, 1994) and even since its mass mortality, *Diadema* is still a significant source of bioerosion on shallow Jamaican forereefs (Perry, 1999). Before *Diadema* mortality, Hunter (1977) calculated that *Diadema* produced 9.7 kg carbonate m^{-2} yr^{-1} and was probably the major sediment producer in Barbados. Comparative figures for fishes and boring sponges were 0.1–0.2 kg m^{-2} yr^{-1} and 0.5–1 kg m^{-2} yr^{-1}, respectively. Also in Barbados, Scoffin *et al*. (1980) calculated rates of 0.4×10^6 g $CaCO^3$ yr^{-1} for *Sp. viride* and 97.5×10^6 g yr^{-1} for *Diadema*, with the latter converted to 5.3 kg $CaCO_3$ m^{-2} yr^{-1} by Glynn (1997). In St. Croix, Ogden (1977) showed that *Diadema* generated 4.6 kg m^{-2} yr^{-1} and *Echinometra lucunter* produced 3.9 kg m^{-2} yr^{-1} compared to 0.49 kg m^{-2} yr^{-1} for the parrotfish *Scarus iserti* in Panama. Hubbard *et al.* (1990) showed that bioerosion in St. Croix was primarily by sea urchins (0.17 kg m^{-2} yr^{-1}). The high rates of bioerosion by urchins are in part because *Diadema*'s grazing rate is much higher than that of parrotfishes (Scoffin *et al*., 1980).

Herbivorous fishes, particularly parrotfishes, may be less significant bioeroders than *Diadema*, although postmortality data are scarce, but they are wider ranging and a geologically significant agent in the transformation of reefs into sediment (Gygi, 1975; Ogden, 1977). For example, parrotfishes have been estimated to reach a summer maximum of $>150{,}000$ bites m^{-2} d^{-1} in the Caribbean (Carpenter, 1986); this is mainly from dead coral areas since living corals are rarely grazed (Scoffin *et al*., 1980; Bruggemann *et al*., 1996; Hixon, 1997). On Jamaican forereefs, grazing rates of all fish species were 800 bites m^{-2} h^{-1} (6–8 m, dominated by *Scarus iserti*) and 121 bites m^{-2} h^{-1} (16–18 m, dominated by *Sparisoma atomarium*), which increased at the shallower site after *Diadema* mortality (Morrison, 1988). Bioerosion rates of parrotfishes, using a range of techniques, have been estimated at 7.62, 2.40, 1.43 and 0.69 kg m^{-2} yr^{-1} (*Scarus vetula* and *Sp. viride* only) on a shallow reef, gorgonian zone, dropoff and reef slope in Bonaire (Bruggemann *et al*., 1996), 0.02 kg m^{-2} yr^{-1} in St. Croix (Hubbard *et al*., 1990), 0.11 kg m^{-2} yr^{-1} in Bermuda (Bardach, 1961), 40–168 g m^{-2} yr^{-1} in Barbados (Frydl and Stearn, 1978) and 174 kg ha^{-1} per summer month in Bermuda (Gygi, 1975). Grazing also alters the microtopography of the coral substratum and may determine the success of settlement of internal bioeroders (Sammarco *et al*., 1986) because any condition that causes coral tissue mortality increases the probability of invasion by borers (Glynn, 1997). Damselfishes further influence external bioerosion by reducing grazing pressure (Section 3.4.4) and may influence internal bioerosion by affecting the population dynamics of the boring cryptofaunal community (Sammarco *et al*., 1986).

Microborers (e.g., cyanobacteria, chlorophytes, rhodophytes and fungi) are a further important component of the bioeroding community and there are well-established interhabitat distribution patterns, although actual habitat-specific rates of bioerosion are scarce. Generally the abundances of microborers are linked to light intensities as many are photosynthetic. In Belize, May *et al.* (1982) documented two endolithic microorganisms assemblages in mounted carbonate fragments along a reef transect; the upper photic zone ($<$12 m) was dominated by cyanophytes and chlorophytes and the lower photic zone was characterised by rhodophytes. There was some evidence that the unidentified subsurface microborers in the shallow lagoon were fungi and bacteria. There were no subsurface microborers in the forereef sand zone, indicating that endoliths require organic nutrient sources such as are available in lagoonal seagrass beds. Perry (1998b) also showed that in Jamaican sediments, two distinct microboring communities were associated with the transition from upper to lower photic zone. In water shallower than 18 m, the sediments were dominated by cyanobacteria and chlorophytes, but deeper than 18 m, rhodophytes and fungi were most abundant. In more turbid water with greater rates of light attenuation, the community shift may occur at 5–10 m (Perry and Macdonald, 2002). The highest infestation of carbonate grains by microborers was in low-energy back reef habitats (Perry, 1998b). Vogel *et al.* (2000) measured microbial bioerosion rates at a shallow leeward site in the Bahamas as being up to 520 g m^{-2} yr^{-1}. The bioerosion rate declined with depth and was only 1–2 g m^{-2} yr^{-1} at 275 m.

3.8.2. *Community bioerosion rates*

Estimates of community bioerosion rates are scarce, with the majority of research focusing on specific taxa or characterising bioeroding community composition. The gross $CaCO_3$ destruction for a shallow ($<$10 m) fringing reef in Barbados was estimated as 123×10^6 g yr^{-1} (Scoffin *et al.*, 1980), and bioerosion across a fringing reef in St. Croix, from the beach to a depth of 40 m, was calculated as 0.65 kg $CaCO_3$ m^{-2} yr^{-1} (Hubbard *et al.*, 1990). Furthermore, *Diadema* mortality affected both coral cover and bioerosion, and Bak *et al.* (1984) concluded that postmortality carbonate dynamics had been significantly altered in Curaçao. Before mass mortality, there was a slight negative carbonate budget (production of $\sim$3.1 kg $CaCO_3$ m^{-2} yr^{-1} $<$ bioerosion $\sim$3.3 kg $CaCO_3$ m^{-2} yr^{-1}) on shallow forereefs (5–10 m), but changes in *Diadema* abundance and the consequent reduction of bioerosion (to $\sim$0.4 kg $CaCO_3$ m^{-2} yr^{-1}) meant there could be a net carbonate accumulation.

3.8.3. *Habitat functional values (Figure 1)*

Habitat-specific community bioerosion rates are limited to shallow fringing reefs and appear to range from $\sim$0.4 to 3.3 kg $CaCO_3$ m^{-2} yr^{-1}, although higher rates have been published for individual taxa alone (e.g., Hunter, 1977). Therefore, functional values are assigned here using the densities of *Diadema* and parrotfishes (Section 3.4) and known distributions of boring sponges. Densities of *Diadema* have been reduced significantly by mass mortality in the 1980s (Lessios, 1988; and Section 3.4.5, earlier in this chapter), but there are few quantitative data on changes to bioerosion rates or compensatory changes by other taxa so the putative functional values assigned here refer to reefs with premortality densities of urchins. Mangroves, seagrass beds and sand areas clearly do not have a carbonate structure and so have no functional value for bioerosion. Although there is significant variation, rates of bioerosion by *Diadema* have generally been reported as higher than those of fishes (0.17–9.7 vs 0.02–7.62 kg $CaCO_3$ m^{-2} yr^{-1}, respectively). Patch reefs, reef crests and shallow *Montastraea* reefs had the highest densities of *Diadema*, high or medium densities of *Sp. viride* and the highest percentage cover of boring sponges (e.g., Liddell and Ohlhorst, 1987) and so are assigned high functional values. Back reefs had medium densities of *Diadema* but have high densities of *Sp. viride* and the highest bioerosion by invertebrates (Perry, 1998a) and so are also assigned a high functional value. Gorgonian-dominated forereef habitats and deep *Montastraea* reefs have low or medium densities of *Diadema* and *Sp. viride* and medium or high percentage cover of boring sponges and are given medium functional values. *Diadema*, *Sp. viride* and boring sponges either have low densities or are absent on escarpments, and this habitat is assigned a low functional value.

3.8.4. Sediment transport

The reef crest and lagoon-reef flats are the main sources of local sediment production within a reef (Fagerstrom, 1987). Reef crests are characterised by a high density of rapidly growing corals and bioeroders and the lagoon-reef flats support abundant calcified algae with fast turnover rates. However, reef sediments are moved between habitats by (1) wind-driven shallow water waves and currents that move from the open ocean to the reef flat and lagoon; (2) tide-driven currents moving across the reef in both directions; and (3) gravity-driven movements to, for example, shallow depressions and deep reef slopes. Sediment transport processes are supplemented by biologically induced transport, but this is less important than physical processes (Sadd, 1984). However, burrowing and bioturbation by the infauna of flat and lagoon communities can be important in resuspending sediments in areas where currents are too weak to resuspend them but are strong enough to move them (Fagerstrom, 1987). An understanding of sediment transport is vital for understanding reef growth; at some sites sediment can constitute ~40% of a reef's interior, which is more than that of recognisable corals

(Hubbard *et al*., 1990). Sediment, particularly on reefs, can be constantly reworked. Scoffin *et al*. (1980) showed that 17% of the weight of coral skeletal carbonates was incorporated back into a Barbados reef and may later be reworked by bioerosion.

As discussed in Section 3.1, the reef crest plays a vital role in energy dissipation and, along with being a significant source of sediment, is a critical demarcation between the two main directions of sediment transport. Sediment moves from the reef crest to the reef flat or by gravity from the crest down the seaward slope. Wave-driven currents continuously flow onshore over reef crests and have the greatest velocity at low tide when wave breaking is at its most intense. Reef crest currents provide a mechanism for moving water and sediment from the forereef shelf into back reef lagoon (Suhayda and Roberts, 1977). Similarly, Lugo-Fernández *et al.* (1994) highlighted that reef-produced sediment (i.e., mainly from shallow areas) was transported primarily into back reef lagoons. Turbulence causes grain size to be largest at the reef crest and decrease with decreasing turbulence towards the deeper forereef (Gischler, 1994). Although the reef crest is a zone of high calcification rates, the topography and turbulence make it effectively ‘‘self-cleaning’’ with little or no accumulation of fine calcareous sediments, which are transported to the lagoon and deep reef slope (Goreau and Goreau, 1973). Gischler (1994) showed that on Belizean atolls, back reefs and lagoons had more fine-grained sediment than forereefs (more fragments of coral, coralline algae and *Halimeda*). Molluscs, and consequently mollusc fragments, are more abundant in back reefs than forereef habitats.

Seaward of the reef crest, some calcareous detritus is exported from shallower zones into deeper water under the impetus of currents induced by gravity waves. Gravity-induced movement generally increases with increasing slope angle and is influenced by reef topography. For example, the grooves of spur-and-groove formations act as sediment ‘‘chutes’’ (Goreau and Goreau, 1973). In Jamaica, movement caused by gravity results in a sand-covered slope starting at 30–35 m with sand from shallower zones and sedimentary fans with apices at forereef canyons (Goreau and Goreau, 1973). On the Belizean atolls, the constant transport of sediment over the brow of the reef and down the reef walls has led to a distinct increase in coarse *Halimeda* fragments in sediments on the ledges of the wall and finer sediment in deeper areas (Gischler, 1994).

Except during storms, gravity-induced sediment movement down forereef slopes is relatively limited (Sadd, 1984). During winter storms, a significant seaward movement of sediment occurs because of wave-generated oscillatory currents (Scoffin *et al*., 1980; Sadd, 1984; Macintyre *et al*., 1987). Sand channels are important ‘‘corridors’’ of sediment transport during both storm and nonstorm conditions (e.g., Hubbard *et al*., 1990). Movement of sediments during storms has been studied in detail on a narrow (300-m) shelf in a semiprotected bay in St. Croix. Sadd (1984) showed that sediment accumulates on the shelf for most of the year and then is moved seaward during winter storms across a sandy forereef terrace and through sand-filled channels at the shelf edge. Sediments are not transported under nonstorm conditions because an algal mat binds the upper layer of grains in sediment-rich habitats. Currents generated during winter storms exceed a critical energy threshold that destroys the algal mat and facilitates sediment movement. Storm events are vital because calculations indicate that sediment transport processes occurring under nonstorm conditions could not remove all the sediment produced by reef organisms. Hurricanes and storms stop the reef "drowning" in its own sediment (Sadd, 1984). Macintyre *et al.* (1987) suggest that the differential transport by high bottom-water velocities during storm periods affect the size distribution of sediments in Belize. Finer sediments are further away from the reef crest and this is an important factor leading to the zonation of five back reef zones. Lugo-Fernández *et al.* (1994) showed that changes to the amount of exposed sediment and the size of seagrass beds in Puerto Rico were a product of sediment transport by hurricane-generated waves. Hubbard (1992) assessed the importance of a hurricane for moving sediments and showed that at least 2 million kg of sand were removed from a reef in St. Croix during the event. Sediment transport rates were 11 orders of magnitude higher during the hurricane than those during calm conditions.

Sediment deposition is a function of the dissipation of wave energy by baffling and then trapping and stabilisation (Fagerstrom, 1987). For example, habitats such as spurs and grooves or seagrass can act as a baffle leading to sediment deposition (Fagerstrom, 1987), and at a smaller scale, turf algae trap sediment (e.g., Birkeland, 1977). Patterns of sediment deposition on some reef flats cause a concentric zonal arrangement of grain size linked to turbulence, and similar sediment zonations are present across whole reef complexes (Fagerstrom, 1987). Similarly, in the Caymans, Suhayda and Roberts (1977) showed that the sediment distribution in a lagoon reflected current patterns and wave characteristics at the shore. Scoffin *et al.* (1980) showed that compositional variations in sediment across a fringing reef in Barbados were highly irregular and did not reflect the ecological zonation of the reef. Gischler (1994) showed on Belizean atolls that no reef zones could be distinguished from their sediments alone.

3.9. Habitat recovery

Hatcher (1997a) lists maintenance of biodiversity as a major ecosystem process of coral reefs. Measures of this process occur at a range of spatial and temporal scales and include ecosystem speciation and extinction, community succession and response and recovery from disturbance and interorganism competition. Detailed long-term studies of Caribbean habitat recovery are surprisingly scarce, at least partly because of the stochastic nature of disturbances and the lack of funding for long-term monitoring. There is even less information on spatial variation in recovery rates of different habitat types under different disturbance regimens. Setting recovery in the context of specific disturbance regimens is important because each type of disturbance has different effects. For example, temperature, sedimentation, pollutants and predation cause organism mortality, but reef structure and topography are not altered significantly. Storms, blasting and dredging cause both mortality and dramatic changes of reef topography (Smith, 1988). Furthermore, it is clear that recovery rates from disturbances are far from predictable because of factors such as synergistic effects of different disturbance types (Pearson, 1981; Hughes and Connell, 1999). In St. Croix, the competitive ability of *A. palmata* had been reduced by white band disease; thus, *D. strigosa* was more abundant than normal. The shift in community structure led to more destruction (loss of coral cover) on a shallow forereef during a hurricane because *A. palmata* is better adapted to recovery from hurricanes by the reestablishment of living fragments (Bythell *et al.*, 1993). Pearson (1981) reviewed early work on reef recovery, but few data were available. More recent monitoring programmes have provided some empirical insights into habitat recovery. Dustan and Halas (1987) reported increasing coral cover in a shallow (0–7 m) reef zone in Florida and decreases in deeper forereefs (10–22 m). The changes in Florida were caused by *A. agaricites*, *Helioseris cucullata*, *Favia fragum* and *P. porites* colonising the shallows, possibly because of physical damage to the dominant *A. palmata*.

Data on reef recovery have been generated by monitoring reef communities following hurricanes. Available data show how the suite of spatial factors affecting reef damage and fragment survival contribute to widely variable rates of reef recovery. Recovery at small scales can be relatively rapid because of coral growth and regeneration (Steneck, 1994). Indeed *A. palmata* is adapted to life in high-energy environments with fast growth rates and its main form of propagation being by colony fragmentation, which enables it to rapidly repopulate areas disturbed by intense physical disturbances (Highsmith *et al.*, 1980; Highsmith, 1982). However, massive, encrusting and foliaceous corals may become more abundant on reefs frequently exposed to higher wave energies than *A. cervicornis* can withstand because, if there is almost total mortality, the latter has slow rates of sexual recruitment (Woodley *et al.*, 1981). Furthermore, simultaneous hurricane and bleaching events can reduce coral recruit densities to ~20% of predisturbance levels (Mumby, 1999a). Variations in the reduction of recruit densities may have been caused by protective microhabitats or the proximity of habitats to reef cuts, which may aid the dissipation of storm surge.

Given the timeframes necessary for studying reef recovery, modelling approaches represent an attractive method to assess the putative effects of different disturbance regimens. Simulations by Hughes and Tanner (2000) based on data from Jamaican reefs provided an example of how species-specific data can be used in modelling reef recovery. Hughes and Tanner (2000) showed that for three species (*M. annularis*, *A. agaricites* and *Leptoseris cucullata*), the levels of larval recruitment required to maintain populations at relatively "natural" (1977) levels increased significantly with time, but actual recruitment rate declined. Furthermore, the simulations showed that *M. annularis* could survive long periods with minimal larval input (because of its life history traits), but recruitment failure was much more important to *A. agaricites* and *L. cucullata*. The simulations indicate that *M. annularis*, and by extension *Montastraea*-dominated forereefs, will recover more slowly than other species because of the species' slow rates of recruitment and growth.

The remainder of this section is dedicated to variations in two key factors driving the recovery of coral populations: coral reproduction and recruitment. The growth of corals following recruitment has been addressed in Section 3.7. We have focused on coral reproduction and recruitment, as opposed to other components of the benthic community, because of the importance of corals in many reef processes and the fact that corals have received the most research effort. Habitat-specific functional values are only assigned for coral recruitment because there are insufficient data for coral reproduction.

3.9.1. Coral reproduction

Coral reproduction has been reviewed by Fadlallah (1983), Szmant (1986), Richmond and Hunter (1990), Harrison and Wallace (1990) and Richmond (1997). Within the body of literature on coral reproduction, there are few empirical data on how, or if, reproductive strategies and success vary across the seascape. Theoretically, it is possible to assess the reproductive potential of a given habitat based on the species present, their relative abundances and age structure (sexual maturity) and the ratio of brooders to broadcasters (Endean, 1976). However, it is conceivable that factors that vary between habitats might influence a given species' reproductive success such as inter-habitat and intrahabitat competition, depth and water movement and these are poorly understood.

Szmant (1986) suggested that species in shallow disturbed habitats with much spatial rearrangement must withstand disturbance or rapidly recolonise by having high rates of local recruitment, resistant skeletons or a high rate of survival of fragments. Szmant (1986) concluded that iteroparous brooding is an optimal strategy in shallow water because it leads to high local settlement and is often used by species with a small adult size (i.e., have high adult mortality). The principles outlined by Szmant (1986) are well demonstrated by *Acropora* species, which are generally limited to shallow areas and largely depend on asexual reproduction caused by wave-induced fragmentation (Highsmith, 1982), along with some sexual recruitment. Johnson (1992) showed that *Manicina areolata*, commonly associated with seagrass and mangroves, is self-seeding and has life history characteristics suitable for life in a patchy chronically disturbed environment. *M. areolata* is a brooding species and is not reproductive until large enough to escape the high probability of mortality associated with small size. The restricted dispersal allows dense populations of *M. areolata* to develop in patchy but nutrient-rich environments such as reef flats. Furthermore, brooding species in shallow habitats may have different reproductive traits compared to those in deeper water. Van Moorsel (1983) demonstrated that differences between the reproductive strategies of two brooding *Agaricia* species were explained by the predictability of their preferred habitats. *Agaricia humilis*, which is found mainly in relatively disturbed shallow reef flats and dropoff zones (5–12 m), had an opportunistic reproductive strategy involving planulation throughout year, smaller maximum size, larger planulae production per unit of living tissue and smaller planulae volume. In contrast, *A. agaricites* on the less-disturbed deeper reef slope (10–30 m) shed planulae in spring and summer and had the opposite traits to *A. humilis*.

3.9.2. Coral recruitment

Following coral larval production and their supply to a reefal area, recruitment to the reef is dependent on four major factors: (1) the phototactic behaviour of planulae; (2) the nature of the surface; (3) reproductive seasonality; and (4) the survival of spat under pressures of predation and competition (Baggett and Bright, 1985). The second and fourth factors are particularly influenced by habitat type and hence are within the scope of this review. The nature of the reef surface is especially important for larval settlement and the presence of crustose coralline algae are important metamorphosis cues. In laboratory experiments, Morse *et al.* (1988) showed that *Agaricia tenuifolia*, *humilis* and *danai* were induced to metamorphose by particular crustose coralline algal species, and in the field, this cue did not appear to vary between forereef, reef crest and back reef habitats in Bonaire. In Jamaica, *A. agaricites* settled and had the highest levels of metamorphosis on the coralline alga *Paragoniolithon typica*, with the coralline *Spongites* also an important cue, but little metamorphosis on bare rubble and none on coral fragments and filamentous algae (Carlon and Olson, 1993). Planulae generally do not settle on sediment and those that do have poor survival rates (Richmond, 1997). The presence of coralline algae on a consolidated substrate varies considerably between habitat types (see Section 3.3).

Habitat rugosity is a key factor influencing the spatial pattern of coral recruitment. The requisite rugosity may be at a very small scale and Gunkel (1997) showed higher recruitment to rough surfaces in the Bahamas and proposed that rough surfaces had a greater development of a bioorganic film compared to smoother surfaces. In contrast, Lewis (1974) showed *Favia fragum* had no preference for rough or smooth surfaces. The role of rugosity has generally been investigated at a larger scale than surface roughness, with many researchers reporting differential recruitment rates between vertical and horizontal surfaces. Overall, it seems that coral recruitment in shallow water is most frequent on downward facing surfaces or crevices to avoid high grazing pressure and sedimentation. In deeper water, recruitment is highest on upper (horizontal) surfaces to compensate for reduced light levels (Bak and Engel, 1979; Rogers *et al.*, 1984; Carleton and Sammarco, 1987). It has been hypothesised that recruitment probabilities are higher in microhabitats protected from surge or rapid water movement (Baggett and Bright, 1985). Furthermore, the general pattern of settlement preferences may not be uniform for all species in shallow and deep water; thus, *A. tenuifolia* prefers shaded areas, but *A. humilis* favours direct light (Morse *et al.*, 1988). However, the relative roles of coral larval settlement selection or postsettlement mortality in determining observed patterns of coral recruitment rates remain unclear. A high density of juvenile corals in a particular habitat may be caused by preferential settlement, low mortality rates or both. Examining the roles of settlement selection and postsettlement mortality is particularly difficult for corals, which broadcast their gametes, such as *Montastraea*, because of the rarity of juveniles found on a reef (reviewed by Mumby, 1999b).

