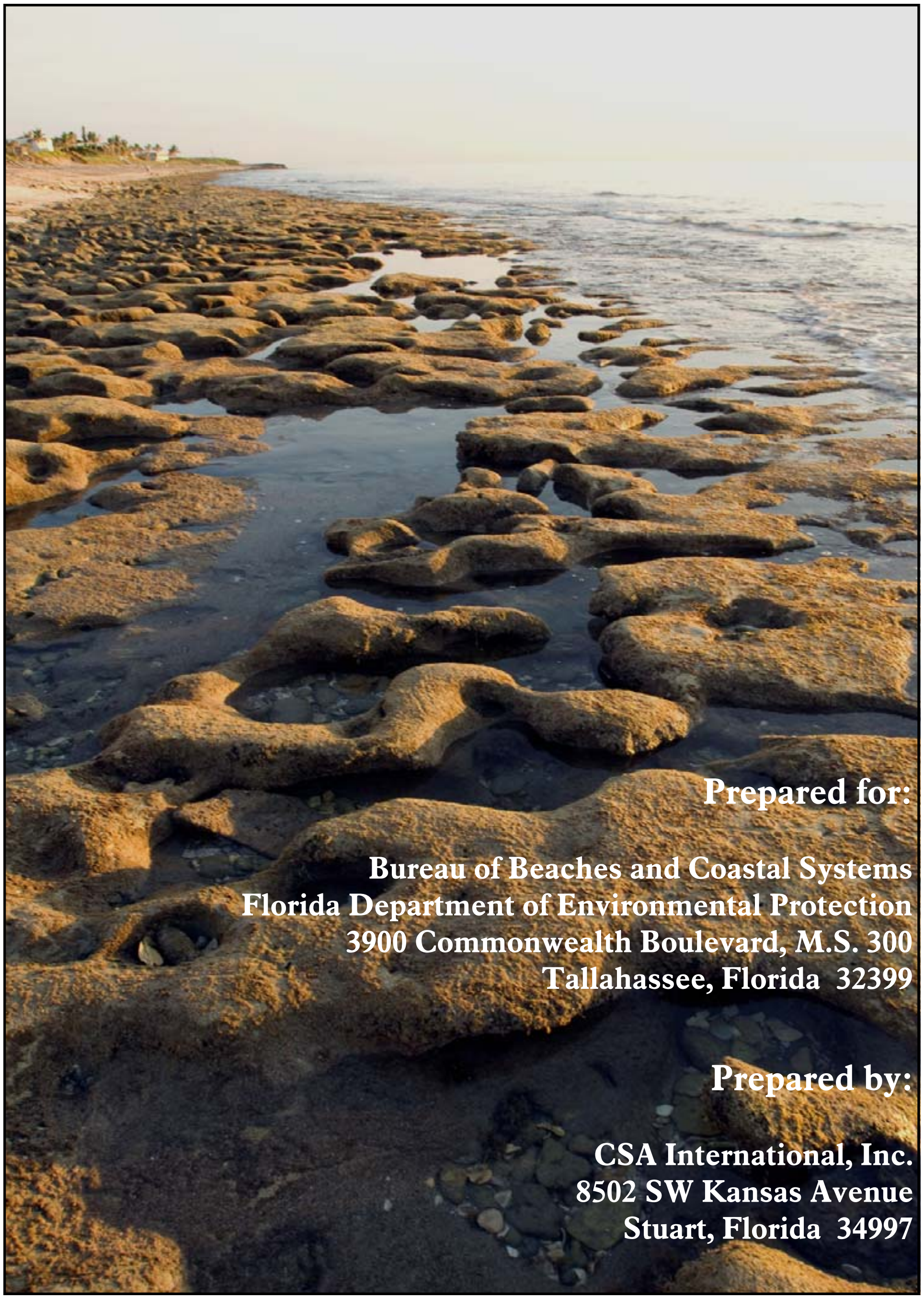
Ecological Functions of Nearshore Hardbottom Habitats in East Florida: A Literature Synthesis

June 2009



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Executive Summary

Given the complex policy questions involving hardbottom burial and mitigation, the consensus need for ecosystem-based management, and the large but unsynthesized literature base, this study responds to four issues: 1) What are specific ecological functions of nearshore hardbottom (NHB) (0 to 4 m depth)?, 2) What is happening to the coastal ecosystem (broader than NHB) when NHB is lost due to nourishment?, 3) Is offshore hardbottom (OHB) (>6 m depth) able to compensate for the loss of NHB?, and 4) If the NHB habitat has specific properties and functions that cannot be compensated for by existing OHB habitat, what are the best mitigation alternatives for the loss of natural NHB?

Very little depth-specific data exist for a majority of taxa throughout the region, which currently limits some of our ability to summarize core functional differences between NHB and OHB. However, a good deal of new information has been assembled and examined on shallow hardbottom structure and distributions (**Section 1**); the algal, invertebrate, fish, and turtle assemblages associated with shallow hardbottom (**Section 2**); and primary ecological functions of shallow hardbottom with a focus on latitudinal and depth variations, and implications for improved mitigation planning and implementation (**Section 3**).

ALGAE, INVERTEBRATE, FISH, AND TURTLE ASSEMBLAGES

Shallow hardbottom of southeast and east central Florida supports a sometimes diverse reef assemblage consisting of algae, invertebrates, fishes, and sea turtles. The fish and sea turtle components of the assemblage tend to be dominated by juvenile life stages. Patches of NHB exist in portions of Broward, Palm Beach, Martin, St. Lucie, Indian River, and Brevard Counties. Although these areas typically are separated by kilometers of sand, there are some areas where there is a semi-continuous hardbottom gradient from the beach into depths exceeding 6 m. Offshore, many mid-shelf areas are also dominated by expanses of sand, despite the variable occurrence of several mid-shelf reefs. Therefore, in many shallow areas, there are no natural habitats in the same or adjacent nearshore areas that can support equivalent abundances of early life stages of fishes and the invertebrates on which they largely feed. Absences of nursery structure can result in increased predation and lowered growth. In newly settled and juvenile stages, such conditions could foster demographic bottlenecks that ultimately result in lowered local population sizes (Jones, 1991).

Algae

The total number of recorded algal taxa, both identified and unidentified, is approximately 340, including 277 known species. Potentially dominant genera are *Ceramium, Dictyota, Hypnea, Laurencia, Gelidium, Caulerpa*, *Jania*, and *Ulva*, depending on subregions and other factors. Sunlight converted into macroalgal tissue is directly eaten by as many as 20 genera of invertebrates, at least 14 genera of fishes, and the juvenile stage of the endangered green turtle, *Chelonia mydas*.

Algae are a dominant driver of the food web and also contribute to shelter used by hundreds of species of invertebrates and fishes. All algal species contribute to oxygen and nutrient production. In terms of functional form groups, jointed-calcareous algae are most responsible for sediment enrichment and sand building. The abundance and diversity of macroalgae on NHB vary substantially with changes in latitude from Cape Canaveral to Miami Beach.

Invertebrates

Over 533 species of invertebrates have been identified along the east Florida coast, and there are likely to be more. The diversity of sessile species is greatest for cnidarians (~21%), bryozoans (~29%), and sponges (~19%). Some sessile groups may not be represented with such high diversity but can occur in very high biomass. A primary example is the sabellariid polychaete *Phragmatopoma lapidosa*, which can be very abundant along the mid- to north sections of the project area and is a habitat engineer that creates structure supporting high diversities of many other invertebrates.

The most diverse and generally abundant motile invertebrates are arthropods and polychaetes, which represent 47% and 28%, respectively, of the total number of motile invertebrate species. Over 100 species of crustaceans are extremely abundant, especially on worm reef-dominated hardbottoms. These include crabs, stomatopods, shrimp, isopods, and amphipods. There are over 87 reported polychaete species that are likely to be very abundant, although more research is needed to confirm this. There are also fairly high numbers of gastropods, flat worms, ribbon worms, and echinoderms on these habitats.

Primary ecological functional roles of invertebrates along the east Florida coast include 1) shelter-enhancing organisms that increase local diversity of fishes and invertebrates, and 2) predators or prey in local food webs. Generally, the highest community biomasses along the mainland east Florida coast occur in hardbottom areas with higher abundances of sessile invertebrate species (some may be considered foundational or keystone contributors to the community) that enhance local shelter. Along the Florida coast, important shelter-enhancing taxonomic groups are hard and soft corals, sponges, tunicates, molluscs, barnacles, and polychaetes (i.e., *P. lapidosa*). However, their importance in this function may vary dramatically with depth and latitude. In terms of contribution to local food webs, important taxonomic groups are sponges, polychaetes, echinoderms, crabs, and shrimp.

The loss of NHB would result in a significant reduction of a high biomass of invertebrates (sponges, corals, crabs, shrimp, worms, gastropods, bivalves) that could significantly change the nearshore food web. Before a dredging event, the nearshore community can be fairly diverse, consisting of a number of opportunistic (common) and longer-lived (often uncommon) species. The diversity contributes to a nearshore food web that consists of suspension feeders, herbivores, omnivores, and various levels of carnivores. However, after a dredging event occurs that results in high mortality and habitat elimination, there is likely to be a less diverse community consisting of more opportunistic species and fewer rare species such as corals. Further, conditions where there are significant reductions in shelter enhancement in these areas (via fewer sessile species) could reduce the number of small carnivore trophic levels and have possible adverse effects on the higher trophic levels within the assemblage.

Natural recovery of hardbottom habitats depends on both re-exposure of substrate as well as the recruitment capability of sessile shelter-enhancing invertebrates which in turn likely affect associated motile invertebrate species. Although it requires further investigation, it appears that very few older adult motile invertebrates would migrate into the area of impact. Consequently, habitat recovery requires ample larval supply and recruitment of the shelter-enhancing species to facilitate what could be a slow recovery of many associated motile invertebrates. The slow recovery of crevice-dwelling species (e.g., small crabs, shrimp, worms) may in turn affect prey availability for many motile invertebrate predators and some fishes. Further, degradation in water quality (most likely via fine resuspension and chronic turbidity) may affect fitness and/or survival of suspension feeders.

It is unlikely that OHB is able to compensate for the loss of NHB, particularly in the northern areas of the east Florida coast. Mitigation efforts to restore hardbottom habitats in some areas likely depend on recruitment capability of shelter-enhancing species such as *P. lapidosa*. Local hydrodynamics and the type, rugosity, and relief of construction materials must be considered for artificial reefs to maximize recruitment and subsequent recovery of the habitat. For instance, in the case of *P. lapidosa*, abundance decreases significantly in water deeper than 4 m. Even within the 0 to 4 m depth range, the highest abundances occur more towards the intertidal zone. This may be related to better feeding and reproductive opportunities and greater availability of suspended sand particles for tube-building in these more turbulent shallow waters. However, the mechanism by which worms settle and survive in these habitats is via large-scale hydrodynamics that affect larval supply and various biotic/abiotic factors that affect juvenile mortality. It is likely (though it requires further investigation) that settling *P. lapidosa* larvae may touch bottom in deeper waters, but actively postpone metamorphosis and choose to settle when they encounter shallower waters (McCarthy, 2001).

Consequently, if the goal is to mitigate for loss of worm reefs (and associated organisms), then structures deployed in the OHB would not be successful unless chemical cues, hydrodynamics, or other environmental factors could be created that accurately mimic the shallower waters and induce larvae to settle. Further, if settlement does occur at these depths, growing juveniles must survive, and recruitment of associated species must occur to properly mitigate for lost habitat.

Fishes

Currently, 257 species of fishes are recorded from NHB habitats. Species composition for the NHB ichthyofaunal assemblage is similar to that from shallow coral reef faunas from the region. Empirical information is highly limited on the amount of connectivity between shallow patches of hardbottom and deeper reefs for fishes and invertebrates of east Florida. The available information suggests that diverse fish species that ontogenetically migrate into deeper water can use NHB during early life stages. The physical environment is subject to wind and wave disturbance of sometimes high levels at intermediate temporal and spatial scales, and NHB assemblages are disturbance-mediated. If the NHB in use is close enough to intermediate hardbottom (IHB) or OHB, some of these species, depending on many changing ecological drivers (predation, growth, larval recruitment), could ontogenetically migrate into deeper habitats. Answers to the question “How close is close enough?” will vary by species, site, and time. Tagging studies using either conventional or acoustic methods that compare cross-shelf movements of fishes associated with isolated bands of NHB with movements of fishes associated with hardbottom extending continuously across the depth gradient from NHB to OHB would provide valuable insights.

Some differences among ichthyofaunal assemblages are present between the southern and northern areas of mainland southeast and east central Florida in terms of the most abundant species. This information suggests there is a southern NHB ichthyofauna and a less diverse northern fauna, particularly north of the deflection of the Gulf Stream offshore. Potential explanations for such difference in dominant species within 100 to 200 km north-south distances may include temporal recruitment variations, NHB structural differences between the two areas, species reaching their biogeographic distributional limits between the northern and southern areas, and other factors.

NHB structural differences probably exist between these areas as described above, but many of the more prominent species appear to be relatively opportunistic in their use of differing NHB and IHB microhabitat structure. At least three of the prominent species (black margate, sailors choice, and hairy blenny) are listed by Gilmore and Hastings (1983) as species whose Florida distributions are restricted to east Florida, not occurring in the Gulf of Mexico as congeners do. More research is required to parse the multiple factors and examine the above alternatives to better understand these and other north-to-south differences in fish assemblage pattern.

Turtles

Juvenile sea turtles of three species commonly associate with shallow hardbottom of mainland east Florida. Juvenile stages of the endangered green turtle, *Chelonia mydas*, can associate with shallow hardbottom for years, feeding on macroalgae and using structure for shelter. NHB certainly represents facultative habitat for juvenile green turtles that may utilize estuarine areas, as well. However, juvenile green turtle populations residing in bays and lagoons have shown high occurrences of disease and injury. As human populations and construction increase in Florida, nearshore reef habitat may play a comparatively more significant role in the recovery of these endangered species. There also are many interactions between turtles and an array of organisms that utilize shallow hardbottom. For example, hawksbill turtles *Eretmochelys imbricata* fragment sponges when foraging, creating space and habitat for other organisms, as well as increasing sponge growth through fragmentation. Globally, DNA evidence indicates juvenile marine turtles on NHB represent a mixed stock of progeny from the Caribbean, Mexico, Costa Rica, and Mediterranean nesting grounds.

ECOLOGICAL FUNCTIONS AND MESOSCALE CONNECTIVITY

Many species use NHB, IHB, and OHB as settlement and juvenile grow-out areas. The majority of the fish species are abundantly recorded from coral reefs, as are many other resident and transient organisms. For fishes, NHB assemblages are not only juvenile dominated, they are reef-species dominated. As the only natural habitat structure within a radius of 0.5 to 5 km of sand in any direction, NHB structural features potentially serve a variety of ecosystem functions, including settlement and nursery areas, spawning sites (for over 100 species of invertebrates and fishes), economic drivers, and recreational service providers.

For sessile invertebrates, there appears to be a trend towards limited dispersal of larvae or juveniles along the east Florida coast. Of those species that reproduce sexually and asexually, many seem to propagate more via asexual reproduction. Recent molecular research supports this idea, as there appears to be restricted gene flow among Caribbean populations. Considerable information has been amassed regarding a variety of biotic and abiotic factors that contribute to retention in larvae.

Developing better information on population connectivity can allow greater understanding of impact cascades at more refined spatial, temporal, and population scales. Efforts are underway to assign select species or families of primary groups to appropriate connectivity categories. Species with short larval periods show attributes of populations that could be categorized in patterns reflecting either 1) mesoscale dispersal structured by physics, resulting in several metapopulation substructures, or 2) diffusive dispersal with stepping-stone metapopulations. These connectivity patterns may change markedly above and below the St. Lucie deflection of the Florida Current.

MITIGATION AND RESEARCH NEEDS

Increasingly important and expensive questions involve the use of mitigation projects to offset impacts from large dredge and fill projects. Typically, these questions represent key steps in the finalization of permitting processes. Preliminary conclusions regarding the functional attributes of NHB and the application of that information to the evaluation of mitigation alternatives include the following:

- Mitigation of NHB impacts by utilizing artificial reefs can often provide adequate replacement of lost structural habitat and therefore some structure- and trophic-associated ecological functions.
- Not all mitigation reef designs and deployments will be successful in all situations, and site-specific factors must be considered. Different approaches and designs will be required for different locations in southeast and east central Florida.
- For worm reef areas, ensuring successful local larval recruitment events is essential. To this end, project designs need to ensure that sediment size range is suitable to incoming recruits.
- In terms of Issue 4, NHB functions from Brevard to mid-Palm Beach County will not be fully replaced with artificial reefs in deeper NHB, IHB, or OHB water depths because of the depth limits of the habitat engineering worm species *P. lapidosa* and the high numbers of associated species that depend on *P. lapidosa* structure for shelter.
- A full conceptual ecological model (CEM) needs to be developed; this will be more efficient if a thorough food web draft is available. Much of the information to build a larger CEM is now available.
- Artificial reef mitigation does not appear to remove or provide compensatory mitigation for the direct and indirect physiological and potential population scale impacts of turbidity and sediment resuspension.
- The intermediate or long term water quality effects on shallow hardbottom from turbidity and sedimentation events, long-shore and cross-shelf, that result from dredge and fill projects (and relationships to natural turbidity levels) require examination. Without this type of information, responses to Issue 2 regarding whole ecosystem effects when NHB is buried or to Issue 3 regarding OHB compensation roles will be not be fully resolvable.
- Approximately 340 algal taxa can associate with NHB, and most are subject to high mortality on a site that is filled. Mitigation reefs can provide new attachment sites for algae. Algal growth on mitigation reefs should correlate in part with water clarity.

