AN ABSTRACT FOR THE DISSERTATION OF

Elise F. Granek for the degree of Doctor of Philosophy in Zoology presented on June 21, 2006.

Title: Linkages Between Mangrove Forests and Coral Reefs: Quantifying Disturbance Effects and Energy Flow Between Systems

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Interface habitats are considered valuable natural systems, tightly linked to adjacent habitats through the flow of matter and energy. However, there is limited research on mechanisms of connectivity such as movement of organisms and particulate matter and ways in which anthropogenic disturbance to interface habitats may affect immediate and adjacent ecosystems. Mangrove forests, a common interface habitat in tropical coastal zones, once lined much of the tropical and subtropical shores worldwide. However, anthropogenic influences on these systems have led to a ~35% reduction in mangrove area over the last fifty years. In light of the perceived importance of mangrove forests as coastal habitat, the rapid decline of this habitat type, and the potential implications of mangrove habitat loss to adjacent ecosystems, it is important to build upon the current state of knowledge for mangrove forests. The chapters in this dissertation report on the following topics.

First I review the published literature to examine the available evidence for connections between mangrove forests and coral reefs. I synthesize previous research findings, highlight areas of future research priorities, and propose a conceptual model of how areas of mangrove disturbance and resulting impacts on coral reefs are related.

Second, I assess the effects of mangrove clearing on the immediate habitat. I examine how the physical environment changes following mangrove clearing by examining abiotic factors. I also measure changes in algal biomass and diversity to determine what

effects physical changes have on the primary producer community. My results indicate that mangrove clearing has dramatic effects on both the physical and biotic environment.

Based on measured changes in abiotic and biotic conditions, K. Frasier and I investigate how larval and zooplankton communities differ between intact and cleared mangrove areas. We find that diversity and community composition differ between intact and cleared mangrove areas, highlighting an additional effect of mangrove disturbance with potential implications for adjacent systems.

To address the unanswered question of whether and how abiotic and biotic changes in cleared mangrove areas impact adjacent coral reefs, I repeat and expand upon the study I had conducted on abiotic and biotic changes following mangrove removal. The results in the immediate habitat indicate that the effects of mangrove disturbance are broad. Results from the reefs indicate that mangrove disturbance does have effects on adjacent coral reefs.

To determine the relative importance of mangrove-derived nutrients to adjacent coral reef ecosystems and to examine how distance from mangroves to reefs and clearing of mangroves affected energy transfer, I sample sessile reef invertebrates. I employ carbon, nitrogen and sulfur stable isotope analysis as a tool to evaluate whether sessile invertebrates: corals, sponges, a bivalve and feather duster worm, utilize mangrove-derived nutrients. Though the pattern varies by taxon, this research provides evidence that sessile reef invertebrates utilize mangrove-derived nutrients.

Finally, I examine the effect of two consecutive storm events, the 2005 Tropical Storm (later Category 5 Hurricane) Wilma and the subsequent Tropical Storm Gamma, on the coastal zone. The retention rate of field equipment following storm events provides a picture of how coastal protection changes following anthropogenic mangrove disturbance and the implications of continuing mangrove loss as storm frequency and intensity increase in parallel with climate change.

These studies provide new evidence on the effects of disturbance to mangroves on coastal and reef systems. Many new research areas are raised by the results presented here. However, these data provide a useful framework for considering conservation and management strategies for mangrove forest – coral reef systems.

Linkages Between Mangrove Forests and Coral Reefs:

Quantifying Disturbance Effects and Energy Flow Between Systems

by
Elise F. Granek

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Dean of the Graduate School

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Elise F. Granek, Author

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CONTRIBUTION OF AUTHORS

Kaitlin E. Frasier assisted with field sampling and identified larvae and zooplankton in collected samples for her Senior Honors Thesis and is a co-author on Chapter 4. Jana Compton assisted me with the research design and protocol development, taught me isotope sample preparations, contributed to the brainstorming and problem-solving involved with data interpretation, and allowed me access to lab resources and space for isotope preparation and processing. Don Phillips assisted extensively with the development and tweaking of mixing model analyses and data interpretation. Jana Compton and Don Phillips are co-authors on Chapter 6.

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Chapter 1. General Introduction

Interface habitats, areas where aquatic and terrestrial habitats intersect, play important functional roles. Interface habitats mediate the exchange of resources (e.g., energy, nutrients, water), alter abiotic gradients (e.g., temperature, salinity, pH, sedimentation, nutrients), insulate abutting habitats from disturbances, and serve as critical habitat in their own right for certain life history stages of species from the adjacent habitats. Though often referred to as transition zones or ecotones (e.g., rocky shores, salt marshes, riparian zones), they are not just a mixture of species from the abutting ecosystems, but also harbor unique species assemblages.

There is strong scientific evidence for functional roles of interface habitats. Marshes and mangroves buffer the seaward system from terrestrial source sedimentation (Golbuu et al. 2003, Kathiresan 2003, Bertness et al. 2004, Neumeier and Ciavola 2004) while protecting adjacent coastal zones from the impacts of waves and storms (Dahdouh-Guebas et al. 2005). Estuaries, marshes, rocky shores, sandy beaches, mangroves and riparian zones provide habitat for early life stages of invertebrates and fish that reside in upstream or downstream habitats as adults (Hering and Plachter 1997, Nagelkerken et al. 2001, Nagelkerken et al. 2002, Akamatsu et al. 2004, Dorenbosch et al. 2004). Riparian zones (Pusey & Arthington 2003; Schade et al. 2005; Wilkinson et al. 2005) and marshes (De La Lanza Espino and Rodriguez Medina 1993, Osgood 2000) alter nutrient, temperature, and/or salinity dynamics in adjacent habitats, and some intertidal zones provide marine food resources for terrestrial fauna (Polis and Hurd 1996, Anderson and Polis 1999).

Interface habitats are considered valuable natural systems tightly linked to adjacent habitats via mechanisms such as organism and particle movement. However, there is limited research on these mechanisms of connectivity and how anthropogenic disturbance to interface habitats may affect the immediate system and adjacent ecosystems.

Mangrove forests, a common interface habitat in tropical coastal zones, once lined much of the tropical and subtropical shores worldwide. However, anthropogenic influences on these systems have led to a ~35% reduction in mangrove area over the last fifty years (Alongi 2002), with half to three-quarters of mangrove area lost in parts of Southeast Asia (Field et al. 1998). In light of the perceived importance of mangrove forests as coastal habitat and the rapid decline of this habitat type, it is important to consider the current state of knowledge for mangrove forests. This includes examining where gaps in our knowledge exist and what research priorities are most relevant to mangrove conservation and management.

The scientific literature refers to connections between mangrove forests and coral reefs (Ogden 1980, UNEP 1995), but here, too, there are gaps in what is known about the level of connectivity between the two habitats. Coral reefs are frequently in close proximity to mangrove forests, house high levels of biodiversity, and provide a suite of ecosystem services to humans and other species. Coral reefs are in decline globally with approximately 30% of reefs severely damaged; predictions estimate that 60% of coral reefs may be lost in the next 25 year (Hughes et al. 2003) due to stressors including climate change, disease, overfishing, and pollution (UNEP 1995, White et al. 2000).

As with mangroves, anthropogenic disturbance to coral reefs continues to threaten their survival and the impacts of mangrove disturbance on nearby coral reefs has not been addressed. There is a need for further research into the effects of anthropogenic mangrove disturbance on the immediate habitat and resultant changes that managers might expect to see on adjacent coral reefs. My dissertation addresses the need for a synthesis of our current knowledge and attempts to fill gaps in the available data on mangrove forest-coral reef connections and implications of anthropogenic mangrove disturbance.

In Chapter *2*, *Habitat connectivity: A review of terrestrial to marine flows between mangrove forest and coral reef systems*, I conduct a review of the literature on mangrove forest-coral reef connectivity. To evaluate the current state of empirical evidence for mangrove forest – coral reef connectivity, I surveyed the literature on three key topics, asking the questions: 1) How does nutrient transfer link mangrove and coral

reef habitats? 2) How are mangroves and reefs linked via organism movement? What effects do these linkages have on community structure and ecosystem health on coral reefs? 3) To what extent are mangroves serving as a trap for terrestrial and mangrove-derived sediments, protecting coral reefs from sedimentation? For each topic, I summarize the general importance of the factor, present findings from a review of the literature on mangrove-reef systems, and highlight key areas in need of further research. Though some data exist to answer each of the aforementioned questions, the body of published literature is disparate, insufficient, and does not specifically examine the effects of mangrove loss on coral reefs. I propose a conceptual model of how areas of mangrove disturbance and resulting impacts on coral reefs are related and identify research priorities for topics on which the available data is insufficient to make predictions about the impacts of mangrove management and restoration decisions.

There is a paucity of research examining mangrove habitat changes following removal making it difficult to assess how mangrove transformation affects the immediate habitat. To address this gap in knowledge, I conducted a study examining how abiotic factors differ between intact and cleared mangrove areas and how these differences impact the biotic algal and herbivore communities. In Chapter 3, *Changes in biotic and abiotic processes following mangrove removal,* I report on this study conducted in Bocas del Toro, Panama. During this study, I observed a difference in the algal growth on coral reefs adjacent to intact versus cleared mangrove areas leading me to question whether this pattern was correlated with mangrove clearing.

In Chapter 4, *The impacts of mangrove deforestation on zooplankton communities*, I address one impact of anthropogenic mangrove disturbance on mangrove community structure, using zooplankton communities as a model. Here I examine whether zooplankton communities differ between intact mangrove areas and adjacent cleared mangrove areas. Determining how the zooplankton community differs between intact and cleared mangrove habitat will clarify the role that mangroves play in entraining zooplankton and larvae, and the importance of mangrove habitat as a settlement site. Light traps and plankton tows were used to quantify and compare meroplankton and

holoplankton communities between intact and cleared mangrove areas in Bocas del Toro, Panama. Taxon diversity, abundance and community structure were all examined. Although the mechanisms responsible for different community composition were not examined in this study, the results highlight an area in need of future research.

To address the unanswered question of whether and how abiotic and biotic changes in cleared mangrove areas impact adjacent reefs, I repeated and expanded upon the study I had conducted in Panama. This next study is presented in Chapter 5, *Anthropogenic mangrove removal: effects of disturbance to interface habitat on adjacent patch reefs*. This study was conducted at sites around Turneffe Atoll, Belize and included examination of sedimentation and algal growth on reefs adjacent to either intact or cleared mangrove areas. In addition, a test of the effects of light as a driving factor influencing algal growth in cleared mangrove areas was added using shades and shade controls.

In Chapter 6, *Mangrove-exported nutrients on coral reefs?,* I present a study examining the relative importance of mangrove-derived nutrients to adjacent systems and the open ocean. This study was conducted to shed light on the variable and, at times conflicting information in the published literature on this potentially important linkage between adjacent ecosystems. Earlier workers hypothesized that organisms and currents carry mangrove-derived nutrients to reefs (Odum and Heald 1972), but the data available are insufficient to confirm this transfer. Duarte and Cebrian (1996) report that an estimated 30% of mangrove-fixed carbon is exported to other systems. In contrast, however, others suggest that little of the mangrove-fixed carbon is transferred to reefs (Jennerjahn and Ittekkot 2002). To address these inconsistencies in the literature, and because only mobile reef species have previously been sampled to examine mangrove nutrient transfer, I sought to test whether mangrove-derived nutrients are incorporated into sessile coral reef-dwelling invertebrates in adjacent reef habitat. I also examined how distance from mangroves to reefs and clearing of mangroves affects this energy transfer. I employed carbon, nitrogen and sulfur stable isotopes as a tool to evaluate whether sessile

invertebrates: corals, sponges, a bivalve and feather duster worm, utilize mangrove-derived nutrients.

Finally, Chapter 7, *The protective capacity of intact mangroves: A case study from Hurricane Wilma and Tropical Storm Gamma in Belize*, examines the effect of two consecutive storm events, 2005 Tropical Storm Wilma (later a Category 5 Hurricane) and the subsequent Tropical Storm Gamma on the ecology of the reef-mangrove interface. Prior to the storm events, field equipment including herbivore cages, sediment traps, and shades, were deployed for the study presented in Chapter 5. The retention rate of field equipment following storm events provides a picture of how coastal protection changes following anthropogenic mangrove disturbance and the implications of continuing mangrove loss as storm frequency and intensity increase in parallel with changing climate.

In light of the rapid loss of mangrove habitat globally, it is important to consider how this habitat degradation will affect the immediate area, adjacent coral reefs and shorelines. Though it is assumed that mangrove forests are important to reef ecosystems, on many fronts the empirical knowledge necessary to test this idea is lacking. This dissertation adds to the overall understanding of how anthropogenic mangrove disturbance affects zooplankton communities, algal and herbivore communities, abiotic factors, and potentially mangrove-derived nutrient transfer to coral reefs. In addition to filling some of the existing gaps in our understanding, this synthetic project raises numerous questions and identifies future research priorities fundamental to successful mangrove conservation and management planning.

Chapter 2:

Habitat connectivity: A review of terrestrial to marine flows between mangrove forest and coral reef systems

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Abstract

Although many ecosystems are affected by changes to their neighbors, the influence of mangroves on adjacent coral reefs remains ambiguous. Mangrove forests and coral reefs are threatened tropical systems suspected of being linked via transfer of nutrients, species and other matter. I used a literature-based analysis to evaluate the hypothesis that a decline of mangrove habitat may have adverse effects on adjacent coral reefs and vice versa. My analysis revealed that there is substantial evidence of cross-system linkages between mangroves and reefs via nutrient subsidies, terrestrial sediment trapping, and complementary habitat utilization for reef-associated species. However, for each of these categories of influence, many questions remain unanswered, limiting our ability to make predictions about how disturbances to mangroves will affect adjacent coral reefs. Based on the available data, I model the probable relationship between mangrove degradation and adjacent reef impacts to provide a conceptual framework and testable hypotheses. Understanding these linkages will provide needed information to managers, landowners and communities for improved management and conservation of these threatened tropical marine systems.

Introduction

Transfers of organisms and materials across habitats and ecosystems are well known for many terrestrial and freshwater systems (Whitney and Smith 1998, Clausen et al. 2002), but are less well understood in marine systems (Helfield and Naiman 2001, Naiman et al. 2002, Schindler et al. 2003, Menge et al. 2003). Ecosystem subsidies moving in one direction, either from sea-to-land (Polis and Hurd 1996, Helfield and Naiman 2001, Naiman et al. 2002), or the inverse land-to-sea (Tea and Valiela 1976, Weinstein et al. 2000) have been examined in a variety of habitats. Very little research has focused on the bi-directional exchange between systems (but see Slim et al. 1996). Successful conservation and management requires consideration of how adjacent habitats outside of the conservation focus may affect the target habitat.

Interface habitats, those systems that lie at the boundary between aquatic and terrestrial zones (Bradstreet 1979, Stunz et al. 2002), are useful for looking at bi-

directional (aquatic-to-terrestrial-to-aquatic) subsidies. Mangrove forests are an ideal interface habitat to examine these flows because they span the terrestrial-intertidal-subtidal zones.

Mangrove forests have declined worldwide by over 35%, with half to three-quarters of mangrove area lost in parts of Southeast Asia (Field et al. 1998). The primary threats to mangrove forests are exploitation for lumber and increasingly, deforestation for agriculture, aquaculture and coastal construction (UNEP 1995, Ogden 2001, Valiela et al. 2001). In addition to the immediate alterations to mangrove habitat, mangrove loss may impact systems beyond the mangroves themselves because of linkages between mangroves and other tropical marine ecosystems such as coral reefs.

In light of the rapid loss of mangrove habitat globally, it is important to consider how this habitat degradation will affect coral reef systems. It is often assumed or asserted that mangrove forests are important to reef ecosystems (Ogden 1983; Cintron and Schaeffer-Novelli 1983), but what is the evidence? This review examines the available data and highlights the importance of considering the following questions relevant to current management and policy decisions: (1) Are flows between mangroves and reefs bidirectional or primarily unidirectional? (2) Are mangroves critical habitats in tropical coastal systems? (3) How important are mangroves to coral reefs as nutrient sources, nursery habitats, and sediment traps? (4) Is there a threshold size of mangroves necessary to provide ecosystem services to adjacent reefs? Alternatively, how large of a mangrove area can be disturbed before adjacent reefs are affected?

If mangrove disturbance directly affects reefs, mangrove loss may be an additional threat to reefs already suffering from multiple stresses including increasing seawater temperatures and solar radiation, overfishing, and sedimentation (UNEP 1995, White et al. 2000, Ogden 2001). Studies on mangrove-coral reef connectivity imply that mangroves may sustain coral reefs, thereby functioning as *keystone habitats* (Kloor 2000, Beck et al. 2004, Golbuu et al. 2005) in tropical coastal waters. *Keystone habitats* are those habitats whose influence on species diversity and ecosystem processes is much larger than predicted based on their abundance.

To evaluate the current state of empirical evidence for mangrove forest – coral reef connectivity, I surveyed the literature on three key topics. 1) How does nutrient transfer link mangrove and coral reef habitats? 2) How are mangroves and reefs linked via organism movement? What effects do these linkages have on community structure and ecosystem health on coral reefs? 3) To what extent are mangroves serving as a trap for terrestrial and mangrove-derived sediments, protecting coral reefs from sedimentation? For each topic, I: (a) summarize the general importance of the factor, (b) present findings from a review of the literature on mangrove-reef systems, and (c) highlight key areas in need of further research.

How mangrove disturbances or perturbations of varying sizes differentially impact adjacent tropical coastal systems is critical to management, but has not been studied. Building on the literature review, I propose a hypothetical model of how areas of mangrove disturbance and resulting impacts on coral reefs are related. I identify research priorities for topics on which the available data is insufficient to make predictions about the impacts of mangrove management and restoration decisions.

Methods

To examine the available evidence for mangrove forest – coral reef connectivity, I conducted a literature review by searching three databases/sources: Cambridge's Aquatic Sciences and Fisheries Abstracts from 1978-present; Web of Science from 1996-Present; and Google Scholars. In addition, I found items from the older literature, book chapters, and additional articles by reading the Literature cited sections of the papers I identified in my initial database search. I searched in the above databases by using key words including mangrove(s), coral reef(s), sediment(ation), nutrient exchange, stable isotope, organism movement, reef fish. The list of papers and chapters included is evident in the Literature cited section below.

Results

Connections via nutrient transport

General importance. Although nutrient transfer across many adjacent marine ecosystems is well known, coral reefs are generally assumed to be relatively closed systems (Duarte and Cebrian 1996). However, few natural systems are closed in terms of nutrient dynamics; for example, terrestrial forests receive marine-derived nutrients carried upstream by anadromous fishes (Helfield and Naiman 2001), and intertidal systems utilize open-ocean nutrients delivered by abiotic (upwelling currents) and biotic (fish and invertebrate movement) pathways (Menge et al. 1997a, Menge et al. 1997b).

Recognizing allochthonous sources is essential to understanding nutrient connectivity among habitats. Recent studies suggest such connectivity exists between mangroves and coral reefs and, therefore, that tropical reefs are more open than previously considered (Sheaves and Molony 2000, Nagelkerken 2000a, Nagelkerken and van der Velde 2004b). However, we lack a comprehensive understanding of the extent and significance of nutrient transfer between mangrove forest and coral reef habitats and how diversity and productivity in one system may be affected by changes to another.

Findings of review. Though nutrient cycling on coral reefs seems to be fairly closed (Duarte and Cebrian 1996), studies employing stable isotope and gut content analyses (Sheaves and Molony 2000; de la Moriniere et al. 2003; Chittaro et al. 2004) indicate pathways of nutrient transfer between mangroves and reefs (Table 2.1). This includes evidence that several reef species feed in adjacent habitats including mangrove forests, seagrass beds, sand and mud flats, and channel systems (John and Lawson 1990, Rooker and Dennis 1991). These individuals are believed to import allochthonous nutrients into reef systems after feeding elsewhere. For instance, mangrove red snapper (*Lutjanus argentimaculatus*) depend heavily on Sesarmid crabs as a food source; these crabs live in mangroves and acquire up to 80% of their nutrients from mangrove detrital leaves (Sheaves and Molony 2000). Mangrove red snapper then spawn on coral reefs. It is thought that this habitat shift leads to a transfer of some portion of uptaken mangrove-derived nutrients out of the mangrove forest when the snapper migrates (Table 2.1).

Table 2.1. Species that feed in mangroves and may transfer mangrove-derived nutrients to coral reef habitat via movement or as a food source for reef-associated organisms feeding in mangroves.

Species	**Common name**	**Food items**	**Location**	**Research tool**
Acanthurus chirurgus	Doctorfish	Filamentous algae, macroalgae[1]	Curacao, Netherlands Antilles	Gut content; stable isotope
Epinephelus coioides	Orange-spotted grouper	Sesarmid crabs[2]	NE Australia	Gut content; stable isotope
Epinephelus malabaricus	Malabar grouper	Sesarmid crabs[2]	NE Australia	Gut content; stable isotope
Haemulon flavolineatum	French grunt	Tanaids[3]	Curacao, Netherlands Antilles	Gut content
Haemulon chrysargyreum	Smallmouth grunt	Taneids, ostracods[1]	Curacao, Netherlands Antilles	Gut content; stable isotope
Haemulon sciurus	Bluestriped grunt	Tanaids[3, 4]	Curacao, Netherlands Antilles	Stable isotope
Lutjanus apodus	Schoolmaster	Decapods[3, 4]	Curacao, Netherlands Antilles	Stable isotope
Lutjanus argentimaculatus	Mangrove red snapper	Sesarmid crabs[2]	Queensland, AU Albatross Bay, AU	Gut content; stable isotope
Metapenaeus brevicornis	Yellow prawn	Mangrove detritus[5]	West Coast, Malaysia	Stable isotope
Mulloidichthys martinicus	Yellow goatfish	Juvenile feeding in mangroves as seagrass resident[1]	Curacao, Netherlands Antilles	Gut content; stable isotope
Ocyurus chrysurus	Yellowtailed snapper	Tanaids, Decapods, Mysids[1,3,4]	Curacao, Netherlands Antilles	Gut content; stable isotope
Penaeus merguiensis	Banana prawn	Mangrove detritus[5]	West Coast, Malaysia	Stable isotope
Penaeus penicillatus	Redtail prawn	Mangrove detritus[5]	West Coast, Malaysia	Stable isotope

Table 2.1. (Continued) Species that feed in mangroves and may transfer mangrove-derived nutrients to coral reef habitat via movement or as a food source for reef-associated organisms feeding in mangroves.				
Species	**Common name**	**Food items**	**Location**	**Research tool**
Polymesoda (Geloina) erosa	Mangrove cockle	Mangrove tree carbon[5]	West Coast, Malaysia	Stable isotope
Sesarma spp.	Sesarmid crabs	Mangrove detritus[5]	West Coast, Malaysia	Stable isotope

[1] Nagelkerken and van der Velde 2004b, [2]Sheaves and Molony 2000, [3]Nagelkerken and van der Velde 2004a, [4]Nagelkerken et l. 2000a, [5]Rodelli et al. 1984

Duarte and Cebrian (1996) report that an estimated 30% of mangrove-fixed carbon is exported to other systems. A portion of this carbon is utilized by reef-associated fish species that visit mangroves to feed (de la Moriniere et al. 2003b), yet we do not know how much of this carbon is exported to inshore habitats or lost to the open ocean. Some research documents nutrient contributions from seagrass beds to coral reefs via fishes that migrate daily between the two habitats to feed (Meyer et al. 1983). It is hypothesized (Odum and Heald 1972) that similar processes are carrying mangrove-derived nutrients to reefs, but there is no empirical data available to confirm this transfer. If reef-associated fishes take up some portion of the 30% of exported mangrove carbon, it is unknown how much of this productivity is incorporated into adjacent reef ecosystems. In addition to nutrients and carbon fixed by mangroves themselves, there is a suite of mangrove-associated primary producers including cyanobacteria and microalgae that contribute to tropical coastal food webs. The mangrove detritus-associated microfauna is proposed to be an important component of the mangrove-coral reef food web (Rivera-Arriaga et al. 2003). Though these mangrove-associated taxa make mangroves one of the most productive marine ecosystems in terms of fixed carbon, other work suggests that little of the mangrove-fixed carbon is transferred to reefs. Jennerjahn and Ittekkot (2002) conclude that, although half of the mangrove leaf litter is exported to the coastal ocean, this mangrove carbon is exported only locally and is a minor contributor to higher trophic levels. The remainder of the leaf litter is accumulated in mangrove sediment or remineralized within mangrove forests (Jennerjahn and Ittekkot 2002). This range of data and interpretations on mangrove-derived nutrient uptake in allochthonous systems represents a paradox and the question remains whether mangrove nutrients are or are not incorporated in adjacent systems and further offshore.

Research priorities. Mangrove-derived nutrients are indirectly utilized by a variety of mobile reef-resident species, yet it is unknown whether this food source is providing essential nutrients to consumers. If this is the case, determining whether mangrove removal will reduce the abundance and survival of reef-associated taxa (Fry and Smith 2002, Fry and Ewel 2003) is a top research priority.

While these few studies suggest that there is some nutrient exchange between reefs and mangroves, we currently do not know at which trophic levels mangrove-derived nutrients are incorporated into reef systems or the significance of these mangrove-derived nutrients to reef productivity and essential nutrient availability. Nutrient delivery may be important to a subset of reef species, but our ability to predict changes in productivity and diversity on reefs in various scenarios of mangrove disturbance is limited because of insufficient research on transport pathways (via organisms versus water movement) and incorporation rates.

The threshold size of mangrove clearing above which we would expect to see a decline in mangrove nutrient inputs to reefs is another research priority. Identifying uptake of mangrove-derived nutrients in organisms in adjacent systems will increase our ability to predict the effects of human disturbance to mangroves on functioning of adjacent systems. Without knowing the composition of sessile and sedentary reef species that incorporate mangrove-derived nutrients, we lack a comprehensive understanding of the importance mangrove nutrient dynamics play on coral reefs. We also lack the ability to predict potential changes in reef nutrients following mangrove disturbance.

Connectivity through organism movement

There are various ways in which organisms connect habitats and this is frequently related to how they utilize the different habitats. Organisms that make ontogenetic habitat shifts utilize multiple habitats sequentially during their life cycle and connect these habitats through their movement (Steneck et al. 2002, Halpern 2004b). Other organisms utilize multiple habitats concurrently, on a daily or seasonal basis, shifting between ecosystems to feed or hunt or with changing seasonal variables (Sheaves and Molony 2000; de la Moriniere et al. 2003; Sheridan and Hays 2003). These two mechanisms of habitat linkage – ontogenetic habitat shifts and multiple habitat utilization daily or seasonally – are sufficiently different to warrant separate examination here.

Ontogenetic habitat shifts

General importance. Many adjacent or linked habitats are known to influence each other via organism movement resulting from ontogenetic habitat shifts (e.g. estuaries and rocky reefs or kelp forests [Steneck et al. 2002, Halpern 2004b]; streams and open ocean [Naiman et al. 2002, Schindler et al. 2003]). For many marine organisms, adult and larval abundance are decoupled by long-distance dispersal of larvae on ocean currents, whereas for short distance dispersers adult populations and settlement are linked. Since different taxa have varying dispersal distances as juveniles (Shanks et al. 2003, Dorenbosch et al. 2004, Kieckbusch et al. 2004, Kinlan et al. 2005), the proximity of suitable nursery habitat affects community composition on adjacent reefs.

Some evidence suggests that mangrove forests, seagrass beds, sand and mud flats are among the suite of coastal marine habitats serving as nursery areas, habitat where species spend their juvenile stage before migrating to adult habitat. In a review of nursery habitats, Beck et al (2001) suggest that nursery habitats with high abundance of juvenile individuals may be sinks if juvenile growth or survival is lower than in adjacent habitats and are not true nurseries if they fail to serve as a source for adult habitats. The ongoing debate over criteria for nurseries and whether certain areas qualify as nursery habitat (Beck et al. 2001) necessitates further research into this role for mangroves.

Findings of review. A survey of the mangrove-coral reef literature reveals that a variety of coral reef-resident species are purported to be facultative or obligate users of mangrove habitat for some life stage (Table 2.2). Mumby et al. (2004) found that coral reef communities near mangroves had higher biomass of commercially important species than reefs with little or no proximal mangrove habitat supporting the nursery habitat theory for mangroves. The area of mangroves may also be important for certain reef-associated species (Halpern 2004a).

Nursery habitats are not all equal. Robertson and Duke (1987) and Blaber et al. (1989) found that species composition and abundance varied by tropical estuarine habitat type (seagrass beds, mangrove forests, sand flats, etc.) and vegetation cover (tall vs. short seagrass). Several studies have identified characteristics that make mangroves ‘preferable’ nursery or juvenile habitat, such as shading, availability of smaller prey

Table 2.2. Species that utilize both mangrove and coral reef habitat (obligate - O, facultative - F, or unknown - U)

Species	**Common name**	**Use of mangroves**	**Locations**	**Obligate vs. facultative mangrove residents**
Abudefduf saxatillis	Sergeant major	Juvenile and adult habitat [1,2]	La Parguera, Puerto Rico Andros Island, Bahamas	F
Acanthurus bahianus	Ocean surgeonfish	Juvenile feeding habitat (while seagrass resident) [3], late juvenile habitat[1]	Curacao, Netherlands Antilles La Parguera, Puerto Rico	U
Acanthurus chirurgus	Doctorfish	Juvenile feeding habitat (while seagrass resident) [3, 4]	Curacao, Netherlands Antilles	U
Apogon ceramensis	Ceram cardinalfish	Unknown/not specified[5]	Queensland, AU	U
Arripis trutta	Eastern Australian salmon	Unknown/not specified [6]	Victoria Coast, AU	F
Atherinomorus stipes	Hardhead silverside	Juvenile and adult habitat [2]	Andros Island, Bahamas	U
Canthigaster rostrata	Sharpnose puffer	Juvenile and adult habitat [2]	Andros Island, Bahamas	F
Caranx hippos	Crevalle jack	Late juvenile habitat[1], feeding ground for juveniles[7]	La Parguera, Puerto Rico Gulf of Guinea, West Africa	U
Caranx rubber	Bar jack	Juvenile and adult habitat [2]	Andros Island, Bahamas	U
Caranx sexfasciatus	Bigeye trevally	Juvenile habitat[8]	Albatross Bay, AU	U
Chaetodon capistratus	Four eyed butterflyfish	Ontogenetic habitat shift-juvenile habitat[1, 2, 4]	Curacao, Netherlands Antilles Andros Island, Bahamas	U

Table 2.2. (Continued) Species that utilize both mangrove and coral reef habitat (obligate - O, facultative - F, or unknown - U)				
Species	**Common name**	**Use of mangroves**	**Locations**	**Obligate vs. facultative mangrove residents**
Chelonodon patoca	Milkspotted puffer	Juvenile habitat[10]	Queensland, AU	O
Coryphopterus punctipectophorus	Spotted goby	Adult habitat[2]	Andros Island, Bahamas	U
Coryphopterus glaucofraenum	Bridled goby	Adult habitat [2]	Andros Island, Bahamas	U
Encrasicholina devisi	Devi's anchovy	Juvenile habitat[10]	Queensland, AU	F
Epinephelus coioides	Orange-spotted grouper	Juvenile feeding habitat[11]	NE Australia	U
Epinephelus malabaricus	Malabar grouper	Juvenile feeding habitat[11]	NE Australia	U
Epinephelus striatus	Nassau grouper	Juvenile habitat[2]	Andros Island, Bahamas	U
Eubalichthys mosaicus	Mosaic leatherjacket	Unknown/not specified [6]	Victoria Coast, AU	U
Gerres argyreus	Common mojarra	Unknown/not specified[5]	Queensland, AU	U
Gerres cinereus	Yellow-fin mojarra	Juvenile habitat[12, 4]	U.S. Virgin Islands	O
Haemulon chrysargyreum	Smallmouth grunt	Juvenile feeding habitat (while seagrass resident) [3]	Curacao, Netherlands Antilles	U
Haemulon flavolineatum	French grunt	Ontogenetic habitat shift-juv. habitat[4, 9, 13, 14]; Juv. feeding habitat[3], late juv. habitat[1]	Curacao, Netherlands Antilles La Parguera, Puerto Rico	O

Table 2.2. (Continued) Species that utilize both mangrove and coral reef habitat (obligate - O, facultative - F, or unknown - U)

Species	Common name	Use of mangroves	Locations	Obligate vs. facultative mangrove residents
Haemulon parra	Sailors choice	Ontogenetic habitat shift-juvenile habitat[9]; Juvenile and adult habitat [2]	Curacao, Netherlands Antilles Andros Island, Bahamas	O
Haemulon plumieri	White grunt	Nursery habitat[13], late juvenile habitat[1]	Curacao, Netherlands Antilles La Parguera, Puerto Rico	O
Haemulon sciurus	Bluestriped grunt	Ontogenetic habitat shift-juvenile habitat[2,4, ,9, 13,14]; Juvenile feeding habitat[3], adult feeding habitat[15], late juv. habitat[1]; Juvenile and adult habitat [2]	Curacao, Netherlands Antilles Belizean Barrier Reef La Parguera, Puerto Rico Andros Island, Bahamas	O
Harengula jacuana	Scaled sardine	Juvenile and adult habitat[16]	Everglades Ntl. Park, FL[15]	U
Harengula humeralis	Redear sardines	Juvenile and adult habitat[16]	Everglades Ntl. Park, FL[15]	U
Jenkinsia lamprotaenia	Dwarf herring	Juvenile and adult habitat[16]	Everglades Ntl. Park, FL[15]	U
Lutjanus analis	Mutton snapper	Juvenile and adult habitat[2]	Andros Island, Bahamas	U
Lutjanus apodus	Schoolmaster	Ontogenetic habitat shift-juvenile habitat[9, 12, 13, 14]; Juvenile feeding habitat[3, 17], adult feeding habitat[3] small juvenile habitat[1], juvenile and adult habitat [2]	Curacao, Netherlands Antilles Belizean Barrier Reef U.S. Virgin Islands Andros Island, Bahamas	O

Table 2.2. (Continued) Species that utilize both mangrove and coral reef habitat (obligate - O, facultative - F, or unknown - U)

Species	**Common name**	**Use of mangroves**	**Locations**	**Obligate vs. facultative mangrove residents**
Lutjanus argentimaculatus	Mangrove red snapper	Juvenile feeding habitat[11,10, 8]	Queensland, AU Albatross Bay, AU	O
Lutjanus cyanopterus	Cubera snapper	Juvenile and adult habitat[2]	Andros Island, Bahamas	U
Lutjanus griseus	Gray snapper	Small juvenile habitat[1], juvenile and adult habitat [2]	La Parguera, Puerto Rico Andros Island, Bahamas	U
Lutjanus mahogoni	Mahogany snapper	Ontogenetic habitat shift[9]-juvenile habitat[9]; late juvenile habitat[1]; adult habitat[2]	Curacao, Netherlands Antilles La Parguera, Puerto Rico Andros Island, Bahamas	O
Lutjanus russelli	Russell's snapper	Juvenile habitat[8]	Albatross Bay, AU	U
Lutjanus synagris	Lane snapper	Juvenile and adult habitat[2]	Andros Island, Bahamas	U
Mulloidichthys martinicus	Yellow goatfish	Juv. feeding in mangroves while seagrass resident[3]	Curacao, Netherlands Antilles	U
Ocyurus chrysurus	Yellowtailed snapper	Ontogenetic habitat shift-juv. habitat[13, 14, 17]; Juv. feeding habitat[3], late juv. habitat[1]	Curacao, Netherlands Antilles Belizian Barrier Reef La Parguera, Puerto Rico	F
Panulirus argus	Spiny lobster	Mangrove juvenile habitat[18]	S. Belize	F
Pranesus endrachtensis	Eendracht Land silverside	Juvenile habitat[10]	Queensland, AU	O
Scarus guacamaia	Rainbow parrotfish	Ontogenetic habitat shift-juvenile habitat[9, 13]	Curacao, Netherlands Antilles Belizean Barrier Reef	O

Table 2.2. (Continued) Species that utilize both mangrove and coral reef habitat (obligate - O, facultative - F, or unknown - U)

Species	Common name	Use of mangroves	Locations	Obligate vs. facultative mangrove residents
Scarus iserti	Striped parrotfish	Nursery habitat[13]	Belizean Barrier Reef	O
Scomberoides lysan	Doublespotted queenfish	Juvenile feeding habitat[10]	Queensland, AU	O
Siganus guttatus	Orange-spotted spinefoot	Juvenile habitat[5]	Queensland, AU	U
Sparisoma chrysopterum	Redtail parrotfish	Ontogenetic habitat shift-juvenile habitat[9]	Curacao, Netherlands Antilles	O
Spheroides testudineus	Checkered puffer	Juvenile and adult habitat[2]	Andros Island, Bahamas	U
Sphyraena barracuda	Great barracuda	Ontogenetic habitat shift-juv. habitat[9]; adult feeding at mangrove-seagrass interface[3], small juv. habitat[1]	Curacao, Netherlands Antilles La Parguera, Puerto Rico	O
Stegastes leucostictus	Beaugregory	Juvenile and adult habitat[2]	Andros Island, Bahamas	U
Stegastes planifrons	Threespot damselfish	Adult habitat[2]	Andros Island, Bahamas	U
Stegastes variabilis	Cocoa damselfish	Juvenile and adult habitat[2]	Andros Island, Bahamas	U

[1]Rooker and Dennis 1991, [2]Layman and Silliman 2002, [3]Nagelkerken and van der Velde 2004a, [4]Nagelkerken et al. 2000b, [5]Robertson and Duke 1987, [6]Hindell and Jenkins 2004), [7]John and Lawson 1990, [8]Blaber et al. 1989), [9]Nagelkerken and van der Velde 2002, [10]Robertson and Duke 1990, [11]Sheaves and Molony 2000, [12]Halpern 2004b, [13]Mumby et al. 2004), [14]de la Moriniere et al. 2003b, [15]Nagelkerken et al. 2000a, [16]Thayer et al. 1987, [17]de la Moriniere et al. 2004, [18]Acosta and Butler 1997

items, lower predator densities, and increased cover resulting in lower predation risk (Laegdsgaard and Johnson 2001, de la Moriniere et al. 2003a, de la Moriniere et al. 2004). Research indicates that growth triggers ontogenetic habitat shifts from mangrove forests to seagrass beds or reefs due to a shift in diet to larger or different prey species, reproductive maturity, or changes in predation risk and access to cover (de la Moriniere et al. 2003a). These findings suggest that remaining intact estuarine habitat of one type (such as seagrass beds) may not compensate for loss of another habitat type (such as mangroves).