Quantitative data on recruitment rates in a variety of habitats has been conducted using both artificial (e.g., settlement tiles) and natural substrata. The link between densities of recruits on settlement plates and those found on reefs is equivocal, so here we assign functional values using surveys of natural substrata alone. On canyon walls at 9, 18, 27 and 37 m in St. Croix, there was a general decrease in the number of juveniles and species with increasing depth (Rogers *et al.*, 1984). Rogers *et al.* (1984) showed that recruits were most abundant at 9 m and 18 m (13–33 and 28–42 juveniles m^{-2}, respectively) with densities decreasing to 8–18 m^{-2} (27 m) and 3–5 m^{-2} (37 m). Also in the U.S. Virgin Islands, the median density of juvenile corals in a shallow (<6 m) boulder field with low coral cover was 0–8 0.25 m^{-2} (Edmunds, 2000, 2004). At a deeper forereef site in the U.S. Virgin Islands, along with forereef sites in Florida and Belize, densities were 1.8–44 juveniles m^{-2} with highest densities in the *Agaricia*-dominated Belize site and densities on *Montastraea* reefs were ~6 m^{-2} (Edmunds *et al*., 1998). In high-relief spur and groove, relict reef flat and relict spur-and-groove habitats across a reef profile from 4 to 18 m in Florida, the number of species as juveniles was significantly greater in deeper (>10 m) relict spur-and-groove sites (2.81 juveniles m^{-2}) compared to the other two zones (1.61–1.65 m^{-2}) (Chiappone and Sullivan, 1996). The density of juveniles of spawning species (*M. annularis*, *M. cavernosa* and *Siderastrea siderea*) increased with increasing depth with a fivefold increase in the density of *M. cavernosa* from a shallow high-relief spur-and-groove habitat to a deeper relict spur-and-groove zone. Conversely the brooding *A. agaricites* decreased fourfold in abundance between the same habitats. On patch reefs and offshore bank reefs in Florida, juvenile densities using two methods were ~0.75–24.0 m^{-2} and ~0.75–10.0 m^{-2}, respectively (Miller *et al*., 2000). Further data from macroalgal-dominated reefs in the Florida Keys gave relatively constant densities of 1.9–2.1 corals 0.25 m^{-2} at four depth intervals from 12 to 29 m (Edmunds *et al*., 2004). At a shallow (5–8 m) control reef in Bermuda, Smith (1992) documented densities on the natural substratum of 18.0–21.1 recruits m^{-2}. Recruit density on an 8–10 m *Montastraea* reef in Belize was ~11–14.5 m^{-2}, which decreased to ~2.5 m^{-2} after a bleaching event and hurricane (Mumby, 1999a). At a series of spur-and-groove forereef sites in Mexico (~10 m depth), densities varied from 1.0 to 6.4 juveniles m^{-2} (Ruiz-Zárate and Arias-González, 2004). In Curaçao, densities of juvenile corals were 16.8 m^{-2} (shallow terrace, 3–9 m), 12.9 m^{-2} (dropoff, 9–17 m), 13.7 m^{-2} (upper slope, 17–26 m) and 17.9 m^{-2} (lower slope, 26–37 m) (Bak and Engel, 1979). Mean recruitment of *Manicina areolata* to a series of *Thalassia testudinum*–dominated carbonate reef flats in Panama was 1.62 m^{-2} (Johnson, 1992).

3.9.3. Habitat functional values (Figure 1)

Data on recruitment density to natural substrata are scarce and generally restricted to forereef habitats. Published densities for patch reefs, *Montastraea* reefs and escarpments range from 0.75–21.1 corals m^{-2} but are generally toward the higher end of this range and are assigned high functional values. Turbulent back reefs and reef crests and gorgonian-dominated forereef habitats are likely to have lower densities of recruits and are assigned putative medium functional values in the absence of quantitative data. Seagrass beds and mangrove stands are assigned low functional values as some recruitment is required to maintain the occasional colonies of hardy genera such as *Manicina*, *Porites* and *Siderastrea*. Forereef sand beds have no coral cover (poor recruitment to soft sediments; Richmond, 1997) and have no functional value.

3.10. Community biodiversity

Although maintenance of biodiversity is a major ecosystem process of coral reefs (Hatcher, 1997a), arguably the actual number of species or diversity in a habitat is a *property* of each community rather than a *functional value*. However, the biodiversity of Caribbean reef habitats is reviewed here because of the importance of this property. Biodiversity, along with conservation of fish stocks, is frequently cited as a key reason for establishing marine reserves (e.g., Roberts and Hawkins, 2000). Furthermore, research interest in the correlation between biodiversity and ecosystem functioning is expanding but is yet poorly understood in marine systems (Done *et al*., 1996; Loreau *et al*., 2002). It is likely, therefore, that researchers would wish to generate maps of biodiversity from standard habitat maps along with maps of functional values.

Despite a long history of describing reef zonation patterns (e.g., Goreau, 1959), the published literature describing the full diversity of a particular taxon across a range of habitat types is limited. Typically, descriptive papers list only the characteristic species for each habitat type documented or cover only part of a full shoreline-escarpment transect. For many taxa, inventories of species richness and diversity are limited by current taxonomic knowledge (Mikkelsen and Cracraft, 2001). Scleractinian corals are perhaps the best known and studied taxon, so variations in their diversity between habitats are reviewed here.

3.10.1. Scleractinian diversity

Scleractinians have well-established requirements of, for example, available space on a hard substratum for settlement (and possibly the presence of appropriate cues), limited sedimentation and some water movement to transport food and remove metabolic wastes (e.g., Sheppard, 1982; Morse *et al*., 1988; Maida *et al*., 1994; Sebens, 1997). Clearly the conditions within lagoons and mangrove stands are unsuitable for most coral species and these habitats have low scleractinian diversity. Only hardy species such as *Manicina areolata* and *Siderastrea radians* can survive in seagrass beds (e.g., Johnson, 1992).

The intermediate disturbance hypothesis (Connell, 1978) has frequently been invoked to explain the patterns of scleractinian diversity across hard-bottom habitats. This hypothesis posits that intermediate disturbance intensities (frequency and magnitude) may maintain benthic species diversity by reducing the abundance of competitive dominants, which may occur under low disturbance conditions. Similarly, high disturbance conditions limit the number of species that can become established compared to intermediate disturbance intensities. Across coral reefs, the effects of disturbance by hurricanes and wave action generally decrease with increasing water depth. However, the relationship between disturbance and diversity is confounded by a range of factors, particularly decreasing light intensity. Although it might be expected that diversity should be low in shallow (disturbed zones), high at intermediate depths and low in deeper zones (competitive exclusion), reduced light intensity (and perhaps other variables) appears to limit competitive exclusion by slowing growth rates (Huston, 1985c). Therefore, the intermediate disturbance hypothesis may only be applicable across relatively shallow reef zones subject to varying disturbance regimens (Rogers, 1993b). Such a pattern across a single habitat (shallow spur-and-groove zone) has been shown by Aronson and Precht (1995) in Belize. At a landscape scale (>10 m^2), coral diversity was highest (Shannon-Wiener diversity $\sim$1.2 compared to a minimum of $\sim$0.2) at intermediate levels of disturbance, as measured by substratum topographical complexity. Disturbance reduced the percentage cover of the competitive dominant *A. tenuifolia* (Aronson and Precht, 1995).

Jamaican reefs, particularly those close to Discovery Bay, are some of the best studied in the Caribbean and provide data on patterns of scleractinian diversity across whole reefs. Huston (1985a) provides data showing that coral diversity was relatively low at the reef crest and increased with increasing depth to a maximum between 15 and 30 m. Shannon–Wiener diversity values were 0.01 (reef crest), 0.75–1.18 (5 m), 1.57–1.68 (10 m), 1.65–2.12 (15 m), 1.54–2.16 (20 m) and 1.26–1.81 (30 m). As predicted, these data support the intermediate disturbance hypothesis at shallow depths but suggest that increasing diversity with increasing depth is caused by limits to competitive dominance. Liddell *et al.* (1984) provided further data from Discovery Bay at depths below the maximum limit of the study by Huston (1985a). Liddell *et al.* (1984) showed that coral diversity, using the Shannon–Wiener index, increased from 15 m (1.87) to 22 m (2.12) and then decreased at 30 m (1.54), and minimum values were found at 56 m (1.49) on the unstable steeply sloping escarpment. Surveys on the same reefs following *Diadema* mortality and hurricane disturbance document the same patterns of coral diversity, despite significant changes to community structure (Andres and Witman, 1995).

Data on interhabitat coral diversity patterns, all using the Shannon–Wiener index, are also available from other reef systems. Sullivan *et al.* (1994b) reported no discernible trends between diversity and evenness indices for linear patch reef (diversity 2.09), transitional reef (2.19) and high- and low-relief spur-and-groove zones (2.17) in the Turks and Caicos Islands. Mean diversity values for a reef in Florida (taken in 1975 and again in 1982) were 0.66–0.68 (reef terrace), 0.48–0.52 (gorgonian zone), 0.46–0.47 (ridge/trough zone), 0.4–0.5 (*A. palmata* zone) and 0.35–0.36 (reef flat)

(Dustan and Halas, 1987). Further assessments of diversity for sponge/octocoral habitats in Florida were 0.49–1.36 (Sullivan and Chiappone, 1993). Work in Mexico showed that the highest coral diversity was on the forereef (1.78 at 5 m; 2.03 at 10 m; 1.66 at 15 m; 1.72 at 20 m; 1.76 at 25 m) compared to the breaker (reef crest, 1.40) and rear (back reef, 1.62) zones (Jordan *et al.*, 1981). Diversity on a *Montastraea* reef (10.7–12.7 m) in St. John before and after Hurricane Hugo in 1989 was 1.94–2.13 (Rogers *et al.*, 1991) and 1.44–1.81 before and after Hurricane David (1979) in St. Thomas (Rogers *et al.*, 1983). Mean diversity for three types of patch reefs in the Bahamas was 1.56 (Chiappone and Sullivan, 1991). For spur-and-groove zones (12–15 m) in Belize, Jamaica and Florida, diversity values were 1.04–1.81 (Aronson *et al.*, 1994). For two sites on a Puerto Rican forereef (8–17 m), diversity was 1.89–2.20, compared to 1.97 at 18–20 m (Loya, 1976).

3.10.2. Habitat functional values (Figure 1)

Highest diversities (Shannon–Wiener index generally >1.5) have been reported from patch reefs, *Montastraea* reefs and escarpments and are assigned high functional values. Diversity values for back reefs, reef crest and gorgonian-dominated forereefs are generally <1.5 and are given medium functional values. Seagrass beds and mangrove stands are assigned low functional values because they may contain occasional colonies of hardy genera such as *Manicina*, *Porites* and *Siderastrea*. Forereef sand beds have no coral cover and have no functional value.

4. FUNCTIONAL LINKS BETWEEN HABITATS

This chapter has so far concentrated on how functional values vary between habitat types, but there are also numerous functional links between habitats. For example, the reef crest dissipates a significant proportion of wave energy and this influences conditions in the back reef and lagoon zones. Similarly, upstream habitats affect the nutrient concentrations reaching downstream zones, and the internal fabric of a given part of a reef can be largely composed of debris and carbonate sediments from elsewhere. Furthermore, many species undertake ontogenetic shifts, with juveniles and adults having different habitat preferences and individuals migrating between habitats as they grow older. However, interhabitat functional links have received relatively little research attention. For example, there is limited insight into questions such as whether the biomass or behaviour of a species in its preferred habitat varies depending on the nature of adjacent habitats or the role of "corridors" of suitable habitat during ontogenetic shifts. Advances in landscape ecology (see Gutzwiller, 2002, for a review of this topic) may assist with a better understanding of the consequences of particular habitat patterns. The remainder of this section explores the links between reefs, mangroves and seagrass beds, which exemplify functional interactions between tropical marine habitats.

4.1. Links between reefs, seagrass beds and mangroves

The link between reefs, seagrass beds and mangroves is multifaceted and includes reefs acting as breakwaters that lead to low-energy environs for mangroves and seagrass beds (see Section 3.1). Seagrass beds and mangroves buffer reefs from excessive nutrients (Done *et al*., 1996) and sediment load (Ogden, 1997) but supply detritus and essential nutrients. Mangroves may also cause more nutrients to be available to adjacent seagrass beds, but this does not appear to increase seagrass net community primary productivity (Koch and Madden, 2001). Seagrass beds are used by some reef fishes for foraging, and both seagrass and mangroves are used by many fish species as nurseries before juveniles undertake ontogenetic shifts to reef habitats (Mumby *et al*., 2004a). A full review of the links between reefs, seagrass beds and mangroves is beyond the scope of this chapter, but we illustrate the interactions by highlighting the movement of organic matter, ontogenetic shifts from nursery areas and trophic connections.

The export of organic production from seagrass beds and mangrove stands to reefs is dependent on a range of factors. A mangrove stand inundated by frequent large tides and strong currents will lose more of its litter production than a stand in a more sheltered environment (Hogarth, 1999). However, there appears to be a net movement of dissolved organic matter from mangroves to seagrass beds and then to reefs. Despite the export of inorganic and organic material from mangroves, the productivity of downstream systems are rarely enhanced (Ogden, 1997). Even 1 km away from a mangrove swamp in the Bahamas, only $\sim$10% of dissolved organic matter was attributable to the vascular plant-derived material (Moran *et al*., 1991). Hogarth (1999) also indicates that mangroves tend to have significant net imports of soluble forms of nitrogen (and phosphorus) but a net export of particulate nitrogen. In contrast, it has been estimated that export from Caribbean seagrass beds ranged from up to 10% of leaf productivity from *Thalassia*-dominated areas to >60% for *Syringodium* beds (Greenway, 1976; Zieman *et al*., 1979). The lower export rate of *Thalassia* is caused by herbivore bites having little effect on the whole blade, but a similar bite on *Syringodium* severs the blade and the upper portion is carried away from the site of growth by water movement (Thayer *et al*., 1984).

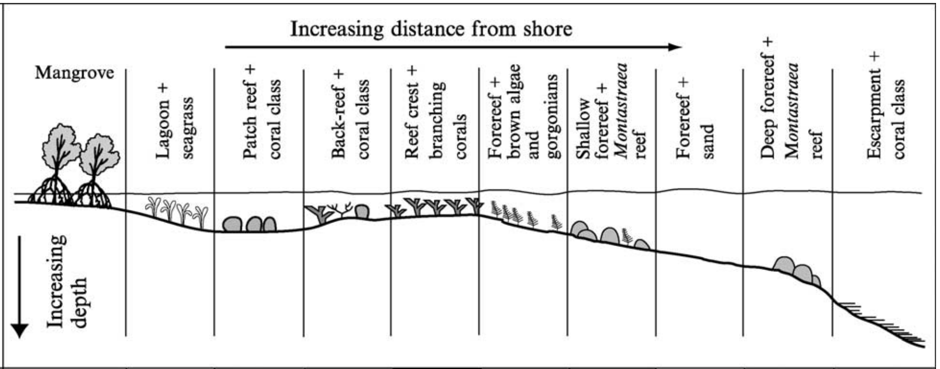
A seagrass bed or mangrove stand acts as a nursery if "its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur" (Beck *et al.*, 2001). Creeks, mangroves and seagrass beds intercept large numbers of fish larvae and provide abundant food resources and protection from predators (e.g., Eggleston, 1995; Nagelkerken *et al.*, 2000a,c). Fishes eventually migrate to near-shore patch reefs and offshore reefs as they mature so that few adults are seen. As noted by Adams and Ebersole (2002), for species that use lagoons as nurseries, these habitats must provide advantages that offset the energy expense and predation risk incurred by incoming larvae both when travelling across the reef to the lagoon and subsequently when returning to the reef. Evidence is provided by both Shulman (1985) and Sweatman and Robertson (1994) that at least part of the advantage of nursery habitats lies in the reduced predation risk associated with settling in seagrass areas compared to the edges of a bank-barrier reefs or patch reef. As recruits grow larger, the seagrass blades no longer offer concealment, but the animals are faster swimmers, may manoeuvre with more agility and achieve a size refuge from predators, which facilitates a move to favourable hard-bottom areas (Shulman, 1985). In Bonaire, van der Velde *et al.* (1992) showed that seagrass beds were important for juvenile *Haemulon flavolineatum*, *H. sciurus*, *Ocyurus chrysurus*, *Sp. viride* and *Acanthurus chirurgus*. Mangroves were particularly used by *Lutjanus apodus*, *L. griseus*, *Sphyraena barracuda* and *Chaetodon capistratus*. Nagelkerken *et al.* (2000a) showed that in a Curaçao bay, variations in the density of juveniles within seagrass and mangrove habitats were caused by the distance to the mouth of the bay, water transparency, amount of shelter and structural complexity. Mumby *et al.* (2004a) show that the presence of mangroves significantly affects fish community structure on nearby reefs and increases the biomass of many species compared to reefs without adjacent mangroves. Nagelkerken *et al.* (2000c) demonstrated that although most species had habitat preferences, many used multiple biotopes.

Trophic links, particularly between seagrass beds and hard-bottom communities, have received considerable attention and are an important component of tropical marine food webs. For example, patch reef–associated predators such as *E. striatus* are significant predators of nocturnally foraging crabs in adjacent seagrass meadows and are an important trophic link between these habitats (Eggleston *et al.*, 1998a). At a lower trophic level, Kirsch *et al.* (2002) showed that small vertebrate grazers consumed substantial amounts of seagrass production in the Florida Keys. Vertebrate grazing led to a large amount of primary production reaching higher consumers, some of which enter seagrass beds from surrounding reefal areas to feed. Grazing of seagrass beds by both fishes and sea urchins, aided by wave and current action, around patch reefs creates the "halos" of sand where seagrass blades have been removed (e.g., Randall, 1965; Ogden and Zieman, 1977). Herbivorous fishes also recycle nutrients (largely ammonium) from feeding on seagrass blades by defaecation on adjacent reef resting areas rather than the feeding areas themselves (Thayer *et al*., 1984). Not only does the defecation process transfer nutrients from seagrass beds to reefs, it is also more rapid than rates of natural seagrass decay.

The trophic link between reefs and seagrass beds is perhaps best demonstrated by grunts (Haemulidae), which feed on seagrass beds by night and cause an enhanced biomass on reefs near seagrass (Ogden and Zieman, 1977). Reefs near seagrass experience a strong reduction in fish density and richness at night as fishes migrate to areas with a high availability of preferred food (Nagelkerken *et al*., 2000b). The dusk and dawn migration distances of *Haemulon plumieri* may be up to 560 m and increase with increasing fish size (Tulevech and Recksiek, 1994). Helfman *et al.* (1982) showed that on patch reefs in St. Croix, small, medium, transitional and large juvenile stages of *H. flavolineatum* and *H. plumieri* each differed in age, size, colouration, habitat preference, diel foraging patterns and twilight migratory behaviour, concluding that ontogenetic differences may be caused by learning and development of visual apparatus. The route of migration paths are also affected by interspecific differences in foraging habitat preferences. Burke (1995) studied *H. flavolineatum* and *H. sciurus* leaving a back reef in Belize; *H. flavolineatum* preferentially used sand flats, whereas *H. sciurus* were usually found in seagrass beds. Working in St. Croix, Meyer *et al.* (1983) showed that juvenile grunts (Haemulidae), which feed in seagrass beds at night, excrete substantial quantities of ammonium, particulate nitrogen and phosphorus onto their daytime resting sites (generally coral heads). Furthermore, excreted nutrients were demonstrated to be more beneficial to corals than had previously been assumed and those colonies with resident fish schools grew faster than those without. Further work (Meyer and Schultz, 1985) showed that the excretions were rich in nitrogen (mainly ammonium), whereas faecal matter was richer in phosphorus and half of a fish's daily excretion and defecation was during the first 4 hr after return to the reef, doubling the amount of ammonium available to corals.

5. SUSCEPTIBILITY OF TROPICAL MARINE HABITATS TO DISTURBANCE

The susceptibility of a range of habitat types to hurricanes and coral bleaching and diseases is addressed in separate subsequent sections as key examples of spatial variation in disturbance regimens (summarised in Figure 2). Synergistic interactions between different types of disturbances are poorly



Disturbance (Section in text) (Units)	Mangrove	Lagoon + seagrass	Patch reef + coral class	Back-reef + coral class	Reef crest + branching corals	Forereef + brown algae and gorgonians	Shallow forereef + *Montastraea* reef	Forereef + sand	Deep forereef + *Montastraea* reef	Escarpment + coral class
Hurricane damage (5.1) (% loss of coral cover)	?	?	░ 3.5 (1)	▓ ?	■ 47.6–93.7 (4)	▓ 19.5–26.6 (1)	▓ 25.3–84.7 (6)		░ ?	░ 0.0–3.0 (2)
Coral bleaching (5.2) (% of dominant species colonies affected)	?	?	■ 15–99.4[a] (4)	■ ?	░ 0–21[b] (2)	■ ?	■ 15–99.4[a] (4)		▓ ?	▓ ?
Coral diseases (5.3) (% of dominant species colonies affected)	?	?	▓ 0.5–5.7[a] (4)	■ ?	■ 2.4–32.2[b] (2)	░ ?	▓ 0.5–5.7[a] (4)		░ ?	░ ?

[a] *Montastraea annularis* complex.
[b] *Acropora palmata*.

Figure 2 Susceptibility of habitats to disturbances across a schematic profile of a Caribbean tropical marine seascape, derived from empirical literature reviewed in the text. Black, dark grey, light grey and no shading indicate high, medium, low and no susceptibility, respectively. Figures represent range of published values. The number of studies (some of which may contribute more than one value) used to derive the ranges are in parentheses. ? indicates a putative class but quantitative data have not been found in the literature.

understood, but Figure 2 summarises the patterns of susceptibility that can form the basis of maps and models of reef resilience to disturbance. In addition to hurricanes and coral bleaching and diseases, other disturbances affect Caribbean reef habitats. The effects of oil pollution are generally most severe in shallow areas, which are the only zones where the oil, which is less dense than water, can accumulate in close contact with the benthos. Jackson *et al.* (1989) documented damage to intertidal reef flats in Panama, which was most extensive at the seaward border where oil accumulated at low tide and caused a bloom of microalgae. Zooanthids, *Millepora* spp., *Porites* spp. and *Echinometra* urchins were also severely affected by the oil. The effects of oil were also seen on shallow subtidal reefs where coral cover decreased by 76%. Similar damage of shallow reefs was seen in Aruba by Bak (1987) as a result of chronic effects from an oil refinery. The *A. palmata* zone at $\sim$2 m was affected, and this habitat appears to be particularly susceptible because of the sensitivity of the characteristic species to oiling (Bak, 1987; Guzmán *et al*., 1991; Brown, 1997).

Sediment rejection is a function of colony morphology, orientation, growth habit and behaviour (e.g., Stafford-Smith and Ormond, 1992). Heavy sedimentation can lead to reduced coral species richness and cover, lower coral growth rates, reduced recruitment, decreased calcification, decreased net productivity of corals and slower rates of reef accretion and affects the structure and function of coral reef ecosystems by altering both physical and biological processes (e.g., Loya, 1976; Rogers, 1990). Most empirical research on the effects of sedimentation has been focused on comparing sedimented habitats to nonsedimented areas or interspecific variations of corals in susceptibility to sediment damage. Such data are difficult to interpret in terms of habitat-specific sedimentation effects and hence are discussed in detail in this chapter. Furthermore, sedimentation has a wide variety of effects and is referenced elsewhere as appropriate (e.g., the effects on settlement of coral recruits). However, corals such as *Siderastrea radians*, *S. siderea*, *Diploria strigosa* and *Meandrina meandrites* appear tolerant of heavy sediment regimens (e.g., Loya, 1976) and habitats dominated by these species are likely to be sedimentation resistant. Similarly, the most profuse coral growth in Jamaica occurred where sediment drainage was most efficient (Goreau and Wells, 1967). More generally, Stoddart (1969) suggested that the main controls of natural sedimentation on a reef are reef geometry and wave energy.

