

**EVALUATING THE ROLE OF GREEN TURTLES IN THEIR ECOSYSTEMS:  
DEVELOPMENT OF ECOPATH MODELS FOR THE CARIBBEAN SEAGRASS  
AND THE HAWAIIAN ALGAL ECOSYSTEMS**

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**EVALUATING THE ROLE OF GREEN TURTLES IN THEIR ECOSYSTEMS:  
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**BACKGROUND:**

The primary goal of this project was to develop a quantitative model of the role of green turtles in seagrass ecosystems in the Greater Caribbean and in algal ecosystems in Hawaii using Ecopath with Ecosim (EwE) software. The past roles of sea turtles as major consumers in many marine ecosystems from tropical to sub-arctic waters have only recently been recognized (Jackson et al. 2001; Bjorndal and Jackson 2003; Pandolfi et al. 2003). The models evaluate the population level of green turtles needed to fulfill their ecological function and restore healthy seagrass ecosystems. This estimate will serve as the target for recovery of green turtles in the Greater Caribbean. The Marine Turtle Specialist Group (MTSG) of the World Conservation Union (IUCN) has defined the recovery goals for sea turtles as the level at which their ecological roles are fulfilled (MTSG 1995). This goal was reaffirmed at the MTSG Visioning Meeting held in December 2003 (the 3 PI's of this project were among the 30 participants). The population levels at which sea turtles fulfill their ecological roles are also the levels with the greatest probability of being sustained indefinitely (Bjorndal and Bolten 2003). But how many sea turtles are needed in order to fulfill their ecological roles? This is not an easy question to answer, but it is the responsibility of those committed to conservation and management of sea turtle populations to determine those population levels.

When sea turtle populations are in decline, reversal of the decline is a sufficient goal for conservation and management programs. However, some green turtle populations have responded to conservation efforts over last few decades and are now demonstrating increases in population size (Chaloupka et al. 2008), such as the nesting populations at Tortuguero, Costa Rica (Bjorndal et al. 1999), Florida (Bagley et al. 2000), Australia (Chaloupka and Limpus 2001), and Hawaii (Balazs and Chaloupka 2004). With these successes comes increased pressure to re-open or increase quotas for directed takes and to reduce regulatory restrictions on commercial fisheries designed to reduce sea turtle bycatch. Thus, specific targets for recovery are essential. In the US, management authorities are required to define specific demographic goals in Recovery Plans for each species under the Endangered Species Act. Throughout the world, management agencies are under constant pressure from groups that wish to kill turtles, either directly or indirectly (e.g., in commercial fisheries or coastal construction), to define levels at which sea turtle populations will be considered "recovered" so that they can resume their activities.

The population abundance at which sea turtles fulfill their ecological roles has never been determined for any population. We are in an excellent position to develop an estimate for the Caribbean green turtle because of the foundation of research on this population. In addition, recent research has resulted in new estimates of the sustainability of green turtle – seagrass grazing systems (Moran and Bjorndal 2005, 2007). We know that green turtle populations in the Greater Caribbean have declined drastically as a result of over-exploitation by humans since their arrival in the region (Parsons 1962, Frazier 2003). Our best estimate is that the present

population represents only 3-7% of the green turtle population in the region before humans (Jackson et al. 2001). Because of reductions in seagrasses in the Caribbean region (Creed et al. 2003) and other forms of habitat degradation, the past level of green turtles cannot be supported in the Caribbean today. If we can estimate the population abundance necessary for the green turtle to fulfill its function in the Greater Caribbean, we will have established the recovery goal for this region.

This project is a partnership between the Archie Carr Center for Sea Turtle Research at the University of Florida and the Sea Around Us Project (SAUP) at the Fisheries Centre (FC), University of British Columbia, Vancouver, Canada. This project is also a partnership with the Marine Turtle Research Program of the Pacific Islands Fisheries Science Center, Honolulu Laboratory (NMFS).

#### **OBJECTIVES:**

1. Develop quantitative models of the ecological roles of the green turtles in the Greater Caribbean seagrass ecosystem and the Hawaiian algal ecosystem. The Greater Caribbean model is based on data collected over the past 3 decades on green turtles and the seagrass pastures on which they graze (e.g., on growth, reproduction, nutrition, survival probabilities, density dependent effects, effects of grazing on seagrass productivity). The Hawaiian algal – green turtle model is based on the longterm research program at the Honolulu Laboratory. These models will be constructed using Ecopath with Ecosim (EwE) software.
2. Improve present estimates of the area of seagrasses in the Greater Caribbean region from synthesized and updated habitat maps in ArcGIS.
3. From the results of the first two objectives, develop targets for green turtle recovery in the Greater Caribbean based on the abundance required to fulfill their ecological roles and the maximum number of green turtles that could be supported in the Greater Caribbean (= carrying capacity).

#### **RESULTS:**

The objectives of this project have been successfully completed. The following documents are attached as Appendices in support of completion of this project:

**Appendix A:** Restoration of *Chelonia mydas* populations in the Caribbean: Ecosystem impacts resulting from a reduction in seagrass habitat complexity [**addresses Objectives 1 and 3**]

**Appendix B:** Regional-scale seagrass habitat mapping in the Wider Caribbean region using Landsat sensors: applications to conservation and ecology. In press in *Remote Sensing of Environment*, Special Issue on Earth Observation for Biodiversity and Ecology. [**addresses Objective 2**]

**Appendix C:** Can success towards the international tropical marine biodiversity conservation targets of 2010-2012 be measured? Abstract of manuscript to be submitted to *Science*.  
[addresses Objective 3]

**Appendix D:** Inputs and outputs for an EwE model of a Hawaiian algal ecosystem in Kaloko Honokōhau National Historic Park [addresses Objective 1]

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## **Appendix A**

Restoration of *Chelonia mydas* populations in the Caribbean: Ecosystem impacts  
resulting from a reduction in seagrass habitat complexity  
[addresses Objectives 1 and 3]

## Restoration of *Chelonia mydas* population in the Caribbean: Ecosystem impacts resulting from a reduction in seagrass habitat complexity

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### Introduction

Populations of the megaherbivore *Chelonia mydas* have suffered substantial reduction in numbers throughout the Caribbean (Seminoff, 2002; McClenachan et al., 2006). Following the arrival of Europeans in the New World, sea turtles have been subject to a long history of human exploitation (Parsons, 1962; Witzell, 1994), which, in addition to threats resulting from disease, incidental capture by fishers, and destruction of critical nesting and foraging habitat, has resulted in the decline of many stocks. Over the last few decades, conservation and management programmes have been implemented throughout the region to help reverse these severe declines. Some green turtle populations, such as the nesting populations at Tortuguero, (Costa Rica), and Florida (USA) (Chaloupka et al., 2008), have responded to protection efforts and are now demonstrating increases in population size. With such successes comes increased pressure to re-open or increase quotas for directed takes and to reduce regulatory restrictions on commercial fisheries designed to reduce sea turtle bycatch. This response is a classic example of the “shifting baseline syndrome” (*sensu* Pauly (1995)), where inappropriate baselines (in this case historic low levels) are used to assess population trends. In the case of the green turtle, it is clear that population levels at the onset of conservation initiatives can not be considered as a reliable baseline against which to assess current trends, with archaeological and palaeontological data demonstrating historical turtle abundances 93% to 97% greater than current estimates (Jackson et al., 2001).

Although the “shifting baseline syndrome” should be avoided when population trends are assessed and recovery goals defined (Bjorndal & Jackson, 2003), the alteration of food webs by decades of overexploitation and habitat degradation means that ecosystems in the present day are unlikely to be able to sustain historic population levels. In the context of current environmental status, a more meaningful

goal for the management and conservation of sea turtles would therefore be a population level at which they can fulfil their ecological role (Bjorndal & Jackson, 2003). Implicit to such an objective is the need to manage single species within the framework of the ecosystem that they are part of. Ecosystem based management (EBM), as this approach is commonly referred to, describes a set of practices that aims to take into account ecological interactions that have been identified as fundamental to maintaining or enhancing ecosystem health. By adopting a more holistic approach, EBM shifts the management focus from the short term to that of long-term sustainability. Within an EBM framework then, actions taken to help green turtle populations recover to a healthy level need to include aspects of this species population biology, as well as its interactions with other species in the ecosystems it interacts with at all stages of its life history. Therefore, seagrasses, which constitute the main foraging grounds for green turtles in the Caribbean, need to be explicitly considered in any management and recovery plan.

### *1. Importance of seagrass beds*

Seagrasses fulfil a key role in coastal ecosystems (Hemminga & Duarte, 2000) and are some of the most productive systems on earth (Duarte & Chiscano, 1999; Mateo et al., 2006). Forming dense meadows in subtidal, soft-bottomed marine and estuarine environments (Phillips & Menez, 1988), they represent important foraging grounds for a variety of organisms, thereby enhancing the biodiversity of coastal waters (Hemminga & Duarte, 2000). Other species, many of which are of commercial importance (e.g., snappers and groupers), benefit from the shelter and the nursery function of seagrass beds (Beck et al., 2003; Heck et al., 2003; Dahlgren et al., 2006) supporting directly or indirectly entire fisheries (Gillanders, 2006).

The value of seagrass habitats as 'nursery areas' (Beck et al., 2001) or effective juvenile habitats (Dahlgren et al., 2006) is often used as one of the chief arguments to support initiatives aimed at their conservation and restoration. The nursery function of seagrass beds is understood to be the provision of a habitat where juveniles of species have greater survival and growth rates than on nearby unvegetated substrate and make successful ontogenetic shifts to adult populations (Adams et al., 2006). It is assumed that such impacts are primarily the result of the increased refuge role provided by seagrasses to those

organisms (Heck & Crowder, 1991; Heck & Orth, 2006). As major grazers of seagrass beds it is possible that green turtles have a significant impact on their nursery function, although, as outline below, their are limited field data (and none from the Caribbean) on this subject.

Seagrass ecosystems are recognised as under increasing threat and their global distribution and spatial extent is currently in a state of decline (Short & Wyllie-Echeverria, 1996; Orth et al., 2006; Short et al., 2006). Destruction or loss has commonly resulted from human impacts (Orth & Moore, 1983; Orth et al., 2006; Short et al., 2006) either directly (e.g., dredging and eutrophication) or indirectly (e.g., seawater temperature rise and large scale changes to marine food webs linked to seagrasses), and these are seen as the major source of change to seagrass ecosystems (Hemminga & Duarte, 2000; Jackson, 2001; Jackson et al., 2001; Duarte, 2002; Valentine & Heck, 2005; Valentine et al., 2007). In addition, the decline in the health of Caribbean seagrass meadows may be partly attributable to the demise of green turtle populations. In the 1980s, seagrasses along the Florida coast experienced mass mortality because of a wasting disease. High temperatures and increased salinities, sulfide toxicity, self-shading, hypoxia, and infection by the slime mold *Labyrinthula* sp. were all correlated with mortality (Robblee et al., 1991; Fourqurean & Robblee, 1999; Rudnick et al., 2005). Jackson (2001) postulated that except for salinity and temperature, all other mortality factors may have been due to the extensive exploitation of sea turtles and manatees throughout the region and thus specific removal of their grazing function.

## 2. *Role of turtles as herbivores*

Green turtles have had the strongest ecological and evolutionary impacts on seagrasses since the extinction of the diverse dugongid fauna before the Pleistocene (Domning, 2001) and may have been as important in determining productivity as terrestrial herbivores were in grasslands (McNaughton, 1979; Pandolfi et al., 2003).

Although current *Thalassia testudinum* (turtle grass) beds in the Caribbean support relatively high levels of herbivory in places (Heck & Valentine, 1995; Valentine & Heck, 1999; Valentine et al., 2000), these rates were undoubtedly higher in pre-Columbian times (ca. 1500AD) when green turtles and manatees were more abundant,

despite sustained exploitation by Amerindian populations (Johnson, 1952; Wing & Wing, 2001). Over evolutionary time, seagrasses developed a number of adaptations in response to intense grazing pressure by these large vertebrate grazers such as belowground carbohydrate reserves and clonal propagation (Valentine & Duffy, 2006).

Sustained grazing by green turtles has been shown to significantly affect life history characteristics of seagrasses and is likely to play an important role in community dynamics. Green turtles remove a large proportion of the standing stock by cropping seagrass blades 2-4 cm above the base without disturbing the underground rhizome system (Lanyon et al., 1989; Brand-Gardner et al., 1999). Individuals commonly show a high degree of fidelity to feeding sites by repeatedly returning to the same grazing plots (Bjorndal, 1980; Ogden, 1980). At comparatively high turtle densities, these individual grazing plots may merge into one single cropped seagrass bed (Williams, 1988). Repeated blade cropping at grazing plots (i.e., feeding philopatry) has been shown to influence the physiology, chemistry, and community composition of seagrasses at a local scale (Bjorndal, 1980; Thayer et al., 1984; Bjorndal, 1985; Aragones & Marsh, 2000; Moran & Bjorndal, 2005; Aragones et al., 2006; Moran & Bjorndal, 2007). Specifically for turtle grass, clipping experiments mimicking turtle grazing resulted in compensatory growth (Moran & Bjorndal, 2005) and led to increases in the nutritional quality of the blades, i.e. increase in nitrogen content (Moran & Bjorndal, 2007).

Available evidence as outlined above clearly demonstrates that grazing of seagrass tissue can lead to changes such as increases in productivity and adjustments in nutrient composition of seagrass leaves. However, the community-wide changes that sustained high level grazing activity (i.e., higher green turtle biomass than present) would have on seagrass community dynamics are less clear.

We had two broad objectives through which we sought to address the overarching goal:

- (i) to develop a Caribbean coral reef ecosystem model, using the widely used mass-balance modeling software Ecopath with Ecosim, that explicitly includes green turtles; and describe the structure and function of this system using a broad number of ecological indicators related to trophic flow description, thermodynamic concepts, information theory, and network analysis (Christensen & Walters, 2004);

- (ii) to assess the impacts a hypothetical increased green turtle biomass would have on the system. As highlighted above, as megaherbivores, at historical abundance levels, green turtles used to play an important role in seagrass beds, significantly affecting seagrass community structure, productivity, and nutritional attributes. Recent studies have confirmed these effects. Such changes are likely to have important ramifications in an ecosystem context, yet to date these have not been considered explicitly. This study then particularly sought to investigate how a dramatic reduction in the canopy height (i.e., loss of refuge) as a result of repeated and increased turtle grazing would impact the species assemblage in Caribbean *Thalassia testudinum* dominated seagrass beds.

Given a number of significant limitations and lack of conclusive information, results should be considered as preliminary in nature until more focused field data have been collected pertaining to the nursery function of seagrass beds in particular. Also, although we recognise that associated fauna and thus changes in species composition and abundance may impact nutrient cycling, substrate stability, and water quality within the meadows, these processes fall outside of the purview of the present study.

## **Model development and considerations**

### *1. Study area*

The coastal waters, from the water's edge to a depth of approximately 100m, around the US Virgin Islands (USVI) and Puerto Rico were modelled here and chosen as representative of a Wider Caribbean region coastal system (Figure 1). The model represents an average annual mid-1990s situation in the coastal waters around the USVI and Puerto Rico. The area below 100m was not included as the model sought to focus chiefly on system dynamics in seagrass beds/coral reefs. Analyses of the products of a recent mapping effort reveal that Puerto Rico harbours a total 1,599km<sup>2</sup> of coastal habitats (3% of which are unconsolidated sediment, 45% submerged vegetation, 5% mangroves, and 47% coral reef and colonized hardbottom), whilst the US Virgin islands coastal habitats cover 487km<sup>2</sup> (5% of which are unconsolidated sediment, 33% submerged vegetation, and 62% coral reef and hard bottom) (Kendall et al., 2001).

### *2. Modeling approach: Ecopath with Ecosim*

The foundation of the Ecopath with Ecosim (EwE) suite is an Ecopath model (Polovina, 1984; Christensen & Pauly, 1992), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass 'pools' (Christensen & Pauly, 1992). At any time within the system and within the elements of that system, the matter fluxes into the system must balance amounts that leave the system plus any change in biomass of individual groups (Pauly & Christensen, 2002). The biomass pools, hereafter referred to as functional groups, consist of a single species, single size/age group of a given species or species groups representing ecological guilds. These may be further split into ontogenetic (juvenile/adult) groups that can then be linked in Ecosim (see stanzas below).

In other words, Ecopath operates under two main assumptions. The first assumption is that biological production within a functional group equals the sum of mortality due to fisheries and predators, net migration, biomass accumulation, and other unexplained mortality. The principle behind this modeling approach is that, on an annual basis, biomass and energy in an ecosystem are conserved (Walters et al., 1997; Walters & Martell, 2004b).

This relationship can be expressed as follows:

$$B_i \cdot (P/B)_i = Y_i + \sum_{j=1} B_j \cdot (Q/B)_j \cdot DC_{ij} + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) \quad (1.1)$$

where  $B_i$  and  $B_j$  are biomasses of prey (i) and predator (j) respectively;

$(P/B)_i$  is the production to biomass ratio – usually determined to be equivalent to total mortality (i.e., fishing and natural mortality);

$Y_i$  is the total fishery catch rate of group (i);

$(Q/B)_j$  is the food consumption per unit biomass of (j);

$DC_{ij}$  is the fraction of prey (i) in the average diet of predator (j);

$E_i$  is the net migration rate (emigration – immigration);

$BA_i$  is the biomass accumulation rate of group (i); and

$EE_i$  is the ecotrophic efficiency – the fraction of production that is utilised within or caught from the system.

The second assumption is that consumption within a group equals the sum of production, respiration, and unassimilated foods. This relationship can be expressed as follows:

$$B \cdot (Q/B) = B \cdot (P/B) + (1 - GS) \cdot Q - (1 - TM) \cdot P + B(Q/B) \cdot GS \quad (1.2)$$

where GS is the proportion of food unassimilated; and TM is the trophic mode expressing the degree of heterotrophy – with 0 representing autotrophs and 1 heterotrophs.

The model is considered balanced when all values for EE < 1 (Christensen & Walters, 2004; Christensen et al., 2005).

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model (Walters et al. 1997). Ecosim was used here to investigate the impact an increased turtle biomass would have on the system modeled. Using a system of differential equations, biomass fluxes amongst functional groups are calculated as a function of time by accounting for changes in predation, consumption and emigration rates, as well as fishing (Christensen & Pauly, 2004). Predator-prey interactions are moderated by prey behaviour to limit exposure to predation, such that biomass flux patterns can show either bottom-up or top down (trophic cascade) control.

Biomass dynamics are described by the following equation (1.3):

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^n f(B_j, B_i) - \sum_{j=1}^n f(B_j, B_i) + I_i - (M_i + F_i + e_i) \cdot B_i \quad (1.3)$$

where  $dB_i/dt$  represents biomass growth rate of group (i) during the interval  $dt$ ;

$g_i$  is the net growth efficiency (production/consumption) ratio;

$I_i$  is the immigration rate;

$M_i$  and  $F_i$  are natural and fishing mortality rates of group (i), respectively;

$e_i$  is the emigration rate of group (i); and

$f(B_j, B_i)$  is a function used to determine the consumption rates of predator (j) on prey (i) according to 'foraging arena' concepts (Walters et al., 1997; Walters & Martell, 2004b).

This function is modified according to a predator-prey vulnerability parameter (see below) assigned to the interaction.

### 3. *Functional groups and model parameters*

Based in part on a species list drawn up by Delgado (2004), data were obtained for 282 species of fish (Appendix 1). These were then aggregated according to their diet and feeding preferences into 17 functional groups (for a total of 36 functional groups including non-fish groups). For each group, four input parameters were estimated: biomass, production per unit of biomass (P/B), consumption per unit of biomass (Q/B) and diet composition (Table 1).

At the start of this project, CW was recommended to utilise transect data stratified by habitat type and collected yearly by NOAA at La Parguera for fish biomass estimates. However, this approach was not adopted here as:

- (i) La Parguera is not considered representative of the remainder of Puerto Rico. Indeed, coral reefs off Puerto Rico near La Parguera, have the highest abundance and percent cover of living coral (Turgeon et al., 2002). As such it cannot be assumed that species sighted in the area commonly occur elsewhere and extrapolations of fish biomasses to the remainder of the zone modelled would have led to significant overestimates (M Kendall, pers. comm.).
- (ii) Sand and seagrass strata were combined into one soft bottom strata at all La Parguera monitoring locations (NOAA, 2007).

Hence, data required to parameterise the model were primarily adapted from Opitz (1996). Fish biomass was calculated according to the following empirical relationship (1.4):

$$W_{mean} = W_{\infty} \cdot 0.3 \cdot 0.86 \quad (1.4)$$

Where  $W_{mean}$  is the mean individual weight and  $W_{\infty}$  is asymptotic weight.

Complementary data, specifically for fish groups, were obtained from the published literature for the USVI and Puerto Rico preferentially, and other regions of the Caribbean where necessary.

The P/B ratio is thought of as the instantaneous total mortality,  $Z$ . As the model developed here does not include fishing mortality the ratio was set to natural mortality for all stocks and estimated using empirical relationships integrating length and weight data obtained from Fishbase (Pauly, 1980; Palomares & Pauly, 1989; Pauly et al.,

1990) (Appendix 2). The Q/B ratio is defined as the food intake by a group during a certain period of time (here: a year) divided by its biomass. For all finfish, Q/B was calculated using the following empirical equation (Christensen et al., 2005) (1.5):

$$\text{Log}\left(\frac{Q}{B}\right) = 7.964 - 0.204 \cdot \log W_{\infty} - 1.965 \cdot T' + 0.083 \cdot A + 0.532 \cdot h + 0.398 \cdot d \quad (1.5)$$

where  $W_{\infty}$  is the asymptotic weight (g),  $T'$  is the annual temperature of the water, expressed using  $T' = 1000/\text{Kelvin}$  (Kelvin = °C + 273.15),  $A$  is the aspect ratio expressed as  $(h^2/s)$  where  $h$  is the height and  $s$  is the surface area of the caudal fin,  $h$  is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), and  $d$  is a dummy variable also expressing food type (1 for detritivores, and 0 for herbivores and carnivores) (Christensen et al., 2005).

Diet information was compiled from the published literature (primarily Randall (1967)). Individual parameters were set for each of the fish species in the model. Groups were then aggregated into functional pools and values weighted according to individual species biomass contribution to those pools.

Q/B values for sea turtles were adapted from Moran and Bjorndal (2005) and Bjorndal and Jackson (2003); P/B values for seagrass were adjusted giving special attention to results in Zieman et al. (1984) as well as Moran and Bjorndal (2005) and Bjorndal and Jackson (2003).

To evaluate the impact of increased turtle abundance in the region, an hypothetical bio-accumulation rate was allowed to vary between  $0.01 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$  and  $0.1 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ . These values were chosen within a range that did not violate mass-balance considerations. The duration of simulation under Ecosim was adjusted to vary between 100 to 200 years. This was assumed to be an acceptable timeframe over which to run the model as trends tended to stabilise between 50 and 150 years depending on the scenario run.

#### 4. *Network analysis*

Total trophic flows within the ecosystem in terms of consumption, production, respiration, exports and imports and flow to detritus ( $\text{t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ ) were quantified. The sum of all these flows, the Total System Throughput (TST), can be seen as an indirect indicator of the size of the ecosystem (Christensen & Pauly, 1993).

Measurements of the flow, efficiency of assimilation, transfer and dissipation of material and energy among the various ecosystem components can provide significant information on the fundamental structure and function of the whole ecosystem. The algorithms used for such measurements are known collectively as network analysis. The following system parameters and flow indices were determined by Ecopath: sum of all consumption; sum of all respiratory flows; sum of all flows into detritus; total system throughput, which is the total of all flows occurring in the system, represents the size of an ecosystem in terms of flows, and is indexed in terms of how much matter the system processes; calculated total net primary production; total primary production/total respiration; total biomass (excluding detritus); total primary production/total biomass; total biomass/total throughput, which represents the amount of biomass necessary for maintaining one unit of flow and can be used as an indicator of system maturity *sensu* Odum (Odum, 1969; Christensen et al., 2005); Finn's cycling index (FCI), which is the proportion of total system throughput that is devoted to recycling of material (Finn, 1976); and the system Omnivory Index, defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake (Christensen & Walters, 2004). The index is a measure of how feeding interactions are distributed between trophic levels and is an indicator of whether the system represented displays web like features or not.

Ecosystem attributes of the generic Caribbean reef system were then compared with six other Ecopath reef system models, including Tiahura, French Polynesia (Arias-Gonzalez et al., 1997), Bolinao, Philippines (Aliño et al., 1993), and three Mexican Caribbean reef systems (Arias-Gonzalez et al., 2004).

## 5. Stanzas

For species with complex life histories (here species making up the intermediate carnivorous reef fish groups), individual life history stages can be incorporated into Ecosim through stanzas. The stanzas are linked to each other and usually the adults are set as the leading group. This then allows for the reproduction per unit biomass ( $P/B \text{ year}^{-1}$ ), consumption per unit biomass ( $Q/B \text{ year}^{-1}$ ), and growth to be calculated for individual stanzas from the leading's group baseline estimates. Growth for each group is inferred from the von Bertalanffy growth curve and assumes stable survivorship within individual age groups (Coll et al., 2006).

## 6. *Predator-prey relationships*

Predation plays an important role in shaping community composition. In this model the functional predator-prey relationship is based on the foraging arena theory, dividing the prey biomass into vulnerable and invulnerable pools (Walters & Kitchell, 2001; Walters & Martell, 2004a). The transfer rate between these two pools (in both directions), also termed 'vulnerability', is directly related to the carrying capacity of the system and can take on a value from one to infinity. Low rates imply a donor-driven (prey is limiting), density-dependent interaction where (i) predator abundance is close to carrying capacity; (ii) prey can remain hidden or otherwise unavailable; (iii) predators are never satiated and prey handling time does not limit prey mortality (Essington et al., 2000); and (iv) an increase in predator abundance will not result in a dramatic increase in prey mortality. High rates on the other hand indicate a predator-driven interaction where (i) the behaviour of both prey and predator have weaker effects on limiting predation rates; (ii) predation mortality is proportional to the product of prey and predator abundance; and (iii) the predator's initial biomass is low compared to its carrying capacity (Christensen et al., 2005). This functional response equation dictates changes in prey composition due to changes in the relative availability of individual prey, but does not allow for predators to switch to new prey items.