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List of Acronyms

BACI	before-after-control-impact
CEM	conceptual ecological model
CERA	comparative ecological risk assessment
CL	carapace length
CPUE	catch-per-unit-effort
EBM	ecosystem-based management
ECB	East Coast Biologists, Inc.
EFH	Essential Fish Habitat
ESA	Endangered Species Act
FDEP	Florida Department of Environmental Protection
FP	fibropapillomatosis
FWC	Florida Fish and Wildlife Conservation Commission
FWRI	Florida Wildlife Research Institute
HAPC	Habitat Areas of Particular Concern
IHB	intermediate hardbottom
MHW	mean high water mark
NEPA	National Environmental Policy Act
NHB	nearshore hardbottom
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
OHB	offshore hardbottom
PALM	propagule and larval measurement
SAB	South Atlantic Bight
SAFMC	South Atlantic Fishery Management Council
SCL	straight carapace length
SFCREMP	Southeast Florida Coral Reef Evaluation and Monitoring Project
SL	standard length
TL	total length
UMAM	Uniform Mitigation Assessment Method
USACE	U.S. Army Corps of Engineers
USEPA	U.S. Environmental Protection Agency
USFWS	U.S Fish and Wildlife Service

Section 1
Project Objectives and Nearshore Hardbottom within the East Florida Seascape

Chapter 1
Introduction

1.1 INTRODUCTION AND OBJECTIVES

Nearshore hardbottom (NHB) habitats take many forms around the Greater Caribbean, from the coquina and worm reefs of mainland east Florida to the ironshore of the Bahamas and Turks and Caicos to the razor sharp *dientes del perro* (dog teeth) of northern Cuba (including much of Havana's shore). There is a deservedly large research literature on a dozen or more geological or biological aspects of the deeper coral reefs of the Florida Keys; yet, there is a paucity of research information in peer-review journals on the approximately 400-km stretch of discontinuous, nearshore ahermatypic reefs of mainland east Florida, at the current northern limits of the subtropical Northwest Atlantic.

Major coastal economies including sun-and-sand tourism and resident-driven recreational-use markets converge in mainland east Florida, with subtropical to warm temperate beaches intergrading with NHB in some locations between Miami/Dade County and Cape Canaveral (**Figure 1.1**). The beaches of this region are subject to many challenges to long-term sustainable management. Many of these challenges are amplified by continuing pressures for coastal development, diminishing natural resource status, and the probabilities of sea level rise. This distance is subject to semi-continuous wind and wave events and periodic erosion events. Southeast Florida is now a pending coastal mega-city. With a continued push of coastal growth northward, over 5 million people will soon exist within a narrow low-elevation corridor between Miami-Dade and Palm Beach Counties (Wallis et al., 2000).

NHB habitats are the primary natural habitat at depths of 0 to 4 m for many organisms in this region. Currently, the majority of these structures are within a narrow, 200- to 400-m strip of the most nearshore marine waters and display a variety of structural forms, ranging from flat expanse with little relief to vertical mounds emergent at low tide to deeper structures that are much less subject to tidal effects. These habitats are patchily distributed from north to south, composing less than 50% of the alongshore distance of six of the seven county shorelines in the region and are often separated by kilometers of sand expanses. Indian River County is an exception, with NHB present along well over 50% of its shore, often extending into depths beyond 4 m (V. Kosmynin, Bureau of Coastal Systems, Florida Department of Environmental Protection [FDEP], Tallahassee, FL, personal communication). Structural complexity of the rock structures can vary latitudinally (**Figures 1.2** and **1.3**) and is enhanced by framework-building organisms such as tube-building polychaete worms (Gram, 1965; Kirtley and Tanner, 1968; Pandolfi et al., 1998; McCarthy, 2001), other invertebrates (e.g., sponges, anthozoans, bryozoans), and macroalgae (Goldberg, 1973; Gore et al., 1978; Nelson, 1989; Nelson and Demetriades, 1992).

Situated among broad expanses of bare sand bottom, NHB structural features potentially serve a variety of ecosystem functions, including settlement and nursery areas, spawning sites, feeding areas, and shelter for hundreds of species of resident crabs, worms, shrimp, fishes, and many other animals and plants, many of which occur in close proximity (**Figure 1.4**). These functions translate into important ecosystem services such as improved water quality, recreational opportunities (e.g., fishing, surfing, diving for local communities), aesthetics, and wildlife habitat (**Figure 1.5**).

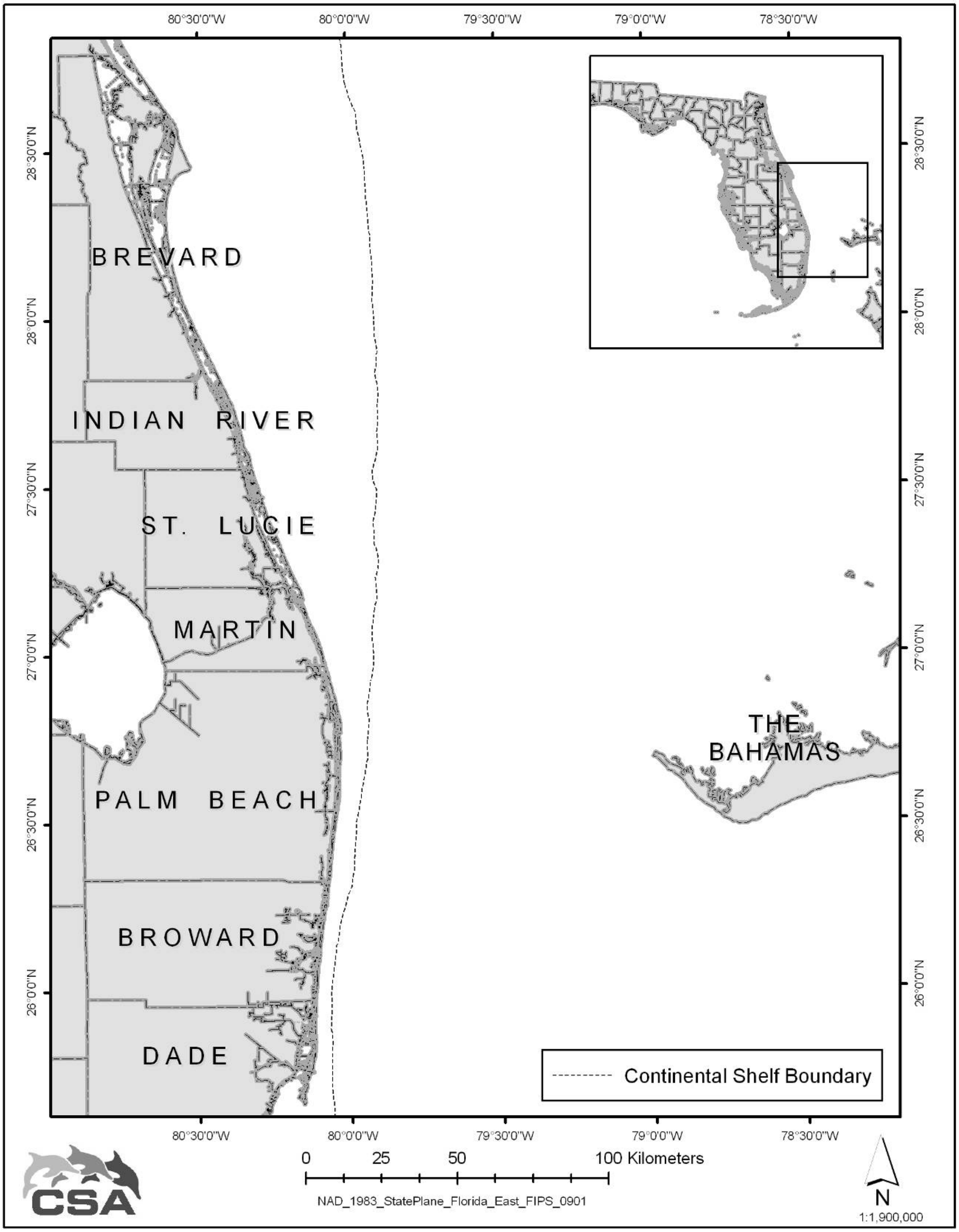


Figure 1.1. Overview of the seven-county project area. Shallow hardbottom distributional information by county is presented in **Table 2.1**.

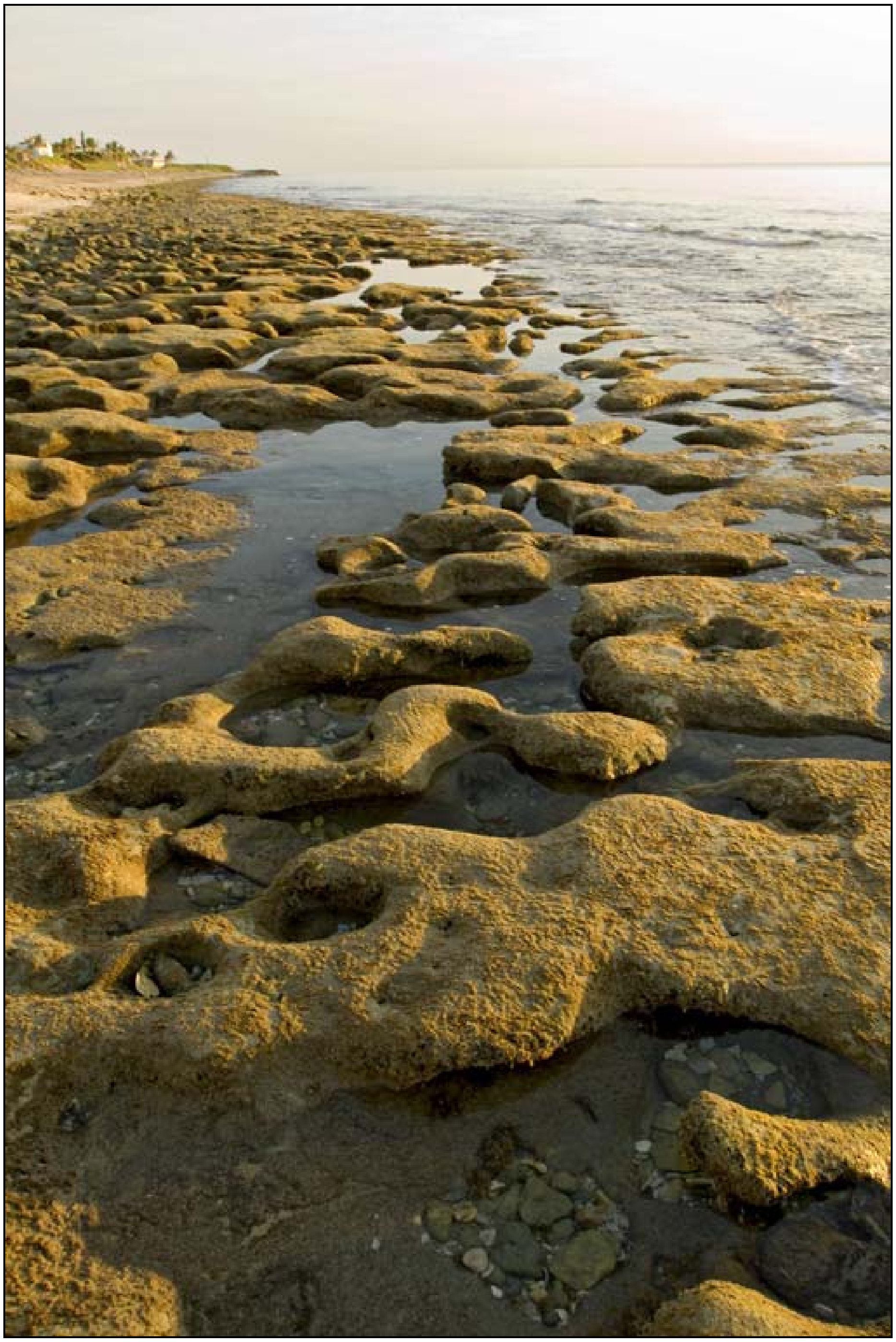


Figure 1.2. Nearshore hardbottom tide pools, Coral Cove County Park, south Jupiter Island, northern Palm Beach County, Florida. *Photo by D. Snyder*.

Figure 1.3. Broken pavement structure, nearshore hardbottom, central Brevard County, Florida. *Photo by K. Lindeman.*

Figure 1.4. Microhabitat complexity among diverse taxa under a nearshore hardbottom ledge, MacArthur Beach State Park, Palm Beach County, Florida. Sponges, tunicates, hydrozoans, macroalgae, and fish are present. *Photo by D. Snyder*.

Figure 1.5. Juvenile stage of the green sea turtle (*Chelonia mydas*) feeding on nearshore hardbottom algae, Boca Raton, Palm Beach County, Florida. *Photo by K. Jones*.

Based on consensus federal and state concerns over the declining condition of fisheries, reefs, and other coastal resources, some management policies have migrated towards potentially more precautionary, ecosystem-based management (EBM) tools, ranging from marine protected areas to increased protection of high value fishery habitats to interdisciplinary use of decision support tools to build more logical, multi-stakeholder governance policies (U.S. Executive Order on Coral Reefs, 1998; National Academy of Sciences, 1999; U.S. Commission on Ocean Policy, 2004). An ongoing example of the focus on new management approaches involves the recent listing of the elkhorn and staghorn corals (*Acropora* spp.) as threatened under the Endangered Species Act (ESA). Listing a colonial invertebrate species that also plays a large role for many other species as a structural habitat feature as threatened is an unprecedented step for ESA. This action has important implications for the management of NHB because the proposed critical habitat designation for ESA includes features essential to the conservation of threatened corals, i.e., *natural consolidated hardbottom or dead coral skeleton that is free from fleshy macroalgae cover and sediment cover* (South Atlantic Fishery Management Council [SAFMC], in prep.), to maximize the potential for successful recruitment and population growth. The recognition and designation of federal Essential Fish Habitat (EFH) is an earlier and broader example of the mandate for more application of EBM tools. NHB of the federal SAFMC's four-state jurisdictional area (east Florida through North Carolina) was administratively designated as EFH in 1998 in response to a statutory mandate from the reauthorization (the Sustainable Fisheries Act of 1996) of the primary federal fisheries statute (the Magnuson-Stevens Fishery Conservation and Management Act of 1976). Federal action agencies that fund, permit, or carry out activities that may adversely affect EFH are required to consult with the National Marine Fisheries Service (NMFS) regarding the potential impacts of their actions on EFH, including consultations for coastal construction activities permitted or funded by the U.S. Army Corps of Engineers (USACE). The final rule on EFH determinations recognized that subunits of EFH may be of higher value. Such areas, termed Essential Fish Habitat-Habitat Areas of Particular Concern (EFH-HAPCs) by the SAFMC, can be identified using four criteria from the rule: a) importance of ecological functions; b) sensitivity to human degradation; c) probability and extent of effects from development activities; and d) rarity of the habitat. All NHB under SAFMC jurisdiction is also designated as EFH-HAPC (SAFMC, 1998); this potentially affects some life stages of the majority of the 73 species of 10 families within the SAFMC Snapper-Grouper Management Plan (Lindeman et al., 2000). NHB is also designated as EFH in the SAFMC's Fishery Management Plan for corals and coral reefs (SAFMC, 1982).

The FDEP is central in efforts to minimize and mitigate impacts to NHB under Florida state administrative rules defining coastal construction permitting procedures. In east Florida, the primary source of anthropogenic impacts to NHB are large beach renourishment projects that involve the offshore dredging and inshore filling of up to 2,300,000 cubic meters of sediments per current project and can potentially result in effects upon various resources and habitats across the shelf (Marszalek et al., 1977; Nelson, 1989; Bush et al., 2004). Increasingly important and expensive issues involve the use of mitigation projects to offset impacts, typically a key step in the finalization of permitting processes. It is in the best interest of all parties to characterize the functional attributes of NHB and apply that information to the evaluation of mitigation alternatives and final decision-making. To this end, the FDEP Bureau of Beaches and Coastal Systems has contracted the production of this report to synthesize available information pertaining to the ecological characteristics and functions of NHB habitat to help guide future management of these resources.

Although many gaps are present, much information can be brought to bear on NHB ecological functions from an array of research, industry, and permitting literature that includes fields such as organismal and population biology, community ecology, coastal geology, physical oceanography, fishery science, engineering design, and economic valuation. Given the consensus need for EBM, the still complex policy questions involving hardbottom burial and mitigation, and the large but unsynthesized literature that already exists, this project uses existing and new information to address the following issues:

1. What are specific ecological functions of NHB?
2. What can happen to the coastal ecosystem (broader than NHB) when NHB is lost due to nourishment?
3. Is the offshore hardbottom (OHB) habitat able to ecologically compensate for the loss of NHB?
4. If the NHB habitat has specific properties and functions that cannot be compensated for by existing OHB habitat, what are the best mitigation alternatives for the loss of natural NHB?

To address these issues, we assembled and examined relevant peer-reviewed journals and texts as well as unpublished or gray literature into a document hierarchically examining the primary assemblages, which collectively contain over 1,000 species. In part to manage this diversity, this synthesis report consists of three sections. **Section 1** (**Chapters 1** and **2**) contains an introduction to the objectives, a physical description of the hardbottom, and terminology of this document. **Section 2** (**Chapters 3** to **6**) contains assemblage-scale chapters on macroalgae and cyanobacteria, invertebrates, fishes, and marine turtles, reviewing known NHB diversity and functional groupings. **Section 3** (**Chapters 7** to **9**) synthesizes the information from prior chapters to address functional ecology, stress characterization, and mitigation alternatives. The following sections of this chapter characterize NHB and OHB and examine fundamental ecological concepts and terms as they relate to this synthesis.