There is a huge literature devoted to increases in global concentrations of CO$_2$ (and other gases) caused by human activities, particularly burning fossil fuels and changes in land use, leading to rising atmospheric temperatures (e.g., Vitousek, 1992; Houghton, 1997; IPCC, 2001). Rising temperatures have been predicted to lead to changing sea levels, but there is little empirical research on how sea-level rise will affect tropical marine ecosystems. However, there have been a number of proposed consequences of rising sea level and it is suggested that shallow reef habitats will be most affected. For example, the areal extent of reef flats could increase because of the release from sea-level constraints of further growth and the putative expansion of reef flats may cause concomitant changes in the fauna and flora of their communities (Cubit *et al.*, 1986; Smith and Buddemeier, 1992). Brown (1997) suggests that reef flats currently constrained by present sea levels in protected waters might be expected to show increases in diversity and productivity. However, the increases in diversity and productivity will be swamped by natural variations in the short term. Empirical evidence of the effects of sea-level rise on shallow water communities is scarce, but predictions are supported by evidence from Panama where movement of a zone of *Laurencia papillosa* at the seaward edge of a reef flat has been linked to sea-level change (Cubit, 1985). The effects of sea-level rise on deeper habitat types is unclear, but they may become subject to greater wave action (Brown, 1997). Furthermore, an increase in the partial pressure of atmospheric CO_2 will decrease the saturation states of calcite, aragonite and Mg-calcite (e.g., Smith and Buddemeier, 1992). Aragonite is deposited by scleractinians and calcareous green algae, and Mg-calcite is commonly precipitated by coralline red algae and many other taxa. The effects of the changes of saturations states on coral reef communities are poorly understood, but it seems likely that calcification rates will decrease and there may be a shift to noncalcifying organisms and bioeroders (Smith and Buddemeier, 1992; Kleypas *et al.*, 1999a).

In lagoonal habitats, sea-level rises may affect seagrass and mangrove habitats. Short and Neckles (1999) indicated that there may be shifts in seagrass bed distributions and community structures because of changes in water depth and movement. A key factor of the response of mangrove forests will be the balance between sedimentation and sea-level rise and the geometry of the shoreline (Woodroffe, 1995; Nicholls *et al.*, 1999). If sediment accumulates at the same rate as sea-level rises, the coastal wetland will grow upwards in place. If accretion is too slow, wetlands are submerged longer during tidal cycles and may die because of water logging (Nicholls *et al.*, 1999). More generally, wave inundation will threaten the buffering capacity of coastal systems because seagrass beds and mangroves will be eroded (Ogden, 1997). In enclosed lagoons, sea-level rise may increase the similarity between the properties of lagoonal seawater and those of local oceanic water and reduce the environmental extremes that limit reef development (Smith and Buddemeier, 1992).

Habitats rich in branching corals are generally the most susceptible to degradation from breakage caused by reef walkers, snorkellers, divers and boat anchors, but much of the work on mechanical breakage has been undertaken in the Red Sea and Indo-Pacific. In Bonaire, Hawkins *et al.*

(1999) showed that sublethal effects of diver damage may alter coral communities; direct physical damage was relatively minor, but diving pressure was causing the proportion of branching corals to increase and reducing the number of large massive colonies. Hawkins *et al.* (1999) hypothesised that there were synergistic effects between diver-induced abrasions, rather than actual breakages, and subsequent coral diseases, on mortality. In the Florida Keys, Davis (1977) showed that 20% of an extensive *A. cervicornis* reef was damaged by boat anchors and suggested that anchor-sensitive areas should be identified and closed to anchoring.

5.1. Susceptibility to hurricane disturbance

There is a large body of literature on the role of hurricanes in Caribbean reef systems, highlighting that the damage to each habitat type is dependent on factors such as benthic community composition, reef topography, previous disturbance regimens and storm type, but we use percentage loss of coral cover to assess susceptibility of different habitats. The most obvious pattern of hurricane effects is the damage to shallow habitats compared to deeper reef areas. Wave energy is highest in shallow water, and many authors describe damage to reef crests while deeper forereefs are less affected (e.g., Woodley *et al.*, 1981). Within shallow areas, *Acropora*-rich habitats are repeatedly reported to be most affected because of the susceptibility of these branching species to breakage compared to massive poritids and faviids (e.g., Stoddart, 1985; Brown, 1997). Severe damage to *Acropora* communities has been reported in many locations including Jamaica (76% loss, Woodley *et al.*, 1981; 93.7% at depths of 3–8 m, Crawford, 1995), Puerto Rico (Armstrong, 1981), Belize (Stoddart, 1965, 1974), the U.S. Virgin Islands (mean of 3.9 broken branches m^{-2}; Rogers *et al.*, 1982), Mexico (82% loss; Jordán-Dahlgren and Rodríguez-Martínez, 1998) and Florida (>90% colonies damaged; Lirman and Fong, 1997). Shallow water *A. palmata* is particularly susceptible to breakage because of its high surface area to volume ratio (e.g., Lirman and Fong, 1997).

Although shallow zones are most affected by hurricanes, reef disturbances have been recorded to 20–30 m (Highsmith *et al.*, 1980; Kjerfve *et al.*, 1986; Scoffin, 1993) and occasionally 50 m (Woodley *et al.*, 1981). After Hurricane Allen in Jamaica (1980), Crawford (1995) reported decreases in coral cover of 84.7% in a mixed zone of *Montastraea* and *A. cervicornis* (5–11 m) and 78.9% in an *A. cervicornis* zone (8–25 m). The loss of coral cover in a similar Jamaican mixed zone after Hurricane Allen was assessed as 62.5% by Steneck (1994). In St. Croix, loss of coral cover on a shallow (4-m) *Diploria*-dominated forereef was ~96.9% but was only ~28% on a deeper (7 m) *Montastraea* reef (Bythell *et al.*, 2000). On St. John, the loss of coral cover on a *Montastraea* reef (10.7–12.7 m) after Hurricane Hugo (1989) was ~40% (Rogers *et al.*, 1991) but insignificant after Hurricanes Luis and Marilyn in 1995 (Rogers *et al.*, 1997). Mean loss of coral cover on St. Thomas after Hurricane David (1979) at four *Montastraea* reef sites (4–6 m deep) was 25.3% compared to 0% on a steep wall in St. Croix (Rogers et al.*, 1983). On a foliaceous coral–dominated wall following Hurricane Allen, coral cover was reduced by only 0–3% (Woodley* et al.*, 1981)*.

In addition to direct wave effects, hurricanes cause a ''domino effect,'' where if one colony is shattered, fragments can cause a cascade of damage to its neighbours (Lirman and Fong, 1996, 1997). The fragments of a coral shattered in one habitat may break corals in both the same habitat and adjacent habitats. Lirman and Fong (1996) document Hurricane Andrew in South Florida causing corals, mainly *A. palmata*, from the reef flat to break corals in the rubble zone. Scoffin (1993) highlights that some deeper corals can be broken by colonies ''falling'' from the shallows. Whether breakage is caused directly by waves or indirectly by collisions between colonies, bioerosion can weaken colonies and introduce further spatial variability to patterns of hurricane damage. Kjerfve *et al.* (1986) noted the importance of bioerosion weakening *Acropora* and making colonies more susceptible to damage. Secondary tissue damage of corals is caused by sand scouring in turbulent water, especially to colonies close to sandy areas (Highsmith *et al.*, 1980; Scoffin, 1993). Layers of sand are also a significant factor in the damage caused to sponges by hurricanes (Fenner, 1991).

Tissue mortality following mechanical breakage by hurricanes is spatially variable within shallow water *Acropora* communities. Knowlton *et al.* (1981, 1990) suggested that during the 5 mo after Hurricane Allen, secondary mortality was >1 order of magnitude more severe than the immediate effects of the storm and eliminated >98% of the original survivors. The complex pattern of mortality involved disease and predation, with predation by *Coralliophila* particularly severe in shallow water. However, patterns of mortality on sections of the back reef epitomised the complex spatial variables that affect coral survival. Some sections of the back reef were protected by *A. palmata* reef crest that survived the hurricane. In protected sections, the mean volume of 22% of patches of *A. cervicornis* remained unchanged or increased in volume and only 9% was reduced to rubble (Williams, 1984). The increase in broken *A. cervicornis* then led to an increase in the abundance of *Diadema* (additional food available) and *S. planifrons* (which are negatively correlated with *A. cervicornis* patch size). There was a competitive interaction between the fish, and urchin species and coral patches occupied by both *Diadema* and *S. planifrons* had a high proportion of living tissue. Coral patches dominated solely by one of the species were overgrazed and <5% of the substratum was covered by living coral (Williams, 1984). In Florida, survival of fragments of *A. palmata* on a patch reef was influenced by the distance from a patch of mature (standing) *A. palmata* (Lirman and Fong, 1997). Standing *A. palmata* may have protected regenerating fragments from wave removal.

Reef topography, the location of the reef relative to the path of the storm, reef orientation with respect to wave direction, the character of prestorm communities and ecological history are important factors determining hurricane damage to reef habitats (e.g., Rogers, 1993a; Bries *et al*., 2004). For example, the prevalence of reefs on the southwestern coast of Cozumel reduced the impact of Hurricane Gilbert (1988) because the largest waves approached from the east, and there is a limited fetch between the western side of the island and the Yucatan Peninsula (Fenner, 1991). Mean loss of coral cover in Cozumel was 47.6% (shallow fringing reefs), 61.2% (deep fringing reefs), 3.5% (patch reefs), 58.5% (top of shelf-edge reefs) and 30.7% (slopes of shelf-edge reefs). At a smaller scale, reef topography is particularly important as it has a direct effect on wave height and hence energy dissipation. Hind casting of Hurricane Allen in Jamaica demonstrated a correlation between the tallest breaking waves and maximum damage (Kjerfve *et al*., 1986). The eastern forereef at Discovery Bay had the tallest waves because of a greater seaward extension of the reef and the effect was exacerbated by the storms being from the east. Furthermore, flow deflection by reef topography was important because this creates high turbulence that breaks *A. palmata* as the water moves in untypical directions (Kjerfve *et al*., 1986). Spur-and-groove formations appear to baffle wave energy more effectively than areas with less topographical relief (Scoffin, 1993). Woodley *et al.* (1981) stated that hurricane damage was more significant on sloping or level areas of reef in Jamaica compared to vertical sections, presumably because vertical areas are generally found in deeper water and wave energy is higher on sloping forereefs. Hurricane damage is also dependent on the distance of a reef from shore. Blair *et al.* (1994) found that in Florida after Hurricane Andrew in 1992, the forereef slope of an offshore reef (between 17 and 29 m) was most heavily affected (26.6% loss) with lesser impacts on a middle reef (21.7%; 11–17 m) and least damage on an inner reef (19.5%; 8–12 m), although all sites initially had low coral cover and could be classified as gorgonian dominated.

Disturbance history is an important consideration in predicting hurricane damage of reef habitats. Hughes and Connell (1999) state that the effect of a given disturbance is significantly affected by previous disturbances and ‘‘blurs the line’’ between single and multiple disturbances. Bythell *et al.* (2000) provide data for the effects of three hurricanes within 6 yr on benthic communities in a protected area in St. Croix, a system with relatively low levels of anthropogenic impacts. Data from three sites (7 m diverse but moderate coral cover; 4 m, high coral cover; 3 m, dominated by dead *A. palmata*) showed that only the 7-m site experienced significant changes in community composition. The change was caused by the interaction of hurricane-induced mortality, some recovery of coral cover, recovery of species richness to higher than prehurricane levels and the role of a major coral recruitment event after the first hurricane. However, variations in community composition between sites (effectively habitats) were much greater than changes over time and landscape community composition appears to remain stable. Bythell *et al.* (2000) conclude that coral communities in St. Croix are resilient to repeated hurricane impacts over a period of 10 yr. The severe damage to shallow water communities during Hurricane Allen in Jamaica (1980) might be atypical because *A. palmata* may have been so abundant only because of lack of hurricanes in the preceding years (Woodley, 1992).

5.1.1. Habitat susceptibilities (Figure 2)

Reef crests are clearly the most susceptible habitats to hurricane damage with generally >60% of coral cover lost (high susceptibility). We assign medium susceptibility to coral loss of generally 10–60% (shallow *Montastraea* reefs and gorgonian-dominated forereefs). Note that although gorgonian-dominated forereefs appear to lose 10–60% of their corals during hurricanes, *Montastraea* reefs have higher initial coral cover, so absolute losses of cover are greater. Although there are few data, shallow back reefs are also assigned medium susceptibility as large coral heads are broken, but some patches of *A. cervicornis* may receive limited damage (Williams, 1984). Low susceptibility is defined as loss of coral cover of generally 1–10% (patch reefs and escarpments). Deep *Montastraea* reefs are also assigned low susceptibility, although data are scarce. Mangroves, seagrass beds and sand channels are assigned no susceptibility because coral colonies are only very occasional or absent.

5.2. Susceptibility to coral bleaching

Mass coral bleaching involves the loss of symbiotic zooxanthellae following chronic photoinhibition, and more frequent bleaching events may represent a symptom of global climate change (see Hoegh-Guldberg, 1999). Bleached coral colonies may recover by regaining zooxanthellae after initial bleaching, but rates of mortality are generally positively correlated with initial susceptibility. Patterns of bleaching susceptibility may be at least partially explained by different tolerances of zooxanthellae (Fitt and Warner, 1995). However, tolerances of different clades of zooxanthellae, how the clades are distributed intraspecifically and interspecifically and whether particular zooxanthellae will spread across reefs to make corals in a range of habitats more tolerant of bleaching (and hence alter the susceptibility values presented here) is the subject of intense research and speculation (e.g., Baker *et al*., 2004; Rowan, 2004; Sotka and Thacker, 2005).

Between 3.4 and 8.7% of corals were bleached in four reef sites in Panamá following the 1982–1983 El Niño event (Glynn, 1984). Across a series of Caribbean sites 3–4 mo after the 1987 bleaching event, mean percent of all ''pale'' corals was 19.9% on patch reefs and 21.7% on forereefs (Lang *et al*., 1992). The 1995 bleaching event in Belize affected 52% of coral colonies and caused 10–25% of bleached colonies to experience at least partial tissue mortality with a 10–13% loss of coral cover (McField, 1999; Kramer *et al*., 2000). The proportions of corals affected in Belize were ~43% (back reef), ~50% (forereef) and ~57% (patch reef) (McField, 1999). Following the 1998 bleaching event in Belize, there was an average of 18% mortality on shallow reefs and 14% on forereefs across the Mesoamerican Barrier Reef System but reached 75% in some locations (Kramer *et al*., 2000).

However, most research on the effects of bleaching has tended to focus on interspecific comparisons of susceptibility, but this work does indicate which habitat types are most affected. The major reef builder *M. annularis* typically has the highest rates of both initial bleaching and tissue mortality (e.g., Goenaga *et al*., 1989; 90% of colonies at 30 m and 14% at 46 m, Ghiold and Smith, 1990; 76% of colonies affected, McField, 1999; 25–50% mortality, Kramer *et al*., 2000). CARICOMP (1997a) gave an extensive assessment of bleaching across the Caribbean following the 1995–1996 bleaching event, and bleaching in *Montastraea* varied from 15 to 99.4% (mean ~70%) and tissue mortality ranged from 0 to 30%. Other taxa regularly affected by bleaching are *Millepora* spp., *Agaricia* spp., *Colpophyllia natans*, *Diploria* spp. and *Porites* spp. and *Siderastrea siderea* (Glynn, 1984; Ghiold and Smith, 1990; Lang *et al*., 1992; CARICOMP, 1997a; McField, 1999). For example, *Agaricia tenuifolia* underwent almost total mortality at all depths in Belize after the 1997–1998 bleaching event (Aronson *et al*., 2000), and *A. agaricites* was significantly affected by bleaching in 1995–1996 on patch reefs in the Bahamas (McGrath and Smith, 1998). Similarly, all *Agaricia undata* colonies were bleached at 46, 62 and 77 m in the Cayman Islands, and only *A. palmata* escaped severe bleaching (Ghiold and Smith, 1990). *Acropora* was also only minimally affected by bleaching in Jamaica and the Mesoamerican Barrier Reef System (Goreau, 1990; Kramer *et al*., 2000), although up to 21% of *palmata* colonies and up to 54% of *cervicornis* colonies have been affected at specific locations (CARICOMP, 1997a).

Intraspecific variations of bleaching susceptibility and subsequent mortality are in part caused by water depth. Depth is important because of its effects on attenuating light and hence thermal stress from radiative energy (e.g., Mobley, 1994). Bleaching mortality generally decreases with increasing depth, and this has been recorded in, for example, the Cayman Islands

(Ghiold and Smith, 1990) and Panama (Glynn, 1984). However, shallow water corals may be able to adapt or acclimatise to high temperatures and light intensities. Brown (1997) states that hardy reef-flat and shallow water corals may show considerable scope for nongenetic adaptations to bleaching-induced mortality, which may be much reduced in species living subtidally. For example, in the Florida Keys and Bahamas, colony recovery rates from initial bleaching seemed more rapid in shallower habitats (Lang *et al.*, 1992). Shallow water adaptations to high temperatures and light intensities may vary between species; a comparison of initial bleaching rates in Belizean back reefs and forereefs and demonstrated that *Siderastrea siderea* and *M. annularis* colonies had higher rates in the forereef, but *P. porites* and *Agaricia* spp. had higher rates in the back reef (McField, 1999).

5.2.1. Habitat susceptibilities (Figure 2)

There are insufficient habitat-specific data to assess the effects of bleaching in terms of loss of coral cover across whole communities. Therefore, we assign susceptibility values using the proportion of colonies of the dominant coral species that is typically affected during bleaching events. *M. annularis* is one of the most susceptible species, with ~70% of colonies affected in a Caribbean wide survey (CARICOMP, 1997a), and shallow *Montastraea* reefs and patch reefs (where *Montastraea* is commonly a major frame building coral along with susceptible *Agaricia* species) are assigned high susceptibility. Deep *Montastraea* reefs are assessed as having medium susceptibility, as the effects of bleaching generally decrease with increasing depth. Similarly, escarpments are assigned medium susceptibility, as they are in deeper water, but characteristic species such as *A. undata* may be severely bleached (Ghiold and Smith, 1990). *A. palmata* is generally resistant to bleaching, and reef crests are assessed as having low susceptibility. *Acropora* may also be present in back reefs but are typically dominated by a mix of susceptible species (e.g., *Agaricia* spp., *Millepora* spp. and *Porites* spp) and are assessed as having high susceptibility. Similarly, the corals present in gorgonian-dominated forereefs are generally susceptible species, and this habitat is assigned high susceptibility, although the coral cover is low. Seagrass beds, mangroves and sand beds have no susceptibility because corals are only occasional or absent.

5.3. Susceptibility to coral diseases

Diseases are defined as any impairment of vital body functions, systems or organs (Peters, 1997). Incidents of coral diseases may be increasing in frequency because of anthropogenic stresses to reef systems (Peters, 1997;

Green and Bruckner, 2000) and appear to be having deleterious impacts on reef communities. A range of diseases have been defined in the Caribbean, such as white pox (Patterson *et al*., 2002) and yellow band (Santavy and Peters, 1997), but here we concentrate on two that are perhaps best studied: black band and white band (e.g., Peters *et al*., 1983; Rützler and Santavy, 1983).

Diploria strigosa and the *M. annularis* complex are most prone to black band disease, and typically ~0.5–1.0% of the population is affected (Antonius, 1981; Peters, 1997; Green and Bruckner, 2000). Antonius (1981) found that *M. cavernosa*, *Diploria labyrinthiformis* and *D. clivosa* are also relatively susceptible, whereas *A. palmata*, *A. cervicornis* and *A. prolifera* appear totally resistant. In Jamaica, Bruckner and Bruckner (1997) documented similar interspecific patterns of black band susceptibility, with the addition of effects to *S. siderea*. A summary of data from across the Caribbean for colonies >25 cm in diameter gave incidence rates as follows: *M. annularis* 1.0%, *faveolata* 1.0, *franksi* 3.7% and *cavernosa* 0.6%, *Siderastrea siderea* 0.8%, *Diploria strigosa* 0.5%, *Agaricia* spp. 0.1%, *Colpophyllia natans* 1.5%, *Diploria labyrinthiformis* 0.6%, *Agaricia agaricites* 0.3%, *M. complanata* 0.4%, *Stephanocoenia intersepta* 1.5% and *Meandrina meandrites* 1.3% (Kramer, 2003). Bruckner and Bruckner (1997) showed that black band disease was rarely found below 10 m, that 47.9% of infected coral died and that the loss of coral was greatest in the back reef, which was exposed to physiological and environmental stresses. Bleached corals may also be more susceptible to black band disease with 34% of *M. faveolata* colonies in Honduras infected after the 1995 bleaching event (Kramer *et al*., 2000).

Corals of the genus *Acropora* are most, and possibly exclusively, susceptible to white band disease (Gladfelter, 1982; Peters, 1997; Aronson and Precht, 2000, 2001). Other species have been reported as being affected by white band, but it seems likely that these reports are misidentifications of the disease (Green and Bruckner, 2000). A summary of data from across the Caribbean for colonies >25 cm in diameter gave incidence rates of 2.4% for *A. palmata* and 12.4% for *A. cervicornis*, with the disease not reported for any other species (Kramer, 2003), but these values inevitably reflect the severe depletion of *Acropora* populations. In 1977–1979 in St. Croix, 32.2% of 90 *A. palmata* colonies were diseased, with a further 41.1% dead (Gladfelter, 1982) and can reach 64% for *Acropora* communities (Peters *et al*., 1983). Aronson and Precht (2001) suggest that white band disease has probably been the primary factor reducing populations of acroporids, with hurricane damage also important on some reefs, and that this event is unique in the late Holocene. The effects of white band disease were documented by Aronson and Precht (2000) in Belize where coral cover decreased in a relatively deep spur-and-groove zone dominated by *A. cervicornis*. In comparison, a shallower spur-and-groove zone was less affected because the resistant *Agaricia tenuifolia* was the dominant coral. In St. Croix, white band disease in *A. palmata* facilitated access to coral skeletons for a variety of boring organisms so that colonies were weakened and collapsed (Clarke, 1996). The massive mortality of *A. palmata* in shallow habitats will have consequences including reduced carbonate deposition, increased wave energy reaching shorelines, mangroves and seagrass beds and affect sand production and beach dynamics (Gladfelter, 1982; Bythell and Sheppard, 1993).