Habitat structure has been recognised to play an important role in mediating predation and therefore determining prey abundance. A number of studies have investigated predator-prey dynamics in seagrass beds under various seagrass structural complexity settings (see Heck and Orth (2006) and Horinouchi (2007b) for recent reviews). Most have been performed in temperate or subtropical locations making it challenging to adapt potential scenarios to Caribbean seagrass beds as tropical systems are typically subjected to higher predation rates (Virnstein et al., 1984; Peterson et al., 2001; Heck & Orth, 2006). Hence, a hypothetical relationship was drawn up and applied to all groups that benefit from the sheltering capacity of seagrass.

## 7. *Mediation functions*

Non-trophic effects whereby the biomass of a particular group affects the vulnerability of  $i$  prey to a given predator  $j$  can be captured in

Ecosim through mediation functions. A key mediation function is that of habitat complexity and its role in providing refuge from predation. Comparison of survival rates of infauna and small fishes have mostly been conducted between unvegetated substrates and a structurally more complex seabed (Beck et al., 2003; Heck et al., 2003). Fewer studies have looked at the impact of differing densities of seagrass on survival rates of resident fauna.

However, evidence seems to indicate that increasing habitat complexity (i.e., via seagrass density mostly) (but see Warfe and Barmuta (2004)) will provide increasing refuge to prey species by interfering with predator search and pursuit behaviour (e.g., Coull & Wells, 1983; e.g., Gotceitas & Colgan, 1989; Lipcius et al., 1998). A threshold density of seagrass has been hypothesized as being necessary before a significant reduction in predation is noted (Heck & Orth, 1980; Bartholomew et al., 2000).

In addition to shelter from predation greater habitat complexity has been postulated to afford more abundant prey to populations supported by seagrasses (Hixon & Beets, 1993). Both of these factors have been highlighted as essential to the nursery function played by seagrasses (Beck et al., 2003; Heck et al., 2003). However, research to date has highlighted the sheltering effect against predators as the most discernible advantage conferred to small and juvenile fish species in particular in seagrass beds (Orth et al., 1984; Heck & Crowder, 1991; Heck & Orth, 2006), with support for the role of increased food provision in the nursery grounds being less compelling (but see Connolly (1994), Boström and Mattila (1999) and Horinouchi (2007a)). According to Beck et al. (2001) the nursery function of a habitat for juveniles of a given species results from a combination of density, growth, survival and ontogenetic shifts to adult habitats. In most studies to date, findings supporting the nursery function of given habitats has been inferred rather than directly demonstrated (Beck et al., 2001), with experiments chiefly taking place in temperate waters (e.g., Beck et al. (2003), Gillanders et al. (2003)). Relative to temperate systems then, the nursery value of tropical coastal habitats remains poorly understood (but see Verweij et al. (2007)).

Given our hypothesis that turtle grazing will significantly impact the structure of seagrass beds, it is important that the model take into account the potential impacts of grazing on the nursery function fulfilled by this ecosystem. The model presented here assumes that the density of seagrass beds in the system is a constant and that an

increase in turtle abundance will result in a decline in seagrass biomass. Since it is assumed that seagrass biomass is positively correlated with height, the change to habitat complexity imparted by turtles is therefore in the height of the available habitat. In view of the two advantages conferred by greater habitat complexity outlined above, i.e. (i) shelter from predation and (ii) more abundant prey afforded to juvenile and infauna populations, the effects of decreasing seagrass cover as a result of increased cropping by large numbers of green turtles on the vulnerability of prey were modeled using two mediation functions (Figure 2). The first one (a) describes the impact of decreasing seagrass biomass on the vulnerability of small fish. It assumes that as vegetation cover declines (moving from the current status, green line, to the left) vulnerability to predators will increase. The second mediation function (b), depicts the impact of decreasing vegetation on the vulnerability of benthic infauna, which feature in the diet of small fish and other seagrass/reef fish. The effects are weighted so that the vulnerabilities of all prey species increase to all their predators as the biomass of seagrass declines due to the greater abundance of green turtles. This assumption is supported by the contention put forth by Hixon (1991) and by findings on coral reefs in Hawaii (Hixon & Beets, 1993), namely that predators may non-selectively reduce all prey populations in proportion to their initial relative abundances. It is important to note that since the system as modelled here does not include catch statistics for any group considered in the modelling effort, the interpretation of the impacts of reduced habitat complexity are not confounded by changes in biomasses attributable to fishing effort.

#### 8. *Carrying capacity*

Carrying capacity estimates were calculated based on previously published estimates of seagrass turtle intake and seagrass productivity under different grazing regimes (Moran & Bjorndal, 2005), and utilizing a new estimate of seagrass extent throughout the Caribbean of 77,000 km<sup>2</sup>, a value attained from the classification of Landsat ETM+ imagery (see Wabnitz et al. (in press) for methodology; Wabnitz unpublished data).

### **Results and discussion**

Modified input parameters and resulting output parameters of the model are shown in Table 1. Ecotrophic efficiencies (EE) were high for most functional groups, whilst respiration/assimilation ratios (R/A),

production/respiration ratios (P/R) and net food conversion efficiencies were within the expected range (Christensen et al., 2005).

Results of the model showed that functional groups were organized within four trophic levels (TL) with the highest TLs corresponding to seabirds, sharks/scombrids, cephalopods, large/intermediate jacks and large/intermediate schooling pelagics (Table 1). The lowest groups, by definition, were the primary producers and detritus groups (TL=1).

Generally, predation mortality accounted for the greatest proportion of total mortality, with the exception of top predators, such as sharks. This finding was also reflected in the high EE values obtained.

### 1. *Network analysis*

Results from the ecological model in terms of aggregated summary statistics, network flows and information indices are shown in Table 2. Total consumption dominated the Total System Throughput (TST) with 45% of the total flows, followed by flow to detritus (32%) and total respiration (23%). Total system throughput, also an index of the ecosystem size (Christensen and Pauly, 1993b) was estimated at  $113,372 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ; this is high when compared to other reef systems (Table 3). Flows into the detrital pool were also large when compared to other reef system models. This is likely due to the fact that the current model includes a greater proportion of benthic autotrophs. Total fish biomass was comparable to Tampalan but lower than Tiahura and Boca Paila. The strikingly low fish biomass in Bolinao can easily be explained by the high exploitation rates of the resource base (Aliño et al., 1993).

The ecological indicators related to community energetics, community structure, cycling of nutrients and information theory suggest that the coastal systems surrounding the USVI and Puerto Rico are at a mature stage *sensu* Odum's theory (Odum, 1969; Odum, 1971). For example, the primary production/respiration ratio ( $Pp/R$ ) was close to one, indicating that the energy that is fixed is approximately balanced by the cost of maintenance (Table 2). Moreover, the primary production/biomass ratio ( $Pp/B$ ) was low suggesting a high level of biomass accumulation within the system relative to primary production (Table 2). This is in accordance with the notion that coral reef ecosystems are often viewed as 'mature' systems, in which structures and processes are maximized within the system's entity. They tend to also be characterized by high rates of direct recycling with relatively

low transfer efficiencies between trophic levels so as to ultimately most effectively recycle matter back into the detrital pool.

The recycling of nutrients is typically considered to enhance stability of a system and is viewed as one of the principal reasons for ecosystem complexity. In 1976, Finn proposed a simple and effective measure (later known as the Finn cycling index [FCI]) to quantify the importance of recycling flows in ecosystems (Finn, 1976). FCI measures the retentiveness of a system, i.e., the higher the index, the greater the proportion recycled and has been shown to correlate strongly with system maturity and resilience. Calculated as a percentage, it is dimensionless, allowing for easy comparisons between series of diverse ecosystems (Allesina & Ulanowicz, 2004). FCI was estimated at 24.6%, indicative of cycling rates typical of relatively 'closed' systems where decomposition and cycling represent important major functional processes (Heymans & Baird, 2000). The FCI estimated here was higher than 2 reefal areas modelled in the Mexican Caribbean, but higher than that derived for the reef sector at Tiahura, French Polynesia (Table 3). The system omnivory index is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake (Heymans & Baird, 2000) and, in this system, is equal to 0.219. A comparatively high FC, combined with a relatively low omnivory index, is also suggestive of relatively low internal stability and may reflect a degree of stress in the system (Christensen & Walters, 2004; Christensen et al., 2005).

## 2. *Ecosim – increase in turtle abundance*

With a forced increase in turtle biomass over a 200 year period, and high vulnerability of seagrass to sea turtle grazing, large intermediate reef fish, lobsters, and crabs underwent significant increases in biomass largely due to a decline in predation pressure on these functional groups. Biomass of large groupers also increased, but due to an increase in the biomass of a number of their prey. As expected from the applied mediation functions, small scaridae, carnivorous reef fish juveniles, benthic invertebrates and decomposers all declined in biomass, due to either a reduction in the refuge role afforded by a grazed seagrass canopy or an increase in predation pressure.

Raising the biomass accumulation rate of turtles incrementally from 0.05 – 0.1 t year<sup>-1</sup> produced the same pattern, but merely brought forward the onset of system perturbations by about 50 years. The system's response relied on and was particularly sensitive to changes

in the vulnerability of seagrass to turtle grazing: Increasing the vulnerability value led to larger differences in biomass gains/losses in the functional groups highlighted above. The system's response was also sensitive to where on the mediation function graph the dynamic simulation was started (i.e., where the green line is placed). Unsurprisingly the most significant changes were registered when the amplitude in vulnerabilities between the start and the end of the simulations was the greatest.

### 3. *Carrying capacity*

Carrying capacity estimates based on a revised estimate of seagrass extent throughout the Caribbean, led to carrying capacity estimates of between 44,968,000 turtles (assuming heavy grazing and an intake of  $0.74 \text{ kg DM seagrass} \cdot \text{kg}^{-1} \cdot \text{green turtle} \cdot \text{yr}^{-1}$ ) and 285,824,000 turtles (assuming moderate grazing and an intake of  $1.77 \text{ kg DM seagrass} \cdot \text{kg}^{-1} \cdot \text{green turtle} \cdot \text{yr}^{-1}$ ) (Table 4). Previous estimates spanned the range of 38,544,000 - 244,992,000 individuals, given the same assumptions (Table 4).

### 4. *Important considerations* a. *Predator prey dynamics*

It was assumed here that changes in predation rate as a result of grazed seagrass would generally follow the existing, and generally accepted, model proposed by Heck and Orth (1980, 2006). This model is based on changes in seagrass *density*, which according to Moran and Bjorndal (2005) remains unaffected by turtle grazing. However, it is likely that patterns observed as a result of changes to seagrass density are comparable to those that would be witnessed as a result of a decline in canopy height (Bjorndal *pers. comm.*). Nevertheless, for the purpose of completeness, a discussion of studies have specifically looked at changes due to differences in blade length (e.g., Bell (1986a), Horinouchi (1999)). Of those that have manipulated canopy height, most were conducted over short periods of time, a few months on average, and were conducted in subtropical seagrass habitats. However, an important finding in experiments carried out by Bell and Westoby (1986a) are worthy of mention here. Results showed that species richnesses in *Zostera* often decreased when leaves were shortened, but overall, numbers of individuals did not significantly change (six species decreased in abundance, seven showed no

significant change).<sup>1</sup> This lack of significant change in total number of individuals reflects the greater abundance of individuals in the non-responding species. Hence, this study's results do not support the existing model developed by Heck and Orth (1980), which predicts that a greater complexity of seagrass habitat leads to increased species richness and abundance due to a reduction in predator success on invertebrates and juvenile fish. Importantly, instead, experimental results showed that the model could only be expected to operate at the individual species level (Heck & Orth, 1980). Although carried out on *Halodule wrightii*, Young and Young (1978) found similar results, with seagrass blade clipping over a period of one year resulting in species specific changes. They also found that the variations in responses did not consistently correspond to taxonomic groupings or feeding types. Ideally therefore, simulations of increases in turtle biomass and their impact on seagrass associated fauna should be run at the species level. However, this is logistically unrealistic to implement within Ecosim. In order to gain greater understanding of predator-prey interactions in seagrass beds the experiments discussed above should be repeated, preferably in *T. testudinum* beds, and expanded upon.

#### *b. Other trophic considerations*

Correlative field studies have found a significant positive relationship between leaf nitrogen content and grazing by parrotfishes, suggesting preferential feeding on leaves enriched in nitrogen (e.g., Goecker et al. (2005)). Invertebrates such as sea urchins have not been found to exhibit such preferential grazing behaviour. Instead, individuals exhibit compensatory feeding, whereby their consumption is increased when presented with low nitrogen leaves compared to enriched blades (Valentine & Heck, 2001). Interestingly, this raises the question whether the occasional observed overgrazing behaviour of the urchin *Lytechinus variegatus* (Camp et al., 1973; Valentine & Heck, 1991) may at least partly be due to the lower quality forage available to them, i.e., urchins need to eat more to satisfy their energy requirements.

Given that turtles have been shown to improve the nutritional content of their food by regular re-cropping of the same plots, it is likely that

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<sup>1</sup> Interestingly, this response, was not observed when repeated at a larger scale of study, among seagrass beds within a bay Bell, J. D. & Westoby, M. (1986b) Variation in seagrass height and density over a wide spatial scale - Effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology*, **104**, 275-295..

herbivorous fishes will in turn preferentially feed on these turtle-grazed leaves. However, feeding on higher palatable fronds probably occurs according to some trade off relationship given increased predation risk amongst shorter seagrass. At this time, however, it is impossible to draw firm conclusions about how the increase in seagrass palatability as a result of the cultivating function of turtle grazing determines the foraging strategies and feeding preferences of different types of herbivores. Moreover, EwE automatically adjusts items in a group's diet according to its proportional availability. In other words, here, with declining seagrass biomass, EwE will automatically increase the proportion of algae and other prey consumed. As mentioned above, this may not reflect reality.

An essential component of the primary production of seagrass bed communities is the contribution of epiphytes. Epiphytic algae attach themselves to seagrass leaves and can account for over 50% of the standing stock and primary production in *T. testudinum* beds (Wear et al., 1999). Studies have revealed that, at least in temperate systems, a large number of organisms seem to feed predominantly on epiphytic algae rather than the seagrass itself (see review by Jernakoff et al. (1996), and in turn these small grazers constitute an important prey for higher order consumers (Heck et al., 2000). Such top-down control of epiphytes by the assemblage of small invertebrates that inhabit seagrass beds may limit the negative effect (e.g., shading) epiphytes can have on seagrasses (Valentine & Duffy, 2006). However, compared to temperate systems, few studies have looked at the structure, biomass and particularly tropho-dynamics of *T. testudinum* epiphytic communities (Hays, 2005). Despite indications that herbivores feeding on epiphytes are likely to be more prevalent than species feeding on seagrass directly (Hays, 2005), it remains difficult to assess whether such links simply aren't as prevalent and important in tropical systems or whether simply evidence supporting the importance of such links for tropical *T. testudinum* dominated beds is lacking. Sub-tropical research indicates that herbivores feeding on epiphytes are likely to be more prevalent than those feeding on seagrass directly (Hays, 2005). However, the strength of interactions among turtle grass, epiphytes, and grazers has been shown to vary significantly according to the source population of turtle grass (genetic background) (Hays, 2005). This suggests that, even in turtle grass meadows with similar community composition, the role of trophic interactions may differ, and implies that factors that structure turtle grass communities may (i) not be generalizable over space or (ii)

extrapolated to other sites (especially given that the study by Hays (2005) was conducted in subtropical seagrass beds).

EwE was primarily developed to describe and explore changes in trophic interactions and to some degree can account for indirect changes in vulnerability to predators through mediation functions (see below). It cannot at this time model the dramatic reduction in epiphyte *biomass* that would occur from turtle grazing, as older portions of seagrass fronds (i.e., epiphyte laden portions) would be lost from the system when turtles first start cropping plots.

### *c. Caveats in determining mediation functions*

The degree to which and precisely how predator-prey interactions are affected by changing amounts of vegetation (in previous studies generally equated with changes in density) depends in part on seagrass species, as well as prey and predator sizes, visual acuities, foraging behaviours on the part of both predator and prey, and on the presence of more than one predator (Bartholomew et al., 2000; Williams & Heck Jr., 2001; Scharf et al., 2006). In a recently published review, Horinouchi (2007b) highlighted predator foraging behaviour as particularly important when determining whether prey capture efficiencies would be lowered in the presence of (denser) seagrass (see also Flynn and Ritz (2001)). No evidence is available to determine how predators that forage from above the seagrass might be impacted by changes in leaf height. Changes in anti-predatory behaviour by prey in response to less structurally complex habitat may also significantly alter capture success. Work by Main (1987) demonstrated that prey behaviours can be more important than physical interference of the habitat with predators whilst foraging.

Another aspect of canopy height that needs to be considered is that fishes and invertebrates tend to use shelter commensurate with their body size. One of the postulated impacts of a shorter canopy height therefore is that predation-induced competition may result in shelter of optimal size being a limiting resource. It is therefore possible that a reduction in canopy height will likely more significantly affect a subset of groups. However, based on the system of equations that define EwE, such dynamics can not at present be modelled using the EwE software.

Predator and prey behaviour have been suggested as important parameters to consider when defining the relationships between

capture success and habitat complexity. Results generally support the idea that increased habitat complexity affords prey greater survival rates. However, this may depend on prey (and predator) behaviour. Flynn & Ritz (2001) for example showed that an increase in habitat complexity led to a breakdown in swarm size (protective mechanism) of the prey, increasing its vulnerability to predation. Interestingly, Flynn & Ritz (2001) also showed that foraging behaviour can just as significantly affect the relationship between capture success and habitat complexity. Contrary to previous findings, the selected predator, an ambush predator, experienced an increase in predation success with increasing habitat complexity. Thus, predator and prey behaviours can strongly affect population dynamics and should be investigated (Table 5).

Multiplicity of predators is also of particular interest as investigations, albeit in freshwater systems, have shown that their impacts tend to be non-additive (Soluk, 1993). Negative non-additivity occurs when multiple predators consume fewer prey than would be expected by adding their individual predator impacts (Swisher et al., 1998). Positive non-additivity occurs when more prey are consumed by predators than expected by adding their separate effects and usually is a result of facilitative interactions as a result from prey behaviour (e.g., fleeing one predator). The inclusion of such considerations are likely to be important in determining the true impact a reduction in habitat complexity would have on predator-prey interactions as a result of green turtle cropping. However, too little is currently known of individual prey behaviour to its suite of predators as well as behavioural changes that may result from predator competition and intraguild predation to incorporate these here. However, such investigations would constitute compelling avenues for future research (see Table 5).

The mediation functions describing changes in vulnerability of prey to their predators and implemented here follow the model proposed by Heck and Orth (1980). It was assumed that the same mediation function could be applied to all potentially impacted groups. This was based on a model drawn up by Hixon (1991) for coral reefs and supported by findings by Hixon and Beets (1993), asserting that predators may non-selectively reduce all prey populations in proportion to their initial relative abundances. However, Hixon (1991) also suggested that in some instances a second model may be more appropriate to describe interactions that take place: should a competitive hierarchy exist among prey species, predators may

disproportionately reduce subordinate prey abundances. Here too then, future endeavours should try to determine which model most adequately describes changes in predator-prey dynamics as a result of turtle grazing, and thus biodiversity, in seagrass systems.

Moreover, since each functional group comprised several species of similar diet, habitat and activity level, equal susceptibility to predation and mortality were assumed. However, community measures, and even abundance of individuals in feeding guilds, are unreliable variables for testing the effects of leaf height and density – they mask different responses by component species and can give different results depending on the relative abundance of species (Young & Young, 1978; Bell & Westoby, 1986a).

An observation on the interpretation of field data is that numerically abundant species from routine surveys are often singled out as the most ecologically important. However, it may well be that the less abundant species are regularly overlooked in sampling designs that do not take their high vulnerability to predators into account (i.e., they are consumed too quickly to be sampled). The contribution of these species to the trophic dynamics of seagrass ecosystems may therefore be more important than indicated by their sampled abundance alone.

Contributing to the difficulty in attributing a clear nursery role to specific habitats for given species, is the fact that many species exhibit considerable plasticity in habitat use as juveniles at different locations. For example, some juveniles of a given species may be obligate users of seagrass beds at one site, use additional habitats at another site (Nagelkerken et al., 2001; Adams & Ebersole, 2002), or vary in their use of habitats over different sampling years (Adams et al., 2006). This inherent variability calls for caution when extrapolating findings from one location to another and makes it difficult to make with confidence reliable inferences on the impact of turtle grazing on the nursery function of seagrasses. Aside from increasing their vulnerability to predation, other factors that significantly influence juvenile abundance and may be affected by a reduced canopy height include competition and other interspecific interactions. However, here again species' plasticity in habitat use as juveniles renders the interpretation of results more complex. As a result of increased predation risk (and/or increased competition, and/or lowered food availability) juveniles may decide to migrate in search of other locations so as to minimize their ratio of mortality risk to growth rate.

A recent review (Adams et al., 2006) emphasized the general lack of baseline data on juvenile habitat use for many species in tropical coastal systems, underscoring their overall poorly understood function as nursery sites. This then makes the testing of hypotheses related to how turtle grazing may impact the nursery function of seagrass habitats and generation of results with confidence difficult. In this context, future research should focus on gaining a better understanding of the nursery functions of different habitats and their importance to the maintenance of coral reef fishes and invertebrate populations (see 4-level approach research approach suggested by Adams et al. (2006) and Verweij et al. (2007)).

#### *d. Recruitment*

Larval processes are considered crucial for the abundance and diversity of fish and invertebrates in seagrass habitats. Indeed, in addition to predation rates and competition for refuge, abundances of predators and prey are also determined by the relative magnitudes of local recruitment by larvae and habitat colonization by juveniles, which are typically highly variable (Hixon & Beets, 1993). The variable survivorship in juvenile fishes can have significant consequences for population regulation. Although seagrasses are known to enhance the survivorship of young fishes (e.g., Rooker et al. (1998)), the extent to which survivorship is dependent on predator foraging and/or prey avoidance behaviours has not been comprehensively investigated. As such, in addition to changes in water flux resultant from a shorter seagrass canopy it isn't clear how recruitment may be affected by changes in seagrass canopy height.

#### *e. Small-scale spatial aspects of seagrass bed ecology*

Green turtles have been shown to maintain grazing plots in seagrass beds by regular regrazing (Bjorndal, 1980; Ogden et al., 1980). Simulations conducted here did not account for the degree of heterogeneity or patchiness of vegetation that may result from increased turtle grazing activity, due to absence of information on such aspects. However, the patterns created by the selective grazing of turtles (short blade, long blade, and bare patches (Ogden et al., 1983)) may be sufficiently common to cause small-scale changes in sedimentation and turbidity. It has been postulated for example that grazing by green turtles may reduce up to 20-fold the flux of detritus and nitrogen to seagrass sediments, and alter their microbial ecology

(Ogden, 1980; Thayer et al., 1982; Ogden et al., 1983; Thayer et al., 1984).

It is also likely, that the pattern created by grazing turtles will significantly alter:

- (i) the bed's water flow regime, in turn impacting the height and composition of the detritus layer and thus associated prey organisms. Sediment particle size is an important factor determining the types of infaunal species that inhabit the substrate. Hence, changes in the detrital layer (independently from changes to predation rates) are likely to be accompanied by changes in infauna composition;
- (ii) the distribution, abundance and predatory behaviour of mobile organisms found within the seagrass canopy through influence on (a) costs of mobility and foraging, (b) recruitment or dispersal, and/or (c) food supply (Bell et al., 1995; Murphy & Fonseca, 1995).

Moreover, the diet composition of fish species and their juveniles will most likely reflect changes in infauna species composition as a result of changes to the height and composition of the detrital layer (note that such changes, if they do take place, cannot be accommodated in EwE).

To date these relationships have not been investigated and are thus poorly understood. Future research should thus seek to evaluate the impact of grazed/ungrazed edge zones on seagrass community structure and dynamics. Particular attention will have to be paid to discerning impacts on abundance and species composition of the infaunal community that result from changes in predation pressure versus changes in erosion and detritus accumulation rates (Table 4).

#### *f. Landscape level spatial aspects of seagrass bed ecology*

At the landscape level, the patchwork-like pattern of grazed and ungrazed blades is likely to significantly (i) increase the 'edge' effect along which erosion may occur and (ii) impact predator-prey dynamics. This type of heterogeneity is likely to be particularly important for juvenile fishes that may prefer the open spaces for feeding but are simultaneously in close proximity to effective protection from predators. Therefore, these edges or 'ecotones' may facilitate foraging, leading to a higher proportion of predators (fish and invertebrates) and fewer prey species than homogenous areas (Heck &

Orth, 1980; Irlandi, 1994). Thus, one could hypothesise that intermediate turtle densities would create the most heterogeneous seagrass habitat and thus potentially sustain the greatest diversity (and/or abundance) of species.

However, field data seem to indicate that this is not the case; densities of juveniles of larger fish species showed a negative relationship with increased seagrass fragmentation (albeit in a temperate system) (Jackson et al., 2006b). This may be in part attributable to more continuous and homogenous seagrass landscapes having less of an edge effect (areas of enhanced species interactions (Fagan et al., 1999)), providing a more stable environment (less disturbance, physical and biological, predation) where more species can survive (Jackson et al., 2006b). Jackson et al. (2006a) also found that more fragmented seagrass beds supported lower diversity and numbers of species (fish and decapod assemblages) than more homogenous seagrass landscapes. Total species number in this instance reflects all fish and decapods sampled. While smaller prey items may find protection, larger predator species may do so too from their own predators. Bowden et al. (2001) proposed such predator-mediated coexistence as a possible reason for higher species diversity in large patches of seagrass. With increasing fragmentation of the seagrass bed, species number declines, perhaps because larger patches no longer afford protection to higher-order predators. In the case of temperate seagrass blue crabs Hovel and Lipcius (2001) suggested that, although predators may not avoid patchy areas, foraging efficiency may be reduced since the search for appropriate feeding patches takes longer in fragmented habitat.