1.2 ECOLOGICAL CONCEPTS AND TERMS

Unlike the physical sciences, where seemingly immutable laws govern processes, ecology (Shrader-Frechette and McCoy, 1993; Sagoff, 2003) and evolutionary biology (Mayr, 1982, 2004) are founded on concepts. Unfortunately, there is much imprecision with usage and meaning of ecological terms and concepts. Foundational concepts such as diversity, stability, succession, community, and ecosystem can vary greatly in their meaning among ecologists. These problems are considerable, often commented on, and amplified by the difficulties in establishing what an ecosystem, community, or habitat actually is among different workers and perspectives (Strong et al., 1984; Underwood, 1986; Noss, 1996; Simberloff, 2004).

The problem of defining communities was described by Whittaker (1975) as follows: “Most communities intergrade continuously along environmental gradients rather than forming distinct clearly defined zones.” A significant example of imprecise meaning was demonstrated by Grimm and Wissel (1997) for the term *stability*. They reviewed the ecological literature and found that the term *stability* had at least 163 definitions based on 70 concepts. This is an unfortunate situation for managers or non-ecologists seeking scientific guidance. They concluded that a six-point checklist had major utility to “… classify ecological systems and provide a system of coordinates for communication” (Grimm and Wissel, 1997). To best manage ambiguity introduced by the imprecise terminology, basic ecological terms used throughout the text are defined in **Table 1.1**. We are not proposing these definitions for universal application, they simply have utility to the seascape and objectives addressed in this study.

Table 1.1. Ecological terms used in the present study. Conceptual background and caveats summarized in text.

Assemblage – a group of organisms defined according to phylogenetic, ecological, or other study-dependent criteria.

Community – a group of species living and interacting together within a particular area.

Disturbance – a natural or anthropogenic perturbation that will disrupt the extant ecological processes of assemblages or successional processes within an area.

Diversity – the number of species in a given area and their proportional abundances.

Ecological functions – substantive ecological processes that occur within a community or ecosystem.

Ecological services – the beneficial outcomes resulting from ecological functions that include human influence (e.g., fishing, snorkeling, bird watching, and nature photography).

Ecosystem – an interacting group of biological communities and abiotic factors within a single geographic area.

Ecosystem engineers – organisms that directly or indirectly modulate the availability of resources to other organisms by modifying, maintaining, or creating habitat architecture.

Keystone species – particular species (or functional group) that influence control over critical processes that can affect the greater assemblage.

Larval supply – the quantity or potential quantity of invertebrate or fish larvae that are transported into an area when competent to settle, metamorphose, and begin a benthic-associated existence.

Metapopulation – a species system in which 1) local populations inhabit relatively discrete habitat patches and 2) dispersal among patches allows demographic connectivity but local population dynamics remain relatively asynchronous from other populations.

Opportunistic species – species with life history strategies that involve facultative, not obligate (dependent), resource use. Such species can utilize a wide array of shelter or food resources.

Recruitment – a generic term referring to organismal entry into a given area. Specific examples include

- *Larval recruitment* – addition of new individuals into a population by arrival of incoming larvae into bottom habitats (e.g., larval settlement).
- *Inter-habitat recruitment* – shifts from one benthic habitat to another; not the first larval settlement event but a later habitat shift.
- *Fishery recruitment* – the size or age at which individuals are first retained by fishing gears (i.e., when they enter the fishery).

Species richness – the total number of species within a project-specific area.

1.3 NEARSHORE, INTERMEDIATE, AND OFFSHORE HARDBOTTOM

For many comparative questions, distinguishing between NHB and OHB habitats is often complicated, particularly among differing latitudes in east Florida. Dozens of physical and biological continua co-vary within a highly dynamic shallow environment that does not obey strict rules about depth zonation. Many metrics therefore often respond in quasi- or non-linear manners to both natural and anthropogenic disturbances, prohibiting discrete line-drawing or flawless terminology. Nevertheless, means to distinguish measurement benchmarks (e.g., NHB and OHB) are logical and necessary to frame and inform answers to complex and interwoven questions about species, communities, fisheries, and coastal management.

Our focus here is on comparative analyses of macroalgae, invertebrates, fishes, and marine turtles between NHB (0 to 4 m), intermediate hardbottom (IHB) (4 to 6 m), and OHB (>6 m) depths. The use of the 0 to 4 m depth range is based on the near-maximum depth of many NHB habitats and some associated biotic assemblages in the region. In addition, this can be a depth of the toe-of-fill subsequent to dredge-related burial of NHB. Within NHB, it can also be useful to refer to an intertidal area (0 to 1 m) and a subtidal area (1 to 4 m), which can be further subdivided in the case of some invertebrate and algal species. Among and within these intervals are gradual transitions in many population- and community-scale metrics, some of utility in examining ecological functions. We re-emphasize that the depth "boundaries" between NHB, IHB, and OHB are artificial benchmarks to allow some measureable stratification of a highly variable abiotic and biotic continuum; they are not self-contained zones.

Currently, the majority of typically uncovered NHB structural features are within 200 m of the mean high water mark (MHW), though there are notable exceptions in which hardbottom structure is emergent west-to-east through two to three depth areas (NHB, IHB, and OHB), including Riomar Reef in St. Lucie County, Bathtub Reef and Peck's Lake Reef in Martin County, Breakers Reef in Palm Beach County, and wide NHB eastern extensions in the area of Broward County (Fort Lauderdale). More detailed examination of NHB, IHB, and OHB occurrence and latitudinal variation is provided in **Chapter 2**.

There can be substantial physical and biotic differences between NHB in the intertidal zone (0 to 1 m) and the subtidal zone (approximately 1 to 4 m). Both zones are populated by disturbance-mediated assemblages, and biotic distributional patterns can vary due to the dynamics of the physical environment. Disturbance examples include storms and the frequency and duration of hardbottom burial (more pronounced in fall and winter periods, and varying by latitude). The issue of ephemeral/seasonal changes in NHB is relevant to analyses of habitat functions discussed in **Chapter 7**.

1.4 SPECIES: WINDOWS INTO ASSEMBLAGES?

The use of particularly prominent species to stratify the analysis and/or management of assemblage complexity has been attempted for many decades in theoretical and applied ecology, and focal or indicator species have been discussed in detail. Simberloff (1998) reviewed a variety of constructs that have evolved for species-enhanced EBM, often based on single-species management models. Unusually representative or analytically valuable species constructs included indicator, flagship, umbrella, and keystone species used as diverse surrogates or representatives of a much wider array of species from local assemblages at risk from environmental impacts. Indicator species were considered tenuous, often because of imprecise metrics of performance and unclear objectives (Simberloff, 1998), though various reviews and many studies still employ differing types of indicator species (Zacharias and Roff, 2001). Umbrella species, those needing so much habitat for protection that other species are protected as well, could be useful, but are typically constrained in reflecting fundamental community functions and measurement, as are flagship species (Walpole and Leader-Williams, 2002). A possible umbrella species in NHB areas is the sabellariid reef-building worm *Phragmatopoma lapidosa* (**Chapters 4** and **7**).

In part based on the work of Paine (1969) on nearshore rocky intertidal community changes, Simberloff (1998) concluded that keystone species played the most significant role in influencing assemblage structure and could potentially be useful tools for multispecies management. A fundamental criterion is that removal of the keystone species should substantially shift assemblage structure. In addition, the roles of some keystone species are highly context-dependent (Simberloff, 1998). Based on empirical information from Australian reefs, Bellwood (2008) has identified a phenomenon termed sleeping functional groups or species. In one case, a siganid rabbitfish of little prior significance in most metrics assumed a keystone-like role when the long-standing system of macro-herbivorous fishes changed in response to a fishing-induced phase shift.

Zacharias and Roff (2001) concluded that the keystone species concept was both relatively strong and of varying utility in management. They also concluded that it was possible to define and measure indicator species under some conditions and suggested two categories: composition indicators and condition indicators. The former species reflect a specific niche or range of measurable environmental tolerances and are relatively independent of sample size. Condition indicators are species that somehow "provide an assessment over a range of stress" and can "differentiate between natural and anthropogenic stress" (Zacharias and Roff, 2001). With the exception of keystone species, we do not currently use any of these other terms. However, some NHB species may have utility as indicator species in some studies (e.g., black margate, *Anisotremus surinamensis*, as a composition indicator), if specific indicator criteria are well-defined.

1.5 EQUILIBRIUM AND SCALE

In addition to ambiguity in concepts and terms, agreement between theory and application in ecology has been generally lacking. Conceptual paradigms in ecology today may be broadly divided into equilibrium and non-equilibrium views (Wiens, 1984; Walter and Hengeveld, 2000; Rohde, 2005; Wallington et al., 2005), and, as with most dichotomies, the truth probably lies somewhere in between the two poles. Theory formulated before the 1990's was largely based on notions of equilibrium in natural assemblages (e.g., MacArthur, 1972). For example, this paradigm viewed ecological succession as a linear sequence of events leading to a stable climax, with any disturbance to that sequence considered something outside of the "system." This viewpoint has been replaced by more probabilistic and non-equilibrium viewpoints (e.g., Botkin, 1990; Sale, 1991; Shrader-Frechette and McCoy, 1993; Drury, 1999; Rohde, 2005; Wallington et al., 2005).

In the non-equilibrium world, disturbance is considered an inherent property of the ecosystem and equilibria are artifacts of observation, not real properties of the system. Unfortunately, many of these new ideas have not been translated into the regulatory arena (Wallington et al., 2005). Schrader-Frechette and McCoy (1993) summarized key conceptual issues and emphasized the importance of case study approaches, contending that ecological problem-solving would be most effective when ecological knowledge (natural history), not ecological theory, was applied.

In this report, a basic conceptual assumption supported by the data is that biota inhabiting NHB are not in any kind of static or spatial equilibrium over long time scales. We state this now and throughout the text to ensure that managers realize the implications of a strict equilibrium stance (**Chapters 7**, **8**, and **9**) when assessing impacts and the results of mitigative measures employed to offset those impacts (Wiens and Parker, 1995; Parker and Wiens, 2005).

Another fundamental component is that scale and assessment of equilibrium is inherently based on the scales of the system under examination. The structure of all levels of ecological hierarchies depends upon spatial and temporal scale. Consideration of spatial scale is paramount to an understanding of assemblage patch dynamics, particularly in disturbance-mediated environments such as NHB (Levin and Paine, 1974; Pickett et al., 1989; Wiens, 1989; Kotliar and Wiens, 1990; Wu and Loucks, 1995). The relationships between species richness and functional diversity (Hooper et al., 2002) can be tenuous but potentially useful in comparing NHB and OHB functional equivalencies and dissimilarities.

1.6 ECOLOGICAL FUNCTIONS

Several project objectives involve identifying ecological functions within natural and artificial habitat types and the subsequent comparison of functions among subregions. Function can be addressed in terms of processes and in terms of functional groups of characteristics and similar species (sometimes known as guilds) (Wilson, 1999). A major challenge at the interface of ecological research and applied management involves the difficulties in merging the conceptual landscape implied by the term *function* with immediate political management needs.

The conceptual underpinnings and terminology associated with the word *function* are highly variable, encompassing dozens of metrics. At least four broad meanings for the term *function* were identified by Jax (2005): 1) processes of changes of state (e.g., organismal feeding); 2) the merging of multiple processes in a whole system context (e.g., system functioning); 3) ecological roles within systems (e.g., functional groups such as producers or consumers); and 4) particular services of the system to humans and society (e.g., ecosystem services such as pollination and photosynthesis). Based on a comprehensive examination of the literature on NHB and ongoing examination of much of the literature on functions and functional groups, we identified nominal functional groupings within shallow hardbottom assemblages. Studies of habitats often have focused on two basic categories of functional attributes: 1) structure and shelter resource use and 2) feeding assemblage relationships. We use the following non-exhaustive categories that are compatible with the framework employed by the Uniform Mitigation Assessment Method (UMAM) protocol (e.g., Continental Shelf Associates, Inc. et al., 2006).

- Structure-shelter associated functional groupings. Examples include groups of species sharing one or more of the following attributes and associations with NHB through OHB:
  - Habitat engineering functions (keystone framework builder);
  - Nesting and spawning site usage;
  - Substrate as attachment resource for sessile organisms;
  - Settlement and post-settlement nursery area usage; and
  - Juvenile and adult patterns of cross-shelf distribution.

- Trophic functional groupings. Food capture patterns, larger energetic fluxes, and physical dynamics drive food web dynamics (e.g., intercommunity nutrient exchange functions of carnivores and herbivores on NHB and OHB [Parrish, 1989]), such as the following:
  - Herbivory;
  - Carnivory;
  - Autotrophy;
  - Detritivory and omnivory; and
  - Cleaning symbioses.

The relationship between ecological function analysis and societal measures has a considerable history (Hooper et al., 2002). Human societies can describe functions within an ecosystem and functions of the whole system (Jax, 2005). Tens of thousands of year-round local residents use the beach not only for sunbathing but also to take advantage of the nearshore waters, occasional reefs, and many coastal recreational activities (**Figure 1.6**) available in the warmest waters of the continental U.S., which also offer some of the highest coastal biodiversity. The services provided by nearshore reefs for humans are often family-based and multi-generational, including fishing, diving, surfing, and other forms of recreational resource use.

Figure 1.6. Anglers fishing from nearshore hardbottom to capture pompano and other coastal pelagic species known to occur near sand-rock interfaces, central Brevard County, Florida. *Photo by K. Lindeman*.

Chapter 2
Shallow Hardbottom of East Florida and the Regional Shelf Setting

2.1 INTRODUCTION

The study region is bounded on the south by Government Cut, the southern boundary of Miami Beach, (**Figure 1.1**). To the north, the study region is bounded by Port Canaveral. There are geological, biological, and climatic differences between the northern and southern portions of the study region. For many coastal marine organisms, the zoogeographic break between subtropical and warm temperate regions typically occurs between the Jupiter Inlet and Cape Canaveral, approximately 230 km to the north (Briggs, 1974; Gilmore, 1995). Transitional warm temperate, wide-shelf systems compared to subtropical, narrow-shelf systems are increasingly represented north and south of the Jupiter Inlet.

Seven of Florida's 35 counties with marine shores are within the study region. **Table 2.1** provides the shoreline lengths and NHB acreages per year available. Brevard and Palm Beach Counties have the longest shorelines within the full project area, while the shorelines of the remaining counties are highly similar in length, ranging from 34.5 to 38.4 km. Primary economic drivers are concentrated in the southern three counties and pushing economic growth and coastal construction into northern counties where relatively less-disturbed coastal reaches can be found. There are substantial structural and NHB areal variations present across the 355-km north-south project reach, as well as considerable variation in the availability of areal NHB data (**Table 2.1**). The information in **Table 2.1** is further evaluated in **Section 2.1.2** and later chapters.

Table 2.1. Study counties from north to south with shallow hardbottom acreage by depth strata by year. Most data were provided from county agencies.

County	Latitude at Southern Border (N)	Shoreline Length km (mi)	% Shoreline in Study Region	Total Hardbottom (acres)	Location[c]	Year
Brevard	27° 51´	114.9 (71.4)	32	42.3	R-70 to R-118	2004
Indian River	27° 33´	36.1 (22.4)	10	278.5[a]	R-37 to R-49	2007
St. Lucie	27° 15´	34.6 (21.5)	10	56.6	R-77 to R 118	2008
Martin	26° 58´	34.5 (21.4)	10	N/A	N/A	N/A
Palm Beach	26° 19´	72.8 (45.2)	21	27.0	R-59 to R-71	2007
				337.4	County	2004
				283.3	County	2003
				4.2	R-59 to R-71	2003
				361.3	County	2001
				375.0	County	2000
				8.8	R-59 to R-71	2000
				16.8	R-59 to R-71	1998
				444.1[b]	County	1993
Broward	25° 58´	38.4 (23.9)	11	125.2	County	N/A
Miami-Dade	25° 46´	23.6 (14.7)[d]	7	N/A	N/A	N/A
Total Shoreline Length	---	354.9 (220.5)	100%		---	---

[a] Mapped out only to ~450 m offshore; hardbottom beyond this is not quantified.
[b] Includes areas within inlets that were not counted in other years.
[c] Florida Department of Environmental Protection Reference Monument.
[d] Measured to southernmost point of Miami Beach (north side of Government Cut).
N/A = Not available.

2.2 GEOLOGICAL AND BIOLOGICAL ATTRIBUTES OF NEARSHORE HARDBOTTOM

Most NHB structures of mainland east Florida are current marine components of the Anastasia formation, which is composed of sediments and mollusc shells (particularly the coquina clam *Donax*). This material accumulated on shorelines during the last Pleistocene interglacial period approximately 80,000 to 120,000 years ago and was later lithified during low sea level stands (Cooke and Mossom, 1929; Cooke, 1945; Duane and Meisburger, 1969). The bulk of the NHB along mainland east Florida is composed primarily of this lithified shellrock; however, there is a transition in the area of Deerfield Beach in north Broward County where the Anastasia formation intergrades with and may be replaced to the south by the Miami Oolite formation and other features (Cooke, 1945; Hoffmeister, 1974). These limestone strata are significant features with east-west reaches that extend across coastal east Florida and still represent terrestrial landscape features. Prominent coastal ridges of these features occur along U.S. Highway 1 throughout the study region (e.g., Rockledge, Brevard County and Silver Ridge, Coconut Grove, Miami-Dade County).

NHB habitats are the natural ahermatypic reef structures at depths of 0 to 4 m of this region, and a diverse array of users refer to them by names that include coquina reefs, worm rock, Anastasia outcrops, worm reef, and nearshore reefs. In some areas, NHB reaches heights of 1.5 to 2 m above the bottom and is highly convoluted (**Figure 1.2**). In other areas, NHB is low-relief and forms pavement-like surfaces, often with small overhangs and crevices (**Figure 1.3**). Currently, little information is readily available on *in-situ* differences in physical and biotic properties of submerged Anastasia NHB compared to submerged NHB of differing origin in Broward County.