5.3.1. Habitat susceptibilities (Figure 2)

There are insufficient, habitat-specific data to assess the effects of white and black band diseases in terms of loss of coral cover across whole communities. Therefore, we assign susceptibility values using the proportion of colonies of the dominant coral species that is typically infected. White band disease causes the greatest loss of coral cover, and *A. palmata* is highly susceptible (2.4–32.2% of colonies infected) and reef crests and back reefs are assessed as having high susceptibility. The *M. annularis* complex is one of the most susceptible species to black band disease, with ~0.5–5.7% of colonies affected, and shallow *Montastraea* reefs and patch reefs (where *Montastraea* is commonly a major frame building coral) are assigned medium susceptibility, although both these communities would previously have also supported *A. cervicornis* communities that would have been susceptible to white band disease. Deep *Montastraea* reefs are assessed as having low susceptibility, as black band disease is rarely found below 10 m (Bruckner and Bruckner, 1997). Escarpments are also assigned low susceptibility, as they are in deeper water with small populations of *Acropora* and *Montastraea*. Similarly, the few corals present in gorgonian-dominated forereefs are generally tolerant of disease, and this habitat is assigned low susceptibility. Seagrass beds, mangroves and sand beds have no susceptibility because corals are only occasional or absent.

6. EXAMPLE MAPS AND MODELS UTILISING FUNCTIONAL VALUES

6.1. Maps of functional values

One of our key aims is to review the empirical data that are available in published literature to assist the generation of maps that facilitate further insight into ecosystem processes and aid conservation. Static maps can be created using a combination of remotely sensed imagery and the proposed functional values (Figure 1) and individual maps, or combinations of data layers, will have a range of applications. We develop this concept by generating maps of "hot spots" of functional value for populations of the commercially important *Epinephelus striatus*, *Panulirus argus* and *S. gigas* (Figure 3). The traditional habitat map used (Figure 3A) is from Andros Island, Bahamas, created using IKONOS imagery with three spectral bands and resampled to 100 m^2 pixels. The map shows a typical barrier reef zonation (total of 15 habitat types) with mangroves (pink), lagoonal seagrass beds (green) and patch reefs (blue) in shallow water behind the reef crest

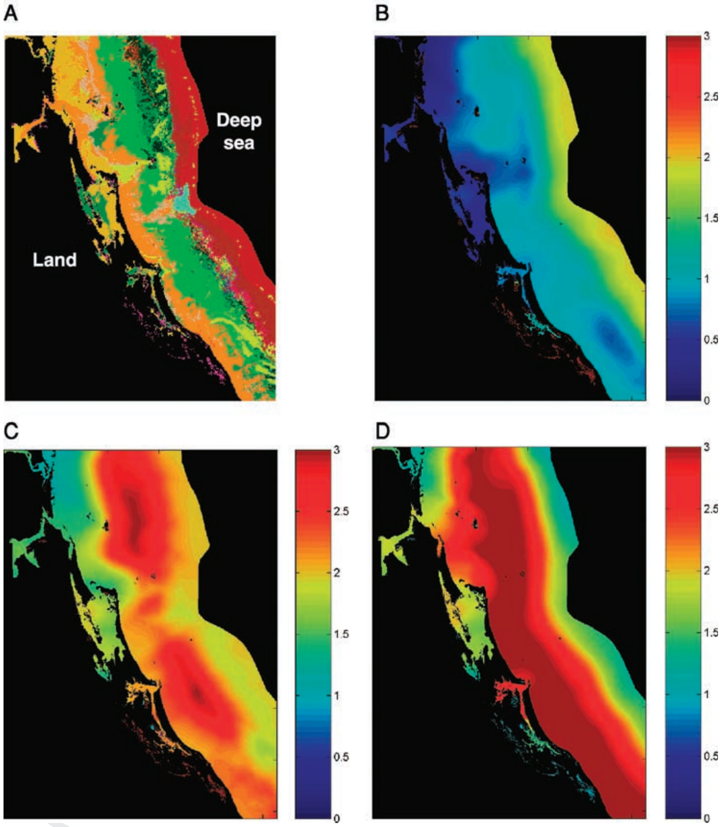


Figure 3 Maps of (A) habitat types off the east coast of Andros Island (Bahamas) and mean functional values of the seascape for populations of (B) Epinephelus striatus, (C) Panulirus argus and (D) Strombus gigas. Mean functional values calculated using 2-km^2 windows centred on each pixel. Colour bars show mean functional value (no functional value = 0; low = 1; medium = 2; high = 3). Functional value of each habitat taken from Figure 1. Area represented is 14.3 × 10.5 km and centred on 24°51′41″ N, 77°53′49″ W.

(purple) and offshore gorgonian-dominated and *Montastraea* reefs (brown shades). For details on standard processing techniques of remotely sensed imagery, see Green *et al.* (2000).

The three derived layers (Figure 3B–D) were generated by first assigning each pixel a functional value based on its habitat type (none = 0, low = 1, medium = 2, high = 3; derived from Figure 1). Note that the use of satellite imagery does not allow the parameterisation of steeply sloping habitats, such as escarpments, and their functional values are significantly underestimated in Figure 3. Additional data, such as those generated by an acoustic ground discrimination system (White *et al*., 2003), could be used to ensure escarpments are correctly represented in assessments of functional value. The mean functional value was then calculated in 2-km^2 "windows" (an arbitrary size to demonstrate the approach) centred on each pixel using a bespoke computer algorithm. The windows grew outwards from the initial centre "seed" pixel in a method analogous to conducting a pixel-to-pixel random walk in all possible directions simultaneously. The walk was iterated until the number of pixels in the locality window was equal to the required number (i.e., the desired area of the window was achieved). In an entirely marine area this method generated circular windows, and when land was encountered, the shape of the window "grew" around, for example, headlands and small islands. Mean functional values (minimum 0, maximum 3) were then assigned to each pixel. Although traditional maps allow the identification of locations of habitats with high functional value (e.g., patch reefs for *E. striatus*), the maps in Figure 3 allow quantitative identification of areas with consistently high functional values across multiple habitats. Furthermore, the hot-spot areas are at a scale appropriate for management and could assist managers to identify priority sites for marine reserves, particularly if used in combination with maps of susceptibility to disturbance that could be generated from both Figure 2 and location-specific data (e.g., fishing pressure).

6.2. Models of ecosystem processes

Of the published habitat-scale ecological models, perhaps only that of Wolanski *et al.* (1984) can be considered a seascape model; most focus on a specific habitat within an ecosystem. Given the obvious patchiness in our habitat-level understanding of processes, it still remains a considerable challenge to create meaningful models of individual tropical marine ecosystem habitats. However, habitat-level models provide useful insights into processes and management of marine resources, particularly when the habitat being modelled is widely used for extractive activities. For example, Mumby (2005) used a spatial-simulation model to explore the link between resilience of *Montastraea* reefs and one of the proxies of secondary production reviewed in this chapter (density of parrotfishes). In the absence of the sea urchin *D. antillarum* (Lessios *et al*., 1984), Caribbean forereefs are largely dependent on parrotfishes to control the cover of macroalgae. Even relatively minor depletions of grazer density can reduce the resilience of *Montastraea* habitats, leading to a reduction in coral cover, which, if left unresolved, will cause a decline in the structural complexity and quality of the habitat (Glynn, 1997). The papers reviewed here on secondary production and coral recruitment and growth, along with new data, allowed parameterisation of the model and similar efforts could be undertaken both for different processes within this habitat and for other habitats. Extending individual-habitat models to seascape scales, either by varying the parameters (e.g., depending on the presence of adjacent nurseries areas) or by linking dynamic models of different habitats using established functional links, will reveal potentially surprising but important phenomena. More importantly, seascape-level models are more likely to become decision-support tools because they must, by definition, embody suitably large spatial scales, such as entire reefs. Reconciling the competing needs of multiple users at these scales is the very essence of coastal management.

7. CONCLUSIONS

7.1. Current status of empirical knowledge

The last 50 years of research on coral reefs has led to great increases in understanding their biology, ecology and underlying processes. However, perhaps the most obvious conclusion from this chapter is the disparate nature of empirical research that has limited attempts to synthesise overarching principals of how whole reef seascapes function spatially and temporally. It is obvious that, even for well-researched processes, there are few documented patterns of how functional values change between habitats and affect the resulting interactions and emergent properties. This chapter has attempted to draw together the disparate and extensive literature and provide spatially explicit functional values of typical Caribbean habitat types to some ecosystem processes clearly derived, where possible, from quantitative data (Figure 1). We have also generated assessments of susceptibility of each habitat to three important disturbances (Figure 2).

Hatcher (1988) provided a review of rates of primary productivity in a range of geomorphological zones and benthic communities and showed that data were relatively abundant for back reef, reef crest and shallow forereef areas, but there was very little information available for deeper forereefs and escarpments. The relative lack of data for deeper reef areas has been borne out by this chapter for other processes and represents a significant gap in the framework of data required for mapping and modelling these processes across tropical marine seascapes. The lack of information in deeper reef zones is largely caused by experimental difficulties, but with considerable coral growth possible to at least 40 m and remotely sensed imagery able to discriminate habitats beyond 20 m in good conditions (Green *et al*., 2000), additional experimental work is imperative. Incorporating the functional values of mangrove and seagrass habitats is also impeded by a lack of empirical data, despite their importance in a number of processes. The limited data available for mangrove stands and seagrass beds has been highlighted previously (e.g., Hatcher *et al*., 1989).

In addition to a lack of data for particular habitat types, much of the published data are essentially related to clear water (''optimal'') environmental conditions. There are very few empirical data on how functional values change when environmental parameters are altered by natural or anthropogenic influences (e.g., increased turbidity). Furthermore, much of the key empirical data on the functional values of many habitats pre-dates significant changes to Caribbean coral reefs. It is clear that the mass mortality of *Diadema* in the early 1980s (e.g., Lessios, 1988) catalysed a shift from coral domination to algal domination in some parts of the region (e.g., Hughes, 1994). Such changes will have profound effects on processes such as biological production, biogeochemical cycling and accretion, and further empirical work may be required for these ''modified'' habitats to parameterise models. Similarly, populations of *A. palmata* and *A. cervicornis*, which were previously dominant in many reef crest and forereefs zones, have decreased significantly throughout the Caribbean because of white band disease (e.g., Aronson and Precht, 2001). Again, the loss of many *Acropora* stands will have significant effects on rates of, for example, calcification and wave-energy dissipation, and previous data may no longer be applicable. An understanding of the changes caused by the loss of *Acropora* in shallow water seems particularly important because of the importance of coral-rich reef crests in many of the processes reviewed in this chapter (Figure 1). Despite the importance of research on the changing nature of reef crests, few empirical data have been published since, for example, Bythell and Sheppard (1993) highlighted the mortality of *A. palmata* in the British Virgin Islands and raised concerns about increased wave energies reaching shorelines and alterations to patterns of sand production, beach dynamics and erosion.

The functional values presented in this chapter must also be placed in a longer term historical context. It is easy, particularly in a relatively new discipline such as tropical marine science, to view recent data as the baseline for monitoring subsequent changes when in fact the current status is dramatically altered from the ''natural'' situation (the ''shifting baseline'' syndrome). Fossil data are important to provide historical context and show that, for example, the decline of *Acropora* is indeed unique in the late Holocene (Aronson and Precht, 2001). In the context of this chapter, the *relative* pattern of many functional values has probably remained similar over long timescales. For example, coral-rich forereef habitats have always had higher calcification rates than gorgonian-dominated habitats, although the actual calcification rates have decreased in coral-rich habitats since the loss of *Diadema* and subsequent decline in coral cover (e.g., Hughes, 1994). However, there are certainly examples of how relative functional values have changed so that patterns described in this chapter represent an ‘‘unnatural’’ scenario. Perhaps the best example of changing patterns is the dramatically reduced densities of megavertebrates (e.g., manatee and green turtle). The loss of these vertebrates cannot be compensated for by fishes and invertebrates and must have altered herbivory in seagrass beds (now significantly lower), patterns of loss of production to adjacent ecosystems and the structure of food chains (Jackson, 1997).

We recognise that the functional value of a given habitat will vary significantly across the seascape. Perhaps most obviously, the functional value of a specific habitat will be affected by its spatial context within the seascape. For example, a patch of habitat may not fulfil an ‘‘adult microhabitat’’ function for a given species if the patch is isolated from the species’ juvenile microhabitat (e.g., Acosta, 1999). Lindeman *et al.* (1998) provide a demonstration of how settlement rates of lutjanids and haemulids to a habitat type will vary depending on its cross-shelf position. At a larger scale, the benthic communities of reef crests (and hence functional values) have been shown to vary dramatically depending on wave energy and storm frequency (Hubbard, 1997). Further complications in describing the functional value of a habitat arise because multiple processes may be linked across habitat boundaries. Wave-energy dissipation varies across different types of reef crests, which then affects primary production, grazing pressure, calcification rates and bioerosion rates in back reefs and lagoons (e.g., Smith and Kinsey, 1976; McGehee, 1994; Hatcher, 1997b). Thus, the functional value of a habitat is far from consistent across a whole seascape and may depend on its size and spatial context. The effects of habitat configurations have been reported where possible, but studies rarely address spatial changes in a habitat’s functional value depending on the nature of adjacent areas. Models of reef processes will need to incorporate such intrahabitat variation and it is likely that the application of landscape ecology approaches (e.g., Liu and Taylor, 2002) will be profitable.

Despite the inevitable caveats associated with Figure 1, it does represent the first time that functional values have been summarised for such an extensive range of processes and habitats. Furthermore, it raises a number of important questions: Which habitats are the most ‘‘important’’ overall and how is their importance influenced by their areal extent? What are the effects of anthropogenic impacts to functional values? Can functional values be weighted depending on their importance to overall reef ecosystem health? Such questions are beyond the scope of this chapter and require specific targeted research programmes. However, it is possible to gain some insight into overall functional roles of habitats by converting functional values to ordinal values (no functional value = 0, low = 1, medium = 2, high = 3; derived from Figure 1 and using pre-1983 densities of *D. antillarum*) and generating an ordination using nonmetric multidimensional scaling (MDS; Figure 4) (see Clarke, 1993, for more details). Sand is so different from the other habitats that it is omitted from the MDS for clarity. Perhaps the most striking feature of the ordination is the spread of habitats, indicating that each habitat has a relatively unique set of functional values. The ‘‘Reef crest + branching corals’’ and ‘‘Back reef + coral class’’ are close together, showing that they have similar functional values for each process. Rather than representing any kind of ‘‘habitat redundancy,’’ we would suggest that this pairing actually represent limitations of the empirical data where such habitats are frequently grouped together. Care must also be taken when suggesting that the ordination shows that each habitat is equally ‘‘important.’’ However, even this basic analysis,

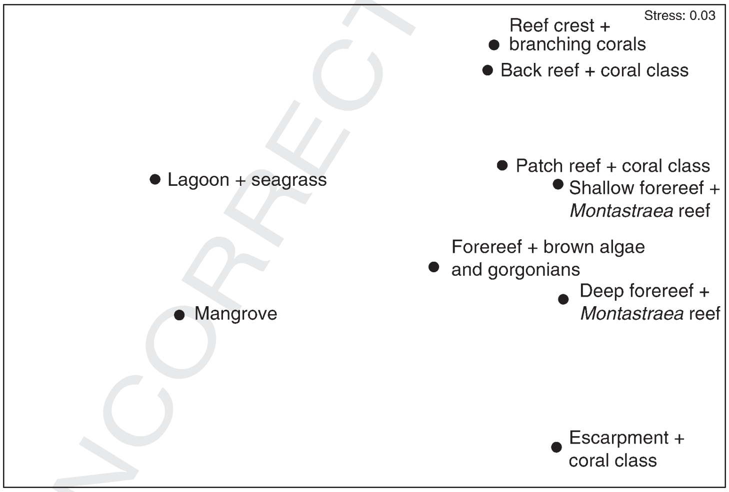


Figure 4 Ordination of nine of the generic habitats (sand omitted) assigned functional values within each section of this chapter (Figure 1). Variables used were those represented in Figure 1, with the exception of post-1983 Diadema densities. Functional values for each variable were converted to an ordinal value (no functional value = 0; low = 1; medium = 2; high = 3). The relatively low stress indicates that the two-dimensional distances are a good representation of the multidimensional similarity between habitats.

which requires much further research to fully explore, appears to show how different habitats may have different and specific functional roles that combine to maintain ecosystem functioning.

7.2. Limitations of the review

The complexity of the processes reviewed in this chapter is such that separating them into separate sections is often artificial. For example, primary productivity and the density of secondary producers (herbivores) are inextricably linked, as are calcification rates and patterns of reef recovery, and indeed multiple processes might be investigated within a single research paper. Some of the most obvious links between processes have been addressed by cross-referencing between sections, but others are not made explicitly in deference to the readability of the text. Finally, space limitations meant that we have limited our review to what we consider the most ecologically and economically important functions. Readers will be aware that, for example, all habitats across a reef seascape function as nursery or adult habitats for a whole range of taxa in addition to the key primary, secondary and tertiary producers discussed.

The functional value of a habitat will vary at a range of temporal scales. Algal communities (and hence primary productivity) vary between seasons (e.g., Lirman and Biber, 2000) and the calcification rates of *Acropora palmata* in Jamaica were anomalously high in the 1970s because of the unusual infrequency of major hurricanes in preceding years (Woodley, 1992). Temporal aspects of processes are arguably better understood than the importance of spatial context, but we have not attempted to review temporal variation. Modelling of reef processes is at such a nascent stage that the inclusion of spatial information alone remains problematic.

7.3. Research priorities and future directions

This chapter aimed to provide a basic framework of information on the functional value of different habitats, particularly those that can be delineated by remotely sensed imagery, in a range of reef processes. Figure 1 highlights clear gaps in our knowledge, which could guide future research. In the context of building maps or models of reef processes, studies working simultaneously in multiple habitats will be particularly important because they provide directly comparable functional values. Ideally, such studies would also include an assessment of functional links between habitats and across their boundaries because these links are poorly understood. If links have been studied, it is normally at large scales between major habitat types (e.g., seagrass beds, mangroves and reefs). Currently, understanding of reef processes is inhibited by a "dearth of system-level information about coral reefs and a poor understanding of how population and community parameters relate to functions at the system level" (Johnson *et al.*, 1995). An alternative approach is to take existing framework models of reef processes and make them spatially explicit. For example, a trophic model has been developed (ECOPATH with Ecosim, e.g., Christensen and Pauly, 1992) and has been parameterised to study trophic structure (and energy flows) of the back reef, reef front and slope zones of three coral reef complexes in the Mexican Caribbean (Arias-González, 1998).

Individual researchers will inevitably have specific aims during their work and may not be concerned with building maps and models of reef processes across multiple habitats. However, most data collected are useful for modelling reef processes if it is clear which habitats were the basis for their experiments. It was clear while reviewing literature for this chapter that the particular habitat used for many studies received only a cursory description or was commonly limited to a geomorphological zone (e.g., "forereef"), even though the benthic community in a given zone can vary widely. We would encourage researchers to provide enough information so that their study site could be allocated to a habitat within a typical classification scheme for remotely sensed imagery.

There are clear limitations in our understanding of how each Caribbean marine habitat contributes to important reef processes and how these functional values are affected by the spatial context of the habitat. However, it does seem that there is sufficient empirical data to combine with remotely sensed imagery and to start building spatially explicit maps and models of reef processes. We feel that such maps and models represent an exciting direction for furthering our understanding of these complex environments. A transect from shore to reef wall encompasses such a panoply of biotopes that it is of interest to even the casual observer how these habitats function together so that reefs are so much more productive and diverse than the open ocean. Perhaps more pertinently, the functional values of reef habitats are increasingly under threat from a suite of factors and a more sophisticated understanding of the implications of these changes, and how to mitigate and reverse them, is vital for the ecological and economic health of tropical marine ecosystems.

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REFERENCES

Acosta, C. A. (1999). Benthic dispersal of Caribbean spiny lobsters among insular habitats: Implications for the conservation of exploited marine species. *Conservation Biology* **13**, 603–612.

Acosta, C. A. and Butler, M. J. (1997). Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Marine and Freshwater Research* **48**, 721–727.

Acosta, C. A. and Butler, M. J. (1999). Adaptive strategies that reduce predation on Caribbean spiny lobster postlarvae during onshore transport. *Limnology and Oceanography* **44**, 494–501.

Acosta, C. A. and Robertson, D. N. (2003). Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* **22**, 1–9.

Adams, A. J. and Ebersole, J. P. (2002). Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series* **228**, 213–226.

Adey, W. H. and Goertemiller, T. (1987). Coral reef algal turfs: Master producers in nutrient poor seas. *Phycologia* **26**, 374–386.

Adey, W. H. and Steneck, R. S. (1985). Highly productive eastern Caribbean reefs: Synergistic effects of biological, chemical, physical, and geological factors. *In* ''The Ecology of Coral Reefs. NOAA's Undersea Research Program'' (M. L. Reaka, ed.), Vol. 3, No. 1, pp. 163–187. U.S. Department of Commerce, Washington, D.C.

Adey, W. H. and Vassar, J. M. (1975). Colonisation, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* **14**, 55–69.

Adey, W. H., Adey, P. J., Burke, R. and Kaufman, L. S. (1977). The Holocene reef systems of Eastern Martinique, French West Indies. *Atoll Research Bulletin* **218**, 1–40.

Alevizon, W., Richardson, R., Pitts, P. and Serviss, G. (1985). Coral zonation and patterns of community structure in Bahamian reef fishes. *Bulletin of Marine Science* **36**, 304–318.

Andres, N. G. and Witman, J. D. (1995). Trends in community structure on a Jamaican reef. *Marine Ecology Progress Series* **118**, 305–310.

Antonius, A. (1981). The ''band'' diseases in coral reefs. *In* ''Proceedings of the Fourth International Coral Reef Symposium, Manila'' (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 2, pp. 7–14. University of the Philippines, Quezon City, The Philippines.

Appeldoorn, R. S. and Rolke, W. (1996). ''Stock Abundance and Potential Yield of the Queen Conch Resource in Belize'' CARICOM Fisheries Resource Assessment and Management Program and Belize Fisheries Department, Belize City.

Appeldoorn, R. S., Recksiek, C. W., Hill, R. L., Pagan, F. E. and Dennis, G. D. (1997). Marine protected areas and reef fish movements: The role of habitat in controlling ontogenetic migration. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. II, pp. 1917–1922. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Arias-González, J. E. (1998). Trophic models of protected and unprotected coral reef ecosystems in the south of the Mexican Caribbean. *Journal of Fish Biology* **53** (suppl. A), 236–255.

Armstrong, R. A. (1981). Changes in a Puerto Rican coral reef from 1936–1979 using aerial photography. *In* "Proceedings of the Fourth International Coral Reef Symposium, Manila" (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 1, pp. 309–315. University of the Philippines, Quezon City, The Philippines.

Aronson, R. B. and Precht, W. F. (1995). Landscape patterns of reef coral diversity: A test of the intermediate disturbance hypothesis. *Journal of Experimental Marine Biology and Ecology* **192**, 1–14.

Aronson, R. B. and Precht, W. F. (2000). Evolutionary paleoecology of Caribbean coral reefs. *In* "Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change" (W. D. Allmon and D. J. Bottjer, eds.), pp. 171–234. Columbia University Press, New York.

Aronson, R. B. and Precht, W. F. (2001). White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* **460**, 25–38.

Aronson, R. B., Edmunds, P. J., Precht, W. F., Swanson, D. W. and Levitan, D. R. (1994). Large-scale, long-term monitoring of Caribbean coral reefs: Simple, quick, inexpensive techniques. *Atoll Research Bulletin* **421**, 1–19.