Possible confounding issues in the interpretation landscape level interactions include the dependence of results on the size and foraging strategy of the predator, and variation in density distribution depending on whether species have a fidelity to the core areas of the seagrass, the area of the patch edge, or an alternative habitat. This relatively new field requires further attention as it has important implications for the largescale management of seagrass ecosystems (e.g., size of marine protected areas).

## 5. *Study limitations*

The model would significantly benefit from incorporating catch statistics as well as time series data on catch per unit effort for individual species. The way it is currently designed, the model

represents what would happen to a coral reef/seagrass system in the absence of perturbations to other groups – which is not realistic in the current resource management context. In Puerto Rico for example, reef fish are under intense fishing pressure from a variety of user groups, including commercial fishers and recreational anglers. Over the last two decades García-Sais et al. (2005) report that reef fisheries, particularly for groupers and snappers (Rogers & Beets, 2001). have undergone marked declines in biomass. Hawkins and Roberts (2004) and Hawkins et al. (2007) also report that artisanal fishing levels can be considered moderately high in Puerto Rico (0.83 fishers per km reef). In the USVI, reef fish assemblages and species composition of catches have also undergone evident changes over the past 40 years (Appeldoorn et al., 1992; Rogers & Beets, 2001).

Furthermore, the model does not include:

- Export of mature leaves from the system when clipping first occurs;
- With a decline in the availability of seagrass as forage due to its elevated consumption by green sea turtles, ecosim automatically increases the proportion of other food types consumed by species that normally include seagrass in their diet. However, a number of species include items in their diets that are not considered food types from which they would derive significant energy for growth and reproduction. Consequently, Ecosim increasing their proportion following a significant decline in seagrass is unlikely to be an adequate representation of real events. For example, parrotfish are common and important herbivores on Caribbean reefs, which use cutting-edged beaks to graze algae from the coral surface. Based on anatomical features of their jaws, a number of parrotfish species has been labelled as excavators. When feeding, these species actively remove coral substrate in the process leaving marked scars on the substratum (Bellwood & Choat, 1990). In addition, they are known to take random, individual bites scattered over the surface of the coral (spot biting) and at times to engage in 'focused biting' (extensive removal of tissue) (Bruckner et al., 2000). It is believed that in conjunction with their unique digestive system, the coral fragments may help these fishes to grind up algae and seagrass (Randall, 1965). Thus, stomach content analyses of parrotfishes will include coral. However, it is unlikely that following a decline in seagrass availability parrotfish will resort to feeding on coral to fulfil their nutritional requirements or metabolic needs.
- Changes to nutrient content of leaves as a result of grazing by turtles (Moran & Bjorndal, 2007) and how this may alter grazing behaviour by other herbivores. In other words, as a result of

increased seagrass productivity the balance between feeding versus seeking refuge from predation may be tipped towards seeking higher quality food resulting in greater exposure to predators. It has been postulated that, at least for selective vertebrate herbivores such as parrotfish and green turtles, the extent of herbivory may be limited by the nutrient content of the leaves, with higher nutrient content being conducive to greater herbivory (Bjorndal, 1980; Zieman et al., 1984; Williams, 1988). However, other studies (e.g., Cebrián & Duarte (1998), Valentine & Heck (2001)) have shown that there appears to be very little correlation between leaf nitrogen and phosphorus contents and herbivory.

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Table 1 – Modified input parameters and output parameters (in italics) for the Caribbean model. TL = Trophic level; B = biomass (t-km<sup>-2</sup>); P/B = production/biomass ratio; Q/B= consumption/biomass ratio; EE = Ecotrophic efficiency; P/Q = production/consumption ratio or Gross efficiency

	<b>Group name</b>	<b>TL</b>	<b>B</b>	<b>P/B</b>	<b>Q/B</b>	<b>EE</b>	<b>P/Q</b>
1	Sharks/rays/scombrids	3.95	0.714	0.298	7.364	<i>0.522</i>	<i>0.04</i>
2	Large/Intermediate jacks	3.67	1.811	1.106	8.805	<i>0.42</i>	<i>0.126</i>
3	Large/intermediate schooling pelagics	3.47	12.172	0.692	12.408	<i>0.93</i>	<i>0.056</i>
4	Intermediate carnivorous reef fish, 1 - ADLT	3.44	5.8	0.58	6.85	<i>0.461</i>	<i>0.085</i>
5	Intermediate carnivorous reef fish, 1 - JUV	3.44	0.13	3.4	33.936	<i>1</i>	<i>0.1</i>
6	Intermediate carnivorous reef fish, 2 - ADLT	3.38	6.493	1.265	10.3	<i>0.852</i>	<i>0.123</i>
7	Intermediate carnivorous reef fish, 2 - JUV	3.44	0.665	2.5	32.05	<i>0.29</i>	<i>0.078</i>
8	Hemiramphidae	2.04	1.125	1.23	39.1	<i>0.888</i>	<i>0.031</i>
9	Intermediate herbivorous reef fish	2.01	12.071	0.52	20.722	<i>0.89</i>	<i>0.025</i>
10	Large/Intermediate reef fish	3.36	11.206	0.57	5.786	<i>0.93</i>	<i>0.099</i>
11	Small carnivorous reef fish	3.38	5.719	2.155	10.902	<i>0.939</i>	<i>0.198</i>
12	Small schooling fish	3.22	13.471	3.366	24.91	<i>0.644</i>	<i>0.135</i>
13	Large groupers	3.83	0.725	0.37	2.3	<i>0.51</i>	<i>0.161</i>
14	Small omnivorous reef fish	2.62	5.659	1.789	20.315	<i>0.831</i>	<i>0.088</i>
15	Large/Intermediate scaridae	2	24.492	0.919	15.131	<i>0.451</i>	<i>0.061</i>
16	Small scaridae	2	5.075	0.94	33.9	<i>0.799</i>	<i>0.028</i>
17	Blenniidae	2.06	0.6	2.84	36.1	<i>0.854</i>	<i>0.079</i>
18	Sea birds	4.19	0.017	5.4	80	<i>0.32</i>	<i>0.068</i>
19	Cephalopods	3.81	1.5	1.3	17.5	<i>0.904</i>	<i>0.074</i>
20	Sea turtles	2.83	0.5	0.15	3.5	<i>0.857</i>	<i>0.043</i>
21	Green turtles	2	0.32	0.15	10.42	<i>0.364</i>	<i>0.014</i>
22	Lobsters	2.9	3.27	1	7.4	<i>0.96</i>	<i>0.135</i>
23	Crabs	2.44	19	1.6	14	<i>0.995</i>	<i>0.114</i>
24	Benthic invertebrates	2.39	25	4.12	86.06	<i>0.983</i>	<i>0.048</i>
25	Echinoids/Asteroids	2.27	125	0.978	3.608	<i>0.688</i>	<i>0.271</i>
26	Gastropods	2.37	46.8	2.8	14	<i>0.976</i>	<i>0.2</i>
27	Worms	2.33	101.24	1.904	22.344	<i>0.915</i>	<i>0.085</i>
28	Bivalves/Chitons/Octopi	2.25	179.65	1.569	10.131	<i>0.901</i>	<i>0.155</i>
29	Sponges/Tunicates	2.14	937.4	1.617	7.199	<i>0.395</i>	<i>0.225</i>
30	Corals/sea anemones	2.34	121	1.09	9	<i>0.739</i>	<i>0.121</i>
31	Zooplankton	2.6	32	40	165	<i>0.993</i>	<i>0.242</i>
32	Decomposers/microfauna	2	15	280	1900	<i>0.982</i>	<i>0.147</i>
33	Phytoplankton	1	40	70	-	<i>0.73</i>	-
34	Seagrass	1	300	6	-	<i>0.906</i>	-
35	Benthic autotrophs	1	1300	13.25	-	<i>0.233</i>	-
36	Detritus	1	2000	-	-	<i>0.999</i>	-

Table 2 – – Ecological indicators of the Caribbean model as pertaining to community energetics, community structure, and cycling of nutrients. The 'cycling index' is the fraction of an ecosystem's throughput that is recycled and is expressed here as percentage.

<b>Parameter</b>	<b>Value</b>	<b>Unit</b>
Sum of all consumption	51022.09	t/km <sup>2</sup> /year
Sum of all respiratory flows	25931.58	t/km <sup>2</sup> /year
Sum of all flows into detritus	36395.04	t/km <sup>2</sup> /year
Total system throughput	113,372	t/km <sup>2</sup> /year
Calculated total net primary production	21,825	t/km <sup>2</sup> /year
Total primary production/total respiration	0.842	
Total primary production/total biomass	6.504	
Total biomass/total throughput	0.03	
Total biomass (excluding detritus)	3,355.63	t/km <sup>2</sup>
<b>Network flow indices</b>		
		% of total
Finn's cycling index	24.6	throughput
System Omnivory Index	0.219	

Table 3 – Comparison between system summary attributes and network flow indices estimated here with reef systems in Tiahura (French Polynesia ) (Arias Gonzalez, 1994; Arias-Gonzalez et al., 1997), Bolinao (Philippines) (Aliño et al., 1993), Boca Paila, Tampalan, and Mahahual (Mexico) (Arias-Gonzalez et al., 2004). (\*) indicate derived from (Heymans & Baird, 2000).

	Tiahura	Bolinao	Boca Paila	Tampalan	Mahahual	Caribbean
Sum of all flows into detritus (t/km <sup>2</sup> /year)		18,405	11,397	12,253	3,503	36,395
Total system throughput (t/km <sup>2</sup> /year)		39,307	48,037	45,202	13,169	113,372
Total net primary production (t/km <sup>2</sup> /year)	11,350		15,889	14,293	4,152	21,825
Total biomass(excluding detritus) (t/km <sup>2</sup> )	4,554	1,879	1,019	1,015	333	0
Biomass/total system throughput		0.048	0.021	0.022	0.025	0.03
Net primary production/total respiration	1.1		1.3	1.3	1.3	0.842
Net primary production/total biomass			15.6	14.1	12.5	6.504
Finn cycling index (% of total throughput)	58		11.7-15 (*)	13.6-15 (*)		24.6
Fish/total biomass	0.032	0.004	0.146	0.107	0.13	0.032185
Fish biomass (t/km <sup>2</sup> )	145.728	7.516	148.774	108.605	43.29	108

Table 4 – Carrying capacities for green turtles on seagrass beds in the Caribbean. Calculations are based on: (i) 3 levels of intake ( $\text{kg DM seagrass} \cdot \text{kg}^{-1} \cdot \text{green turtle} \cdot \text{yr}^{-1}$ ) estimated by 3 different methods; (ii) 3 levels of seagrass productivity (DM = dry mass); (iii) an average 50kg turtle estimate; and (iv) a revised Caribbean wide seagrass extent estimate of 77,000  $\text{km}^2$ . Values derived based on 66,000  $\text{km}^2$  of seagrass in the Caribbean are included in parentheses for comparative purposes. Modified from Moran and Bjorndal (2005).

<i>T. testudinum</i> productivity ( $\text{kg} \cdot \text{DM} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$ )	Intake 0.74 <sup>a</sup>		Intake 1.17 <sup>b</sup>		Intake 1.77 <sup>c</sup>	
	$\text{kg} \cdot \text{turtle} \cdot \text{km}^{-2}$	No. of turtles in the Caribbean	$\text{kg} \cdot \text{turtle} \cdot \text{km}^{-2}$	No. of turtles in the Caribbean	$\text{kg} \cdot \text{turtle} \cdot \text{km}^{-2}$	No. of turtles in the Caribbean
Heavy grazing <sup>d</sup>	29,200	44,968,000 (38,544,000)	18,500	28,490,000 (24,420,000)	12,200	18,788,000 (16,104,000)
Simulated grazing <sup>e</sup>	374,800	577,192,000 (494,736,000)	237,100	365,134,000 (312,972,000)	156,700	241,318,000 (206,844,000)
Moderate grazing <sup>f</sup>	443,900	683,606,000 (585,948,000)	280,800	432,432,000 (370,656,000)	185,600	285,824,000 (244,992,000)

<sup>a</sup> Bjorndal (1982); based on energy budget calculation for adult female.  
<sup>b</sup> Bjorndal (1980); based on indigestible lignin ratio and daily feces production  
<sup>c</sup> Williams (1988); based on estimates of daily bite counts and bite size  
<sup>d</sup> 21,600  $\text{kg DM} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$  (re-calculated from Table 4 in Williams (1988))  
<sup>e</sup> 277,400  $\text{kg DM} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$  (Moran & Bjorndal, 2005)  
<sup>f</sup> 328,500  $\text{kg DM} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$  (Zieman et al., 1984)

Table 5 – Examples of suggestions for future research priorities based on limitations that came to the fore in developing the model presented here

Aspect	Postulated impact	Examples of questions that need to be addressed in future research	Examples of key references
Fishes use shelter commensurate with body size	Reduced availability of shelter of appropriate size > predation-induced competition	Does the size distribution and density of fishes that seek shelter in seagrass beds vary over a gradient of seagrass canopy heights?	(Hixon & Beets, 1993);
Epiphytes		Who are the consumers of epiphytes? Do their diets in terms of species composition vary & do they preferentially feed on some species? Who are the predators of seagrass epiphyte consumers (SEC)? Are there significant differences in the abundance of SEC over a gradient of fishing pressure? [Both mesocosm and field studies will be required here ]	(Hays, 2005)
Vulnerability of species benefiting from sheltering capacity of seagrass	Increased vulnerability of certain species to their predators. The relationship is likely to vary between species.	What is the predation rate of species known to benefit from the refuge role of long bladed seagrass? How does this rate change following a reduction in canopy height? [e.g., tethering experiments]	
Diet composition	Prey items consumed different, mirroring changes in infauna species composition a result of changes to the height of the detrital layer.	How does the diet composition of key species differ between grazed and ungrazed scenarios? Care will need to be applied to make sure that differences registered are indeed attributable to differences in grazing intensity (canopy height) and not due to seasonal or other changes. Are prey becoming limiting?	
Increased palatability	Fish herbivores whose diet consists mainly of seagrass will increase their intake of turtle cropped seagrass. Invertebrate herbivores will need to consume less to satisfy their energy needs.	What are the grazing rates on seagrass of herbivores known to consume <i>T. testudinum</i> in ungrazed conditions? How do these compare when seagrass has been continuously cropped by turtles.	(Goecker et al., 2005) (Valentine & Heck, 2001)
Nursery function	Sheltering capacity of grazed seagrass is reduced compared to non-grazed seagrass	What is the community composition in non-grazed versus grazed seagrass beds? What is the size composition of species in grazed and non-grazed seagrass beds? What is the predation rate in grazed and non-grazed seagrass beds Are there significant differences between predators foraging in grazed versus non-grazed beds? What are their size distribution? Do they preferentially forage during the day or at night? What are their predation strategies? Are there any interactions between these predator species? Are larger predators (i.e. organisms that prey on studied predators) more commonly sighted over grazed seagrass beds?	

		<p>If multiple predators are present can their impact on prey be categorized as positive or negative non-additive?</p> <p>Is there evidence of a threshold in terms of seagrass biomass beyond which (i) potential changes in refuge seeking individuals' size does not significantly vary and/or (ii) predation rates do not show significant differences?</p>	
Edge effects	Significant reduction in detritus layer and thus impact on infauna abundance and composition	<p>1. Erosion</p> <p>What effect does turtle grazing have on the height of the detritus layer?</p> <p>How do sedimentation rates and turbidity levels differ between grazed and ungrazed plots?</p> <p>How do potential changes to the detritus layer influence the community composition within the detrital layer as well as the seagrass bed?</p> <p>2. Predator /prey dynamics</p> <p>Are edge effects discernible at the boundary between grazed and ungrazed seagrass in terms of for example fewer invertebrates species but greater fish abundance?</p> <p>If increased predation rates are prevalent what relationship do they follow?</p> <p>[need to consider these interactions both at both the level of individual patches and seagrass landscape]</p>	<p>(Ogden, 1980; Thayer et al., 1982; Ogden et al., 1983; Thayer et al., 1984; Moran &amp; Bjorndal, 2005)</p> <p>(Heck &amp; Orth, 1980; Bell &amp; Westoby, 1986)</p> <p>(Boström et al., 2006; Jackson et al., 2006a; Jackson et al., 2006b)</p>
Predator foraging behaviour	Ambush predators will suffer from whereas most other visual predators will benefit from a decrease in habitat complexity	<p>What foraging tactics do existing predators in the observed seagrass bed use? How does predation success vary with changes in seagrass habitat complexity?</p> <p>How does foraging success vary depending on number and 'type' of predator present?</p>	<p>(Flynn &amp; Ritz, 2001)</p> <p>(Swisher et al., 1998)</p>

Figure 1 – Map of the US Virgin Islands (reproduced from Grober-Dunsmore et al. (2007) and Puerto Rico (CIA, 2008)

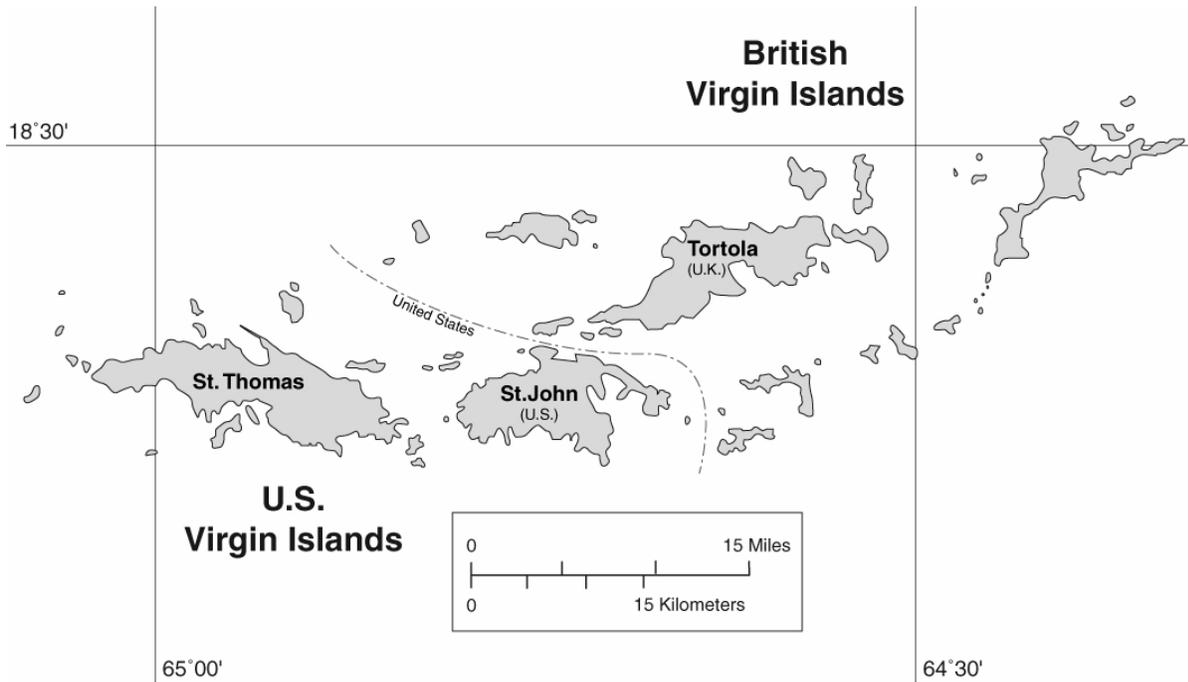
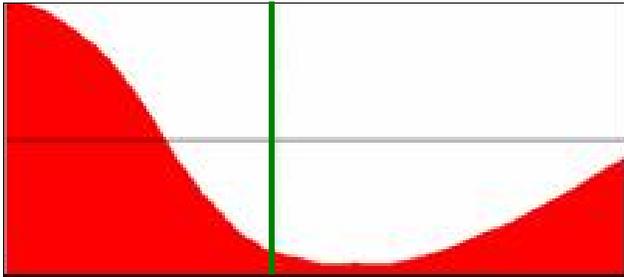
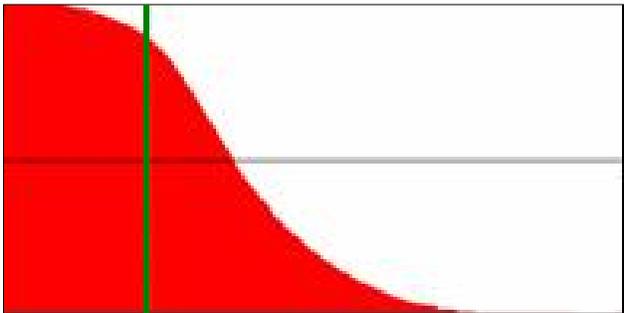


Figure 2 – Mediation functions where the mediating group is on the x-axis and changes to the vulnerability of the impacted group is depicted on the y-axis. In both instances seagrass biomass is the mediating parameter. Seagrass biomass is assumed to decline as moving from left to right. (a) describes the decline in refuge afforded to small and juvenile fish by seagrass in an ungrazed state (b) describes the increase in vulnerability of infauna to their predators with a reduction in the canopy height and concomitant greater exposure to predation



(a)



(b)

Appendix 1 – List of Caribbean fish species and their habitat association – R = reef ecosystem, here can include seagrass; BP= benthypelagic; D= demersal

Family	Genus	Species	Habitat
Acanthuridae	Acanthurus	bahianus	R
Acanthuridae	Acanthurus	chirurgus	R
Acanthuridae	Acanthurus	coeruleus	R
Albulidae	Albula	vulpes	R
Antennariidae	Antennarius	multicellatus	R
Antennariidae	Antennarius	striatus	R
Apogonidae	Phaeoptyx	conklini	R
Apogonidae	Apogon	maculatus	R
Atherinidae	Hypoatherina	harringtonensis	R
Atherinidae	Atherinomorus	stipes	R
Aulostomidae	Aulostomus	maculatus	R
Balistidae	Balistes	capriscus	R
Balistidae	Balistes	vetula	R
Balistidae	Canthidermis	sufflamen	R
Balistidae	Melichthys	niger	R
Balistidae	Xanthichthys	ringens	R
Belonidae	Tylosurus	crocodilus	R
Belonidae	Ablennes	hians	R
Belonidae	Platybelone	argalus argalus	R
Belonidae	Strongylura	marina	R
Belonidae	Strongylura	timucu	R
Belonidae	Tylosurus	acus acus	R
Blenniidae	Entomacrodus	nigricans	R
Blenniidae	Ophioblennius	atlanticus	R
Blenniidae	Parablennius	marmoreus	R
Blenniidae	Scartella	cristata	R
Bothidae	Bothus	lunatus	R
Bothidae	Bothus	ocellatus	R
Bothidae	Paralichthys	tropicus	
Carangidae	Selar	crumenophthalmus	R
Carangidae	Alectis	ciliaris	R
Carangidae	Carangoides	bartholomaei	R
Carangidae	Caranx	crysos	R
Carangidae	Caranx	hippos	R
Carangidae	Caranx	latus	R
Carangidae	Caranx	lugubris	BP
Carangidae	Carangoides	ruber	R
Carangidae	Decapterus	macarellus	R
Carangidae	Decapterus	punctatus	R
Carangidae	Oligoplites	saurus	R
Carangidae	Selene	vomer	D
Carangidae	Seriola	dumerili	R

Carangidae	Seriola	rivoliiana	R
Carangidae	Trachinotus	falcatus	R
Carangidae	Trachinotus	goodei	R
Carangidae	Elagatis	bipinnulatus	R
Carcharhinidae	Carcharhinus	acronotus	R
Carcharhinidae	Carcharhinus	falciformis	R
Carcharhinidae	Carcharhinus	leucas	R
Carcharhinidae	Carcharhinus	limbatus	R
Carcharhinidae	Carcharhinus	longimanus	R
Carcharhinidae	Carcharhinus	perezii	R
Carcharhinidae	Galeocerdo	cuvier	R
Carcharhinidae	Negaprion	brevirostris	R
Carcharhinidae	Rhizoprionodon	porosus	R
Chaetodontidae	Chaetodon	aculeatus	R
Chaetodontidae	Chaetodon	ocellatus	R
Chaetodontidae	Chaetodon	striatus	R
Chaetodontidae	Chaetodon	capistratus	R
Chaetodontidae	Chaetodon	sedentarius	R
Cirrhitidae	Amblycirrhitus	pinos	R
Labrisomidae	Labrisomus	nuchipinnis	R
Labrisomidae	Labrisomus	guppyi	R
Clupeidae	Harengula	clupeola	R
Clupeidae	Harengula	humeralis	R
Clupeidae	Jenkinsia	lamprotaenia	R
Clupeidae	Opisthonema	oglinum	R
Clupeidae	Sardinella	aurita	
Congridae	Heteroconger	longissimus	R
Coryphaenidae	Coryphaena	`	P
Dactylopteridae	Dactylopterus	volitans	R
Dasyatidae	Dasyatis	americana	R
Dasyatidae	Urolophus	jamaicensis	R
Diodontidae	Chilomycterus	antennatus	R
Diodontidae	Chilomycterus	antillarum	R
Diodontidae	Diodon	holocanthus	R
Diodontidae	Diodon	hystrix	R
Echeneidae	Echeneis	naucrates	R
Echeneidae	Remora	remora	R
Elopidae	Elops	saurus	R
Emmelichthyidae	Inermia	vittata	
Engraulidae	Anchoa	hepsetus	P
Engraulidae	Anchoa	lyolepis	P
Engraulidae	Anchoa	mitchilli	P
Engraulidae	Anchoa	parva	P
Ephippidae	Chaetodipterus	faber	R
Exocoetidae	Exocoetus	volitans	P
Fistulariidae	Fistularia	tabacaria	R
Gerreidae	Eucinostomus	argenteus	R