A number of fishes are reported to move from nursery habitats in mangrove forests to adult habitats on coral reefs (Nagelkerken et al. 2002, Nagelkerken and van der Velde 2002). Some of these species are found exclusively in mangroves during their juvenile stage (obligate) and others utilize various nursery habitats including mangroves (facultative) (Halpern 2004a) (Table 2.2). In the absence of mangrove habitat in close proximity to coral reefs, the adult density of these obligate species in adjacent reef habitat is reportedly much lower (Dorenbosch et al. 2004, Mumby et al. 2004). Even among species for which mangrove habitat is facultative as a nursery area, lower densities have been observed on nearby reefs when mangroves are not in close proximity (Halpern 2004a, Mumby et al. 2004).

Given the number of predatory and herbivorous reef-resident species that appear to utilize mangrove habitat as nursery grounds and juvenile habitat (Table 2.2), as mangrove forests continue to decline, a parallel decline in diversity and abundance of mobile species on adjacent coral reefs is predicted (Layman and Silliman 2002). For example, Mumby et al. (2004) found juvenile *Scarus guacamaia* exclusively in mangrove habitat. Adult *S. guacamaia* are large mobile reef herbivores important to Caribbean reef systems. Mumby et al. (2004) suggest that loss of mangrove habitat may lead to a disappearance of *S. guacamaia* on adjacent reefs. Decline of such herbivorous reef fishes due to loss of juvenile habitat is predicted to result in increases in reef algal cover and decreases in coral cover (Lirman 2001, Jompa and McCook 2002).

Research priorities. Though correlative evidence exists supporting the mangroves-as-nursery hypothesis (Mumby et al. 2004, Halpern 2004a), further

experimental research using mark-and-recapture, caging, and tagging studies are needed to empirically test and confirm this role. Additional examination of reef-associated organism movement into and out of mangrove habitat, differing juvenile growth rates in mangroves versus alternative inshore nursery areas, and studies on how organisms respond to degraded mangroves in terms of foraging and growth would provide important evidence of how coral reef community structure may change following alteration of or human disturbance to adjacent, linked mangroves. Further experimental research on the effects of mangrove patch size, condition and distance to reefs on mobile reef communities will further clarify potential impacts of mangrove removal on these communities. The threshold area and proximity of intact mangroves to maintain reef-mangrove organism movement is as yet unknown.

Ontogenetic habitat shifts have been examined for a variety of commercially important reef species (see Table 2.2), but such transitions for other fish and invertebrate taxa are less studied (Clynick and Chapman 2002, Hindell and Jenkins 2004, Kieckbusch et al. 2004). Further study of prey species movement will provide a more comprehensive understanding of the breadth of impacts that mangrove disturbance may have on coral reef systems and resident communities (Weerts and Cyrus 2002).

Daily and seasonal movement

General importance and Findings of review. Habitats may also be linked via species that concurrently or seasonally utilize multiple habitats for different functions (i.e. feeding, spawning, or residence habitats). Using a combination of gut content observations and stable isotope analysis, several studies have identified mangroves as important feeding habitats for various taxa of fish (Tables 2.1and 2.2) (Sheaves and Molony 2000; de la Moriniere et al. 2003; Sheridan and Hays 2003; Nagelkerken and van der Velde 2004; Nagelkerken and van der Velde 2004) with some seasonal variability (Rooker and Dennis 1991).

A number of commercially important Caribbean reef fishes are coral reef residents during their adult stage, but, as juveniles, utilize mangrove forests for daytime shelter and a combination of mangroves and adjacent seagrass beds as nocturnal feeding

grounds (see Table 2.2) (Nagelkerken and van der Velde 2004a). Some adult reef-resident species also migrate to mangrove and seagrass habitat nocturnally to forage (Nagelkerken et al. 2000a). Thayer et al. (1987) found that mangrove fish density was 35 times that in adjacent inshore habitat, proposing greater shelter in mangroves (compared with adjacent coastal feeding grounds) as a possible cause.

Research priorities. Species that use different habitats for feeding grounds versus shelter contribute to the community structure of both habitats. Though mangrove removal is predicted to affect its functioning as feeding grounds, how consumer use of mangroves changes following mangrove degradation is not well known. Therefore, we are unable to predict the effects of mangrove disturbance on consumer populations in adjacent systems. Additionally, the maximum distance that consumers will transit to travel between mangrove and reef habitats has not been assessed for most taxa.

It remains unconfirmed whether removal of mangrove feeding and nursery habitat will have a direct effect on reef-residents by changing the abundance of consumers in mangroves and what indirect effects there will be on their prey and/or predators on nearby coral reef. There is potential that mangrove removal will affect reef resident species and communities as suggested by Mumby et al. (2004). If so, such shifts in the community structure of mobile reef species may have cascading effects on coral community composition and diversity.

Buffering marine systems from terrestrial sedimentation

General importance. As a coastal habitat, mangroves are believed to fulfill an important role buffering downstream marine habitats including seagrass beds and coral reefs from terrestrial sedimentation (e.g. UNEP 1995; Golbuu et al. 2003). External sediment trapping is important to habitat integrity in coastal marine systems because high sedimentation loads can suffocate corals and associated sessile invertebrates leading to transitions from coral-dominated to algal dominated reefs (Golbuu et al. 2003). Removal of biotic sediment trap buffers has additional implications as sea levels rise and coastal areas are increasingly exposed to wave action and erosion.

Findings of review. In addition to trapping land-based sediments, mangroves trap suspended sediment brought in from coastal waters during high tides (Furukawa et al. 1997; Wolanski et al. 1998). Though an earlier study indicates that mangroves are more efficient at trapping riverine clay than as net sediment trappers (Wolanski et al. 1998), more recent research attributes a greater role in sediment trapping to mangroves.

Sediment trapping in mangroves is related to root structure complexity (Kathiresan 2003) as well as tidal dynamics (Mazda et al. 2002; Victor et al. 2004) and wind (Wolanski et al. 1998). Therefore, degraded mangrove forests may be less efficient at trapping sediment if root structure and complexity are altered. Kathiresan (2003) has identified varying efficiencies in sediment trapping among zones with the *Avicennia-Rhizophora* interface zone as the most efficient, trapping 30% of suspended sediment carried in at high tide. Estimates vary greatly on the amount of sediment trapped by mangroves, but research indicates 15-40% of riverine sediment is trapped by estuarine mangroves when not degraded (Kathiresan 2003; Victor et al. 2004). On the other hand, degraded mangroves trap 1-10% *less* sediment than intact, undegraded mangrove systems (Brinkman et al. 2005).

Despite the considerable sediment trapping ability of mangroves, Victor et al. (2004) point out that in areas of extensive land transformation and resultant sedimentation, the routine trapping of sediment by mangroves may be insufficient to protect coral reefs. Furthermore, Mazda et al. (2002) surmise that not only the fringing forest mangroves, but inland mangroves are necessary to prevent coastal erosion.

Research priorities. It is unknown whether merely protecting mangroves along the coastal edge without addressing upstream land-use and inland mangrove condition will be sufficient to protect coastal marine habitats. The threshold size (width and length) of mangrove disturbances above which land-based sedimentation impacts are seen on reefs is not known. Effective management of mangrove forests as sediment buffers for reefs requires further research on buffering ability and effects of land development on the sediment-trapping function.

Conservation Implications – Community structure and ecosystem health on reefs

Bi-directional habitat connectivity (Beier and Noss 1998, Webster et al. 2002), has not been well documented for tropical coastal systems (Mora and Sale 2002, Appeldoorn et al. 2003). Some evidence exists for the role of ontogenetic and daily/seasonal movement of organisms between mangrove and coral reef habitats in affecting nutrient transfer and community structure in each habitat. Mangrove structure and complexity may protect coastal marine systems from sedimentation and resultant suffocation. However, we need to know more about such interactions to effectively manage and protect these globally threatened coastal marine habitats. If mangrove habitat is a keystone habitat in tropical coastal systems, its loss may dramatically affect coral reefs due to the hypothesized degree of connectivity.

Is there a critical size above which mangrove removal triggers significant downstream impacts? What are the appropriate units of area at which a threshold is surpassed? And how do various types of degradation (thinning, trimming, clearcutting, etc.) trigger cascading effects? For example, mangrove habitat conversion may have direct and indirect effects on algal growth and coral cover on nearby reefs as light regimes and herbivore composition or abundance changes (Granek In Review). How effects will differ based on variations in size of mangrove clearing as well as differing tidal exchange, current directions and amount of water circulation is also unknown.

I suggest a hypothetical relationship between mangrove disturbance and reef impacts (Figure 2.1) based on existing literature and personal experience in mangrove ecosystems. We might expect that very small clearings (e.g. 10s of meters) have little effect, but that above some size (maybe 100s to 1000s of meters), we would expect to see increasing effects of mangrove disturbance on adjacent reefs (E.G. pers.obs.). Sedimentation is predicted to impact reefs when only smaller patch clearings occur, whereas changes in nutrient cycling is likely detectable only in areas impacted by larger (perhaps kms) clearings and on reefs closer to mangroves (see Jennerjahn and Ittekkot 2002). Effects on reef fish and invertebrate communities are predicted from intermediate size clearings, with some variability due to different home ranges and motilities of various species (see Mumby et al. 2004; Halpern 2004a). The threshold area (of

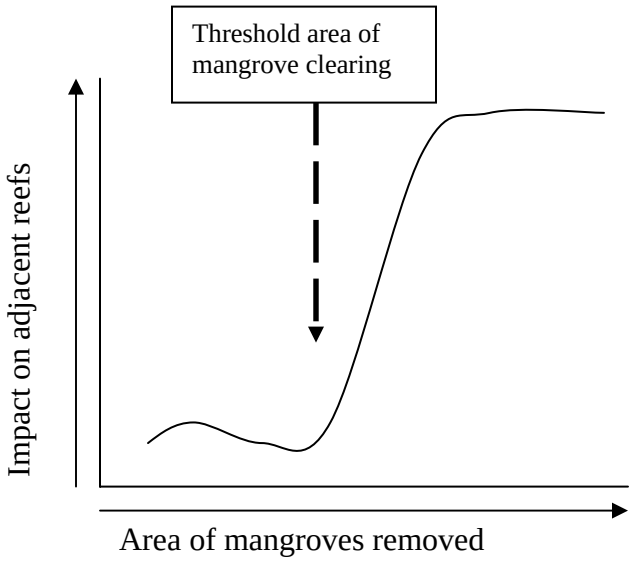

Figure 2.1. Available data and previous observations following mangrove degradation lead us to predict that impacts on adjacent reefs occur after a threshold size of mangrove clearings has occurred. This threshold area of removed mangroves and the rate of increased impact on adjacent reefs will likely vary based on the type of reef effect (sedimentation, community composition, nutrient availability, etc.).

mangrove clearing) and the slope of increased impacts on adjacent reefs will presumably vary depending on the factor (sedimentation, nutrients, biotic community) and any interactions among these factors of interest (Figure 2.1). Since we have few data to facilitate a determination of the threshold size of mangrove clearings above which a manager, land owner or community might expect to see effects on reef sedimentation, nutrient availability or community composition (Figure 2.1) testing this model to identify these thresholds is a top research priority.

Conclusions and Future Directions

I examined several extant assumptions commonly made about mangrove forest – coral reef connectivity. The literature documents specific evidence for some components of these assertions. For example, that mangrove removal may lead to reduced nutrient export due to loss of primary production (Jennerjahn and Ittekkot 2002) is supported, but it is unclear how this might affect reefs. There may be changes in species composition both in mangroves and reefs resulting from changing habitat structure for juveniles and food availability for adult consumers (Mumby et al. 2004), but there is no empirical evidence that this happens. Nor are the impacts on community composition on reefs known. Mangrove removal eliminates the zone of water filtration and sediment trapping created by intact habitat (Golbuu et al. 2003); but it is not known how large of a clearing or how proximal to mangroves the clearing must be to lead to reduced water quality and increased sediment cover on adjacent reefs.

Identifying what is known and what holes exist in our understanding of mangrove-coral reef connectivity allows us to identify research priorities. Determining the threshold area of mangrove clearings above which effects of this disturbance impact coral reefs is priority information for managers, policy makers and restoration planners. Mangroves may be keystone tropical habitats sustaining coral reefs (via nutrient input, species abundance, feeding grounds for multiple reef species, and filters for sedimentation), but further research into their roles as nutrient sources, nursery habitats and sediment traps is imperative to determine the verity of this assumption. How close and how extensive must mangroves be to reefs to allow for inter-habitat organism

movement? Do degraded mangroves provide similar ecosystem services to reef systems as do intact mangroves? To what extent do mangrove nutrients contribute to nutrient availability on reefs? On which habitats do mangrove prey species depend during various life stages? Testing assumptions of the model presented in Figure 2.1 will clarify the degree of connectivity between mangrove and reef systems and answer some of these questions.

The multiple unanswered research questions identify critical gaps in the current knowledge of mangrove forest-coral reef systems and this knowledge is necessary to improve mangrove-reef management and conservation. In the absence of this information, it is important to invoke the precautionary principle when writing policy and creating management plans, given the limited data we do have illustrating some connections. This approach highlights the value of ecosystem-based management strategies that incorporate adjacent habitat types to protect the various ecosystem functions they fulfill (Browman and Stergiou 2004).

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Chapter 3:

Changes in biotic and abiotic processes following mangrove removal

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Abstract

Human disturbance to natural systems can alter ecosystem productivity through direct effects on abiotic factors such as nutrient supply or through changes in biotic factors such as consumer density. The extent to which human impacts are mediated through abiotic and biotic factors is related to disturbance type and has important implications for ecosystem management. Mangrove forests, important tropical coastal habitats, are in decline worldwide primarily due to removal by humans. I examined the relative importance of biotic and abiotic mechanisms on algal productivity following red mangrove (*Rhizophora mangle L.*) removal in Panama. In this first study examining community effects of mangrove disturbance, I found that mangrove removal areas had higher algal biomass and richness than intact mangrove areas. This increase in algal biomass and richness was due to changes in the abiotic factors of light intensity, temperature, sedimentation, but not due to the biotic factor of fish herbivory following removal. Additionally the algal and cyanobacterial genera dominating mangrove removed areas are competitors with coral for space on reefs and include *Dictyota* sp., *Acanthophora* sp., *Spyridea* sp. and the cyanobacterium *Lyngbya* sp.; these taxa differed from algal genera in intact mangrove areas. *Synthesis and applications:* Removal of dominant mangroves changes biotic and abiotic processes inshore and may lead to an increased supply of algal spores from cleared mangrove areas. This may promote overgrowth on inshore tropical coastal habitats such as coral reefs and seagrass beds by fast-growing algae and cyanobacteria compounding increased reef sedimentation and reduced habitat for juvenile reef species.

Introduction

Human disturbance has consequences for ecosystem functioning via changes to physical or abiotic conditions (e.g. light, temperature, water, nutrients) as well as species interactions or biotic factors (e.g. predation, herbivory, competition). The relative importance of these factors depends on the disturbance frequency and intensity, the type of disturbance (i.e. removal of strongly interacting species such as keystone and dominant

species *sensu* Power et al. 1996 or weakly interacting species with little community influence), and the resilience of the ecosystem (Hughes 2005). The relative importance of biotic versus abiotic mechanisms in ecosystem processes can be strongly controlled by such disturbances (Connell 1975; Menge and Sutherland 1976; Menge 1995; Nielsen 2001). However, this conceptual information has not been sufficiently applied in mangrove systems to assess mechanisms by which human disturbance affects community structure and the implications for management, conservation and restoration of impacted systems (Katharensis 2004). Management and restoration strategies are dependent on whether the species removed is a keystone or dominant species and the resulting direct and indirect effects on both biotic and abiotic factors. For example, successful restoration of forest understory following clearcutting, recovery of coral cover on reefs overgrown by macroalgae, or re-establishment of predatory fish upstream of human-made barriers requires an understanding of how the type of human disturbance contributes to shifts in ecosystem functioning (Power et al. 1996).

Removal of a keystone species has a direct biological effect on other species, which, in turn, indirectly affects physical characteristics such as space. For example, removal of the sea star *Pisaster ochraceus* from the rocky intertidal zone caused an increase in abundance of the mussel *Mytilus californianus* (a biotic effect) leading to an indirect effect of space reduction (a physical/abiotic effect) (Paine 1966, 1974). On the other hand, removal of a dominant such as an ecosystem engineer (organism that modifies its own habitat) or a structure-creating species has a direct physical effect on its habitat, leading to an indirect biological effect on other species in the community (Hacker and Gaines 1997; Bruno et al. 2003). For example, clearcutting a forest precipitates physical changes (light, temperature, nutrient shifts) that affect which early successional species colonize that area (a biological consequence) (Messier 1993). Identifying the type of human disturbance and the category or guild of species affected is important to understanding the cascading effects that will result. I use this conceptual framework of species roles and impacts of their removal to understand consequences of human alteration of a globally imperiled ecosystem, tropical mangrove forests.

Tropical coastal marine ecosystems including mangrove forests are severely threatened by anthropogenic alteration. Mangrove forests have declined worldwide by at least 35%, primarily due to human disturbance (Field et al. 1998). These disturbances include cutting and clearing swaths of mangroves for lumber, clearing and filling mangrove areas for agriculture and coastal development, and removal and replacement of mangrove habitat with aquaculture (UNEP 1995, Ogden 2001, Valiela et al. 2001). Concomitantly, coral reefs are suffering multiple stresses affecting their condition and long-term persistence such as increasing seawater temperatures, solar radiation, overfishing, and sedimentation (Hughes 1994, UNEP 1995, White et al. 2000, Ogden 2001). Mangrove habitat protects neighboring coral reefs from terrestrial runoff (UNEP 1995) and shelters coastlines from storm damage (Naylor and Drew 1998, Kathiresan and Rajendran 2005). Mangroves also serve as nursery grounds for juvenile reef fish and invertebrates (Nagelkerken et al. 2000, 2001) and feeding grounds and shelter for adult reef fish (Mumby et al. 2004), including commercially important species. Mangroves contribute both structurally and functionally to the stability of adjacent coral reef systems.

Degradation of mangrove forests through removal of the dominant species (e.g mangrove clearing or pruning that kills the trees) may damage the immediate habitat via both biotic and abiotic pathways. In addition to removing the buffer that moderates reef sedimentation and reducing juvenile fish habitat (Valiela et al. 2001), mangrove deforestation may have other important effects. For example, algal growth may increase as a result of greater light intensity, nutrient availability, and frequency of high temperature events (though see also Gwyth and Fairweather 2002) or decreases in sedimentation resulting from mangrove removal. These direct changes to the physical features of the mangrove habitat may indirectly result in shifts in the biotic community where mangroves have been removed (Eston et al. 1992). Fish communities and resulting herbivory may change as mangrove cover and root structure are removed because the rugosity or 3-dimensionality of the habitat becomes more homogeneous without subtidal prop roots.

Here I test the hypothesis that algal productivity and richness increase as a response to abiotic changes including light, temperature, and sedimentation rather than decreasing in response to biotic shifts in herbivory following removal of red mangrove (*Rhizophora mangle L.*) trees, the dominant species in this community. I provide the first evidence that mangrove removal affects algal community structure in removal areas through a direct abiotic to indirect biotic pathway, with potential implications for adjacent habitats.

Materials and Methods

Study area. This study was conducted at five sites in Almirante Bay, Bocas del Toro Province in Panama (Figure 3.1). Sites were located within 15 kilometers of each other, three on Isla Colon, one on Isla Pastores, and one on the mainland south of Almirante. All sites that met the following criteria were selected for this study: (1) at least 100 m long stretch of cleared red mangroves adjacent to stretches of at least 100 m of intact red mangroves; (2) fringing or patch reefs within 100 meters of the seaward mangrove edge; (3) > 2 km from major human development or construction to exclude potential sources of anthropogenic nutrients. The sites along Isla Colon include, from the northwest to southeast, Red Point, Punta Caracole North, and Punta Caracole South. The site on Isla Pastores is referred to as Pastores and the site on the mainland as Gallinazo due to its proximity to Punta Gallinazo. The coastline at all sites was characterized by *Rhizophora mangle* trees, except where stands had been removed for agriculture, construction, or viewsheds. Mangrove-removal areas ranged from 100 to 300 meters in length along the shore. On Isla Colon, mangrove removal occurred approximately 8 years prior to this study and mangrove-removed areas were characterized by submerged decaying prop roots on the substrate with significant macroalgal growth inshore and the seagrass *Thalassia testudinum* growth further from shore. Little 3-dimensional structure remained in these mangrove-removed areas. At the Isla Pastores and Gallinazo sites, removal had occurred during the previous 12 months and disturbed areas retained dead, exposed mangrove stands covered subtidally with algae and fringed by seagrass along the seaward edge. At Pastores and Gallinazo, subtidal root structure in removed areas was

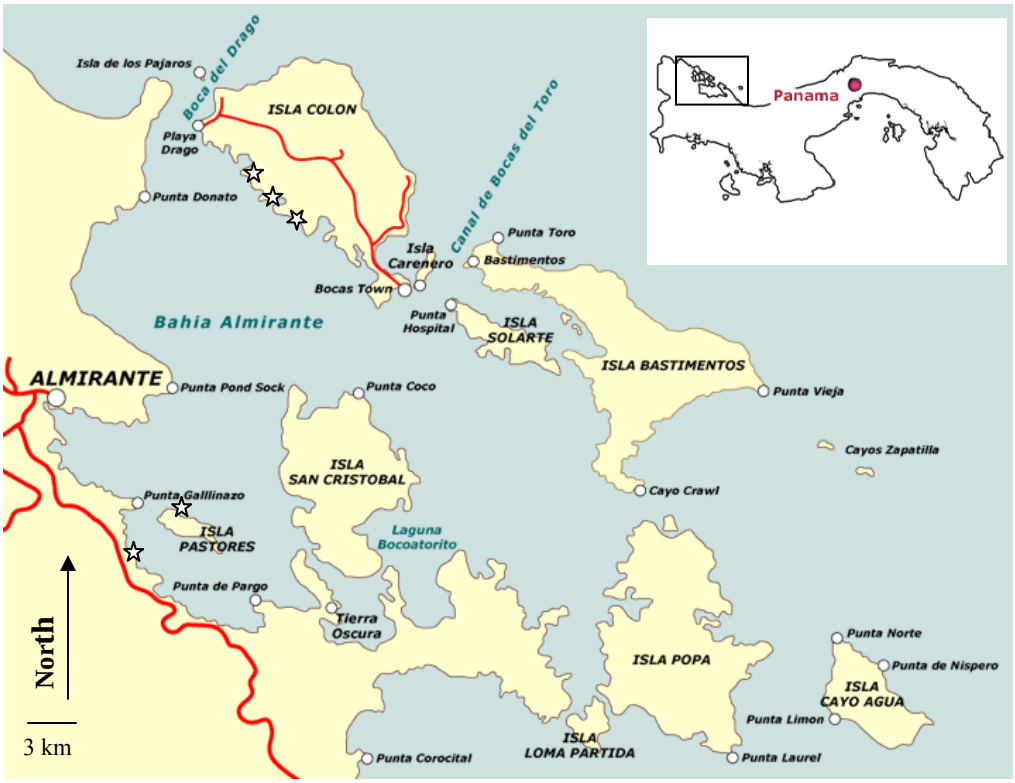


Figure 3.1. Map of Panama with Bocas del Toro region boxed. Sites are marked on inset map by symbols (on Isla Colon from NW to SE – Red Point, Punta Caracole North, Punta Caracole South; Pastores and Gallinazo)

substantially greater leading to subtidal structure intermediate between intact mangroves and the three Isla Colon mangrove removed areas. Intact mangrove areas were characterized by submerged prop roots colonized by oysters, sponges, sporadic coral heads, and infrequently epibiotic algae with occasional non-forested channels between trees. In intact areas at the five sites examined in this study, epibiotic algal cover on mangrove prop roots and trunks as well as on soft sediment substrate was extremely low; cyanobacterial mats on the substratum were sporadic. Overall, the proportion of hard surfaces (mangrove roots, dead coral, etc.) within the soft bottom substrate was comparable between mangrove cleared and intact mangrove areas.

Algal Biomass and Richness. Algal biomass was quantified at the five sites along a total of forty 20-meter long transects. Site design included two sub-habitats (mangrove edge and mangrove center) in each of two areas (intact mangrove and mangrove removed); there were two replicates of each area type at each site. The sub-habitats were parallel to shore: along the seaward edge of the mangroves (ME) and in the center of the mangroves through the roots (MC). Each transect was delineated by a 20-m long by 1-mm thick yellow nylon cord located approximately 30 cm above the substratum. Because the substrate along transects is not solid (i.e. detritus/mud/sand with macroalgae and cyanobacteria), this cord (simulating remaining root structure or hard substrata including dead coral) was the substrate from which algal growth was sampled. Nylon cord was used as a substrate because it allowed for easy sampling and is known to facilitate macroalgal growth in aquaculture (Buck and Buchholtz 2004). The rough surface of the nylon cord resembles the irregular surface of mangrove prop roots to which new algal propagules may attach though the cord may experience some differences in flow. The nylon cord was used as a standard surface to minimize differences in substrate heterogeneity but was not intended to exactly mimic the natural substrate or the community thereon.

Samples were taken by removing six randomly selected 15-cm long segments from the line at 3, 6 and 9 weeks after the cord was deployed. The data reported here are from week nine. Sampled segments were replaced with a different color nylon cord to

denote that the section had been sampled. Sample lines were rinsed to remove detritus and sand, and algal taxa (genera were used as a proxy for functional groups) were identified under a dissecting scope based on Littler and Littler (2000). Identification of some algal taxa to species depends on microscopic examination of reproductive or other fine structures and was impossible in the field. Since ecological studies involving marine algae often take a functional-form approach (i.e. Steneck and Dethier 1994), and most genera observed had few species, here taxon diversity is quantified as the number of genera. After identification, all algal and cyanobacterial biomass was scraped off the line and dried at 60°C. Dried samples were weighed to determine biomass.

Herbivory. To quantify the influence of herbivorous fishes on differences in algal biomass between intact and disturbed areas, herbivore exclusion cages were deployed at Red Point, Punta Caracole North, and Pastores. I constructed herbivore exclusion cages of Naltex tubular diamond mesh bag (1.4 cm mesh) stretched to ~20 cm in length and held open with three rings of ¾ cm x 15 cm PVC rings; the ends were covered with Vexar L-30 mesh (Redden Net Company Inc., Port Coquitlam, BC, Canada) attached with cable ties. Cage controls were similar but had two 6-cm diameter holes cut in the mesh on each side of the cage. The cages were threaded onto the lines when the experiment was deployed. This design excluded herbivorous fishes from the 20-cm stretch of cord surrounded by the cage. Herbivorous stocky ceriths (the gastropod *Cerithium litteratum*) occasionally entered the cages but were removed during bi-weekly monitoring visits. The line in cages and cage controls was sampled after nine weeks as described above. The effects of herbivory are defined as the difference between algal biomass in cages and cage controls. Cage effects were quantified by comparing algal biomass in cage controls to that on the open line.

Water temperature and light variation. Two i-button data loggers (i-button Temperature Loggers DS1921G, Maxim Direct, Dallas, TX) were deployed along each transect line at the beginning of the experiment and programmed to measure temperature hourly. I calculated mean temperature, temperature variance over the course of the

experiment, and the number of high temperature events exceeding 30.5°C (selected because local reef temperatures rarely exceed 30°C; E. Granek, unpublished data).

Light intensity was measured using a Li-cor Underwater Quantum Sensor (LI-192) and a Li-cor Atmospheric Quantum Sensor (LI-190) to standardize light measurements to ambient light conditions with a Li-cor data logger (LI-1400). Four light readings were taken per point at five points along each transect on a clear sunny day. Measurements were standardized to ambient light readings and averaged to determine mean light intensity per transect line (μmoles).

Sedimentation. Sedimentation rates were measured using 3.81-cm diameter x 19.05-cm PVC tubes capped at the bottom and anchored to rebar stakes. Three sediment traps were deployed on each transect line for approximately 8 weeks. Sediment was removed from each trap and dried at 60ºC until no further weight loss occurred. Final dry weight was recorded and mean sedimentation per transect was calculated.

Statistical analysis. For each analysis, the residuals were examined for normality and variance. Algal biomass and high temperature events were normalized using a $\log_{10}$ +1 transformation; light intensity and sedimentation were square-root transformed.

I used a nested ANOVA to determine how much of the variability in algal biomass was accounted for by physical location (mangrove edge vs. mangrove center and site) and mangrove presence (+mangrove vs. -mangrove). Number of algal taxa per line was averaged for each transect to determine differences in algal taxon diversity in +mangrove vs. -mangrove transects. A fixed effects ANOVA was employed to determine if generic richness was greater in -mangrove areas than in +mangrove areas. Differences in frequency of occurrence of genera on the sampling substrates were tested using a X^{2}– test.

A MANOVA and single factor ANOVAs were run to test how each factor (light intensity, high temperature events, variance of temperature and sediment accumulation) differed between -mangrove and +mangrove habitat and whether these factors

contributed to differences in algal biomass. In univariate tests, P-values were adjusted using a Bonferroni correction (0.05/n = 0.0125).

I used a three-way fixed-effects ANOVA to test the effects of herbivory (+herbivores= partial cages, -herbivores= complete cages), mangroves (+mangrove=mangrove-intact sites, -mangroves=mangrove-removed sites) and transect (center vs. edge). The response variable was algal biomass.

Results

Algal biomass. Algal biomass was higher in -mangrove than in +mangrove areas (ANOVA, $F = 38.83$; $p < 0.003$) (Figure 3.2a, Table 3.1). Algal biomass at three weeks was very low; since biomass at weeks six and nine had similar patterns, week nine data are reported here. There were no differences between transects (center vs. the edge of mangroves), among sites, or any interactions among these factors (Table 3.1).

Algal communities. The average number of algal and cyanobacterial genera per line was greater in -mangrove areas than in +mangrove areas (ANOVA, $F=7.34$, $p<0.02$) (Figure 3.3). Similarly, taxon richness was greater in -mangrove areas ($X^2 = 31.1178$, df = 16, $p = 0.013$; Figure 3.2b). The proportion of line segments with >50% cover of at least one algal or cyanobacterial taxon (referred to hereafter as dominant) was greater in -mangrove than in +mangrove areas ($F=57.02$; $p<0.002$). Three cyanobacterial genera dominated transects in cleared areas whereas two dominated in intact areas (Figure 3.3). In -mangrove areas, 14 algal genera were dominant, whereas in +mangrove areas, only seven genera were dominant. *Lyngbya* sp. and *Dictyota* sp. were most common overall. Field observations indicate that *Dictyota* sp., *Acanthophora* sp., and cyanobacteria were overgrowing live and dead coral on *Porites* patch reefs adjacent to -mangrove areas at Punta Caracole South and Red Point (E. Granek, unpublished data) (Figure 3.3). A survey of the literature showed that macroalgal genera found in mangrove-removed areas in this study were coral competitors at other Caribbean locations (McClanahan et al. 2002; McCook et al. 2001) (Figure 3.3, starred genera).

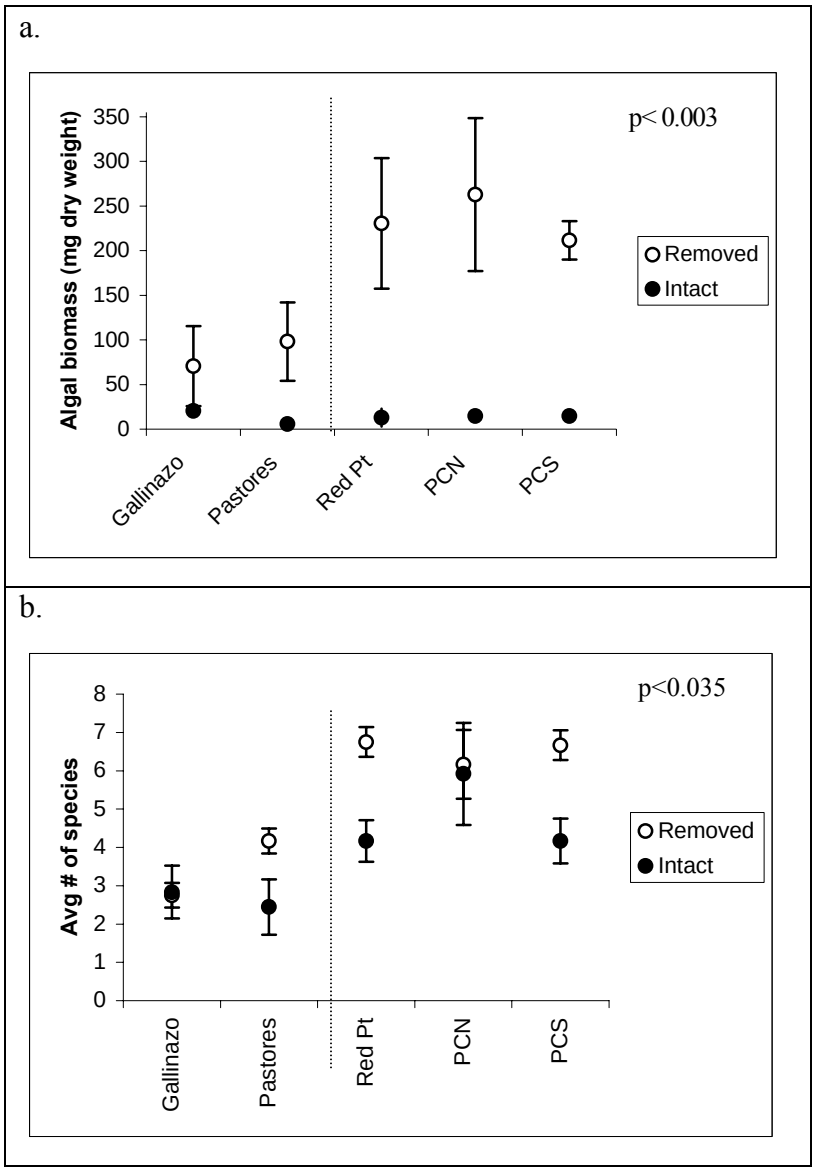


Figure 3.2. Averages of biotic factors (a. algal biomass and b. diversity) for –mangrove (hollow circles) and +mangrove (solid circles) areas by site. Bars are standard error of the mean. Dashed vertical line separates -mangrove areas with above-water and substantial subtidal structure still remaining (left) from sites at which -mangrove areas have only minimal subtidal structure remaining (right).