Aronson, R. B., Precht, W. F., Macintyre, I. G. and Murdoch, T. J. T. (2000). Coral bleach-out in Belize. *Nature* **405**, 36–36.

Atkinson, M. J. and Grigg, R. W. (1984). Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs* **3**, 13–22.

Bach, S. D. (1979). Standing crop, growth and production of calcareous siphonales (Chlorophyta) in a south Florida lagoon. *Bulletin of Marine Science* **29**, 191–201.

Baggett, L. S. and Bright, T. J. (1985). Coral recruitment at the East Flower Garden Reef (northwestern Gulf of Mexico). *In* "Proceedings of the Fifth International Coral Reef Congress, Tahiti" (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 4, pp. 379–384. Antenne Museum–EPHE, Moorea, French Polynesia.

Bak, R. P. M. (1976). The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* **10**, 285–337.

Bak, R. P. M. (1985). Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. *In* "Proceedings of the Fifth International Coral Reef Congress, Tahiti" (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 5, pp. 267–272. Antenne Museum–EPHE, Moorea, French Polynesia.

Bak, R. P. M. (1987). Effects of chronic oil pollution on a Caribbean coral reef. *Marine Pollution Bulletin* **18**, 534–539.

Bak, R. P. M. (1994). Sea urchin bioerosion on coral reefs: Place in the carbonate budget and relevant variables. *Coral Reefs* **13**, 99–103.

Bak, R. P. M. and Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology* **54**, 341–352.

Bak, R. P. M. and van Eys, G. (1975). Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia* **20**, 111–115.

Bak, R. P. M., Carpay, M. J. E. and de Ruyter van Steveninck, E. D. (1984). Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Marine Ecology Progress Series* **17**, 105–108.

Baker, A. C., Starger, C. J., McClanahan, T. R. and Glynn, P. W. (2004). Corals' adaptive response to climate change. *Nature* **430**, 741.

Barber, B. J. and Behrens, P. J. (1985). Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* Banks Ex König and *Syringodium filiforme* Kutzing. *Aquatic Botany* **22**, 61–69.

Bardach, J. E. (1958). On the movements of certain Bermuda reef fishes. *Ecology* **39**, 139–146.

Bardach, J. E. (1961). Transport of calcareous fragments by reef fishes. *Science* **133**, 98–99.

Barlow, G. W. (1975). On the sociobiology of four Puerto Rican parrotfishes (Scaridae). *Marine Biology* **33**, 281–293.

Barnes, D. J. and Devereux, M. J. (1984). Productivity and calcification on a coral reef: A survey using pH and oxygen electrode techniques. *Journal of Experimental Marine Biology and Ecology* **79**, 213–231.

Bauer, J. C. (1976). Growth, aggregation, and maturation in the echinoid, *Diadema antillarum*. *Bulletin of Marine Science* **26**, 273–277.

Bauer, J. C. (1980). Observations on geographical variations in population density of the echinoid Diadema antillarum within the western North Atlantic. *Bulletin of Marine Science* **30**, 509–515.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F. and Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**, 633–641.

Beets, J. and Hixon, M. A. (1994). Distribution, persistence, and growth of groupers (Pisces, Serranidae) on artificial and natural patch reefs in the Virgin Islands. *Bulletin of Marine Science* **55**, 470–483.

Béné, C. and Tewfik, A. (2003). Biological evaluation of marine protected area: Evidence of crowding effect on a protected population of queen conch in the Caribbean. *P.S.Z.N.: Marine Ecology* **24**, 45–58.

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *In* ''Proceedings, Third International Coral Reef Symposium'' (D. L. Taylor, ed.), Vol. 1, ''Biology'', pp. 16–21. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Birkeland, C. (1997). Introduction. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 1–12. Chapman & Hall, New York.

Blair, S. M., McIntosh, T. L. and Mostkoff, B. J. (1994). Impacts of Hurricane Andrew on the offshore reef systems of central and northern Dade County, Florida. *Bulletin of Marine Science* **54**, 961–973.

Boettcher, A. A. and Targett, N. M. (1996). Induction of metamorphosis in queen conch, *Strombus gigas* Linnaeus, larvae by cues associated with red algae from their nursery grounds. *Journal of Experimental Marine Biology and Ecology* **196**, 29–52.

Bolden, S. K. (2000). Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fishery Bulletin* **98**, 642–645.

Booth, D. J. and Beretta, G. A. (1994). Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* **13**, 81–89.

Borowitzka, M. A. (1983). Calcium carbonate deposition by reef algae: Morphological and physiological aspects. *In* "Perspectives on Coral Reefs" (D. J. Barnes, ed.), pp. 16–28. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Bosscher, H. and Meesters, E. H. (1993). Depth related changes in the growth rate of *Montastrea annularis*. *In* "Proceedings of the Seventh International Coral Reef Symposium, Guam" (R. H. Richmond, ed.), Vol. 1, pp. 507–512. University of Guam Marine Laboratory, Mangilao, Guam.

Brawley, S. H. and Adey, W. H. (1977). Territorial behaviour of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environmental Biology of Fishes* **2**, 45–51.

Bries, J. M., Debrot, A. O. and Meyer, D. L. (2004). Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. *Coral Reefs* **23**, 297–307.

Briones-Fourzán, P. and Lozano-Álvarez, E. (2001). The importance of *Lobophora variegata* (Phaeophyta: Dictyotales) as a habitat for small juveniles of *Panulirus argus* (Decapoda: Palinuridae) in a tropical reef lagoon. *Bulletin of Marine Science* **68**, 207–219.

Brown, B. E. (1997). Adaptations of reef corals to physical environmental stress. *Advances in Marine Biology* **31**, 221–299.

Bruckner, A. W. and Bruckner, R. J. (1997). The persistence of black-band disease in Jamaica: Impact on community structure. *In* "Proceedings of the 8th International Coral Reef Symposium" (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 601–606. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Bruckner, A. W. and Bruckner, R. J. (2003). Condition of coral reefs off less developed coastlines of Curaçao (Part 2: Reef fishes). *Atoll Research Bulletin* **496**, 394–403.

Bruggemann, J. H., Begeman, J., Bosma, E. M., Verburg, P. and Breeman, A. M. (1994a). Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein and energy. *Marine Ecology Progress Series* **106**, 57–71.

Bruggemann, J. H., Kuyper, M. W. M. and Breeman, A. M. (1994b). Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* **112**, 51–66.

Bruggemann, J. H., van Oppen, M. J. H. and Breeman, A. M. (1994c). Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different socially determined habitats. *Marine Ecology Progress Series* **106**, 41–55.

Bruggemann, J. H., van Kessel, A. M., van Rooij, J. M. and Breeman, A. M. (1996). Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* **134**, 59–71.

Buddemeier, R. W. and Kinzie, R. A. (1976). Coral growth. *Oceanography and Marine Biology Annual Review* **14**, 183–225.

Burke, N. C. (1995). Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. *Environmental Biology of Fishes* **42**, 365–374.

Butler, M. J., Hunt, J. H., Herrnkind, W. F., Childress, M. J., Bertelsen, R., Sharp, W., Matthews, T., Field, J. M. and Marshall, H. G. (1995). Cascading disturbances in Florida Bay, USA: Cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series* **129**, 119–125.

Butler, M. J., Herrnkind, W. F. and Hunt, J. H. (1997). Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in Macroalgae. *Bulletin of Marine Science* **61**, 3–19.

Butler, M. J., Dolan, T., Herrnkind, W. and Hunt, J. (2001). Modelling the effect of spatial variation in postlarval supply and habitat structure on recruitment of Caribbean spiny lobster. *Marine and Freshwater Research* **52**, 1243–1252.

Bythell, J. and Sheppard, C. (1993). Mass mortality of Caribbean shallow corals. *Marine Pollution Bulletin* **26**, 296–297.

Bythell, J. C., Gladfelter, E. H. and Bythell, M. (1993). Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* **12**, 143–152.

Bythell, J. C., Hillis-Starr, Z. M. and Rogers, C. S. (2000). Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series* **204**, 93–100.

Camoin, G. F., Gautret, P., Montaggioni, L. F. and Cabioch, G. (1999). Nature and environmental significance of microbialites in Quaternary reefs: The Tahiti paradox. *Sedimentary Geology* **126**, 271–304.

Capone, D. G., Penhale, P. A., Oremland, R. S. and Taylor, B. F. (1979). Relationship between productivity and N_2 (C_2H_2) fixation in a *Thalassia testudinum* community. *Limnology and Oceanography* **24**, 117–125.

CARICOMP (1997a). Studies on Caribbean coral bleaching, 1995–96. *In* "Proceedings of the 8th International Coral Reef Symposium" (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 673–678. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

CARICOMP (1997b). Variation in ecological parameters of *Thalassia testudinum* across the CARICOMP network. *In* "Proceedings of the 8th International Coral Reef Symposium" (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 663–668. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Carleton, J. H. and Sammarco, P. W. (1987). Effects of substratum irregularity on success of coral settlement: Quantification by comparative geomorphological techniques. *Bulletin of Marine Science* **40**, 85–98.

Carlon, D. B. and Olson, R. R. (1993). Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. *Journal of Experimental Marine Biology and Ecology* **173**, 247–263.

Carpenter, R. C. (1981). Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal of Marine Research* **39**, 749–765.

Carpenter, R. C. (1985a). Relationships between primary production and irradiance in coral reef algal communities. *Limnology and Oceanography* **30**, 784–793.

Carpenter, R. C. (1985b). Sea urchin mass-mortality: Effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. *In* "Proceedings of the Fifth International Coral Reef Congress, Tahiti" (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 4, pp. 53–59. Antenne Museum–EPHE, Moorea, French Polynesia.

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**, 345–363.

Carpenter, R. C. (1988). Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. *Proceedings of the National Academy of Sciences of the United States of America* **85**, 511–514.

Carpenter, R. C. (1990a). Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Marine Biology* **104**, 79–86.

Carpenter, R. C. (1990b). Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* **104**, 67–77.

Carpenter, R. C. (1997). Invertebrate predators and grazers. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 198–229. Chapman & Hall, New York.

Chapman, M. R. and Kramer, D. L. (1999). Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: Effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series* **181**, 81–96.

Chappell, J. (1980). Coral morphology, diversity and reef growth. *Nature* **286**, 249–252.

Chave, K. E., Smith, S. V. and Roy, K. J. (1972). Carbonate production by coral reefs. *Marine Geology* **12**, 123–140.

Chiappone, M. and Sullivan, K. M. (1991). A comparison of line transect versus linear percentage sampling for evaluating stony coral (Scleractinia and Milleporina) community similarity and area coverage on reefs of the central Bahamas. *Coral Reefs* **10**, 139–154.

Chiappone, M. and Sullivan, K. M. (1996). Distribution, abundance and species composition of juvenile scleractinian corals in the Florida Reef Tract. *Bulletin of Marine Science* **58**, 555–569.

Chiappone, M., Sluka, R. and Sullivan Sealey, K. (2000). Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series* **198**, 261–272.

Chiappone, M., Swanson, D. W. and Miller, S. L. (2002a). Density, spatial distribution and size structure of sea urchins in Florida Keys coral reef and hard-bottom habitats. *Marine Ecology Progress Series* **235**, 117–126.

Chiappone, M., Swanson, D. W., Miller, S. L. and Smith, S. G. (2002b). Large-scale surveys on the Florida Reef Tract indicate poor recovery of the long-spined sea urchin *Diadema antillarum*. *Coral Reefs* **21**, 155–159.

Childress, M. J. and Herrnkind, W. F. (1994). The behaviour of juvenile Caribbean spiny lobster in Florida Bay: Seasonality, ontogeny and sociality. *Bulletin of Marine Science* **54**, 819–827.

Childress, M. J. and Herrnkind, W. F. (1997). Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: Cooperation or coincidence? *Marine and Freshwater Research* **48**, 751–758.

Christensen, V. and Pauly, D. (1992). ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* **61**, 169–185.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.

Clarke, R. D. (1996). Population shifts in two competing fish species on a degrading coral reef. *Marine Ecology Progress Series* **137**, 51–58.

Claro, R. and Ramos, K. C. (2003). Rapid assessment of coral communities of María La Gorda, southeast Ensenada de Corrientes, Cuba (Part 2: Reef fishes). *Atoll Research Bulletin* **496**, 278–293.

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I. and van der Velde, G. (2002). Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine Coastal and Shelf Science* **55**, 309–321.

Cochrane, K. L. and Chakalall, B. (2001). The spiny lobster fishery in the WECAFC region—an approach to responsible fisheries management. *Marine and Freshwater Research* **52**, 1623–1631.

Colin, P. L., Laroche, W. A. and Brothers, E. B. (1997). Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bulletin of Marine Science* **60**, 656–667.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1309.

Connell, J. H. (1997). Disturbance and recovery of coral assemblages. *Coral Reefs* **16**, S101–S113.

Connor, J. L. and Adey, W. H. (1977). The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. *Atoll Research Bulletin* **211**, 1–39.

Constantz, B. (1985). Taxon-specific diagenetic variation among scleractinian corals (Barbados, West Indies). *In* ''Proceedings of the Fifth International Coral Reef Congress, Tahiti'' (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 3, pp. 229–234. Antenne Museum–EPHE, Moorea, French Polynesia.

Cox, C., Hunt, J. H., Lyons, W. G. and Davis, G. E. (1997). Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. *Marine and Freshwater Research* **48**, 671–679.

Crawford, J. A. (1995). The effects of Hurricane Allen at Discovery Bay, Jamaica, and a post-hurricane survey of the living hermatypic corals. *Caribbean Journal of Science* **31**, 237–242.

Cubit, J. D. (1985). Possible effects of recent changes in sea level on the biota of a Caribbean reef flat and predicted effects of rising sea levels. *In* ''Proceedings of the Fifth International Coral Reef Congress, Tahiti'' (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 3, pp. 111–118. Antenne Museum–EPHE, Moorea, French Polynesia.

Cubit, J. D., Windsor, D. M., Thompson, R. C. and Burgett, J. M. (1986). Water-level fluctuations, emersion regimes, and variations of echinoid populations on a Caribbean reef flat. *Estuarine Coastal and Shelf Science* **22**, 719–737.

Dahl, A. L. (1973). Benthic algal ecology in a deep reef and sand habitat off Puerto Rico. *Botanica Marina* **16**, 171–175.

Dahlgren, C. P. and Eggleston, D. B. (2000). Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81**, 2227–2240.

Dahlgren, C. P. and Eggleston, D. B. (2001). Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology Progress Series* **217**, 145–156.

Davies, P. J. (1983). Reef growth. *In* ''Perspectives on Coral Reefs'' (D. J. Barnes, ed.), pp. 69–106. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Davis, G. E. (1977). Anchor damage to a coral reef on the coast of Florida. *Biological Conservation* **11**, 29–34.

Davis, M. and Stoner, A. W. (1994). Trophic cues induce metamorphosis of queen conch larvae (*Strombus gigas* Linnaeus). *Journal of Experimental Marine Biology and Ecology* **180**, 83–102.

de Boer, B. A. (1978). Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curaçao, Netherlands Antilles. *Bulletin of Marine Science* **28**, 550–565.

de Ruyter van Steveninck, E. D. (1984). The composition of algal vegetation in and outside damselfish territories on a Florida reef. *Aquatic Botany* **20**, 11–19.

de Ruyter van Steveninck, E. D. and Breeman, A. M. (1981). Biomass and relative coverage of benthic algae in the fore-reef of Curaçao (Netherlands Antilles) in relation to production. *Marine Ecology Progress Series* **6**, 257–265.

D'Elia, C. F. and Wiebe, W. J. (1990). Biogeochemical nutrient cycles in coral-reef ecosystems. *In* ''Coral Reefs'' (Z. Dubinsky, ed.), pp. 49–74. Elsevier Science Publishers, Amsterdam.

Demicco, R. V. and Hardie, L. A. (2002). The ''carbonate factory'' revisited: A reexamination of sediment production functions used to model deposition on carbonate platforms. *Journal of Sedimentary Research* **72**, 849–857.

Deschamps, A., Desrochers, A. and Klomp, K. D. (2003). A rapid assessment of the Horseshoe Reef, Tobago Cays Marine Park, St. Vincent, West Indies (stony corals, algae and fishes). *Atoll Research Bulletin* **496**, 438–459.

Diekmann, O. E., Bak, R. P. M., Tonk, L., Stam, W. T. and Olsen, J. L. (2002). No habitat correlation of zooxanthellae in the coral genus *Madracis* on a Curaçao reef. *Marine Ecology Progress Series* **227**, 221–232.

Domeier, M. L. and Colin, P. L. (1997). Tropical reef fish spawning aggregations: Defined and reviewed. *Bulletin of Marine Science* **60**, 698–726.

Done, T. J., Ogden, J. C., Wiebe, W. J. and Rosen, B. R. (1996). Biodiversity and ecosystem function of coral reefs. *In* ''Functional Roles of Biodiversity: A Global Perspective'' (H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala and E.-D. Schulze, eds.), pp. 393–429. John Wiley & Sons.

Downing, J. A., McClain, M., Twilley, R., Melack, J. M., Elser, J., Rabalais, N. N., Lewis, W. M., Turner, R. E., Corredor, J., Soto, D., Yanez-Arancibia, A., Kopaska, J. A. and Howarth, R. W. (1999). The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems: Current conditions and projected changes. *Biogeochemistry* **46**, 109–148.

Dubin, R. E. and Baker, J. D. (1982). Two types of cover-seeking behaviour at sunset by the princess parrotfish, *Scarus taeniopterus*, at Barbados, West Indies. *Bulletin of Marine Science* **32**, 572–583.

Dustan, P. and Halas, J. C. (1987). Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* **6**, 91–106.

Ebersole, J. P. (1985). Niche separation of two damselfish species by aggression and differential microhabitat utilisation. *Ecology* **66**, 14–20.

Edmunds, P. J. (2000). Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Marine Ecology Progress Series* **202**, 113–124.

Edmunds, P. J. (2004). Juvenile coral population dynamics track rising seawater temperature on a Caribbean reef. *Marine Ecology Progress Series* **269**, 111–119.

Edmunds, P. J. and Carpenter, R. C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5067–5071.

Edmunds, P. J. and Spencer Davies, P. (1986). An energy budget for *Porites porites* (Scleractinia). *Marine Biology* **92**, 339–347.

Edmunds, P. J., Aronson, R. B., Swanson, D. W., Levitan, D. R. and Precht, W. F. (1998). Photographic versus visual census techniques for the quantification of juvenile corals. *Bulletin of Marine Science* **62**, 937–946.

Edmunds, P. J., Bruno, J. F. and Carlon, D. B. (2004). Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. *Marine Ecology Progress Series* **278**, 115–124.

Eggleston, D. B. (1995). Recruitment in Nassau grouper *Epinephelus striatus*: Post-settlement abundance, microhabitat features, and ontogenic habitat shifts. *Marine Ecology Progress Series* **124**, 9–22.

Eggleston, D. B. and Dahlgren, C. P. (2001). Distribution and abundance of Caribbean spiny lobsters in the Key West National Wildlife Refuge: Relationship to habitat features and impact of an intensive recreational fishery. *Marine and Freshwater Research* **52**, 1567–1576.

Eggleston, D. B. and Lipcius, R. N. (1992). Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* **73**, 992–1011.

Eggleston, D. B., Lipcius, R. N. and Grover, J. J. (1997). Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Marine Ecology Progress Series* **149**, 43–59.

Eggleston, D. B., Grover, J. J. and Lipcius, R. N. (1998a). Ontogenetic diet shifts in Nassau grouper: Trophic linkages and predatory impact. *Bulletin of Marine Science* **63**, 111–126.

Eggleston, D. B., Lipcius, R. N., Marshall, L. S. and Ratchford, S. G. (1998b). Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: Lunar and seasonal periodicity, spatial coherence, and wind forcing. *Marine Ecology Progress Series* **174**, 33–49.

Endean, R. (1976). Destruction and recovery of coral reef communities. *In* ''Biology and Geology of Coral Reefs. III: Biology 2'' (O. A. Jones and R. Endean, eds.), pp. 215–254. Academic Press, New York.

Fadlallah, Y. H. (1983). Sexual reproduction, development and larval biology in scleractinian corals—a review. *Coral Reefs* **2**, 129–150.

Fagerstrom, J. A. (1987). ''The Evolution of Reef Communities'' John Wiley & Sons, New York.

Fenner, D. P. (1991). Effects of Hurricane Gilbert on coral reefs, fishes and sponges at Cozumel, Mexico. *Bulletin of Marine Science* **48**, 719–730.

Findley, J. S. and Findley, M. T. (2001). Global, regional, and local patterns in species richness and abundance of butterflyfishes. *Ecological Monographs* **71**, 69–91.

Fitt, W. K. and Warner, M. E. (1995). Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin* **189**, 298–307.

Fonseca, A. C. and Gamboa, C. (2003). A rapid assessment at Cahuita National Park, Costa Rica, 1999 (Part 2: Reef fishes). *Atoll Research Bulletin* **496**, 258–267.

Forcucci, D. (1994). Population density, recruitment and 1991 mortality event of *Diadema antillarum* in the Florida Keys. *Bulletin of Marine Science* **54**, 917–928.

Forcucci, D., Butler, M. J. and Hunt, J. H. (1994). Population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, Florida. *Bulletin of Marine Science* **54**, 805–818.

Foster, A. B. (1980). Environmental variation in skeletal morphology within the Caribbean reef corals *Montastraea annularis* and *Siderastrea siderea*. *Bulletin of Marine Science* **30**, 678–709.

Foster, S. A. (1985). Size-dependent territory defense by a damselfish: A determinant of resource use by group-foraging surgeonfishes. *Oecologia* **67**, 499–505.

Foster, S. A. (1987). The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: Effects of habitat and surge. *Journal of Experimental Marine Biology and Ecology* **105**, 1–20.

Fourqurean, J. W., Zieman, J. C. and Powell, G. V. N. (1992). Phosphorus limitation of primary production in Florida Bay: Evidence from C : N : P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* **37**, 162–171.

Fourqurean, J. W., Willsie, A., Rose, C. D. and Rutten, L. M. (2001). Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* **138**, 341–354.

Freile, D. and Hillis, L. (1997). Carbonate productivity by *Halimeda incrassata* in a land proximal lagoon, Pico Feo, San Blas, Panama. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 767–772. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Freile, D., Milliman, J. D. and Hillis, L. (1995). Leeward bank margin *Halimeda* meadows and draperies and their sedimentary importance on the western Great Bahama Bank slope. *Coral Reefs* **14**, 27–33.

Frydl, P. and Stearn, C. W. (1978). Rate of bioerosion by parrotfish in Barbados reef environments. *Journal of Sedimentary Petrology* **48**, 1149–1157.

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A. and Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science* **301**, 958–960.

Gattuso, J.-P., Frankignoulle, M. and Wollast, R. (1998). Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* **29**, 405–434.

Gattuso, J.-P., Allemand, D. and Frankignoulle, M. (1999). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *American Zoologist* **39**, 160–183.

Gaut, V. C. and Munro, J. L. (1983). The biology, ecology and bionomics of the grunts, Pomadasyidae. *In* ''Caribbean Coral Reef Fishery Resources'' (J. L. Munro, ed.), pp. 110–141. International Center for Living Aquatic Resources Management, Manila.