NHB habitats are patchily distributed among expanses of relatively barren sediments (**Table 2.1**; **Figure 2.1**) and commonly possess worm reef structure in shallow areas from southern Palm Beach County to the north. NHB habitats of the region show very low coral diversities, yet have moderate to high diversities of other invertebrates, algae, and fishes. Nelson (1989) recorded 325 species of invertebrates and plants from NHB habitats at Sebastian Inlet. Hard corals are rare or uncommon in many NHB patches due to high turbidities and wave energy, but several species can be locally present (e.g., *Oculina diffusa* and *O. varicosa* in St. Lucie County; *Acropora cervicornis* in Broward County). Both *Siderastrea radians* and *S. siderea* can occur on shallow hardbottom in all counties from Brevard to Dade. A locally prominent contributor to habitat structure and biological diversity of NHB along east Florida is the polychaete *Phragmatopoma lapidosa*, also known as *P. caudata* (Nelson and Demetriades, 1992; Kirtley, 1994; Drake et al., 2007). Worms of this species (Family Sabellariidae) settle on hardbottom and glue together sedimentary particles of specific sizes and origins to build sand tubes, forming shallow reefs in intertidal and shallow subtidal hardbottom areas (Gram, 1965; Kirtley and Tanner, 1968; Pandolfi et al., 1998; McCarthy, 2001). This species meets all the attributes and is the primary habitat engineer (Jones et al., 1994; Coleman and Williams, 2003; Jones et al., 2004) of NHB communities in mainland east Florida. Its distribution extends southward to Santa Catarina, Brazil (Kirtley, 1994), though it is often uncommon or absent on many islands and the Florida Keys (McCarthy et al., 2008). There are significant differences in the invertebrate fauna of intertidal NHB habitats in comparison to subtidal NHB habitats, driven in part by the high abundance of *P. lapidosa* in intertidal NHB habitats (McCarthy et al., 2003; also see **Chapters 4**, **5**, and **7**).

In east Florida, the structure provided by NHB and associated habitat engineers (e.g., polychaete worms) supports a higher diversity and abundance of many marine invertebrate species than that of neighboring sand or hardbottom habitats (Gore et al., 1978; Nelson, 1989). The differences between areas with and without hardbottom can exceed an order of magnitude in terms of both species richness and abundance. At least 8 federal- and 15 state-listed species are associated with nearshore reefs off east Florida (U.S. Fish and Wildlife Service [USFWS], 1999), and NHB is considered an important source of food and shelter for juvenile green turtles (*Chelonia mydas*) (Ehrhart et al., 1996; Wershoven and Wershoven, 1989; Holloway-Adkins, 2001).

Figure 2.1. Aerial image of Bathtub Reef, Stuart, Martin County, Florida.

Prior to the current synthesis report, NHB was recorded to provide shelter for over 325 invertebrate species (Gore et al., 1978; Nelson, 1988, 1989; Nelson and Demetriades, 1992) and 192 fish species (Gilmore, 1977; Gilmore et al., 1981; Lindeman, 1997a; Lindeman and Snyder, 1999). Substantial geological evidence suggests that NHB and worm reefs are also important in the maintenance and persistence of beaches and barrier islands by retention of sediments and the progradation of beaches (Kirtley, 1966, 1967; Multer and Milliman, 1967; Gram, 1965; Kirtley and Tanner, 1968; Mehta, 1973; Kirtley, 1974; Pandolfi et al., 1998). It is important to emphasize, however, that the vast majority of hardbottom is not encrusted by nor derived from tube worms (**Figure 2.2**). Worm reefs also can monopolize space, precluding other algae and sessile invertebrates.

Figure 2.2. Nearshore hardbottom algal and invertebrate colonization on ledge exposed at full moon low tide, Brevard County, Florida. Algal species represented include *Caulerpa racemosa, C. prolifera, Ulva lactuca, Laurencia* sp.*, Aghardiella subulata, Gelidiopsis* sp., and others. Cuban stone crabs (*Menippe nodifrons*) are visible in ledge on lower left. *Photo by K. Lindeman.*

NHB structures are largely carbonate composed via lithification of biogenic components (often calcareous microstructures of the small coquina bivalve *Donax*) and current framework-building organisms, particularly *P. lapidosa* (=*caudata*). Is the structure typical of NHB properly termed a reef? A fundamental way to examine this question is to go to the original source marine geological literature that described east Florida NHB. Early papers refer to NHB structures as reefs with geological and biological rationale, often including the role of the sabellariid worm species *P. lapidosa* in beach stabilization (Gram, 1965; Kirtley, 1967; Kirtley and Tanner, 1968). These structures reflect and absorb wave energy, influence sediment movements, maintain structure position over time, support substantial biotic populations, and display fundamental attributes of ahermatypic, inorganic, or marginal reefs as described in Gram (1965), Kirtley and Tanner (1968), Fagerstrom (1987), Pandolfi et al. (1998), and Kleypas et al. (2001). Ichthyofaunal compositions are dominated by reef-associated species (Lindeman and Snyder, 1999; Baron et al., 2004).

The term NHB is also applied in the Florida Keys (Hoffmeister, 1974; Chiappone and Sullivan, 1996). NHB habitats of the Florida Keys can differ both geologically and biologically from mainland east Florida areas (**Table 2.2**). Emergent upland components of the Florida Keys are derived from ancient reefs of the Florida Reef Tract and typically do not have sizeable beaches nor a nearshore current regime for delivery of beach-quality sediments. Compared to mainland east Florida, most Florida Keys NHB habitats are distributed among areas with higher organic sediments, increased seagrasses, more corals, and reduced wave conditions, though there are exceptions offshore (Ginsburg, 1956). In contrast to the Keys, beach systems are common in mainland east Florida areas and their geologically distinct, sedimentary barrier islands (**Table 2.2**).

Table 2.2. Geological and biological comparisons between nearshore areas of the mainland east Florida coast and the northern margin of the Florida reef tract and the Florida Keys (Adapted from: Cooke, 1945; Kirtley and Tanner, 1968; Hoffmeister, 1974). Transition areas are given for each attribute.

Geological or Biological Component	Mainland North of Transition	Geographic Transition Areas	Florida Keys South of Transition
Island type	Sedimentary barrier islands	Key Biscayne – Soldier Key	Coral/limestone islands
Bedrock type	Anastasia limestone	Palm Beach – Broward Counties	Miami Oolite and limestone
Sabellariid worm reefs	Locally common	Broward – Dade Counties	Rare
Shallow corals	Uncommon	Key Biscayne – Soldier Key	Common
Seagrasses	Absent	Miami Beach – Fisher Island	Abundant
Predominant sediment type	Quartz – calcium carbonate	Key Biscayne – Soldier Key	Calcium carbonate – quartz
Predominant sediment size	Coarse	Key Biscayne – Soldier Key	Fine
Wave energy	Intermediate to high	Martin – Broward Counties	Low

2.3 DISTRIBUTION OF SHALLOW HARDBOTTOM IN EAST FLORIDA, MIAMI TO CANAVERAL

Recent information on distributions and areal amounts of shallow hardbottom habitats are housed most comprehensively at the county scale from Miami to Canaveral (Dade through Brevard Counties, respectively) by the responsible county agencies and, at the federal level, by the USACE and NMFS in the form of various National Environmental Policy Act (NEPA)-associated documents from past dredge and fill projects. **Table 2.1** summarizes some of the currently available macro-level information on NHB acreage and distributions. The construction of coastal inlets probably has contributed to the exposure of NHB in some areas by interrupting the littoral movement of sand. Based on available information (i.e., county mapping products), the counties with the most NHB are Palm Beach and Indian River, each appearing to have at least 250 acres of areal coverage. This value is essentially an average of a single snapshot (aerials) taken annually in each county. Broward has significant amounts of IHB at depths of 4 to 6 m, with NHB as well. NHB is distributed near ridge complexes of substantial geomorphological complexity that occupy at least 125 acres (K. Banks [Broward County Department of Environmental Protection], B. Walker [National Coral Reef Institute, Nova Southeastern University Oceanographic Center], and Q. Robertson [Coastal Planning & Engineering, Inc.], pers. comm.). Martin and St. Lucie counties have comparatively less NHB, but can have substantial outcrops. Dade currently has no shallow NHB (<4 m water depth), though hardbottom with limited epibiota occurs in some areas around the 4 m depth contour, often grading into more densely colonized hardbottom by 6 m depths (B. Flynn, Miami-Dade Department of Environmental Resources Management, pers. comm.). Brevard's NHB is very discrete, consisting of an approximately 40-acre system in the central part of the county that does not intergrade with deeper hardbottom.

Table 2.1 is not comprehensive, as some data from aerial overflight imagery are not available (or have not been digitized to delineate hardbottom), and a full survey of other information sources (e.g., past NEPA documents) was outside the scope of this project. In addition to data summaries such as **Table 2.1***,* aerial imagery can be assembled to show NHB distribution patterns among the seven counties for the years when mapping was conducted. In addition, there are substantial state and federal efforts underway both to map hardbottom resources as funding develops and also to gather existing information in publicly accessible manners (e.g., www.safmc.net).

Evaluating NHB areal distributions and biological relationships is complicated by the burial dynamics of lower elevation NHB outcrops resulting from the many storms and wave events in the region (Nelson, 1989; McCarthy et al., 2003; Bush et al., 2004; Continental Shelf Associates, Inc., 2006; Lybolt and Tate, 2008; Montague, 2008). Therefore, the presence of hardbottom in mapping efforts is seasonally and annually variable according to trends in local wind and wave activity and extra-regional storms; such trends may often vary interannually as well. Imagery of the system shows substantial hardbottom structures and their point-in-time position on the seascape for multi-year time steps, as at Singer Island in Palm Beach County where acreage has increased approximately three-fold in recent years (**Figure 2.3**). Typically, more NHB is exposed during summer and lower overall nearshore energy periods (also the only feasible photographic periods for most areas).

The South Atlantic Bottom Mapping Work Group of the Atlantic States Marine Fisheries Commission generated hardbottom mapping information for the South Atlantic Bight, including the study region from the beach to a depth of 200 m. The project ended in 2007, and the information is available at www.safmc.net. **Figures 2.4** and **2.5** are from a summary of NHB and OHB mapping information from the Southeast Area Monitoring and Assessment Program (SEAMAP) (Perkins et al., 1997). There are fundamental differences in cross-shelf NHB habitat distribution among counties (e.g., Broward and northern Palm Beach). In Broward, the level of hardbottom structural overlap of the NHB, IHB, and OHB depth ranges exceeds that of many reaches to the north, with particular exceptions in southern Martin and Indian River Counties.

Depth contours at 4 and 6 m are highly variable in terms of distance from shore throughout the study region. This complicates efforts to segregate patterns according to the nominal NHB, IHB, and OHB categories (**Figure 2.1**). The available data by county are also patchy in quantity and quality, and the ability to accurately segregate data by the three nominal categories currently is not possible for most counties. Nonetheless, there are many areas of Palm Beach and Brevard Counties, for example, where the NHB is not continuous with IHB and OHB. The NHB, IHB, and OHB designations are useful benchmarks for beginning to examine the complex interrelationships between the shallowest hardbottom assemblages and those in depths greater than 6 m. The challenges are amplified by the absence of depth-stratified information for most taxa and localities as well as by the dynamic spatial environment.

2.4 OFFSHORE HARDBOTTOM AREAS

Recognizing the difficulties in defining depth boundaries discussed earlier, this study uses a depth range of >6 m to represent OHB. There are many ways in which to characterize hardbottom and live coral habitats from >6 m to the shelf edge, with most available studies concentrated on the southern part of the project region (Goldberg, 1973; Moyer et al., 2003; Banks et al., 2008). We refer to shallow OHB (6 to 10 m) and midshelf OHB (>10 m) based on physical and biotic characteristics that are actually distributed across a continuum (see **Chapter 1** regarding the high permeability of these depth “ranges”). In the present study, our emphasis is almost entirely on shallow OHB compared to midshelf OHB. Complex physical and biological assemblage relationships exist between OHB and the intermediate, transitional depth range for hardbottom, 4 to 6 m (IHB). OHB from shallow and midshelf areas potentially receives a portion of the grunt, wrasse, and other species of fish and invertebrate settlers that survive and eventually redistribute into deeper waters, sometimes across the broader shelf. These relationships are discussed by major biotic group in **Chapters 3**, **4**, **5**, and **6**, as well as in **Chapter 7** with respect to ecological functions.

The relict Holocene reefs from Palm Beach to Dade Counties are the most-examined within the study region, with Lighty (1977), Moyer et al. (2003), and Banks et al. (2007) referring to shore-parallel inner, middle, and outer reefs. The latter papers also refer to a nearshore beach ridge complex (see **Chapter 1**); this is the depth zone of NHB. Though not frame-building, the hardbottom across the three reef lines is colonized by reef fauna characteristic of the Caribbean (Goldberg, 1973; Banks et al., 2008).

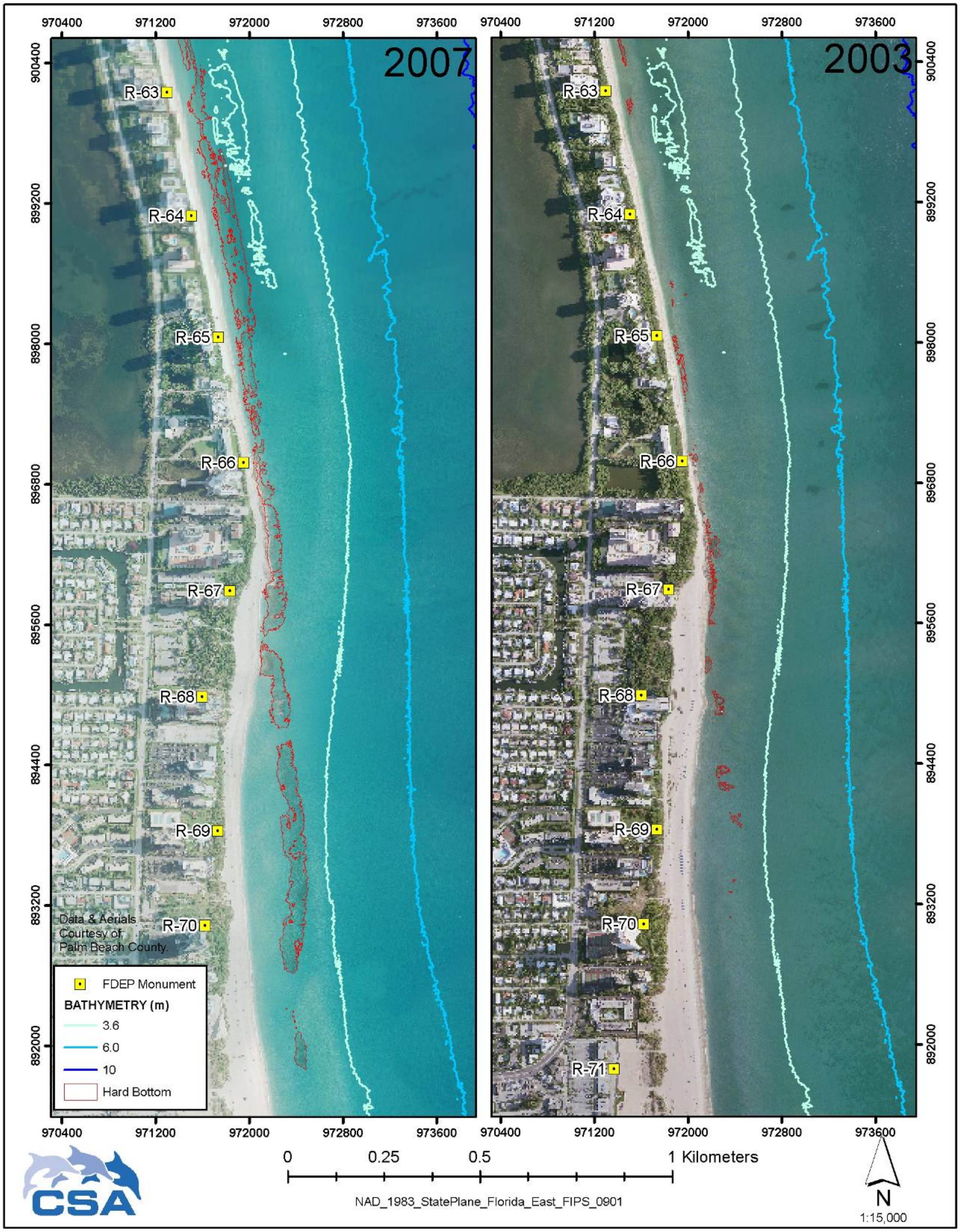


Figure 2.3. Aerial views of nearshore hardbottom structures and sediment change at northern Singer Island, Palm Beach County, Florida, 2003-2007.