Gerreidae	Eucinostomus	lefroyi	R
Gerreidae	Gerres	cinereus	R
Ginglymonstomalidae	Ginglymostoma	cirratum	R
Gobiidae	Gobiosoma	evelynae	R
Gobiidae	Bathygobius	soporator	R
Gobiidae	Coryphopterus	glaucofraenum	R
Gobiidae	Gnatholepis	thompsoni	R
Gobiidae	Gobiosoma	horsti	R
Serranidae	Rypticus	saponaceus	R
Grammatidae	Gramma	loreto	R
Grammatidae	Gramma	melacara	R
Haemulidae	Anisotremus	surinamensis	R
Haemulidae	Anisotremus	virginicus	R
Haemulidae	Haemulon	carbonarium	R
Haemulidae	Haemulon	chrysargyreum	R
Haemulidae	Haemulon	striatum	R
Haemulidae	Haemulon	boschmae	R
Haemulidae	Haemulon	macrostomum	R
Haemulidae	Haemulon	steindachneri	R
Haemulidae	Orthopristis	poeyi	D
Haemulidae	Pomadasys	corvinaeformis	D
Haemulidae	Pomadasys	crocro	D
Haemulidae	Haemulon	album	R
Haemulidae	Haemulon	aurolineatum	R
Haemulidae	Haemulon	bonariense	R
Haemulidae	Haemulon	flavolineatum	R
Haemulidae	Haemulon	melanurum	R
Haemulidae	Haemulon	parrai	R
Haemulidae	Haemulon	plumieri	R
Haemulidae	Haemulon	sciurus	R
Haemulidae	Orthopristis	ruber	D
Haemulidae	Orthopristis	chrysoptera	D
Hemiramphidae	Hemiramphus	balao	R
Hemiramphidae	Hemiramphus	unifasciatus	R
Hemiramphidae	Hemiramphus	brasiliensis	R
Holocentridae	Myripristis	jacobus	R
Holocentridae	Holocentrus	coruscus	
Holocentridae	Neoniphon	marianus	R
Holocentridae	Plectrypops	retrospinis	R
Holocentridae	Sargocentron	vexillarium	R
Holocentridae	Holocentrus	ascensionis	R
Holocentridae	Holocentrus	rufus	R
Kyphosidae	Kyphosus	sectator	R
Kyphosidae	Kyphosus	incisor	R
Labridae	Xyrichtys	splendens	R
Labridae	Thalassoma	bifasciatum	R
Labridae	Bodianus	rufus	R

Labridae	Clepticus	parrae	R
Labridae	Halichoeres	bivittatus	R
Labridae	Halichoeres	garnoti	R
Labridae	Halichoeres	maculipinna	R
Labridae	Halichoeres	poeyi	R
Labridae	Lachnolaimus	maximus	R
Labridae	Xyrichtys	novacula	R
Labridae	Halichoeres	radiatus	R
Lutjanidae	Pristipomoides	macrophthalmus	BP
Lutjanidae	Lutjanus	cyanopterus	R
Lutjanidae	Apsilus	dentatus	R
Lutjanidae	Lutjanus	analis	R
Lutjanidae	Lutjanus	apodus	R
Lutjanidae	Lutjanus	buccanella	R
Lutjanidae	Lutjanus	campechanus	R
Lutjanidae	Lutjanus	griseus	R
Lutjanidae	Lutjanus	jocu	R
Lutjanidae	Lutjanus	synagris	R
Lutjanidae	Lutjanus	vivanus	R
Lutjanidae	Ocyurus	chrysurus	R
Lutjanidae	Rhomboplites	aurorubens	D
Lutjanidae	Lutjanus	mahogoni	R
Malacanthidae	Malacanthus	plumieri	R
Megalopidae	Tarpon	atlanticus	R
Monacanthidae	Aluterus	monoceros	R
Monacanthidae	Aluterus	schoepfii	R
Monacanthidae	Aluterus	scriptus	R
Monacanthidae	Cantherines	pullus	R
Monacanthidae	Monacanthus	ciliatus	R
Monacanthidae	Monacanthus	tuckeri	R
Monacanthidae	Cantherines	macrocerus	R
Monacanthidae	Stephanolepis	setifer	R
Mugilidae	Mugil	curema	R
Mullidae	Mulloidichthys	martinicus	R
Mullidae	Pseudupeneus	maculatus	R
Muraenidae	Enchelycore	nigricans	R
Muraenidae	Echidna	catenata	R
Muraenidae	Gymnothorax	funnebris	R
Muraenidae	Gymnothorax	miliaris	R
Muraenidae	Gymnothorax	vicinus	R
Muraenidae	Gymnothorax	moringa	R
Myliobatidae	Aetobatus	narinari	R
Ogcocephalidae	Ogcocephalus	nasutus	R
Ophichthidae	Myrichthys	breviceps	R
Ophichthidae	Myrichthys	ocellatus	R
Ophichthidae	Ophichthus	ophis	D
Opisthognathidae	Opisthognathus	aurifrons	R

Opisthognathidae	Opisthognathus	macrognathus	R
Opisthognathidae	Opisthognathus	maxillosus	R
Opisthognathidae	Opisthognathus	whitehurstii	R
Ostraciidae	Acanthostracion	quadricornis	R
Ostraciidae	Lactophrys	bicaudalis	R
Ostraciidae	Lactophrys	trigonus	R
Ostraciidae	Lactophrys	triqueter	R
Ostraciidae	Acanthostracion	polygonius	R
Pempheridae	Pempheris	schomburgki	R
Pempheridae	Pempheris	poeyi	R
Pomacanthidae	Centropyge	argi	R
Pomacanthidae	Holacanthus	ciliaris	R
Pomacanthidae	Pomacanthus	arcuatus	R
Pomacanthidae	Holacanthus	tricolor	R
Pomacanthidae	Pomacanthus	paru	R
Pomacentridae	Abudefduf	saxatilis	R
Pomacentridae	Abudefduf	taurus	R
Pomacentridae	Chromis	multilineata	R
Pomacentridae	Microspathodon	chrysurus	R
Pomacentridae	Chromis	cyanea	R
Pomacentridae	Stegastes	fuscus	R
Pomacentridae	Stegastes	leucostictus	R
Pomacentridae	Stegastes	variabilis	R
Pomacentridae	Stegastes	planifrons	R
Pomatonidae	Pomatomus	saltatrix	P
Priacanthidae	Heteropriacanthus	cruentatus	R
Priacanthidae	Priacanthus	arenatus	R
Rachycentridae	Rachycentron	canadum	R
Scaridae	Scarus	iserti	R
Scaridae	Cryptotomus	roseus	R
Scaridae	Nicholsina	usta	R
Scaridae	Scarus	coelestinus	R
Scaridae	Scarus	taeniopterus	R
Scaridae	Sparisoma	radians	R
Scaridae	Sparisoma	aurofrenatum	R
Scaridae	Scarus	vetula	R
Scaridae	Sparisoma	rubripinne	R
Scaridae	Sparisoma	viride	R
Scaridae	Scarus	coeruleus	R
Scaridae	Scarus	guacamaia	R
Scaridae	Sparisoma	chrysopterum	R
Sciaenidae	Equetus	lanceolatus	R
Sciaenidae	Equetus	punctatus	R
Sciaenidae	Odontoscion	dentex	R
Sciaenidae	Pareques	acuminatus	R
Scombridae	Scomberomorus	regalis	R
Scombridae	Auxis	rochei rochei	P

Scombridae	Auxis	thazard thazard	P
Scombridae	Scomberomorus	cavalla	R
Scombridae	Thunnus	atlanticus	P
Scombridae	Euthynnus	alletteratus	R
Scombridae	Scomberomorus	maculatus	R
Scorpaenidae	Scorpaena	plumieri	R
Scorpaenidae	Scorpaena	brasiliensis	R
Scorpaenidae	Scorpaena	grandicornis	R
Scorpaenidae	Scorpaena	inermis	R
Scorpaenidae	Scorpaenodes	caribbaeus	R
Serranidae	Dermatolepis	inermis	R
Serranidae	Liopropoma	rubre	R
Serranidae	Serranus	tabacarius	R
Serranidae	Alphestes	afer	R
Serranidae	Hypoplectrus	aberrans	R
Serranidae	Hypoplectrus	chlorurus	R
Serranidae	Hypoplectrus	nigricans	R
Serranidae	Serranus	tortugarum	R
Serranidae	Cephalopholis	cruentata	R
Serranidae	Cephalopholis	fulva	R
Serranidae	Diplectrum	formosum	R
Serranidae	Epinephelus	adscensionis	D
Serranidae	Epinephelus	guttatus	R
Serranidae	Epinephelus	itajara	R
Serranidae	Epinephelus	morio	R
Serranidae	Epinephelus	striatus	R
Serranidae	Hypoplectrus	puella	R
Serranidae	Mycteroperca	bonaci	R
Serranidae	Mycteroperca	interstitialis	R
Serranidae	Mycteroperca	phenax	R
Serranidae	Mycteroperca	tigris	R
Serranidae	Mycteroperca	venenosa	R
Serranidae	Paranthias	furcifer	R
Serranidae	Serranus	tigrinus	R
Sparidae	Calamus	calamus	R
Sparidae	Calamus	penna	R
Sparidae	Calamus	pennatula	R
Sparidae	Diplodus	argenteus caudimacula	R
Sparidae	Archosargus	rhomboidalis	R
Sparidae	Calamus	bajonado	R
Sphryaenidae	Sphyaena	barracuda	R
Sphryaenidae	Sphyaena	picudilla	R
Sphyrnidae	Sphyrna	mokarran	R
Sphyrnidae	Sphyrna	lewini	P
Sphyrnidae	Sphyrna	tiburo	R
Synodontidae	Synodus	intermedius	R
Synodontidae	Synodus	synodus	R

Synodontidae	Synodus	foetens	R
Tetraodontidae	Sphoeroides	spengleri	R
Tetraodontidae	Canthigaster	rostrata	R
Tetraodontidae	Sphoeroides	testudineus	R
Triakidae	Mustelus	canis	D

## Appendix 2 – Basic estimates for Caribbean reef fish species. Natural mortality values were derived for 28°C

Family	Genus	Species	M	Temp	Winf	Q/B				Food (general)	Food (detailed)
						Detr	Herb	Omni	Carn		
Acanthuridae	Acanthurus	bahianus	0.95	28.0	1616.9		26.7			plants, detritus	92% algae, 8% seagrass
Acanthuridae	Acanthurus	chirurgus	0.64	28.0	823.4		30.6			plants, detritus	94% algae, 5.7% seagrass, rest mollusks, worms
Acanthuridae	Acanthurus	coeruleus	0.32	28.0	2056.3		25.4			plants, detritus	93% algae, 7% seagrass, rest benthic invertebrates, cnidarians
Albulidae	Albula	vulpes	0.51	28.0	31449.6				4.3	zoobenthos, mainly animals	70% zoobenthos, 20% fish, 3% worms, 5.2% mollusks, 1.5% algae
Antennariidae	Antennarius	multiocellatus	1.50	28.0	93.9				14.0	nekton, mainly animals	75% fish, 25% benthic crustaceans
Antennariidae	Antennarius	striatus	1.28	28.0	181.9				12.2	nekton, mainly animals	100% nekton
Apogonidae	Phaeoptyx	conklini	2.63	28.0	8.8			50.0			n/a
Apogonidae	Apogon	maculatus	2.27	28.0	30.9				17.6	zoobenthos, mainly animals	87.2% benthic crustaceans, 9% zooplankton, 4% worms
Atherinidae	Hypoatherina	harringtonensis	2.44	28.0	12.3				21.2	zooplankton, mainly animals	worms & zooplankton
Atherinidae	Atherinomorus	stipes	2.44	28.0	12.3				21.2	zooplankton, mainly animals	80% zooplankton, 20% finfish
Aulostomidae	Aulostomus	maculatus	0.48	28.0	2335.8				7.3	nekton, mainly animals	74% nekton, 26% zoobenthos
Balistidae	Balistes	capriscus	0.75	28.0	2678.7				7.1	zoobenthos, mainly animals	benthic crustaceans, echinoderms, mollusks
Balistidae	Balistes	vetula	0.63	28.0	4551.0				6.3	zoobenthos, mainly animals	73% echinoderms, 1% seastars, 13% benthic crustaceans, 5% mollusks, rest worms
Balistidae	Canthidermis	sufflamen	0.65	28.0	6614.6				5.9	zoobenthos, mainly animals	29% echinoderms, 25% mollusks, 3% algae, rest zooplankton; 90% benthic crustaceans, 10% mollusks
Balistidae	Melichthys	niger	0.78	28.0	1406.1		27.4			plants, detritus+animals	76% algae, 9% benthic crustaceans, 7% mollusks, 3% fish, 5% zooplankton
Balistidae	Xanthichthys	ringens	1.28	28.0	181.9				12.2	zooplankton, mainly animals	zooplankton
Belonidae	Tylosurus	crocodilus	0.39	27.5	8086.4				5.5	nekton, mainly animals	91% finfish (acanthurus, harengula), 9% benthic crustaceans
Belonidae	Ablennes	hians	0.86	28.0	3898.5				6.5	nekton, mainly animals	finfish
Belonidae	Platybelone	argalus argalus	0.78	28.0	1406.1				8.1	nekton, mainly animals	97% finfish, 3% zoobenthos
Belonidae	Strongylura	marina	0.45	28.0	14815.4				5.0	mainly animals	nekton, benthic crustacean & zooplankton
Belonidae	Strongylura	timucu	0.68	28.0	2524.4				7.2	nekton, mainly animals	96% finfish, 4% benthic crustacean

Belontiidae	Tylosurus	acus acus	0.36	28.0	38183.6			4.1	nekton, mainly animals	96% finfish, 1.5% benthic crustacean, 2.5% zooplankton
Blenniidae	Entomacrodus	nigricans	2.44	28.0	12.3		72.1		plants, detritus	96% algae, 4% worms
Blenniidae	Ophioblennius	atlanticus	1.55	28.0	81.2		49.1		plants, detritus	99.5% algae, 0.5% zooplankton
Blenniidae	Parablennius	marmoreus	2.74	28.0	7.5		45.1		plants/detritus + animals	algae, zooplankton, detritus
Blenniidae	Scartella	cristata	2.14	28.0	1.3		114.1		plants, detritus	100% algae
Bothidae	Bothus	lunatus	0.83	28.0	2237.8			7.3	nekton, mainly animals	86% finfish, 11% benthic crustacean, 3% mollusks
Bothidae	Bothus	ocellatus	1.61	28.0	68.6			14.9	zoobenthos, mainly animals	28% finfish, 72% benthic crustaceans
Bothidae	Paralichthys	tropicus	0.78	28.0	1406.1			17.8		n/a
Carangidae	Selar	crumenophthalmus	0.55	27.6	11584.0			5.2	zoobenthos, mainly animals	50% finfish, 50% zooplankton; 98% benthic crustacean, 2% finfish
Carangidae	Alectis	ciliaris	0.36	28.0	69773.8			3.6	nekton, mainly animals	65% benthic crustacean, 31% finfish, 4% detritus
Carangidae	Carangoides	bartholomaei	0.48	28.0	18372.8			4.8	nekton, mainly animals	100% finfish (parrotfish, ocyurus chrysurus, Halichoeres)
Carangidae	Caranx	cryos	0.53	28.0	6987.1			5.0	nekton, mainly animals	87% finfish (Engraulidae), 12% benthic crustaceans, 1% zooplankton
Carangidae	Caranx	hippos	0.41	28.0	33460.4			7.0	zoobenthos, mainly animals	100% shrimps and crabs; 50% finfish, 50% benthic crustaceans
Carangidae	Caranx	latus	0.48	28.0	44949.1			4.0	nekton, mainly animals	100% benthic crustaceans; 87% finfish (Myripristis, Harengula), 8% mollusks, 5% benthic crustaceans
Carangidae	Caranx	lugubris	0.27	28.0	18721.2			4.8	nekton, mainly animals	100% finfish (parrotfish, ocyurus chrysurus, Halichoeres)
Carangidae	Carangoides	ruber	0.33	28.0	5918.0			10.6	nekton, mainly animals	91% finfish (acanthuridae, engraulidae, mullidae, blennidae, pomacentridae), 6% benthic crustaceans, 3% zooplankton
Carangidae	Decapterus	macarellus	1.36	28.0	1670.1			7.8	zooplankton, mainly animals	98% zooplankton, 2% benthic crustaceans
Carangidae	Decapterus	punctatus	0.75	28.0	319.6			10.9	zooplankton, mainly animals	66% zooplankton, 28% benthic crustaceans, 6% detritus
Carangidae	Oligoplites	saurus	1.01	28.0	490.3			10.0	nekton, mainly animals	98% finfish, 2% zooplankton
Carangidae	Selene	vomer	0.80	28.0	3342.4			6.8	nekton, mainly animals	finfish & benthic crustaceans
Carangidae	Seriola	dumerili	0.25	28.0	32302.3			3.5	nekton, mainly animals	100% finfish (balistidae, caranx ruber, haemulon)
Carangidae	Seriola	rivoliana	0.34	28.0	66274.5			3.7	nekton, mainly animals	100% finfish

Carangidae	Trachinotus	falcatus	0.52	28.0	16788.1				11.8	mainly animals	65% mollusks, 25% urchins, 10% benthic crustaceans
Carangidae	Trachinotus	goodei	0.78	28.0	1406.1				8.1	nekton, mainly animals	85% finfish (Engraulidae), 12% mollusks, 3% benthic crustaceans
Carangidae	Elagatis	bipinnulatus	0.24	28.5	54885.8				3.8	nekton, mainly animals	finfish, benthic crustaceans, mollusks, worms, zooplankton
Carcharhinidae	Carcharhinus	acronotus	0.22	28.0	121036.3				3.2	nekton, mainly animals	98% finfish, 1% benthic crustaceans, 1% mollusks
Carcharhinidae	Carcharhinus	falciformis	0.17	28.0	445811.9				2.5	nekton, mainly animals	64% finfish, 33% squids, 3% benthic crustaceans
Carcharhinidae	Carcharhinus	leucas	0.09	28.0	321197.5				4.3	nekton, mainly animals	88% finfish, 4% algae, 3% mammals, 3% benthic crustaceans, 0.5% birds, 1.5% turtles
Carcharhinidae	Carcharhinus	limbatus	0.34	28.0	73418.2				3.6	nekton, mainly animals	93% finfish, 4% squids, 2% benthic crustaceans, 0.5% mollusks, 0.5% algae
Carcharhinidae	Carcharhinus	longimanus	0.18	28.0	954388.8				2.1	nekton, mainly animals	44% squids, 46% finfish, 4% mammals, 4% algae, 1% birds, 1% benthic crustaceans, 1% mollusks.
Carcharhinidae	Carcharhinus	perezii	0.22	28.0	278732.5				2.7	nekton, mainly animals	100% finfish
Carcharhinidae	Galeocerdo	cuvier	0.09	28.0	2735926.9				1.7	nekton, mainly animals	50% finfish, 50% turtles
Carcharhinidae	Negaprion	brevirostris	0.09	28.0	543757.3				2.5	nekton, mainly animals	100% finfish
Carcharhinidae	Rhizoprionodon	porosus	0.94	28.0	19.2				19.4	nekton, mainly animals	100% finfish (Halichoeres)
Chaetodontidae	Chaetodon	aculeatus	3.54	25.0	12.3				21.2	zoobenthos, mainly animals	38% worms, 27% detritus, 11% echinoderms, 24% benthic crustaceans; 69% worms, 25% benthic crustaceans, 5% zooplankton, 1% detritus
Chaetodontidae	Chaetodon	ocellatus	1.86	25.0	284.5				11.2	zoobenthos, mainly animals	53% polyps, 40% worms, 5.5% algae, 2.5% benthic crustaceans
Chaetodontidae	Chaetodon	striatus	2.28	25.0	159.2				12.6	zoobenthos, mainly animals	59% worms, 33% polyps, 6% benthic crustaceans, 3% mollusks
Chaetodontidae	Chaetodon	capistratus	3.00	28.0	16.7				19.9	zoobenthos, mainly animals	44% polyps, 31% worms, 17% detritus, 6% zooplankton, 2% sponges; 84% polyps, 12% worms, 3% benthic crustaceans, 1% zooplankton
Chaetodontidae	Chaetodon	sedentarius	1.83	28.0	124.5				13.2	zoobenthos, mainly animals	44% detritus, 17% worms, 28% benthic

										crustaceans, 12% polyps	
Cirrhitidae	Amblycirrhitus	pinos	2.54	28.0	7.2				23.6	zooplankton, mainly animals	45% zooplankton, 42% benthic crustaceans, 13% worms
Labrisomidae	Labrisomus	nuchipinnis	1.36	28.0	141.7				12.9	zoobenthos, mainly animals	40% benthic crustaceans, 16% mollusks, 24% echinoderms, 10% finfish, 10% worms
Labrisomidae	Labrisomus	guppyi	2.22	28.0	18.2				19.6	zoobenthos, mainly animals	75% benthic crustaceans, 25% mollusks
Clupeidae	Harengula	clupeola	1.61	28.0	115.2				13.4	zooplankton, mainly animals	90% zooplankton, 5% mollusks, 5% worms; 99% zooplankton, 1% worms
Clupeidae	Harengula	humeralis	2.07	28.0	102.4				13.8	zooplankton, mainly animals	62% finfish, 29% worms, 56% zooplankton, 3% algae (incl. thalassia); 74% zooplankton, 26% worms; 41% zooplankton, 36% benthic crustaceans, 24% worms
Clupeidae	Jenkinsia	lamprotaenia	7.75	28.0	1.7				31.7	zooplankton, mainly animals	96% zooplankton, 4% benthic crustaceans; 99% zooplankton, 1% worms
Clupeidae	Opisthonema	oglinum	0.78	28.0	1011.5				8.6	zooplankton, mainly animals	65% zooplankton, 22% worms, 10% finfish, 3% sponges
Clupeidae	Sardinella	aurita									
Congridae	Heteroconger	longissimus	0.77	28.0	1488.8				8.0	plants, detritus+animals	73% zooplankton, 19% sponges, 6% benthic crustaceans, 2% mollusks
Coryphaenidae	Coryphaena		1.01	28.0	1638000.0				8.5	nekton, mainly animals	100% finfish
Dactylopteridae	Dactylopterus	volitans	0.52	28.0	8511.2				5.6	zoobenthos, mainly animals	88% benthic crustaceans, 5% finfish, 7% mollusks
Dasyatidae	Dasyatis	americana	0.29	28.0	226522.1				2.9	zoobenthos, mainly animals	22% finfish (acanthurus, scorpaena), 38% worms, 28% benthic crustaceans, 12% mollusks
Dasyatidae	Urolophus	jamaicensis	0.58	28.0	5002.8				6.2	mainly animals	finfish, benthic crustaceans, mollusks, worms
Diodontidae	Chilomycterus	antennatus	0.95	28.0	625.7				9.5	zoobenthos, mainly animals	57% mollusks, 43% benthic crustaceans
Diodontidae	Chilomycterus	antillarum	1.12	28.0	312.6			24.1			n/a
Diodontidae	Diodon	holocanthus	0.78	28.0	8050.8				5.6	zoobenthos, mainly animals	81% mollusks, 12% echinoderms, 7% benthic crustaceans
Diodontidae	Diodon	hystrix	0.51	28.0	11983.2				5.2	zoobenthos, mainly animals	35% echinoderms, 44% mollusks, 30% benthic crustaceans, 1%

											detritus
Echeneidae	Echeneis	naucrates	0.45	28.0	5683.7				6.1	zooplankton, mainly animals	
Echeneidae	Remora	remora	0.53	28.0	7073.5				5.8	zooplankton, mainly animals	40% zooplankton, 30% benthic crustaceans, 10% finfish, 20% detritus
Elopidae	Elops	saurus	0.56	28.0	7493.5				5.7	zoobenthos, mainly animals	40% zooplankton, 35% detritus, 25% benthic crustaceans
Emmelichthyidae	Inermia	vittata	1.36	28.0	141.7				11.1	zooplankton, mainly animals	95% zooplankton, 3% finfish, 2% worms
Engraulidae	Anchoa	hepsetus	1.81	28.0	93.3				14.0	zooplankton, mainly animals	100% zooplankton; 52% benthic crustaceans, 38% zooplankton, 8% mollusks, 2% sponges
Engraulidae	Anchoa	lyolepis	2.14	28.0	21.0				19.0	plants, detritus+animals	zooplankton
Engraulidae	Anchoa	mitchilli	1.56	28.0	9.0				22.6	zooplankton, mainly animals	zooplankton
Engraulidae	Anchoa	parva	3.49	28.0	0.9				36.1	zooplankton	zooplankton
Ephippidae	Chaetodipterus	faber	0.96	28.0	1689.3				7.8	zoobenthos, mainly animals	46% sponges, 28% polyps, 14% worms, 5% algae, 3% benthic invts, 2% echinoderms, 2% zooplankton
Exocoetidae	Exocoetus	volitans	1.12	28.0	312.6				11.0	zooplankton, mainly animals	50% zooplankton, 50% sponges; 100% zooplankton
Fistulariidae	Fistularia	tabacaria	0.29	28.0	5045.5				6.2	nekton, mainly animals	100% finfish
Gerreidae	Eucinostomus	argenteus	1.50	28.0	256.3				11.4	zoobenthos, mainly animals	71% benthic crustaceans, 23% worms, 6% mollusks; 92% benthic crustaceans, 5% algae, 3% worms
Gerreidae	Eucinostomus	lefroyi	1.36	28.0	141.7			28.3			n/a
Gerreidae	Gerres	cinereus	1.15	28.0	1370.5				8.1	zoobenthos, mainly animals	91% benthic crustaceans, 6% mollusks, 3% algae; 78% benthic crustaceans, 38% mollusks, 22% worms, 2% echinoderms
Ginglymonstomalidae	Ginglymostoma	cirratum	0.17	28.0	439844.3				2.2	nekton, mainly animals	89% finfish (acanthurus, clupeids, scarids), 11% squids; 56% benthic crustaceans, 25% finfish, 19% squids
Gobiidae	Gobiosoma	evelynae	4.69	28.0	0.8				37.0	zoobenthos, mainly animals	polyps, sponges, benthic inverts
Gobiidae	Bathygobius	soporator	1.83	28.0	40.2				16.6	mainly animals	benthic crustaceans
Gobiidae	Coryphopterus	glaucofraenum	2.85	28.0	7.8		71.8			plants, detritus+animals	50% algae, 30% benthic crustaceans, 10% echinoderms, 10% mollusks
Gobiidae	Gnatholepis	thompsoni	2.80	28.0	12.6		71.8			plants, detritus+animals	74% algae, 18% zooplankton, 8% benthic