Table 3.1. Effects of location variables (site, transect, and presence or absence of mangroves) on algal biomass.

Residual standard error: 0.84

Factor	Df	Sum of Sq	F Value	Pr(F)
Mangrove (intact vs. removed)	1	27.35	38.83	0.003
Site	4	2.58	0.91	0.53
Transect (center vs. edge)	1	0.41	0.58	0.49
Mangrove x site	4	3.59	1.27	0.41
Site x transect	4	2.04	0.72	0.62
Mangrove x Transect	1	0.05	0.07	0.81
Residuals	4	2.82	0.70	

Herbivory. Algal biomass in +herbivore treatments was lower than in –herbivore treatments indicating a strong effect of herbivory ($F=10.21$; $p < 0.01$) even after accounting for the cage effect. Herbivory did not vary with transect (edge vs. center of mangroves) or site ($p> 0.5$). There was no difference in the magnitude of herbivory between +mangrove and -mangrove areas (i.e., there was no herbivore x mangrove interaction) (Table 3.2).

Abiotic factors. Abiotic conditions including light intensity, high temperature events, and sedimentation, differed in -mangrove areas and +mangrove areas (Figure 3.4; MANOVA $F= 53.52$; 4, 15 df; $p<0.0001$; Wilks' Lambda = 0.65). The differences in abiotic condition were primarily due to light, temperature and sedimentation (Figure 3.4a, b, c). As expected, light intensity was greater in - than in + mangrove areas (ANOVA, $F=209.84$; 1, 18 df; $p<0.0001$). The number of high temperature events was also greater in -mangrove than in +mangrove areas (ANOVA, $F= 17.68$; 1, 18 df; $p=0.0001$) (Figure 3.4b). Sedimentation rate was lower in -mangrove than in +mangrove areas (ANOVA, 1, 18 df; sedimentation $F= 41.91$; $p< 0.0001$).

Discussion

Although cyanobacterial mats occur naturally in mangrove habitat (Joye and Lee 2004), macroalgal growth is generally low in the undisturbed mangrove systems in this study. Removal of mangroves increases light availability and frequency of high temperature events and decreases sedimentation leading to increased macroalgal biomass and taxon diversity relative to areas with undisturbed mangrove forests. This suggests that tropical mangroves directly alter their local abiotic environment by providing shade and retaining sediment, acting as ecosystem engineers to indirectly control regional algal community structure. In addition, algal taxon diversity associated with the nylon cord was greater in areas where mangroves had been removed than in areas with intact mangroves over the course of this study. In contrast, herbivore consumption of algae was not affected by mangrove removal. The similar differences between exclusion cages and cage controls indicate that grazing impact was comparable in mangrove-intact and

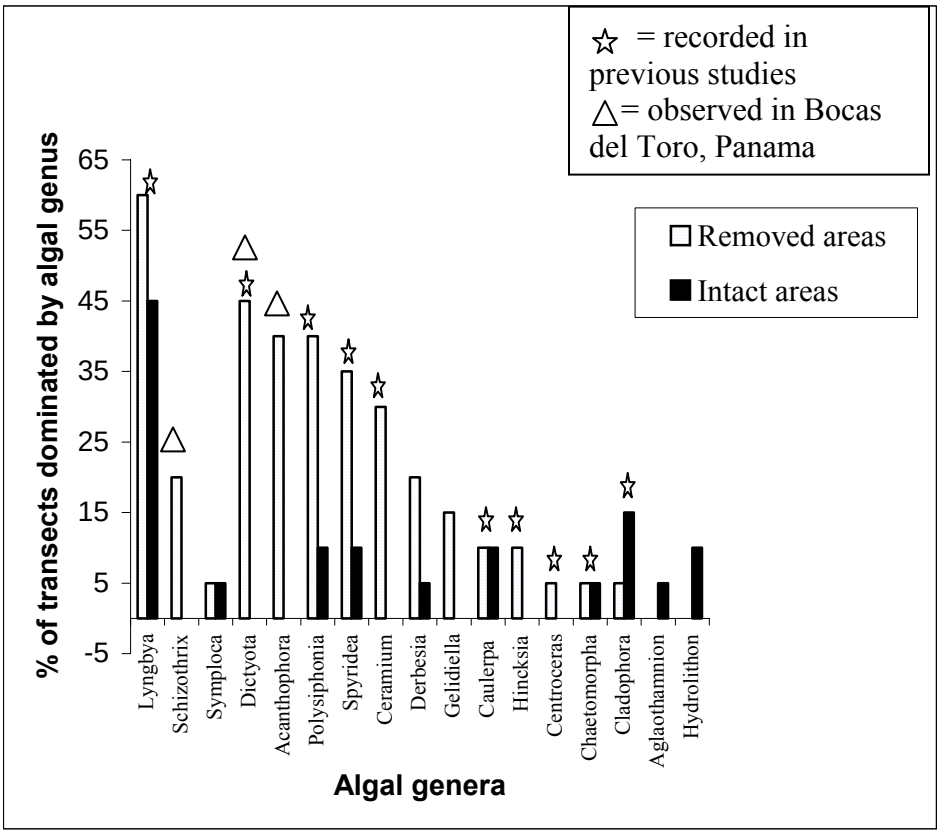
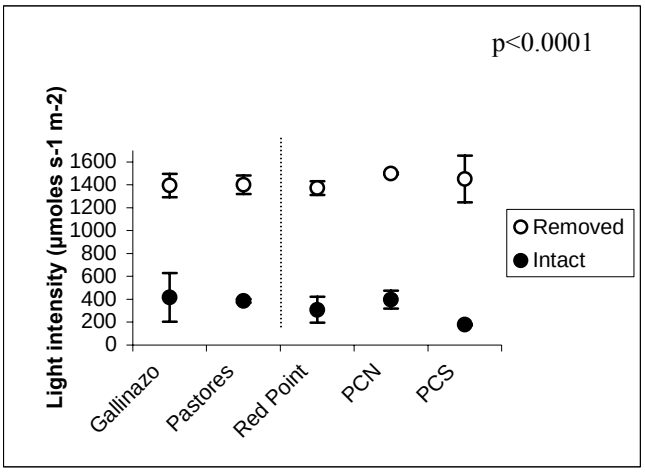


Figure 3.3. Frequency of line segments in which each genus occurred along > 50% of segment in cleared and intact mangrove transects: Percent of transects on which genera dominated at least one segment sampled. ☆ denotes genera observed overgrowing coral in other studies (McClanahan et al. 2002; McCook et al. 2001) and △ denotes species observed overgrowing adjacent reefs (E. Granek unpublished data).

Table 3.2. Four-way analysis of variance on the effects of herbivory on algal biomass. Treatments were mangrove presence (+ or -), transect (edge or center), site and herbivory (+ in partial cage, - in complete cage).

	Df	Sum of Sq	F Value	Pr(F)
Herbivory	1	12.05	10.21	0.01
Transect	1	0.58	0.49	0.50
Mangrove	1	16.78	14.21	0.004
Site	2	0.16	0.066	0.95
Herbivory x Transect	1	1.11	0.94	0.36
Herbivory x Site	2	1.01	0.43	0.66
Herbivory x Mangrove	1	0.06	0.05	0.82
Transect x Mangrove	1	0.68	0.58	0.46
Transect x Site	2	6.02	2.55	0.13
Mangrove x Site	2	2.42	1.02	0.40
Residuals	9	10.62	1.18	

a.



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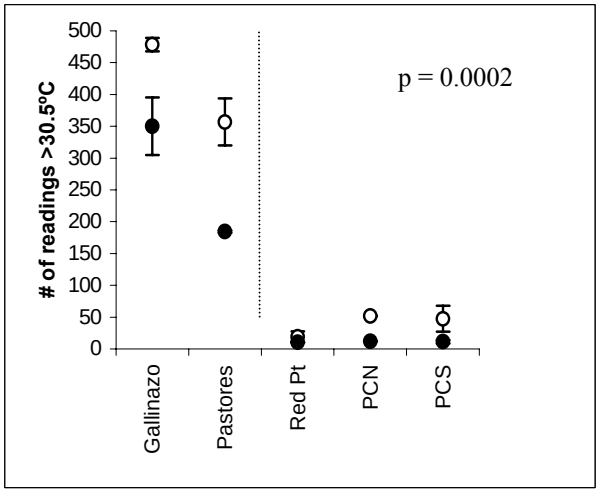

Figure 3.4. Averages of abiotic factors (a. light intensity, b. high temperature events, c. sedimentation) for –mangrove (hollow circles) and +mangrove (solid circles) areas by site. Bars are standard error of the mean. Dashed vertical line separates -mangrove areas with above-water and substantial subtidal structure still remaining (left) from sites at which -mangrove areas have only minimal subtidal structure remaining (right). P-values are from univariate ANOVA tests examining effect of mangrove removal.

c.

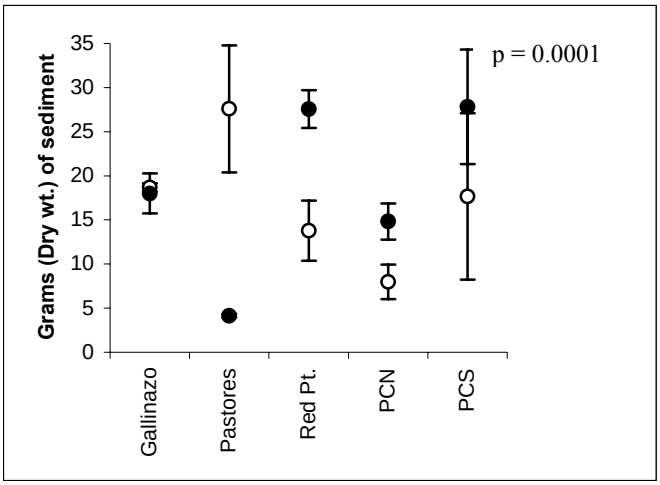

Figure 3.4. (Continued) Averages of abiotic factors (a. light intensity, b. high temperature events, c. sedimentation) for –mangrove (hollow circles) and +mangrove (solid circles) areas by site. Bars are standard error of the mean. Dashed vertical line separates -mangrove areas with above-water and substantial subtidal structure still remaining (left) from sites at which -mangrove areas have only minimal subtidal structure remaining (right). P-values are from univariate ANOVA tests examining effect of mangrove removal.

mangrove-removal areas, though herbivore assemblages may have shifted. These patterns support the hypothesis that disturbance to mangrove structure increased the dominance of macroalgae via shifts in abiotic (light, temperature, sedimentation) rather than biotic (herbivory) factors.

Intact mangrove cover limited light and maintained lower temperatures than in areas from which mangroves were removed, resulting in differing algal growth both on the sample surface and on the substrate at each site (E. Granek, pers. obs.). The importance of light in altering community structure is further supported by observations that patches below canopy gaps in intact mangroves had higher light intensity and greater algal biomass (E. Granek, pers. obs.). Further, increased sedimentation in mangrove-intact areas may interfere with propagule establishment possibly burying growing algae or reducing light penetration, limiting its ability to colonize the community (see also Kercher and Zedler 2004). Low light levels and high sedimentation rates are less than optimal for growth of many macroalgal and cyanobacterial genera (Irving and Connell 2002; Pang and Luning 2004). Variation in sedimentation rates in the mangroves was probably affected by the amount of remaining structure following clearing, with lower sedimentation rates in the more extensively cleared sites (those on Isla Colon). For example, the majority of the trunk and prop root structure were still present in the mangrove- removed areas at Isla Pastores, which may have caused its sedimentation rate to more closely resemble intact mangroves. This demonstrates how the extent of disturbance to an ecosystem dominant has varying degrees of impact on abiotic processes.

Although there was no difference in herbivory between intact and cleared mangroves, there was high site-to-site variability and this may be confounded by the variation in mangrove root structure following removal. Herbivorous fish composition and abundance are related to the amount of shelter habitat (complexity of root structure) and shade available (de la Moriniere et al. 2004) and this varied among sites. For example, at Pastores, where significant root structure remained in mangrove removal areas, higher herbivory in the mangrove-removed area than in the mangrove-intact area is likely due to the combination of greater availability of root structure habitat and increased

algal resources. In fact, herbivorous fish abundance was higher in mangrove removal areas at Pastores than any other mangrove-removed area (E.Granek, unpublished data). Additionally, the similarity in herbivory detected between mangrove-intact and mangrove-removed areas may be scale-dependent. The pattern could be a byproduct of the fairly small extent of mangrove removal, i.e. the distance to the removal areas may be sufficiently short for herbivores to transit from adjacent intact mangrove habitat to feed on algae in removal areas.

Mangrove-removed areas increased algal generic richness relative to mangrove-intact areas (Figure 3.3). This was observed not only on the transect lines but on the substrate as well. Diversity and dominance of cyanobacteria (e.g., *Lyngbya* sp., *Symploca* sp., and *Schizothrix* sp.) and a variety of red, green and brown macroalgal taxa uncommon in local mangrove habitat were consistently higher in disturbed mangroves, indicating more favorable algal growth conditions in mangrove removal areas due to higher light. Similarly in terrestrial savannahs and grasslands, higher primary producer diversity (Keeley et al. 2003) and higher frequency of genera dominating the substrate (Symstad and Tilman 2001) have been found following human disturbance. My results demonstrate an indirect biotic effect following mangrove removal, a shift similar to those in terrestrial systems, suggesting that human disturbance to dominants may have consistent effects on biotic communities across ecosystems.

Shifts in abiotic factors and resultant algal community structure caused by mangrove removal could influence adjacent habitats with significant implications for management of tropical coastal ecosystems. Changes in light, temperature and sedimentation contributed to increased richness of certain alga and cyanobacteria in mangrove-removed areas. The algal genera dominating line segments in these mangrove-removed areas included *Centroceras, Hincksia, Cladophora, Spyridea, Caulerpa, Ceramium, Chaetomorpha* and *Polysiphonia*, some of which have been recorded on mangrove prop roots (Farnsworth and Ellison 1996; Littler et al. 2000). These genera were also observed by McClanahan et al. (2002) growing on coral reefs in Belize and leading to coral-algal competition for light and space (McClanahan et al. 2002). By increasing algal biomass, facilitating algal compositional shifts and changing local

biogeochemistry, mangrove deforestation may indirectly alter the competitive balance between corals and algae on nearby patch reefs.

Mangrove removal may provide favorable habitat for algal and cyanobacterial genera that are known to be aggressive competitors with corals and in areas where historically many of these primary producers did not thrive (in the mangroves). These shifts may be similar to the impacts of forest clearings on adjacent streams (Likens et al. 1970) and of river pollution on inshore marine habitat hundreds of miles downstream (Bricker et al. 1999). This study suggests an important area for further research to examine whether mangrove removal leads to higher macroalgal biomass in nearby seagrass beds and coral reefs through possible mechanisms including increased propagules of competitive algae or changes in nutrient and sediment conditions on already-stressed adjacent coral reef.

In this study, disturbance to an ecosystem dominant, mangroves, changed abiotic factors including light intensity, temperature, and sedimentation, triggering shifts in the biotic community resulting in increased algal and cyanobacterial abundance and diversity (Noe and Zedler 2000) with potential implications for management and conservation of adjacent habitats. Understanding these cascading processes may be useful for examining the mechanisms underlying shifts in ecosystem functioning following other disturbances including deforestation, dam removal, eutrophication of rivers and lakes, invasion of grasslands, or overfishing of coral reefs. Identifying processes that influence shifts in ecosystem functioning and community structure, be they the effects of competitive dominants or other strong interactors, and the biotic or abiotic consequences of their activities, is necessary for addressing management, restoration, and conservation of both human-disturbed ecosystems and potentially adjacent, un-manipulated natural systems.

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Chapter 4:

The impacts of red mangrove (*Rhizophora mangle*) deforestation on zooplankton communities in Bocas del Toro, Panama

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Abstract

Deforestation impacts ecosystems via changes in habitat structure and community composition. The composition of the zooplankton and larval community in marine habitats can be an important indicator of potential food availability, propagule arrival, and settlement. Determining how this community differs between intact and cleared red mangrove (*Rhizophora mangle* Linneaus 1773) habitat could clarify the role that mangroves play in entraining zooplankton and larvae and the importance of mangrove habitat as a settlement site. Light traps and plankton tows were used to quantify and compare zooplankton communities between intact and cleared mangrove areas in Bocas del Toro, Panama. Plankton communities within intact mangrove areas had greater species richness and a distinct composition compared to plankton communities in cleared mangrove areas. The meroplankton communities, in particular, were distinct between intact and cleared areas. Amphipods and ostracods, as well as larval, postlarval and reproductive mysids (all prey of juvenile and adult reef fish), were more common in intact mangrove areas. Mangrove removal had effects on the structure of larval and zooplankton communities. This difference in community structure has potential implications for food and propagule availability for seagrass bed and coral reef systems adjacent to degraded mangroves.

Introduction

Deforestation impact studies generally focus on tropical rainforests or temperate coniferous woodlands. However, extensive clear-cutting is currently occurring in a wide-ranging, but far less recognized habitat: the world's mangrove forests. These coastal forests thrive in areas of low wave action and high sediment availability, where mangrove trees develop dense and productive ecosystems (Alongi 2002). Extensive aerial and subtidal prop root networks, a dense canopy, and varying water conditions allow these forests to support unique assemblages of flora and fauna.

Mangrove forests in tropical coastal areas provide important ecosystem services and protective functions that include buffering coastlines, protecting seagrass beds and coral reefs from terrestrial sedimentation, and serving as nursery areas for juvenile reef

fishes and invertebrates. An estimated 70 species of mangroves cover approximately 181,000-km^2 worldwide (Alongi 2002). However, Alongi (2002) estimates that mangroves currently cover approximately two-thirds of the area they covered 50 years ago, and their decline is expected to continue at similar rates for at least the next two decades in the absence of large-scale intervention. Causes of deforestation include cutting mangroves for lumber, clearing and filling mangrove areas for agriculture and coastal development, and removal and replacement of mangrove habitat for aquaculture facilities (UNEP 1995; Ogden 2001; Valiela et al. 2001). Potential consequences of mangrove deforestation include increased coastal sedimentation, excess nutrient flow from terrestrial runoff, altered food chains and changes in tidal flow (Alongi 2002). However, the ecological impacts of these changes are largely unstudied.

Even as mangrove deforestation continues to alter coastlines worldwide, these forests are becoming increasingly recognized as important nursery habitats and feeding grounds for many larval, juvenile and adult fish and invertebrate species (Nagelkerken et al. 2000a,b; Nagelkerken et al. 2001; Nagelkerken et al. 2002; Mumby et al. 2004; Nagelkerken and van der Velde 2004). Larval populations of a wide variety of marine species recruit to these sheltered, structurally complex, shaded and nutrient-rich ecosystems (Krishnamurthy 1982, Dennis 1992). However, it is not known whether zooplankton communities differ between intact and cleared mangrove areas. Structural complexity should affect flow and hence the availability of food and the retention rates of larvae. However, results from different systems indicate various patterns. In kelp forests, structural complexity inhibits deposition of suspended particles possibly reducing food availability for benthic organisms and retarding zooplankton dispersal (Eckman et al. 1989). As with inhibited flow in kelp forests, Toffart (1983) suggests that there is a rapid decrease in species diversity as one penetrates inward from the open water edge of a mangrove forest towards the shore because of the reduction in flow. This may have an effect particularly on less active swimmers. However, direct measurements of zooplankton inside and outside mangroves do not yet exist. Mangroves may be preferred settlement sites for some highly mobile species that can actively select this habitat. Some fish larvae can swim at speeds approaching 30 cm/min

and can detect and swim towards favorable habitats such as reefs that may be more than 1 km away (Leis et al. 1996). Many invertebrates are also highly mobile. For example, copepods swim at maximum speeds of 60cm/min (Ferrari et al. 2003) and crab larvae at 12.6 cm/second (Luckenbach, 1992). This capacity for swift directional travel could allow mobile larval species to actively select mangrove habitat over less complex, more open environments (i.e. cleared mangrove areas).

The complexity of root systems in mangrove forests, in combination with reduced light penetration beneath dense foliage, is beneficial for larvae and zooplankton for several reasons. These include increased number of niches (due to the structural complexity) and food availability, and decreased predation risk. Whether lower flow areas like mangroves increase (or decrease) the abundance of larvae and thus create retention zones where larvae can develop without traveling too far from suitable habitat (Grothues et al. 2002) is unclear (Paula et al. 2004).

Larval abundance in mangroves may be high because of high larval survival resulting from more favorable substrate, greater food availability and reduced predation (Cocheret de la Moriniere et al. 2004, Laegdsgaard and Johnson 1995). The extensive and often dense root networks of mangrove forests retain nutrients and sediments carried in runoff from adjacent land or produced *in situ* which has the dual effect of fueling productivity (Bouillon et al. 2000) and creating murky water conditions, reducing visibility for predators. The structural complexity of mangrove roots themselves may also provide settling larvae with shelter from predators and open water currents. On the other hand, the differences in structural complexity within mangrove forests may also lead to variable larval supply and diversity within different areas of intact mangroves (Krumme and Liang 2004; Osore et al. 2004).

Some of the larvae found in mangroves, after growing to the juvenile or pre-adult stage, migrate to adjacent seagrass bed or coral reef habitats where they spend their adult life (Sheridan and Hays 2003). Examining zooplankton and larval communities in mangroves is likely to be relevant to the understanding of community patterns in these adjacent habitats.

To date little research has examined larval and zooplankton communities in mangrove habitat (but see Paula et al. 2001; Barletta-Bergan et al. 2002; Osore et al. 2004). In this study, we examine the effects of mangrove habitat loss on larval and zooplankton communities by comparing the diversity and abundance of community composition between areas cleared of mangroves and areas with intact mangroves in the Bocas del Toro region of Panama. We tested the hypothesis that different meroplankton and holoplankton communities inhabit intact and cleared mangrove environments. We define meroplankton as those organisms that spend the early part of their lifecycle in the water column and settle out into benthic habitat at a later stage whereas holoplankton spend their entire lifecycle in the plankton. Because higher complexity habitats are usually characterized by higher biological diversity (i.e. Kohn and Leviten 1976, Taniguchi and Tokeshi 2004; Gratwicke and Speight 2005a,b; Kostylev et al. 2005; Lassau et al. 2005; Le Hir and Hily 2005) we expected to find higher diversity in the intact mangrove habitat.

Methods

Study Area

This study was conducted adjacent to Isla Colon in the Bocas del Toro Province off the Caribbean coast of Panama. The coastline at the study area was characterized by *Rhizophora mangle* (Linneaus 1773; red mangrove) trees, except where stands had been removed for agriculture, construction, or viewsheds. Cleared mangrove areas ranged from 100 to 300 meters in length along the shore and were bordered on either end by intact mangrove habitat. Mangrove removal occurred approximately 8 years prior to this study. Intact mangrove areas were characterized by submerged prop roots colonized by oysters, sponges, sporadic coral heads, and infrequently epibiotic algae with occasional unforested channels between trees. Cleared areas were characterized by similar depth and distance from the shoreline, but they lacked the complex 3-dimensional underwater root structure (generally limited to a few remaining snags), overhead cover available under the mangrove canopies, and high sediment levels and nutrients resulting from

organic production of a healthy mangrove community (Krishnamurthy 1982; Granek, unpublished data). Mangrove-removed areas were characterized by submerged decaying prop roots on the substrate with significant macroalgal growth inshore and seagrass (*Thalassia testudinum*) growth further from shore. Tidal exchange in the region is ~50 cm.

Six sites on Isla Colon were selected for this study because they met the following criteria: (1) At least 100 m long stretch of cleared *R. mangle* adjacent to stretches of at least 100 m of intact red mangroves; (2) fringing or patch coral reefs within 100 meters of the seaward mangrove edge; (3) > 2 km from *major* human development or construction, to exclude potential immediate anthropogenic sources of nutrients. Nearby development in the study region was limited, primarily consisting of subsistence farming and mangrove clear-cutting. Commercial and industrial development was >10 km from all sampling sites. Below, we refer to areas of intact mangrove as +mangrove areas and to areas cleared of mangroves as –mangrove areas.

Larval Sampling

Previous assessments demonstrate that community composition and taxa collected differ between light trap and plankton tow sampling methods (Porter et al. 2002, Hickford and Schiel 1999). Because larvae and zooplankton display a range of swimming abilities and photosensitivity, we simultaneously used light traps and plankton tows to assess the plankton communities in the +mangrove and -mangrove areas. Positively phototactic swimming larvae are drawn into the light traps, while non-phototactic and slow-moving or negatively phototactic larvae are more effectively sampled through plankton tow collections (Doherty 1987).

Larval Light Traps

Larval light traps have the potential to trap positively phototactic, mobile larvae (Watson et al. 2001; Porter et al. 2002). Larval light trap design was based on that used by Roegner et al. (2003). The traps were constructed using 7.6-liter (2 gallon) clear plastic water jugs, inverted, with an attached, 220-um, mesh-lined cod-end made of

perforated PVC tubing (Figure 4.1). A yellow glow stick, suspended inside the bottle from the top of each inverted trap, was used as the light source. Three funnel-shaped entry points were available to larvae in the bottle's sides, leading inward to a hole measuring approximately 1 cm in diameter. The small size of entry points and the funnel shapes were designed to limit, as much as possible, the ability of larvae to leave the traps after entering. Larvae were flushed into the cod-end of the trap when it was lifted from the water.

Traps were deployed for one hour after sunset, between 7:00 and 8:30 pm. In intact mangrove areas, light traps were anchored by suspended dive weights within the root structure approximately 1-1.5 m above the substrate. In the cleared areas, the traps were deployed within the area previously occupied by mangroves. The differences in habitat complexity may have led to undersampling in +mangrove areas where light penetration was reduced due to root structure and increased turbidity blocking light dispersal. Therefore, the effective sampling area is smaller for traps in +mangrove areas than for traps in –mangrove areas. In June 2004, sampling was conducted for 6 nights around the new moon, the period of the lunar cycle when spawning is most common, and therefore, when the larval community is likely at its peak density (McFarland et al. 1985). We began collections two days prior to and continued 3 days after the new moon. Two sites were sampled per night, (two intact and their two associated cleared areas) and each site was sampled twice in the course of the study.

Plankton Tows

Plankton tows sample less mobile larvae in the water column, primarily trapping individuals lacking the ability to actively avoid the tow net mouth (Porter et al. 2002, Hickford and Schiel 1999). Unlike larval light traps, tows do not preferentially trap phototactic larvae. Diver-pulled plankton tows were conducted in the vicinity of the traps for 1 minute (approximately 20 meters) during the time period in which the light trap was deployed. The 200-μm mesh plankton net had an opening diameter of 30 cm. In intact mangrove areas, the net was pulled through partially open waters found behind the most seaward trees and through small channels within the mangrove forest. Tows were

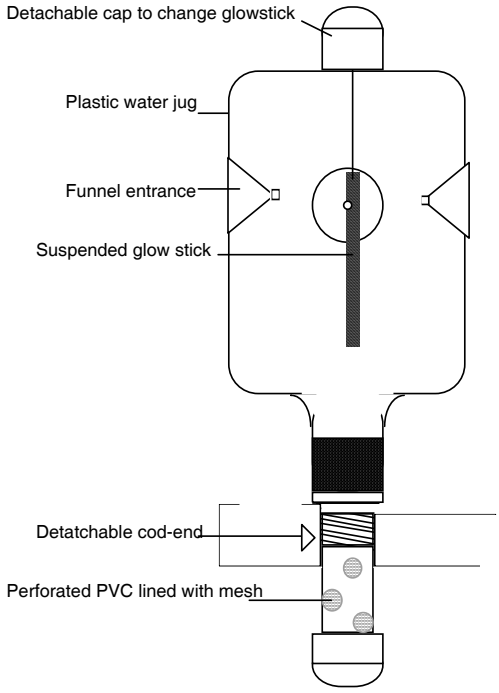

Figure 4.1. Diagram of larval trap design (modified from C. Roegner and A. Shanks; not to scale).

conducted as close to the light traps as feasible within the root structure, given the size of the net. In the cleared mangrove areas, the tows were pulled along a straight line, parallel to the shore and adjacent to light traps.

Sample Processing

The contents of the cod-ends of the traps and tows were preserved in 2-4% formalin solution. A light microscope was used for sample identification. All individuals in each sample were counted and identified to phylogenetic order when possible. Decapods were further categorized by developmental stage (i.e. zoea, megalopae, or postlarval). Reproductive individuals were recorded.

Statistical Analysis

Prior to analysis, data were log +1 transformed for analysis of variance (ANOVA) tests and square root transformed for non-parametric multidimensional scaling analysis. Three-factor ANOVA was used to determine how much of the variability in taxonomic abundance was accounted for by physical location (site), mangrove presence (+mangrove vs. –mangrove), and sampling night. Shannon-Weiner diversity index was used to determine differences in taxon diversity between +mangrove and -mangrove areas. A non-parametric multidimensional scaling analysis (nMDS) was run to examine differences between communities at each site, and whether +mangrove sites were more similar to each other than to -mangrove sites. All analyses were run separately for light trap and plankton tow data. Communities were then separated into meroplankton and holoplankton, and nMDS was run for each sub-community (meroplankton; holoplankton).

Results

Light traps

In light trap samples, abundance of meroplankton taxa (e.g. amphipods, isopods, ostracods, crab and mysid larvae; see Figure 4.2A) and daphnia were greater in +mangrove areas (Table 4.1A). For three meroplankton taxa (crab zoeae, shrimp zoeae and megalopae and worms) and two holoplankton taxa (copepods and cumaceans; Figure 4.2A), abundance was greater in –mangrove areas (Table 4.1C). For all other taxa sampled in light traps there was no difference in taxon abundance between +mangrove and–mangrove areas (Figure 4.2A). There was no difference in the total zooplankton abundance between cleared and intact mangrove areas (Paired t-test: t = -1.8141, df = 10, p-value = 0.0997) though there was a trend toward greater abundance in –mangrove areas.

Overall diversity was more than 50% higher in intact mangrove areas relative to cleared areas (Shannon Weiner diversity index: intact = 1.4, removed = 0.92; Figure 4.3A). A nMDS analysis demonstrates differences in larval and zooplankton communities between +mangrove and -mangrove areas (R^2 = 0.506, Stress in randomized runs: p <0.0099; Figure 4.4A). Community differences in light traps were primarily driven by higher abundances in +mangrove areas of meroplankton including amphipods, reproductive mysids, and porcellanid megalopae larvae as well as *Daphnia* and jellies. A nMDS analysis examining only the meroplankton community demonstrated differences between +mangrove and -mangrove areas (R^2 = 0.50, Stress in randomized runs: p <0.0099; Figure 4.4) as did an analysis on the holoplankton community (R^2 = 0.422, Stress in randomized runs: p <0.012; Figure 4.4).

Plankton tows

In plankton tows, several meroplankton taxa (amphipods, euphausids, mysids, and ostracods; see Figure 4.2B) were more abundant in +mangrove than -mangrove areas

a. Light trap

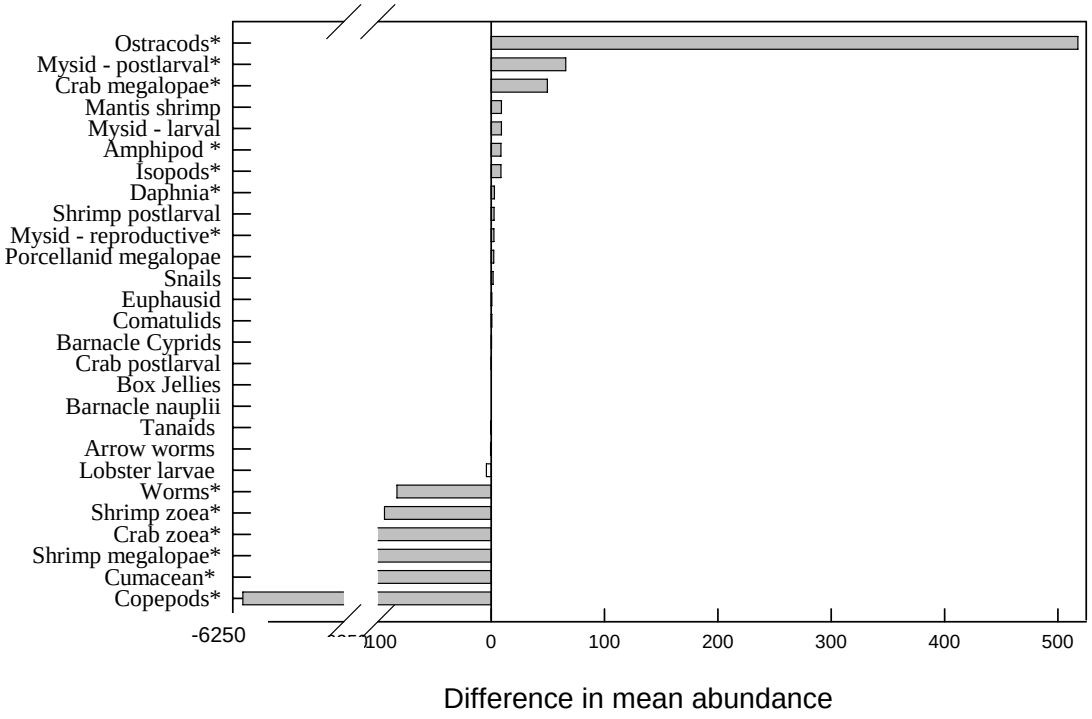

Figure 4.2. Difference in mean taxon abundance between +mangrove areas and –mangrove areas. * indicates significant difference. Grey bars indicate taxa that are key food items for reef fish (Randall 1967); white bars are taxa that are not known as important food items.

b. Plankton tow

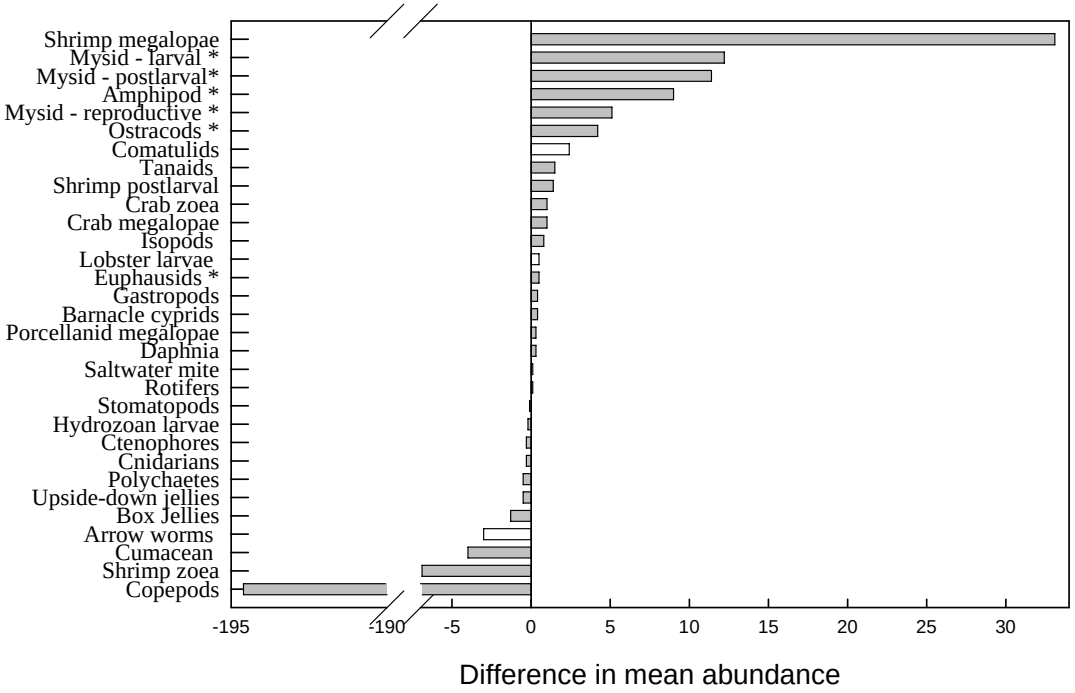

Figure 4.2. (Continued) Difference in mean taxon abundance between +mangrove areas and –mangrove areas. * indicates significant difference. Grey bars indicate taxa that are key food items for reef fish (Randall 1967); white bars are taxa that are not known as important food items.