Ghiold, J. and Smith, S. H. (1990). Bleaching and recovery of deep-water, reef-dwelling invertebrates in the Cayman Islands, B.W.I. *Caribbean Journal of Science* **26**, 52–61.

Gischler, E. (1994). Sedimentation on three Caribbean atolls: Glovers Reef, Lighthouse Reef and Turneffe Islands, Belize. *Facies* **31**, 243–254.

Gladfelter, E. H. and Monahan, R. K. (1977). Primary production and calcium carbonate deposition rates in *Acropora palmata* from different positions in the reef. *In* ''Proceedings, Third International Coral Reef Symposium'' (D. L. Taylor, ed.), Vol. 2, ''Geology'', pp. 389–394Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Gladfelter, E. H., Monahan, R. K. and Gladfelter, W. B. (1978). Growth rates of five reef-building corals in the northeastern Caribbean. *Bulletin of Marine Science* **28**, 728–734.

Gladfelter, W. B. (1982). White-band disease in *Acropora palmata*: Implications for the structure and growth of shallow reefs. *Bulletin of Marine Science* **32**, 639–643.

Glazer, R. A. and Kidney, J. A. (2004). Habitat associations of adult queen conch (*Strombus gigas* L.) in an unfished Florida Keys back reef: Applications to essential fish habitat. *Bulletin of Marine Science* **75**, 205–224.

Glynn, P. W. (1984). Widespread coral mortality and the 1982–83 El Niño warming event. *Environmental Conservation* **11**, 133–146.

Glynn, P. W. (1997). Bioerosion and coral-reef growth: A dynamic balance. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 68–95. Chapman & Hall, New York.

Goenaga, C., Vicente, V. and Armstrong, R. A. (1989). Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: A precursor of change in the community structure of coral reefs? *Caribbean Journal of Science* **25**, 59–65.

Goering, J. J. and Parker, P. L. (1972). Nitrogen fixation by epiphytes on sea grasses. *Limnology and Oceanography* **17**, 320–323.

Goldner, L. L. (1980). Nitrogen fixation (acetylene reduction) in shallow water Bahamian environments. *Bulletin of Marine Science* **30**, 444–453.

González-Salas, C., Nàñez-Lara, E., Ruiz-Zárate, M. A., Hernández-Landa, R. and Arias-González, J. E. (2003). Condition of coral reef ecosystems in central-southern Quintana Roo (Part 3: Juvenile reef fishes). *Atoll Research Bulletin* **496**, 598–610.

Goreau, T. F. (1959). The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* **40**, 67–90.

Goreau, T. F. and Goreau, N. I. (1973). The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. *Bulletin of Marine Science* **23**, 403–464.

Goreau, T. F. and Wells, J. W. (1967). The shallow-water Scleractinia and their vertical distribution range. *Bulletin of Marine Science* **17**, 442–453.

Goreau, T. J. (1990). Coral bleaching in Jamaica. *Nature* **343**, 417.

Green, E. P. and Bruckner, A. W. (2000). The significance of coral disease epizootiology for coral reef conservation. *Biological Conservation* **96**, 347–361.

Green, E. P., Mumby, P. J., Edwards, A. J. and Clark, C. D. (1996). A review of remote sensing for the assessment and management of tropical coastal resources. *Coastal Management* **24**, 1–40.

Green, E. P., Mumby, P. J., Edwards, A. J. and Clark, C. D. (2000). ''Remote Sensing Handbook for Tropical Coastal Management''. Coastal Management Sourcebooks 3, UNESCO, Paris.

Greenway, M. (1976). The grazing of *Thalassia testudinum* in Kingston Harbor, Jamaica. *Aquatic Botany* **2**, 117–126.

Gunkel, F. (1997). Effects of different substrate surface roughness on sessile invertebrate recruitment off Lee Stocking Island, Exuma Cays, Bahamas—preliminary results. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. II, pp. 1185–1190. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Gutiérrez, L. (1998). Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*. *Oecologia* **115**, 268–277.

Gutzwiller, K. J. (ed.) (2002). ''Applying Landscape Ecology in Biological Conservation''. Springer Verlag, New York.

Guzmán, H. M., Jackson, J. B. C. and Weil, E. (1991). Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* **10**, 1–12.

Gygi, R. H. (1975). *Sparisoma viride* (Bonnaterre), the stoplight parrotfish, a major sediment producer on coral reefs of Bermuda. *Ecologae Geologicae Helvetiae* **68**, 327–359.

Hamner, W. M. and Wolanski, E. (1988). Hydrodynamic forcing functions and biological processes on coral reefs: A status review. *In* ''Proceedings of the 6th

International Coral Reef Symposium, Australia'' (J. H. Choat, ed.), Vol. 1, pp. 103–113. 6th International Coral Reef Symposium Executive Committee, Townsville, Australia.

Hanisak, M. D. (1992). The importance of macroalgae to the queen conch, *Strombus gigas*. *Journal of Phycology* **28**, 12.

Hanley, F. (1984). Time-budgeting and foraging strategy of the stoplight parrotfish *Sparisoma viride* Bonnaterre, in Jamaica. *Journal of Experimental Marine Biology and Ecology* **83**, 159–177.

Harrison, P. L. and Wallace, C. C. (1990). Coral reproduction. *In* ''Coral Reefs'' (Z. Dubinsky, ed.), pp. 133–208. Elsevier Science Publishers, Amsterdam.

Hatcher, B. G. (1988). Coral reef primary productivity: A beggar's banquet. *Trends in Ecology & Evolution* **3**, 106–111.

Hatcher, B. G. (1990). Coral reef primary productivity: A hierarchy of pattern and process. *Trends in Ecology & Evolution* **5**, 149–155.

Hatcher, B. G. (1997a). Coral reef ecosystems: How much greater is the whole than the sum of the parts? *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 43–56. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Hatcher, B. G. (1997b). Organic production and decomposition. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 140–174. Chapman & Hall, New York.

Hatcher, B. G., Johannes, R. E. and Robertson, A. I. (1989). Review of research relevant to the conservation of shallow tropical marine ecosystems. *Oceanography and Marine Biology Annual Review* **27**, 337–414.

Hawkins, C. M. and Lewis, J. B. (1982). Ecological energetics of the tropical sea urchin *Diadema antillarum* Philippi in Barbados, West Indies. *Estuarine Coastal and Shelf Science* **15**, 645–669.

Hawkins, J. P., Roberts, C. M., van't Hof, T., de Meyer, K., Tratalos, J. and Aldam, C. (1999). Effects of recreational scuba diving on Caribbean coral and fish communities. *Conservation Biology* **13**, 888–897.

Hay, M. E. (1981a). Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *American Naturalist* **118**, 520–540.

Hay, M. E. (1981b). Spatial patterns of grazing intensity on a Caribbean barrier reef: Herbivory and algal distribution. *Aquatic Botany* **11**, 97–109.

Hay, M. E. (1984). Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology* **65**, 446–454.

Hay, M. E. (1985). Spatial patterns of herbivore impact and their importance in maintaining algal species richness. *In* ''Proceedings of the Fifth International Coral Reef Congress, Tahiti'' (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 4, pp. 29–34. Antenne Museum–EPHE, Moorea, French Polynesia.

Hay, M. E. and Goertemiller, T. (1983). Between-habitat differences in herbivore impact on Caribbean coral reefs. *In* ''The Ecology of Deep and Shallow Coral Reefs. Symposia Series for Undesea Research'' (M. L. Reaka, ed.), Vol. 1, pp. 97–102. Office of Undersea Research NOAA, Rockville, Maryland USA.

Hay, M. E. and Taylor, P. R. (1985). Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* **65**, 591–598.

Hay, M. E., Colburn, T. and Downing, D. (1983). Spatial and temporal patterns in herbivory on a Caribbean fringing reef: The effects on plant distribution. *Oecologia* **58**, 299–308.

Helfman, G. S., Meyer, J. L. and McFarland, W. N. (1982). The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Animal Behaviour* **30**, 317–326.

Herrnkind, W. and Cummings, W. C. (1964). Single file migrations of the spiny lobster, *Panulirus argus* (Latreille). *Bulletin of Marine Science* **14**, 123–125.

Herrnkind, W. F. and Butler, M. J. (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. *Marine Ecology Progress Series* **34**, 23–30.

Herrnkind, W. F., Butler, M. J., Hunt, J. H. and Childress, M. (1997). Role of physical refugia: Implications from a mass sponge die-off in a lobster nursery in Florida. *Marine and Freshwater Research* **48**, 759–769.

Hesse, K. O. (1979). Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. *Bulletin of Marine Science* **29**, 303–311.

Highsmith, R. C. (1982). Reproduction by fragmentation in corals. *Marine Ecology Progress Series* **7**, 207–226.

Highsmith, R. C., Riggs, A. C. and D'Antonio, C. M. (1980). Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* **46**, 322–329.

Highsmith, R. C., Lueptow, R. L. and Schonberg, S. C. (1983). Growth and bioerosion of three massive corals on the Belize Barrier Reef. *Marine Ecology Progress Series* **13**, 261–271.

Hillis-Colinvaux, L. (1980). Ecology and taxonomy of *Halimeda*: Primary producer of coral reefs. *Advances in Marine Biology* **17**, 1–327.

Hinds, P. A. and Ballantine, D. L. (1987). Effects of the Caribbean threespot damselfish, *Stegastes planifrons* (Cuvier), on algal lawn composition. *Aquatic Botany* **27**, 299–308.

Hixon, M. A. (1991). Predation as a process structuring coral reef fish communities. *In* ''The Ecology of Fishes on Coral Reefs'' (P. F. Sale, ed.), pp. 475–508. Academic Press, Inc, San Diego.

Hixon, M. A. (1997). Effects of reef fishes on corals and algae. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 230–248. Chapman & Hall, New York.

Hixon, M. A. and Brostoff, W. N. (1983). Damselfish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. *Science* **220**, 511–513.

Hobson, E. S. (1991). Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. *In* ''The Ecology of Fishes on Coral Reefs'' (P. F. Sale, ed.), pp. 69–95. Academic Press, Inc, San Diego.

Hobson, E. S. and Chess, J. R. (1978). Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fisheries Bulletin* **76**, 133–153.

Hobson, E. S. and Chess, J. R. (1986). Diel movements of resident and transient zooplankters above lagoon reefs at Enewetak Atoll, Marshall Islands. *Pacific Science* **40**, 7–26.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839–866.

Hogarth, P. J. (1999). ''The Biology of Mangroves''. Oxford University Press, Oxford.

Holmes, K. E. (2000). Effects of eutrophication on bioeroding sponge communities with the description of new West Indian sponges, *Cliona* spp. (Porifera : Hadromerida : Clionidae). *Invertebrate Biology* **119**, 125–138.

Horn, M. H. (1989). Biology of marine herbivorous fishes. *Oceanography and Marine Biology Annual Review* **27**, 167–272.

Hoshino, K., Brandt, M., Manfrino, C., Riegl, B. and Steiner, S. C. C. (2003). Assessment of the coral reefs of the Turks and Caicos Islands (Part 2: Fish communities). *Atoll Research Bulletin* **496**, 480–499.

Houghton, J. T. (1997). ‘‘Global Warming: The Complete Briefing’’. Cambridge University Press, Cambridge and New York.

Howe, M. A. (1912). The building of ‘‘coral’’ reefs. *Science* **35**, 837–842.

Hubbard, D. K. (1992). Hurricane-induced sediment transport in open-shelf tropical systems—an example from St. Croix, U.S. Virgin Islands. *Journal of Sedimentary Petrology* **62**, 946–960.

Hubbard, D. K. (1997). Reefs as dynamic systems. *In* ‘‘Life and Death of Coral Reefs’’ (C. Birkeland, ed.), pp. 43–67. Chapman & Hall, New York.

Hubbard, D. K. and Scaturo, D. (1985). Growth rates of seven species of scleractinean corals from Cane Bay and Salt River, St. Croix, USVI. *Bulletin of Marine Science* **36**, 325–338.

Hubbard, D. K., Burke, R. B. and Gill, I. P. (1986). Styles of reef accretion along a steep, shelf-edge reef, St. Croix, U.S. Virgin Islands. *Journal of Sedimentary Petrology* **56**, 848–861.

Hubbard, D. K., Miller, A. I. and Scaturo, D. (1990). Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* **60**, 335–360.

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–1551.

Hughes, T. P. and Connell, J. H. (1999). Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* **44**, 932–940.

Hughes, T. P. and Tanner, J. E. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250–2263.

Hughes, T. P., Reed, D. C. and Boyle, M. J. (1987). Herbivory on coral reefs: Community structure following mass mortalities of sea urchins. *Journal of Experimental Marine Biology and Ecology* **113**, 39–59.

Hughes, T., Szmant, A. M., Steneck, R., Carpenter, R. and Miller, S. (1999). Algal blooms on coral reefs: What are the causes? *Limnology and Oceanography* **44**, 1583–1586.

Hunte, W., Côté, I. and Tomascik, T. (1986). On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. *Coral Reefs* **4**, 135–139.

Hunter, I. G. (1977). Sediment production by *Diadema antillarum* on a Barbados fringing reef. *In* ‘‘Proceedings, Third International Coral Reef Symposium’’ (D. L. Taylor, ed.), Vol. 2, pp. 106–109. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Huston, M. (1985a). Patterns of species diversity in relation to depth at Discovery Bay, Jamaica. *Bulletin of Marine Science* **37**, 928–935.

Huston, M. (1985b). Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* **4**, 19–25.

Huston, M. A. (1985c). Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* **16**, 149–177.

IPCC (2001). ‘‘Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of Intergovernmental Panel on Climate Change’’ (J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, C. A. Johnson and K. Maskell, eds.) Cambridge University Press, Cambridge and New York.

Itzkowitz, M. (1977a). Spatial organisation of the Jamaican damselfish community. *Journal of Experimental Marine Biology and Ecology* **28**, 217–241.

Itzkowitz, M. (1977b). Group organisation of a territorial damselfish, *Eupomacentrus planifrons*. *Behaviour* **65**, 125–137.

Iversen, E. S., Jory, D. E. and Bannerot, S. P. (1986). Predation on queen conchs, *Strombus gigas*, in the Bahamas. *Bulletin of Marine Science* **39**, 61–75.

Jackson, J. B. C. (1991). Adaptation and diversity of reef corals. *Bioscience* **41**, 475–482.

Jackson, J. B. C. (1997). Reefs since Columbus. *Coral Reefs* **16**, S23–S32.

Jackson, J. B. C., Cubit, J. D., Keller, B. D., Batista, V., Burns, K., Caffey, H. M., Caldwell, R. L., Garrity, S. D., Getter, C. D., Gonzalez, C., Guzman, H. M., Kaufmann, K. W., Knap, A. H., Levings, S. C., Marshall, M. J., Steger, R., Thompson, R. C. and Weil, E. (1989). Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* **243**, 37–44.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.

Johnson, C., Klumpp, D., Field, J. and Bradbury, R. (1995). Carbon flux on coral reefs: Effects of large shifts in community structure. *Marine Ecology Progress Series* **126**, 123–143.

Johnson, K. G. (1992). Population dynamics of a free-living coral: Recruitment, growth and survivorship of *Manicina areolata* (Linnaeus) on the Caribbean coast of Panama. *Journal of Experimental Marine Biology and Ecology* **164**, 171–191.

Jones, G. P., Ferrell, D. J. and Sale, P. F. (1991). Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. *In* "The Ecology of Fishes on Coral Reefs" (P. F. Sale, ed.), pp. 156–179. Academic Press, Inc, San Diego.

Jordan, E., Merino, M., Moreno, O. and Martin, E. (1981). Community structure of coral reefs in the Mexican Caribbean. *In* "Proceedings of the Fourth International Coral Reef Symposium, Manila" (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 2, pp. 303–308. University of the Philippines, Quezon City, The Philippines.

Jordán-Dahlgren, E. and Rodríguez-Martínez, R. E. (1998). Post-hurricane initial recovery of *Acropora palmata* in two reefs of the Yucatán Peninsula, Mexico. *Bulletin of Marine Science* **63**, 213–228.

Kaldy, J. E. and Dunton, K. H. (2000). Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. *Marine Ecology-Progress Series* **193**, 271–283.

Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). *In* "The Biology and Management of Lobsters" (J. S. Cobb and B. F. Phillips, eds.), Vol. II, pp. 59–96. Academic Press, New York.

Kanciruk, P. and Herrnkind, W. (1978). Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): Behaviour and environmental correlates. *Bulletin of Marine Science* **28**, 601–623.

Keller, B. D. (1983). Coexistence of sea urchins in seagrass meadows: An experimental analysis of competition and predation. *Ecology* **64**, 1581–1598.

Kinsey, D. W. (1981). The Pacific/Atlantic reef growth controversy. *In* "Proceedings of the Fourth International Coral Reef Symposium, Manila" (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 1, pp. 493–498. University of the Philippines, Quezon City, The Philippines.

Kinsey, D. W. (1983). Standards of performance in coral reef primary production and carbon turnover. *In* "Perspectives on Coral Reefs" (D. J. Barnes, ed.), pp. 209–220. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Kinsey, D. W. (1985). Metabolism, calcification and carbon production. I. Systems level studies. *In* "Proceedings of the Fifth International Coral Reef Congress, Tahiti" (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 4, pp. 505–526. Antenne Museum–EPHE, Moorea, French Polynesia.

Kirsch, K. D., Valentine, J. F. and Heck, K. L. (2002). Parrotfish grazing on turtlegrass *Thalassia testudinum*: Evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. *Marine Ecology Progress Series* **227**, 71–85.

Kjerfve, B., Magill, K. E., Porter, J. W. and Woodley, J. D. (1986). Hindcasting of hurricane characteristics and observed storm damage on a fringing reef, Jamaica, West Indies. *Journal of Marine Research* **44**, 119–148.

Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J. P., Langdon, C. and Opdyke, B. N. (1999a). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118–120.

Kleypas, J. A., McManus, J. W. and Menez, L. A. B. (1999b). Environmental limits to coral reef development: Where do we draw the line? *American Zoologist* **39**, 146–159.

Klomp, K. D. and Kooistra, D. J. (2003). A post-hurricane, rapid assessment of reefs in the windward Netherlands Antilles (stony corals, algae and fishes). *Atoll Research Bulletin* **496**, 404–437.

Knowlton, N., Lang, J. C., Rooney, M. C. and Clifford, P. (1981). Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature* **294**, 251–252.

Knowlton, N., Lang, J. C. and Keller, B. D. (1990). Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. *Smithsonian Contributions to the Marine Sciences* **31**, 1–25.

Koch, M. S. and Madden, C. J. (2001). Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves. *Marine Ecology Progress Series* **219**, 109–119.

Kramer, P. A. (2003). Synthesis of coral reef health indicators for the western Atlantic: Results of the AGRRA program (1997–2000). *Atoll Research Bulletin* **496**, 1–57.

Kramer, P. A. and Bischof, B. G. (2003). Assessment tables for Abaco, Bahamas (fish), Lighthouse Atoll, Belize (corals, algae, fishes), and Bonaire, Netherlands Antilles (corals, algae, fishes). *Atoll Research Bulletin* **496**, 590–597.

Kramer, P., Kramer, P. R., Arias-González, E. and McField, M. (2000). Status of coral reefs of northern Central America: Mexico, Belize, Guatemala, Honduras, Nicaragua and El Salvador. *In* "Status of Coral Reefs of the World: 2000" (C. R. Wilkinson, ed.), pp. 287–313. Australian Institute of Marine Science, Cape Ferguson, Queensland and Dampier.

Kramer, P. A., Marks, K. W. and Turnbull, T. L. (2003). Assessment of the Andros Island reef system, Bahamas (Part 2: Fishes). *Atoll Research Bulletin* **496**, 100–123.

Land, L. S. (1979). The fate of reef-derived sediment on the north Jamaican island slope. *Marine Geology* **29**, 55–71.

Landsea, C. W., Pielke, R. A., Mestas-Nunez, A. and Knaff, J. A. (1999). Atlantic basin hurricanes: Indices of climatic changes. *Climatic Change* **42**, 89–129.

Lang, J. C., Lasker, H. R., Gladfelter, E. H., Hallock, P., Jaap, W. C., Losada, F. J. and Muller, R. G. (1992). Spatial and temporal variability during periods of "recovery" after mass bleaching on western Atlantic coral reefs. *American Zoologist* **32**, 696–706.

Langmead, O. and Sheppard, C. (2004). Coral reef community dynamics and disturbance: A simulation model. *Ecological Modelling* **175**, 271–290.

Lapointe, B. E. and O'Connell, J. (1989). Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: Eutrophication of a confined, phosphorus-limited marine ecosystem. *Estuarine Coastal and Shelf Science* **28**, 347–360.

Larkum, A. W. D. (1983). The primary productivity of plant communities on coral reefs. *In* ''Perspectives on Coral Reefs'' (D. J. Barnes, ed.), pp. 221–230. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Larned, S. T. (1998). Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology* **132**, 409–421.

Lawson, G. L., Kramer, D. L. and Hunte, W. (1999). Size-related habitat use and schooling behaviour in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Environmental Biology of Fishes* **54**, 19–33.

Leboeuf, B. J., Kenyon, K. W. and Villaramirez, B. (1986). The Caribbean monk seal is extinct. *Marine Mammal Science* **2**, 70–72.

Lessios, H. A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* **19**, 371–393.

Lessios, H. A. (1991). Presence and absence of monthly reproductive rhythms among eight Caribbean echinoids off the coast of Panama. *Journal of Experimental Marine Biology and Ecology* **153**, 27–47.

Lessios, H. A., Robertson, D. R. and Cubit, J. D. (1984). Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**, 335–337.

Levitan, D. R. (1988). Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **119**, 167–178.

Lewis, J. B. (1960). The coral reefs and coral communities of Barbados, W.I. *Canadian Journal of Zoology* **38**, 1133–1145.

Lewis, J. B. (1974). Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. *In* ''Proceedings of the Second International Coral Reef Symposium'' (A. M. Cameron, B. M. Cambell, A. B. Cribb, R. Endean, J. S. Jell, O. A. Jones, P. Mather and F. H. Talbot, eds.), Vol. 2, pp. 201–206. The Great Barrier Reef Committee, Brisbane, Australia.

Lewis, J. B. (1977). Processes of organic production on coral reefs. *Biological Reviews* **52**, 305–347.

Lewis, J. B. (1981). Estimates of secondary production of reef corals. *In* ''Proceedings of the Fourth International Coral Reef Symposium, Manila'' (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 2, pp. 369–374. University of the Philippines, Quezon City, The Philippines.

Lewis, S. M. (1985). Herbivory on coral reefs: Algal susceptibility to herbivorous fishes. *Oecologia* **65**, 370–375.

Lewis, S. M. (1986). The role of herbivorous fishes in the organisation of a Caribbean reef community. *Ecological Monographs* **56**, 183–200.

Lewis, S. M. and Wainwright, P. C. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology* **87**, 215–228.

Liddell, W. D. and Ohlhorst, S. L. (1986). Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *Journal of Experimental Marine Biology and Ecology* **95**, 271–278.

Liddell, W. D. and Ohlhorst, S. L. (1987). Patterns of reef community structure, north Jamaica. *Bulletin of Marine Science* **40**, 311–329.