											crustaceans
Gobiidae	Gobiosoma	horsti	3.98	28.0	1.6			70.8			n/a
Serranidae	Rypticus	saponaceus	1.01	28.0	490.3				10.0	nekton, mainly animals	48% finfish (halichoeres, thalassoma bifasciatum), 52% benthic crustaceans
Grammatidae	Gramma	loreto	2.85	28.0	6.4				20.3	zoobenthos, mainly animals	benthic crustaceans, zooplankton
Grammatidae	Gramma	melacara	2.44	28.0	12.3				17.8	zoobenthos, mainly animals	benthic crustaceans
Haemulidae	Anisotremus	surinamensis	0.58	28.0	11773.7				5.2	zoobenthos, mainly animals	61% echinoderms, 17% mollusks, 20% benthic crustaceans, 2% finfish
Haemulidae	Anisotremus	virginicus	0.91	28.0	2109.3				7.4	zoobenthos, mainly animals	17% echinoderms, 58% benthic crustaceans, 14% worms, 10% mollusks, 1% zooplankton
Haemulidae	Haemulon	carbonarium	0.99	28.0	957.4				8.7	zoobenthos, mainly animals	44% benthic crustaceans, 25% mollusks, 17% echinoderms, 13% worms, 1% finfish
Haemulidae	Haemulon	chrysargyreum	1.36	28.0	257.9				11.4	zoobenthos, mainly animals	41% zooplankton, 20% worms, 17% mollusks, 23% benthic crustaceans
Haemulidae	Haemulon	striatum	1.18	28.0	621.5				9.5	zooplankton	zooplankton
Haemulidae	Haemulon	boschmae	1.55	28.0	81.2				14.4	mainly animals	benthic crustaceans, mollusks
Haemulidae	Haemulon	macrostomum	0.87	28.0	1988.0				7.5	zoobenthos, mainly animals	benthic crustaceans, echinoderms
Haemulidae	Haemulon	steindachneri	1.12	28.0	893.6				8.8	zoobenthos, mainly animals	benthic inverts
Haemulidae	Orthopristis	poeyi	1.31	28.0	161.9			27.6			n/a
Haemulidae	Pomadasys	corvinaeformis	1.28	25.0	683.7				9.3	mainly animals	finfish & benthic crustaceans
Haemulidae	Pomadasys	crocro	0.95	28.0	625.7				9.5	nekton, mainly animals	nekton, zoobenthos (benthic crustaceans)
Haemulidae	Haemulon	album	0.43	28.0	8151.6				5.6	zoobenthos, mainly animals	43% worms, 25% echinoderms, 21% benthic crustaceans, 9% mollusks, 1% finfish, 1% sponges
Haemulidae	Haemulon	aurolineatum	0.55	28.0	584.0				7.5	zoobenthos, mainly animals	49% zooplankton, 31% worms, 16% benthic crustaceans, 4% mollusks
Haemulidae	Haemulon	bonariense	0.45	28.0	1231.1			18.2			n/a
Haemulidae	Haemulon	flavolineatum	0.82	28.0	532.0				8.0	zoobenthos, mainly animals	50% worms, 27% benthic crustaceans, 13% mollusks, 10% echinoderms
Haemulidae	Haemulon	melanurum	0.72	28.0	1069.8				8.5	zoobenthos, mainly animals	benthic inverts & benthic crustaceans

Haemulidae	Haemulon	parrai	0.57	28.0	1365.8				8.1	zoobenthos, mainly animals	80% benthic crustaceans, 8% mollusks, 3% polyps, 6% echinoderms, 3% worms; 69% worms, 19% benthic crustaceans, 6% mollusks, 6% echinoderms
Haemulidae	Haemulon	plumieri	0.58	28.0	1765.6				7.7	zoobenthos, mainly animals	42% benthic crustaceans, 24% worms, 22% echinoderms, 9% mollusks, 3% finfish; 91% benthic crustaceans, 7% worms, 1% mollusks, 1% echinoderms
Haemulidae	Haemulon	sciurus	0.67	28.0	1352.0				7.0	zoobenthos, mainly animals	50% benthic crustaceans, 23% mollusks, 15% echinoderms, 8% worms, 3% finfish, 1% sponges; 95% benthic crustaceans, 3% worms, 1% mollusks, 1% echinoderms
Haemulidae	Orthopristis	ruber	0.75	28.0	837.5				9.0	mainly animals	finfish, benthic crustaceans, mollusks, worms
Haemulidae	Orthopristis	chrysoptera			1004.4				8.6	zoobenthos, mainly animals	58% benthic crustaceans, 13% detritus, 11% mollusks, 10% worms, 7% finfish, 1% algae
Hemiramphidae	Hemiramphus	balao	2.14	28.0	411.3				10.4	zooplankton, mainly animals	54% zooplankton, 36% mollusks, 10% worms
Hemiramphidae	Hemiramphus	unifasciatus	1.12	28.0	90.0		48.1			zooplankton, mainly animals	50% algae, 50% seagrass
Hemiramphidae	Hemiramphus	brasiliensis	1.19	28.0	1070.4		29.0			plants, detritus+animals	81% algae/seagrass; 19% finfish
Holocentridae	Myripristis	jacobus	1.28	28.0	808.4				9.0	zooplankton, mainly animals	76% benthic crustaceans, 12% zooplankton, 7% worms, 5% finfish
Holocentridae	Holocentrus	coruscus	2.19	25.0	79.0				14.5	zoobenthos, mainly animals	100% benthic crustaceans
Holocentridae	Neoniphon	marianus	1.84	25.0	68.6				14.9	zoobenthos, mainly animals	100% benthic crustaceans
Holocentridae	Plectrypops	retrospinis	2.19	25.0	40.2				16.6	zoobenthos, mainly animals	50% benthic crustaceans, 50% worms
Holocentridae	Sargocentron	vexillarium	1.84	25.0	68.6				14.9	zoobenthos, mainly animals	55% benthic crustaceans, 35% mollusks, 5% finfish, 5% worms
Holocentridae	Holocentrus	ascensionis	0.68	28.0	5250.7				5.7	zoobenthos, mainly animals	74% zoobenthos; 95.1% benthic crustaceans, 4% worms,

											1% mollusks
Holocentridae	Holocentrus	rufus	1.69	28.0	455.7				10.1	zoobenthos, mainly animals	50% benthic crustaceans, 50% worms
Kyphosidae	Kyphosus	sectator	0.58	28.0	11932.9			17.7		plants, detritus	99% algae, 1% seagrass
Kyphosidae	Kyphosus	incisor			7966.0			10.9		plants, detritus	100% algae
Labridae	Xyrichtys	splendens	1.65	28.0	63.3				15.2	zooplankton, mainly animals	73% zooplankton, 17% benthic crustaceans, 8% mollusks, 2% finfish,
Labridae	Thalassoma	bifasciatum	1.28	28.0	209.4				11.9	zooplankton, mainly animals	55% zooplankton, 20% benthic crustaceans, 10% echinoderms, 10% finfish, 5% worms
Labridae	Bodianus	rufus	0.92	28.0	1281.3				8.2	zoobenthos, mainly animals	36% zoobenthos; benthic crustaceans, echinoderms, mollusks
Labridae	Clepticus	parrae	1.12	28.0	312.6				11.0	zooplankton, mainly animals	75% zooplankton, 20% jellyfish, 5% sponges
Labridae	Halichoeres	bivittatus	0.72	25.0	790.8				9.1	zoobenthos, mainly animals	32% benthic crustaceans, 26% echinoderms, 18% worms, 21% mollusks, 3% finfish
Labridae	Halichoeres	garnoti	1.53	28.0	136.8				13.0	zoobenthos, mainly animals	45% benthic crustaceans, 20% echinoderms, 25% mollusks, 7% worms, 3% finfish
Labridae	Halichoeres	maculipinna	1.61	28.0	147.8				12.8	zoobenthos, mainly animals	49% worms, 10% zooplankton, 26% benthic crustaceans, 15% mollusks
Labridae	Halichoeres	poeyi	1.50	28.0	93.9				14.0	zoobenthos, mainly animals	39% benthic crustaceans, 30% mollusks, 19% echinoderms, 7% worms, 5% finfish
Labridae	Lachnolaimus	maximus	0.22	28.0	15245.8				5.0	zoobenthos, mainly animals	84% mollusks, 10% benthic crustaceans, 1% mollusks, 5% echinoderms; 56% benthic crustaceans, 44% mollusks
Labridae	Xyrichtys	novacula	0.95	28.0	185.1				12.2	zoobenthos, mainly animals	73% mollusks, 7% worms, 14% benthic crustaceans, 6% detritus
Labridae	Halichoeres	radiatus	0.40	28.2	2267.9				7.3	zoobenthos, mainly animals	47% mollusks, 27% echinoderms, 25% benthic crustaceans, 1% worms
Lutjanidae	Pristipomoides	macrophthalmus	0.78	28.0	1406.1				2.8	nekton, mainly animals	finfish & zooplankton
Lutjanidae	Lutjanus	cyanopterus	0.21	27.2	89863.1				3.3	nekton, mainly animals	100% finfish (diodon, haemulon, scarids); 72% finfish, 28% benthic crustaceans
Lutjanidae	Apsilus	dentatus	1.07	28.0	3895.4				6.5	nekton, mainly animals	cephalopods, finfish, sponges

Lutjanidae	Lutjanus	analis	0.35	28.0	8022.6				5.7	zoobenthos, mainly animals	52% benthic crustaceans, 30% finfish (acanthurus, diodon, haemulon, holocentrus), 18% mollusks; 60% benthic crustaceans, 31% finfish, 7% echinoderms, 2 mollusks
Lutjanidae	Lutjanus	apodus	0.48	28.0	6372.2				5.9	nekton, mainly animals	100% benthic crustaceans; 85% benthic crustaceans, 15% finfish
Lutjanidae	Lutjanus	buccanella	0.68	28.0	1498.5				8.0	nekton, mainly animals	squids, finfish, benthic crustaceans, sponges
Lutjanidae	Lutjanus	campechanus	0.36	28.0	13457.0				5.2	nekton, mainly animals	squids, finfish, benthic crustaceans
Lutjanidae	Lutjanus	griseus	0.25	28.0	9964.2				5.4	zoobenthos, mainly animals	54% benthic crustaceans, 39% finfish, 7% mollusks; 74% finfish, 24% benthic crustaceans, 1% mollusks, 1% worms
Lutjanidae	Lutjanus	jocu	0.24	28.0	20397.9				4.7	nekton, mainly animals	61% finfish (labridae, murrenidae, haemulidae, holocentridae), 26% benthic crustaceans, 11% mollusks, 2% squids; 10% algae, 10% finfish, 80% benthic crustaceans
Lutjanidae	Lutjanus	synagris	0.53	28.0	2312.1				7.3	nekton, mainly animals	100% benthic crustaceans; 47% finfish, 45% benthic crustaceans, 4% mollusks, 2% worms, 1% echinoderms, 1% algae
Lutjanidae	Lutjanus	vivanus	0.25	28.0	9166.6				5.5	zoobenthos, mainly animals	squids, finfish, benthic crustaceans, mollusks, sponges
Lutjanidae	Ocyurus	chrysurus	0.36	28.0	10051.0				5.4	nekton, mainly animals	23% benthic crustaceans, 64% zooplankton, 3% detritus; 50% finfish, 26% benthic crustaceans, 11% zooplankton, 8% mollusks, 5% echinoderms
Lutjanidae	Rhomboplites	aurorubens	0.45	28.0	4367.9				6.4	nekton, mainly animals	80% zooplankton, 15% worms, 5% finfish
Lutjanidae	Lutjanus	mahogoni	0.81	28.0	1772.5				7.7	mainly animals	75% finfish, 16% benthic crustaceans, 9% mollusks
Malacanthidae	Malacanthus	plumieri			2084.5				7.4	zoobenthos, mainly animals	25% echinoderms, 37% benthic crustaceans, 12% finfish, 20% worms, 6% mollusks

Megalopidae	Tarpon	atlanticus	0.16	28.0	83710.1				3.5	nekton, mainly animals	83% imports, 17% benthic crustaceans; 100% finfish; 75% benthic crustaceans, 25% finfish
Monacanthidae	Aluterus	monoceros	0.58	28.0	7941.2				5.7	mainly animals	43% polyps, 33% zooplankton, 24% benthic crustaceans
Monacanthidae	Aluterus	schoepfii	0.68	28.0	1741.8		26.3			plants, mainly plants/detritus	67% seagrass, 32% algae, 1% benthic crustaceans
Monacanthidae	Aluterus	scriptus	0.45	28.0	3174.4			15.0		zoobenthos, plants/detritus+animals	54% polyps, 34% algae, 9% seagrass, 2% sponges
Monacanthidae	Cantherines	pullus	1.50	28.0	169.3		42.3	27.3		zoobenthos, plants/detritus+animals	44% algae, 38% sponges, 7% polyps, 5% seagrass, 3% benthic crustaceans, 3% echinoderms
Monacanthidae	Monacanthus	ciliatus	1.50	28.0	222.9		40.0	25.8		zoobenthos, plants/detritus+animals	22% algae, 16% seagrass, 37% zooplankton, 16% benthic crustaceans, 5% worms, 4% mollusks
Monacanthidae	Monacanthus	tuckeri	2.44	28.0	12.3	53.0				detritus, plants/detritus+animals	41% detritus, 42% zooplankton, 7% benthic crustaceans
Monacanthidae	Cantherines	macrocerus	0.83	28.0	1610.2				7.8	zoobenthos, mainly animals	86% sponges, 10% polyps, 3% algae, 1% echinoderms
Monacanthidae	Stephanolepis	setifer	1.50	28.0	93.9				14.0	mainly animals	benthic invertebrates, algae
Mugilidae	Mugil	curema	0.49	28.0	9028.8		18.8			plants, mainly plants/detritus	100% algae & seagrass
Mullidae	Mulloidichthys	martenicus	0.74	27.0	1075.0				8.5	zoobenthos, mainly animals	26% worms, 28% zooplankton, 22% mollusks, 9% echinoderms, 15% benthic crustaceans; 46% worms, 39% benthic crustaceans, 15% zooplankton, 14% mollusks, 8% finfish, 3% worms
Mullidae	Pseudupeneus	maculatus	1.39	28.0	432.2				10.3	zoobenthos, mainly animals	69% benthic crustacean, 18% worms, 8% mollusks, 4% finfish, 1% echinoderms
Muraenidae	Enchelycore	nigricans	0.48	28.0	10863.7			11.7			n/a
Muraenidae	Echidna	catenata	0.34	28.0	47755.8				3.9	zoobenthos, mainly animals	100% benthic crustaceans
Muraenidae	Gymnothorax	funnebris	0.25	28.0	30064.6				4.3	zoobenthos, mainly animals	finfish & benthic crustaceans
Muraenidae	Gymnothorax	miliaris	0.62	28.0	67.4				15.0	mainly animals	finfish & benthic crustaceans
Muraenidae	Gymnothorax	vicinus	0.42	28.0	4518.2				6.4	nekton, mainly animals	63% finfish (scarus), 15% benthic

											crustaceans, 12% mollusks
Muraenidae	Gymnothorax	moringa	0.42	28.0	3990.6				6.5	nekton, mainly animals	100% finfish (haemulon, lutjanus)
Myliobatidae	Aetobatus	narinari			345672.2				2.6	zoobenthos, mainly animals	
Ogcocephalidae	Ogcocephalus	nasutus	0.95	28.0	625.7				9.5	zoobenthos, mainly animals	48% zoobenthos; benthic custraceans, mollusks, algae & fish
Ophichthidae	Myrichthys	breviceps	0.47	28.0	11543.2				5.2	zoobenthos, mainly animals	100% mollusks
Ophichthidae	Myrichthys	ocellatus	0.15	28.0	14429.0				5.0	zoobenthos, mainly animals	62% zoobenthos; 95.6% benthic crustaceans, 3.2% nekton; 1.2% polychaetes
Ophichthidae	Ophichthus	ophis	0.28	28.0	97181.4				3.4	nekton, mainly animals	50% finfish (haemulon), 50% mollusks
Opisthognathidae	Opisthognathus	aurifrons	2.44	28.0	12.3				21.2	zooplankton, mainly animals	88% zooplankton, 9% benthic crustaceans, 2% detritus, 1% worms
Opisthognathidae	Opisthognathus	macrognathus	1.50	28.0	93.9				14.0	zoobenthos, mainly animals	100% benthic crustaceans
Opisthognathidae	Opisthognathus	maxillosus	2.03	28.0	26.3			40.0			n/a
Opisthognathidae	Opisthognathus	whitehurstii	1.92	28.0	29.9				17.7	zoobenthos, mainly animals	70% benthic crustaceans, 22% finfish, 8% echinoderms
Ostraciidae	Acanthostracion	quadricornis	0.73	28.0	4331.3			14.1		zoobenthos, mainly animals	55% sponges, 17% polyps, 10% benthic crustaceans, 8% algae, 4% seagrass, 3% zooplankton, 2% worms, 1% mollusks
Ostraciidae	Lactophrys	bicaudalis	0.81	28.0	3653.0			14.6		zoobenthos, plants/detritus+animals	21% sponges, 51% echinoderms, 9% seagrass, 8% algae, 6% worms, 4% benthic crustaceans, 1% mollusks
Ostraciidae	Lactophrys	trigonus	0.73	28.0	4635.8			14.9		zoobenthos, mainly animals	53% benthic crustaceans, 14% mollusks, 9% worms, 10% echinoderms, 5% algae, 5% sponges, 4% seagrass
Ostraciidae	Lactophrys	triqueter	0.82	28.0	3613.1			17.4		zoobenthos, mainly animals	51% worms, 25% benthic crustaceans, 13% sponges, 6% mollusks, 2% echinoderms, 3% seagrass
Ostraciidae	Acanthostracion	polygonius			2516.9				7.2	mainly animals	benthic crustaceans, sponges, polyps
Pempheridae	Pempheris	schomburgki	1.83	28.0	80.5				14.4	zooplankton, mainly animals	27% worms, 4% benthic crustaceans, 69% zooplankton
Pempheridae	Pempheris	poeyi	1.83	28.0	40.2			36.7			n/a
Pomacanthidae	Centropyge	argi	2.85	28.0	6.4			82.4		plants, mainly plants/detritus	100% algae



Priacanthidae	Priacanthus	arenatus	1.19	28.0	1502.0				8.0	zooplankton, mainly animals	52% zooplankton, 36% benthic crustaceans, 11% worms, 1% squids
Rachycentridae	Rachycentron	canadum	0.37	28.0	76275.7				3.6	nekton, mainly animals	100% finfish (lactophrys); 40% finfish, 37% benthic crustaceans, 23% squids
Scaridae	Scarus	iserti	1.01	28.0	874.6		30.2			plants, mainly plants/detritus	100% algae
Scaridae	Cryptotomus	roseus	2.03	28.0	214.0		40.3			plants, mainly plants/detritus	algae mainly
Scaridae	Nicholsina	usta	1.12	28.0	312.6		37.3			plants, mainly plants/detritus	algae mainly
Scaridae	Scarus	coelestinus	0.58	28.0	10083.6		18.4			plants, mainly plants/detritus	97% algae, 3% zoobenthos & zooplankton
Scaridae	Scarus	taeniopterus	1.01	28.0	867.8		30.3			plants, mainly plants/detritus	81% algae, 17% thalassia, 2% zoobenthos
Scaridae	Sparisoma	radians	1.50	28.0	93.9		47.7			plants, mainly plants/detritus	88% Thalassia, 12% algae
Scaridae	Sparisoma	aurofrenatum	0.53	27.2	475.5		34.2			plants, mainly plants/detritus	98% algae, 1% seagrass, 1% polyps
Scaridae	Scarus	vetula	1.05	28.0	1672.8		26.5			plants, mainly plants/detritus	94% algae, 4% seagrass, 1% sponges, 1% polyps
Scaridae	Sparisoma	rubripinne	1.04	28.0	2498.5		24.4			plants, mainly plants/detritus	92% algae, 8% seagrass
Scaridae	Sparisoma	viride	0.63	28.0	5231.0		21.0			plants, mainly plants/detritus	96% algae, 3% seagrass, 1% polyps
Scaridae	Scarus	coeruleus	0.26	28.2	39465.2		13.9			plants, mainly plants/detritus	algae, some seagrass
Scaridae	Scarus	guacamaia	0.26	28.2	39155.4		13.9			plants, mainly plants/detritus	92% algae, 8% seagrass
Scaridae	Sparisoma	chrysopterum			1432.1		27.3			plants, mainly plants/detritus	83% algae, 17% seagrass
Sciaenidae	Equetus	lanceolatus	1.45	25.0	316.0				10.9	zoobenthos, mainly animals	69% benthic crustacean, 31% worms,
Sciaenidae	Equetus	punctatus	1.36	25.0	229.1				11.7	zoobenthos, mainly animals	90% benthic crustaceans, 5% worms, 5% mollusks
Sciaenidae	Odontoscion	dentex	1.23	25.0	336.2				10.8	zooplankton, mainly animals	78% zooplankton, rest zoobenthos (benthic crustaceans)
Sciaenidae	Pareques	acuminatus	1.58	25.0	234.7				11.6	zooplankton, mainly animals	95% benthic crustaceans, 4% finfish, 1% zooplankton
Scombridae	Scomberomorus	regalis	0.30	27.2	45983.3				4.0	nekton, mainly animals	97% finfish (carangidae, blennidae, labridae), 2% squids, 1% benthic crustaceans
Scombridae	Auxis	rochei rochei	0.80	28.0	1952.3				21.0	nekton, mainly animals	47% finfish (clupeidae), 25% squids, 24% zooplankton, 4% benthic crustaceans
Scombridae	Auxis	thazard thazard	1.54	28.0	2280.1				7.3	nekton, mainly animals	50% finfish, 45% zooplankton, 5% benthic crustaceans
Scombridae	Scomberomorus	cavalla	0.30	28.0	18687.4				4.8	nekton, mainly animals	93% finfish (carangidae,

											ocyurus, harengula), 7% squids
Scombridae	Thunnus	atlanticus	0.62	28.0	10355.5				5.4	nekton, mainly animals	49% finfish, 34% mollusks, 17% benthic crustaceans
Scombridae	Euthynnus	alletteratus	0.37	28.0	24790.3				4.5	nekton, mainly animals	57% finfish, 36% squids, 7% worms
Scombridae	Scomberomorus	maculatus	0.61	28.0	3286.9				6.8	nekton, mainly animals	100% finfish (engraulidae, labridae, clupeidae, balistidae)
Scorpaenidae	Scorpaena	plumieri	0.84	28.0	2068.6				7.5	zooplankton, mainly animals	42% zooplankton, 6% mollusks, 52% benthic crustaceans
Scorpaenidae	Scorpaena	brasiliensis	1.01	28.0	490.3				10.0	zoobenthos, mainly animals	86% benthic crustaceans, 14% finfish
Scorpaenidae	Scorpaena	grandicornis	1.12	28.0	312.6				11.0	zoobenthos, mainly animals	87.5% benthic crustacean, 12.5% nekton
Scorpaenidae	Scorpaena	inermis	2.29	28.0	16.0				20.1	zoobenthos, mainly animals	93% benthic crustaceans, 7% detritus
Scorpaenidae	Scorpaenodes	caribbaeus	2.14	28.0	21.0				16.3	zoobenthos, mainly animals	92% benthic crustaceans, 8% zooplankton
Serranidae	Dermatolepis	inermis	0.51	28.0	8226.6				5.6	mainly animals	finfish
Serranidae	Liopropoma	rubre	0.48	28.0	10863.7			11.7			n/a
Serranidae	Serranus	tabacarius	1.40	28.0	124.9				13.2	nekton, mainly animals	100% finfish
Serranidae	Alphestes	afer	1.05	28.0	410.6				10.4	zoobenthos, mainly animals	91% benthic crustaceans, 7% fish, 2% octopus
Serranidae	Hypoplectrus	aberrans	2.03	28.0	26.3				18.2	mainly animals	benthic crustaceans
Serranidae	Hypoplectrus	chlorurus	2.06	28.0	24.6				18.4	zoobenthos, mainly animals	75% benthic crustaceans, 25% blennidae
Serranidae	Hypoplectrus	nigricans	1.81	28.0	42.5				16.5	mainly animals	nekton, benthic crustaceans
Serranidae	Serranus	tortugarum	2.85	28.0	6.4				20.8	zooplankton, mainly animals	92% zooplankton; 100% zooplankton
Serranidae	Cephalopholis	cruentata	0.79	28.0	635.0				9.5	nekton, mainly animals	66% finfish (apogon, holocentrus, haemulon, abudedefduf), 30% benthic crustaceans, 4% mollusks
Serranidae	Cephalopholis	fulva	1.22	28.0	617.1				9.5	nekton, mainly animals	46% finfish (acanthuridae, balistidae, scaridae), 54% benthic crustaceans
Serranidae	Diplectrum	formosum	2.45	28.0	313.9				10.9	nekton, mainly animals	97% finfish, 3% zooplankton
Serranidae	Epinephelus	adscensionis	0.40	28.0	1901.0				7.6	zoobenthos, mainly animals	75% benthic crustaceans, 20% finfish (cantherhines), 5% mollusks
Serranidae	Epinephelus	guttatus	0.31	28.0	2306.0				2.8	zoobenthos, mainly animals	60% benthic crustaceans, 21% finfish (murraenidae, balistidae, mullidae,

										scaridae), 7% mollusks, 2% worms	
Serranidae	Epinephelus	itajara	0.24	28.0	143165.5				3.1	zoobenthos, mainly animals	81% benthic crustaceans (lobsters), 13% finfish (dasyatis, diodon), 6% turtles; 76% benthic crustaceans, 24% finfish
Serranidae	Epinephelus	morio	0.28	28.0	10955.9				5.3	zoobenthos, mainly animals	83% benthic crustaceans, 17% finfish; 4% mollusks, 10% finfish, 86% benthic crustaceans
Serranidae	Epinephelus	striatus	0.23	28.0	13278.9				5.1	nekton, mainly animals	53% finfish, 39% benthic crustaceans, 5% squids, 3% mollusks; 82% finfish, 12% benthic crustaceans, 6% mollusks
Serranidae	Hypoplectrus	puella	1.43	28.0	42.8				16.4	zoobenthos, mainly animals	81% benthic crustaceans, 10% finfish, 9% zooplankton
Serranidae	Mycteroperca	bonaci	0.33	28.0	36479.2				4.1	nekton, mainly animals	100% finfish (haemulon)
Serranidae	Mycteroperca	interstitialis	0.17	28.0	8966.9				5.5	nekton, mainly animals	100% finfish (chromis, scarus, atherinidae)
Serranidae	Mycteroperca	phenax	0.22	28.0	12597.1				5.2	mainly animals	97% finfish, 3% benthic crustaceans
Serranidae	Mycteroperca	tigris	0.28	28.0	6384.6				5.9	nekton, mainly animals	100% finfish (acanthuridae, clupeidae, balistidae, blennidae, pomacentridae, scaridae)
Serranidae	Mycteroperca	venenosa	0.37	28.0	7759.9				5.7	nekton, mainly animals	96% finfish (labridae, holocentridae, pomacentridae, balistidae, scaridae), 4% cephalopods; 85% finfish, 15% mollusks
Serranidae	Paranthias	furcifer	0.52	28.0	1334.6				8.1	zooplankton, mainly animals	64% zooplankton, 12% sponges, 15% benthic crustaceans, 1% mollusks, 1% finfish, 7% other
Serranidae	Serranus	tigrinus			479.9				10.0	zoobenthos, mainly animals	90% benthic crustaceans, 10% finfish
Sparidae	Calamus	calamus	0.72	28.0	5093.2				6.2	zoobenthos, mainly animals	19% worms, 25% echinoderms, 25% mollusks, 30% benthic crustaceans, 1% detritus
Sparidae	Calamus	penna	0.83	28.0	2582.6				7.1	zoobenthos, mainly animals	50% benthic crustaceans, 50% mollusks
Sparidae	Calamus	pennatula	0.97	28.0	1542.4				7.9	zoobenthos, mainly animals	38% benthic crustaceans, 22% echinoderms, 19% worms, 20% mollusks