Table 4.1. Taxa for which abundance was greater in + mangroves using (a) light traps and (b) plankton tows; (c) taxa for which abundance was greater in -mangrove areas. Significant results are indicated in bold face type.

a. Light traps: +mangrove > -mangrove		Amphipods			Crab megalope			Daphnia			Isopods		
Factor	DF	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)
Mangrove (+ vs -)	1	8.32	11.78	**0**	4.47	3.7	0.07	3.32	9.86	**0.007**	2.85	6.15	**0.03**
Site	5	5	1.41	0.28	9.6	1.59	0.23	5.68	3.37	0.03	8.67	3.74	0.02
Night	1	1.62	2.29	0.15	0.89	0.74	0.4	2.29	6.77	0.02	0.72	1.55	0.23
Residuals	14	9.89			16.91			4.72			6.49		
		Mysids - postlarval			Mysids -reproductive			Ostracods					
Factor	DF	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)			
Mangrove (+ vs -)	1	13.6	5.84	**0.03**	3.51	7.91	**0.01**	37.87	8.39	**0.01**			
Site	5	10.57	0.91	0.5	2.95	1.33	0.31	9.35	0.41	0.83			
Night	1	1.48	0.64	0.44	0.28	0.62	0.44	3.78	0.84	0.38			
Residuals	14	32.54			6.21			63.2					
b. Plankton tow: + mangrove > -mangrove		Amphipods			Euphausid			Mysid larvae			Mysids - postlarval		
Factor	DF	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)
Mangrove (+ vs -)	1	8.78	17.18	**0**	0.51	4.16	0.06	17.23	22.7	**0**	17.66	39.02	**0**
Site	5	5.52	2.16	0.13	0.6	0.99	0.46	8.12	2.14	0.13	7.16	3.16	0.05
Night	1	1.15	2.26	0.16	0.01	0.04	0.84	0.07	0.09	0.77	0.12	0.26	0.62
Residuals	12	6.13			1.46			9.11			5.43		

Table 4.1. (Continued) Taxa for which abundance was greater in + mangroves using (a) light traps and (b) plankton tows; (c) taxa for which abundance was greater in -mangrove areas. Significant results are indicated in bold face type.

		Mysids -reproductive			Ostracods		
Factor	DF	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)
Mangrove (+ vs -)	1	9.16	17.75	**0**	3.07	5.76	**0.03**
Site	5	4.47	1.73	0.2	3.02	1.13	0.39
Night	1	0.14	0.28	0.61	1.33	2.5	0.14
Residuals	12	6.19			6.39		

c. Light traps: -mangrove > + mangrove		Crab zoea			Copepods			Cumaceans			Shrimp zoea		
Factor	DF	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)	Sum of Sq	F-value	Pr(F)
Mangrove (+ vs -)	1	25.08	7.45	**0.02**	36.15	9.45	0.01	11.96	11.3	**0.005**	11.33	5.23	**0.04**
Site	5	8.79	0.52	0.76	15.7	0.82	0.56	7.88	1.49	0.026	21.11	1.95	0.15
Night	1	0.53	0.16	0.7	0.19	0.05	0.82	3.4	3.21	0.09	3.08	1.42	0.25
Residuals	14	47.12			53.55			14.83			30.3		

		Shrimp megalope			Worms		
Factor	DF	Sum of Sq	F-value	P-value	Sum of Sq	F-value	Pr(F)
Mangrove (+ vs -)	1	26.03	14.26	**0**	14.11	11.31	**0.01**
Site	5	12.19	1.34	0.31	1.69	0.27	0.92
Night	1	0.01	0.01	0.94	1	0.8	0.39
Residuals	14	25.55			17.46		

(Table 4.1B) with some taxa being 10 to 100 times greater in +mangrove areas. For all other taxa sampled in plankton tows, there was no difference in taxon abundance between +mangrove and -mangrove areas (Figure 4.2B). There was also no difference in the total zooplankton abundance between +mangrove and -mangrove areas (Paired t-test: $t = 1.3487$, $df = 10$, p-value = 0.2072).

Overall diversity was more than 50% higher in +mangrove areas compared to -mangrove areas (Shannon Weiner diversity index: intact = 2.13, removed = 1.34) (Figure 4.2B). A nMDS analysis demonstrates differences in larval and zooplankton communities between +mangrove and -mangrove areas ($R^2 = 0.724$, Stress in randomized runs: $p < 0.0099$; Figure 4.3B). Community differences in plankton tows were primarily driven by higher abundances in +mangrove areas of holoplankton including *Daphnia*, jellies, and rotifer larvae; and meroplankton including comatulids, euphausids, hydrozoan larvae, mantis shrimp, and snails. A nMDS analysis examining only meroplankton demonstrated differences in communities between +mangrove and -mangrove areas ($R^2 = 0.454$, Stress in randomized runs: $p < 0.012$; Figure 4.4) though there was no difference in the holoplankton communities between +mangrove and -mangrove areas ($R^2 = 0.214$, Stress in randomized runs: $p < 0.03$; Figure 4.4).

Discussion

Our study focused on invertebrates and demonstrates that taxonomic diversity of zooplankton communities, and, in particular, meroplankton, is different in +mangrove and -mangrove areas. For example, amphipods, euphausids, mysids and ostracods were more abundant in undisturbed mangrove areas regardless of sampling method. Using light traps, crab megalopae and isopods were shown to be more abundant in undisturbed mangroves, whereas copepods, cumaceans, worms, and crab and shrimp zoeae were more abundant in –mangroves areas. It is important to note that light traps in +mangrove areas were likely sampling a smaller effective area than light traps in –mangrove areas due to decreased light penetration from roots and higher turbidity in +mangrove areas. On the other hand, the general patterns for these taxa were similar in both tows and traps giving some confidence that the results are reliable. Various factors may contribute to the

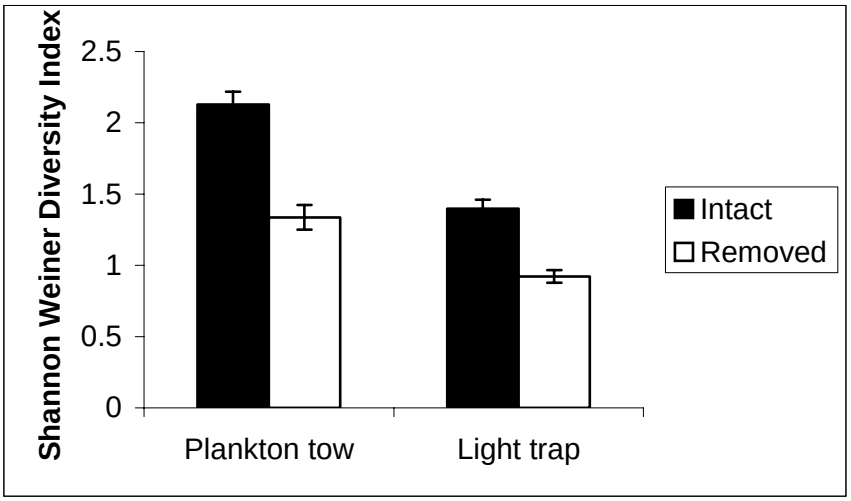

Figure 4.3. Shannon-Weiner Diversity Index comparing taxon diversity between +mangrove and –mangrove areas for light traps and plankton tows. Error bars are standard errors.

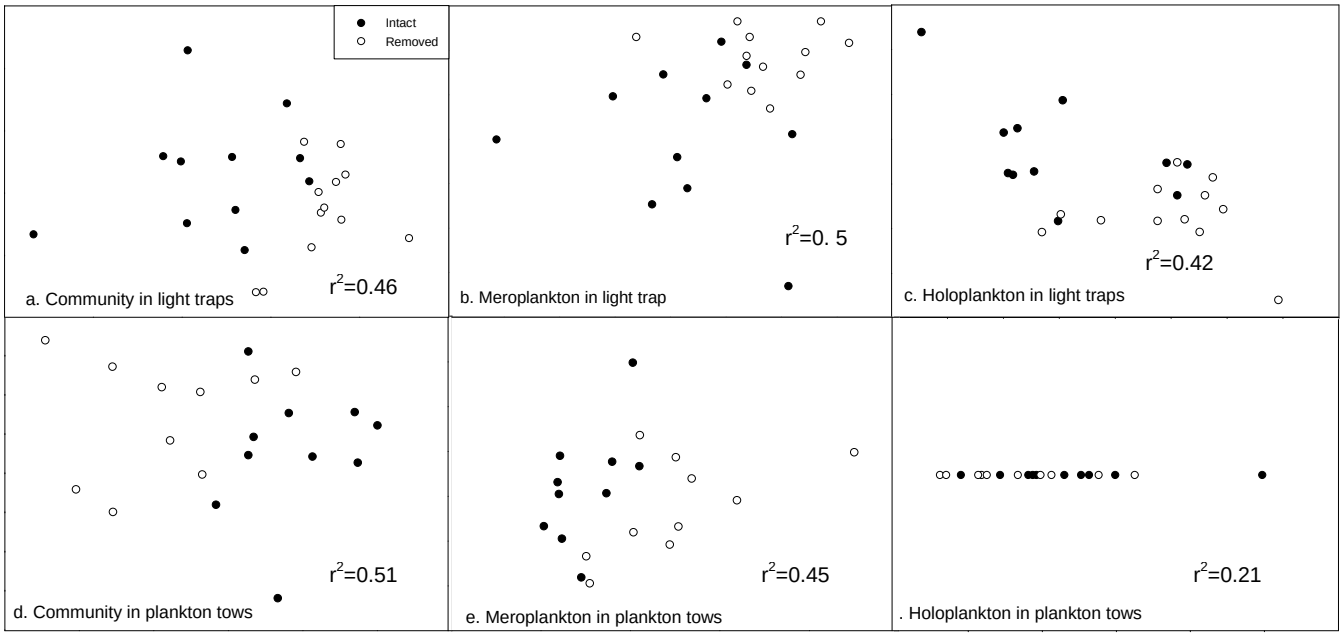

Figure 4.4. Nonparametric multidimensional scaling ordinations of differences in communities between intact and cleared mangrove areas from light traps (a-c) and plankton tows (d-f). Closed circles are +mangrove areas and open circles are -mangrove areas. f. is linear because only one axis explains any of the variability among samples.

observed differences in community structure between +mangrove and –mangrove areas. Two major processes could be responsible, separately or in conjunction, for this difference: (1) differential mortality among the different taxa and/or (2) differential habitat preference among taxa.

Differential mortality could affect the community composition sampled in the two habitats. Increased three-dimensional structure (Primavera 1997; Sheridan and Hays 2003) and turbidity both increase the ability of prey to escape or hide from predators, potentially increasing survival rates. One mechanism that could potentially create the observed difference in zooplankton assemblage structure between +mangrove and –mangrove areas could thus be differential predator avoidance ability among the different taxonomic groups, and thus differential mortality rates. On the other hand, mangrove structure provides greater shelter and protection against predators for a suite of juvenile reef fish, including several zooplankton feeders (Randall 1967), and is identified as an important nursery and feeding area (Nagelkerken et al. 2000a,b; Nagelkerken et al. 2001; Nagelkerken et al. 2002; Mumby et al. 2004; Nagelkerken and van der Velde 2004). The abundance of these juvenile reef fish is believed to be greater in +mangrove areas (see Mumby et al. 2004). This would imply that predation pressure on zooplankton in mangrove areas should be high. But it is unknown how lower predator abundance and reduced shelter against predators interact to affect the abundance of preferred prey items such as shrimp larvae, cumaceans, copepods and polychaete worms in cleared areas where reef fish populations are purported to be lower (e.g. Mumby et al. 2004). Teasing apart how these conflicting mechanisms contribute to differences in community structure between +mangrove and –mangrove areas necessitates further experimental investigation.

Differential habitat preference influences the taxa located in a system. Mangrove habitat may be a more favorable settlement site to pre-settlement meroplankton because of increased structure and food availability (Schwamborn et al. 2002) and lower thermal stress. Zooplankton are capable of responding to temperature cues (Yurista 2000; Metaxas 2001; Ouimet 2001; Bell and Weithoff 2003), and thermally stressful events are more frequent in -mangrove areas (E. Granek, Oregon State University, unpubl. data). Therefore, zooplankton may be attracted to temperature-related aspects of +mangrove

areas relative to cleared areas. Greater abundance of certain meroplankton taxa in +mangrove areas may therefore be caused by selection for habitat with reduced predation risk and preferred settlement characteristics of the more structurally complex and turbid habitat and greater nutrient source (Mohan et al. 1997; Kingsford et al. 2002). Different swimming abilities (Holzman et al. 2005) may contribute to the taxonomic variability in intact mangrove areas, as only strong swimmers may be able to actively select mangrove root structure. Meroplankton are at a pre-settlement stage whereby selection of settlement sites is relevant. On the other hand, holoplankton do not settle out and are thus more likely to be evenly distributed across habitat types. Our finding that meroplankton are more abundant in +mangrove areas whereas holoplankton are similar (in tows) or slightly more abundant (in traps) in –mangrove areas supports this possible mechanism.

The observed differences in diversity and community composition between +mangrove and -mangrove areas suggest a potential impact of mangrove removal on coastal marine communities. Previous studies in diverse habitats demonstrate that habitat loss or transformation can lead to changes in community composition and species diversity (Boulinier et al. 2001; Silliman and Bertness 2004; Stoner and Joern 2004; Watson et al. 2004). Loss of an important habitat type like mangrove forests has implications for communities and species, and may influence adjacent habitats, such as seagrass beds and coral reefs that depend on mangroves for juvenile supply or as feeding areas for resident adults.

Mangrove deforestation may change zooplankton communities due to a decrease in physical features of the mangrove habitat, changes in food availability and water flow. Based on Randall (1967), most of the taxa sampled in this study are common or preferred food items for juvenile and adult reef fish (Figure 4.2A and B). Further research is needed to determine whether the change in zooplankton community composition observed in this study may lead to reduced food availability for juvenile and adult reef fish feeding in mangrove habitat. Whether changes in zooplankton abundance and diversity cascades into changes in fish communities on adjacent reefs following shifts in preferred prey items subsequent to mangrove removal warrants further research. In

addition, the source of larval invertebrates for adult populations on adjacent reefs may decline as the meroplankton population shifts in nearby cleared mangrove areas.

In conclusion, our study is the first to demonstrate changes in zooplankton community structure due to mangrove deforestation. Lacking still are the mechanisms responsible for those changes. There is a need for further research to understand the underlying processes driving the difference in larval and zooplankton diversity and community structure between +mangrove and -mangrove areas. We have suggested two hypotheses that may explain why larval communities differ between intact and cleared areas: differential survivorship or differential habitat preference. In addition, different settlement rates may result from differences in source populations within mangroves or differing delivery of pelagic larvae and zooplankton for short-distance dispersers. Different survivorship, habitat preference and/or settlement rates may also act synergistically to facilitate greater diversity and different community structure in intact mangrove areas than in adjacent cleared mangrove areas. Patterns observed in this study indicate potential effects of mangrove removal on trophic interactions and food web structure in inshore tropical habitats. Further research on the importance of flow rates, abiotic cues, food availability and predation risk will clarify the mechanisms behind these differences in zooplankton community structure. Examination of how differences in larval and zooplankton community structure might directly (as a larval source) or indirectly (as a food source for reef species) affect adjacent reef systems is also essential.

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Chapter 5:

Effects of anthropogenic mangrove removal on adjacent coral patch reefs

Elise Granek

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Abstract

Human disturbance to natural systems can alter not only the impacted ecosystem but also adjacent habitats. Mangrove forests, important tropical coastal habitats, are in decline worldwide primarily due to removal by humans. Similarly, coral reefs are declining due to a suite of anthropogenic influences including reduced herbivore populations and increased sedimentation. I examined the consequences of mangrove removal on adjacent inshore coral patch reefs, specifically, changes in sedimentation and algal productivity. In addition, this study evaluates changes in mangroves following removal to better understand likely impacts on downstream coral reefs. Patch reefs adjacent to cleared mangroves had higher rates of sedimentation than those adjacent to intact mangroves, but there was no difference in algal growth on patch reefs adjacent to +mangrove vs. –mangrove areas. In the inshore habitat, algal biomass was higher in –mangrove than +mangrove areas due to changes in abiotic factors (light intensity, temperature). Herbivory reduced algal biomass in both +mangrove and -mangrove areas with no effect of mangrove clearing on intensity of herbivory. Shading reduced algal biomass in both +mangrove and -mangrove areas. This study supports the hypothesis that mangrove habitat degradation can have significant impacts on downstream subtidal marine habitats, thus highlighting the importance of incorporating upstream habitat use into management and conservation strategies.

Introduction

Interface habitats are critical habitats where ecosystems intersect. Often referred to as transition zones or ecotones (e.g., rocky intertidal shores, salt marshes, riparian zones), they are not just a mixture of species from the abutting ecosystems but also harbor unique species assemblages (van der Maarel 1990). Interface habitats play important functional roles by mediating the exchange of resources (e.g., energy, nutrients, water), altering abiotic gradients (e.g., temperature, salinity, pH, sedimentation, nutrients), insulating

adjacent habitats from disturbances, and serving as critical habitat in their own right for certain life history stages of species from the adjacent habitats (van der Maarel 1990, Clark 1991).

Vegetated coastal habitats provide numerous ecosystem services. Marshes and mangroves buffer the seaward system from terrestrial source sedimentation (Golbuu et al. 2003; Kathiresan 2003; Bertness et al. 2004; Neumeier & Ciavola 2004) while protecting adjacent coastal zones from the impacts of waves and storms (Dahdouh-Guebas et al. 2005). Riparian zones (Pusey & Arthington 2003; Schade et al. 2005; Wilkinson et al. 2005) and marshes (De la Lanza Espino & Rodriguez Medina 1993; Osgood 2000) alter nutrient, temperature, and/or salinity dynamics in adjacent habitats, and some intertidal zones provide marine food resources for terrestrial fauna (Polis & Hurd 1996; Anderson & Polis 1999). Estuaries, marshes, rocky shores, sandy beaches, mangroves and riparian zones provide habitat for early life stages of invertebrates and fish that reside in upstream or downstream habitats as adults (Hering and Plachter 1997; Nagelkerken et al. 2001; 2002; Akamatsu et al. 2004; Dorenbosch et al. 2004).

Increasing evidence indicates that protecting marine habitat without consideration of interface terrestrial habitat may lead to unsuccessful conservation of target marine systems (see Stoms et al. 2005). Disturbance to interface habitat may influence community structure and ecosystem functioning in downstream habitats. Increased inputs (e.g., of sediments, nutrients or pollutants) from disturbances upstream accumulate and concentrate downstream. Upstream (terrestrial) degradation may further impede the buffering capacity of interface habitats and their ability to protect downstream habitats from disturbance.

Previous research demonstrates that mangrove removal alters abiotic conditions in the immediate habitat, leading to changes in algal growth and diversity in areas from which mangroves have been cleared (E. Granek, in review). Mangrove reduction or removal also reduces the sediment trapping ability of these coastal zones (Golbuu et al. 2003; E. Granek, in review). If mangrove disturbance alters abiotic processes and biotic communities in the immediate habitat, it is logical to postulate that downstream habitat (e.g. coral reefs) will be affected by these upstream changes.

This study examines whether mangrove removal impacted adjacent patch reefs. This necessitated establishing the types and extent of changes that occurred following mangrove removal to determine whether there were corresponding effects on reefs adjacent to each mangrove condition. On coral reefs, I predicted that sedimentation and algal growth would increase on reefs adjacent to cleared mangrove areas relative to those adjacent to intact mangrove areas. In mangrove habitat, I predicted that cleared\ mangrove areas would exhibit higher algal growth, sedimentation rates, light levels and temperature anomalies but lower levels of herbivory than adjacent +mangrove areas.

Materials and Methods

Study area. This study was conducted at Turneffe Atoll, Belize, at five paired sites (each with an intact [+mangrove] and cleared [-mangrove] area; and a patch reef adjacent to each), one unpaired cleared mangrove site (no adjacent intact area available), and three control sites (intact mangroves only). Sites were located within 30 kilometers from each other (Figure 5.1 and Table 5.1). All sites met each of the following criteria: (1) at least 75 m long stretch of cleared *Rhizophora mangle* (red mangroves) adjacent to stretches of at least 100 m of intact red mangroves; (2) fringing or patch reefs within 200 meters of the seaward mangrove edge; (3) > 2 km from major human development to exclude potential sources of anthropogenic nutrients. The coastline at all sites was characterized by *R. mangle* trees, except where stands had been removed for agriculture, construction, or viewsheds. The reef flats consisted of patch reefs at depths ranging from 1-3 meters. The -mangrove areas ranged from 75 to 250 meters in length along the shore and were either recent (within 12 months of the study deployment) or historic (~15 years prior) removals.

Recently cleared -mangrove areas retained substantial 3-dimensional structure of submerged decaying prop roots, covered subtidally with algae and fringed by seagrass along the seaward edge. In contrast, historically cleared –mangrove areas were characterized by minimal residual submerged decaying prop roots with some macroalgal

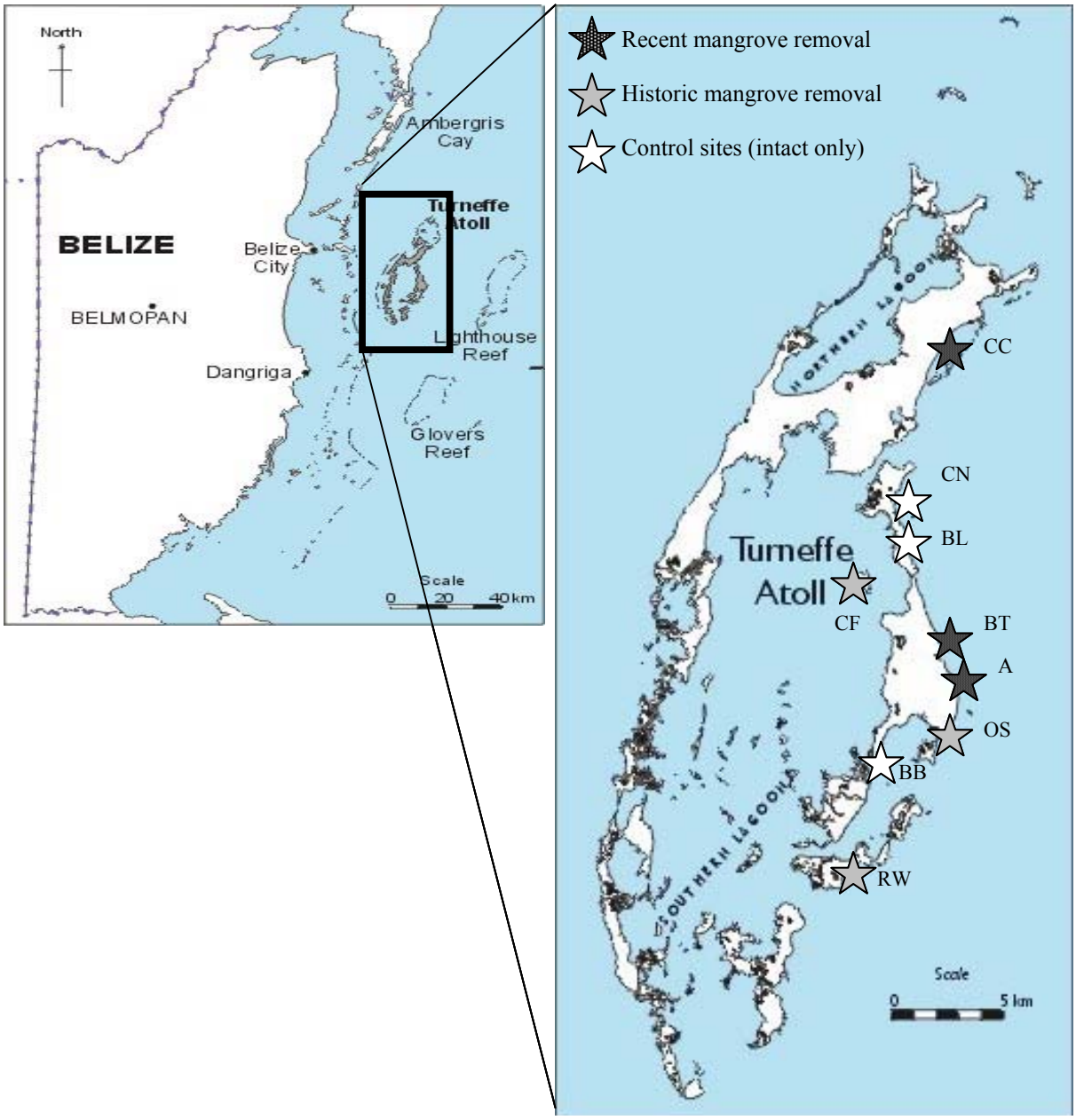

Figure 5.1. The nine sites in this study included 5 paired sites, 1 cleared only site and 3 control sites (only intact mangrove areas). Recent mangrove removal areas were cleared within 12 months prior to study deployment; historic mangrove removal areas were cleared >10 years prior. Sites include from north to south Cockroach Caye (CC), Control North (CN), Blackbird Control (BL), Crayfish Caye (CF), Blue Tarp (BT), Airport (A), Oceanic Station (OS), Bull Bay Control (BB), and Rope Walk (RW).

growth inshore and seagrass growing into the previous mangrove habitat. Submerged regions of +mangrove areas were characterized by prop roots colonized by epibiotic algae, sponges, tunicates and anemones. Detailed characteristics of each site can be found in Table 5.1.

Each site included two areas (+ mangrove and -mangrove) with two habitats (mangrove edge and reef flat) sampled in each area. Control sites had only +mangrove areas. Transects were parallel in both mangrove edge (ME) and reef flat (RF) habitat.

Algal Biomass and Richness. Algal and cyanobacterial biomass were quantified at the nine sites along thirty-five 20-meter long transects parallel to shore. The natural community was sampled by point counts conducted along all transects to determine the percent natural algal cover along the substrate. However, because the natural substrate is so variable and, along mangrove transects, is not solid (i.e. detritus/mud/sand with macroalgae and cyanobacteria), I also placed 1-mm diameter yellow nylon cord approximately 30 cm above the substratum. Nylon cord was used as a substrate because it allowed for easy sampling and is known to facilitate macroalgal growth in aquaculture (Buck and Buchholtz 2004). The cord simulates hard substratum including root structure or dead coral and was suitable as a uniform substrate from which algal growth could be sampled in both habitat types. The nylon cord was used as a standard surface to minimize differences in substratum heterogeneity but was not intended to simulate the natural substrate or to serve as areas with exact replicas of the natural community.

Samples were taken by removing six randomly selected 15-cm long segments from each line at three (September 2005) and six (January 2006) months after the experiment was initiated. Sampled segments were replaced with a different color nylon cord to denote that the section had been sampled. Sample lines were rinsed to remove detritus and sand, and algal taxa (genera were used as a proxy for functional groups) were identified under a dissecting scope based on Littler and Littler (2000). Since ecological studies involving marine algae often take a functional-form approach (i.e. Steneck and Dethier 1994), and most genera observed had few (1-3) species, here taxon diversity is quantified as the number of genera (based on similar functional form). After

Table 5.1. Characteristics of mangrove areas by site. N/a refers to 'not applicable' because these sites were intact controls with no mangrove clearings.

Site	**Location**	**ME transects**	**Time cleared**	**Mangrove removal size**	**Subtidal structure in -mangrove**	**Fringing seagrass**
Airport (A)	Blackbird Caye	+ and -	< 1 yr	75 m	Intact	*Thalassia testudinum*
Blue Tarp (BT)	Blackbird Caye	+ and -	< 1 yr	75 m	Reduced	*Thalassia testudinum*
Cockroach Caye (CC)	Cockroach Caye	+ and -	< 1 yr	250 m	Intact	*Thalassia testudinum*
Rope Walk (RW)	Ropewalk Bogue	+ and -	~15 yrs	250 m	Minimal	*Thalassia testudinum Syringodium filiforme*
Crayfish Caye (CF)	Lagoon	+ and -	~15 yrs	75 m	Reduced	*Thalassia testudinum*
Oceanic Station (OS)	Blackbird Caye	- only	~15 yrs	250 m	Minimal	*Thalassia testudinum Halodule wrightii*
Blackbird (BL)	Blackbird Caye	+ only	n/a	n/a	n/a	*Thalassia testudinum*
Bull Bay (BB)	Calabash Caye	+ only	n/a	n/a	n/a	*Thalassia testudinum*
Control N (CN)	Blackbird Caye	+ only	n/a	n/a	n/a	*Thalassia testudinum*

identification, all biomass was scraped off the line and dried at 60°C until no further weight loss occurred. Dried samples were weighed to determine biomass.

Herbivory. To quantify the influence of herbivorous fishes on differences in algal biomass between +mangrove and -mangrove areas, herbivore exclusion cages (-herbivores) were deployed along the mangrove transects. I constructed herbivore exclusion cages of Naltex tubular diamond mesh bag (1.4 cm mesh) stretched to ~20 cm in length and held open with three rings of ¾ cm x 15 cm PVC rings. Mesh-lined ends were covered with Vexar L-30 mesh (Redden Net Company Inc., Port Coquitlam, BC, Canada). Cage controls (+herbivores) were similar but had two 6-cm diameter holes cut in the mesh on each side of the cage to allow herbivore access. The cages were threaded onto the lines when the experiment was deployed. This design excluded herbivorous fishes from the 20-cm stretch of cord surrounded by the cage. The central 15-cm of line in cages and cage controls was sampled after six months as described above. The effects of herbivory are defined as the difference between algal biomass in cages and cage controls. Cage effects were quantified by comparing algal biomass in cage controls to that on 15 cm-long segments of open line.

Water temperature and light variation. Two i-button data loggers (i-button Temperature Loggers DS1921G, Maxim Direct, Dallas, TX) were programmed to measure temperature hourly and deployed along each ME (mangrove edge) transect line at the beginning of the experiment. To focus on temperature anomalies, I calculated the number of high temperature events exceeding 30.5°C (selected because reef temperatures rarely exceed 30°C; E. Granek, unpublished data) over the course of the experiment.

Light intensity was measured on ME transects using a Li-cor Underwater Quantum Sensor (LI-192) and a Li-cor Atmospheric Quantum Sensor (LI-190) to standardize light measurements to ambient light conditions; measurements were recorded with a Li-cor data logger (LI-1400). Four light readings were taken per point at five points along each transect. Measurements were standardized to ambient light readings and averaged to determine mean light intensity per transect line (μmoles).

Shading. An experiment was established to further examine the effects of light on algal growth and test whether light limitation is the primary driver of differences in algal growth between +mangrove and –mangrove areas. The experiment consisted of shades (+shade) and shade controls (-shade). Shades were constructed of 0.25 x 0.25 m PVC quadrats covered with Vexar L-30 mesh (Redden Net Company Inc., Port Coquitlam, BC, Canada), attached to the PVC frame with cable ties. and placed over 4 rebar stakes at each corner of the quadrat. Shade controls consisted of PVC quadrats without a Vexar mesh cover.

Sedimentation. Sedimentation rates were measured on all transects (ME and RF [reef flat]) using 3.81-cm diameter x 19.05-cm PVC tubes capped at the bottom and anchored to rebar stakes. Three sediment traps were deployed on each transect line. Sediment traps were sampled at 3 months and redeployed and resampled at six months. Sediment was removed from each trap, characterized qualitatively, and dried at 60ºC until no further weight loss occurred. Final dry weight was recorded and mean sedimentation per transect was calculated.

Statistical analysis. Prior to analysis, algal biomass, light intensity, high temperature events, sedimentation, shading and herbivory were normalized using a $\log_{10}$ +1 transformation.

Reefs. I used a one-way analysis of variance (ANOVA) to determine if algal growth and sedimentation differed between reefs adjacent to +mangrove versus -mangrove areas. The land activity and reef characteristics among the three historic -mangrove sites were highly variable. Therefore, I analyzed the three paired sites at which mangroves had been cleared in the last year separately from the historic set. Number of algal taxa per line was averaged for each transect to determine differences in algal taxon diversity in reefs adjacent to +mangrove vs. -mangrove transects. An ANOVA was employed to determine if generic richness and sedimentation differed on reefs adjacent to +mangrove versus –mangrove areas.

*Mangroves***.** The above analyses were repeated to examine differences in algal biomass and richness between -mangrove and +mangrove areas. A multivariate analysis of variance (MANOVA) and single factor ANOVAs were run to quantify the extent to which each factor (light intensity, high temperature events and sediment accumulation) was contributing to the differences in algal biomass between -mangrove and +mangrove habitat. For the grazing component, I used a fixed-effects ANOVA to test the effects of herbivory (cage controls vs. complete cages), mangroves (+mangroves, -mangroves), time since clearing (recent versus >10 years) and all possible interactions on algal biomass. Similarly, for the shading experiment I used a fixed-effects ANOVA to examine effects of shading (+shade, -shade), mangrove condition (+mangroves, -mangroves), time since clearing (recent versus >10 years) and all possible interactions on algal biomass.

Results

Reefs

Algal biomass and richness. Algal biomass on reefs adjacent to -mangrove areas did not differ from that on +mangrove areas in either September 2005 (ANOVA, $F = 0.14$; $p = 0.72$) or January 2006 (ANOVA, $F = 0.02$; $p = 0.90$). Similarly, the average number of algal and cyanobacterial genera per line did not differ between patch reefs near +mangrove areas and those near -mangrove areas (January 2006; ANOVA, $F = 0.32$; $p = 0.6$). Algae covered 74.2% (standard error = 4.16) of the coral and rubble (hard) substrate across all reef transects.

***Sedimentation*.** At recently disturbed sites, sedimentation rates were greater on reefs adjacent to -mangrove than those adjacent to +mangrove areas after three months (Figure 5.2a)(ANOVA, $F=7.74$; df 1, 4; $p<0.05$), but not between three and six months (Figure 5.2b) (ANOVA, $F=1.61$; df 1, 4; $p=0.27$).

Mangroves

Algal biomass and richness. In the ME areas (+mangrove and -mangrove areas), algal biomass was higher in -mangrove than in +mangrove areas both after three months (ANOVA, $F = 5.99$; $p = 0.03$) and six months (ANOVA, $F = 13.27$; $p < 0.005$) (Figure 5.3). However, the average number of algal and cyanobacterial genera per line did not differ between +mangrove and -mangrove areas (January 2006; ANOVA, $F = 0.46$; $p = 0.55$).

Herbivory. Algal biomass in +herbivore treatments was lower than in -herbivore treatments indicating a strong effect of herbivory (ANOVA, $F=8.12$; $p< 0.009$) even after accounting for the strong cage effect (ANOVA, $F=3.02$, $p=0.07$). Herbivory did not vary with site ($p> 0.5$) but was higher at the historically cleared site than the recently cleared sites (ANOVA, $F=8.29$; $p< 0.002$). There was no difference in the magnitude of herbivory between +mangrove and -mangrove areas (i.e., there was no herbivore x mangrove interaction) (Table 5.2a).

Shading Algal biomass in +shade treatments was lower than in –shade treatments indicating a strong effect of shading on algal growth (ANOVA, $F=6.74$; $p= 0.02$).

Furthermore, there was greater algal biomass in -mangrove than in +mangrove areas (ANOVA, $F=10.6$; $p<0.005$). There was no difference in the magnitude of shade effect between +mangrove and -mangrove areas (i.e., there was no shade x mangrove interaction) (Table 5.2b).

Abiotic factors. Abiotic conditions (light intensity, high temperature events, sedimentation) differed in -mangrove areas and +mangrove areas (MANOVA, $F= 51.55$; df 1, 12; Wilks' Lambda = 0.06; $p<0.0001$). The differences in abiotic conditions were primarily due to light and temperature. As expected, light intensity was greater in -mangrove than in + mangrove areas (ANOVA, $F=6.2$; df 1, 12; $p<0.0001$) (Fig. 5.4a).