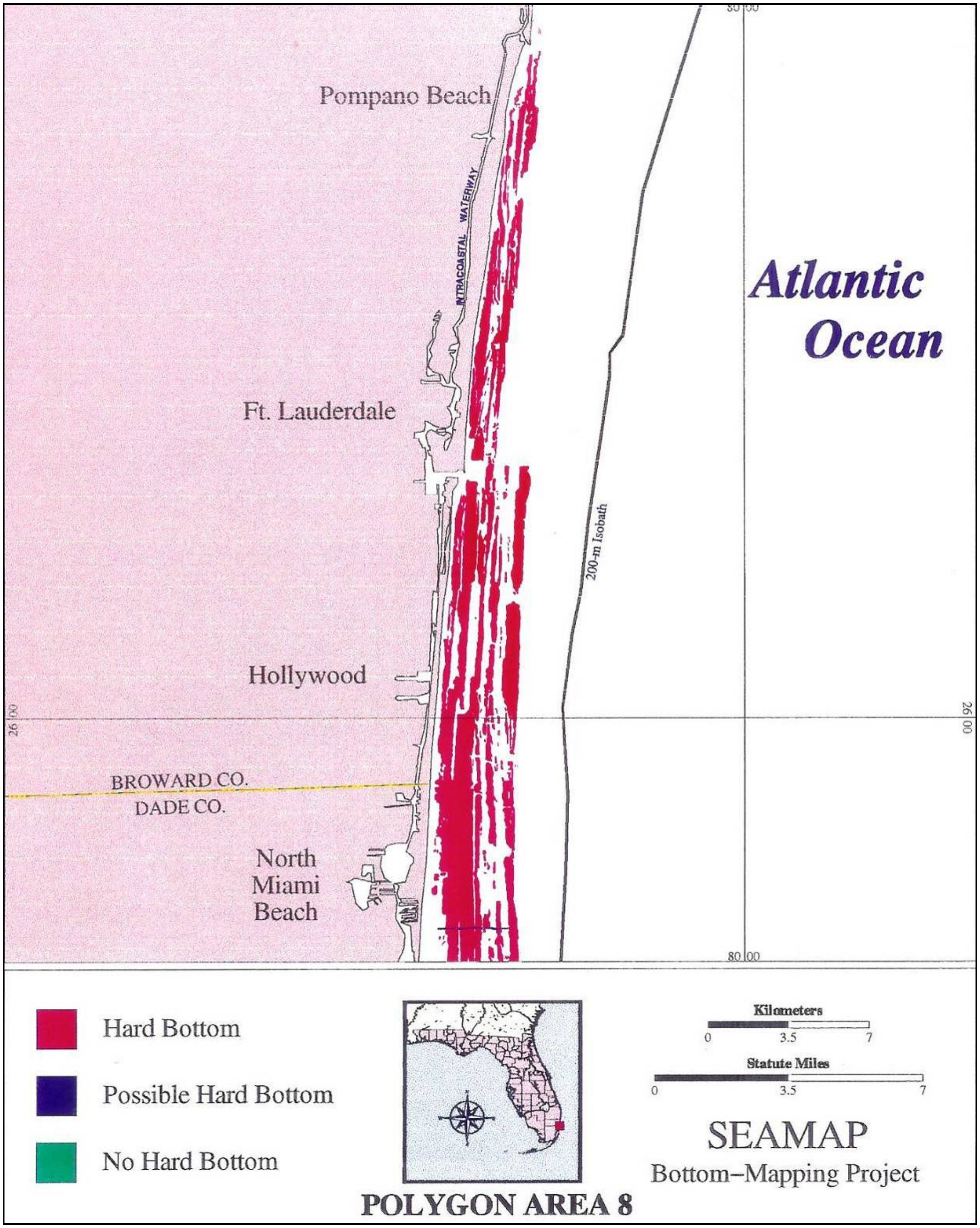


Figure 2.4. Broward and northern Dade County plots from a summary of nearshore and offshore hardbottom information from the Southeast Area Monitoring and Assessment Program (SEAMAP) (Perkins et al., 1997).

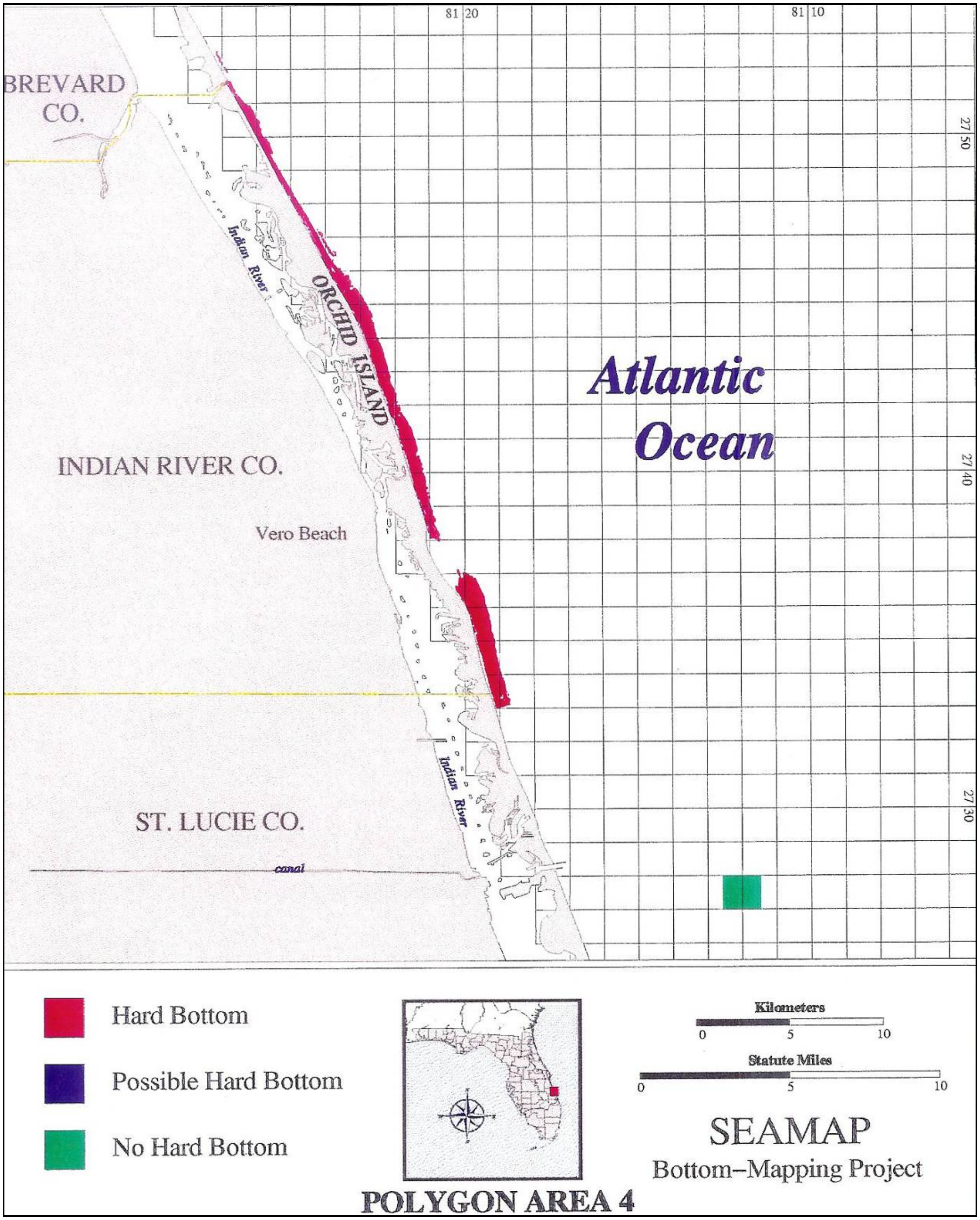


Figure 2.5. Indian River County hardbottom from a summary of nearshore and offshore hardbottom (From: Perkins et al., 1997).

The inner reef crests at a depth of approximately 8 m and consists of discontinuous patch reef outcrops along a shore-parallel axis that periodically form elongate reefs (Banks et al., 2008), representing the OHB and IHB components of the southern project region in the present study. Throughout most of Palm Beach County, however, no inner or middle reefs are found (Banks et al., 2008). The nature and extent of shallow OHB varies with latitude along the study area. In some areas, most notably Breakers Reef, Palm Beach; Bathtub Reef and Peck's Lake, Stuart; and Riomar, Vero Beach (**Figure 2.5**), hardbottom extends seaward from NHB to OHB depth ranges. In most other areas, NHB is not continuous with hardbottom in greater depths.

Epibiota colonizing shallow OHB vary in taxonomic composition and diversity in both north-south and cross-shelf directions. Summaries for the Palm Beach through Dade County area are provided in Banks et al. (2008). Variations in light penetration, water temperature, sedimentation, and circulation are particularly present in shallow hardbottom areas and greatly influence the structure and dynamics of epibiotic assemblages (Rogers, 1990). Moyer et al. (2003) found substantial differences in benthic communities between the inner reef and the middle and outer reefs. For example, densities of octocorals and sponges were lower on the inner reef, presumably in response to greater environmental variability in shallower waters. There has been little directed study of hardbottom and reef structures and their epibiotic assemblages north of the Palm Beach area. General trends such as the north-south gradient in species diversity and basic taxonomic composition have been described peripherally for some epibiotic taxa, including corals and algae (Humm, 1969; Briggs, 1974; van den Hoek, 1975; Searles and Schneider, 1980; Jaap, 1984), but specific details of most assemblages in 6 to 10 m depths within the region remain poorly known. Taxa-specific discussions of known shallow OHB, IHB, and NHB associations among fishes, algae, invertebrates, and marine turtles are presented in **Section 2** and summarized in terms of functional ecological attributes in **Section 3**.

2.5 REGIONAL SETTING: THE FLORIDA CURRENT AND THE CONTINENTAL SHELF

The continental shelf and associated waters off the southeastern U.S., collectively termed the South Atlantic Bight, extend from Cape Hatteras, North Carolina to southeast Florida. Shelf widths vary from just 3 km off Palm Beach County, Florida to a maximum of 120 km off Georgia. Climatically and biogeographically, the area contains the transition region between many tropical and warm temperate organisms of the Greater Caribbean and the Carolinas. Influences on oceanographic regimes of the continental shelf of mainland east Florida include 1) activities of the Florida Current and meanders of the western frontal boundary; 2) seasonal heating and cooling; and 3) bottom topography. Winds and tides can also modify circulation patterns, especially nearshore or where density gradients are weak (SAFMC, in prep.). Relatively brief consideration of the underlying oceanographic processes in this faunal break is provided below. More thorough summaries for the southern and central project regions exist within Smith (1983), Miller and Lee (1995), Banks et al. (2008), and Entrix, Inc. (2008).

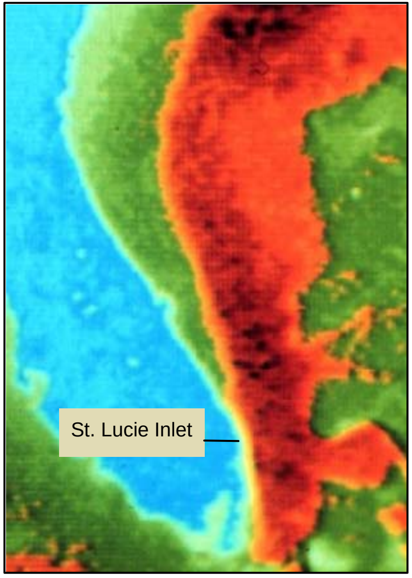


Figure 2.6. Florida Current (shown in orange) with offshore deflection near the southern boundary of Martin County, Florida (Image from: National Oceanic and Atmospheric Administration).

2.5.1 Currents and Upwelling Events

The driving oceanographic characteristic of the project area is the northerly Florida Current and the dynamics of its warm, fast-moving waters derived from the Gulf of Mexico and the Caribbean through the Yucatan Channel. In southeast Florida, coastal circulation is strongly related to the dynamics of the Florida Current and wave oscillations in the relatively narrow trough between Florida and the Bahamas (Soloviev et al., 2007). In the vicinity of the Jupiter and St. Lucie Inlets, the continental shelf platform abruptly extends wide to the east, deflecting the Florida Current much further offshore than in southeast mainland Florida (**Figure 2.6**), influencing the assemblages that utilize shallow hardbottom in manners examined in **Sections 2** and **3**.

Upwelling occurs in the region from wind, eddies, or current meanders that displace surface waters and drive replacement by cooler and usually nutrient-rich water from deeper depths (Atkinson and Targett, 1983; Smith, 1983). The location of the western frontal boundary of the Florida Current varies considerably both north and south of the inflection of the current. Small frontal eddies and meanders propagate along the western edge of the Florida Current, typically at 1- to 2-week intervals. These features can transport significant nutrient and plankton patches into shallower water and contribute to small-scale upwelling of nutrients along midshelf and shelf break areas of this South Atlantic Bight subregion. Seasonal upwelling events that persist for 1 to 3 weeks typically occur during the late summer along some areas of east Florida (Smith, 1983).

A high number of upwelling events occurred off north Hutchinson Island in the summer of 2003. Six events occurred with low temperatures ranging from 16°C to 21°C. Upwelling periods in early and late summer averaged 12 and 5 days, respectively (McCarthy, 2005). Analyses suggest that the longer upwelling events in early summer eventually resulted in similar surface and bottom temperatures. Shorter upwelling events during late summer appear to have resulted in stronger thermoclines because of less time for mixing between surface and bottom waters. Analysis of local meteorological data suggests that wind stress was not favorable to upwelling during most of the summer yet may have played a supplementary role in producing some of the upwelling events (McCarthy, 2005). In contrast to transient upwelling events, there is at least one area on the northern boundary of the study region where upwelling of nutrient-rich deep water is more permanent, an area of diverging isobaths just to the north of Cape Canaveral (SAFMC, in prep.).

In Broward County, in southern portion of the project area, the Florida Current typically flows toward the north or northeast and the current from the surface to the bottom flows relatively consistently in the same direction. However, countercurrents have been recorded where the near-bottom currents flowed in a southerly direction (Soloviev et al., 2007). Strongest currents usually occurred near the surface, with a mean speed of approximately 3.4 ft/sec and a peak speed of greater than 6.8 ft/sec (Entrix, Inc., 2008). When the western edge of the current was closest to shore, the currents were strongest. When the location shifted to the east, currents sometimes weakened and for brief periods reversed and flowed southward. These oscillations were on the order of 14 days; however, 1- to 2-day periods were also recorded.

The complexity of the system constrains full understanding of the effects of current behavior, winds, and upwelling on primary production and cross-shelf fluxes of nutrients and plankton. Biophysical simulations at mesoscale-resolution compared well with *in-situ* observations of shelfbreak upwelling on daily to seasonal timescales in east Florida (Fiechter and Mooers, 2007). Nitrate inputs associated with upwelling were mainly due to bottom Ekman transport as the Florida Current jet interacts with the shelf topography and summer winds that favor coastal upwelling. Upwelling-induced additions of nutrients and phytoplankton blooms can possibly increase decapod larval survival (Pitts, 1999). Brooke (2002) suggests that deep *Oculina* colonies could provide larvae to shallow-water colonies during upwelling events. Hare and Cowen (1996) examine a variety of physical transport mechanisms associated with ichthyoplankton transport and survival to the north of the study area.

2.5.2 Tides, Wind Events, Wave Activity, and Hurricanes

The semidiurnal tides of the South Atlantic Bight vary in manners that can correspond to shelf width. The maximum coastal tides of 2.2 m occur at Savannah, Georgia, where the shelf is widest, and decrease to 1.1 m at Cape Canaveral. NHB is exposed at low tides in a variety of locations, some of which are well-known local geologic features with intertidal habitat structure, e.g., Bathtub Reef in Martin County (**Figure 2.7**). Winds, in general, are from the northeast in fall-winter and from the southwest or southeast in spring-summer, but they can switch directions and form a new pattern for five or more days with little predictability, and with rapid increases in nearshore coastal energetics via wind and wave activity. Waves in the area are often wind-derived, typically from the north and northeast. Approximately half of the waves approach from the northeast; the largest waves approach from the north. Below northern Palm Beach County, wave development from the east and southeast is impeded by the Little and Great Bahama Banks. Banks et al. (2008) provide a recent summary of climate and wind seasonality in the southern and central project region.

Figure 2.7. Southward view of Bathtub Reef, Stuart, Martin County, Florida. Worm rock (*Phragmatopoma lapidosa*) mounds are visible on the lower left. An aerial view of this intertidal reef system is shown in **Figure 2.1**. *Photo by D. McCarthy.*

During large wave events, often associated with nor'easters during fall and winter atmospheric cold fronts, substantial erosional events can occur. In the background, relatively typical summer-winter seasonal beach profiles are seen. Latitudinal differences in the impacts of these events are seen between Canaveral and Miami. Primary differences include 1) the very wide to very narrow north to south shelf width, with major shelf width change in the St. Lucie Inlet area, and 2) the positioning of the northern Bahama Banks off of southeast Florida, particularly from north Palm Beach County to the south. This wave shadow influences a variety of coastal process and sedimentary phenomena in southeast Florida.

Hurricanes and tropical storms can produce intense wind-generated wave action during late summer and early fall, resulting in significant changes to the circulation in a given area. Under normal conditions, the Florida Current would be the dominant transport mechanism, with wave and tidal action having less influence. During a storm event, however, water circulation and transport are dominated by waves and tidal surge. During a hurricane with peak winds of at least 86 mph, the near-bottom currents on the inner- and mid-shelf approximately triple compared to non-storm conditions, increasing from approximately 0.5 to 1.5 ft/sec. During 2004 and 2005, the number of hurricane and tropical storm paths that impacted mainland east Florida (**Figure 2.8**) was higher than had been observed for many years. This hurricane activity may have contributed to higher post-hurricane NHB exposure in some areas (for example, at Singer Island, Palm Beach County, **Figure 2.3**).