Sparidae	Diplodus	argenteus caudimacula	1.12	28.0	312.6		32.5		plants/detritus+animals	seagrass, phytoplankton, benthic crustaceans & mollusks
Sparidae	Archosargus	rhomboidalis	2.64	28.0	1060.7		29.1		plants, plants/detritus+animals	45% seagrass, 39% algae, 5% benthic crustaceans, 7% benthic crustaceans, 4% zooplankton
Sparidae	Calamus	bajonado			10079.7			5.4	zoobenthos, mainly animals	45% echinoderms, 23% benthic crustaceans, 24% mollusks, 7% worms, 1% detrtus
Sphryaenidae	Sphyraena	barracuda	0.19	28.0	99480.4			4.3	nekton, mainly animals	96% finfish (balistidae, acanthuridae, carangidae, muraenidae, haemulidae, diodontidae), 3% mollusks, 2% zooplankton; 100% finfish
Sphryaenidae	Sphyraena	picudilla			1329.8			7.0	nekton, mainly animals	82% finfish, 17% cephalopods
Sphyrnidae	Sphyrna	mokarran	0.13	28.0	1266855.0			2.0	nekton, mainly animals	86% finfish, 11% benthic crustacean, 3% cephalopods
Sphyrnidae	Sphyrna	lewini	0.32	28.0	194990.0			2.9	nekton, mainly animals	62% finfish, 22% benthic crustaceans, 16% cephalopods
Sphyrnidae	Sphyrna	tiburo	0.49	28.0	7802.9			6.0	nekton, mainly animals	72% benthic crustaceans, 25% algae, 2% cephalopods, 2% finfish; 90% benthic crustaceans, 10% finfish; 61% benthic crustaceans, 39% cephalopods
Synodontidae	Synodus	intermedius	0.83	28.0	1083.8			8.5	nekton, mainly animals	94% finfish (carangidae, haemulon, serranus), 5% cephalopods, 1% benthic crustaceans
Synodontidae	Synodus	synodus	1.05	28.0	390.1			10.5	nekton, mainly animals	100% finfish
Synodontidae	Synodus	foetens			1008.0			9.5	nekton, mainly animals	100% finfish (anchoa)
Tetraodontidae	Sphoeroides	spengleri	1.12	28.0	840.2			9.0	zoobenthos, mainly animals	29% mollusks, 36% benthic crustaceans, 9% algae, 12% worms, 14% echinoderms
Tetraodontidae	Canthigaster	rostrata	2.14	28.0	21.0		36.0		plants/detritus + animals	20% algae, 17% sponges, 25% benthic crustaceans, 13% worms, 13% mollusks, 7% echinoderms, 3% cnidarians
Tetraodontidae	Sphoeroides	testudineus	1.08	28.0	60.2			15.3	zooplankton, mainly animals	50% zooplankton, 50% mollusks
Triakidae	Mustelus	canis	0.50	28.0	7101.3			5.8	zoobenthos, mainly animals	80% benthic crustaceans, 10% finfish, 6% mollusks, 2% cephalopods, 2% detritus; 78% benthic



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## **Appendix B**

Regional-scale seagrass habitat mapping in the Wider Caribbean region using Landsat sensors: applications to conservation and ecology. In press in *Remote Sensing of Environment*, Special Issue on Earth Observation for Biodiversity and Ecology.  
[addresses Objective 2]

*In press: Remote Sensing of Environment*  
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**Title:**

Regional-scale seagrass habitat mapping in the Wider Caribbean region using Landsat sensors: applications to conservation and ecology

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## **Abstract**

Seagrass meadows occupy a large proportion of the world's coastal oceans and are some of the most productive systems on Earth. Direct and indirect human-derived impacts have led to significant seagrass declines worldwide and the alteration of services linked to their biodiversity. Effective conservation and the provision of sustainable recovery goals for ecologically significant species are limited by the absence of reliable information on seagrass extent. This is especially true for the Wider Caribbean Region (WCR) where many conservation initiatives are under way, but impaired by the lack of accurate baseline habitat maps.

To assist with such a fundamental conservation need using high resolution remote sensing data, both environmental and methodological challenges need to be tackled. First, the diversity of environments, the heterogeneity of habitats, and the vast extent of the targeted region mean that local expertise and field data are seldom available. Second, large-scale high-resolution mapping requires several hundred Landsat 5 and 7 images, which poses substantial processing problems.

The main goal of this study was to test the feasibility of achieving Landsat-based large-scale seagrass mapping with limited ground-truth data and acceptable accuracies. We used the following combination of methods to map seagrass throughout the WCR: geomorphological segmentation, contextual editing, and supervised classifications. A total of 40 Landsat scenes (path-row) were processed. Three major classes were derived ("dense seagrass", "medium-sparse seagrass", and a generic "other" class). Products' accuracies were assessed against (i) selected *in situ* data; (ii) patterns detectable with very high-resolution IKONOS images; and (iii) published habitat maps with documented accuracies. Despite variable overall classification accuracies (46-88%), following their critical evaluation, the resulting thematic maps were deemed acceptable to (i) regionally provide an adequate baseline for further large-scale conservation programs and research actions; and (ii) regionally re-assess carrying capacity estimates for green turtles. They certainly represent a drastic improvement relative to current regional databases.

**Keywords:** seagrass; coral reef; *Thalassia testudinum*; ETM+; IKONOS; Millennium Coral Reef Mapping Project; conservation management; habitat database; biodiversity; sea turtle; *Chelonia mydas*.

## 1. Introduction

Seagrasses are submerged flowering plants (angiosperms) that can form dense beds in shallow subtidal, mostly clear and sheltered, soft-bottomed marine and estuarine environments (Phillips and Menez, 1988). These ‘seagrass meadows’ are important tropical, temperate, and subarctic coastal habitats (Hemminga and Duarte, 2000; den Hartog and Kuo, 2006), covering the equivalent of approximately 0.05-0.15% of the surface area of the oceans globally (Spalding et al., 2003). By providing substratum for epiphytic algae, shelter for invertebrates and fishes, and foraging areas for a variety of organisms, they significantly contribute to the biodiversity of coastal waters (Williams and Heck Jr., 2001; Duffy, 2006). The combined productivity of seagrasses and epiphytic algae rank them among the most productive systems on Earth (Duarte and Cebrián, 1996; Duarte and Chiscano, 1999). These meadows also serve as critical breeding and nursery grounds for juvenile stages of many economically and ecologically important species (Beck et al., 2003; Heck et al., 2003; Dahlgren et al., 2006; Gillanders, 2006).

Established in coastal zones, seagrass beds are inherently dynamic systems prone to natural physical disturbance, particularly in temperate regions (Fonseca et al., 2002). However, changes or losses in abundance, species composition, structure, and extent have commonly resulted from activities such as eutrophication, overfishing, and habitat alteration or destruction (Short and Wyllie-Echeverria, 1996; Duarte, 2002). Until recently, relatively little attention had been paid to the impacts of human activities on seagrass food webs (Jackson, 2001; Duarte, 2002), with most studies focusing on how physical disturbance alters the structure and function of the ‘seagrass habitats’ themselves. The presence of green turtles (*Chelonia mydas*) may have had substantial ecological and evolutionary effects: increasing the productivity of seagrass in the same way as grazers in terrestrial grasslands (McNaughton, 1979; Pandolfi et al., 2003; Moran and Bjorndal, 2005; Moran and Bjorndal, 2007). Changes in temperature, nutrient levels, and salinity, as well as a 93-97% reduction in the Caribbean green turtle population compared to its size prior to human contact (Jackson et al., 2001), have been implicated in die-offs of seagrass throughout the region (Robblee et al., 1991; Jackson, 1997; Fourqurean and Robblee, 1999). Overall, anthropogenic impacts have contributed to seagrasses now ranking among the most threatened of marine habitats (Green and Short, 2003; Lotze et al., 2006; Orth et al., 2006).

Given ongoing coastal zone development around the globe, it is imperative to design and implement effective ways to protect coastal resources. Specifically, at the Fifth World Parks Congress (WPC) in 2003, the recommendation was made to develop extensive networks of Marine Protected Areas (MPAs) that “include strictly protected areas [amounting] to at least 20-30% of each habitat” by 2012. However, exact predictions of the potential status of seagrasses in the future and best ways to protect them are hampered – chiefly by the absence of consistent and reliable information concerning the present extent of this habitat. Similarly, current carrying capacity estimates of green turtles for the Caribbean Sea, ranging between 16 million and 586 million turtles, are based on only a very rough idea of seagrass extent thought of as available for foraging (Jackson et al., 2001).

A literature review conducted for this study suggests that there are many site specific studies and records of seagrass bed extent and distribution for the Wider Caribbean Region (WCR). However, with few exceptions (e.g., Puerto Rico and the U.S. Virgin Islands), relevant documents are difficult to access and rarely, or poorly, document mapping methods or accuracies. Digital maps in GIS formats are often unavailable, or their use restricted. The only existing database generating a global overview was developed by the United Nations Environment Program-World Conservation Monitoring Centre (UNEP-WCMC) in 2003. The resulting “*World Atlas of Seagrasses*” was the first synthesis of the distribution and status of seagrass habitat at that scale (Green and Short, 2003). However, direct habitat maps (i.e., chiefly derived from remotely sensed data), which provide the most accurate data on habitat distribution, were only available for a very limited subset of the world. The majority of geographic information thus falls into two main categories: (i) interpolation of expert knowledge and observations; and (ii) point-based samples, which are useful in providing information regarding species presence, but give no information as to actual seagrass extent (Spalding et al., 2003). As a result, the worldwide UNEP-WCMC database, including the Caribbean section, suffers from substantial inaccuracy (vast commission or omission errors (i.e., including a seagrass pixel in a non-seagrass area and vice versa)), poor spatial representation, and limited spatial resolution.

Satellite remote sensing provides a tool to develop a reliable, methodologically consistent database of seagrass extent over large regions, in a cost-effective, objective,

and timely fashion (Mumby et al., 1999; Krause-Jensen et al., 2004; Balmford et al., 2005). Habitat mapping on the scale of a region poses new environmental and methodological challenges rarely addressed in tropical initiatives to date (but see the Millennium Coral Reef Mapping Project (Andréfouët and Guzmán, 2005; Andréfouët et al., 2005)). First, the diversity of environments (estuaries, cross-shelf areas, banks, atolls, and narrow continental reef terraces), the heterogeneity of habitats, and the vast extent of the targeted region imply that expertise and field data are seldom available with comparable quality, and often cannot be acquired due to their prohibitive costs. Secondly, high-resolution regional mapping requires hundreds of Landsat images to achieve complete cloud-free coverage. Working with such a large dataset presents substantial calibration problems in marine environments, and complicates or even prevents the use of standard analytical and statistical image processing approaches (Andréfouët et al., 2001; Thome, 2001; Teillet et al., 2006).

This paper reports on the approach used to map seagrass beds using consistent methods, throughout the Wider Caribbean Region, given the constraints associated with working at large spatial scales. First, we provide results obtained for well-documented sites throughout the region, where cross-comparison with ancillary data allowed for direct or indirect measures of accuracy. Second, we outline the implications of our findings for mapping seagrass beds in a cost effective fashion throughout the WCR. Finally, we discuss the relevance of our products and results for (i) generally advancing future biodiversity research, conservation, and management in the region and (ii) specifically re-assessing carrying capacity estimates for green turtles.

## **2. Data and Methods**

### *2.1. Landsat data and Millennium Coral Reef Mapping Project*

The archive of Landsat 7 Enhanced Thematic Mapper Plus (ETM+) images compiled by the Millennium Coral Reef Mapping Project (MCRMP) (Andréfouët et al., 2005) constituted the main data set used for seagrass mapping in this study. Most images in the database were acquired between 2000 and 2002. One to six images were available for each Landsat scene (path-row) intersecting coastlines. Where clouds were persistent, several Landsat Thematic Mapper 5 (TM) images, acquired mainly in the early 1990s, were also available (and often used). Images were all re-sampled to UTM

WGS 84 projection, at 30m spatial resolution. Only the first four bands were considered for the work presented here (blue, green, red, and near infra-red).

For each image path-row, MCRMP created polygons that characterize and delineate coral reef geomorphology according to a typology that is globally relevant (for more detailed information regarding the methodology applied see Andréfouët et al. (2005)). Individual Millennium classes are easily associated with a given set of environmental attributes (zonation, depth, hydrodynamic exposure), which favor the development of some habitats (e.g., seagrass), but not others. Although linkages between “geomorphology” and “habitats” have not been exhaustively quantified to date, preliminary analysis for several Caribbean sites where detailed habitat maps have been produced confirm that Millennium polygons can be used for *a priori* contextual editing. By doing so, areas of the image unlikely to contain seagrasses are excluded, avoiding misclassification in subsequent analyses.

## 2.2. Study areas

Table 1 lists the 19 focal areas of the WCR considered in this study (see also Figure 1). These sites were chosen based on the availability of independent information to: (i) compare our derived accuracies with published values and qualitatively contrast available thematic maps to our products; or (ii) assess the accuracy of seagrass extent estimates derived from Landsat data using IKONOS imagery and/or field data points. The sites represent various levels of geomorphological complexity typical of the region.

## 2.3. Image processing

For each site within a Landsat image, polygons were constructed that encompassed one, several, or all MCRMP classes with any likelihood of containing seagrass (see Figures 2 and 3). For instance, one is unlikely to find seagrass within the deeper classes and on several exposed “reef” areas (i.e., forereefs). The degree to which MCRMP classes were merged depended on the geomorphological complexity of the site.

*A priori* contextual editing has been reported by Andréfouët et al. (2003) and Andréfouët & Guzmán (2005) as a relatively simple and efficient way to enhance classification richness and improve accuracy results. The method consists in applying a

contextual decision rule throughout the image to sets of habitats which have similar spectra, but different yet predictable physical environments (Groom et al., 1996). By removing beforehand image areas that may create spectral confusion for the classes of interest, the classification process is much more accurate (Andréfouët et al., 2003). Given the scale of the area covered, this straight forward and reliable approach was favored here over the use of water column correction techniques, or the construction of depth-invariant indices. However, we are well aware of the benefits of the latter methodology (Andréfouët et al., 2003), and in the few cases where polygons include a large number of habitats and significant depth range (e.g., wide cross-shelf areas), our assumption may not hold. In such instances, low map accuracies indicate Caribbean coastal configurations where bathymetric corrections would be required. Elsewhere, to quantify the validity of our assumption, we compared our results with those obtained from independent studies that corrected for the effects of the water column and published accuracy values.

For very large continuous areas spanning several Landsat scenes (e.g., Bahamas, Belize), images were inter-calibrated and normalized prior to classification (Figure 2). For this, digital counts (DN) were transformed into at-sensor reflectance using the gain/bias coefficients available for each image. A dark pixel correction scheme was then applied to remove part of the atmospheric effect. Specifically, subsequent to Rayleigh correction (Zhang et al., 1999), a deep-water reflectance value (average value of pixels sampled in ‘deep water’ in the short-wave infra-red band) was subtracted from pixels in all other bands, assuming a white aerosol signal (Zhang et al., 1999; Hu et al., 2001). Finally, using one arbitrary reference image, the next Landsat scene in the composition was adjusted using an empirical line calibration approach, based on training areas that have not changed between the different images (i.e., according to shapes of dense seagrass and sand patches, cf. Andréfouët et al. (2001)). This was possible since all Landsat scenes overlap neighboring scenes and we assumed stable conditions between the acquisitions of images (less than two years). All images were joined in a mosaic, which was expanded one image at a time. For all images, where necessary, clouds and shadows were masked out prior to classification.

Image classification training regions (e.g., sand, seagrass of different densities, bare substratum) were selected by visual-interpretation, due to the lack of extensive

field data for the majority of polygons. Generally, 3 to 5 classes were generated, but no more than 8, depending on intra-polygon spectral variability. Standard supervised classification, using ENVI ®'s Maximum Likelihood classifier, was conducted for each image to produce a habitat map. Individual seagrass classes were subsequently merged to a maximum of 3 categories according to the density of the submerged vegetation: (i) dense (70-100% cover); (ii) medium-dense (30-70%); and (iii) sparse (<30%). These closely correspond to categories derived for seagrass cover in other studies within the region (e.g., Mumby & Harborne (1999)). All other habitat classes were merged into a generic "other" class.

The study aimed to map overall seagrass presence/absence and density of cover throughout the region, without reference to particular seagrass species. However, turtle grass (*Thalassia testudinum*) is considered to be the most common of species off the coast of Florida and throughout the Caribbean. *Halodule wrightii* Kütz. and *Syringodium filiforme* Aschers. are the other two species commonly encountered, albeit at lower densities, and they are generally considered to be pioneer species (Gallegos et al., 1994).

#### 2.4. Accuracy assessment

The accuracy of classified images is generally assessed using a set of geo-referenced field data (Lillesand et al., 2004). However, quality ground-truth data that are adequately documented, of comparable quality, and that uniformly cover all areas of interest present a substantial challenge for large-scale mapping efforts. Such information is not available for seagrass beds throughout the Caribbean. Therefore, several strategies were adopted as proxies (Figure 2):

(i) Data were gleaned from non peer-reviewed literature (i.e., consultancy reports, newspaper articles, electronic information, government reports etc). The database developed from this information contains references of disparate quality and level of detail. Only a handful of these references provided detailed thematic maps or geographic coordinates of point observations associated with specific habitat classes. Only information gathered for Roatán Island (Honduras) was considered of sufficient quality to enable accuracy assessment of our product (Porcher et al., 2001a; Porcher et al., 2001b).

(ii) Maps were extracted from published peer-reviewed articles. Documented areas with published thematic maps allowing for qualitative comparisons with our products included Roatán (Maeder et al., 2002), Los Roques (Schweizer et al., 2005), Lee Stocking Island (Armstrong, 1993; Call et al., 2003; Louchard et al., 2003), Martinique and Guadeloupe (Chauvaud, 1997; Chauvaud et al., 1998; Chauvaud et al., 2001), Glovers Atoll (Andréfouët et al., 2003), Alacranes (Bello-Pineda et al., 2005), Vieques Island (Hernández-Cruz et al., 2006; Shapiro and Rohmann, 2006), Puerto Rico (Shapiro and Rohmann, 2005), and Colombia (Díaz et al., 2003; Díaz and Gómez-López, 2003). For these, accuracy values were generally reported. Although a number of other peer-review articles report on their seagrass mapping efforts in the Caribbean, the absence of available habitat maps precluded direct qualitative comparisons (e.g., Garza-Perez et al. (2004), Luczkovich et al. (1993), Mumby et al. (1998) and Mumby & Edwards (2002)).

(iii) *In situ* data from mapping projects undertaken by the National Ocean and Atmospheric Administration (NOAA) for coastal waters under US jurisdiction (NOAA, 2001) were downloaded from NOAA's website. Under this initiative, habitat maps were created by visual interpretation of aerial photos. *In situ* data for Puerto Rico and the US Virgin Islands were available as: (a) "ground-truth" points (large data set, geographically widespread for training) and (b) accuracy assessment data points (estimated at only two locations within the project area). The accuracy of our seagrass products was assessed using the larger "ground-truth" dataset.

(iv) Habitat survey points collected by authors of this study (Serge Andréfouët and Phil Kramer) between 2001 and 2003 were collated into a single database (see Table 2). The dataset, providing seagrass presence/absence observations, spans San Blas (Panama), Los Roques (Venezuela), and Lee Stocking and Andros Islands (Bahamas).

(v) "Virtual ground truthing" points were derived from high spatial resolution IKONOS imagery (Figure 4). High resolution images, such as aerial photographs, allow enhanced visual-interpretation of many benthic features, including seagrass beds (cf. NOAA's approach). Although confusion with other submerged aquatic vegetation types remains possible, this method allows the practitioner to locate points (or polygons) within specific habitat types effectively and with a high level of confidence – even at depth. IKONOS images, collected between 2000 and 2003, were obtained from the National Aeronautics and Space Administration (NASA) Data Buy program

archive. Several of these images had already been processed for habitat mapping purposes, with the resulting products and analyses published (e.g., Andréfouët et al. (2003) and Mumby & Edwards (2002)). To our knowledge, the use of other scenes is reported here for the first time.

(vi) *in situ* points collected by contributors to the study by Andréfouët et al. (2003) were collated into a separate dataset and augmented for this study by visual-interpretation (Figure 4). Sites processed included: Boca Paila, Majahual and Akumal (Mexico); Andros and Lee Stocking Island (Bahamas) (Figure 5); Roatán (Honduras); Glovers Atoll, Lighthouse Atoll, lagoonal patch reefs and two sites off the barrier reef (Belize).

In general, the time lag between the acquisition of ground observations, Landsat images, and IKONOS images ranged between a few months and a year. It was assumed that for the most part, the delineation of seagrass bed extent would not have dramatically changed during that timeframe.

Accuracy of habitat maps produced here was determined from confusion matrices elaborated using data obtained under (iii), (iv), (v), and (vi) above. Such a matrix allows the calculation of specific accuracy measures including the overall accuracy and user's and producer's accuracies (Congalton, 1991). Overall accuracy is computed by dividing the total number of correctly classified pixels by the total number of pixels in the matrix (Congalton, 1991). Producer's accuracy" refers to the probability of a reference pixel being correctly classified (i.e., measures the error of omission); whereas "user's accuracy" indicates the probability that a pixel classified on the map represents that category on the ground (i.e., measures the error of commission)(Congalton and Green, 1999). An estimate of the Kappa coefficient, which quantifies the improvement of the classified map over a random class assignment, is also provided (Congalton and Green, 1999; Foody, 2002).

Locations used for accuracy assessment spanned the entire WCR and included a large variety of habitat types, depth ranges, and water conditions inherent to the region. Therefore, these estimates were assumed to be representative of accuracies derived for thematic maps produced for the remainder of the Caribbean (ongoing project). NOAA outlined a similar approach to assess the accuracy of their Caribbean products (NOAA,

2001). However, for seagrass beds located in turbid estuaries and large coastal lagoons (e.g., Mexico and Venezuela) this assumption is unlikely to be verified and accuracy assessment of products derived for these areas will require the development of alternative strategies. Such sites were not included in this analysis.

### **3. Results**

Confusion matrices derived when using three seagrass classes of variable densities plus one “other” (all non-seagrass areas) class, showed significant confusion between individual seagrass classes, resulting in low overall accuracy. However, as a whole, ‘seagrass’ was correctly classified. Consequently, the “medium” and “sparse” seagrass classes were merged to form a single “medium-sparse” class (<70% cover) (see discussion for details). Associated ground-truth points were also merged for corresponding accuracy assessments. The “dense” class (>70% cover) was left unchanged. This improved accuracy, with overall values ranging between 46% and 77%.