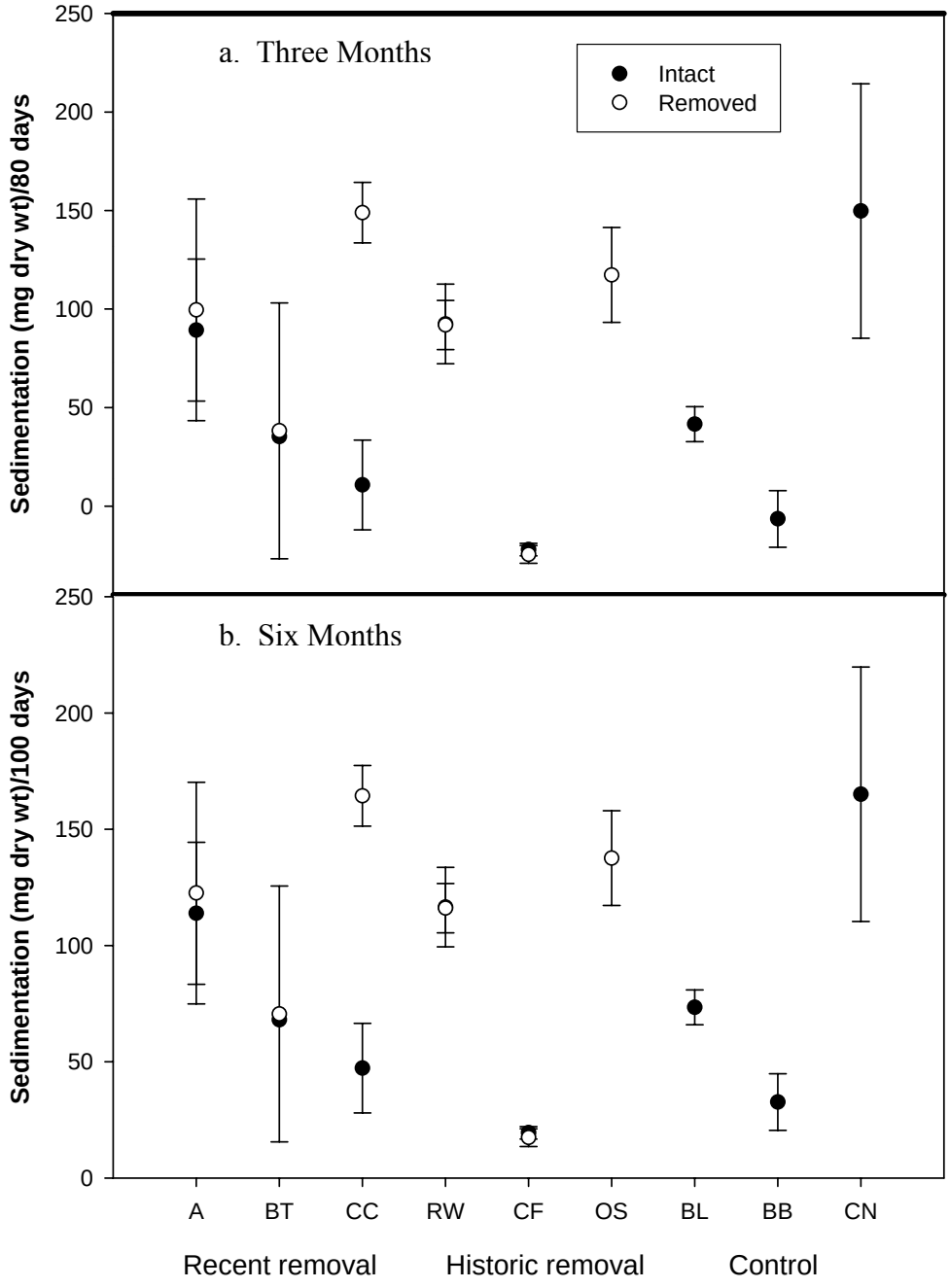

Figure 5.2 Mean (+/- standard error) amount of sediment arriving at reef patches adjacent to intact (+mangrove) and cleared (–mangrove) areas after (a) three and (b) six months. Sites are grouped based on the time since clearing (recent, historic, or control).

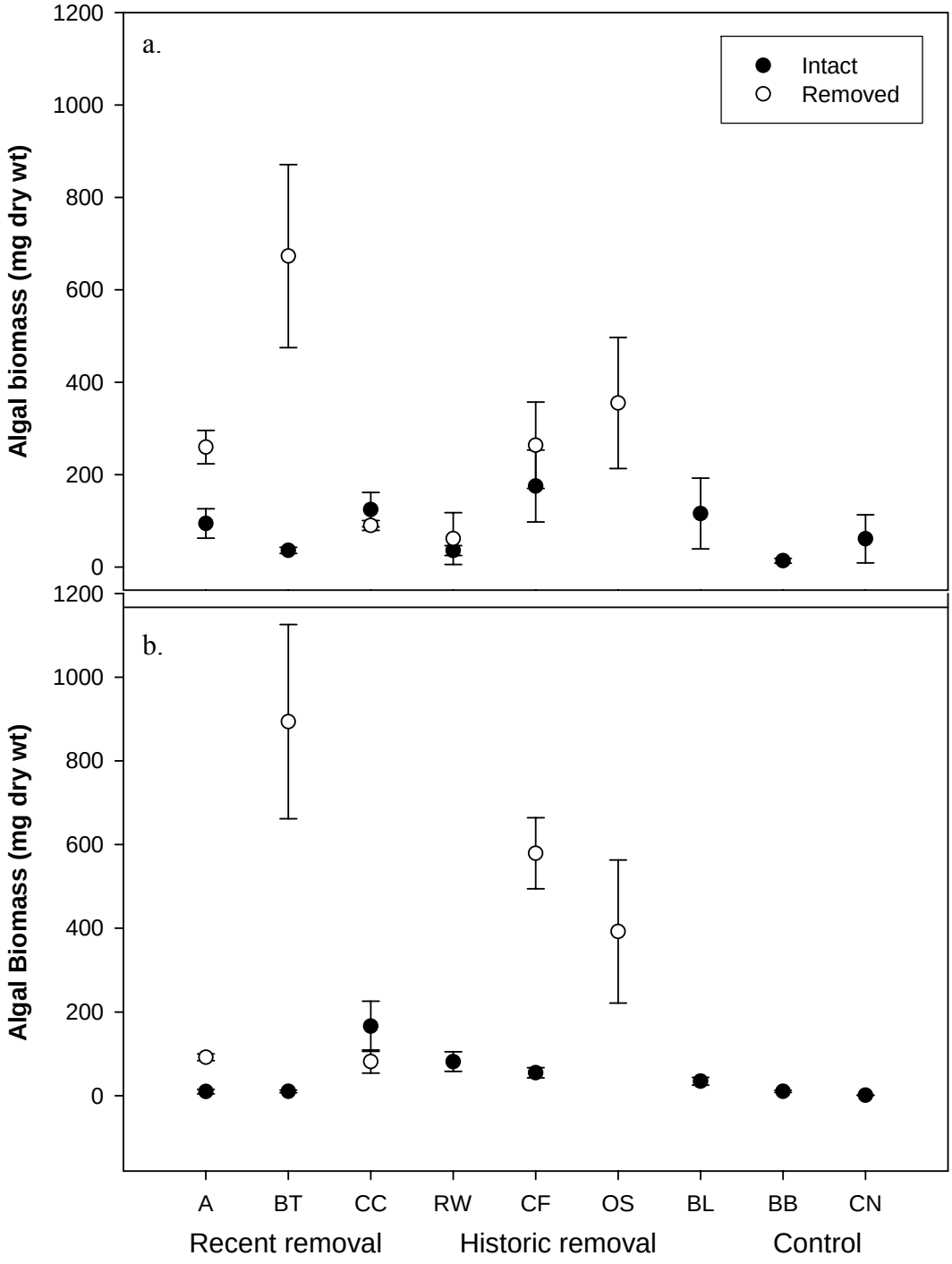

Figure 5.3. Mean (+/- standard error) algal growth in intact (+mangrove) and removed (-mangrove) areas after (a) three and (b) six months.

Table 5.2. Effects of (a) herbivory (cage vs. partial cage) or (b) shading and mangrove condition, time since clearing and all possible interactions on algal biomass in mangrove edge areas.

(a)

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)
Mangrove (+/-)	1	23.22	23.22	16.22	**0.0008**
Time cleared (0, 1 yr, >10yr)	2	8.53	4.27	2.98	0.076
Herbivory (+, partial, -)	2	7.36	3.68	2.57	0.104
Mangrove x Time cleared	1	0. 70	0.697	0.49	0.49
Mangrove x Herbivory	2	3.42	1.71	1.19	0.326
Time cleared x Herbivory	4	2.34	0.59	0.41	0.80
Mangrove x Time cleared x Herbivory	2	0.62	0.31	0.22	0.81
Residuals	18	25.78	1.43		

(b)

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Time cleared (0, 1 yr, >10yr)	2	20.16	10.08	7.86	**0.0042**
Shade (+,-)	1	8.64	8.64	6.74	**0.019**
Mangrove (+,-)	1	13.58	13.58	10.599	**0.005**
Time cleared x Shade	2	0.51	0.25	0.198	0.823
Time cleared x Mangrove	1	0.024	0.02	0.019	0.89
Shade x Mangrove	1	0.108	0.108	0.084	0.776
Time cleared x Shade x Mangrove	1	0.027	0.027	0.021	0.886
Residuals	16	20.507	1.282		

a.

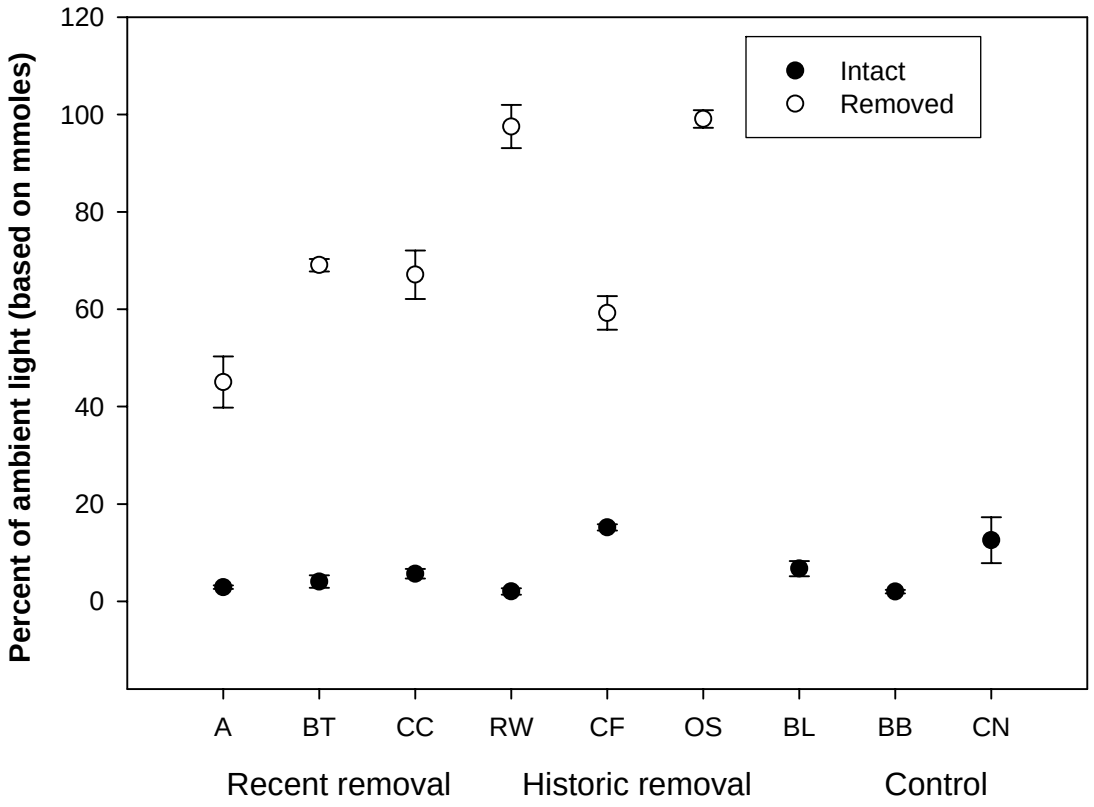

Figure 5.4. Abiotic changes in intact (+mangrove) and removed (-mangrove) areas: (a) light (measured at experiment deployment) (b) temperature during first three months, (c) temperature from three to six months and sedimentation from (d) 0-3 months and (e) 3-6 months. Means (+/- standard error).

The number of high temperature events was also greater in -mangrove than in +mangrove areas both from July to September 2005 (ANOVA, $F= 6.2$; df 1, 12; $p<0.03$) and from October to January 2006 (ANOVA, $F=6.57$, $p<0.03$) (Fig. 5.4b and c). Sedimentation rates were not different between -mangrove and +mangrove areas at three (Fig. 5.4d) (ANOVA, $F=0.05$; df 1, 12; $p=0.82$) or six months (ANOVA, $F= 1.97$; df 1, 10; $p=0.19$) (Fig. 5.4e).

Discussion

To put these results in context, it is important to establish the types and extent of changes that occurred within mangrove habitat after removal to determine probable effects on reefs. Removal of mangroves increases light availability and frequency of high temperature events, leading to increased macroalgal biomass relative to areas with undisturbed mangrove forests. In this study, macroalgal growth was generally lower in undisturbed +mangrove systems than in adjacent -mangrove areas, though Belizean mangrove root and substrate communities contain diverse algal and cyanobacterial taxa (Joye and Lee 2004, Littler et al. 2000). This change indicates that tropical mangroves directly alter their local abiotic environment by both providing shade and moderating temperature, and thus indirectly controlling regional algal abundance.

The importance of light in altering algal community structure is further supported by the shading experiment whereby algal growth was reduced on transects when shaded. The level of algal reduction with shading did not differ between +mangrove and -mangrove areas, but there was greater algal growth at historically cleared sites. This is corroborated by previous studies demonstrating that low light levels are less than optimal for growth of many macroalgal and cyanobacterial genera (Irving and Connell 2002; Pang and Luning 2004).

Sedimentation rates did not differ between +mangrove and –mangrove areas, though there was high among-site variability. Variation in sedimentation rates in -mangrove areas was probably affected by the amount of remaining structure following clearing (at recently cleared sites) and the changes in land use since clearing (at

historically cleared sites). At the two recent mangrove-removal sites (A and CC) with the majority of trunk and prop root structure still present in the -mangrove areas, sedimentation rates more closely resembled adjacent intact mangroves. At the recent mangrove-removal site (BT) where little root structure was left following mangrove removal (and terrestrial clearing is ongoing), sedimentation in -mangrove areas was much higher than adjacent +mangrove areas. At historically cleared sites, land transformation is more variable. At one site (RW), both the -mangrove area and the adjacent terrestrial habitat were filled (by humans) with sand following clearing, reducing the sediment source to the immediate area and to adjacent patch reefs via sediment burial. In contrast, another historic mangrove-removal site (CF) has ongoing land clearing and continues to have high sedimentation from the land into -mangrove areas; however little sediment is carried out to the patch reefs here, perhaps due to reduced flow at this site. This among-site variability demonstrates how extent of disturbance to an interface habitat and compounding effects from upland habitat disturbance influence the degree of impact on immediate and downstream abiotic processes.

Consumption of algae by herbivores was measurable in all ME areas but was not affected by mangrove removal. The similar differences between exclusion cages and cage controls indicate that grazing impact was comparable in +mangrove and -mangrove areas. However, there was an effect of time-since-clearing on the level of herbivory, suggesting that herbivore assemblages may have shifted following mangrove loss. The similarity in herbivory detected between +mangrove and -mangrove areas is likely scale-dependent. The pattern may be a byproduct of the fairly small extent of mangrove removal in the study area, i.e. the distance to the -mangrove areas may be sufficiently short for herbivores (e.g. fishes) to transit from adjacent intact mangrove habitat to feed on abundant algae in -mangrove areas.

Moreover, algal biomass in cages varied based on time since clearing (Table 5.2). This pattern is driven by the higher overall algal biomass at the historical mangrove-removal site in the lagoon (this was the only historically cleared site at which cages were not removed by Tropical Storm Wilma in October 2005). Greater algal biomass and thereby greater food availability in this cleared area may attract herbivorous fishes

sheltering in nearby intact mangrove areas (de la Moriniere et al. 2004). These patterns indicate that disturbance to mangrove structure increased the dominance of algae via shifts in abiotic (light, temperature, sedimentation) (see also Noe and Zedler 2000) rather than biotic (herbivory) factors.

The effect of mangrove removal on adjacent patch reefs was evident only on reefs near recently cleared mangroves. Recent mangrove clearing led to increased sedimentation on inshore patch reefs but with no difference in algal growth associated with mangrove condition. The land use and disturbance at recently cleared sites were quite similar, whereas those sites at which mangroves had been cleared for over a decade, land use was highly variable (filling with sand, deforestation of inland habitat, etc.), which may have accounted for the large variability in impacts on reefs adjacent to these historical clearings. I infer that changes in the sediment trapping efficiency of mangroves following removal led to a short-term increase in sedimentation on adjacent reefs.

Hurricane Wilma hit Turneffe Atoll with tropical storm level surge, wind and waves for five days in October 2005, between the three-month and six-month sampling periods. This disturbance caused significant sand movement at all sites resulting in sediment traps on the reef being filled with sand and *Halimeda* spp. flakes rather than with a combination of sand and detritus as occurs under normal weather conditions. As a result, sedimentation rates at the six-month sampling period did not vary among any of the factors tested.

The increase in sedimentation detected after three months appears to drop off (at historic mangrove-removal sites) after the majority of built-up mangrove detritus has been washed out of the mangrove-cleared areas, unless further deforestation continues on land. This increase in reef sedimentation may alter community structure on adjacent patch reefs as sediment-tolerant coral and algal species will be most likely to thrive with concurrent declines of sediment-sensitive corals (Stafford-Smith 1993). McClanahan and Obura (1997) found that high sedimentation can lead to shifts from hard coral-dominated to soft-coral and sponge dominated communities. Other studies indicate that high sediment loading may decrease settlement success for certain coral species (Babcock and Davies 1991). Therefore, changes in sediment delivery to reefs following mangrove

clearing has implications for coral community composition and structure on nearshore reefs. High sediment loading from mangrove clearing further compounds the stress imposed on Caribbean reefs by declining herbivores, increasing disease, historical hurricane damage, and rising sea surface temperatures (Nyström et al. 2000), UNEP 1995).

On Turneffe Atoll, there is no evidence that mangrove removal had an effect on algal community structure on adjacent reefs. The lack of a mangrove condition effect on reef algal growth may indicate no difference in propagule source between -mangrove and +mangrove areas despite increased algal growth inland in -mangrove areas. However, most likely, the similarity in reef algal growth may be an artifact of the already high levels of algal growth (74% of hard substrate has algal cover) on Belizean reefs off the east coast of Turneffee Atoll, with no additional impact of increased propagules from -mangrove areas. With such high ambient levels of algal growth, it may be difficult to detect additional effects from mangrove clearing. Furthermore, the distance between mangroves and reefs may be too great for an increase in propagule supply inland to affect the community composition on the reefs.

In this study, disturbance to mangrove forests changed abiotic factors including light intensity, temperature, and sedimentation, triggering shifts in the biotic community locally, leading to increased algal abundance. Altered conditions in the mangrove forests impacted an abiotic condition, sedimentation, on adjacent reefs. These results highlight the importance of considering the effects of interface habitat degradation (here, mangrove forests) on functioning and structure in adjacent, downstream systems, i.e. coral reefs and seagrass beds, and how these effects change over time. Understanding these cascading processes is essential for developing effective management strategies in coastal regions. Identifying processes that influence shifts in ecosystem functioning and community structure and the biotic or abiotic consequences of their activities in other, adjacent systems, is necessary for addressing management, restoration, and conservation of both human-disturbed ecosystems and adjacent, un-manipulated natural systems.

Acknowledgements

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Chapter 6:
Mangrove-exported nutrients on coral reefs?

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Abstract

The high net primary production in mangrove forests has led to the investigation of the importance of mangrove habitat as a source of organic matter (OM) for adjacent marine systems. To date, the contribution of mangrove-derived nutrients to marine food webs has focused primarily on mobile fishes or invertebrates and mangrove sediments, whereas the contribution to sessile reef invertebrates such as corals has not been well examined. Understanding the consequences of declining cover of mangroves worldwide due to anthropogenic disturbance necessitates consideration of how mangrove-derived nutrients contribute to threatened coral reef systems nearby. Recent research has suggested that the low nutrient content of mangrove OM would lead to little uptake through the food web. We sampled potential sources of OM (decaying mangrove leaves, phytoplankton, macroalgae, and seagrass) and a suite of sessile reef invertebrate consumers including hard corals, sponges, a bivalve mollusc, polychaete annelid and tunicate, from six sites in Bocas del Toro, Panama in the Caribbean Sea to conduct stable isotope analysis using $\delta^{34}S$ and $\delta^{13}C$. Using IsoSource mixing models, we determined the range of potential contributions to consumers from the various organic matter sources in the system. We identified three major, distinct sources supported by $\delta^{34}S$ and $\delta^{13}C$. Contributions of macroalgae and seagrass were indeterminate due to the high variability in the range of potential source contributions. In contrast, mangrove contribution was often significant and the range of potential contributions was constrained, though this varied by consumer taxon. Mangrove OM contributed substantially to most filter feeders ranging across sites from 11-53% for sponges, 18-44% for file clams, and 29-51% for feather duster worms. One filter feeder, a solitary tunicate, was the exception with only a 0-7% contribution from mangroves. Among the corals, the contribution of mangroves to their organic intake varied by feeding mode of the coral. Mangrove contribution to heterotrophic corals (*Acropora cervicornis, Montastrea annularis,* and *Diploria* sp.) ranged from 7-24% whereas mangrove contribution to more autotrophic corals (*Agaricia fragilis* and *A. tenuifolia*) was more variable (0-31%). To examine how the contribution from mangroves to sessile reef invertebrates varied with distance from a mangrove source we conducted a sponge transplant experiment. Results indicated that the mangrove

contribution to three sponge species declined with increasing distance from shore. These results provide the first evidence that mangrove inputs of organic matter to sessile invertebrate species are substantial , accounting for up to 53% of the composition. Thus, removal of mangroves from tropical shores can potentially generate a serious deficit in the organic inputs to reef organisms, with as yet unknown but possibly major ecological consequences for the integrity and persistence of reefs.

Introduction

Mangrove forests are productive tropical and subtropical coastal marine ecosystems (Odum and Heald 1975, Jennerjahn and Ittekkot 2002). They have net primary production (NPP) in considerable excess of the carbon utilized in the system, with an estimated 40% of NPP exported (Duarte and Cebrian 1996). This high export of NPP has led various researchers to examine the contributions of mangrove-fixed carbon to adjacent inshore habitats and open ocean (John and Lawson 1990, Duarte and Cebrian 1996, Dittmar and Lara 2001, Jennerjahn and Ittekkot 2002), including the incorporation of mangrove-derived nutrients into seagrass systems (Sheaves and Molony 2000). In addition, a suite of studies have examined incorporation of mangrove production into organisms ranging from zooplankton (Bouillon et al. 2000) to mobile marine invertebrates (France 1998, Christensen et al. 2001, Fry and Smith 2002a, Fry and Smith 2002b, Schwamborn et al. 2002, Werry and Lee 2005) and fishes (Sheaves and Molony 2000, Fry and Ewel 2003, Nagelkerken and van der Velde 2004a, b, Benstead et al. 2006). These mobile organisms may serve as a pathway for export of mangrove-derived nutrients. Whether or not sessile reef invertebrates are also directly incorporating mangrove NPP remains an open question.

Stable isotope analysis can provide insights into the relative importance of the various primary producers contributing to a system (Bouillon et al. 2002), as the relative abundance of stable isotopes (e.g., ^{13}C vs. ^{12}C) of the food sources are reflected in the tissues of consumers. Odum and Heald (1972, 1975) stated that mangrove detritus and the high productivity from mangrove trees is incorporated into food webs both in and adjacent to mangroves. However, more recent studies indicate that less abundant primary

producers (phytoplankton, micro- and macro-algae) may be more important than mangrove leaves or detritus because of the higher nitrogen content of microalgae and macroalgae compared to mangrove matter (Stoner and Zimmerman 1988, Ambler et al. 1994, Newell et al. 1995, Primavera 1996, Loneragan et al. 1997, Marguillier et al. 1997, France 1998).

To date, research has not explicitly examined whether mangrove-derived nutrients are incorporated into sessile reef invertebrates. Nor has the primary mechanism of mangrove-nutrient export been determined; possible pathways include export by reef-resident fish and mobile invertebrate species (Fry and Smith 2002a), or via currents (Lee 1995, Jennerjahn and Ittekkot 1997). In this study we examine whether sessile reef invertebrates, including corals, sponges, file clams and feather duster worms, are incorporating mangrove-derived nutrients into their tissues. We also investigate whether distance from mangroves affects the level of incorporation by (1) conducting a sponge transplant experiment and (2) sampling natural populations on reefs at varying distances from mangrove forests. Our ultimate goal in this study was to determine if exported mangrove carbon is contributing to reef structure and community composition and to assess how loss of mangrove habitat may affect nutrient availability on inshore and offshore reef systems.

Methods

Study Area

This study included samples from six sites around Bocas del Toro, Panama (Fig. 1). We sampled five sites in Almirante Bay, located in Bocas del Toro Province and one control site outside of Almirante Bay. The five bay sites were located within 20 kilometers of each other, whereas the control site was located ~30 km from the bay sites. Three were on Isla Colon, one was on Isla Pastores, and one was on the mainland south of Almirante (Figure 1). The sites met the following criteria: (1) they included at least 100 m long stretches of cleared *Rhizophora mangle* red mangroves adjacent to at least 100 m long stretches of intact fringing red mangroves; (2) fringing or patch reefs

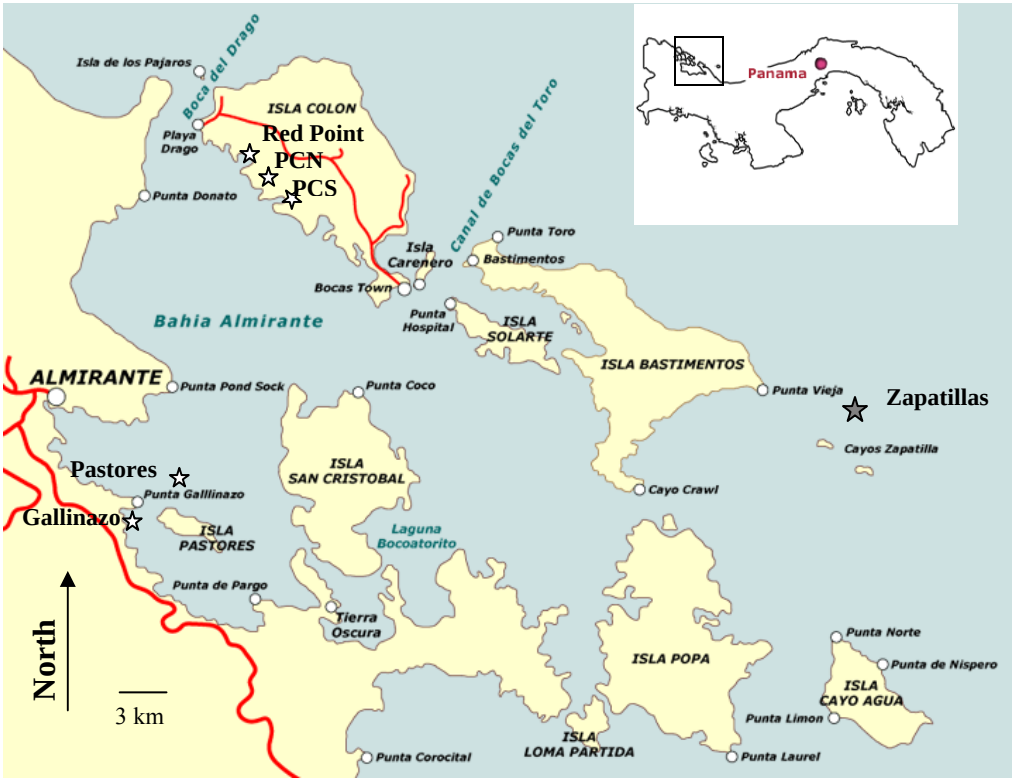


Figure 6.1. Map of study area in Bocas del Toro, Panama in the Caribbean Sea.

occurred within 100 meters of the seaward mangrove edge; and (3) to exclude potential sources of anthropogenic nutrients they were > 2 km from major human development or construction. At all sites, primary producers and sessile reef invertebrates were sampled along transects placed in the following habitat types: center of the mangroves (MC), seaward edge of the mangroves (ME), fringing reef flat (RF) and the reef slope (RS).

The sites along Isla Colon included, from the northwest to southeast, Red Point (RP), Punta Caracole North (PCN), and Punta Caracole South (PCS). The site on Isla Pastores is referred to as Pastores and the site on the mainland as Gallinazo due to its proximity to Punta Gallinazo. The coastline at all Almirante Bay sites was characterized by *Rhizophora mangle* trees, except where stands had been removed for subsistence agriculture, construction, or viewsheds (to create an ocean view for homes). Below we refer to these as "cleared" areas, and contrast them to "intact" areas with undisturbed mangroves. Cleared areas ranged from 100 to 300 meters in length along the shore. On Isla Colon, clearance occurred approximately 8 years prior to this study and cleared areas were characterized by submerged decaying prop roots on the substrate with substantial cover of macroalgae inshore and of the seagrass *Thalassia testudinum* further from shore. Little 3-dimensional structure remained in these cleared areas. At the Pastores and Gallinazo sites, clearance occurred during the 12 months prior to sampling and disturbed areas retained dead, exposed mangrove stands covered subtidally with algae and fringed by seagrass along the seaward edge. At Pastores and Gallinazo, subtidal root structure in cleared areas was substantially greater leading to subtidal structure intermediate between intact areas and the three Isla Colon cleared areas. Intact areas were characterized by submerged prop roots colonized by oysters, sponges, sporadic coral heads, and infrequently epibiotic algae with occasional non-forested channels between trees. At all five sites, reef flats were predominantly *Porites furcata* and *Millepora alcicornis* interspersed with macroalgae. Reef slopes were a mix of hard corals, soft corals, and numerous sponge colonies; turbidity was often high and visibility was generally low on reef slope transects.

A control site (no mangroves present) was located at Zapatillas Caye, ~10 km from the nearest mangroves (Figure 1) outside of Almirante Bay. This site is

characterized by strong wave action, lower turbidity, greater visibility (implying lower nutrients) and flushing and different sessile community composition from the Almirante Bay sites. The Zapatillas Caye reef was dominated by hard corals with few sponge colonies and low algal cover.

Sample collection and preparation

Naturally occurring organisms

In March and July 2004, primary producer and sessile reef invertebrate samples were collected from the six Bocas del Toro sites. Four individuals were collected per species per transect. Primary producers included decaying *Rhizophora mangle* mangrove leaves (Fry and Smith 2002b), collected from the substrate under mangrove trees, *Thalassia testudinum* seagrass blades, dominant macroalgae (*Padina* spp., *Caulerpa* spp., *Dictyota* spp., *Halimeda* spp., and composite filamentous and branching red algae), and phytoplankton. Phytoplankton was sampled by filtering 2-liter samples of seawater collected over the reef slope onto a 25-mm, 0.7 μm Whatman GF/F glass microfibre filter. Sessile reef invertebrates included corals (*Agaricia tenuifolia, A. fragilis, Acropora cervicornis, Porites furcata,* and *Montastrea sp.*), sponges (*Amphimedon compressa, Aplysina fulva, Niphates erecta)*, the rough file clam (*Lima scabra)*, magnificent featherduster worm (*Sabellastarte sp.*) and a solitary tunicate (*Phallusia nigra*). The feather duster worm was only found in sufficient abundance to sample at one site.

Coral samples were prepared by airbrushing tissue off of the coral skeleton to remove live tissue. The extracted tissue was dried for analysis. File clams were removed from their shells and the tissue was retained for analysis. Feather duster worms were separated from their tubes and tissue and tubes were analyzed separately. Samples were rinsed in deionized (DI) water and dried at 60ºC until no further weight loss occurred.

All primary producer and filter feeder samples were ground using a steel tube-and-ball "wiggle-worm" grinder to homogenize whole body tissue. Samples were ground for two minutes, redried at 60ºC for at least 4 hours, then weighed into tin cups for analysis with an Elemental Analyzer. Samples were run for $\delta^{15}N$ and $\delta^{13}C$ on a Costech

ECS 4010 elemental analyzer interfaced through a ThermoFinnigan Conflo III to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer at the EPA Integrated Stable Isotope Research Facility laboratory in Corvallis, Oregon. Samples were run for $\delta^{34}S$ at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University on a Carlo Erba NC2100 Elemental Analyzer interfaced to a Thermo-Finnigan Delta Plus Advantage isotope ratio mass spectrometer. In order to combust high-weight samples with low % sulfur, a Costech Analytical Technologies ECS4010 Elemental Analyzer with a 20-ml O_2 loop was used in place of the CE NC2100.

Isotope values are expressed as $\delta^{34}S$ or $\delta^{13}C$ (with units of ‰) determined by the following equation:

$$\delta^{34}S \text{ or } \delta^{13}C = [(R_{sample}/R_{standard})-1] \times 1000$$

where $R = {}^{13}C/{}^{12}C$, ${}^{34}S/{}^{32}S$. Reference standards were PeeDee Belemnite Carbonate and Canyon Diablo Troilite for $\delta^{13}C$ and $\delta^{34}S$, respectively. Internal standards were interspersed with samples in all runs to control for drift within and among runs.

Sponge transplant experiment

A transplant experiment was carried out to investigate whether distance from mangroves affects the level of incorporation of mangrove-derived nutrients. In March 2004, a large colony of each of three sponge species (*Aplysina fulva, Amphimedon compressa, Niphates erecta*) was identified to use in the transplant experiment. The *Niphates erecta* source colony was along a mangrove edge, the *Aplysina fulva* colony was on a reef flat area, and the *Amphimedon compressa* colony was on a reef slope area. A segment of each sponge colony was removed and cut into 100 3-cm long pieces. Each sponge piece was measured for volume and attached with a zip-tie to a 1.27-cm diameter by 7.62-cm long PVC tube. All sponge segments were strung on a line at the collection site to acclimate to their PVC for 24-48 hours. Following this acclimation period, sponge pieces were randomly out-transplanted to the 16 transects at the Punta Caracole North site on Isla Colon (see Figure 2). Six replicates of each species were attached to rebar stakes in each habitat type including (1) the center of the mangroves (MC), (2) along the seaward edge of the mangroves (ME), (3) on the reef flat (RF) ~50 m from the mangrove

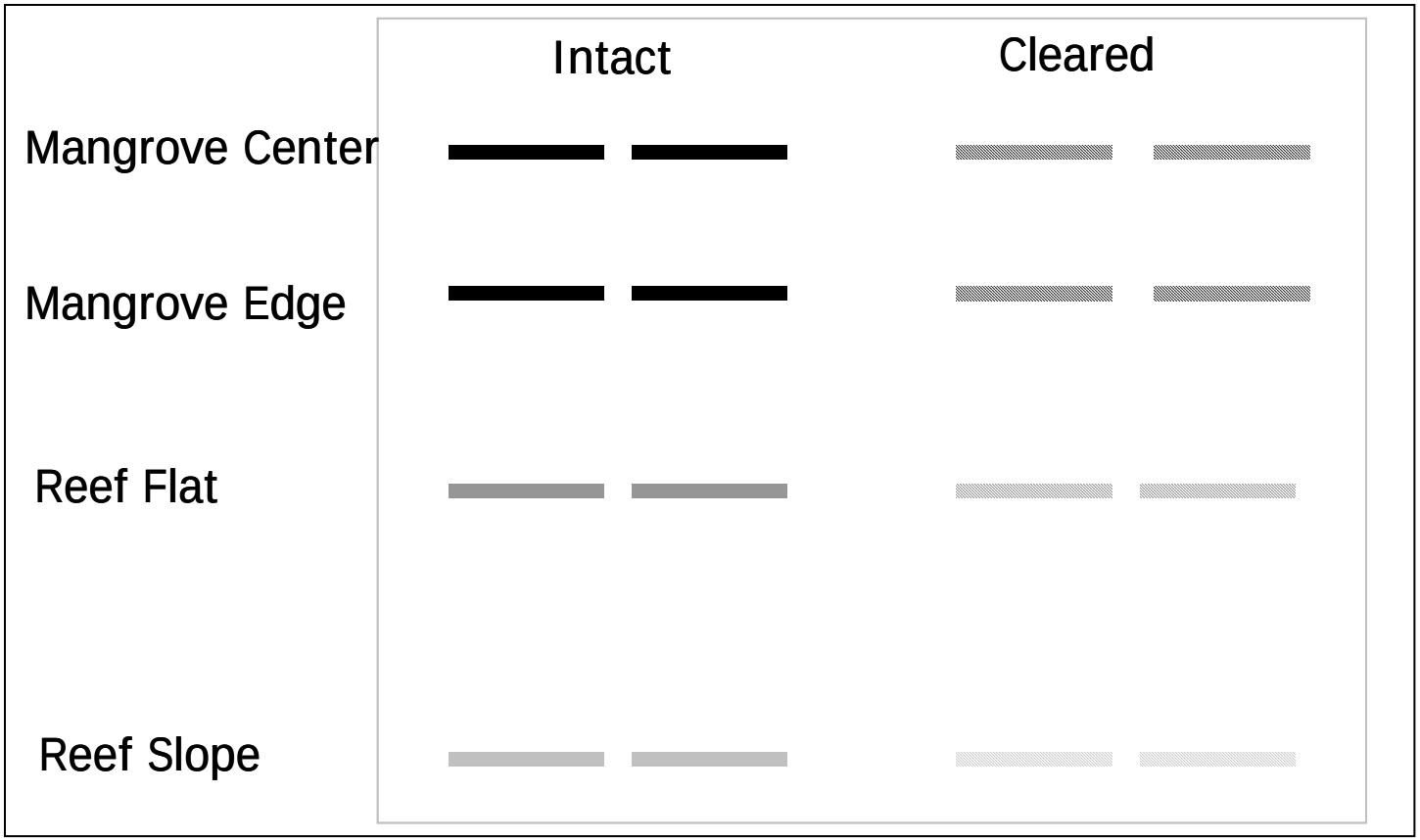


Figure 6.2. Experimental design of transects at each site. Each transect was 20-m long. MC to ME transects were approximately 15 m apart, ME to RF transects approximately 50 m apart, and RF to RS transects approximately 250 m apart. Intact and cleared areas were separated by > 100 m. There were replicate transects in each habitat type and mangrove condition (intact vs. cleared).

edge, and (4) along the reef slope (RS) ~250 m from the mangrove edge. Sponge transplants were left in the field for ~90 days to allow sufficient time for tissue turnover to occur; they were collected and re-measured for length and volume. At ~75 days, an unidentified predator began taking bites out of a subset of the sponges, so length and volume results are not presented. Sponges were then rinsed with DI water and dried at 60ºC until no further weight loss occurred and were prepared as indicated above.