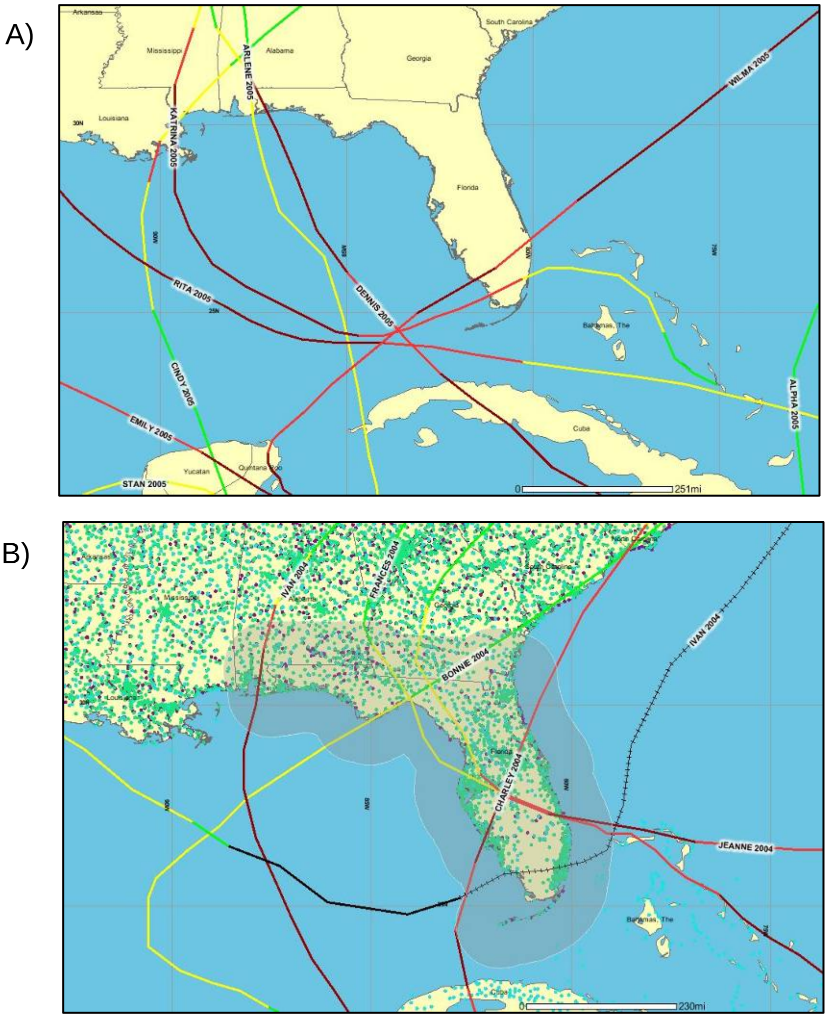


Figure 2.8. Paths of hurricanes and tropical storms impacting east Florida during A) 2005 and B) 2004.

Section 2
Organismal Assemblages of East Florida Shallow Hardbottom

Chapter 3
Macroalgae and Cyanobacteria

3.1 INTRODUCTION

NHBs along the east Florida coast provide substrate for the recruitment and growth of a number of species of macroalgae and cyanobacteria that serve a variety of functions. Macroalgae and cyanobacteria are primary producers in the marine environment and can form the foundation of a highly complex, diverse, and dynamic trophic food web (Duarte, 2000; Paerl, 2000; Kang et al., 2008).

The abundance and diversity of macroalgae vary substantially within the NHB region with changes in latitude from Cape Canaveral to Key Biscayne. Of the varying factors along the east Florida coast that influence macroalgal species distribution in NHB, one of the most important likely is proximity to the relatively warm, oligotrophic waters of the Florida Current. Other important factors include species-specific life history characteristics, small- and large-scale hydrodynamics, substrate type (e.g., worm reefs, limestone, coral reefs) and topography, water clarity, sand scouring and burial, wave energy, and fish and invertebrate grazing pressure (Lobban and Harrison, 1994).

This chapter addresses the distribution, function, and ecology of macroalgae (reds, greens, and browns) and cyanobacteria (blue-greens) found on NHB. Few peer-reviewed studies are available on east Florida coast macroalgal assemblages. Data for this review have largely been extracted from pre- or post-impact monitoring reports, personal communications, and personal observations made during research activities conducted within the study region (**Appendix A**, **Table A.1**). Macroalgae found in juvenile green turtle foraging studies are also listed, since these animals show high site-specificity and their foraging items are indicative of local macroalgal flora. Over 275 different species of macroalgae and cyanobacteria from 108 genera within 57 families were documented from all of the studies reviewed (**Appendix A**, **Table A.2**). Genera and number of species within genera are also documented by county (**Appendix A**, **Table A.3**) in an attempt to elicit some latitudinal perspective for NHB macroalgal distribution patterns, if present. The algal divisions are ultimately organized into functional-form groups as proposed by Littler et al. (1983), which represent useful groupings of macroalgae based on morphological-metabolic-ecological interactions, and has been widely experimented and applied in the marine environment (Littler and Littler, 1980; Steneck and Watling, 1982; Littler et al., 1983).

3.1.1 Functional Form Groups

Functional form grouping as proposed by Littler et al. (1983) assigns species of macroalgae to a particular group based on internal and external characteristics and is applied in this document to describe observed distributional patterns of macroalgae on NHB (**Table 3.1**). Cyanobacteria are treated separately in this document. The functional form algal groups are primarily based on classifying algae by morphological and functional adaptations, and are divided into six main groups: 1) sheet (foliose), 2) filamentous, 3) coarsely-branched, 4) thick-leathery, 5) jointed-calcareous, and 6) crustose. The ranks (or groupings) are based on characteristics of evolutionary strategies that are often similar across divisions. For example, the thick-leathery group contains species from red, green, and brown divisions that are morphologically similar and share metabolic and ecological properties that can be used to examine their patterns or functions within a community (Littler et al., 1983). The sheet group bauplan are characteristically one- to two-layered (mono- or distromatic) or thin-tubed, one to several cells thick, like species of *Ulva* and *Dictyota*. The filamentous group contains species such as *Ceramium*, *Spyridia*, and *Chaetomorpha*, which are lightly branched, multiseriate, and lightly corticated. Macroalgal species such as *Acanthophora*, *Laurencia*, *Liagora*, *Udotea,* and *Penicillus* are placed within the coarsely-branched algal group, characterized as fleshy-wiry textured species with upright coarsely branched structures. Examples from the thick-leathery group are species of *Gracilaria*, *Sargassum*, *Udotea,* and *Padina*, normally several cells in thickness, toughly branched, and heavily corticated. Species in the jointed-calcareous group are typically articulated, calcified, and stony (e.g., *Amphiroa, Jania,* and *Halimeda*). Genera in the crustose group are normally characterized as encrusting, prostrate, and stony (e.g., *Hydrolithum* and *Porolithon*).

Table 3.1. Macroalgal functional form group descriptions as proposed in Littler et al. (1983).

Functional Form Group	External Morphology	Internal Anatomy	Texture	Genera Examined
Sheet	Thin, tubular, and sheet-like (foliose)	Uncorticated, one to several cells thick	Soft	*Ulva, Enteromorpha* (*Ulva*), *Dictyota*
Filamentous	Delicately branched (filamentous)	Uniseriate, multiseriate, or lightly corticated	Soft	*Centroceras, Caulerpa, Spyridia, Chaetomorpha, Ceramium*
Coarsely-branched	Coarsely branched, upright	Corticated	Fleshy-wiry	*Acanthophora, Laurencia, Rhipocephalus, Liagora, Udotea, Caulerpa, Penicillus, Neomeris*
Thick-leathery	Thick blades and branches	Differentiated, heavily corticated, thick-walled	Leather, rubbery	*Sargassum, Lobophora, Gracilaria, Turbinaria, Padina, Stypopodium, Udotea*
Jointed-calcareous	Articulated, calcareous, upright	Calcified genicula, flexible intergenicula with parallel cell rows	Stony	*Halimeda, Galaxaura, Jania, Amphiroa*
Crustose	Prostrate, encrusting	Calcified or uncalcified parallel rows of cells	Stony or tough	*Porolithon, Hydrolithon, Neogoniolithon, Peyssonnelia*

General differences in functional form group responses to environmental conditions (e.g., photosynthesis, sedimentation, grazing, etc.) are presented in **Table 3.2**. Data for NHB macroalgae were extracted from the sources listed in **Appendix A, Table A.1**. Macroalgae are expressed as presence/absence data because different sampling methods were utilized among the studies.

Table 3.2. Effects of environmental conditions on the various algal functional form groups based on Littler et al. (1983).

Functional Form Group	Light	Sedimentation	Water Motion	Nutrients	Herbivory
Sheet (foliose)	High net photosynthesis; Low self-shading	Continuous spore release aids in success	Destructive; Some turf-forming species	High uptake	Low resistance (exceptions [e.g., *Dictyota*]); Delicate thalli but rapid growth
Filamentous	High net photosynthesis	Commonly turf; Vegetation fragmentation aids in success	Many turf-forming species	High uptake	Low resistance (exceptions [e.g., *Caulerpa*]); Delicate thalli but rapid and sometimes conspicuous growth
Coarsely-branched	Moderate net photosynthesis	Commonly turf	Turf forming species; Reduced photosynthesis near holdfast	N/A	Low to moderate resistance; Some secondary metabolic chemical deterrents
Thick-leathery	Moderate net photosynthesis	Robust hold-fasts aid persistence	Strengthens holdfast/reduces height; Some turf-forming species	N/A	High resistance; Morphological deterrent
Jointed-calcareous	Low net photosynthesis	Commonly turf	N/A	Low nutrient uptake rates	High resistance; Morphological deterrent
Crustose	Low net photosynthesis	Tolerant of short burial; Anoxic conditions created under burial	N/A	Low nutrient uptake rates	High resistance; Morphological deterrent

N/A = not available.

3.1.2 Latitudinal Gradients

There are several dramatic and some relatively subtle differences in macroalgal distribution along east Florida NHB that are most likely correlated to two major geographical features: 1) the diverging path of the Florida Current (or Gulf Stream), and 2) gradients in seawater temperatures from warm temperate to subtropical latitudes. The average distance of the Gulf Stream from the nearshore waters of south Florida is approximately 24 km, while the average distance in the northern NHB is approximately 48 km away at Port Canaveral (**Figure 3.1**). Between Cape Canaveral and Palm Beach, Searles (1984) documented the southernmost limit of several warm temperate species (e.g., *Hypnea volubilis, Petroglossum undulatum, Gloioderma blomquistii*) and the northern limits of a number of subtropical species. Macroalgal biomass appears to be relatively higher in northern east Florida coast NHB counties than in the southern NHB counties. While the specific reasons for this have not been experimentally tested, the trend may be due to latitudinal differences in nutrients (possibly a function of the oligotrophic waters of the Florida Current), wave dynamics, and abundance and diversity of grazing fishes and invertebrates. The later explanation may be further supported by the relatively higher percentage of physically- and chemically-defended macroalgae (i.e., thick-leathery, jointed-calcareous, and crustose forms) seen towards southeast Florida (see **Chapter 7**) and, possibly, a relatively higher abundance and diversity of herbivorous fish species seen towards more southern latitudes, as suggested by Floeter et al. (2004). Presence/absence data from NHB studies support some of these general observations (e.g., increase in defended species, especially crustose and jointed-calcareous); however, these data have not been adequately tested.

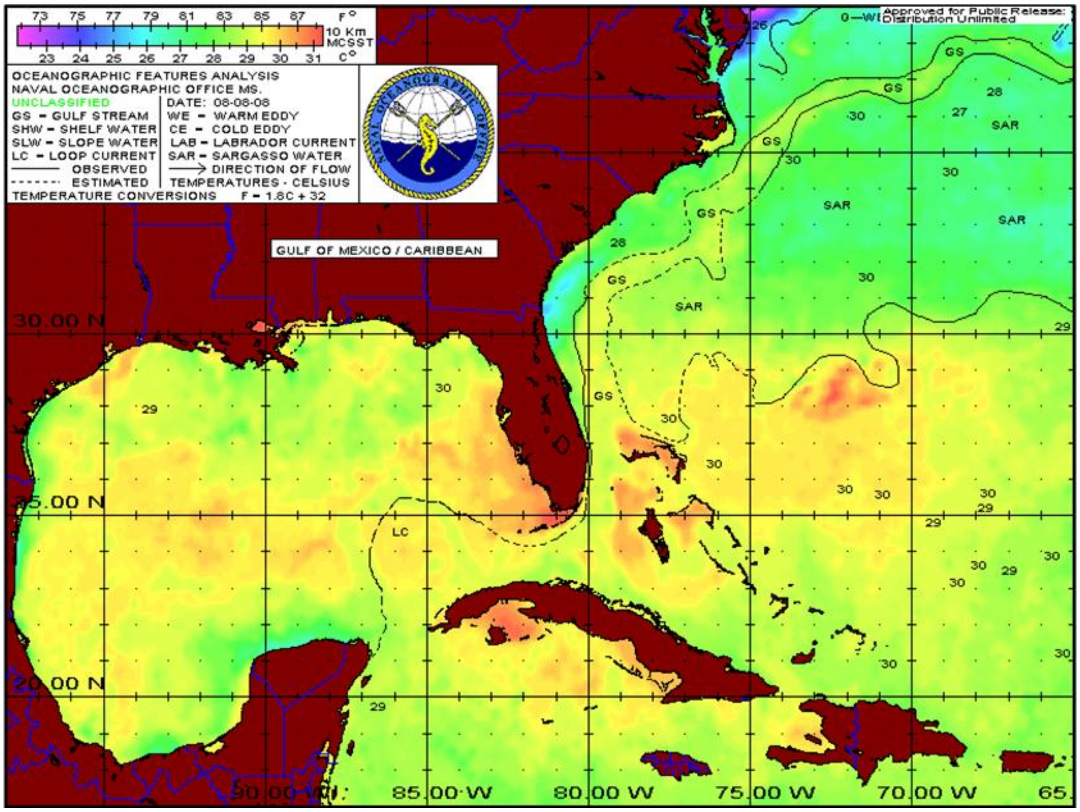


Figure 3.1. Path of the Florida Current (Gulf Stream). Note the increased distance of the Gulf Stream west wall along the east Florida coast from south to north (Image from: Naval Oceanographic Office website [unclassified document]).

3.1.3 Depth Gradients

The overall percent compositions of red (Rhodophyta), green (Chlorophyta), and brown (Phaeophyta) macroalgal species documented in NHB studies (**Figure 3.2**) appear to reflect the overall taxonomic abundance of species of the different divisions. For example, red algae represent the largest taxonomic group of macroalgae, and red algae composed the highest percent composition of total NHB macroalgae. Saffo (1987) and others have more recently questioned Engelmann's theory (1883; see Saffo, 1987) on the depth distributions among green, brown, and red macroalgae. The more-than-century-old hypothesis that predicted chromatic adaptation phylogeny was responsible for the vertical distribution of macroalgae has been tested with more advanced technology. Biologists now recognize that factors other than photosynthetic pigments may affect the distribution of macroalgae, and that seaweeds photoacclimate to light quality as well as light intensity (Saffo, 1987; Dawes, 1998).

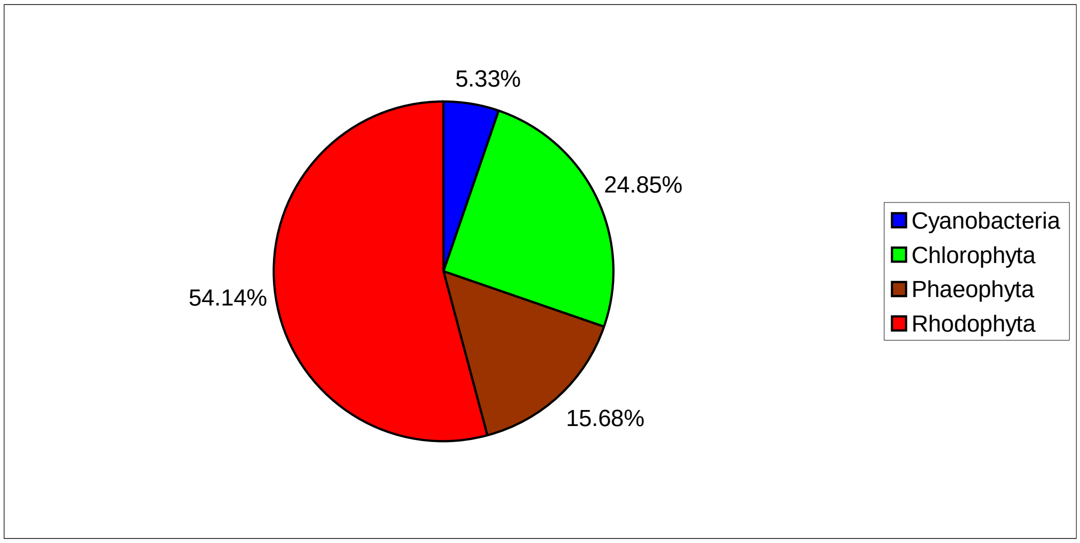


Figure 3.2. Percent composition of macroalgae and cyanobacteria divisions documented from studies conducted on nearshore hardbottom (see **Appendix A**, **Table A.1**).

Macroalgae from the functional form groups of filamentous and thick-leathery represented about 50% of the macroalgae documented from studies conducted on east Florida NHB (**Figure 3.3**). Functional form group representation, however, varied among counties (**Figure 3.4**). Combinations of several different local microhabitat features (e.g., wave dynamics, substrate type, turbidity levels) are most likely responsible for macroalgal zonation patterns of diversity and abundance, as well as changes in form (turfing) on NHB. Turf-forming algae, defined here as macroalgae that form colonial assemblages instead of spatially segregated individuals, normally form in stressful environments, such as areas that experience periodic or frequent sedimentation, exposure, and/or high grazing pressure (Airoldi, 2001). Conditions that induce algal "turfing" are common in low intertidal and shallow subtidal areas. The hardbottoms in these areas are usually well-vegetated with fast-growing and/or turf-forming macroalgae, especially on high-energy beaches. Some patterns elicited among the functional form groups are 1) resilience among many species in the sheet and filamentous groups, and 2) resistant species in the thick-leathery group. Distributional patterns indicate the morphology and productivity strategies of articulated coralline and crustose functional form species enable them to either survive in stressful environments or select against settlement in these habitats.