Overall, Kappa values were found to vary widely between sites, spanning from 0 for a site west of La Parguera, Puerto Rico to 0.64 for Los Roques, Venezuela. Overall accuracy averaged 68%. Lowest overall accuracies were obtained for the classification of a site west of La Parguera, Puerto Rico (45%). Highest accuracies were recorded for Akumal, Mexico (87%) and San Blas, Panama (85%). Given the local topographic complexity and patterns, thematic maps encompassed only one seagrass class for these two sites. Highest overall accuracy for sites with two distinct seagrass classes was registered at Los Roques, Venezuela (77%). The “other” class showed high producer accuracies, except for Puerto Rico. Most misclassifications at all sites still occurred between the two seagrass classes and some seagrass pixels that classified as “other”. Our products can therefore be seen as conservative seagrass distribution maps (i.e., not overestimating seagrass areas) since very few “other” pixels were classified as seagrass (with the exception of Puerto Rico).

Figures 5 and 6 show examples of thematic maps produced for two classes of seagrass, and one “other class” for the Bahamas, Los Roques (Venezuela), and Alacranes (Mexico). Seagrass extent at each site is reported in Table 3. For comparative purposes, Figure 5 also includes current data available for seagrass extent

in the Bahamas from UNEP-WCMC. Figure 6 includes sites for which qualitative comparisons were drawn with previously published seagrass maps. At these two sites and for areas of Martinique, Guadeloupe, and Roátan (not shown here) the two sets of products showed high consistency in distribution and extent of seagrass meadows.

As existing maps for Alacranes and Los Roques had also been derived from Landsat images, further analysis was undertaken for these two sites. At Alacranes, seagrass beds were predominantly found along the eastern rim of the bank. Minor discrepancies included seagrass beds mapped along the north part of the outer slope and areas within reef passes. Seagrass distribution and extent for our product at Los Roques closely matched those provided by Schweizer et al. (2005). Main differences included thinner seagrass margins in our product along the mangrove-lined northern and southeastern portions of the central atoll. While visual comparisons do not constitute quantitative accuracy assessments *per se*, the close agreement between our maps and those produced (i) with significant quantities of ground-truthed data and (ii) using depth correction techniques, provides confidence in the methodology developed for the purposes of this study.

## **4. Discussion**

### *4.1. Remote sensing considerations*

Accuracies reported here span a broad range of values (46-88%; Table 2), but they are comparable to those from previous Landsat-based seagrass mapping efforts. Despite the diverse datasets used to assess the accuracy of thematic maps, values do not reveal any positive or negative bias towards a ‘groundtruthing’ source. For example, two of the three poorest overall accuracies recorded (Majahual, Mexico, and Belize patch reef), and the best overall accuracy (Akumal, Mexico), were evaluated based on IKONOS image interpretation. For the two areas with highest accuracies, San Blas and Akumal, different sources were used in the assessment: *in situ* and IKONOS respectively.

Overall accuracies achieved in this study are well within the range of values reported in previous studies within the Caribbean, including results obtained using water column correction techniques (e.g., Schweizer et al. (2005) for Los Roques). For most areas, the use of Millennium polygons to guide *a priori* contextual editing in this

study has emerged as a useful approach to limit misclassifications in the absence of a formal water column correction step. However, the site west of La Parguera (Puerto Rico) stands out as a clear exception. This location is a wide cross-shelf area with a gentle slope from the shore down to 40m, and is characterized by a variety of different habitats that are spectrally similar (deep diffuse seagrass, shallow dense seagrass, gorgonian plains, coral escarpment, and hard substrate covered with varying densities of algae). Yet, this mosaic of habitats is included in one single Millennium polygon labeled as “Shelf Slope”. In such instances, the practitioner is therefore faced with the usual challenges of benthic habitat mapping. Application of water column correction as an image pre-processing step to these sites is expected to result in improved accuracies. As a note, the very high accuracy reported by NOAA for Puerto Rico (100% for submerged vegetation) is for the area of La Parguera itself (NOAA, 2001), characterized by much shallower seas and several distinct Millennium classes which facilitate classification.

Given the scale of the work presented here, it is necessary to put into perspective the different groundtruth data sets employed and the maps produced in previous studies. Although all mapped “dense”, “medium-dense”, and “sparse” seagrass beds according to some comparable threshold of seagrass density, a closer look at individual studies reveals variations in definitions:

- NOAA has a fairly detailed scheme, with 5 seagrass classes, that needed to be interpreted and simplified into three classes of seagrass density (NOAA, 2001);
- *in situ* data for Lee Stocking Island and Andros were semi-quantitative, using an index of cover on a scale from 0 to 5 during the surveys (Andréfouët et al., 2003);
- *in situ* data for San Blas made use of a continuous measure of seagrass cover along boat tracks (Andréfouët, unpublished data). The data set thus needed to be broken down by Landsat pixels, resulting in only one class of seagrass density, as variations in cover were mostly very patchy and tended to occur within one Landsat pixel;
- data generated through visual-interpretation of IKONOS imagery, even when trained using well-know sites, may not always generate consistent density categories between sites. Consistency is difficult to maintain because of the variability in sediments and seagrass beds themselves, which may produce different signatures for similar benthic cover and densities. Variations such as leaves

colonized by epibionts or calcareous growth, beds temporarily just below or even above the water surface at low tide, and dark background sediments, may all lower the spectral contrast of seagrass blades (Fyfe, 2003), complicating the interpretation of densities. Similar challenges apply to categorizing *in situ* data despite measurable field experience (e.g., Lee Stocking Island, Andros, Glovers).

As algae can easily be mistaken for seagrass on Landsat images due to their highly similar spectral signatures (Green et al., 2000; Schweizer et al., 2005), a brief discussion of how we dealt with the issue follows. All ground-truth data that reported *dominance* (>70%) of algae were included in the “other” class. Seagrass beds with varying levels of algae density were included in the appropriate corresponding seagrass class. Although very few “other” pixels were classified as seagrass, seagrass pixels had a tendency to be attracted to the “other” class. In addition, in some instances, availability of several images acquired at different dates for individual Landsat scenes, recorded significant changes in the extent of submerged vegetation over short time periods (Figure 7). Since tropical seagrass beds are typically stable over the temporal scale of years, even in the advent of severe storms (e.g., Byron & Heck (2006), but see also Bouchon et al. (1991) and Fourqurean & Rutten (2004)), these variations are most likely caused by changes in algal biomass, and/or cyanobacterial blooms. Accounting for this factor during validation of final products allowed us to avoid large errors potentially associated with overestimating the extent of dense seagrass beds. In some instances, such as across the shallow Bahama Banks, this type of image comparison constituted a critical aspect of the mapping effort.

High values registered for producer and user accuracies of the “other” class indicate that the thematic maps do not overestimate seagrass extent. Moreover, confusion between individual seagrass classes explained most of the low accuracy. This is confirmed by the high accuracy results obtained in San Blas and Akumal where only one seagrass class was mapped. In these two focal areas, seagrass beds were primarily located on back reefs and terraces, and were typically small in size. Given the spatial resolution of Landsat images (30m pixels), it was not possible to confidently discriminate between seagrass patches of different densities and thus only one seagrass class was mapped.

Uncertainty in pixels classification (e.g., differentiating between fuzzy ‘medium’ or ‘sparse’ classes given slight differences in class definitions) led us to collate the initial three-class seagrass typology into a two-class seagrass scheme. Although this approach may not be entirely satisfactory for all applications, given the constraints and goals of this study, the methodology adopted is a valuable first attempt at obtaining realistic figures of seagrass extent and distribution across the Caribbean.

Areas with dense seagrass cover are frequently patchy and narrow. These were generally correctly captured in shape and extent in classified images. Yet ground-truth points for dense seagrass often fell just onto the patch’s edge, or just outside the area classified as dense, leading to an incorrect classification assessment for that class. Misregistration of Landsat images, and/or ground-truth points, may partly explain this observation. Landsat image specifications may have up to 250m geolocation errors (up to 7 pixels) (NASA, 2007). Our field experience further demonstrates that common errors are due to being off by one to two pixels (30-60m); a distance still large enough to miss small targets defined on IKONOS images or *in situ*. It is usually possible, following personal data collection, to manually correct either images or GPS points to ensure their proper overlap. Here, such adjustments were impossible as data were collected from widely different sources. The problem was less common for medium and sparse seagrass beds, which generally cover wider areas. Areas of very low cover (<5%), which includes sandy areas, were generally classified as “other”. Since one of our principle mapping objective was to re-estimate green turtle carrying capacity for the Caribbean, accurate mapping of low density seagrass beds was not of primary importance. Optimal turtle foraging grounds tend to consist of dense seagrass beds, so we assumed that accurate mapping of dense and medium-dense seagrass beds was an essential first step towards establishing turtle (and other) conservation targets.

Based on these observations, we suggest that thematic maps are both more useful and more valid for spatial analysis than the results of confusion matrices alone may indicate. Consistently higher values could have been achieved had images with high spectral and/or spatial resolution been used to map seagrass extent (Mumby and Edwards, 2002; Andréfouët et al., 2003; Hochberg and Atkinson, 2003). However, data availability and costs justify the use of Landsat images here. As of 2007, IKONOS and Quickbird licensed data cost 15-20US\$ per km<sup>2</sup> depending on products, availability in

archives, or needs for tasking an acquisition. In comparison, an archived copyright-free Landsat 7 image costs 600US\$, corresponding to a cost of  $\sim 0.02$  US\$.km<sup>-2</sup>. Therefore, although enhancement in accuracies and resolution may be substantial using IKONOS, Quickbird, or hyperspectral data - to date, given acquisition costs - none of these solutions present realistic approaches for large-scale mapping efforts.

#### *4.2. Implications for conservation*

While we recognize that our mapping efforts have limitations, results obtained to date are encouraging given the scale of the achievement, the rapid production of maps applying a consistent and uniform methodology, and the objectives to:

- i. regionally assist with management and conservation planning targets in a cost effective fashion; and
- ii. regionally re-assess carrying capacity estimates for green turtles.

Turtles and many fish species may move over large spatial scales and across different environments over the course of their life histories. Providing Caribbean-wide habitat information therefore significantly improves our ability to manage and conserve the goods and services provided by seagrass beds at biologically relevant scales (Olson and Dinerstein, 2002; Stevens, 2002). Indeed, it has been suggested that effective mapping for successful conservation should be carried out at transboundary (i.e. ecoregional) scale (Beck and Odaya, 2001; Lourie and Vincent, 2004), with a strong emphasis on methodological consistency. The products may also provide researchers and managers with a useful and much needed (Creed et al., 2003) baseline to monitor changes registered in seagrass ecosystems over time due to mounting human pressures on coastal ecosystems (Burke and Maidens, 2004), and to develop spatially explicit models of impacts due to disturbances (e.g., (Kelly et al., 2001)). Even for management at a national level, the maps developed through this research can form the basis of efforts targeted at capturing important landscape patterns that may have significant management implications at a more local scale (Fonseca et al., 2002; Bell et al., 2006).

The average accuracy of 68% across all sites does not adequately reflect the utility of organizing disaggregated spatial data into consolidated map products. Ultimately, which product is more environmentally relevant (i.e., higher classification accuracy but smaller spatial extent versus lower classification accuracy but larger spatial extent) will

depend on the conservation task at hand. In the case of green turtle conservation for instance, deriving a more reliable estimate of seagrass extent represents a critical first step in re-assessing a regional estimate of carrying capacity. This in turn can inform the goals set for population recoveries. In doing so it is noteworthy that the theoretical number of green turtles that could be sustained by present seagrasses might not be consistent with turtle numbers that would assure optimal long-term seagrass productivity. This is clearly demonstrated in the diverse estimates of turtle carrying capacity for the WCR, derived from varying levels of seagrass productivity: from 586 million turtles for highly productive seagrass beds to 39 million in stressed meadows (Bjorndal et al., 2000).

## **5. Conclusion and perspectives**

Recognizing the urgency in establishing enhanced GIS data sets on the spatial distribution of habitats for large-scale ecological and conservation applications, this study assessed the feasibility of using Landsat sensors to map seagrass beds effectively and subsequently apply consistent methods throughout the WCR. We processed a total of 40 Landsat 7 (ETM+) images covering regionally representative sites with contrasted sizes, structure, geomorphology, and seagrass bed extent. The results reported here are encouraging for the completion of a Caribbean-wide map of seagrasses using Landsat images, Millennium Coral Reef Mapping Project coral reef products, and further IKONOS imagery. Such an effort is currently in progress, and builds on the discussion developed here. This is, to our knowledge, the largest such effort worldwide.

Accuracies obtained at individual sites are in agreement with local studies previously published using different methods. Comparison of the regional results also point to where some of the traditional image processing challenges in shallow coastal environments will be the most acute: wide cross shelf areas, such as those around Puerto Rico. Similar environments in the Bahamas, Cuba, and Florida, will require image depth-correction if useful accuracies are to be achieved.

Next steps include the processing of all remaining available images for the region and compiling the results into a GIS layer to facilitate use by the conservation and scientific community. In parallel, further map validation based on local expertise and high resolution images will help to highlight weaknesses and strengths of our products.

There are mounting threats facing coastal areas (Burke & Maidens, 2004), and significant gaps in existing habitat databases. Therefore, availability of consistent regional seagrass habitat maps for the WCR will assist governments and their partners in developing successful conservation plans. Furthermore, the design employed in this study should also be useful in other tropical regions where reliable habitat data are critically needed for integrated coastal management purposes.

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Table 1: List of sites for which thematic seagrass habitat maps were derived in this paper. Available ancillary data and references on previous remote sensing and habitat mapping work at these same sites are also presented. Where applicable, the type of data used to assess accuracy of our products is indicated.

Focal area	Landsat Path-Row	Accuracy assessment data	IKONOS data	References
Bahamas	13-41, 14-41, 14-42, 13-42, 12-42, 15-43, 14-43, 13-43, 12-43, 11-43, 15-44, 14-44, 13-44, 12-44, 11-44, 10-44, 12-45, 11-45, 10-45, 9-45	IKONOS & in situ	Lee Stocking Island Andros Island. (AUTEC)	Armstrong (1993); Andréfouët et al. (2003); Call et al. (2003), and Louchard et al. (2003)
Belize	19-48, 18-48, 19-49, 18-49	IKONOS	Lighthouse Atoll Glovers Atoll Barrier Reef section Patch Reef section	Andréfouët et al. (2003)
Mexico (Yucatán coast)	20-45, 19-45, 18-45, 19-46, 18-46, 19-47, 18-47	IKONOS	Akumal Boca Paila Mahahual	Andréfouët et al. (2003); Garza-Perez et al. (2004)
Roatán (Honduras)	17-49	IKONOS	Roatán	Maeder et al. (2002)
St Croix (US Virgin Island)	4-48	NOAA		NOAA (2001)
Puerto Rico (south coast)	5-48	NOAA		NOAA (2001)
San Blas offshore banks and islands (Panama)	11-53	<i>in situ</i>		Andréfouët & Guzmán (2005)
Los Roques (Venezuela)	4-52	<i>in situ</i>		Schweizer et al. (2005)
Alacranes Bank (Mexico)	20-45	N/A (published value: 77%)		Bello-Pineda et al. (2005)
Guadeloupe	1-49	N/A (published value: 95.7%)		Chauvaud et al. (2001)
Bay du Robert (Martinique)	1-50	N/A (published value: 94%)		Chauvaud et al. (1998)
Providence Island (Colombia)	14-51	N/A		Díaz et al. (2003)
San Andrés (Colombia)	14-51	N/A		Díaz et al. (2003)

Table 2: Accuracy achieved for two seagrass classes (\* with the exception of San Blas and Akumal) and one “other” class using the following data for the assessment: IKONOS imagery; direct ground-truth data collected *in situ*, and NOAA ground-truth data. *n* is the total number of points used for each site.

Focal area	Source	<i>n</i>	Overall		Dense seagrass (>70%)		Medium/Sparse Seagrass (<70%)		Other	
			Accuracy (%)	Kappa	Producer (%)	User (%)r	Producer (%)	User (%)	Producer (%)	User (%)
Lee Stocking Island	IKONOS & <i>in situ</i>	170	71.8	0.48	15.4	50.0	74.0	72.5	86.2	72.3
East Andros	IKONOS & <i>in situ</i>	502	63.3	0.19	41.5	32.3	23.3	50.0	74.1	77.3
Roatán	IKONOS	296	71.3	0.54	65.1	50.0	55.4	64.8	82.7	86.7
Lighthouse Atoll	IKONOS	181	69.1	0.53	25.0	76.5	86.2	53.8	87.3	87.3
Glovers Atoll	IKONOS	120	71.7	0.51	75.0	32.2	31.7	68.5	95.5	87.7
Belize patch reefs	IKONOS	76	64.5	0.05	N/A	N/A	0.0	0.0	96.1	66.2
Belize barrier reef	IKONOS	102	55.9	0.34	33.3	29.6	42.9	85.7	86.1	57.4
Mahahual	IKONOS	54	55.6	0.18	21.8	83.3	0.0	0.0	100	52.1
Boca Paila	IKONOS	87	72.4	0.52	52.4	55.0	57.2	42.1	84.6	91.7
Akumal*	IKONOS	57	87.7	0.46	N/A	N/A	57.1	50.0	92.0	93.9
St Croix	NOAA	294	63.9	0.24	46.8	47.8	24.1	12.3	72.9	83.2
La Parguera	NOAA	81	45.7	0.0	59.4	47.8	100.0	8.3	32.6	60.9
San Blas*	<i>in situ</i>	293	85.3	0.57	66.2	67.2	N/A	N/A	90.8	90.4
Los Roques	<i>in situ</i>	279	77.1	0.64	90.5	79.2	49.4	88.9	86.8	71.2

Table 3: Estimated seagrass surface areas (in km<sup>2</sup>) at each study site, with the exception of Puerto-Rico due to low accuracy achieved for the product.

Site	Seagrass (km <sup>2</sup> )
Bahamas	65436.4
Belize	2092.2
Mexico (Yucatán coast)	1318.9
Roatán (Honduras)	64.4
St Croix (US Virgin Island)	61.7
San Blas offshore banks and islands (Panama)	11.1
Los Roques (Venezuela)	150.1
Alacranes Bank (Mexico)	57.8
Guadeloupe Island (France)	178.8
Providence Island (Colombia)	2.6
San Andrés (Colombia)	16.9

## Figures

Figure 1: Map of the Caribbean and geographic location of sites processed for this study. Belize PR = Belize Patch Reef, Belize BR = Belize Barrier Reef (background map from [www.reefbase.org](http://www.reefbase.org)). The lower panel shows data (both points and polygons) currently available on seagrass distribution for the region as displayed in “World Atlas of Seagrasses” (Green and Short, 2003) as taken here from the interactive IMAPS system (<http://storp.unep-wcmc.org>).

Figure 2: Flow chart of data processing steps involved in mapping seagrasses at the large scale of the Wider Caribbean Region (WCR). “Path-Row” > 1 = is more than one path-row covering the study site? Rounded boxes = objects; square boxes = processing steps; diamond shaped boxes = highlight specific tests or conditions that need to be fulfilled. Bathymetric correction is highlighted in grey as it was not utilized here but is recommended for sites where depth presents a confounding factor (e.g., site west of La Parguera, Puerto Rico).

Figure 3: Examples of Millennium polygons for the Belizean focal area. Detailed geomorphological classes provided by the Millennium Coral Reef Mapping Project allow for *a priori* contextual editing prior to spectral supervised classification. The figure aims to highlight the complexity and details of the structures and products provided. This area includes close to 100 classes, so for the purposes of readability and simplicity, no thematic legend has been provided.

Figure 4: Accuracy assessment points selected for Lee Stocking Island (Exuma, Bahamas) using an IKONOS image and augmented with *in situ* observations. Pink: dense seagrass, yellow: medium-sparse seagrass, green: other.

Figure 5: Thematic map for the entire Bahamas and for the Little Bahama Bank with two seagrass classes (green) and a single “other” class (grey). The “other” category (in grey) includes here areas that were removed by *a priori* contextual editing for the actual seagrass mapping effort as well as processed areas classified as “non seagrass”. The upper right panel shows the current seagrass product available from UNEP-WCMC, displayed with the interactive IMAPS service (<http://storp.unep-wcmc.org>). It is included here for comparative purposes and highlights commission and omission errors in the existing seagrass coverage for the Bahamas.

Figure 6: Examples of habitat maps displaying two seagrass classes and a single “Other” class (as under Figure 5) that can be compared with previous published peer-reviewed studies: Los Roques (to use in comparison with Schweizer et al. (2005)), and Alacranes (to be compared to Bello-Pineda et al. (2005)).

Figure 7: Examples of temporal variation in vegetation cover, probably due to algal blooms, in two pairs of Landsat images taken less than 14 months apart (path-row 12-53, Bahamas). In the top pair, extensive darker areas appear on the bottom image. Note also (arrow most left) that dark areas have shifted to bright areas in the same period of time. In

the second image pair, patches of dark water and darker bottoms appear on the bottom image (left arrow). Over the same time period (right arrow), vegetation has decreased on hard-bottom areas. These rapid changes from dark to bright and vice-versa are not typical of dense or medium-dense seagrass beds and are most likely to be associated with changes in algal cover.