Data analysis techniques

Mixing models were used to determine the proportional contribution of the four organic matter sources to each of the invertebrates. However, with four sources and only two isotopic tracers, there is no unique combination of sources that will result in the observed isotopic signatures of the invertebrates. For these situations, the mixing model software IsoSource (Phillips and Gregg 2003) can calculate the range of source contributions that are consistent with isotopic mass balance. The four organic matter sources were entered into IsoSource: mangrove detrital leaves, seagrass, macroalgae, and microalgae (phytoplankton and zooxanthellae). We chose to use the $\delta^{13}C$ and $\delta^{34}S$ values of detrital leaves (rather than green leaves) since this senesced stage is most biologically available to marine food webs. For the sponge transplant experiment *Niphates erecta* samples from the MT and ME transects, a fifth source, mangrove wood, was added based on data from Fry and Smith (2002b). For each primary producer and each consumer, four individuals were analyzed per transect. Results represent an average of the four individuals.

In IsoSource, the Increment parameter (specificity of range of percent contribution) was set at 1%, and the Tolerance parameter (flexibility within the ‰ range) was set at 0.05‰ and increased when necessary by 0.1‰ up to a maximum of 0.8‰. Only $\delta^{13}C$ and $\delta^{34}S$ were entered into IsoSource due to the difficulty of predicting trophic position, and therefore fractionation factors, for $\delta^{15}N$. Trophic fractionation factors (change in $\delta^{13}C$ and $\delta^{34}S$ as it moves from a lower to higher trophic position) for C and S were assigned as 0.5‰ (France and Peters 1997, Pinnegar and Polunin 1999, Vander Zanden and Rasmussen 2001, McCutchan et al. 2003). Small ranges of percent

contribution indicate well-constrained (more precise) estimates of the source contribution, assuming that all food sources have been included in the model.

To examine whether the contribution of mangrove nutrients varied within a species based on distance from a mangrove source, a Kruskal-Wallis rank sum test was run on samples of each taxon with sufficient data for comparison. For this analysis, the most conservative approach was taken: the highest possible contribution from the far sites was compared with the lowest possible contribution from the near sites. The samples from Zapatillas Caye were excluded from this analysis because of their extreme difference in distance from mangrove source. Due to the high cost of sample processing, sample sizes were small for this analysis.

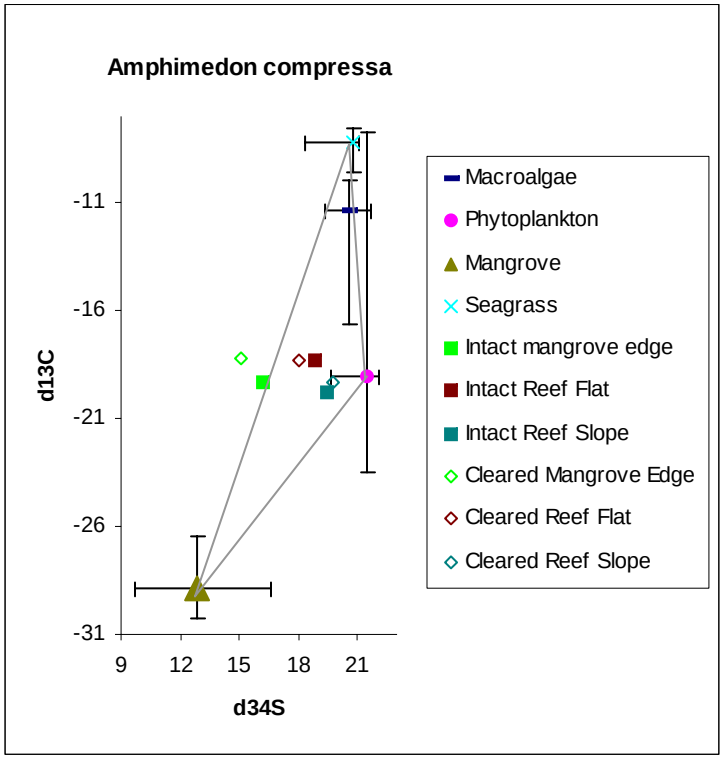
Results

Using carbon and sulfur isotopes, we were able to clearly discriminate among organic matter sources with the $\delta^{13}C$ values of mangrove, phytoplankton, macroalgae and seagrass separated by at least 3‰ and the $\delta^{34}S$ values of mangroves separated from the other sources by >12‰ (see sponge experiment results; Figure 3). The polygon formed by the organic matter sources outlines the range of values that can be explained by the sources considered. The ME values that lie outside the polygon likely reflect incorporation of particulates from mangrove woody matter that has a lower $\delta^{34}S$ value (Fry and Smith 2002b). These sources reflected consistent $\delta^{34}S$ and $\delta^{13}C$ values across sites with primary producer values similar to within 1.5‰ across sites.

Naturally occurring filter-feeders

Filter-feeding invertebrates including the rough file clam (*Lima scabra*), feather duster worm (*Sabellastarte sp.*) and three sponge species (*Amphimedon compressa, Aplysina fulva, Niphates erecta*) all reflected signatures of mangrove-derived nutrients (Table 1 and Figure 4). The rough file clam reflects intermediate levels of contribution from mangroves ranging from 18-44% depending on site. The feather duster worm reflects a substantial contribution of mangrove-derived nutrients both in tissue and tube

a.



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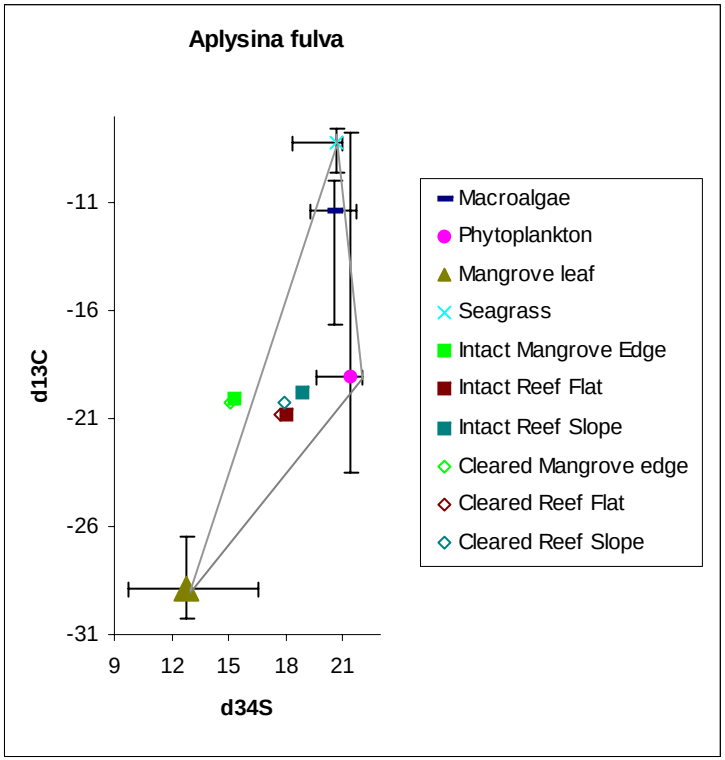


Figure 6.3. $\delta^{34}S$ and $\delta^{13}C$ ratios for primary producer sources and three species of tropical reef sponges. The mixing space of the four primary producer sources is defined by the polygon.

c.

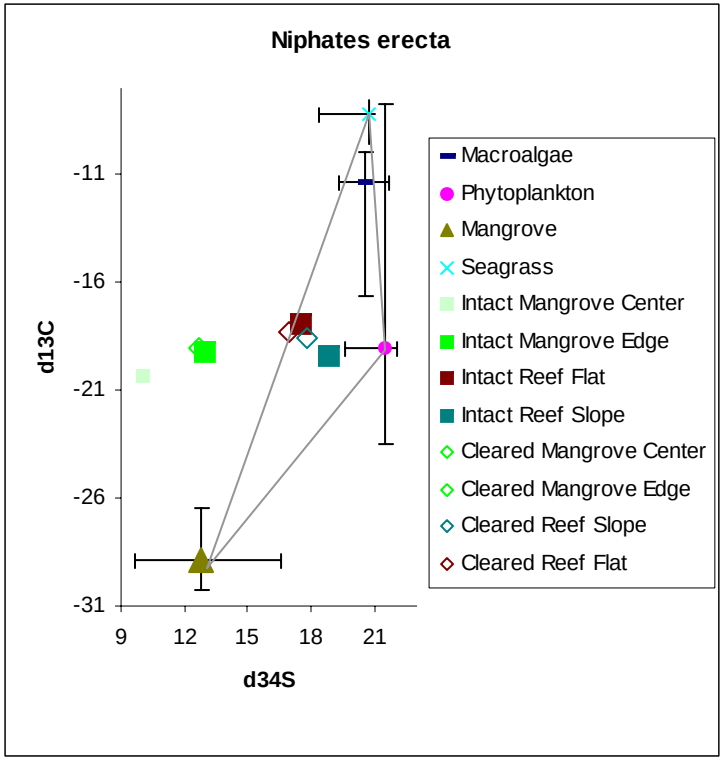


Figure 6.3. (Continued) $\delta^{34}S$ and $\delta^{13}C$ ratios for primary producer sources and three species of tropical reef sponges. The mixing space of the four primary producer sources is defined by the polygon.

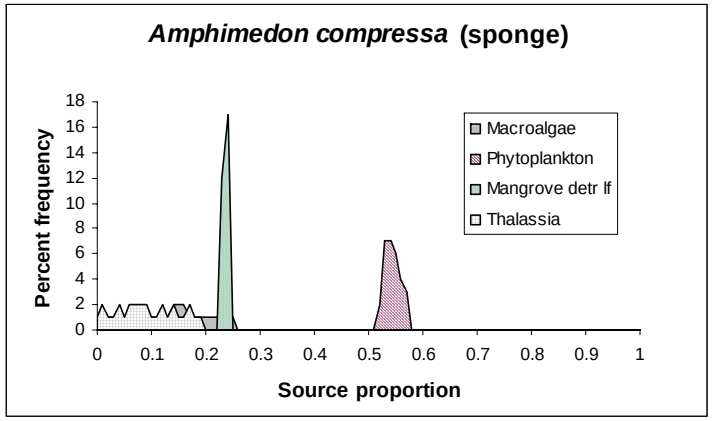
Table 6.1. The range of potential contributions from the four primary producer sources for filter-feeders on the reef at different sites and along different transects. Each row represents the contribution calculated in IsoSource based on the average $\delta^{34}S$ and $\delta^{13}C$ values of four individuals of the species collected at the site.

Species	Phylum	Site	Mangrove Condition	Area	Depth (m)	Distance	Mangrove contribution	Microalgae contribution	Macroalgae Contribution
Amphimedon compressa	Porifera	Gallinazo	Intact	Reef Slope	4.9	100 m	**18%**	82%	0%
		Gallinazo	Cleared	Reef Slope	4.9	100 m	**20-21%**	72-74%	0-8%
		Red Point	Intact	Reef Slope	7.6	250 m	**13%**	86-87%	0-1%
		PCN	Intact	Reef Slope	9.1	300 m	**21%**	70-73%	0-9%
		PCS	Intact	Reef Slope	8.5	300 m	**18%**	69-73%	0-13%
		PCS	Cleared	Reef Slope	8.5	300 m	**19%**	66-71%	0-15%
		Zappatillas	none	Reef Slope	7	10 km	**23-24%**	52-57%	0-25%
Aplysina fulva	Porifera	Gallinazo	Cleared	Reef Flat	1.5	50 m	**37-38%**	43-37%	0-20%
		PCS	Cleared	Reef Flat	1.5	50 m	**51-53%**	4-13%	1-45%
		Red Point	Intact	Reef Flat	7.6	50 m	**44-46%**	16-24%	0-40%
		Red Point	Intact	Reef Slope	7.6	250 m	**27%**	62-65%	0-11%
		PCN	Intact	Reef Slope	9.1	300 m	**33-34%**	42-48%	0-25%
		PCS	Intact	Reef Slope	8.5	300 m	**37-38%**	33-40%	0-30%
		PCS	Cleared	Reef Slope	8.5	300 m	**33-34%**	43-49%	0-22%
		Zappatillas	none	Reef Slope	7	10 km	**35-36%**	37-44%	0-28%
Niphates erecta	Porifera	Gallinazo	Intact	Reef Flat	1.5	50 m	**28-30%**	33-41%	0-39%
		PCN	Intact	Reef Flat	1.5	50 m	**28-31%**	3-18%	0-68%
		Gallinazo	Intact	Reef Slope	4.9	100 m	**28-29%**	54-58%	0-17%
		Red Point	Intact	Reef Slope	7.6	250 m	**12%**	82-84%	0-6%
		PCN	Intact	Reef Slope	9.1	300 m	**11-12%**	83-85%	0-4%
		PCS	Intact	Reef Slope	8.5	300 m	**17-18%**	66-70%	0-17%

Table 6.1. (Continued) The range of potential contributions from the four primary producer sources for filter-feeders on the reef at different sites and along different transects. Each row represents the contribution calculated in IsoSource based on the average $\delta^{34}S$ and $\delta^{13}C$ values of four individuals of the species collected at the site.

Niphates erecta	Porifera	PCS	Cleared	Reef Slope	8.5	300 m	**11%**	82-84%	0-7%
Lima scabra	Mollusca	Red Point	Intact	Reef Flat	1.5	50 m	**43-44%**	0-1%	0-7%
		Red Point	Intact	Reef Slope	7.6	250 m	**29-31%**	19-30%	0-52%
		PCS	Intact	Reef Slope	8.5	300 m	**21-23%**	39-47%	0-39%
		PCS	Cleared	Reef Slope	8.5	300 m	**18-20%**	47-54%	0-35%
Sabellastarte magnifica-tube	Annelida	Gallinazo	Intact	Mangrove Edge	1.5	0 m	**36-39%**	7-19%	0-56%
Sabellastarte magifica		Gallinazo	Cleared	Reef Flat	1.5	50 m	**50-51%**	0-2%	0-7%
Sabellastarte magnifica-tube		Gallinazo	Cleared	Reef Flat	1.5	50 m	**50-51%**	0%	0-7%
Sabellastarte magifica		Gallinazo	Intact	Reef Slope	4.9	100 m	**29-30%**	37-45%	0-34%
Sabellastarte magnifica-tube		Gallinazo	Intact	Reef Slope	4.9	100 m	**33-35%**	25-33%	0-42%
Phallusia nigra	Chordata	Gallinazo	Cleared	Reef Slope	4.9	100 m	**7%**	93%	0%
		Red Point	Intact	Reef Slope	7.6	250 m	**0-4%**	92-100%	0-5%
		Red Point	Cleared	Reef Slope	7.6	250 m	**1-4%**	92-99%	0-4%
		PCS	Cleared	Reef Slope	8.5	300 m	**7-8%**	90-93%	0-2%

a.



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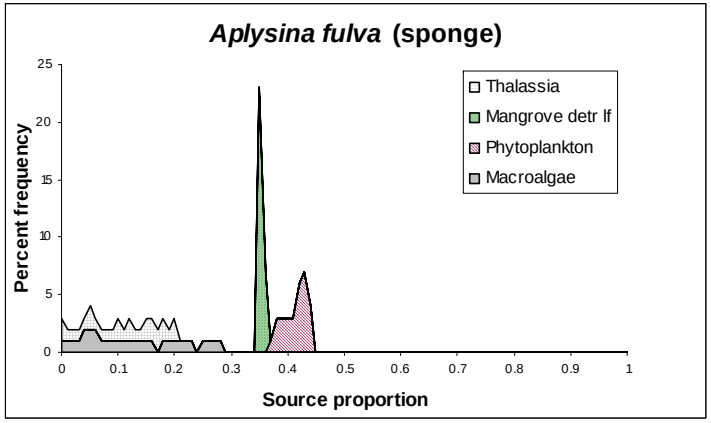

Figure 6.4. The range of potential contributions of each organic matter source (macroalgae, phytoplankton, mangroves, seagrass) for filter feeders and coral using the IsoSource mixing model. Each panel is the average of four individuals sampled in the same habitat type at a site. The consumers in a-e were sampled at Zapatillas Caye, f-g were sampled on the Reef Slope at Red Point, and h was sampled on the Reef Slope at Gallinazo.

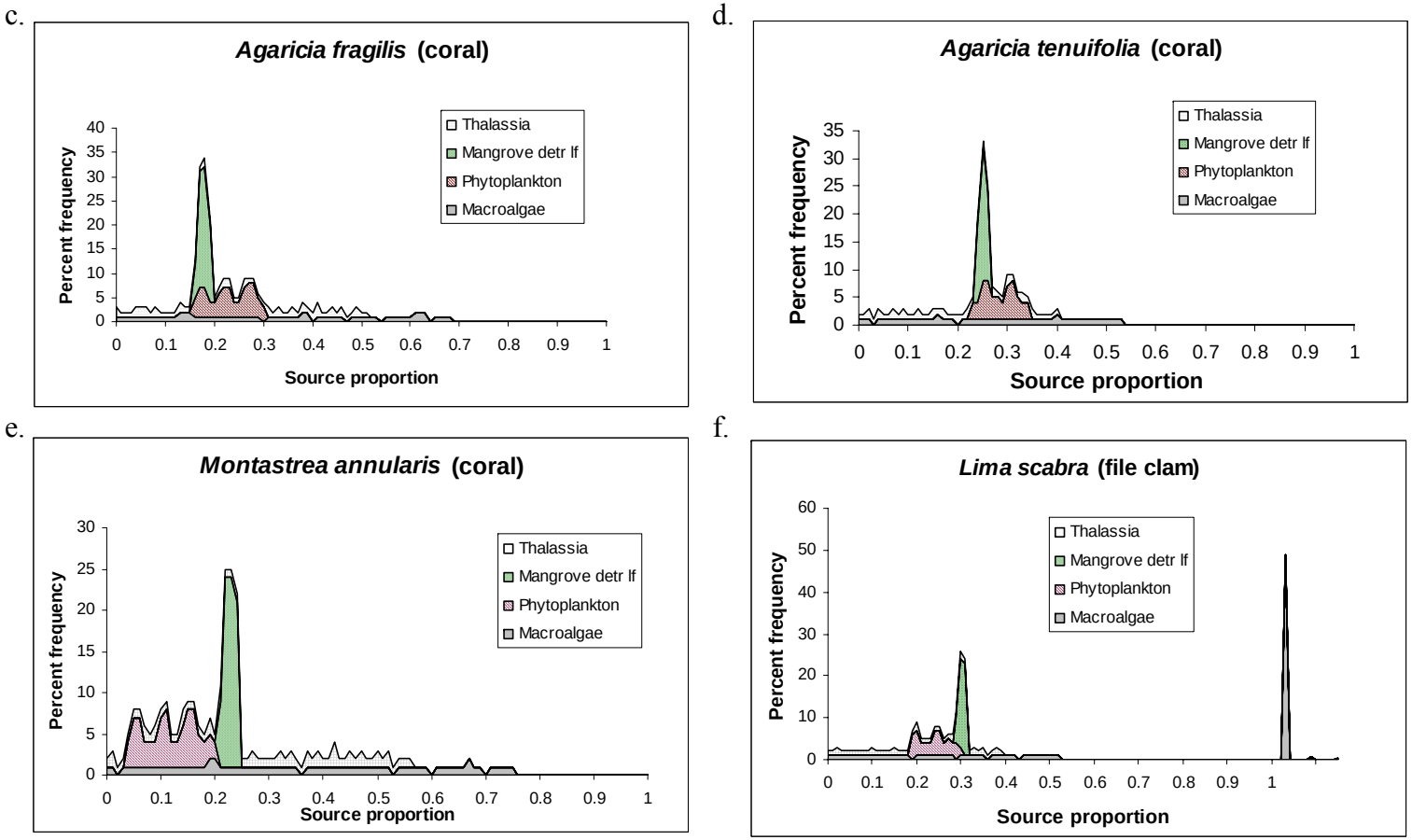

Figure 6.4. (Continued) The range of potential contributions of each organic matter source (macroalgae, phytoplankton, mangroves, seagrass) for filter feeders and coral using the IsoSource mixing model. Each panel is the average of four individuals sampled in the same habitat type at a site. The consumers in a-e were sampled at Zapatillas Caye, f-g were sampled on the Reef Slope at Red Point, and h was sampled on the Reef Slope at Gallinazo.

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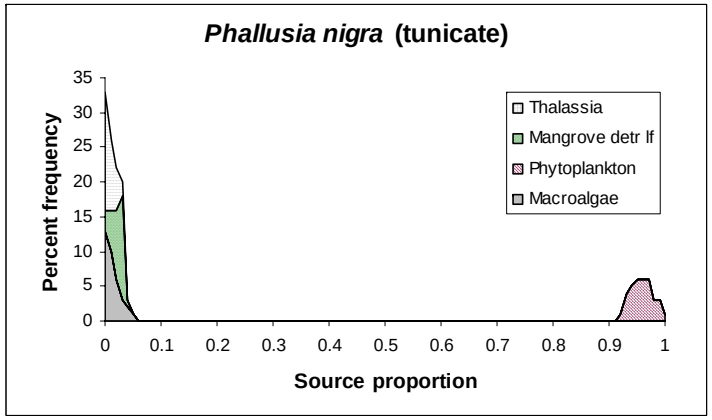

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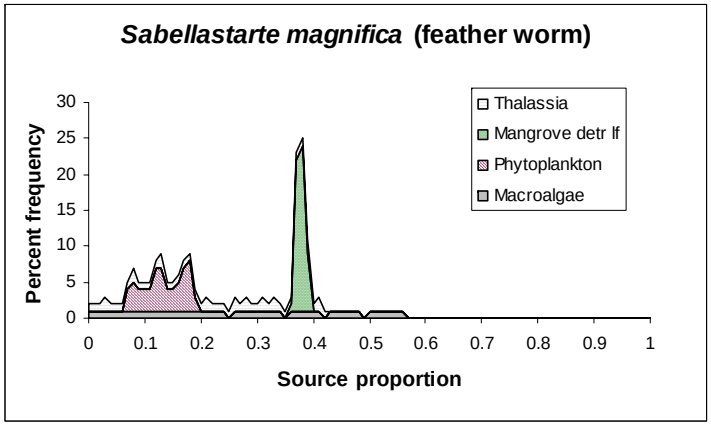

Figure 6.4. (Continued) The range of potential contributions of each organic matter source (macroalgae, phytoplankton, mangroves, seagrass) for filter feeders and coral using the IsoSource mixing model. Each panel is the average of four individuals sampled in the same habitat type at a site. The consumers in a-e were sampled at Zapatillas Caye, f-g were sampled on the Reef Slope at Red Point, and h was sampled on the Reef Slope at Gallinazo.

composition ranged from 29-51% for live tissue and 36-51% for tubes across the transects sampled. For feather duster worms, samples collected along the Reef Flat transect (closer to the mangroves) showed a marginally greater contribution from the mangrove source than those sampled collected on the Reef Slope (Table 1; Kruskal-Wallis chi-square = 3.16, df = 1, $p<0.08$). For file clams, contribution from the mangrove source did not vary with distance from mangroves (Kruskal-Wallis chi-square = 1.8, df = 1, p= 0.18).

The three sponge species reflected consistent contributions (between 11 and 46%) from mangroves, though the percent contribution varied among species, sites, and distance from mangroves (Table 1). *Amphimedon compressa* reflected a contribution from mangroves ranging from 13-24%; the mangrove contribution to *Aplysina fulva* ranged from 27-53%; and *Niphates erecta* reflected a mangrove contribution ranging from 11-31%. For all three sponges, the range of potential contributions from mangroves for all samples along a given transect was tightly constrained (spanned a small range), providing a clear indication of the mangrove contribution along that transect (Figure 4). Furthermore, samples of *Niphates erecta* closer to a mangrove source (i.e. those along the RF transect) demonstrated a higher mangrove contribution than those sampled from the further (RS) transect (Table 1; Kruskal-Wallis chi-square = 4.94, df = 1, $p< 0.03$); for *Aplysina fulva* the contribution was marginally greater (Kruskal-Wallis chi-square = 3.18, df = 1, p-value = 0.07). For *Amphimedon compressa* there is no difference in mangrove-nutrient incorporation with greater proximity to the mangroves (Kruskal-Wallis chi-square = 0.21, df = 1, p = 0.64).

The tunicate *Phallusia nigra,* on the other hand, reflected little incorporation of mangrove-derived nutrients with only a 0-7% contribution across all sampled sites (Figure 4) and no pattern of differential incorporation based on proximity to mangroves (Kruskal-Wallis chi-square = 0.22, df = 1, p = 0.64).

Corals

Corals range from primarily autotrophic to heavily heterotrophic depending on species and ecological variables. Reflecting the variability in feeding ecology and habitat,

Table 6.2. The range of potential contributions from the four primary producer sources for six coral species at different sites and along different transects. Each row represents the contribution calculated in IsoSource based on the average $\delta^{34}S$ and $\delta^{13}C$ values of four individuals of the species collected at the site.

Species	Phylum	Site	Mangrove Condition	Area	Depth (m)	Distance (m)	Mangrove contribution	Microalgae contribution	Macroalgae Contribution	Seagrass Contribution
Acropora cervicornis	Cnidaria	Red Point	Intact	Reef Slope	7.6	250	**15-17%**	37-48%	0-48%	0-36%
Agaricia fragilis	Cnidaria	Red Point	Intact	Mangrove Edge	1.5	0	**29-31%**	16-28%	0-55%	0-41%
	Cnidaria	Gallinazo	Intact	Reef Slope	4.9	100	**9-12%**	27-41%	0-64%	0-48%
	Cnidaria	Pastores	Intact	Reef Slope	5.2	100	**8-12%**	18-35%	0-73%	0-55%
	Cnidaria	Red Point	Intact	Reef Slope	7.6	250	**16-19%**	20-33%	0-64%	0-48%
	Cnidaria	PCS	Intact	Reef Slope	8.5	300	**10-13%**	34-46%	0-55%	0-41%
	Cnidaria	PCS	Cleared	Reef Slope	8.5	300	**1-3%**	55-65%	0-44%	0-33%
	Cnidaria	Zapatilla	none	Reef Slope	7	10 km	**16-19%**	16-30%	0-68%	0-51%
Agaricia tenuifolia	Cnidaria	Red Point	Intact	Mangrove Edge	1.5	0	**29-31%**	16-28%	0-51%	0-41%
	Cnidaria	PCN	Intact	Reef Flat	1.5	50	**3-5%**	66-73%	0-31%	0-24%
	Cnidaria	Gallinazo	Intact	Reef Slope	4.9	100	**13-15%**	26-40%	0-61%	0-45%
	Cnidaria	Pastores	Cleared	Reef Slope	5.2	100	**13-15%**	20-36%	0-67%	0-49%
	Cnidaria	Red Point	Cleared	Reef Slope	7.6	250	**16-18%**	22-37%	0-62%	0-45%
	Cnidaria	PCN	Intact	Reef Slope	9.1	300	**0-1%**	43-53%	0-41%	16-46%
	Cnidaria	Zapatilla	none	Reef Slope	7	10 km	**24-26%**	23-34%	0-53%	0-40%
Millepora	Cnidaria	PCN	Cleared	Reef Flat	1.5	50	**25%**	0%	3-5%	70-72%
Montastrea annularis	Cnidaria	Pastores	Intact	Reef Slope	5.2	100	**17-20%**	27-39%	0-56%	0-42%
	Cnidaria	Red Point	Intact	Reef Slope	7.6	300	**8-11%**	16-32%	0-76%	0-57%
	Cnidaria	Red Point	Cleared	Reef Slope	7.6	250	**7-10%**	19-35%	0-74%	0-55%
	Cnidaria	Zapatilla	none	Reef Slope	7	10 km	**21-24%**	4-20%	0-75%	0-56%
Diploria	Cnidaria	PCN	Intact	Reef Slope	9.1	300	**15-16%**	82-85%	0-2%	0-1%

the mangrove contribution to coral tissue was variable among species (Figure 4), depth, and water exchange (Table 2).

The smaller polyped, more autotrophic Agaricids (Porter 1976) reflect higher variability in the mangrove contribution. *Agaricia fragilis* demonstrated a mangrove contribution ranging from 1-19 % across sites for those samples collected from reef habitat. *Agaricia fragilis* colonies growing directly on mangrove prop roots suggested a higher mangrove contribution with a range of 29-31% than those colonies on the reef (Figure 5; Kruskal-Wallis chi-square = 2.14, df = 1, p = 0.14). *Agaricia tenuifolia* showed a similar range of potential mangrove contribution ranging from 0-26%. Furthermore, the Agaricids collected from the reefs show a weak trend towards lower incorporation of mangrove-derived nutrients (Table 2; Kruskal-Wallis chi-square = 2.21, df = 1, p-value = 0.14). *Acropora cervicornis* revealed a moderate contribution from mangroves ranging from 15-17% as did *Diploria* sp. with a range of 15-16%. *Montastrea annularis*, a more heterotrophic coral, reflected a range of contributions from mangroves ranging from 7-24% with a weak trend towards lower mangrove-nutrient input at the deepest site (Figure 6.5; Kruskal-Wallis chi-square = 1.5, df = 1, p-value = 0.22).

Sponge transplant experiment

All transplanted sponges reflected incorporation of mangrove-derived matter, but at varying rates depending on the proximity of the transplants to mangroves. All sponge species responded similarly, with individuals transplanted into the MC or ME areas demonstrating higher levels of mangrove contribution, pieces transplanted into the RF areas with intermediate levels of mangrove contribution, and those transplanted to the RS areas demonstrating lower levels of mangrove contribution (Figure 6.6). This difference was significant for *Amphimedon compressa* and *Aplysina fulva* (Kruskal-Wallis chi-square = 4.5, df = 1, p = 0.03) but not for *Niphates erecta* (Kruskal-Wallis chi-square = 2.55, df = 1, p-value = 0.11). Sponge pieces transplanted into intact mangroves did not differ in mangrove contribution from pieces transplanted into cleared mangrove areas. However, there was small variability among species with *Aplysina fulva* indicating a 60% contribution from mangroves when placed along the intact ME transects and a 61%

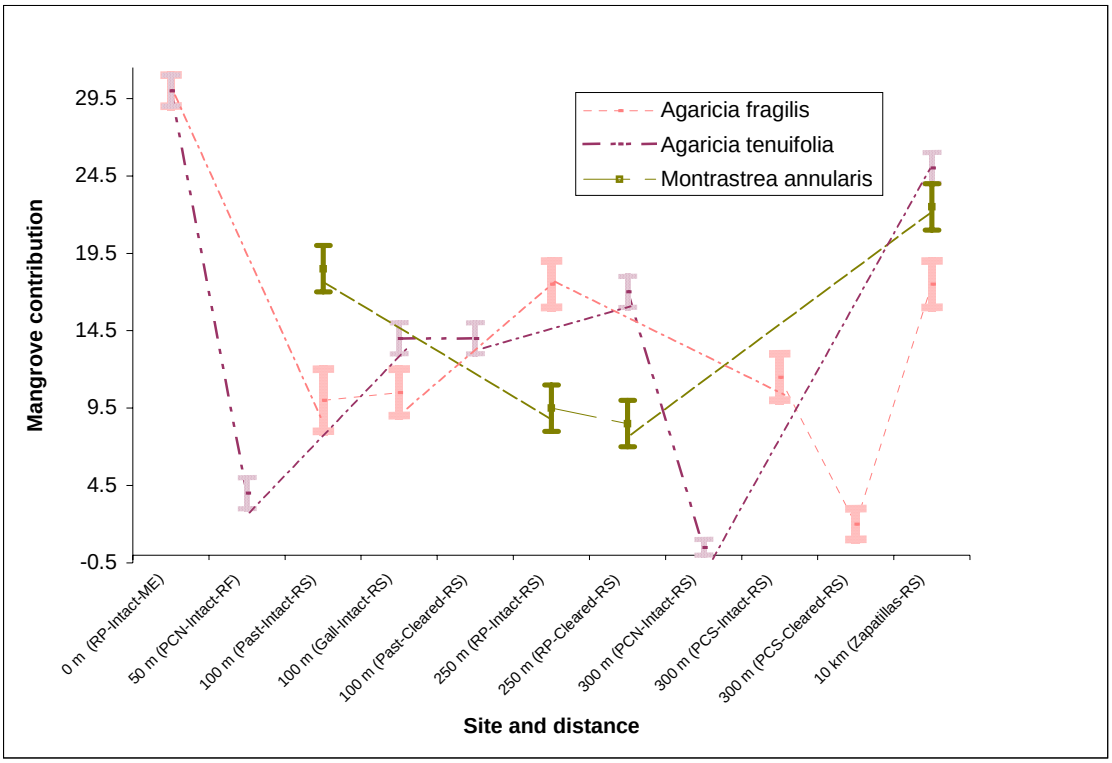

Figure 6.5. The change in mangrove-derived nutrient contribution for three coral species with increasing distance from a mangrove source. The two Agaricids are hashed bars; *Montastrea annularis* is represented by solid bars.