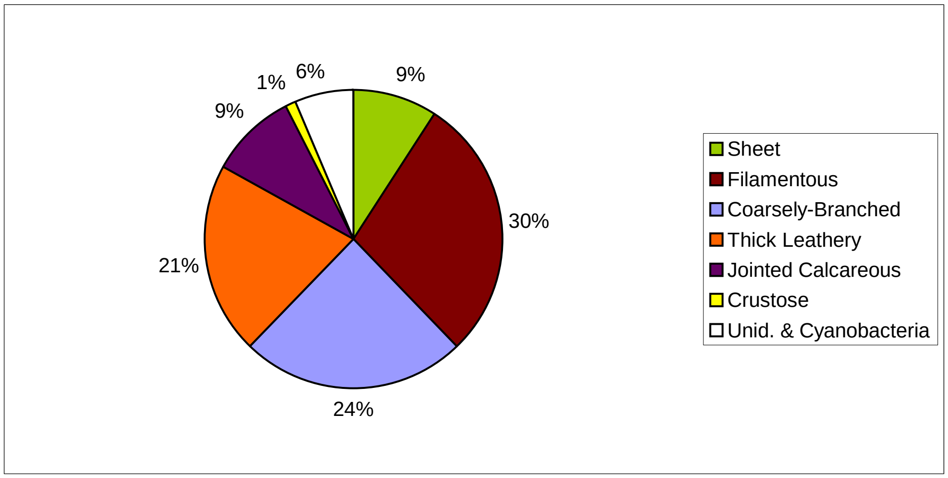


Figure 3.3. Percent composition of macroalgae and cyanobacteria functional form groups documented from studies conducted on nearshore hardbottom (see **Appendix A**, **Table A.1**).

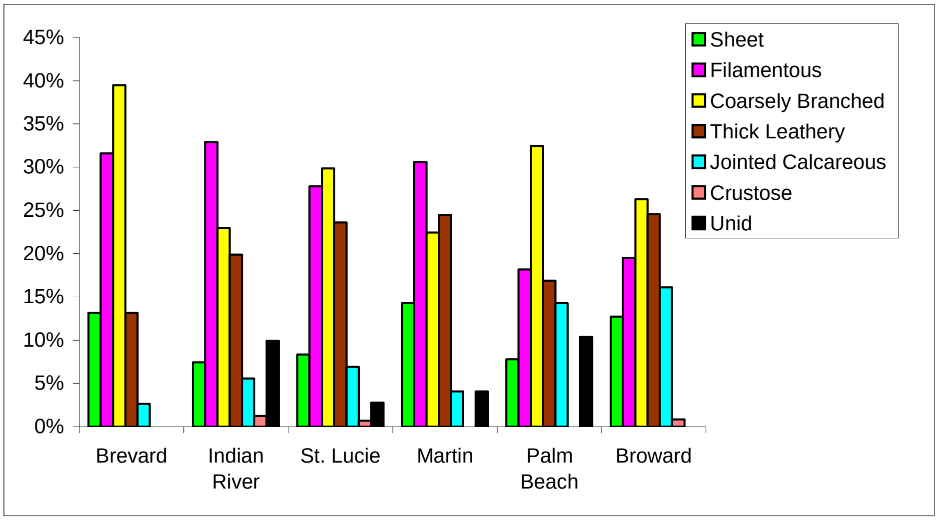


Figure 3.4. Percent composition of macroalgal functional form groups (by county) documented from studies conducted on nearshore hardbottom (see **Appendix A**, **Table A.1**).

3.1.4 Algal Reproduction

3.1.4.1 Sexual Reproduction

Most macroalgae are capable of sexual and asexual reproduction; however, the latter remains less costly. Sexual reproduction promotes variation at the cost of sporophyte and gametophyte production. Thus far, research on the reproductive strategies of certain macroalgae indicates there are several variations within and between species, and generalizations should be cautioned (Lobban and Harrison, 1994). However, for descriptive purposes, a brief definition of the basic reproductive strategies is made here to apply their ecological significance to NHB macroalgae. The three basic life history strategies (from Moore et al., 1998) are as follows:

- sporic meiosis – diploid parents form spores by sporic meiosis; spores produce haploid parents, which produce gametes (i.e., *Ulva lactuca*, *U. flexuosa* [formerly *Enteromorpha*], *Polysiphonia* spp., *Laurencia* spp.).
- gametic meiosis – where diploid parents directly produce gametes by gametic meiosis, bypassing the haploid parent phase (i.e., *Sargassum* spp., *Turbinaria* spp.).
- zygotic meiosis – where haploid parents produce gametes, and gametes fuse into a zygote, which is the only diploid cell in this life cycle (i.e., *Cladophora* spp., *Ulva* spp.).

Heteromorphic or isomorphic haplodiplontic sporic meiosis is a common life history strategy of many NHB macroalgae. Some advantages of this life history (two free-living phases) are that there are different photosynthetic characteristics between gametophytes and sporophytes. There are shade-adapted young sporophytes and gametophytes and sun-adapted (canopy) mature sporophytes (Littler and Littler, 1980 in Dawes, 1998). Other advantages of this life history may include grazer-resistant diploid crustose phases under heavy herbivory levels that alternate with bladed haploid phases when under reduced herbivory pressure (Dawes, 1998).

The dispersal distances of algal propagules vary considerably with species (i.e., 3 m versus 500 m; see Reed et al., 1988) due to species life history in combination with episodic events (i.e., storm events). However, most macroalgae seeds generally settle within a relatively short range (~1 m) from their source (Deysher and Norton, 1982; Lobban and Harrison, 1994). Research to predict rates and distances of dispersal in benthic marine communities has been a recent focus in the marine ecology field. Carr et al. (2003) contends that marine systems are more “open” and dispersal is relatively wider than in terrestrial systems. However, Cowen et al. (2000) reviewed several studies that indicate small-scale circulations in marine systems tend to minimize long-distance dispersal, creating higher-than-expected retention of invertebrate larvae (Cowen et al., 2000) and macroalgal propagules (Santelices, 1990). Bobadilla and Santelices (2005) constructed a model of the predicted spatial distribution of macroalgal dispersal with expected high rates of settlement near the parent plant and progressively less settlement with increasing distance from the propagule source. However, models run with in-field propagule data did not conform to the expected results, with actual propagule dispersal rates being pulsed and highly variable. Source curves that were generated from their data indicated dispersal distance was greater from the source than predicted for many rocky intertidal species. Ultimately, results from Cowen et al. (2000) and Bobadilla and Santelices (2005) support the idea that more accurate models need to be derived that include 1) localized currents and eddies and 2) pulsing events in the capacity of propagules to be imported and exported. Additionally, another important factor to consider is that dispersal distances and survival rates can be enhanced by consumers, where spores successfully pass through the gut of gastropods or fishes and benefit from the sinking, sticking, and nutrient qualities of the fecal pellet (Santelices and Paya, 1989).

3.1.4.2 Asexual Reproduction

Several different strategies exist for clonal (asexual) reproduction: 1) stoloniferous growth (e.g., *Caulerpa* spp. and *Penicillus* spp.), where the plant consists of a prostrate stolon and upright growth, 2) common holdfast growth (e.g., *Corallina officinalis* and *Ascophyllum* spp.), where a basal holdfast gives way to multiple upright thalli, 3) crusts (e.g., *Mesophyllum* spp. and *Ralfsia* spp.), which grow out horizontally, 4) the bending and reattaching of plants to the substrate (e.g., *Laurencia* spp.), where the apical cell attaches to the surface and generates a new thallus, and 5) fragmentation of parts (e.g., *Halimeda* spp., *Dictyota* spp., *Gracilaria* spp.) (Collado-Vides, 2002).

3.1.4.3 Life History Strategy (Perennial vs. Annual Algae)

There are a number of life history strategies of macroalgae, but most can be categorized as either perennial (live for multiple years) or annual (live for 1 year). Perennial algae often represent the final stages of succession and are capable, in some cases, of living for up to 20 years (Lüning, 1990). Perennials exist in, and are dependent on, stable environmental conditions (or at least predictable fluctuating conditions). They are also resilient to low light and nutrient marine environments. Perennial algae can be categorized as **k**-strategist species that optimally utilize environmental resources. Their annually fixed organic carbon stores are used to increase thallus growth (e.g., large canopy species) in lieu of allocating resources toward reproductive structures. In contrast, the biomass of annual species (***r*** strategy) is highly variable since they allocate much of their resources to generate reproductive cells on the thallus and reproduce quickly (Lüning, 1990). Macroalgal species associated with the NHB in Florida appear to have greater numbers of annual species in intertidal and shallow subtidal waters than in deeper (>31 m) waters off the Florida coast, where most of the documented macroalgal species are considered perennial (Hanisak and Blair, 1988).

3.1.5 Functional Form Group Descriptions

3.1.5.1 Sheet Group

Littler et al. (1983) described this group as having a soft, foliose, and uncorticated external morphology with a general cell thickness that ranges from one to several cells. Representative genera from this group are *Ulva* and *Dictyota* (**Figure 3.5**). Predominantly fast-growing and found in shallow waters, species in this group typically have high net photosynthesis rates, are short-lived, and are nitrogen-limited (Littler and Arnold, 1982).

Figure 3.5. Representative species of the sheet functional form group growing on nearshore hardbottom: *Ulva lactuca* (left) and *Dictyota* sp. (right). *Photos by K. Holloway-Adkins*.

Thirty-one different species based from studies conducted on east Florida NHB were from the sheet functional form group: 8 green (*Ulva* spp.), 22 brown (*Dictyopteris delicatula* and *Dictyota* spp.), and 1 red macroalga (*Nitophyllum punctatum*). Macroalgae within this functional group were highly represented in Martin and Brevard Counties (**Figure 3.6**). The number of sheet group species among NHB studies ranged from 0% (Salmon et al., 2004) in Broward County to 20% (Cummings, 1990) in Palm Beach County (**Appendix A**, **Table A.4**). The number of sheet group species was highest in foraging sample analyses of juvenile green turtles in Palm Beach County (27.3%) (Makowski, 2004) (**Appendix A**, **Table A.4**).

The sheet group is abundant throughout east Florida NHB and can be found in both intertidal and subtidal waters. Species of *Ulva* and *Dictyota* were the most frequently represented species from this group and were documented in all counties within the NHB area. Species like *Ulva* that are thin and transparent are less efficient in absorbing submarine illumination than thick, multilayered plants like *Codium*, even though they share the same pigments (Dawes, 1998). However, light can be effectively trapped at depth through morphological adaptations and changes in pigment concentration.

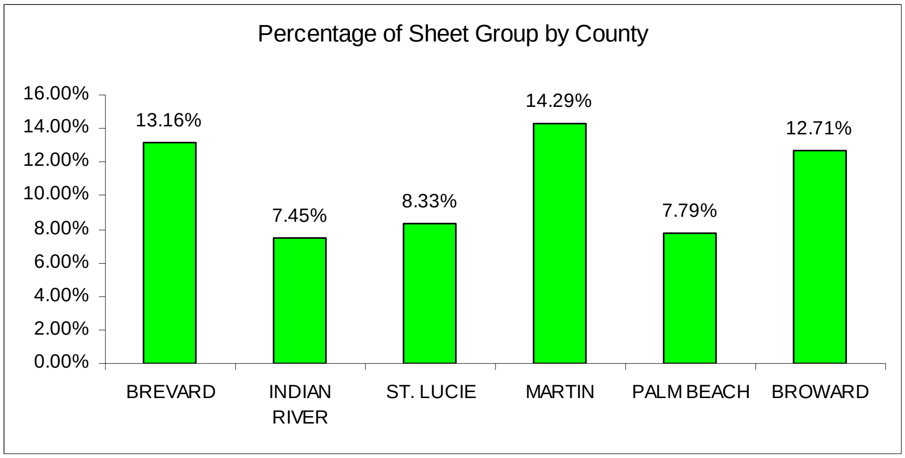


Figure 3.6. Percentage of species in the sheet functional form group documented in studies conducted on nearshore hardbottom in counties from Brevard to Broward, Florida (see **Appendix A**, **Table A.4**).

Most of the green and brown algae within the sheet group display haplodiplontic sporic meiosis life history. Littler et al. (1983) found net productivity was high (second highest of groups) for macroalgae characterized within the sheet group. Species are likely to be opportunistic, with limited life history strategy flexibility (Littler and Littler, 1980); however, because most species from this group have long continuous spore release events (Eriksson and Johansson, 2005), they are highly productive. Species from this group are commonly early successional species, short-lived, and very resilient to environment disturbances.

Many of the sheet group species have bauplans with high surface-to-volume ratios, which promotes a higher uptake of nutrients and accelerates photosynthesis. The ubiquitous *Ulva* was described by Guimaraens and Coutinho (2000) as light-limited during winter and nutrient-limited during summer. However, upwelling events that occur in summer, coupled with the effects of high irradiance and excess nutrients, significantly stimulated algal growth of this species. The sheet group tends to be opportunistic (***r*** strategy), settle, and grow quickly, and be eurytopic (tolerant of a wide range of environmental conditions or habitats); however, this group is more prone to desiccation and grazer damage. Most of these forms are comparatively more susceptible to damage from sedimentary particle abrasion and the shearing action of high-energy waves. Species from this group (i.e., *Ulva* and *Dictyota*) were frequently found in foraging analyses of juvenile green turtles and herbivorous fishes (see **Chapter 7**). However, experimental studies indicate that compounds inherent to *Dictyota* may deter many grazing invertebrates and fishes (Cronin et al., 1997).

3.1.5.2 Filamentous Group

The morphology of this group has been described as delicately branched and filamentous with internal anatomy characterized as uniseriate, multiseriate, or lightly corticated (Littler et al., 1983). Typical genera include *Centroceras*, *Chaetomorpha,* and *Ceramium*. This group represented the largest functional form group (31.0%) found on east Florida NHB and was documented from studies in every county examined.

Ninety-seven macroalgal species were identified as having filamentous functional form. This group included 24 green, 9 brown, and 64 red algae. Most of the same species were abundant and common along the entire east Florida NHB; however, they were most frequently documented in Indian River and Brevard Counties (**Figure 3.7**). The number of filamentous group species for NHB studies ranged from 0% (Continental Shelf Associates, Inc., 2005b) in Palm Beach County to 35.8% (Juett et al., 1976) in Indian River County (**Appendix A**, **Table A.5**). The highest composition of filamentous species found in foraging analysis of juvenile green turtles was 36.3% in Palm Beach County (Makowski, 2004) (**Appendix A**, **Table A.5**).

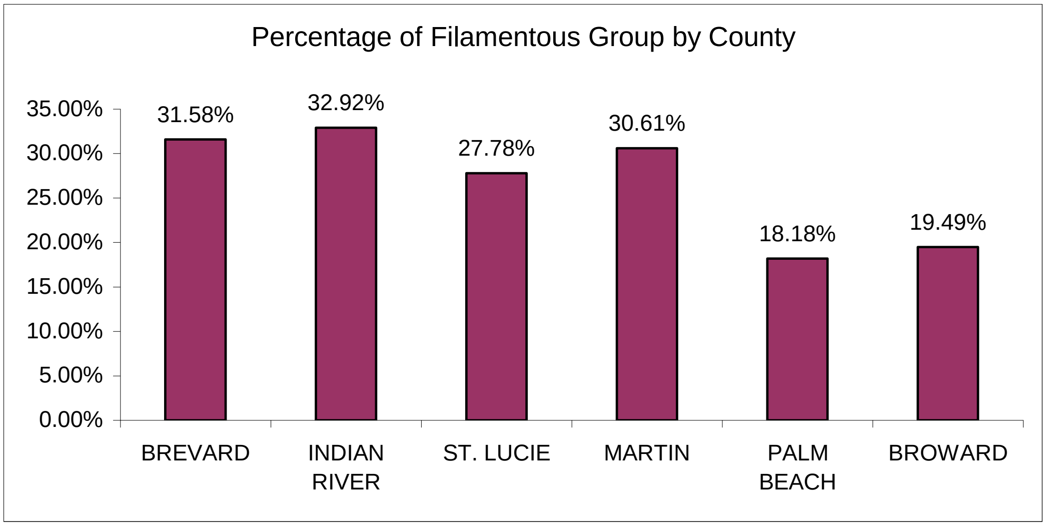


Figure 3.7. Percentage of species in the filamentous functional form group documented in studies conducted on nearshore hardbottom in counties from Brevard to Broward, Florida (see **Appendix A**, **Table A.5**).

Macroalgae from the filamentous form group were documented among most of the east Florida NHB studies. *Bryopsis*, *Caulerpa,* and *Ceramium* were reported in studies within all of the counties, and *Cladophora* was counted in all but Broward County (**Appendix A**, **Table A.3**). These species are present and abundant in both intertidal and subtidal waters (K. Holloway-Adkins, East Coast Biologists, Inc., [ECB], personal observation) and exhibit few inhibitions to growth or distribution. Many species within this group are frequently found in the diet of herbivorous invertebrates, fishes, and juvenile green turtles.

Net productivity was experimentally highest for macroalgae within the filamentous functional form group (Littler et al., 1983). Most macroalgae in this group exhibit high tolerance for changes in sedimentation and will commonly turf to persist in stressful environmental conditions. Dense turfs of filamentous algae are common in lower shallow intertidal waters, and this morphological adaptation helps these species persist and grow under intense grazing pressure and/or high-energy beach conditions (Airoldi, 2001). A few species can grow epiphytically on other macroalgae; however, most form a somewhat distinct holdfast or stolon and require hard substratum for attachment and growth. Most of the species within this group lack defense metabolites and are frequently consumed by many herbivorous fishes, invertebrates, and juvenile green turtles (see **Chapter 7**).