Liddell, W. D., Ohlhorst, S. L. and Boss, S. K. (1984). Community patterns on the Jamaican fore reef (15–56 M). *Palaeontographica Americana* **54**, 385–389.

Lindeman, K. C., Diaz, G. A., Serafy, J. E. and Ault, J. S. (1998). A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute* **50**, 385–416.

Lipcius, R. N., Stockhausen, W. T., Eggleston, D. B., Marshall, L. S. and Hickey, B. (1997). Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: Source-sink dynamics? *Marine and Freshwater Research* **48**, 807–815.

Lipcius, R. N., Eggleston, D. B., Miller, D. L. and Luhrs, T. C. (1998). The habitat-survival function for Caribbean spiny lobster: An inverted size effect and non-linearity in mixed algal and seagrass habitats. *Marine and Freshwater Research* **49**, 807–816.

Lirman, D. (1994). Ontogenic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *Journal of Experimental Marine Biology and Ecology* **180**, 71–81.

Lirman, D. (1999). Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. *Bulletin of Marine Science* **65**, 235–252.

Lirman, D. and Biber, P. (2000). Seasonal dynamics of macroalgal communities of the northern Florida reef tract. *Botanica Marina* **43**, 305–314.

Lirman, D. and Fong, P. (1996). Sequential storms cause zone-specific damage on a reef in the northern Florida reef tract: Evidence from Hurricane Andrew and the 1993 Storm of the Century. *Florida Scientist* **59**, 50–64.

Lirman, D. and Fong, P. (1997). Patterns of damage to the branching coral *Acropora palmata* following Hurricane Andrew: Damage and survivorship of hurricane-generated asexual recruits. *Journal of Coastal Research* **13**, 67–72.

Littler, M. M. and Littler, D. S. (1984). Models of tropical reef biogenesis: The contribution of algae. *Progress in Phycological Research* **3**, 323–364.

Littler, M. M., Littler, D. S. and Taylor, P. R. (1983a). Evolutionary strategies in a tropical barrier reef system: Functional-form groups of marine macroalgae. *Journal of Phycology* **19**, 229–237.

Littler, M. M., Taylor, P. R. and Littler, D. S. (1983b). Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* **2**, 111–118.

Littler, M. M., Taylor, P. R., Littler, D. S., Sims, R. H. and Norris, J. N. (1987). Dominant macrophyte standing stocks, productivity and community structure on a Belizean barrier reef. *Atoll Research Bulletin* **302**, 1–18.

Littler, M. M., Taylor, P. R. and Littler, D. S. (1989). Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* **80**, 331–340.

Liu, J., and Taylor, W. W. (eds.) (2002). ‘‘Integrating Landscape Ecology into Natural Resource Management’’. Cambridge University Press, Cambridge.

Lobel, P. S. (1980). Herbivory by damselfishes and their role in coral reef community ecology. *Bulletin of Marine Sciences* **30**, 273–289.

Lobel, P. S. and Ogden, J. C. (1981). Foraging by the herbivorous parrotfish *Sparisoma radians*. *Marine Biology* **64**, 173–183.

Loreau, M., Naeem, S., and Inchausti, P. (eds.) (2002). ‘‘Biodiversity and Ecosystem Functioning. Synthesis and Perspectives’’ Oxford University Press, New York.

Loya, Y. (1976). Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bulletin of Marine Science* **26**, 450–466.

Lubchenco, J. and Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* **12**, 405–437.

Luckhurst, B. E. and Luckhurst, K. (1977). Recruitment patterns of coral reef fishes on the fringing reef of Curaçao, Netherlands Antilles. *Canadian Journal of Zoology* **55**, 681–689.

Lugo, A. E. and Snedaker, S. C. (1974). The ecology of mangroves. *Annual Review of Ecology and Systematics* **5**, 39–64.

Lugo-Fernández, A., Hernández-Ávila, M. L. and Roberts, H. H. (1994). Wave-energy distribution and hurricane effects on Margarita Reef, southwestern Puerto Rico. *Coral Reefs* **13**, 21–32.

Macintyre, I. G. (1997). Reevaluating the role of crustose coralline algae in the construction of coral reefs. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 725–730. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Macintyre, I. G., Graus, R. R., Reinthal, P. N., Littler, M. M. and Littler, D. S. (1987). The barrier reef sediment apron: Tobacco Reef, Belize. *Coral Reefs* **6**, 1–12.

Maida, M., Coll, J. C. and Sammarco, P. W. (1994). Shedding new light on scleractinian coral recruitment. *Journal of Experimental Marine Biology and Ecology* **180**, 189–202.

Marx, J. M. and Herrnkind, W. F. (1985). Macroalgae (Rhodophyta: *Laurencia* Spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Science* **36**, 423–431.

Mateo, I. and Tobias, W. J. (2004). Survey of nearshore fish communities on tropical backreef lagoons on the southeastern coast of St. Croix. *Caribbean Journal of Science* **40**, 327–342.

May, J. A., Macintyre, I. G. and Perkins, R. D. (1982). Distribution of microborers within planted substrates along a barrier reef transect, Carrie Bow Cay, Belize. *In* ''The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities'' (K. Rützler and I. G. Macintyre, eds.), pp. 93–107. Smithsonian Contributions to the Marine Sciences Number 12, Smithsonian Institution Press, Washington, D.C.

McAfee, S. T. and Morgan, S. G. (1996). Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology* **125**, 427–437.

McClanahan, T. R. (1995). A coral reef ecosystem-fisheries model: Impacts of fishing intensity and catch selection on reef structure and processes. *Ecological Modelling* **80**, 1–19.

McCoy, E. D. and Bell, S. S. (1991). Habitat structure: The evolution and diversification of a complex topic. *In* ''Habitat Structure, the Physical Arrangement of Objects in Space'' (S. S. Bell, E. D. McCoy and H. R. Mushinsky, eds.), pp. 3–27. Chapman & Hall, New York.

McFarland, W. N., Brothers, E. B., Ogden, J. C., Shulman, M. J., Bermingham, E. and Kotchian-Prentiss, N. M. (1985). Recruitment patterns in young French grunts, *Haemulon flavolineatum* (Family Haemulidae), at St. Croix, Virgin Islands. *Fisheries Bulletin* **83**, 413–426.

McField, M. D. (1999). Coral response during and after mass bleaching in Belize. *Bulletin of Marine Science* **64**, 155–172.

McGehee, M. A. (1994). Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Marine Ecology Progress Series* **105**, 243–255.

McGehee, M. A. (1995). Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. *Environmental Biology of Fishes* **44**, 393–401.

McGrath, T. A. and Smith, G. W. (1998). The effects of the 1995/1996 Western Atlantic coral bleaching event on the patch reefs around San Salvador Island, Bahamas. *Revista De Biologia Tropical* **46**, 91–99.

Mejia, L. S. and Garzon-Ferreira, J. (2000). Reef fish community structure in four atolls of the San Andres Providencia archipelago (southwestern Caribbean). *Revista De Biologia Tropical* **48**, 883–896.

Meyer, J. L. and Schultz, E. T. (1985). Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography* **30**, 146–156.

Meyer, J. L., Schultz, E. T. and Helfman, G. S. (1983). Fish schools: An asset to corals. *Science* **220**, 1047–1049.

Mikkelsen, P. M. and Cracraft, J. (2001). Marine biodiversity and the need for systematic inventories. *Bulletin of Marine Science* **69**, 525–534.

Miller, M. W., Weil, E. and Szmant, A. M. (2000). Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* **19**, 115–123.

Moberg, F. and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**, 215–233.

Moberg, F. and Rönnbäck, P. (2003). Ecosystem services of the tropical seascape: Interactions, substitutions and restoration. *Ocean & Coastal Management* **46**, 27–46.

Mobley, C. D. (1994). ‘‘Light and Water: Radiative Transfer in Natural Waters’’. Academic Press, San Diego.

Moore, C. H. and Shedd, W. W. (1977). Effective rates of sponge bioerosion as a function of carbonate production. *In* ‘‘Proceedings, Third International Coral Reef Symposium’’ (D. L. Taylor, ed.), Vol. 2, pp. 499–505. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Moran, M. A., Wicks, R. J. and Hodson, R. E. (1991). Export of dissolved organic matter from a mangrove swamp ecosystem: Evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary production. *Marine Ecology Progress Series* **76**, 175–184.

Morrison, D. (1988). Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* **69**, 1367–1382.

Morrissey, J. (1985). Primary productivity of coral reef benthic macroalgae. *In* ‘‘Proceedings of the Fifth International Coral Reef Congress, Tahiti’’ (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 5, pp. 77–82. Antenne Museum–EPHE, Moorea, French Polynesia.

Morse, D. E., Hooker, N., Morse, A. N. C. and Jensen, R. A. (1988). Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology and Ecology* **116**, 193–217.

Moses, C. S. and Bonem, R. M. (2001). Recent population dynamics of *Diadema antillarum* and *Tripneustes ventricosus* along the north coast of Jamaica, W.I. *Bulletin of Marine Science* **68**, 327–336.

Mueller, K. W., Dennis, G. D., Eggleston, D. B. and Wicklund, R. I. (1994). Size-specific social interactions and foraging styles in a shallow water population of mutton snapper, *Lutjanus analis* (Pisces, Lutjanidae), in the Central Bahamas. *Environmental Biology of Fishes* **40**, 175–188.

Muller-Parker, G. and D'Elia, C. F. (1997). Interactions between corals and their symbiotic algae. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 96–113. Chapman & Hall, New York.

Mumby, P. J. (1999a). Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Marine Ecology Progress Series* **190**, 27–35.

Mumby, P. J. (1999b). Can Caribbean coral populations be modelled at metapopulation scales? *Marine Ecology Progress Series* **180**, 275–288.

Mumby, P. J. and Dytham, C. (2005). Metapopulation dynamics of hard corals. *In* ''Marine Metapopulations'' (J. P. Kritzer and P. F. Sale, eds.), in press. Academic Press, San Diego.

Mumby, P. J. and Edwards, A. J. (2002). Mapping marine environments with IKONOS imagery: Enhanced spatial resolution can deliver greater thematic accuracy. *Remote Sensing of Environment* **82**, 248–257.

Mumby, P. J. and Harborne, A. R. (1999). Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological Conservation* **88**, 155–163.

Mumby, P. J. and Wabnitz, C. C. C. (2002). Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes* **63**, 265–279.

Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., Wabnitz, C. C. C. and Llewellyn, G. (2004a). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**, 533–536.

Mumby, P. J., Skirving, W., Strong, A. E., Hardy, J. T., LeDrew, E. F., Hochberg, E. J., Stumpf, R. P. and David, L. T. (2004b). Remote sensing of coral reefs and their physical environment. *Marine Pollution Bulletin* **48**, 219–228.

Nagelkerken, I. and van der Velde, G. (2002). Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Marine Ecology Progress Series* **245**, 191–204.

Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Morinière, E. and van der Velde, G. (2000a). Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: Patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series* **202**, 175–192.

Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Morinière, E. and van der Velde, G. (2000b). Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series* **194**, 55–64.

Nagelkerken, I., van der Velde, G., Gorissen, M. W., Meijer, G. J., van't Hof, T. and den Hartog, C. (2000c). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science* **51**, 31–44.

Nagelkerken, W. P. (1977). The distribution of the graysby *Petrometopan cruentatum* (Lacepede) on the coral reef at the southwest coast of Curacao. *In* ''Proceedings, Third International Coral Reef Symposium'' (D. L. Taylor, ed.), Vol. 1, ''Biology'', pp. 311–315. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Nagelkerken, W. P. (1981). Distribution and ecology of the groupers (Serranidae) and snappers (Lutjanidae) of the Netherlands Antilles. *Foundation for Scientific Research in Surinam and the Netherlands Antilles, Natural History Series* **3**, 7–71.

Nemeth, R. S. (1997). Spatial patterns of bicolour damselfish populations in Jamaica and St. Croix are determined by similar post-settlement processes. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 1017–1022. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Nemeth, R. S., Whaylen, L. D. and Pattengill-Semmens, C. V. (2003). A rapid assessment of coral reefs in the Virgin Islands (Part 2: Fishes). *Atoll Research Bulletin* **496**, 566–589.

Newman, S. P. and Gruber, S. H. (2002). Comparison of mangrove and seagrass fish and macroinvertebrate communities in Bimini. *Bahamas Journal of Science* **9**, 19–26.

Nicholls, R. J., Hoozemans, F. M. J. and Marchand, M. (1999). Increasing flood risk and wetland losses due to global sea-level rise: Regional and global analyses. *Global Environmental Change-Human and Policy Dimensions* **9**, S69–S87.

Núñez-Lara, E., González-Salas, C., Ruiz-Zárate, M. A., Hernández-Landa, R. and Arias-González, J. E. (2003). Condition of coral reef ecosystems in central-southern Quintana Roo (Part 2: Reef fish communities). *Atoll Research Bulletin* **496**, 338–359.

Odum, H. T. (1956). Primary production in flowing waters. *Limnology and Oceanography* **1**, 102–117.

Odum, H. T., Burkholder, P. and Rivero, J. (1959). Measurements of productivity of turtle grass flats, reefs, and the Bahia Fosforescente of southern Puerto Rico. *Publications of the Institute of Marine Science* **15**, 9–170.

Ogden, J. C. (1976). Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquatic Botany* **2**, 103–116.

Ogden, J. C. (1977). Carbonate-sediment production by parrot fish and sea urchins on Caribbean reefs. *In* ''Reefs and Related Carbonates: Ecology and Sedimentology. American Association of Petroleum Geologists Studies in Geology 4'' (G. H. Frost, M. P. Weis and J. B. Saunders, eds.), pp. 281–288. American Association of Petroleum Geologists, Tulsa, Oklahoma.

Ogden, J. C. (1997). Ecosystem interactions in the tropical coastal seascape. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 288–297. Chapman & Hall, New York.

Ogden, J. C. and Buckman, N. S. (1973). Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* **54**, 589–596.

Ogden, J. C. and Lobel, P. S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* **3**, 49–63.

Ogden, J. C. and Zieman, J. C. (1977). Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. *In* ''Proceedings, Third International Coral Reef Symposium'' (D. L. Taylor, ed.), Vol. 1, ''Biology'', pp. 377–382. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Ogden, J. C., Brown, R. A. and Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science* **182**, 715–717.

Ogden, J. C., Robinson, L., Whitlock, K., Daganhardt, H. and Cebula, R. (1983). Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **66**, 199–205.

Opitz, S. (1996). ''Trophic Interactions in Caribbean Coral Reefs. ICLARM Technical Report 43''. International Center for Living Aquatic Resources Management, Manila.

Overholtzer, K. L. and Motta, P. J. (1999). Comparative resource use by juvenile parrotfishes in the Florida Keys. *Marine Ecology Progress Series* **177**, 177–187.

Parrish, J. D. (1987). The trophic biology of snappers and groupers. *In* ''Tropical Snappers and Groupers. Biology and Fisheries Management'' (J. J. Polovina and S. Ralston, eds.), pp. 405–463. Westview Press, Boulder.

Patterson, K. L., Porter, J. W., Ritchie, K. E., Polson, S. W., Mueller, E., Peters, E. C., Santavy, D. L. and Smiths, G. W. (2002). The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 8725–8730.

Pearson, R. G. (1981). Recovery and recolonisation of coral reefs. *Marine Ecology Progress Series* **4**, 105–122.

Perry, C. T. (1998a). Macroborers within coral framework at Discovery Bay, north Jamaica: Species distribution and abundance, and effects on coral preservation. *Coral Reefs* **17**, 277–287.

Perry, C. T. (1998b). Grain susceptibility to the effects of microboring: Implications for the preservation of skeletal carbonates. *Sedimentology* **45**, 39–51.

Perry, C. T. (1999). Reef framework preservation in four contrasting modern reef environments, Discovery Bay, Jamaica. *Journal of Coastal Research* **15**, 796–812.

Perry, C. T. and Macdonald, I. A. (2002). Impacts of light penetration on the bathymetry of reef microboring communities: Implications for the development of microendolithic trace assemblages. *Palaeogeography Palaeoclimatology Palaeoecology* **186**, 101–113.

Peters, E. C. (1997). Diseases of coral-reef organisms. *In* ''Life and Death of Coral Reefs'' (C. Birkeland, ed.), pp. 114–139. Chapman & Hall, New York.

Peters, E. C., Oprandy, J. J. and Yevich, P. P. (1983). Possible causal agent of white band disease in Caribbean acroporid corals. *Journal of Invertebrate Pathology* **41**, 394–396.

Polunin, N. V. C. and Roberts, C. M. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**, 167–176.

Posada, J. M., Villamizar, E. and Alvarado, D. (2003). Rapid assessment of coral reefs in the Archipiélago De Los Roques National Park, Venezuela (Part 2: Fishes). *Atoll Research Bulletin* **496**, 530–543.

Preece, A. L. and Johnson, C. R. (1993). Recovery of model coral communities: Complex behaviours from interaction of parameters operating at different spatial scales. *In* ''Complex Systems: From Biology to Computation'' (D. G. Green and T. Bossomaier, eds.), pp. 69–81. IOS Press, Amsterdam.

Rakitin, A. and Kramer, D. L. (1996). Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series* **131**, 97–113.

Randall, J. E. (1964). Contributions to the biology of the queen conch, *Strombus gigas*. *Bulletin of Marine Science* **14**, 246–295.

Randall, J. E. (1965). Grazing effect on sea grasses by herbivorous fishes in the West Indies. *Ecology* **46**, 255–260.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**, 665–847.

Randall, J. E., Schroeder, R. E. and Starck, W. A. (1964). Notes on the biology of the echinoid *Diadema antillarum*. *Caribbean Journal of Science* **4**, 421–433.

Rasser, M. W. and Riegl, B. (2002). Holocene coral reef rubble and its binding agents. *Coral Reefs* **21**, 57–72.

Ray, M. and Stoner, A. W. (1994). Experimental analysis of growth and survivorship in a marine gastropod aggregation: Balancing growth with safety in numbers. *Marine Ecology Progress Series* **105**, 47–59.

Ray, M. and Stoner, A. W. (1995). Growth, survivorship, and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. *Marine Ecology Progress Series* **123**, 83–94.

Ray-Culp, M., Davis, M. and Stoner, A. W. (1999). Predation by xanthid crabs on early post-settlement gastropods: The role of prey size, prey density, and habitat complexity. *Journal of Experimental Marine Biology and Ecology* **240**, 303–321.

Reinthal, P. N. and Lewis, S. M. (1986). Social behaviour, foraging efficiency and habitat utilisation in a group of tropical herbivorous fish. *Animal Behaviour* **34**, 1687–1693.

Reiswig, H. M. (1971). *In situ* pumping activities of tropical Demospongiae. *Marine Biology* **9**, 38–50.

Richardson, L. L., Goldberg, W. M., Kuta, K. G., Aronson, R. B., Smith, G. W., Ritchie, K. B., Halas, J. C., Feingold, J. S. and Miller, S. L. (1998). Florida's mystery coral-killer identified. *Nature* **392**, 557–558.

Richmond, R. H. (1997). Reproduction and recruitment in corals: Critical links in the persistence of reefs. *In* ‘‘Life and Death of Coral Reefs’’ (C. Birkeland, ed.), pp. 175–197. Chapman & Hall, New York.

Richmond, R. H. and Hunter, C. L. (1990). Reproduction and recruitment of corals: Comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Marine Ecology Progress Series* **60**, 185–203.

Risk, A. (1998). The effects of interactions with reef residents on the settlement and subsequent persistence of ocean surgeonfish, *Acanthurus bahianus*. *Environmental Biology of Fishes* **51**, 377–389.

Risk, M. J. and MacGeachy, J. K. (1978). Aspects of bioerosion of modern Caribbean reefs. *Revista de Biologia Tropical* **26**(Suppl. 1), 85–105.

Risk, M. J. and Sammarco, P. W. (1982). Bioerosion of corals and the influence of damselfish territoriality: A preliminary study. *Oecologia* **52**, 376–380.

Roberts, C. M. (1995). Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* **9**, 988–995.

Roberts, C. M. and Hawkins, J. P. (2000). ‘‘Fully-Protected Marine Reserves: A Guide’’. WWF Endangered Seas Campaign and Environment Department, Washington, D.C., and University of York, York.

Roberts, H. H., Murray, S. P. and Suhayda, J. N. (1977). Physical processes in a fore-reef shelf environment. *In* ‘‘Proceedings, Third International Coral Reef Symposium’’ (D. L. Taylor, ed.), Vol. 2, pp. 507–515. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Roberts, H. H., Wilson, P. A. and Lugo-Fernández, A. (1992). Biologic and geologic responses to physical processes: Examples from modern reef systems of the Caribbean-Atlantic region. *Continental Shelf Research* **12**, 809–834.

Robertson, D. R. (1988). Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: Due to settlement, or post-settlement events? *Marine Biology* **97**, 495–501.

Robertson, D. R. (1991). Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panamá indicate food limitation. *Marine Biology* **111**, 437–444.

Robertson, D. R. (1996). Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* **77**, 885–899.

Robertson, D. R., Hoffman, S. G. and Sheldon, J. M. (1981). Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. *Ecology* **62**, 1162–1169.

Rogers, C. S. (1979). The productivity of San Cristobal Reef, Puerto Rico. *Limnology and Oceanography* **24**, 342–349.

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**, 185–202.

Rogers, C. S. (1993a). A matter of scale: Damage from Hurricane Hugo (1980) to U. S. Virgin Islands reefs at the colony, community, and whole reef level. *In* ‘‘Proceedings of the Seventh International Coral Reef Symposium, Guam’’ (R. H. Richmond, ed.), Vol. 1, pp. 127–133. University of Guam Marine Laboratory, Mangilao, Guam.

Rogers, C. S. (1993b). Hurricanes and coral reefs: The intermediate disturbance hypothesis revisited. *Coral Reefs* **12**, 127–137.

Rogers, C. S. and Salesky, N. H. (1981). Productivity of *Acropora palmata* (Lamarck), macroscopic algae, and algal turf from Tague Bay Reef, St. Croix, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **49**, 179–187.

Rogers, C. S., Suchanek, T. H. and Pecora, F. A. (1982). Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science* **32**, 532–548.

Rogers, C. S., Gilnack, M. and Fitz, H. C. (1983). Monitoring of coral reefs with linear transects: A study of storm damage. *Journal of Experimental Marine Biology and Ecology* **66**, 285–300.

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J. and Hardin, J. (1984). Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* **3**, 69–76.

Rogers, C. S., McLain, L. N. and Tobias, C. R. (1991). Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Marine Ecology Progress Series* **78**, 189–199.

Rogers, C. S., Garrison, V. and Grober-Dunsmore, R. (1997). A fishy story about hurricanes and herbivory: Seven years of research on a reef in St. John, U.S. Virgin Islands. *In* ‘‘Proceedings of the 8th International Coral Reef Symposium’’ (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 555–560. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Rooker, J. R. (1995). Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. *Bulletin of Marine Science* **56**, 881–894.

Rowan, R. (2004). Thermal adaptation in reef coral symbionts. *Nature* **430**, 742.

Ruiz-Zárate, M. A. and Arias-González, J. E. (2004). Spatial study of juvenile corals in the northern region of the Mesoamerican Barrier Reef System (MBRS). *Coral Reefs* **23**, 584–594.