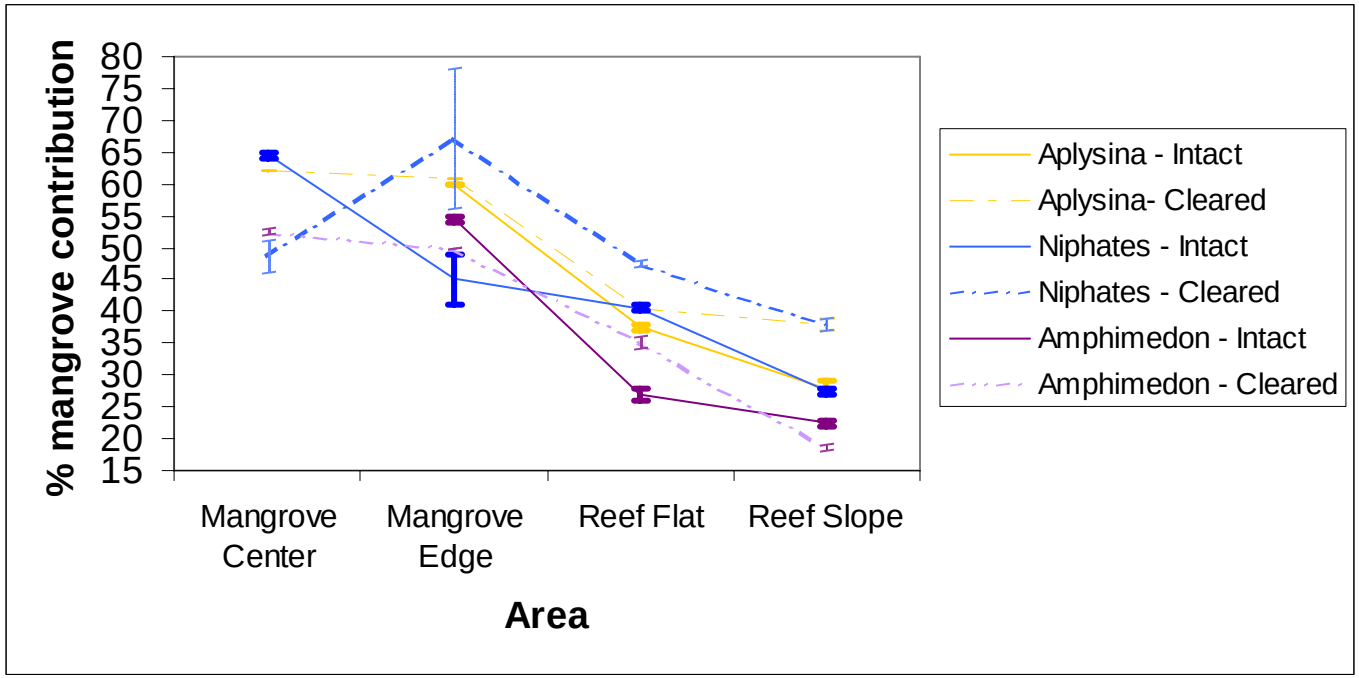

Figure 6.6. For all three species of sponge, the percent contribution from mangroves declines with distance from mangrove habitat. (For *Niphates erecta*, the mangrove edge and mangrove center samples were based on IsoSource analyses including an additional source, mangrove wood [Fry and Smith 2002]).

contribution when placed along the cleared ME transects; and *Amphimedon compressa* reflecting a 54-55% contribution when placed along the intact ME transects and a 50% contribution when placed along the cleared ME transects. Based on the four organic matter sources, the results for *Niphates erecta* were inconclusive, with the sulfur signature of these pieces resembling that of the mangrove source, whereas the carbon signature was intermediate among the four primary producer sources. However, when mangrove wood was added as a source (Fry and Smith 2002b), this became a significant source with a contribution ranging from 41-49% along the intact transects and 56-78% along the cleared transects.

Discussion

Sessile filter-feeding invertebrates on Caribbean coral reefs off of Bocas del Toro, Panama, incorporated up to 53% of their organic matter from mangroves as reflected by $\delta^{34}S$ and $\delta^{13}C$ isotope mixing models. Coral species also reflected incorporation of mangrove-derived nutrients, although this was more variable among species and locations. The level of contribution from mangroves varied among species in a taxon and within a species among sites. This variability was related to distance from a mangrove source. Site-to-site variability was likely due to differences in delivery rates of particulate and dissolved organic matter due to currents. Mangrove-derived nutrient incorporation is reflected in organisms located close to mangroves (e.g., within 0.5 km at the Almirante Bay sites) as well as in organisms far from mangroves (e.g., on reefs >10km away at Zapatillas Caye). These results are based on IsoSource mixing models and assuming all relevant organic matter sources were included in the model.

There are multiple pathways that mangrove-derived nutrients could take that would explain why they are available to corals and reef-dwelling filter feeders on reefs at varying distances from mangroves. First, previous research has demonstrated that reef fishes visiting mangroves incorporate mangrove-derived nutrients to varying degrees (Deegan 1993, Sheaves and Molony 2000, Cocheret de la Moriniere et al. 2003,

Nagelkerken and van der Velde 2004a, b). These fish may carry mangrove-derived nutrients back to reefs as they transit between the two habitats (Deegan 1993), similar to the finding by Meyer et al. (1983) that the reef fish *Haemulon spp. (*grunts) carry seagrass-derived nutrients to reefs thereby contributing to the nutrients available to the coral heads around which the grunts reside.

Another potential pathway through which sessile reef invertebrates may obtain mangrove-derived nutrients is via outwelling of particulate and dissolved organic matter from mangrove systems (Lee 1995). The internal recycling of organic matter and high primary productivity within mangrove forests allows for large quantities of detritus and dissolved matter to be exported to adjacent coastal waters (Odum and Heald 1972, Twilley 1985). Jennerjahn and Ittekkot (1997; 2002) argue that although mangrove leaf litter fall and water exchange with coastal areas is high, leading to significant carbon export to coastal zone areas, mangrove-derived organic matter is only a minor contribution to higher organisms due to lower nutrient content. In contrast, our findings reveal that mangrove-derived nutrients contribute ~10-50% of the nutrients and energy to sessile reef invertebrates as far as 10 km from a mangrove source.

We found high variability among filter feeder taxa in the contribution of the various nutrient sources. This variability may be due to different feeding modes and levels of selectivity among taxa, including varying capacities to filter different particle sizes. For example, previous research indicates that ascidians may feed selectively and that they show seasonal shifts in food preference (Yahel 2003). Similarly, preliminary evidence indicates that some sponges feed selectively, regardless of particle size (Yahel and Eerkes-Medrano, pers. comm.). Our results indicate that the tunicate *Phallusia nigra* is taking in primarily phytoplankton, incorporating little to no organic matter from mangroves, seagrass or macroalgae (Table 1; Figure 4). On the other hand, rough file clams, magnificent feather duster worms, and the three sponge species incorporate significant amounts of mangrove- and phytoplankton-derived nutrients whereas the results for macroalgae and seagrass uptake are so variable that the importance of these sources is inconclusive.

Sponges are important organisms that play a role in cementing reefs, trapping nutrients, and providing food to mobile vertebrates (Wulff 1997, 2000). The three sponges sampled varied in their uptake of mangrove-derived nutrients. *Amphimedon compressa*, the erect rope sponge found predominantly on deeper reefs, reflects intermediate levels of mangrove-derived nutrient incorporation (13-24%), with high incorporation of phytoplankton-derived nutrients (52-87%), and low to variable incorporation from macroalgae (0-25%) and seagrass (0-19%). *Niphates erecta*, the lavender rope sponge, commonly found growing on mangrove prop roots as well as in deeper reef habitat, reflects low to moderate incorporation from mangrove source (11-31%) with generally high incorporation of phytoplankton-based nutrients (3-84%) and highly variable incorporation from seagrass (0-68%) and macroalgal (0-51%) sources (Figure 4). For this species, at sites where mangrove contribution is greater, there is a concurrent decline in phytoplankton contribution. In addition, previous research indicated that attachment to mangrove prop roots enhances growth rates of some species (Ellison et al. 1996); since *Niphates erecta* occurs naturally on mangrove prop roots, this species may be adapted to utilize mangrove-derived nutrients directly from the woody roots as well as from particulate or dissolved organic matter primarily from detrital leaf or woody matter. *Aplysina fulva*, the scattered pore rope sponge commonly found on shallow inshore reefs, reflects a moderate (27-53%) contribution from mangrove derived-nutrients, and an intermediate contribution from phytoplankton (16-65%) that is inverse in magnitude to the mangrove contribution at each site, and variable contribution from seagrass (0-45%) and macroalgae (0-33%).

The molluscan and annelid filter feeders reflect the highest and most consistent contribution from mangrove nutrients, each with confined ranges of contribution per site. The rough file clam (*Lima scabra*) is found predominantly on the reef slope with a moderate (18-44%) contribution from mangroves. The magnificent featherduster worm, *Sabellastarte magnifica,* reflects a consistently high contribution from mangroves (33-51%) both in its tissue and tube composition. Moreover, those individuals located closer to mangroves (on the Reef Flat) demonstrated a greater contribution from mangroves than those located on the Reef Slope, further from a mangrove source (Table 1).

Of the taxa sampled in this study, coral species reflect a greater variability in mangrove-nutrient incorporation rates both within and among species. The variability in mangrove-derived nutrient contribution is both greater and more complex possibly due to the complexity of trophic position among coral species and the heterotrophic plasticity of some coral species (Grottoli et al. 2006) since the coral signature represents a composite of the animal tissues and the endosymbiotic dinoflagellate algae within the coral cells. Within a coral species, the mangrove contribution is also variable among sites; this may be based on distance from mangrove source as well as differences in light availability and depth that can affect heterotrophy (Muscatine et al. 1989, Heikoop et al. 1998). *Montastrea annularis*, a large-polyped, predominantly heterotrophic species, shows significant variability in mangrove-derived nutrient incorporation among sites (Table 2). When indirect, phytoplankton-based nutrient incorporation is high (at the Almirante Bay sites), mangrove nutrient incorporation is low. However, at Zapatillas Caye, an open ocean site with high wave energy, incorporation of mangrove-derived nutrients is higher and phytoplankton-based incorporation is lower. This may be due to a limitation of available phytoplankton at this site, in which case mangrove-derived nutrients appear to be substituted when phytoplankton nutrients are limiting. Current flow into Almirante Bay is predominantly through Bocas del Drago (to the North, Figure 1)(E.G. pers. obs.) and out through the southern openings among the islands. Therefore, the pattern of varying mangrove nutrient incorporation across sites in *Montastrea annularis* may reflect differing nutrient availability due to currents.

Results of the sponge transplant experiment indicate that the three species sampled may be incorporating nutrients based on availability. For all three species, sponges transplanted into the mangrove edge habitat reflect a higher contribution of mangrove-derived nutrients. The mangrove contribution declines with distance from the mangroves (Figure 6) such that mangrove contribution in MC>ME>RF>RS transects. This finding is consistent with the results from the naturally occurring sponges and indicates that sponge selectivity in their uptake of available organic matter sources may be correlated with availability and presents the possibility that loss of mangroves and

therefore mangrove-derived primary production may lead to shifts in the uptake from various sources.

It remains unknown whether mangrove-derived nutrients provide any essential nutrients or minerals that would be limiting if mangrove nutrients were to become unavailable. This research therefore highlights some key areas for further research. For example, do sessile reef invertebrates that have incorporated mangrove-derived nutrients exhibit higher growth rates or reproductive output? Or are mangrove-derived nutrients a less nutritious source that reduces fitness relative to other primary producer sources? Does the nutritional or contribution value of mangrove-derived nutrients vary among consumers? Understanding the importance of mangroves as a nutrient source for sessile reef invertebrates and what shifts in uptake would follow from a loss of mangrove production may be relevant to understanding changes in coral reef communities as both mangrove forests and coral reefs respond to increased threats on a global scale.

In this paper, we present evidence that suggests Odum and Heald (1972, 1975) may have been correct in their assertion that mangrove-nutrients contribute to the food web both within mangroves and in adjacent systems as far away as 10 km. This is interesting since, despite the low OM quality and nutrient content (France 1998, Alongi 1990), mangrove nutrients still contribute to adjacent food webs. If mangrove-derived nutrients are, indeed an important source of essential nutrients or are a necessary nutrient source on reefs with low levels of phytoplankton, loss of mangrove habitat may lead to a reduction in organic matter for sessile reef organisms. How this loss of mangrove-derived nutrients will affect food availability in a changing ocean and on increasingly stressed coral reefs is a critical area for future research.

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Chapter 7:

The protective capacity of mangroves: A case study from Hurricane Wilma and Tropical Storm Gamma in Belize

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Abstract

Mangrove forests are a globally threatened tropical habitat identified as ecologically important buffer zones assumed to protect coastlines from wave and storm impacts and coastal erosion. The paucity of studies assessing the effectiveness of mangroves in protecting shorelines during major storm events is primarily due to the difficulty of predicting where and when a storm will intersect the shoreline in order to collect data before and after the event. Opportunistic results of an ongoing study quantifying physical and biological differences between intact and cleared mangroves on Turneffe Atoll, Belize, reveal the effect of two consecutive storm events, the 2005 Category 5 Hurricane Wilma and the subsequent Tropical Storm Gamma. The differential survival of three types of previously installed experimental devices in intact mangroves versus adjacent cleared mangroves provides an empirical evaluation of the protective capacity of mangroves. The survival of equipment was greater in intact mangroves for two types of experimental devices; a third equipment type revealed a trend towards greater retention in intact mangrove areas. The results of this fortuitous experiment support the conclusion that removal of coastal mangroves diminishes physical protection during significant storm events. This conclusion highlights the importance of coastal zone management in the current scenario of two interacting factors: increased frequency and intensity of storm events in parallel with a changing climate and the concurrent decline of coastal mangrove forests.

Introduction

Significant mangrove deforestation has removed much of the vegetative buffer that once protected tropical and subtropical coastlines. Today, less than 50% of the historic mangrove cover exists along these coasts, with rates of habitat degradation greater than 30% over the last 50 years (Field et al. 1998, Alongi 2002, Williams 2005). This habitat conversion results in the gain of land for shrimp farms, agriculture, towns and resorts, but what ecosystem services are lost in the conversion? The role of mangroves and coral reefs as protective buffers to coastal areas during storm events has

been widely discussed (Ogden 1980, UNEP 1995, Cesar 1996, Field et al. 1998, Moberg and Folke 1999, Alongi 2002, UNEP-WCMC 2006), however, until recently, few studies have quantified the nature of this ecological function.

The December 26, 2004 tsunami in the Indian Ocean provides the first example of a storm event for which mangroves as coastal buffers were examined extensively and quantitatively. Dahdouh-Guebas et al. (2005) and Danielson et al. (2005) report that intact mangroves along coastlines were successful barriers to strong wave action, and reduced coastal and property damage, as well as loss of human life (Kar and Kar 2005) compared with adjacent cleared mangrove areas. Demonstration of this valuable ecosystem service by mangrove forests is critical in the face of continuing global mangrove cover decline due to anthropogenic disturbance.

In contrast, few studies have quantified the level of protection that intact mangroves provide during more frequent storm events, such as hurricanes, cyclones and tropical storms. This lack of documentation is due, in part, to the difficulty of predicting where and when a storm will intersect the shoreline in order to collect data before and after the event. In Belize, during October-November, 2005, an ongoing experiment evaluating the differences between intact mangroves and anthropogenically cleared mangrove areas was hit first by Hurricane Wilma and then by Tropical Storm Gamma providing the rare opportunity to quantify differences in protection.

Methods

The study was designed to evaluate the impact of clearing mangroves on community and ecosystem properties of mangroves and adjacent coral reefs. Study sites were arrayed along a 30-km stretch of coastline on Turneffe Atoll, Belize and consisted of four paired sites (intact and cleared mangrove areas), one cleared site with no paired intact area, and three control sites (large areas of intact mangroves with no nearby clearings) (Figure 7.1). These sites met the following criteria: (1) a minimum of 75 m stretch of cleared *Rhizophora mangle* (red mangroves) adjacent to stretches of at least 100 m of intact red mangroves; (2) fringing

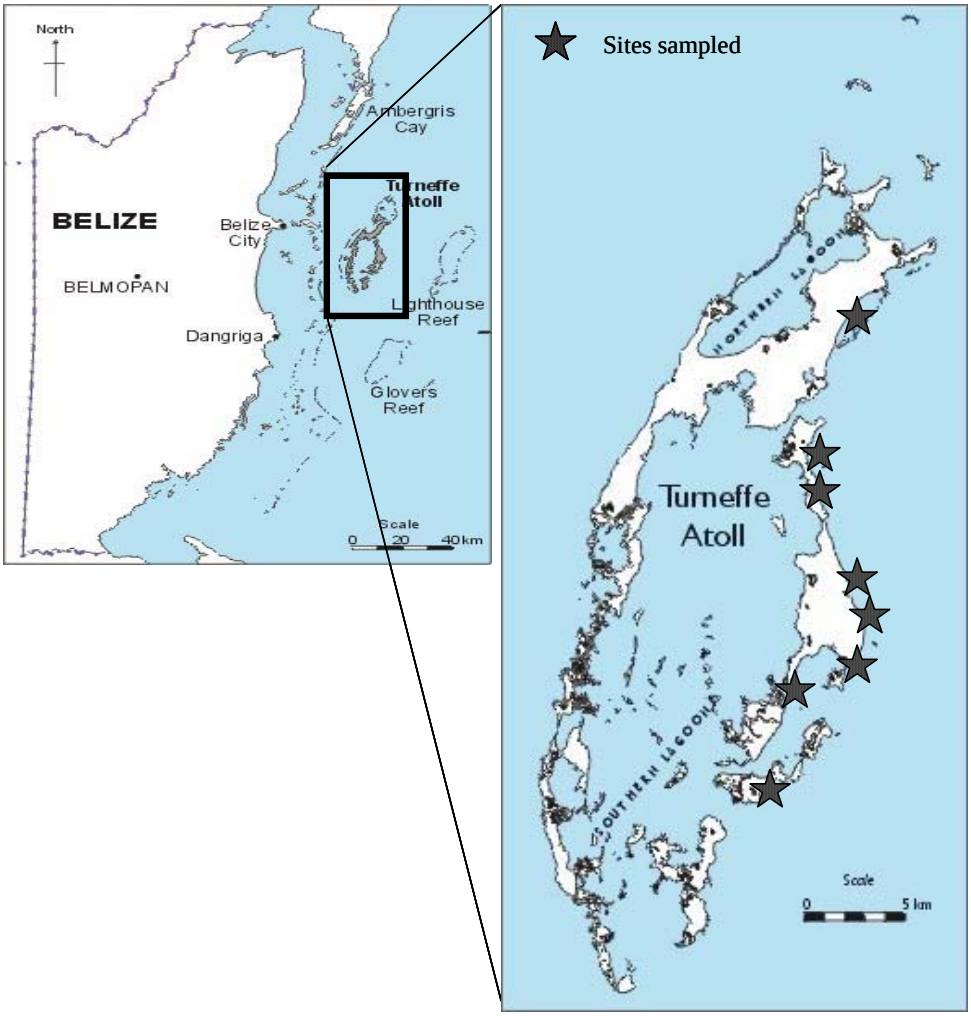

Figure 7.1. Map showing location of study sites on the eastern side of Turneffe Atoll, Belize in the Western Caribbean Sea.

or patch reefs within 200 meters of the seaward mangrove edge; (3) located at least 2 km from major human development to exclude potential sources of anthropogenic nutrients; (4) similar exposure to wave action. All sites were characterized by *R. mangle* trees, except where stands had been removed for agriculture, construction, or viewsheds. The atoll is surrounded by a barrier reef. All sites were 0.75-1.25 m deep (tidal exchange is ~0.5 m). The reef flat areas consisted of patch reefs at depths ranging from 1-3 meters. Mangrove-removal areas ranged from 75 to 250 meters in length along the shore and were either recent (within 12 months of study deployment) or historic (~15 years prior).

Three different types of experiments were in progress when the storms hit. Each experiment entailed replicate treatments deployed along a transect line. At each intact mangrove study area, transects were placed within the seaward edge of mangrove roots; in the cleared sites, transect lines were deployed where the roots once were present. Each experimental transect line had 3 sediment traps and 2 pairs of herbivore exclusion cages and cage controls. A subset of the sites also had shades (testing the effects of light on algal growth) and shade controls. Installation of experimental devices was similar in all areas.

Herbivore exclusion cages were Naltex mesh bags stretched to ~20 cm in length and held open with three ¾ cm x 15 cm PVC rings; the ends were covered with Vexar mesh and cinched down with cable ties. Cages were strung on a line ~1 meter above the substrate and 0.25-0.5 m below the water surface; the line was attached at either end to rebar stakes. Cage controls were similar with two 6-cm holes cut in the mesh walls. Sediment traps were 3.8-cm diameter x 19-cm PVC tubes capped at the bottom and anchored to rebar stakes with cable ties. Shades were constructed of 0.25 x 0.25 m PVC quadrats covered with Vexar mesh and attached to the PVC frame with cable ties. The shades were cinched to four 1-m tall rebar stakes (at each corner of the quadrat). Shade controls were PVC quadrats without Vexar mesh covers. All rebar stakes were 1 m x 1.3 cm and were anchored ~0.4 m below the substrate surface.

An unplanned but useful component of this design was the varying degrees of anchoring utilized for the three field equipment types. Shades were well anchored in the substrate by 4 rebar stakes. Herbivore traps were suspended in the water column and

moderately anchored by two rebar stakes. Sediment traps were anchored directly to the substrate by a single rebar stake.

The experiments were initiated in July 2005. At the end of September 2005, all field equipment was monitored and was intact. Three weeks later (October 18), Hurricane Wilma moved past Turneffe Atoll, Belize with tropical storm-force winds, waves and surge (Pasch et al. 2006). Three weeks after Hurricane Wilma passed, Tropical Storm Gamma stalled off of Belize for 3 days (November 16-18), battering Turneffe Atoll with high winds, surge and flooding rains (Stewart 2005). These two tropical storm-force events were characterized by sustained wind speeds ranging from 40-73 kts with peak gusts up to 81 kts (Saffir Simpson Scale) and surge up to 1.5 meters. There is no weather station at Turneffe Atoll, so wind and surge maxima are not available.

The impact of these two tropical storms on the survivorship of the experimental devices was measured in January 2006. The difference in the loss of deployed field equipment between mangrove-intact and mangrove-cleared areas provides an unplanned, quantitative measure of the protective capacity of the mangroves.

Results

The percent of herbivore exclusion cages lost during the storms was more than 4-fold higher in the cleared areas compared to the intact mangrove areas (Figure 7.2, ANOVA, $F=61.36$; df: 1,6; $p<0.0002$). There was no effect of site on the loss of herbivore cages (ANOVA, $F=1.86$; df: 8,6; $p=0.23$). Sediment traps were also removed at a greater rate (3-fold) from cleared areas than from intact mangrove areas (Figure 7.2, ANOVA, $F=28.7$; df: 8,6; $p<0.002$), though site also was significant (ANOVA, $F=5.87$; df: 8,6; $p<0.02$). A greater number of shades and shade controls were buried or removed in cleared areas, but the differences are not significant [based on mangrove status (intact versus removed, ANOVA, $F=3.2$; df: 1,3; $p=0.17$) or site (ANOVA, $F=2.6$; df: 6,3; $p=0.23$)] (Figure 7.2).

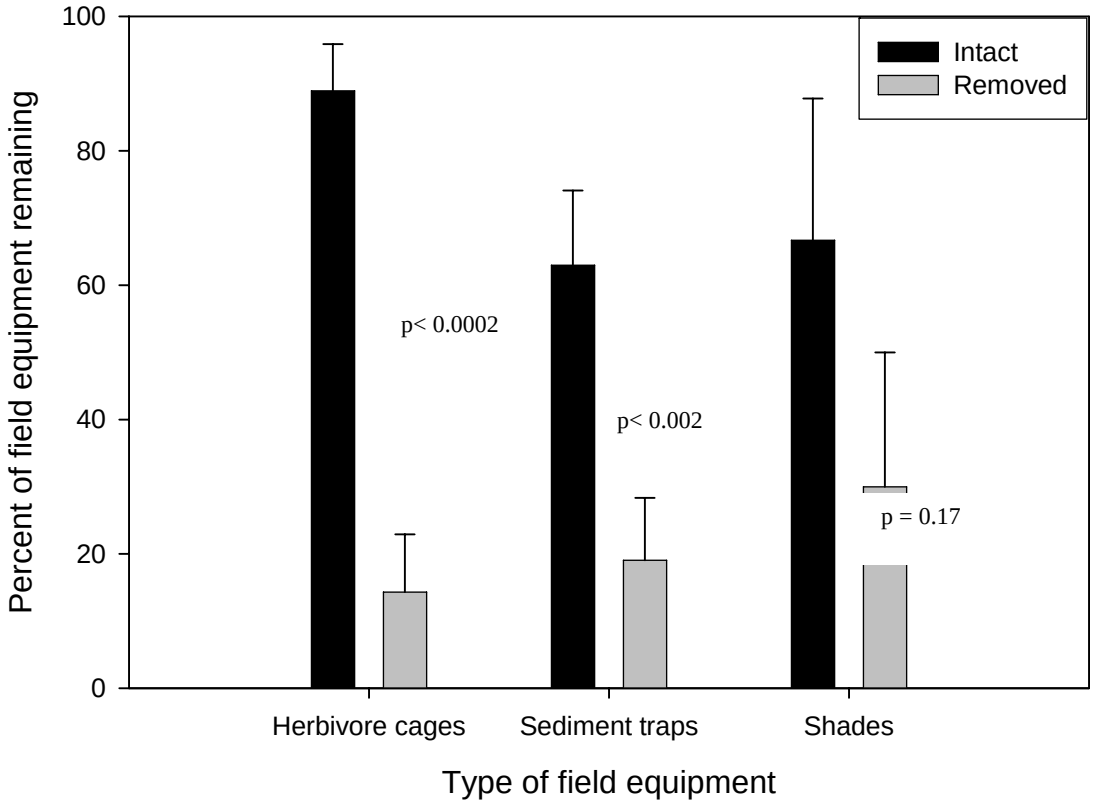

Figure 7.2. Survivorship (mean +/- SE) of 3 types of field equipment during Category 5 Hurricane Wilma and Tropical Storm Gamma in intact mangroves versus adjacent removed areas.

Discussion

The appearance of a Category 5 Hurricane and a Tropical Storm during an ongoing experimental investigation of differences between intact mangrove forests and cleared mangroves provided the rare opportunity to evaluate the role of mangroves in ameliorating impacts of strong storms. The data are consistent with the hypothesis that intact mangroves, like other coastal vegetation (Feagin et al. 2005), diminish wave and surge impacts associated with large storm events (Williams 2005).

Not surprisingly, storm size was important in determining impact. All field equipment remained in place from July to September, despite numerous smaller storms. Significant losses of field equipment did not occur until Hurricane Wilma and Tropical Storm Gamma hit Belize.

The three types of field experiments differed in the strength of their attachment to the substrate. Shades were more securely anchored than either cages or sediment traps. The results suggest that both storm surge and strength of anchoring are important.

The results here provide quantitative support for the hypothesis that mangrove structure is an important biophysical barrier protecting coastlines. Corresponding empirical evidence quantifying this role for coral reefs is similarly needed. Though these local site-level impacts are not easily scaled to coast-wide extents, these results do show that mangrove intact areas react differently than disturbed areas to stochastic and seasonal storm events (Figure 7.3). Moreover, the protective capacity of mangroves will likely vary from one storm event and location to the next. Additional information on differences in flow velocities and tidal intrusion during the storm event would provide further data on mangrove buffering during these high wave action and surge events. Furthermore, studies measuring coastal erosion and sand or sediment extraction between intact and cleared mangrove areas would contribute to our understanding of how these storm events are affecting coastlines over time.

This information on the difference in tropical storm impacts between areas with and without intact mangroves highlights the importance of mangrove conservation and restoration strategies (Field et al. 1998, Ellison 2000, Check 2005). As the frequency and intensity of major storm events is predicted to rise in conjunction with climate change

Figure 7.3. Effect of Hurricane Wilma on removal of sand from a beach where mangroves had been cleared. The bottom two steps were added between Hurricane Wilma and Tropical Storm Gamma due to the extensive sand removal during Hurricane Wilma. The visible exposed rocks were covered with sand prior to Hurricane Wilma (photo by N. Duplaix).

(McCarthy et al. 2001), understanding the capacity of mangroves to buffer shorelines is increasingly relevant. Similar to other coastal vegetation types (Feagin et al. 2005), evidence for the role of mangroves as coastal buffers is increasing as their global coverage declines and warrants greater attention in the policy and management arenas.

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Chapter 8. General Conclusion

The studies presented here represent an effort to better understand how mangrove forests and coral reefs are connected via organism movement and energy flow and to clarify the effects of mangrove degradation on coral reefs. Much effort has been focused on coral reef conservation, but this is less true for mangrove forests. However, if mangrove forests are, indeed, connected via ecological and biogeochemical processes to coral reefs, it is essential to consider mangroves in conservation and management strategies to protect coral reefs.

I begin by reviewing the available literature on known linkages between mangrove forests and coral reefs (Chapter 2). In this review I find that, although there is empirical evidence for many of the perceived connections, including organism movement and nutrient exchange, in fact, many gaps remain in our understanding of habitat connectivity among these tropical marine systems. For example, my review identifies a need to consider and examine how disturbance to mangroves affects the natural connections between these two threatened and declining ecosystems (UNEP 1995, Ogden 2001, Alongi 2002). A major gap and area for further research is to understand the threshold size of mangrove clearings above which sedimentation increases and nutrient availability and species diversity decrease. Identifying critical sizes for mangrove buffers is important to informing future conservation and management planning.

The study presented in Chapter 3 addressed the effects of mangrove disturbance on biotic and abiotic processes in the immediate habitat. To identify potential impacts of mangrove clearing on nearby reefs, it is important to understand what changes occur locally following a disturbance event. I found that areas cleared of mangroves had higher light levels, more frequent high temperature anomalies, and lower sedimentation than adjacent intact mangrove areas. In addition to changes in the abiotic environment, cleared areas had higher algal biomass and algal diversity than adjacent mangrove areas. These changes will have detrimental impacts on organism that depend on mangrove habitat

complexity and shade (Cocheret de la Moriniere et al. 2004), both of which are reduced or lost following mangrove clearing. These results begin to address how mangrove disturbance might affect the ontogenetic habitat use of mangroves and potential implications for adjacent reefs (Mumby et al. 2004).

Changes to the abiotic variables following mangrove clearing and resultant increases in algal biomass are likely to propagate through the food web, affecting higher trophic levels. I was interested in how mangrove clearing affects the zooplankton community, an important food source for higher organisms, and the larval community, an important source for future invertebrate populations in inshore marine habits. In Chapter 4, the study we conducted to evaluate differences in the larval and zooplankton communities between intact and cleared mangrove areas revealed striking differences in the community composition and overall diversity. In cleared areas, the meroplankton community was reduced, whereas the holoplankton communities were similar between the two mangrove conditions. Moreover, overall diversity declined in cleared areas.

Further research would resolve whether the change in zooplankton community composition observed in this study might lead to reduced food availability for juvenile and adult reef fishes feeding in mangrove habitat. Alterations in zooplankton abundance and diversity might cascade into changes in fish communities on adjacent reefs following shifts in preferred prey items subsequent to mangrove removal. Furthermore, the source of larval invertebrates for adult populations on adjacent reefs may decline as the meroplankton population shifts in nearby cleared mangrove areas. This study identifies a potential additional indirect effect of mangrove clearing on coral reef communities. The results answer a piece of the question of whether removal of mangrove habitat will have a direct effect on the prey of reef-resident organisms that reside or feed in mangroves.

Having identified multiple changes in mangrove habitat following clearing, I was interested in determining how this inshore disturbance might affect adjacent coral reef systems. Chapter 5 discussed a study conducted in Belize to identify whether mangrove cleared areas reflect similar changes as those identified in Panama (Chapter 3) and whether there are differences on coral reefs adjacent to the cleared versus intact areas. In Belize, the inshore mangrove areas had similar patterns to those found in Panama with

increased light and high temperature events and higher algal biomass in cleared areas. On the other hand, sedimentation rates were lower in cleared areas in Belize, with sedimentation differing between recently cleared and historically cleared sites.

On the inshore reefs, sedimentation was greater on reefs adjacent to recent clearings and there was no change in sedimentation on reefs adjacent to historic clearings. The effects of increased sedimentation are noteworthy, since previous studies (Babcock and Davies 1991, Stafford-Smith 1993, McClanahan and Obura 1997) have demonstrated that sedimentation can negatively impact coral survival and settlement leading to changes in reef community composition. From this finding, it is clear that even small clearings of less than 0.5 km can have effects on reef sedimentation, a first step in understanding minimum areas of mangroves needed to protect reefs.

Based on observations in Panama of reefs adjacent to cleared mangroves, I expected to see an effect of clearing on reef algal growth. However, in Belize there was no difference in algal growth on coral reefs based on mangrove condition. It is important to note that overall algal cover on the reefs was markedly high, with 74% of the hard substrate covered with algae across all transects. Therefore, any effect of mangrove clearing on algal growth may be overshadowed by the already high algal cover in the area.

I also sought to understand linkages (energy flow) between highly productive mangrove systems and coral reefs by determining whether mangroves provide nutrients and organic materials to sessile reef invertebrates. There has been debate in the literature about whether mangrove-derived nutrients are actually utilized by organisms outside of the mangrove habitat. Recent works suggest that that they are less important to food webs, because mangrove organic matter is lower in nitrogen than other primary producers (Stoner and Zimmerman 1988, Ambler et al. 1994, Newell et al. 1995, Primavera 1996, Loneragan et al. 1997, Marguillier et al. 1997, France 1998).

My results suggest the opposite. Using stable isotope analyses, I was able to track mangrove-derived nutrients in a suite of filter feeding and predatory reef invertebrates to examine uptake and incorporation of this organic matter source. From this study (Chapter 6), we found that filter feeding sponges, clams and feather duster worms reflect a 10-40%

contribution from mangroves, whereas analyses of a tunicate species suggest little or no mangrove contribution. For five hard corals sampled, isotope results indicate ~10-30% contribution from mangroves, varying by species and site. This finding is the first evidence that mangrove-derived nutrients are incorporated into sessile reef invertebrates and indicates and that this organic matter source may be important to the nutrient dynamics on coral reefs. Further research into the nutritive value of mangrove-derived nutrients and whether growth rates of sessile reef invertebrates change in the absence of this organic matter source will help inform our understanding of habitat connections and the effects of mangrove loss on coral and sessile invertebrate communities. Furthermore, examining the relative contribution of mangrove-nutrients to sessile reef invertebrates provides a starting point for determining potential changes in reef nutrients following mangrove disturbance.

Mangroves are considered important vegetative buffers, protecting coastal areas from the impacts of wave action and storm events. However, little empirical research has examined this role (Dahdouh-Guebas et al. 2005, Danielsen et al. 2005, Kar and Kar 2005, Kathiresan and Rajendran 2005). My study in Belize allowed me to opportunistically examine whether mangroves reduced wave and storm surge impacts in the immediate habitat relative to adjacent cleared areas during two major storm events during the hurricane season. I found that field equipment secured in these areas was lost during Tropical Storms Wilma and Gamma; however, loss was up to 60% greater in the cleared areas, though it varied with equipment type. This loss of buffering capacity during storm events has implications both for coastal protection and for coral reefs that may be affected by land erosion and deposition during such events.

The results from this research project have succeeded in: (1) demonstrating additional connections between mangrove forests and coral reefs; (2) identifying effects of mangrove clearing on inshore marine systems; (3) highlighting the importance of considering mangrove habitat in conservation efforts to protect adjacent coral reef systems; and (4) drawing attention to a number of research priorities that will clarify mangrove-reef connections and facilitate effective conservation and management strategies. The results presented here are not intended to be a conclusive statement on

mangrove-coral reef connectivity, but rather are presented as a summary of the current state of knowledge and as impetus for future research and adaptive management to incorporate this and future knowledge on habitat linkages.

From these findings it is clear that managers of coastal and marine systems are not sufficiently managing these areas if mangrove forests are excluded from management. These data highlight the importance of managing and protecting mangrove forests as part of any coastal and marine management plan that focuses on subtidal or coastal habitats. On land, managers consider the impacts of disturbance and connections within a watershed. Similarly, in tropical marine systems, managers and conservation practitioners need to adjust their paradigm to think in terms of a "mangrove-shed": to consider the interactions and impacts of disturbance to mangroves on the rest of the "mangrove-shed". Rather than considering passive protection of mangrove forests for their own sake, alone, management strategies designed to protect coral reefs must acknowledge the role that mangrove forests play in functioning of seagrass and reef systems.

The rapid loss of mangrove forest habitat and continuing decline of coral reefs worldwide necessitates urgent consideration of the results and research gaps presented here. To ensure survival of both mangroves and reefs in the future, it is essential to act on new findings in a timely manner and pursue existing questions and gaps in our understanding to provide needed information for conservation practitioners and resource managers in their efforts to halt the decline of these valuable marine ecosystems.