Figure 1

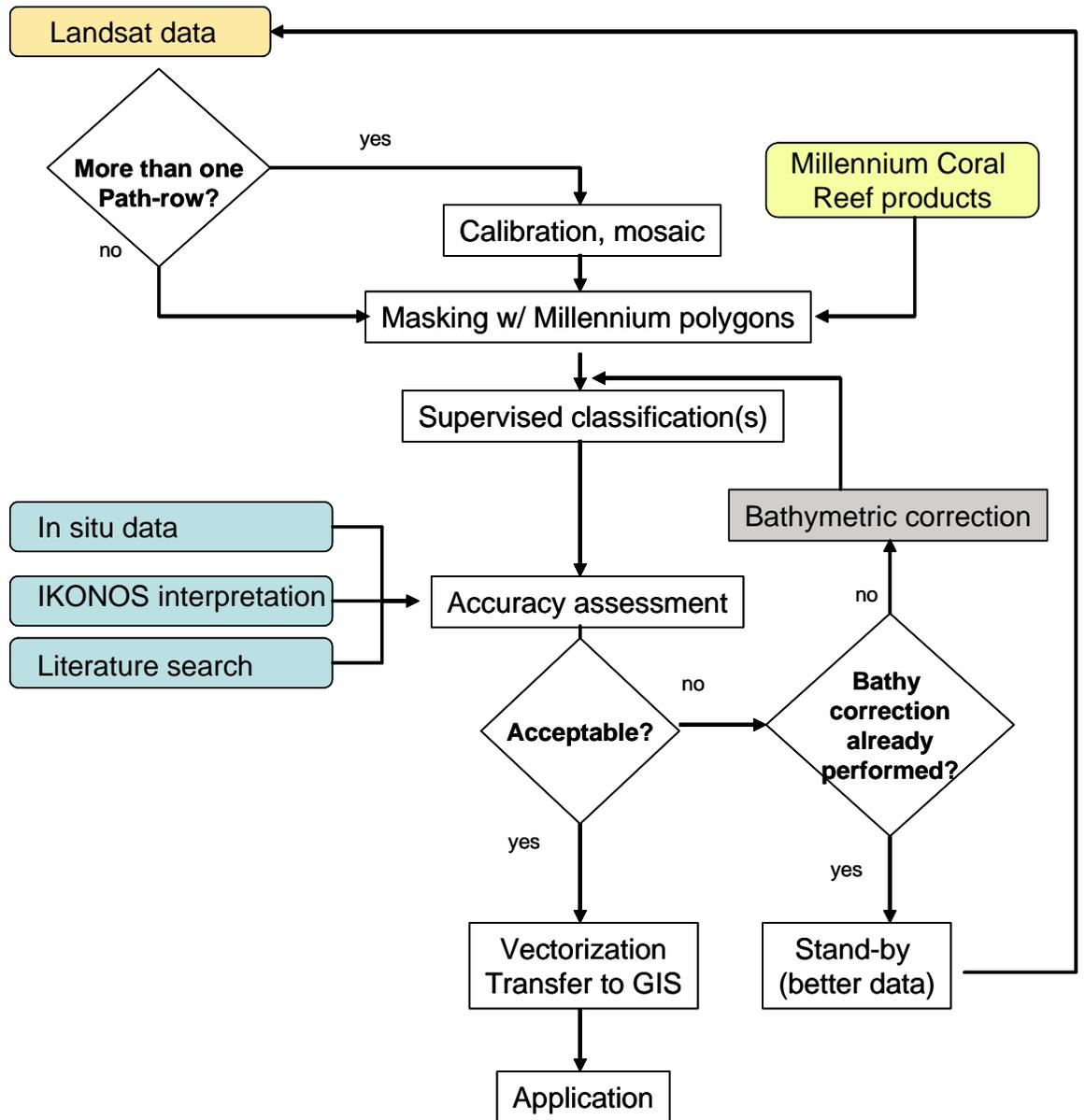


Figure 2

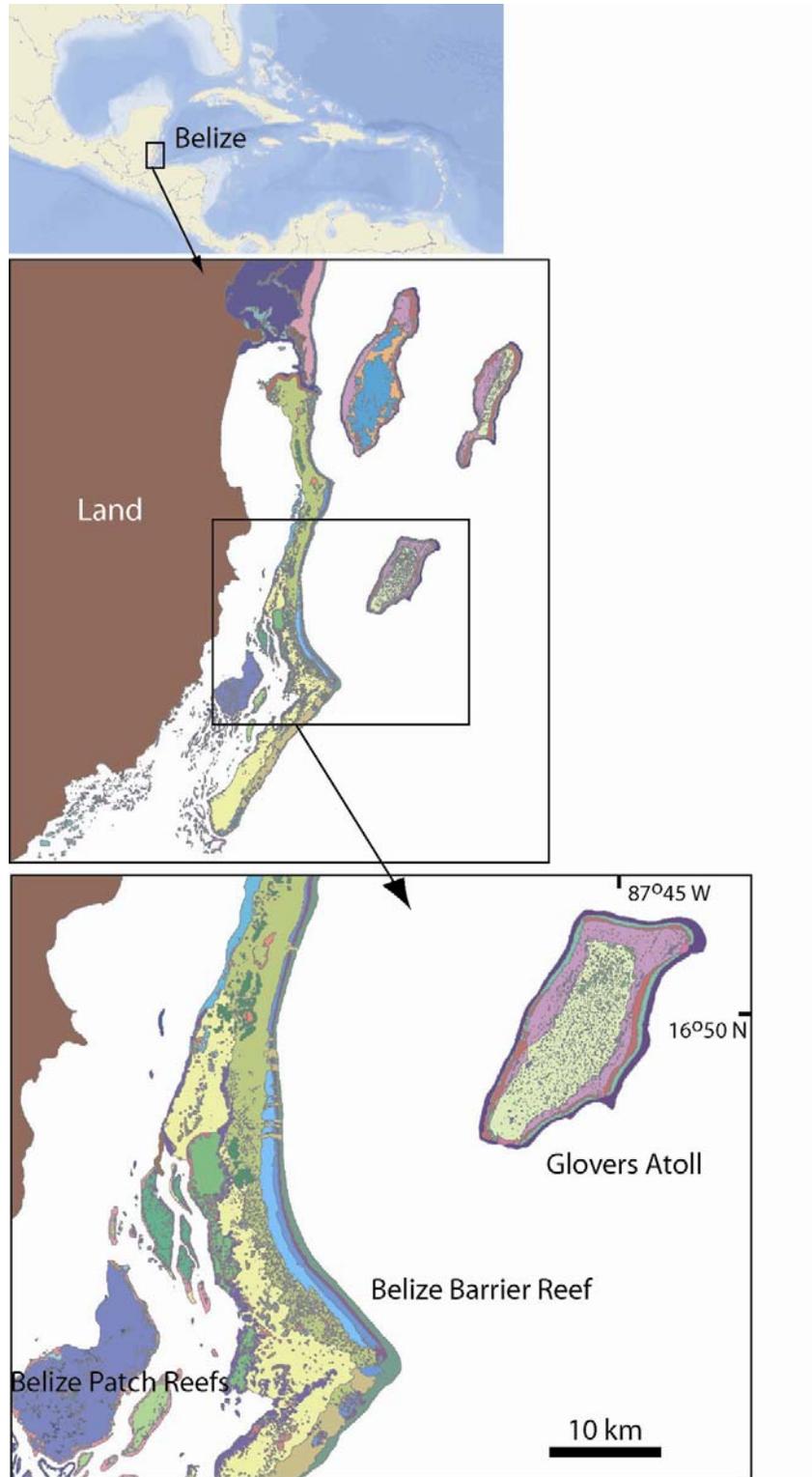


Figure 3

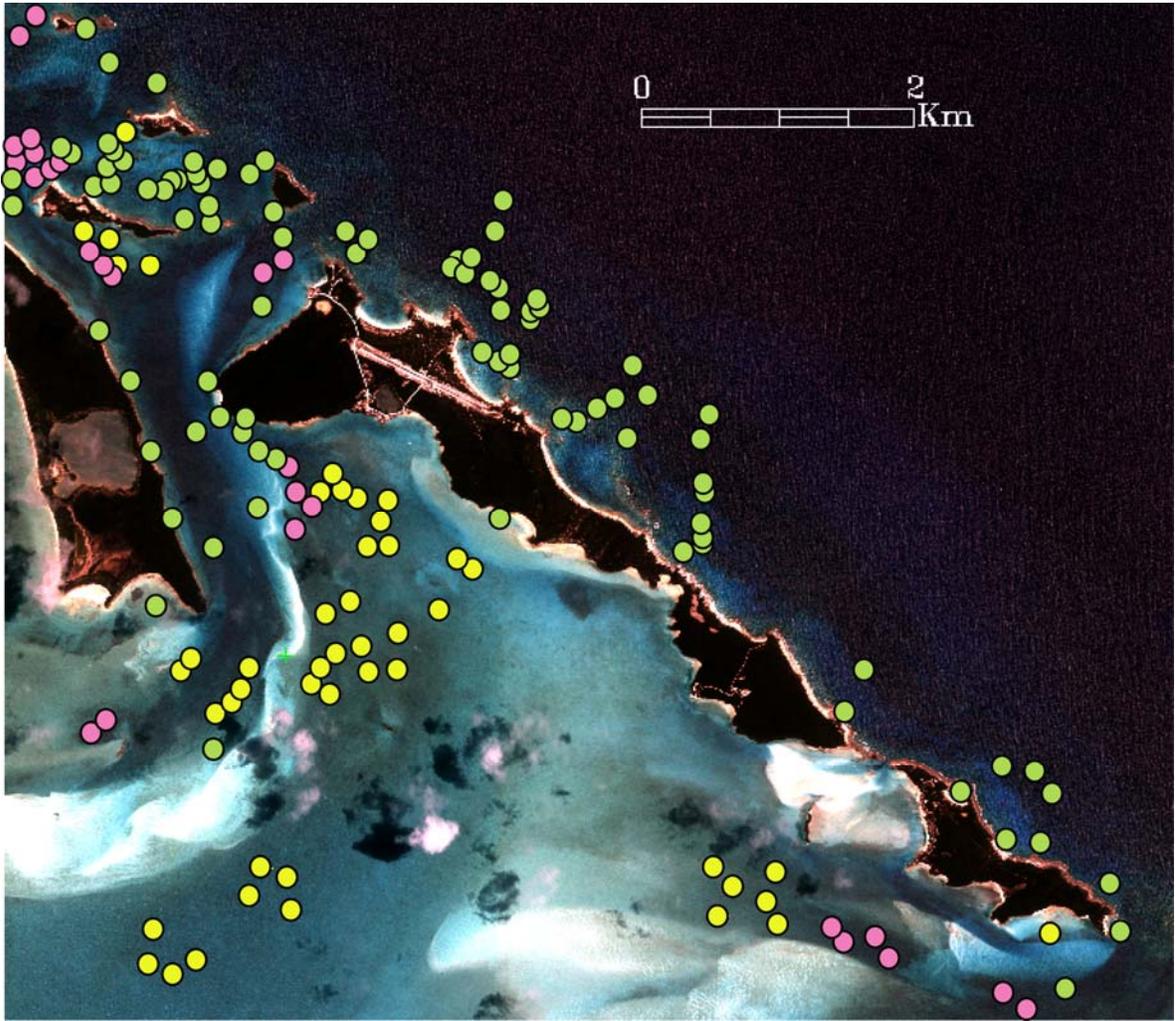


Figure 4

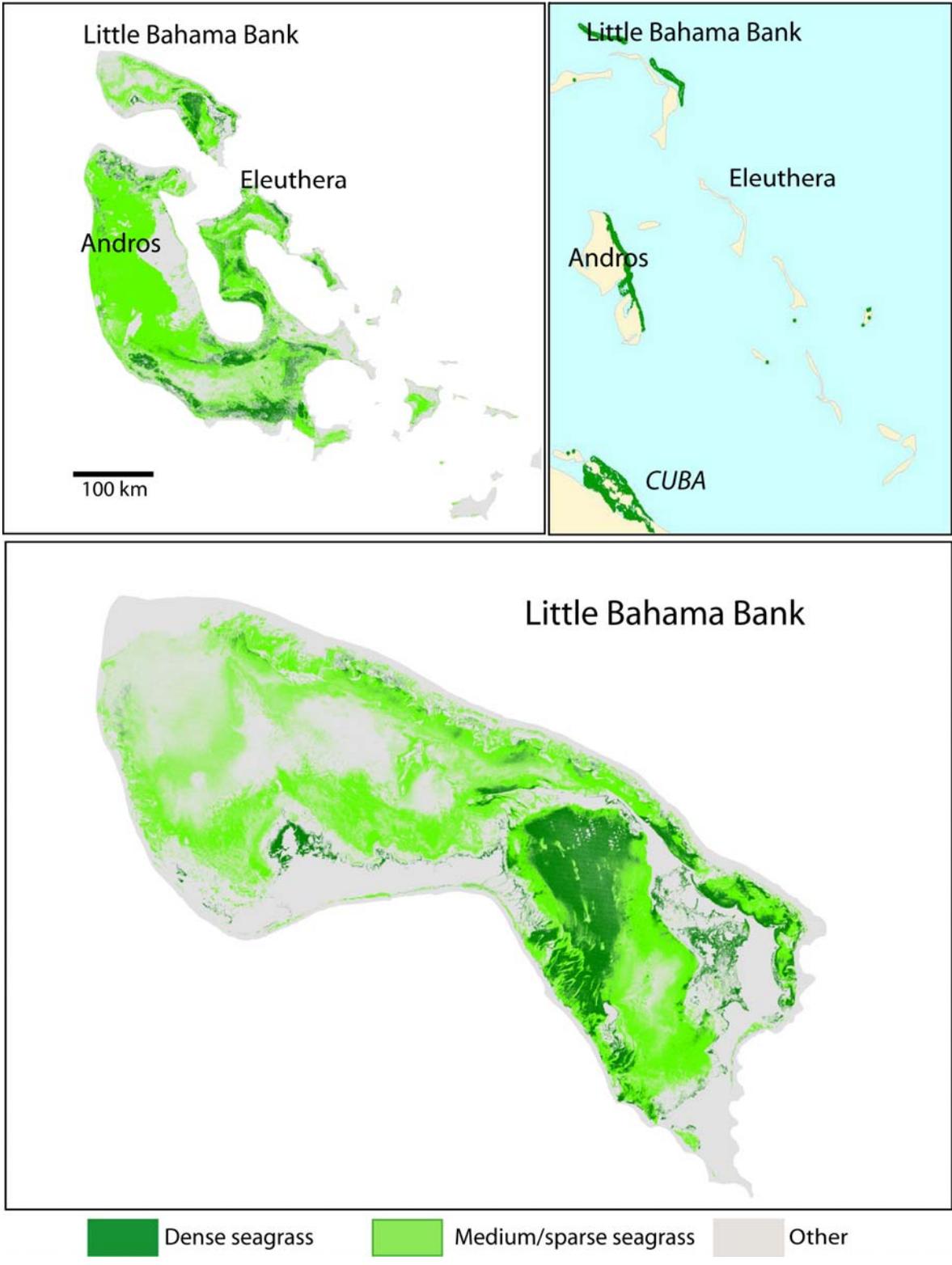


Figure 5

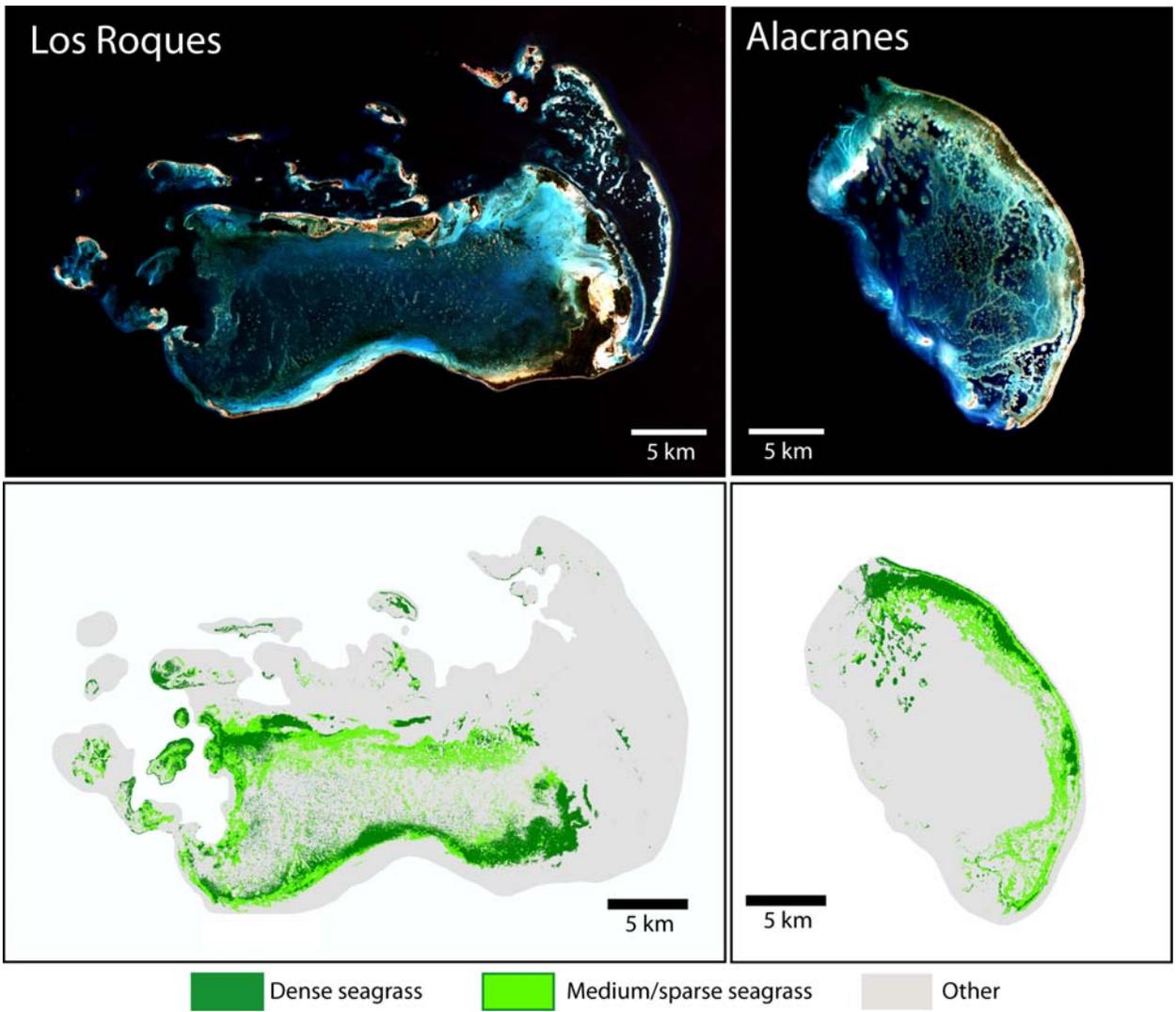


Figure 6

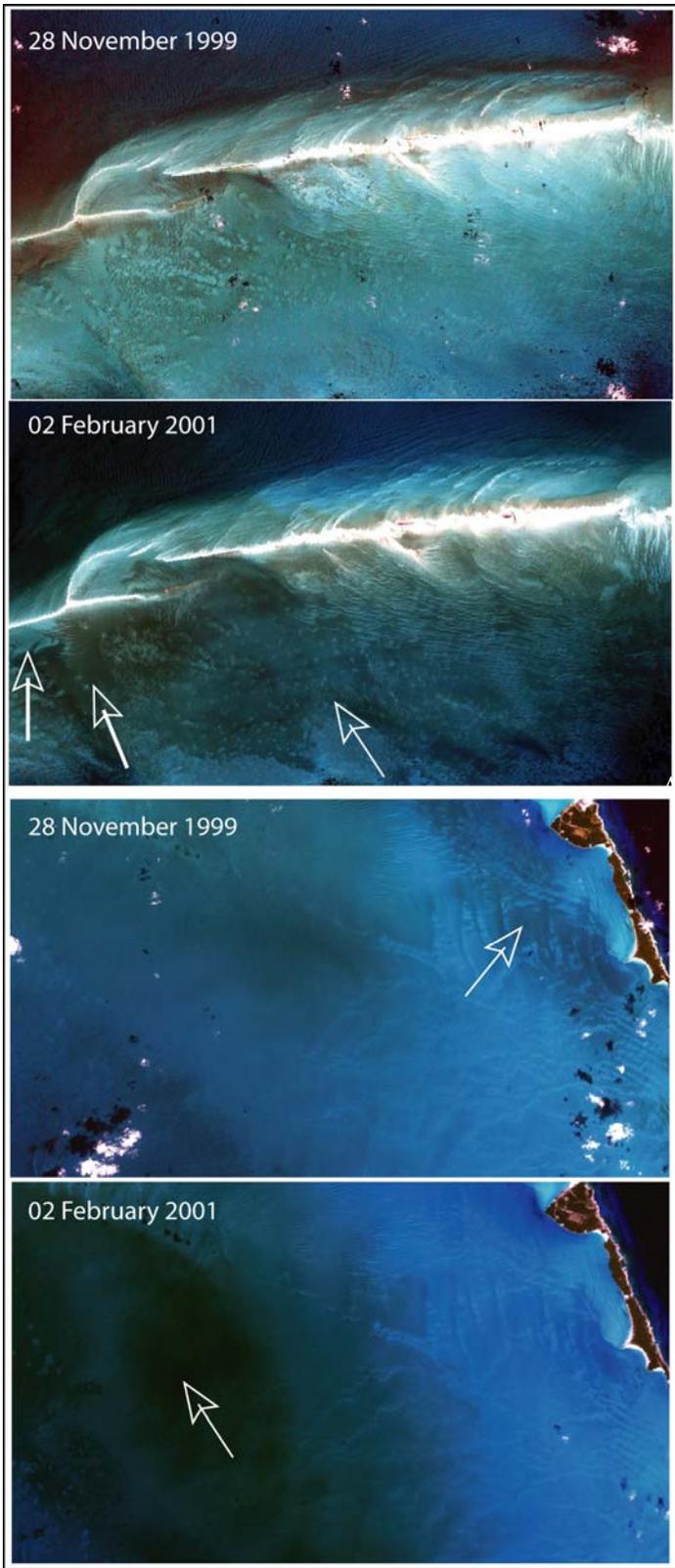


Figure 7

## **Appendix C**

Can success towards the international tropical marine biodiversity conservation targets of 2010-2012 be measured? Abstract of manuscript to be submitted to *Science*.  
[addresses Objective 3]

*Abstract of manuscript to be submitted to Science*

**Can success towards the international tropical marine biodiversity conservation targets of 2010-2012 be measured?**

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**Abstract:**

In response to urgent calls for the protection of species and their habitats in the face of persistent global destruction and overexploitation, the international community has agreed to establish *representative* networks of marine protected areas by 2012 and effectively conserve between 10 and 30% of specific habitats by 2010. In light of information currently available about the extent of coastal marine habitats worldwide, advances in implementing these targets cannot be achieved. We propose that this gap can be filled in a cost effective and timely fashion through the targeted use of mostly already available satellite imagery.

## **Appendix D**

Inputs and outputs for an EwE model of a Hawaiian algal ecosystem  
in Kaloko Honokōhau National Historic Park  
[addresses Objective 1]

Inputs and outputs for an Ecopath with Ecosim model of a Hawaiian algal ecosystem  
in Kaloko Honokōhau National Historic Park

Colette Wabnitz worked closely with George Balazs and Jeffrey Polovina in the development of the inputs for an Ecopath with Ecosim (EwE) model for an algae-based ecosystem with foraging green turtles. After careful review, the area within the Kaloko Honokōhau National Historic Park on the Big Island of Hawaii (see map) was selected because of the data available for that area. Based on this collaboration and the extensive involvement of other colleagues for ground-truthing the inputs, we are confident in the identification and quantification of the model inputs (see Table 1).

For data inputs, particularly for biomass values, preference was given to, in order of importance:

- (i) information collected specifically in Kaloko Honokōhau;
- (ii) from published reports for the Kona coast; and
- (iii) from data collected on the island of Hawaii.

Once an initial input value was determined from available materials, it was discussed with experts with intimate knowledge of the park and local ecosystems and refined accordingly.

Experts consulted include:

- (i) sea birds – K. Uyehara and S. Waddington;
- (ii) green turtles – G. Balazs, S. Kubis, and S. Beavers;
- (iii) reef fishes – E. Brown;
- (iv) urchins – L. Marrack, S. Beavers, and M. Weijerman;
- (v) algae – C. Squair, T. Sauvage, C. Payri, and J. Smith;
- (vi) phytoplankton and zooplankton – P. Bienfang, M. Landry, and R. Scheinberg.

Results from this project will be presented by George Balazs and Jeffrey Polovina at the External Program Review of the Pacific Islands Fisheries Science Center in June 2008.

Map of Kaloko Honokōhau.

Reproduced from: <http://www.nps.gov/kaho/planyourvisit/upload/final%20map%20w%20revised%20trails%20enlarged.pdf>

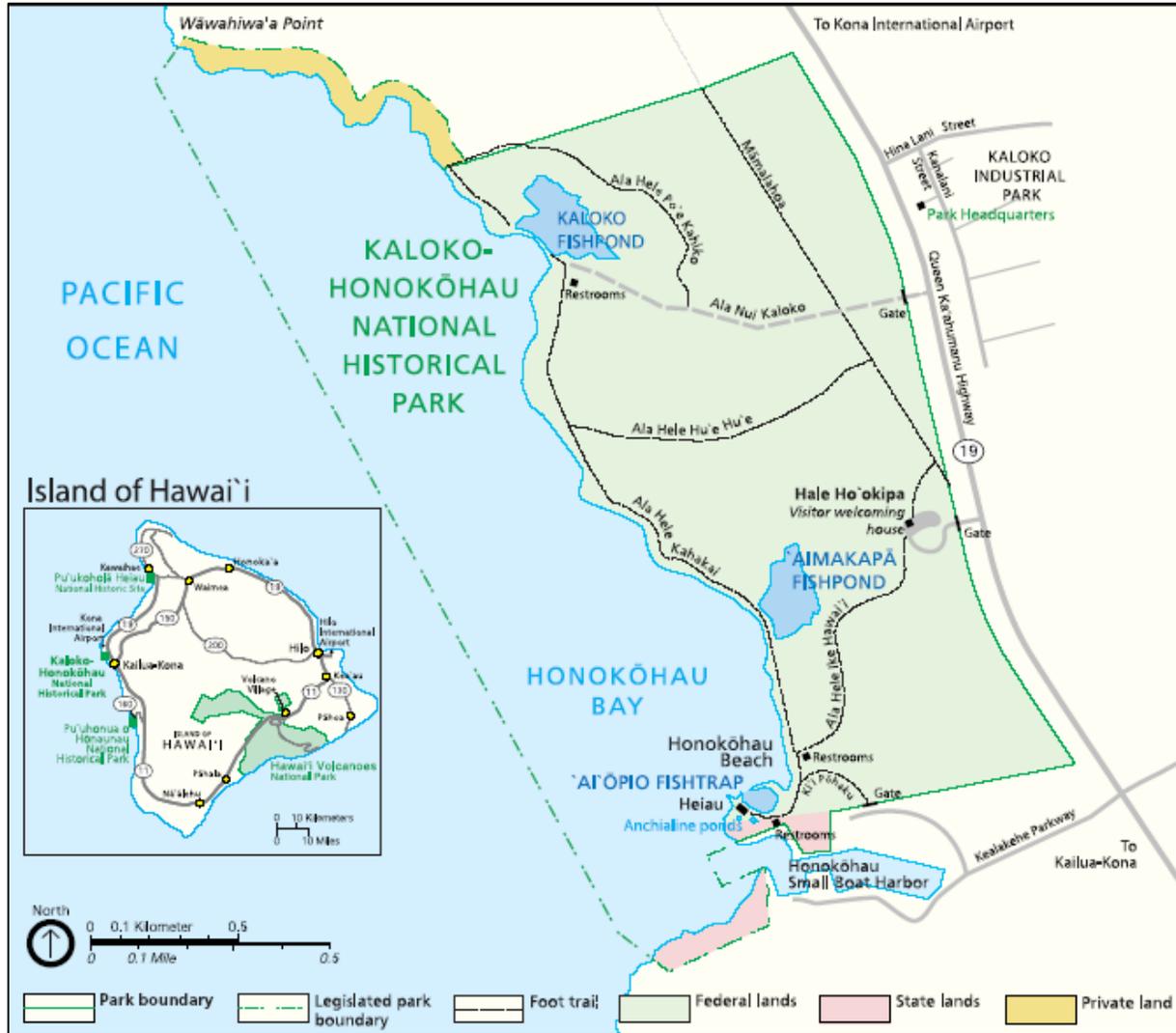


Table 1. Data table for functional groups included in an ecosystem model of Kaloko Honokōhau (Hawaii). Output data are provided in bold. P/B = production/biomass ratio; Q/B= consumption/biomass ratio; MIF = Mobile Invertebrate Feeders; SIF = Sessile Invertebrate Feeders; ZOO = Zooplanktivores; and CCA = Crustose Coralline Algae

Group name	Biomass (t/km <sup>2</sup> )	P/B	Q/B	Ecotrophic efficiency
Spinner dolphins	2.74	0.176	11.52	<b>0.007</b>
Monk seals	0.179	0.23	11.025	<b>0.02</b>
Sea birds	0.00237	0.3	2.314	<b>0</b>
Sharks, jacks and rays	0.1	0.447	4.12	<b>0</b>
Green sea turtles	1.591	0.115	5.187	<b>0.049</b>
Reef fishes - piscivores	2.4	0.48	6.44	<b>0.435</b>
Reef fishes - herbivores	20.42	1.08	22.6	<b>0.269</b>
Reef fishes - corallivores	0.7	2.03	13.71	<b>0.544</b>
Reef fishes - detritivores	2.27	1.6	24.69	<b>0.669</b>
Reef fishes – MIF	10.44	0.75	8.29	<b>0.702</b>
Reef fishes – SIF	0.54	1.48	13.52	<b>0.204</b>
Reef fishes – ZOO	3.06	1.26	16.24	<b>0.772</b>
Urchins	300	0.48	8.547	<b>0.056</b>
Crown of thorn	0.8	0.41	9	<b>0.001</b>
Benthic Invertebrates	<b>41.327</b>	<b>2.91</b>	15.25	0.95
Corals	146.288	0.674	5.527	<b>0.197</b>
Octocorals	2.9	0.9	1.9	<b>0.174</b>
Macro-algae	23.353	3.467	-	<b>0.898</b>
CCA	31.896	2.322	-	<b>0.346</b>
Turf algae	117.962	21.325	-	<b>0.818</b>
Zooplankton	0.768	412	900	<b>0.883</b>
Phytoplankton	2.04	441.219	-	<b>0.973</b>
Detritus	100	-	-	<b>0.942</b>