Rützler, K. (1975). The role of burrowing sponges in bioerosion. *Oecologia* **19**, 203–216.

Rützler, K. and Santavy, D. L. (1983). The black band disease of Atlantic reef corals. I. Description of a cyanophyte pathogen. *P.S.Z.N.: Marine Ecology* **4**, 301–319.

Sadd, J. L. (1984). Sediment transport and $CaCO_3$ budget on a fringing reef, Cane Bay, St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science* **35**, 221–238.

Sammarco, P. W. (1980). *Diadema* and its relationship to coral spat mortality: Grazing, competition, and biological disturbance. *Journal of Experimental Marine Biology and Ecology* **45**, 245–272.

Sammarco, P. W. (1982). Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. *Journal of Experimental Marine Biology and Ecology* **61**, 31–55.

Sammarco, P. W. (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Marine Ecology Progress Series* **13**, 1–14.

Sammarco, P. W. and Carleton, J. H. (1981). Damselfish territoriality and coral community structure: Reduced grazing, coral recruitment, and effects on coral spat. *In* ''Proceedings of the Fourth International Coral Reef Symposium, Manila'' (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh and R. T. Tsuda, eds.), Vol. 2, pp. 525–535. University of the Philippines, Quezon City, The Philippines.

Sammarco, P. W., Carleton, J. H. and Risk, M. J. (1986). Effects of grazing and damselfish territoriality on bioerosion of dead corals: Direct effects. *Journal of Experimental Marine Biology and Ecology* **98**, 1–19.

Sammarco, P. W., Risk, M. J. and Rose, C. (1987). Effects of grazing and damselfish territoriality on internal bioerosion of dead corals: Indirect effects. *Journal of Experimental Marine Biology and Ecology* **112**, 185–199.

Santavy, D. L. and Peters, E. C. (1997). Microbial pests: Coral disease in the western Atlantic. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 607–612. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Schmitt, E. F., Sluka, R. D. and Sullivan-Sealey, K. M. (2002). Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. *Coral Reefs* **21**, 216–223.

Scoffin, T. P. (1993). The geological effects of hurricanes on coral reefs and the interpretation of storm deposits. *Coral Reefs* **12**, 203–221.

Scoffin, T. P., Stearn, C. W., Boucher, D., Frydl, P., Hawkins, C. M., Hunter, I. G. and MacGeachy, J. K. (1980). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II—erosion, sediments and internal structure. *Bulletin of Marine Science* **30**, 475–508.

Sebens, K. P. (1997). Adaptive responses to water flow: Morphology, energetics, and distribution of reef corals. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. II, pp. 1053–1058. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Serafy, J. E., Faunce, C. H. and Lorenz, J. J. (2003). Mangrove shoreline fishes of Biscayne Bay, Florida. *Bulletin of Marine Science* **72**, 161–180.

Sheppard, C. R. C. (1982). Coral populations on reef slopes and their major controls. *Marine Ecology Progress Series* **7**, 83–115.

Sheppard, C. R. C., Matheson, K., Bythell, J. C., Murphy, P., Blair Myers, C. and Blake, B. (1995). Habitat mapping in the Caribbean for management and conservation, use and assessment of aerial photography. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**, 277–298.

Short, F. T. and Neckles, H. A. (1999). The effects of global climate change on seagrasses. *Aquatic Botany* **63**, 169–196.

Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* **74**, 85–109.

Shulman, M. J. (1985). Recruitment of coral reef fishes: Effects of distribution of predators and shelter. *Ecology* **66**, 1056–1066.

Shulman, M. J. and Ogden, J. C. (1987). What controls tropical reef fish populations: Recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series* **39**, 233–242.

Sluka, R. and Sullivan, K. M. (1996). The influence of habitat on the size distribution of groupers in the upper Florida Keys. *Environmental Biology of Fishes* **47**, 177–189.

Sluka, R., Chiappone, M. and Sullivan, K. M. (1994). Comparison of juvenile grouper populations in southern Florida and the central Bahamas. *Bulletin of Marine Science* **54**, 871–880.

Sluka, R., Chiappone, M., Sullivan, K. M. and Wright, R. (1996a). ''Habitat and Life in the Exuma Cays, the Bahamas: The Status of Groupers and Coral Reefs in the Northern Cays''. Media Publishing, Nassau, Bahamas.

Sluka, R. D., Chiappone, M. and Sullivan, K. M. (1996b). Habitat preferences of groupers in the Exuma Cays. *Bahamas Journal of Science* **4**, 8–14.

Sluka, R., Chiappone, M., Sullivan, K. M. and Wright, R. (1997). The benefits of a marine fishery reserve for Nassau grouper *Epinephelus striatus* in the Central Bahamas. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. II, pp. 1961–1964. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Sluka, R., Chiappone, M., Sullivan, K. M., Potts, T. A., Levy, J. M., Schmitt, E. F. and Meester, G. (1998). Density, species and size distribution of groupers (Serranidae) in three habitats at Elbow Reef, Florida Keys. *Bulletin of Marine Science* **62**, 219–228.

Sluka, R. D., Chiappone, M. and Sullivan Sealey, K. M. (2001). Influence of habitat on grouper abundance in the Florida Keys, U.S.A. *Journal of Fish Biology* **58**, 682–700.

Smith, G. B. and van Nierop, M. (1986). Abundance and potential yield of spiny lobster (*Panulirus argus*) on the Little and Great Bahama Banks. *Bulletin of Marine Science* **39**, 646–656.

Smith, K. N. and Herrnkind, W. F. (1992). Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): Influence of size and shelter. *Journal of Experimental Marine Biology and Ecology* **157**, 3–18.

Smith, S. R. (1988). Recovery of a disturbed reef in Bermuda: Influence of reef structure and herbivorous grazers on algal and sessile invertebrate recruitment. *In* ''Proceedings of the 6th International Coral Reef Symposium, Australia'' (J. H. Choat, ed.), Vol. 2, pp. 267–272. 6th International Coral Reef Symposium Executive Committee, Townsville, Australia.

Smith, S. R. (1992). Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: Comparisons to Caribbean and Pacific reefs. *American Zoologist* **32**, 663–673.

Smith, S. V. (1981). The Houtman Abrolhos Islands: Carbon metabolism of coral reefs at high latitude. *Limnology and Oceanography* **26**, 612–621.

Smith, S. V. (1983). Coral reef calcification. *In* ''Perspectives on Coral Reefs'' (D. J. Barnes, ed.), pp. 240–247. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Smith, S. V. and Buddemeier, R. W. (1992). Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* **23**, 89–118.

Smith, S. V. and Kinsey, D. W. (1976). Calcium carbonate production, coral reef growth, and sea level change. *Science* **194**, 937–939.

Sotka, E. E. and Thacker, R. W. (2005). Do some corals like it hot? *Trends in Ecology & Evolution* **20**, 59–62.

Sponaugle, S. and Cowen, R. K. (1996). Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Marine and Freshwater Research* **47**, 433–447.

Stafford-Smith, M. G. and Ormond, R. F. G. (1992). Sediment rejection mechanisms of 42 species of Australian scleractinian corals. *Australian Journal of Marine and Freshwater Research* **43**, 683–705.

Stearn, C. W., Scoffin, T. P. and Martindale, W. (1977). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I—zonation and productivity. *Bulletin of Marine Science* **27**, 479–510.

Steneck, R. S. (1994). Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978–1988). *In* ''Global Aspects of Coral Reefs: Health, Hazards, and History'' (R. N. Ginsburg, ed.), pp. C32–C37. University of Miami, Florida.

Steneck, R. S. (1997). Crustose corallines, other algal functional groups, herbivores and sediments: Complex interactions along reef productivity gradients. *In* ''Proceedings of the 8th International Coral Reef Symposium'' (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 695–700. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

Steneck, R. S. and Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos* **69**, 476–498.

Stockhausen, W. T., Lipcius, R. N. and Hickey, B. M. (2000). Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bulletin of Marine Science* **66**, 957–990.

Stoddart, D. R. (1965). Re-survey of hurricane effects on the British Honduras reefs and cays. *Nature* **207**, 589–592.

Stoddart, D. R. (1969). Ecology and morphology of recent coral reefs. *Biological Reviews of the Cambridge Philosophical Society* **44**, 433–498.

Stoddart, D. R. (1974). Post-hurricane changes on the British Honduras reefs: Resurvey of 1972. *In* ''Proceedings of the Second International Coral Reef Symposium'' (A. M. Cameron, B. M. Cambell, A. B. Cribb, R. Endean, J. S. Jell, O. A. Jones, P. Mather and F. H. Talbot, eds.), Vol. 2, pp. 473–483. The Great Barrier Reef Committee, Brisbane, Australia.

Stoddart, D. R. (1985). Hurricane effects on coral reefs. *In* ''Proceedings of the Fifth International Coral Reef Congress, Tahiti'' (C. Gabrie and M. Harmelin-Vivien, eds.), Vol. 3, pp. 349–350. Antenne Museum–EPHE, Moorea, French Polynesia.

Stoner, A. W. (1989). Density-dependent growth and grazing effects of juvenile queen conch *Strombus gigas* L. in a tropical seagrass meadow. *Journal of Experimental Marine Biology and Ecology* **130**, 119–133.

Stoner, A. W. (2003). What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. *Marine Ecology Progress Series* **257**, 275–289.

Stoner, A. W. and Lally, J. (1994). High-density aggregation in queen conch *Strombus gigas*: Formation, patterns, and ecological significance. *Marine Ecology Progress Series* **106**, 73–84.

Stoner, A. W. and Ray, M. (1993). Aggregation dynamics in juvenile queen conch (*Strombus gigas*): Population structure, mortality, growth, and migration. *Marine Biology* **116**, 571–582.

Stoner, A. W. and Ray-Culp, M. (2000). Evidence for Allee effects in an overharvested marine gastropod: Density-dependent mating and egg production. *Marine Ecology Progress Series* **202**, 297–302.

Stoner, A. W. and Sandt, V. J. (1992). Population structure, seasonal movements and feeding of queen conch, *Strombus gigas*, in deep-water habitats of the Bahamas. *Bulletin of Marine Science* **51**, 287–300.

Stoner, A. W., Lin, J. and Hanisak, M. D. (1995). Relationships between seagrass bed characteristics and juvenile queen conch (*Strombus gigas* Linne) abundance in the Bahamas. *Journal of Shellfish Research* **14**, 315–323.

Stoner, A. W., Pitts, P. A. and Armstrong, R. A. (1996a). Interaction of physical and biological factors in the large-scale distribution of juvenile queen conch in seagrass meadows. *Bulletin of Marine Science* **58**, 217–233.

Stoner, A. W., Ray, M., Glazer, R. A. and McCarthy, K. J. (1996b). Metamorphic responses to natural substrata in a gastropod larva: Decisions related to postlarval growth and habitat preference. *Journal of Experimental Marine Biology and Ecology* **205**, 229–243.

Suhayda, J. N. and Roberts, H. H. (1977). Wave action and sediment transport on fringing reefs. *In* ‘‘Proceedings, Third International Coral Reef Symposium’’ (D. L. Taylor, ed.), Vol. 2, ‘‘Geology’’, pp. 65–70. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

Sullivan, K. M. and Chiappone, M. (1993). Hierarchical methods and sampling design for conservation monitoring of tropical marine hard bottom communities. *Aquatic Conservation-Marine and Freshwater Ecosystems* **3**, 169–187.

Sullivan, K. M., Chiappone, M., Delgado, G. and Schmitt, E. (1994a). ‘‘Rapid Ecological Assessment Methodologies for Marine Ecosystems in the Tropical Western Atlantic’’. Florida and Caribbean Marine Conservation Science Center, Coral Gables, TNC, Miami.

Sullivan, K. M., Chiappone, M. and Lott, C. (1994b). Abundance patterns of stony corals on platform margin reefs of the Caicos Bank. *Bahamas Journal of Science* **1**, 2–11.

Sweatman, H. and Robertson, D. R. (1994). Grazing halos and predation on juvenile Caribbean surgeonfishes. *Marine Ecology Progress Series* **111**, 1–6.

Szmant, A. M. (1986). Reproductive ecology of Caribbean reef corals. *Coral Reefs* **5**, 43–53.

Tait, R. J. (1972). Wave set-up on coral reefs. *Journal of Geophysical Research* **77**, 2207–2211.

Thayer, G. W., Bjorndal, K. A., Ogden, J. C., Williams, S. L. and Zieman, J. C. (1984). Role of larger herbivores in seagrass communities. *Estuaries* **7**, 351–376.

Thayer, G. W., Colby, D. R. and Hettler, W. F., Jr (1987). Utilisation of the red mangrove prop root habitat by fishes in south Florida. *Marine Ecology Progress Series* **35**, 25–38.

Thresher, R. E. (1983). Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. *Marine Ecology Progress Series* **10**, 137–145.

Tolimieri, N. (1995). Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia* **102**, 52–63.

Tolimieri, N. (1998a). Effects of substrata, resident conspecifics and damselfish on the settlement and recruitment of the stoplight parrotfish, *Sparisoma viride*. *Environmental Biology of Fishes* **53**, 393–404.

Tolimieri, N. (1998b). The relationship among microhabitat characteristics, recruitment and adult abundance in the stoplight parrotfish, *Sparisoma viride*, at three spatial scales. *Bulletin of Marine Science* **62**, 253–268.

Tolimieri, N. (1998c). Contrasting effects of microhabitat use on large-scale adult abundance in two families of Caribbean reef fishes. *Marine Ecology Progress Series* **167**, 227–239.

Tolimieri, N., Sale, P. F., Nemeth, R. S. and Gestring, K. B. (1998). Replenishment of populations of Caribbean reef fishes: Are spatial patterns of recruitment consistent through time? *Journal of Experimental Marine Biology and Ecology* **230**, 55–71.

Tomascik, T. and Sander, F. (1985). Effects of eutrophication on reef-building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. *Marine Biology* **87**, 143–155.

Tomascik, T. and Sander, F. (1987). Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Marine Biology* **94**, 53–75.

Tomasko, D. A. and Lapointe, B. E. (1991). Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. *Marine Ecology Progress Series* **75**, 9–17.

Torres, R., Chiappone, M., Geraldes, F., Rodriguez, Y. and Vega, M. (2001). Sedimentation as an important environmental influence on Dominican Republic reefs. *Bulletin of Marine Science* **69**, 805–818.

Tulevech, S. M. and Recksiek, C. W. (1994). Acoustic tracking of adult white grunt, *Haemulon plumieri*, in Puerto Rico and Florida. *Fisheries Research* **19**, 301–319.

Tupper, M. and Juanes, F. (1999). Effects of a marine reserve on recruitment of grunts (Pisces: Haemulidae) at Barbados, West Indies. *Environmental Biology of Fishes* **55**, 53–63.

van der Velde, G., Gorissen, M. W., den Hartog, C., van't Hoff, T. and Meijer, G. J. (1992). Importance of the Lac-Lagoon (Bonaire, Netherlands Antilles) for a selected number of reef fish species. *Hydrobiologia* **247**, 139–140.

Van Moorsel, G. W. N. M. (1983). Reproductive strategies in two closely related stony corals (*Agaricia*, Scleractinia). *Marine Ecology Progress Series* **13**, 273–283.

van Rooij, J. M. and Videler, J. J. (1996). Estimating oxygen uptake rate from ventilation frequency in the reef fish *Sparisoma viride*. *Marine Ecology Progress Series* **132**, 31–41.

van Rooij, J. M. and Videler, J. J. (1997). Mortality estimates from repeated visual censuses of a parrotfish (*Sparisoma viride*) population: Demographic implications. *Marine Biology* **128**, 385–396.

van Rooij, J. M., Bruggemann, J. H., Videler, J. J. and Breeman, A. M. (1995a). Ontogenic, social, spatial and seasonal variations in condition of the reef herbivore *Sparisoma viride*. *Marine Biology* **123**, 269–275.

van Rooij, J. M., Bruggemann, J. H., Videler, J. J. and Breeman, A. M. (1995b). Plastic growth of the herbivorous reef fish *Sparisoma viride*: Field evidence for a trade-off between growth and reproduction. *Marine Ecology Progress Series* **122**, 93–105.

van Rooij, J. M., de Jong, E., Vaandrager, F. and Videler, J. J. (1996a). Resource and habitat sharing by the stoplight parrotfish, *Sparisoma viride*, a Caribbean reef herbivore. *Environmental Biology of Fishes* **47**, 81–91.

van Rooij, J. M., Kok, J. P. and Videler, J. J. (1996b). Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride*. *Environmental Biology of Fishes* **47**, 65–80.

van Rooij, J. M., Kroon, F. J. and Videler, J. J. (1996c). The social and mating system of the herbivorous reef fish *Sparisoma viride*: One-male versus multi-male groups. *Environmental Biology of Fishes* **47**, 353–378.

van Rooij, J. M., Videler, J. J. and Bruggemann, J. H. (1998). High biomass and production but low energy transfer efficiency of Caribbean parrotfish: Implications for trophic models of coral reefs. *Journal of Fish Biology* **53**(Suppl. A), 154–178.

van Tussenbroek, B. I. (1995). *Thalassia testudinum* leaf dynamics in a Mexican Caribbean coral reef lagoon. *Marine Biology* **122**, 33–40.

Vecsei, A. (2001). Fore-reef carbonate production: Development of a regional census-based method and first estimates. *Palaeogeography Palaeoclimatology Palaeoecology* **175**, 185–200.

Vecsei, A. (2004). A new estimate of global reefal carbonate production including the fore-reefs. *Global and Planetary Change* **43**, 1–18.

Vitousek, P. M. (1992). Global environmental change: An introduction. *Annual Review of Ecology and Systematics* **23**, 1–14.

Vogel, K., Gektidis, M., Golubic, S., Kiene, W. E. and Radtke, G. (2000). Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: Implications for paleoecological reconstructions. *Lethaia* **33**, 190–204.

Vooren, C. M. (1981). Photosynthetic rates of benthic algae from the deep coral reef of Curaçao. *Aquatic Botany* **10**, 143–159.

Wanders, J. B. W. (1976a). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles) II. Primary productivity of the *Sargassum* beds on the north-east coast submarine plateau. *Aquatic Botany* **2**, 327–335.

Wanders, J. B. W. (1976b). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I. Primary productivity in the coral reef. *Aquatic Botany* **2**, 235–270.

Watson, M., Munro, J. L. and Gell, F. R. (2002). Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. *Marine Ecology Progress Series* **237**, 247–256.

Weil, E., Losada, F. and Bone, D. (1984). Spatial variations in density and size of the echinoid *Diadema antillarum* Philippi on some Venezuelan coral reefs. *Bijdragen Tot De Dierkunde* **54**, 73–82.

Weinstein, M. P. and Heck, K. L. (1979). Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: Composition, structure and community ecology. *Marine Biology* **50**, 97–107.

Wellington, G. M. (1992). Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia* **90**, 500–508.

Welsh, D. T. (2000). Nitrogen fixation in seagrass meadows: Regulation, plant–bacteria interactions and significance to primary productivity. *Ecology Letters* **3**, 58–71.

Westlake, D. F. (1963). Comparisons of plant productivity. *Biological Reviews* **38**, 385–425.

Whaylen, L., Pattengill-Semmens, C. V., Semmens, B. X., Bush, P. G. and Boardman, M. R. (2004). Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environmental Biology of Fishes* **70**, 305–313.

White, W. H., Harborne, A. R., Sotheran, I. S., Walton, R. and Foster-Smith, R. L. (2003). Using an Acoustic Ground Discrimination System to map coral reef benthic classes. *International Journal of Remote Sensing* **24**, 2641–2660.

Wiebe, W. J., Johannes, R. E. and Webb, K. L. (1975). Nitrogen fixation in a coral reef community. *Science* **188**, 257–259.

Wilkinson, C. R. (1983). Role of sponges in coral reef structural processes. *In* ''Perspectives on Coral Reefs'' (D. J. Barnes, ed.), pp. 263–274. Published for the Australian Institute of Marine Science by Brian Clouston Publisher, Manuka.

Williams, A. H. (1978). Ecology of threespot damselfish: Social organisation, age structure, and population stability. *Journal of Experimental Marine Biology and Ecology* **34**, 197–213.

Williams, A. H. (1984). The effects of Hurricane Allen on back reef populations of Discovery Bay, Jamaica. *Journal of Experimental Marine Biology and Ecology* **75**, 233–243.

Williams, D. M. (1991). Patterns and processes in the distribution of coral reef fishes. *In* "The Ecology of Fishes on Coral Reefs" (P. F. Sale, ed.), pp. 437–474. Academic Press, Inc, San Diego.

Williams, I. D., Polunin, N. V. C. and Hendrick, V. J. (2001). Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* **222**, 187–196.

Williams, S. L. and Carpenter, R. C. (1988). Nitrogen-limited primary productivity of coral-reef algal turfs: Potential contribution of ammonium excreted by *Diadema antillarum*. *Marine Ecology Progress Series* **47**, 145–152.

Williams, S. L. and Carpenter, R. C. (1997). Grazing effects on nitrogen fixation in coral reef algal turfs. *Marine Biology* **130**, 223–231.

Williams, S. L. and Carpenter, R. C. (1998). Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. *Journal of Experimental Marine Biology and Ecology* **226**, 293–316.

Wolanski, E., Richmond, R. H. and McCook, L. (2004). A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. *Journal of Marine Systems* **46**, 133–144.

Woodley, J. D. (1992). The incidence of hurricanes on the north coast of Jamaica since 1870: Are the classic reef descriptions atypical? *Hydrobiologia* **247**, 133–138.

Woodley, J. D., Chornesky, E. A., Clifford, P. A., Jackson, J. B. C., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., Rylaarsdam, K. W., Tunnicliffe, V. J., Wahle, C. M., Wulff, J. L., Curtis, A. S. G., Dallmeyer, M. D., Jupp, B. P., Koehl, M. A. R., Neigel, J. and Sides, E. M. (1981). Hurricane Allen's impact on Jamaican coral reefs. *Science* **214**, 749–755.

Woodroffe, C. D. (1995). Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. *Earth Surface Processes and Landforms* **20**, 65–85.

Wooldridge, S. and Done, T. J. (2004). Learning to predict large-scale coral bleaching from past events: A Bayesian approach using remotely sensed data, *in situ* data, and environmental proxies. *Coral Reefs* **23**, 96–108.

Yates, K. K. and Halley, R. B. (2003). Measuring coral reef community metabolism using new benthic chamber technology. *Coral Reefs* **22**, 247–255.

Zieman, J. C. (1975). Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. *Aquatic Botany* **1**, 107–123.

Zieman, J. C., Thayer, G. W., Robblee, R. B. and Zieman, R. T. (1979). Production and export of sea grasses from a tropical bay. *In* "Ecological Processes in Coastal and Marine Systems" (R. J. Livingston, ed.), pp. 21–34. Plenum Press, New York.

Zieman, J. C., Fourqurean, J. W. and Iverson, R. L. (1989). Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* **44**, 292–311.

FURTHER READING

CARICOMP (1997c). Structure and productivity of mangrove forests in the greater Caribbean region. *In* "Proceedings of the 8th International Coral Reef Symposium" (H. A. Lessios and I. G. Macintyre, eds.), Vol. I, pp. 669–672. Smithsonian Tropical Research Institute, Balboa, Republic of Panamá.

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