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Appendix A. Supplementary Materials, Chapter 6

Table A1. Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Penicillus 4	P Caracole N - CS ME	21.64	0.76	-10.12046	18.76253	2.436785	1.251608
Penicillus 1	P Caracole N - CS ME	19.89	0.99	-11.45136	20.9275	2.379882	1.692841
Halimeda 3	P Caracole N - CS RF	19.66	0.15	-4.477321	12.89827	*	*
Hamelida 1	P Caracole N - CS RF	20.50	0.32	-7.453588	15.2634	1.009128	0.753749
Hamelida 2	P Caracole N - CS RF	19.64	0.09	-5.276673	13.29381	*	*
Avranvilla 2	P Caracole N - IS ME	19.89	0.30	-10.84373	22.00999	1.647255	1.648768
Avranvilla 3	P Caracole N - CN MT	21.48	0.62	-12.34539	24.17992	3.34805	1.619013
Avranvilla 4	P Caracole N - CN MT	19.39	1.41	-14.23502	28.91441	2.803538	2.693961
Thallassia-lo 5	P Caracole N - IN RF	20.62	0.50				
Thallassia-lo 4	P Caracole N - IN RF	20.85	0.58	-8.200568	38.74566	0.088003	3.102057
Thallassia-lo 3	P Caracole N - IS RF	19.39	0.82				
Detritus leaf 4	P Caracole N - IN RS	13.41	0.53	-27.5245	45.61725	2.392904	0.457894
Detritus leaf 3	P Caracole N - IN RS	12.44	0.43	-28.73073	46.34415	2.329656	0.349565
Detritus leaf 1	P Caracole N - IN RS	12.63	0.33	-30.26145	44.59802	1.757319	0.490644
Very decayed detritus leaf 1	P Caracole N - IN RS	5.18	0.71	-28.80833	46.01065	1.705477	0.714929
Green/yellow mangrove leaf (old+on tree) 1	P Caracole N - IN MT	5.76	0.44	-27.81271	47.32221	1.473224	0.787768
Green/yellow mangrove leaf (old+on tree) 2	P Caracole N - IN MT	-0.71	0.40	-27.89836	46.95022	1.419309	0.809305
Green/yellow mangrove leaf (old+on tree) 3	P Caracole N - IN MT	-7.91	0.42	-28.16238	43.42085	1.124845	0.389836
Unidentified whorling red in tuft 1	P Caracole N - CN ME	21.65	4.73	-16.2774	20.33984	2.452004	1.111672

Table A1. (Continued) Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Yellow mangrove leaf (old+on tree) 4	P Caracole N - IN ME	-10.73	0.52				
Caulerpa r 1	P Caracole N - CN RF	20.89	1.10	-27.79851	29.21363		
Green mangrove leaf (new) 5	P Caracole N - IN ME			-27.51241	44.49514	2.250856	0.865715
Caulerpa racemosa 4	Pastores - IN RF	20.83	1.37	-16.34994	22.97868	2.33618	2.378555
Caulerpa racemosa 3	Pastores - IN RF	20.85	1.48	-16.2789	21.13207	2.449785	1.90062
Caulerpa racemosa 2	Pastores - IN RF	20.70	1.39	-16.29791	21.54507	2.917628	1.484512
Epiphytes	Aldabra Lagoon NW - near mangr.	13.98	0.59	4.665921	0.929481		
Detritus leaf 3	Gallinazo - IN - RS	11.20	0.22	-27.48777	49.08737	1.351953	0.412762
Detritus leaf 2	Gallinazo - IN - RS	11.05	0.26	-28.47638	48.15984	2.107939	0.491252
Detritus leaf 1	Gallinazo - IN - RS	17.81	0.32	-27.57683	47.67266	1.477434	0.505754
Thallassia-lo 2	Gallinazo - CS - RF	20.75	0.63	-7.777688	34.48622	0.796324	2.852165
Thallassia-lo 4	Gallinazo - CS - RF	20.84	0.56	-9.585797	35.88187	5.440678	2.661968
Thallassia-lo 1	Gallinazo - CS - RF	20.39	0.88	-8.908382	34.35391	4.294307	2.54717
Thallassia-lo 3	Gallinazo - CS - RF	21.04	0.56	-8.719266	35.66195	5.172159	2.445373
Acanthopora specif 1	Red Point - CN RF	21.77	4.51	-13.77739	17.12612	2.355495	1.086515
		21.35	4.57				
Acanthopora specif 2	Red Point - CN RF	21.58	4.29	-13.93361	18.00534	2.591236	1.321776
Acanthopora specif 3	Red Point - CN RF	21.35	5.11	-13.9255	19.64111	2.244737	1.242766
Detritus leaf 3	Red Point - IN RS	12.45	0.71	-28.43961	45.42027	0.341533	0.400183

Table A1. (Continued) Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where` available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Detritus leaf 5	Red Point - IN RS	12.28	0.71	-26.44124	43.82354	3.0048	0.715457
Detritus leaf 4	Red Point - IN RS	13.96	0.44	-27.88068	46.68544	1.924658	0.5915
Thallassia-lo 1	Red Point - CN RF	19.36	0.52	-8.743912	35.31409	3.428524	2.806733
Thallassia-lo 2	Red Point - CN RF	20.40	0.45	-9.43878	34.92142	6.085694	2.569339
Thallassia-lo 4	Red Point - CN RF	20.56	0.55	-7.599155	34.93628	3.689161	2.740003
Acanth spic 1	PCS - CS - RF	19.88	4.98				
Acanth spic 3	PCS - CS - RF	20.00	4.75				
Acanth spic 2	PCS - CS - RF	20.01	5.57				
Thallasia-lo 4	PCS - CS - RF	19.93	0.72	-8.732065	34.86477	5.15426	2.619116
Thallasia-lo 1	PCS - CS - RF	18.95	0.65	-9.024784	35.17202	4.7705	2.688433
		18.92	0.65				
Thallasia-lo 2	P Caracole S - CS RF	19.78	0.74	-9.14025	30.76988	5.458799	2.284523
Acanthopora musc	P Caracole S - IS RF	21.20	5.28	-14.66443	20.37706	2.975161	1.427833
Acanthopora musc 3	P Caracole S - IS RF	20.99	5.85	-14.62999	21.32219	2.901084	1.443853
Acanthopora musc 4	P Caracole S - IS RF	20.94	5.15	-13.53711	20.61913	3.168584	1.263495
Thallasia-lo 3	P Caracole S - IN RF	18.33	0.46	-8.739155	36.2022	4.785933	2.448769
Thallasia-lo 6	P Caracole S - IN RF	18.78	0.37	-8.239812	36.3793	4.849721	2.440804
Dictyota + Dasya(?) mix 1	P Caracole S - CN ME	19.69	2.44	-14.50743	30.57522	2.86919	1.598653
Dictyota + Dasya(?) mix 2	P Caracole S - CN ME	21.35	5.68	-14.82851	25.74242	2.820834	1.704411
Dictyota 1	P Caracole S - CS ME	19.75	2.08	-14.27042	22.73565	2.528641	1.527844

Table A1. (Continued) Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Unidentified branching red algae 1	P Caracole S - CS ME	21.08	6.74	-16.64559	20.90925	2.456622	1.509216
Unidentified branching red algae 2	P Caracole S - CS ME	20.97	6.75	-15.48384	19.75795	3.204594	1.363771
Dictyota (guineensis?) 1	P Caracole S - IS RF	20.52	3.90	-15.4808	19.84088	2.587285	0.908493
Dictyota + unidentified branching red algae 2	P Caracole S - CS ME	20.77	3.86	-14.62594	26.38562	2.737497	1.897053
Detritus leaf 2	P Caracole S - IN RS	16.57	0.61	-29.38239	39.82847	2.382545	0.660734
Detritus leaf 3	P Caracole S - IN RS	12.63	0.23	-28.75239	45.99724	1.969977	0.449015
Detritus leaf 4	P Caracole S - IN RS	11.82	0.36	-28.10719	45.17281	0.418475	0.473156
Detritus leaf 2	P Caracole S - IN ME	11.21	0.22	-29.15652	45.70145	1.074879	0.325343
Detritus leaf 3	P Caracole S - IN ME	9.69	0.27	-28.53159	45.57753	0.770341	0.538157
		9.89	0.28				
Detritus leaf 1	P Caracole S - IN ME	13.57	0.32	-29.34188	46.47838	1.510082	0.374625
Sediment trap sample	PCN-IN ME 2	2.48	1.60				
Sediment trap sample	PCN-IN RS 3	18.31	0.20	-3.958392	11.10617	2.31	0.355871
Sediment trap sample	PCN-CS RS 2	16.70	1.13	-7.921558	5.389724	2.470736	0.186026
Sediment trap sample	PCN-IN MT 3	-6.65	3.08				
Sediment trap sample	PCN-IN RF 3	11.44	0.64	-7.610109	9.825307	2.219149	0.265442
Sediment trap sample	PCN-CS RF 1	13.42	0.15				
Sediment trap sample	PCN-IN ME 3	9.72	1.55				
Sediment trap sample	PCN-IN MT 2	-1.54	3.49				
Sediment trap sample	PCN-CS MT 2	1.45	0.89				
		1.40	1.05				
Sediment trap sample	PCS-CS ME 1	2.67	0.71				
Sediment trap sample	PCN-IN ME 1	0.62	1.05				

Table A1. (Continued) Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Sediment trap sample	PCS-CS MT 1	-5.22	0.86				
Sediment trap sample	Red Pt - IN - ME 1	2.85	0.67	-17.94034	17.83682	2.597195	0.173445
Sediment trap sample	PCS-IN ME 3	3.02	0.33				
Sediment trap sample	PCN-CS RS 1	16.36	0.81				
Sediment trap sample	PCN-CS RF 3	11.72	0.33	-6.355241	10.02471	2.356923	0.256223
Sediment trap sample	Red Pt -IN ME 3	-1.07	0.80	-23.14746	22.93235	1.229333	0.815739
Sediment trap sample	PCN-CS MT 1	3.08	0.41				
Sediment trap sample	PCN-IN MT 1	-1.32	0.77				
Sediment trap sample	PCN-CS ME 3	10.53	0.92				
		10.80	1.04				
Sediment trap sample	PCS-CS MT 2	-2.86	1.89				
Sediment trap sample	PCS-CS MT 3	-4.29	0.44				
Sediment trap sample	PCN-IN RS 1	21.09	0.49	-4.706273	7.805282	3.709701	0.162395
Sediment trap sample	PCN-CS RF 2	12.84	0.31				
Sediment trap sample	Gallinazo-IN ME 3	-2.87	0.87	-26.10857	18.21241	1.885338	0.741774
Sediment trap sample	PCS-CS ME 2	4.28	1.07				
		4.27	0.97				
Sediment trap sample	PCN-CS ME 2	5.56	0.75				
Sediment trap sample	PCS-CS ME 3	6.33	0.72				
Sediment trap sample	PCN-IN RF 1	16.15	0.80				
Sediment trap sample	PCS-IN ME 2	1.40	1.77				
Sediment trap sample	Gallinazo-IN ME 1	8.68	1.63	-25.43174	10.26141	2.218418	0.511431
Sediment trap sample	PCN-IN RS 2	17.89	0.96	-5.003612	5.875989	2.995874	0.119644
Sediment trap sample	PCS-IN MT 2	0.86	0.47				

Table A1. (Continued) Sample data for primary producers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Sediment trap sample	PCN-CS MT 3	2.23	0.39				
Sediment trap sample	PCN-CS RS 3	11.51	0.75	-10.33756	3.863486	2.801193	0.177887
Sediment trap sample	PCN-CS ME 1	3.36	1.12	-13.25526	14.05543	1.950172	0.520524
Sediment trap sample	Red Point- IN ME 2	0.02	1.42	-21.26353	20.80169	1.033851	0.692649
Water sample 1	Gallinazo -reef			*	*	*	*
Water sample 2	Gallinazo -reef	19.64	0.21	*	*	*	*
Water sample 3	Gallinazo -reef	20.33	0.28	-23.50333	1.209315	*	*
Water sample 4	Gallinazo -reef	20.74	0.35	*	*	*	*
Water sample 1	P Caracole S - reef	21.04	0.49				
		21.31	0.48				
Water sample 3	P Caracole S - reef	21.84	0.36				
Water sample 5	P Caracole S - reef	21.72	0.33				
		21.40	0.34				
		21.48	0.28				
water sample 1 (over coral)	Aldabra NW Lagoon	21.50	0.37	-9.844758	0.718109	*	*
water sample 2 (over coral)	Aldabra NW Lagoon	22.09	0.38	-7.709378	1.306945	*	*
water sample 3 (over coral)	Aldabra NW Lagoon	21.76	0.40	*	*	*	*
			0.28				

Table A2. Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available).

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Agaricia tenu 1	PCN - IN - RF	21.58	1.89	-13.8101	30.93942	3.931842	6.604661
		21.67	2.07				
Agaricia tenu 2	PCN - IS - RF	21.59	2.12	-14.2725	29.80733	4.494149	5.963938
Agaricia tenu 1	PCN - IS - RF	21.25	2.26	-12.9386	38.12468	3.488999	7.174712
Agaricia tenu 1	PCN - IS - RS	21.50	2.23	-17.1098	34.25243	4.194458	6.832937
Agaricia tenu 3	PCN - IS - RS	21.31	2.67	-15.6836	30.38415	4.696003	6.547549
Niphates 3	P Caracole N - IN RF	18.89	0.51	-16.089	8.713247	5.560271	2.042015
Millepora alc 2	PCN - CN - RF	19.16	0.97	-12.9316	49.95408	3.143994	7.76832
Diploria sp. 1	PCN - IS - RS	20.71	3.12	-15.0026	20.68738	5.077054	4.126606
Agaricia tenu 4	Pastores - CS - RS	20.43	2.32	-14.1805	26.81491	*	*
Agaricia tenu 3	Pastores - CS - RS	19.97	2.97	-14.7622	30.53951	*	*
Agaricia tenu 6	Pastores - CS - RS	20.42	1.99	-15.0856	33.47746	3.72195	6.319236
Agaricia frag 1	Pastores - IN - RS	20.43	2.20	-13.7948	22.23987	3.758633	4.087827
Agaricia frag 2	Pastores - IN - RS	20.49	1.54	-14.0208	27.86676	3.610879	4.79865
Agaricia frag 4	Pastores - IN - RS	20.81	1.90	-13.3829	23.48862	3.171691	4.673168
Montestrea ann 2	Pastores- IN - RS	19.96	2.82	-15.9194	37.17263	2.40031	5.800611

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Agaricia frag 1	Red Pt - IN - RS	20.25	3.00	-14.1665	25.57637	3.908426	5.295127
Agaricia frag 4	Red Pt - IS - RS	19.83	3.01	-15.4724	35.48829	3.552796	7.120016
Agaricia frag 5	Red Pt - IS - RS	19.88	2.87	-15.7828	32.33299	3.596613	6.897404
Montestrea ann 1	Red Pt - CN - RS	20.67	1.95	-13.5165	33.67134	5.780324	5.390457
Agaricia tenu 1	Red Pt- CS - RS	x	x	-15.4593	33.87839	4.288512	6.836528
Agaricia tenu 2	Red Pt - CS - RS	20.28	2.51	-15.1007	28.95214	5.155679	5.970875
Agaricia tenu 3	Red Pt - CS - RS	19.82	2.56	-15.5327	32.6729	4.103055	6.878115
Agaricia frag 2	Red Pt - IS - ME	19.03	1.56	-17.6352	25.40152	5.049703	4.420032
		19.09	1.55				
Agaricia frag 1	Red Pt - IS - ME	18.84	1.52	-17.1329	38.83386	4.609496	6.912731
Acropora cerv 1	Red Pt - IN - RS	20.04	1.53	-16.2349	28.06126	3.410136	4.873552
Acropora cerv 2	Red Pt - IN - RS	20.35	1.65	-16.1053	27.72417	3.76169	4.549906
Acropora cerv 3	Red Pt - IN - RS	20.43	1.47	-16.3981	31.79368	3.519169	5.087744
Montestrea ann 1	Red Pt - IN - RF	20.68	2.14	-12.513	22.84004	4.098979	5.190163
Montestrea ann 1	Red Pt - IN - RS	20.48	2.92	-14.4116	31.95831	3.572157	6.014587
File clam 1	Red Point - IN RS	18.99	2.07	-17.2606	40.63854	5.189927	11.00511
File clam 2	Red Point - IN RS	18.84	1.98	-17.7316	40.93697	5.018325	11.41131
File clam 3	Red Point - IN RS	19.03	2.01	-17.0322	40.89977	6.316579	11.47961
File clam 1	Red Point - IN RF	17.56	2.02	-17.0211	43.81566	5.868165	10.71582

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
		17.77	1.99				
File clam 2	Red Point - IN RF	17.43	2.14	-16.8685	43.46614	5.377873	11.07633
File clam 3	Red Point - IN RF	17.41	1.98	-16.154	43.23769	5.870208	11.56832
Phallusia 1	Red Point - IN RS	22.41	5.71	-18.8342	16.0524	6.481031	2.838882
Phallusia 2	Red Point - IN RS	22.41	5.68	-19.1899	15.36655	7.184805	2.599502
Phallusia 3	Red Point - IN RS	22.10	5.39	-19.2222	18.53796	4.871237	3.942579
Phallusia 1	Red Point - CN RS	21.87	5.04	-18.8099	18.93348	2.443267	4.511909
File clam 1	Red Point - CS RS	20.37	1.84	-17.9559	42.64408	4.224664	11.77866
File clam 4	Red Point - IN RF	18.85	2.27	-16.5097	43.23583	5.220571	11.9007
Amphimedon comp 1	Red Point - IN RS	21.34	2.35	-20.1611	18.46095	6.797679	3.995905
Amphimedon comp 2	Red Point - IN RS	21.34	2.11	-19.7296	17.50023	6.888587	3.935913
Amphimedon comp 3	Red Point - IN RS	19.73	1.70	-19.3364	15.17363	7.246092	3.504501
Aplysina fulva 1	Red Point - IN RS	19.64	1.87	-20.3481	35.11973	4.488196	8.680317
		19.68	1.81				
Aplysina fulva 2	Red Point - IN RS	19.55	1.90	-20.345	34.73267	4.049997	8.431503
Aplysina fulva 3	Red Point - IN RS	19.39	1.97	-20.3056	38.01201	4.494325	9.357284
Aplysina fulva 2	Red Point - IN RF	17.56	2.16	-19.6022	36.69642	4.307401	9.057702
Aplysina fulva 3	Red Point - IN RF	17.95	1.78	-20.15	40.45906	2.959096	9.639117
		17.97	1.76				
Aplysina fulva 4	Red Point - IN RF	17.61	2.18	-19.7993	37.21608	3.312515	9.451373
Niphates (pink) 1	Red Point - IN RS	20.99	0.75	-19.203	10.14919	5.365615	2.40985

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Niphates (pink) 2	Red Point - IN RS	20.99	0.89	-19.2748	10.73223	6.179195	2.493056
Niphates (blue) 1	Red Point - IN RS	20.71	0.96	-19.2091	11.57365	5.386044	2.660776
Agaricia tenu 2	Gallinazo - IN - RS	20.37	2.74	-15.133	29.09331	3.71557	5.741647
Agaricia tenu 1	Gallinazo - IN - RS	20.27	2.77	-15.0608	21.80693	3.888588	4.919238
Agaricia frag 2	Gallinazo - IN - RS	20.49	2.30	-15.0026	21.87157	2.900946	4.617295
Agaricia frag 1	Gallinazo - IN - RS	20.79	1.98	-13.4546	29.33227	3.406095	5.112409
Agaricia frag 3	Gallinazo - IN - RS	20.54	5.27	-14.9645	15.13929	2.381893	3.355309
Amphimedon compressa 2	Gallinazo - CS - RF	20.05	3.02	-19.66	21.73	7.58	4.5
Amphimedon compressa 3	Gallinazo - CS - RF	20.15	2.16	-19.98	19.18	7.35	3.89
Amphimedon compressa 4	Gallinazo - CS - RF	20.22	2.21	-20.04	17.46	7.35	3.61
Aphysina fulva 1	Gallinazo - CS - RF	18.66	2.07	-20.86	38.79	3.33	9.38
Aphysina fulva 2	Gallinazo - CS - RF	18.72	2.02	-20.53	39.07	3.44	9.51
Aphysina fulva 4	Gallinazo - CS - RF	18.37	1.92	-20.52	38.89	3.51	9.56
Amphimedon compressa 1	Gallinazo -IN - RS	20.61	1.74	-20.85	20.33	6.61	3.94
Amphimedon compressa 2	Gallinazo -IN - RS	20.17	2.62	-20.24	20.27	6.81	4.16
Amphimedon compressa 4	Gallinazo -IN - RS	20.83	1.44	-20.17	15.39	6.74	3.15
Niphates 1	Gallinazo - IN - RF	17.84	0.41	*	*	**	**
Niphates 2	Gallinazo - IN - RF	20.48	0.51	-18.3	7.9	5.56	1.81
Niphates er 1	Gallinazo - IN - RS	19.27	1.00	-20.05	16.48	5.25	3.58

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Niphates er 2	Gallinazo - IN - RS	19.36	0.89	-20.07	16.74	5.27	3.79
Niphates er 4	Gallinazo - IN - RS	19.45	0.65	-19.68	11.84	5.39	2.64
Sabellastarte magn 1	Gallinazo - IN RS	17.97	1.45	-17.98	40.21	5.66	10.43
Sabellastarte magn (tube) 1	Gallinazo - IN RS	18.64	6.49	-17.59	23.07	6.7	4.52
Sabellastarte magn 1	Gallinazo - IS ME	9.30	1.64	-19.16	39.8	7	8.58
Sabellastarte magn 1	Gallinazo - CS RF	16.81	1.59	-17.74	42.44	7.39	8.94
Sabellastarte magn (tube) 2	Gallinazo - IS RS	17.84	4.49	-18.03	19.71	7.28	3.75
Sabellastarte magn (tube) 1	Gallinazo - CS RF	15.77	3.94	-18.22	19.17	8.21	3.27
Sabellastarte magn (tube) 4	Gallinazo - CS RF	18.70	5.03				
Phallusia 1	Gallinazo - CS RS	22.25	5.72	-20.14	16.47	2.54	4.11
Phallusia 1	Gallinazo - CN RS	22.11	5.69	-19.77	20.81	3.77	5.12
Phallusia 2	Gallinazo - CN RS	21.79	5.50	-19.79	18.79	4.44	3.99
Sabellastarte magn 1	Gallinazo - IS RF	17.76	1.55	-17.71	44.51	5.73	9.23
Sabellastarte magn 2	Gallinazo - IS RF	17.55	1.45	-17.9	43.33	5.65	9.95
Sabellastarte magn 2	Gallinazo - CS RF	18.30	1.36	-17.15	41.41	5.39	11.18
Sabellastarte magn 4	Gallinazo - CS RF	18.03	1.77	-18.04	41.24	6.64	9.66
		18.09	1.77				
Sabellastarte magn 1	Gallinazo - IS RS	19.23	1.60	-19.25	42.91	6.92	9.45

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Sabellastarte magn 2	Gallinazo - IS RS	19.10	1.77	-18.28	41.52	5.58	10.93
Sabellastarte magn (tube) 1	Gallinazo - IS ME	12.51	4.93	-20.45	22.32	4.93	3.3
Agaricia frag (or lepto?) 2	PCS - CS - RS	21.50	2.16	-16.4188	29.55928	4.015261	5.658722
Agaricia frag (or lepto?) 3	PCS - CS - RS	21.52	2.05	-14.4651	31.49681	3.878289	6.08335
Agaricia frag (or lepto?) 1	PCS - CS - RS	21.41	2.08	-14.7288	33.31466	3.681585	6.175423
		21.58	1.99				
Agaricia tenu 1	PCS - IN - RS	20.95	2.30	-15.0478	21.29645	*	*
Agaricia tenu 2	PCS - IN - RS	20.47	2.13	-15.8351	33.14669	*	*
Agaricia tenu 3	PCS - IN - RS	20.25	2.56	-15.2514	28.65342	*	*
Aplysina fulva 2	P Caracole S - CS RF	17.00	2.09	-19.7279	37.78011	1.912824	9.401245
Aplysina fulva 3	P Caracole S - CS RF	17.45	2.09	-20.2187	37.76198	2.839872	9.468497
Aplysina fulva 4	P Caracole S - CS RF	16.90	1.78	-20.3462	38.61215	3.732701	9.692269
Aplysina fulva 1	P Caracole S - IN RS	18.64	1.86	-19.4435	31.94435	4.637973	7.675734
Aplysina fulva 3	P Caracole S - IN RS	18.55	1.99	-20.0213	35.83762	4.775889	8.823102
Aplysina fulva 4	P Caracole S - IN RS	18.38	1.94	-20.1559	35.95656	4.292663	8.793595
Niphates er (blue) 1	P Caracole S - IN RS	20.61	1.18	-18.9122	11.60347	4.487612	2.884738
Niphates er (blue) 2	P Caracole S - IN RS	19.97	0.84	-18.89	11.4411	4.431616	2.860976
Niphates er (blue) 3	P Caracole S - IN RS	20.47	0.88	-18.81	10.53064	5.232155	2.587772
Phallusia 1	P Caracole S - IN RS	22.25	7.75	-19.3109	10.5369	1.606919	2.742318

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Phallusia 2	P Caracole S - IN RS	21.08	6.49	-19.4324	18.34438	0.911114	4.338153
Phallusia 1	P Caracole S - CN RS	21.10	6.06	-19.2958	20.02361	2.036223	4.473894
Amphimedon comp 1	P Caracole S - CS RS	20.48	2.14	-18.8201	14.79763	6.788642	3.473139
Amphimedon comp 2	P Caracole S - CS RS	20.29	2.01	-19.1561	16.89459	6.893375	3.952954
Amphimedon comp 3	P Caracole S - CS RS	19.92	2.92	-19.8119	21.61954	6.394594	4.915198
Amphimedon comp 2	P Caracole S - IN RS	20.32	1.83	-19.3656	16.13827	6.561546	3.724271
Amphimedon comp 3	P Caracole S - IN RS	20.19	1.57	-19.27	16.88196	6.853971	3.927623
Amphimedon comp 4	P Caracole S - IN RS	20.44	1.47	-19.2269	15.49413	7.078992	3.608911
Aplysina fulva 1	P Caracole S - CS RS	18.73	1.71	-19.23	33.96238	4.980172	8.291745
Aplysina fulva 4	P Caracole S - CS RS	18.88	1.90	-19.7076	36.45363	4.693969	9.291284
		18.99	1.85				
Aplysina fulva 5	P Caracole S - CS RS	18.85	1.85	-20.0365	38.5154	4.318587	9.550846
Niphates er (purple) 1	P Caracole S - CS RS	20.75	1.18	-19.2259	12.78455	5.288151	3.242662
Niphates er (purple) 2	P Caracole S - CS RS	21.12	0.81	-18.8151	9.192306	5.167863	2.334436
File clam 1	P Caracole S - IN RS	19.71	1.90	-17.9681	43.92783	4.228371	11.83135
File clam 2	P Caracole S - IN RS	19.81	1.98	-17.1332	43.62049	5.331703	11.96334
File clam 1	P Caracole S - CN RS	20.00	2.42	-17.3159	42.22588	5.259116	12.04737
File clam 2	P Caracole S - CN RS	20.11	2.37	-17.9509	44.47996	5.658348	11.19342
Niphates (blue) 3	P Caracole N - IN RS	20.50	1.36	-19.1872	13.78964	5.542897	3.394645

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Niphates (blue) 4	P Caracole N - IN RS	22.06	0.40	-18.7052	6.562308	5.623633	1.658345
Niphates (pink) 1	P Caracole N - IN RS	20.21	1.38	-19.5073	15.72443	5.171923	3.71043
Niphates (pink) 2	P Caracole N - IN RS	20.93	0.59	-19.6533	9.780216	5.541875	2.061452
Amphimedon comp 1	P Caracole N - IN RS	20.14	2.30	-19.7793	18.5094	6.568952	3.856522
Amphimedon comp 2	P Caracole N - IN RS	20.08	2.70	-19.8743	21.45727	6.660929	4.579071
Amphimedon comp 3	P Caracole N - IN RS	19.99	2.84	-20.1183	21.55991	6.74984	4.52867
Aplysina fulva 1	P Caracole N - IN RS	18.90	2.04	-19.8703	37.13048	4.213319	9.003328
Aplysina fulva 2	P Caracole N - IN RS	18.79	1.91	-19.6853	34.59605	4.586337	8.400602
Aplysina fulva 4	P Caracole N - IN RS	18.88	1.94	-20.0323	38.02825	4.074331	9.139234
Amphimedon comp 3	Zapatillas	19.61	1.62	-19.2152	16.97411	6.299152	3.404013
Amphimedon comp 4	Zapatillas	19.89	1.13	-17.7471	15.45626	6.556688	2.802352
Amphimedon comp 5	Zapatillas	19.73	2.67	-19.5683	22.3013	7.522446	4.577212
Aplysina fulva 3	Zapatillas	18.73	1.83	-19.8333	39.12185	4.029365	9.571714
Montestrea ann 1	Zapatillas	19.72	3.37	-14.8918	23.13268	4.004212	3.071832
Montestrea ann 2	Zapatillas	19.07	4.46	-14.4116	32.98891	3.130931	5.492963
Montestrea ann 3	Zapatillas	19.55	4.00	-15.1529	21.71091	4.214125	6.456535
Agaricia fragilis 1	Zapatillas	19.73	2.45	-15.3991	26.58206	2.980119	3.409716
Agaricia fragilis 2	Zapatillas	19.58	2.47	-14.947	17.9839	3.631259	4.12803
Agaricia fragilis 3	Zapatillas	20.51	1.87	-14.3383	24.16495	3.77188	3.995208
Agaricia tenu 1	Zapatillas	19.04	4.11	-15.9425	26.9485	3.316389	5.758419

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Agaricia tenu 2	Zapatillas	19.65	4.56	-18.4117	31.61739	3.180862	6.5409
Agaricia tenu 3	Zapatillas	19.54	5.05	-15.9767	35.70413	3.409117	6.770862
STRI Pt Amphim host colony 1		19.44	2.82	-19.7014	19.17301	6.21328	4.659172
STRI Pt Amphim host colony 2		19.42	1.64	-19.5391	17.10318	6.461547	3.901607
STRI Pt Amphim host colony 3		18.91	3.06	-19.3628	18.5567	6.648	4.531108
Aplysina fulva 42 f	IN ME - expt	15.55	1.92				
Aplysina fulva 91 f	IN ME - expt	16.00	1.92	-19.5371	34.27905	3.741575	9.296326
Aplysina fulva 28 f	IN RS - expt	19.37	1.72	-19.3263	31.423	3.269749	7.977381
Aplysina fulva 61 f	IN RF - expt	18.56	2.04	-20.2896	35.36748	3.114169	9.078771
Aplysina fulva 18 f	CS RF -expt	19.02	1.84	-20.1816	35.99857	3.027194	9.01293
Aplysina fulva 54 f	CS RF -expt	18.45	1.93	-20.4222	37.86835	2.980291	9.371589
		18.13	1.98				
Aplysina fulva 78 f	CS RF-expt	17.38	1.98	-20.243	36.65151	3.167902	9.020874
Aplysina fulva 86 f / Aplysina fulva 34 f	CS RS - expt	18.45	1.93	-19.9954	37.73264	3.838816	9.772976
Aplysina fulva 95 f	CS RS - expt	18.44	1.88	-19.4991	35.35624	4.515848	9.239021
Aplysina fulva 32 f	CS ME - expt	15.67	1.89	-19.7679	38.71029	3.36367	9.922511
Aplysina fulva 62 f	CS ME - expt	15.44	1.92	-19.5021	38.46412	3.80007	9.957473
Aplysina fulva 57 f	CS ME - expt	15.72	1.94	-19.9618	37.55715	3.057224	10.05053
Aplysina fulva 14 f	CS MT - expt	16.27	1.98	-20.2632	36.0469	3.383043	9.179232
Aplysina fulva 24 f	CS MT - expt	15.98	1.97	-20.1132	36.13268	3.225001	9.430468

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Aplysina fulva 47 f	CS MT - expt	15.28	1.94	-20.0687	38.66007	3.535151	10.20316
Niphates erecta - 56N	IN MT - expt	10.97	1.10	-20.1263	11.83245	5.05523	2.473945
Niphates erecta - 71N	IN MT - expt	13.56	1.31	-20.0717	10.80168	4.92419	2.491711
Niphates erecta - 80N	IN MT - expt	8.65	1.35	-19.3142	15.52808	4.880465	3.420685
		8.91	1.37				
Niphates erecta - 20N	IN ME - expt	13.87	1.36	-18.9434	13.07753	5.646613	2.680564
Niphates erecta - 21N	IN ME - expt	12.89	1.37	-18.5425	14.17747	5.065535	3.124671
Niphates erecta - 100N	IN ME - expt	13.72	1.26	-18.6625	14.78375	4.77166	3.319766
Niphates erecta - 60N	IN RF - expt	18.12	0.98	-17.327	10.089	5.162137	2.354528
Niphates erecta - 25N	IN RF - expt	17.81	0.93	-17.3361	11.13882	5.336021	2.76211
Niphates erecta - 94N	IN RF - expt	18.13	0.98	-17.6377	10.14525	5.568883	2.194319
Niphates erecta - 70N	IN RS - expt	19.59	0.95	-18.601	9.912752	5.486517	2.319141
Niphates erecta - 28N	IN RS - expt	19.19	1.18	-19.1427	11.16912	5.581357	2.708478
Niphates erecta - 35N	IN RS - expt	19.26	1.06	-19.1044	9.753175	5.19671	2.235725
Niphates erecta - 3N	CS MT - expt	14.15	1.42	-18.4924	15.23986	4.996092	3.471623
Niphates erecta - 32N	CS MT - expt	12.41	1.37	-18.6494	17.83775	4.843858	4.058062
Niphates erecta - 36N	CS MT - expt	12.94	1.30	-18.606	15.01759	5.003506	3.218443
Niphates erecta - 38N	CS ME - expt	10.22	1.29	-17.374	14.09965	4.858442	3.256733
Niphates erecta - 51N	CS ME - expt	9.27	0.87	-17.7324	13.41355	5.133741	2.77603
Niphates erecta - 67N	CS ME - expt	7.86	1.00	-17.7535	14.76169	5.13884	3.081255
		8.12	1.00				

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Niphates erecta - 83N	CS RF -expt	16.99	0.99	-17.7799	12.02515	4.905887	2.968125
Niphates erecta - 17N	CS RS - expt	18.38	0.85	-18.5307	8.065739	5.423315	1.979039
Niphates erecta - 31N	CS RS - expt			-18.0012	7.639304	5.632339	1.799451
Niphates erecta - 97N	CS RS - expt	18.16	0.78	-17.7767	7.928818	5.646613	1.871688
Amphim. Comp. 4 c	IN ME - expt	16.86	2.23	-18.7967	18.12698	6.213576	4.402526
Amphim. Comp. 92 c	IN ME - expt	16.28	2.57	-18.8471	20.22517	6.192222	4.715468
		16.45	2.56				
Amphim. Comp. 47 c	IN ME - expt	17.24	2.71	-18.8481	17.93849	6.690486	4.408836
Amphim. Comp. 17 c	IN RF - expt	19.20	2.27	-17.7133	18.38406	6.791156	4.489143
Amphim. Comp. 43 c	IN RF - expt	19.35	2.32	-17.7718	18.25243	6.598968	4.434942
Amphim. Comp. 89 c	IN RF - expt	19.41	2.36	-17.791	18.8951	6.301027	4.613178
Amphim. Comp. 32 c	IN RS - expt	19.96	1.95	-19.1235	16.26859	6.342718	4.048523
Amphim. Comp. 39 c	IN RS - expt	19.70	2.45	-19.528	17.24582	6.421017	4.204771
Amphim. Comp. 86 c	IN RS - expt	20.07	1.76	-19.2325	15.60071	6.177986	3.810037
Amphim. Comp. 35 c	CS MT - expt	16.02	2.28	-18.5246	17.41143	6.951735	4.065145
Amphim. Comp. 99 c	CS MT - expt	17.07	1.68	-18.1683	16.15837	6.428667	3.941785
		17.32	1.66				
Amphim. Comp. 56 c	CS ME - expt	14.00	2.12	-17.8683	19.46827	6.325685	4.726458
Amphim. Comp. 76 c	CS ME - expt	16.16	1.70	-17.8314	14.93276	6.671166	3.607406
Amphim. Comp. 95 c	CS ME - expt	16.54	1.17	-17.4525	12.88798	6.606082	3.108762
Amphim. Comp. 64 c	CS RF - expt	18.57	2.52	-17.8461	17.19358	6.515335	4.166106

Table A2. (Continued) Sample data for consumers from Bocas del Toro, Panama and Aldabra Atoll Seychelles. Results include $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ and % S, C, and N values for each sample (where available)

Sample type	Location and transect	$\delta^{34}S$	%S	$\delta^{13}C$	%C	$\delta^{15}N$	%N
Amphim. Comp. 48 c	CS RS - expt	20.43	1.77	-19.0552	13.35476	6.843655	3.40278
Amphim. Comp. 1 c	CS RS - expt	19.99	2.21	-18.7552	15.60993	6.791654	3.967282
Amphim. Comp. 13 c	CS RS - expt	20.23	1.77	-18.575	14.58212	7.096522	3.583681