Green and brown filamentous group macroalgae exhibit haplodiplontic sporic meiosis life history strategies. The majority of species in this group elicit ***r***-strategy characteristics and are highly resilient but short-lived species. Reproductive strategies of red algae within this group are known to have long continuous spore releases events (Eriksson and Johansson, 2005). Additionally, species from this group are commonly early successional species, highly ephemeral, and characteristically resilient.

3.1.5.3 Coarsely-branched Group

The morphology of this group has been described by Littler et al. (1983) as coarsely-branched, upright, and corticated. Typical genera include species of *Acanthophora*, *Laurencia, Liagora, Udotea, Caulerpa*, and *Penicillus; Laurencia* and *Caulerpa* are pictured in **Figure 3.8**.

Figure 3.8. Representative species of the coarsely-branched functional form group growing on nearshore hardbottom: *Laurencia* sp. (left image, top left and right) and *Caulerpa* sp. (cover in right image). *Photo by K. Holloway-Adkins.*

There were 83 macroalgal species within the coarsely-branched functional form group documented from east Florida NHB studies. The group itself is dominated by species of red and green macroalgae (see Littler et al., 1983). Fifty-seven species of red, 26 species of green, and no species of brown macroalgae were documented in NHB studies for this functional form group.

The percent of macroalgae from this group was highest in Brevard County (39%; **Figure 3.9**). The number of coarsely-branched species per NHB study ranged from 16.7% composition in Broward County (Salmon et al., 2004) to 66.7% in Palm Beach County (Continental Shelf Associates, Inc., 2005b) (**Appendix A**, **Table A.6**). The percent composition of macroalgae from the coarsely-branched functional group was highest in the foraging samples of juvenile green turtles in Broward County (Wershoven and Wershoven, 1992a) at 40.0% (**Appendix A**, **Table A.6**).

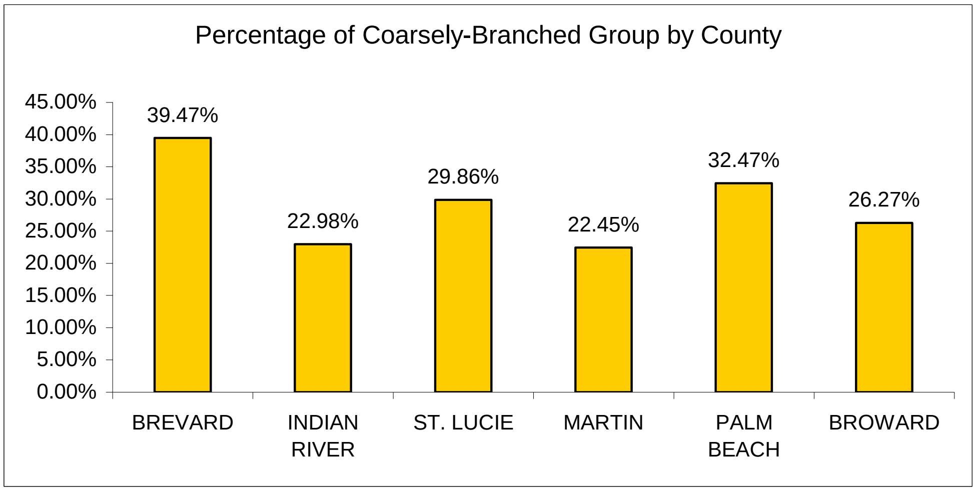


Figure 3.9. Percentage of species in the coarsely-branched functional form group documented in studies conducted on nearshore hardbottom in counties from Brevard to Broward, Florida (see **Appendix A**, **Table A.6**).

This group contains species that extend to the edge of the range and therefore exhibit traits from the two adjacent groups, i.e., on one end some genera like *Udotea* have low net productivity and tough external morphology, but others share other characteristics with the coarsely-branched group (Littler et al., 1983).

Acanthophora spicifera exhibits seasonal patterns of growth and mortality on east Florida NHB (K. Holloway-Adkins, ECB, pers. observ.); however, in tropical Panama it was considered perennial (Kilar and MacLachlan, 1989). Some species within this group have dormant or reduced stages where the plant dies back to the holdfast and regenerates under more favorable (i.e., photoperiod, temperature, salinity level, etc.) conditions (Brawley and Johnson, 1992).

3.1.5.4 Thick-leathery Group

The morphology of this group is described as having thick blades and branches, with internal anatomy being differentiated, heavily corticated, and thick-walled (Littler et al., 1983). Species include *Sargassum, Lobophora, Gracilaria, Turbinaria, Padina, Stypopodium,* and *Udotea.*

A total of 71 different species was documented from east Florida NHB studies (38 red, 21 brown, and 12 green macroalgae). Species within this group were widely distributed across the NHB in every county and were from all three macroalgal divisions. *Gracilaria* and *Padina* occur frequently throughout east Florida NHB, while *Sargassum*, *Lobophora*, *Turbinaria*, and *Udotea* are more frequently found in the central and southern east Florida NHB. Representative species from the thick-leathery functional form group are shown in **Figure 3.10**.

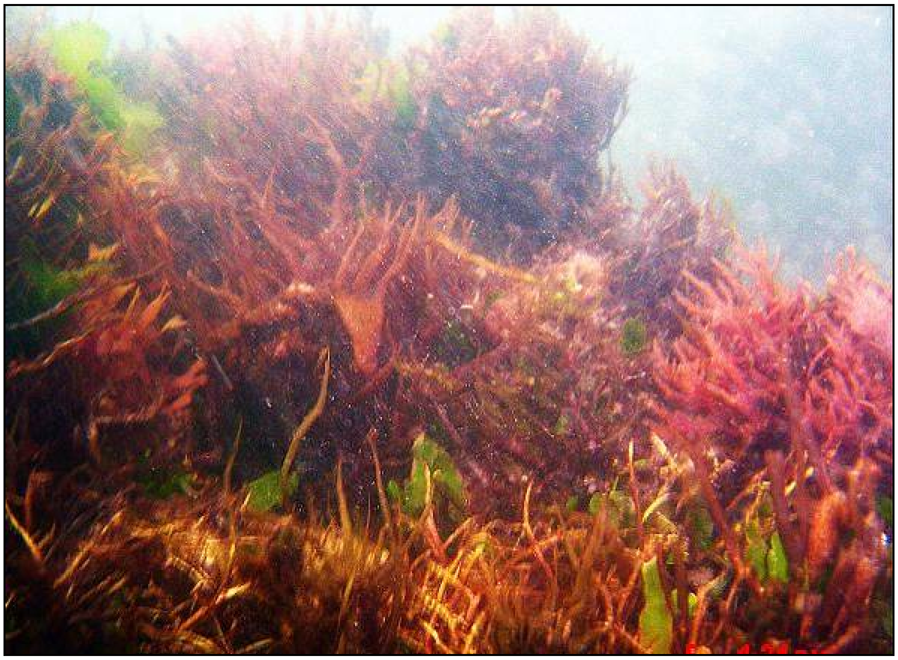


Figure 3.10. Several representative species of the thick-leathery functional form group, including *Agardhiella subulata* and *Gracilaria* sp., growing on nearshore hardbottom. *Photo by K. Holloway-Adkins.*

Distribution – Latitude and Water Depth

The percent of macroalgae from this group was highly represented in Broward and Martin Counties (**Figure 3.11**). Percent composition found in studies conducted along east Florida NHB showed a low percentage (8%) in Palm Beach County (Continental Shelf Associates, Inc., 2005b) and a high percentage (50%) in Broward County (Salmon et al., 2004) (**Appendix A**, **Table A.7**). Species from the thick-leathery group were highest (30.0%) in foraging samples that were analyzed from juvenile green turtles in Broward County (Wershoven and Wershoven, 1992b) (**Appendix A**, **Table A.7**).

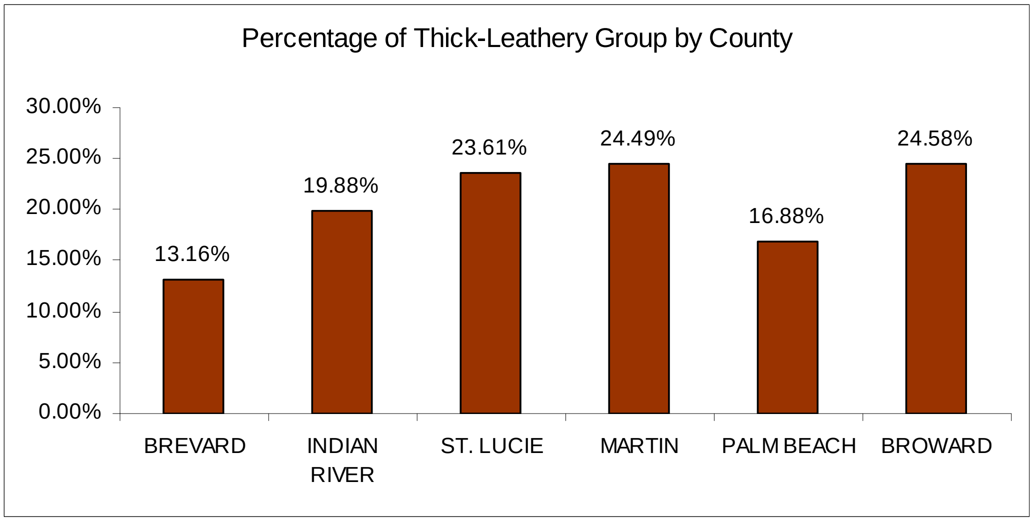


Figure 3.11. Percentage of species in the thick-leathery functional form group documented in studies conducted on nearshore hardbottom in counties from Brevard to Broward, Florida (see **Appendix A**, **Table A.7**).

Robust holdfast structures may promote persistence under short-term burial events. This group's reproductive strategy appears to be not as tolerant of sedimentation (Eriksson and Johansson, 2005); however, their association with turf (understory) species may promote their persistence in stressful environments (Johnson and Brawley, 1998). The majority of species within this group produce secondary metabolites and persist as perennial **k**-strategy plants.

3.1.5.5 Jointed-calcareous Group

External morphology of this group is described as being articulated, calcareous, and upright (Littler et al., 1983). Internal anatomy is calcified genicula and flexible intergenicula with parallel cell rows. Species include *Halimeda*, *Galaxaura*, *Jania*, and *Amphiroa*. Red coralline species (Order Corallinales) are less frequently encountered in the northern reach of the east Florida NHB but are represented by *Amphiroa* sp. and *Jania* spp. throughout the entire east Florida NHB.

There were 32 different species (19 rhodophytes and 13 chlorophytes) from the jointed-calcareous functional form group documented from east Florida NHB studies. Jointed-calcareous functional form group species were represented in every county within the NHB.

Broward County had the highest percent of macroalgae from this group (**Figure 3.12**). Percent composition found in studies conducted along east Florida NHB were highest (21.7%) in the Vare study (1991) in Palm Beach County (**Appendix A**, **Table A.8**). The highest percent composition of jointed-calcareous species found in foraging samples of juvenile green turtles was 10%, in Broward County (Wershoven and Wershoven, 1992b) (**Appendix A**, **Table A.8**).

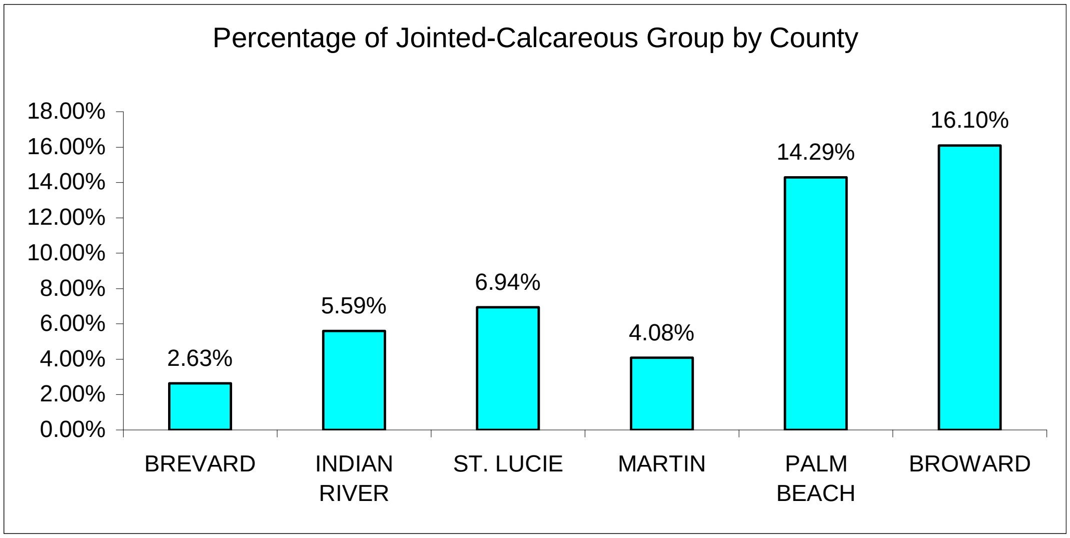


Figure 3.12. Percentage of species in the jointed-calcareous functional form group documented in studies conducted on nearshore hardbottom in counties from Brevard to Broward, Florida (see **Appendix A**, **Table A.8**).

Calcareous species are important contributors to sediment production (as well as species from the crustose group). They exhibit more **k**-strategy life histories, transferring energy towards structural development (e.g., calcareous external morphology) and therefore growing much slower than filamentous and sheet group species. Net productivity of this group and the crustose group are lowest among the functional form groups (Littler et al., 1983). The propagules of articulated coralline species are considered poor dispersers (Dethier et al., 2003), and macroalgal dispersal generally serves to primarily replenish local productivity.

Parrotfish (Scaridae) readily consume calcareous algae (e.g., *Halimeda* spp., *Avrainvillea* spp., *Penicillium* spp.). However, it appears that other herbivorous fish species and most invertebrates avoid calcareous green and red algal species.

3.1.5.6 Crustose Group

Morphology for this group is typically epilithic, prostrate, or encrusting. The internal morphology has been described as calcified or uncalcified parallel rows of cells (Littler et al., 1983). From this group, only species of Rhodophyta were found on east Florida NHB.

The crustose macroalgal group was represented in only two counties, so a multi-county figure similar to **Figures 3.6** through **3.12** is not presented. *Lithophyllum* sp. and *Peyssonnelia rubra* were the only two species documented on east Florida NHB. *Lithophyllum* sp. was documented in a study in Broward County (USACE, 2003a), and *Peyssonnelia rubra* was documented by Juett et al. (1976) in Indian River County.

Studies conducted showed a high percentage (18.5%) for crustose-group in Broward County (USACE, 2003a) and a low percentage (1.8%) in Indian River County (Juett et al., 1976) (**Appendix A**, **Table A.9**). Foraging analysis of juvenile green turtles did not include any species in the crustose functional form group.

Species within this group show low net productivity; however, they are highly resistant to mechanical damage by sedimentation events and grazers, are considered perennial species, and can reproduce both asexually and sexually. Species in this group can grow in deep intertidal and shallow subtidal areas of the reef (as suggested by van den Hoek et al., 1975 in Dawes, 1998).

3.1.5.7 Cyanobacteria

Cyanobacteria are photosynthetic, oxygen-producing bacteria that were formerly known as blue-green algae. They play a major role in nitrogen fixation and are primary producers in most marine environments. Some occur at macroscopic sizes (i.e., *Lyngbya*), but most are microscopic. The paramount importance of cyanobacteria in shaping the supporting marine food webs is sometimes underestimated (Paerl, 2000). In some cases, cyanobacteria have been reported to produce up to 20% of ocean primary production (Moore et al., 1998), while others report it to account for anywhere from 30% to over 50% of the global oceanic primary production (Paerl, 2000). Their ubiquitous presence, eurythermal nature, and, sometimes, dual life-history strategy (auto- and heterotrophic) have made them difficult to classify, as well as characterize. Most likely several hundred different species are associated with NHB on Florida's east coast.

The two basic morphological classifications for marine planktonic cyanobacteria are 1) unicellular, and 2) filamentous. Filamentous forms are further subdivided into heterocystous and non-heterocystous forms (Paerl, 2000). Examples of heterocystous filamentous cyanobacteria documented from NHB studies were *Anabaena* and *Nodularia*. Non-heterocystous blue-green algae found included genera of *Lyngbya* and *Oscillatoria*.

Except for the more epiphytic colonial, filamentous cyanobacteria, most species are microscopic in size. Cyanobacteria can be relatively difficult to identify *in situ* and are predominantly inconspicuous in most cases. The paucity of data on species found on NHB from reviewed studies is most likely due to blue-green algae being overlooked and/or undocumented. Ongoing research by the Smithsonian Marine Station in Fort Pierce, Florida and Nova Southeast University in Ft. Lauderdale is exploring the cyanobacteria interactions with other sessile organisms along the Florida coast. For example, their research suggests that cyanobacteria blooms appear to be more frequent along the Florida coast in recent years and may prohibit coral recruitment (Kuffner et al., 2006; Paul et al., 2007). Species of cyanobacteria were recorded for Indian River (Juett et al., 1976), Martin (Phillips, 1961), and Palm Beach (Vare, 1991) Counties, and from foraging samples of juvenile green turtles in Palm Beach County (Jones et al., 2004) (**Appendix A**, **Table A.1**). High-density *Lyngbya* blooms were documented on Gulf Stream reef (Boynton Beach OHB) from 2002 to 2004 and again in fall 2008 by Palm Beach County Reef Rescue. Also, *Lyngbya* blooms occurred on Broward County NHB and OHB from 2002 through 2004, where they smothered benthic species, particularly octocorals (Paul et al., 2007; Banks et al., 2008). In addition, NHB in Broward County south of Port Everglades was dominated by cyanobacteria during the summer of 2001 (Miller and Cuba, 2003; USACE, 2003a).

Seventeen species from 11 genera and eight different families were documented from east Florida NHB studies (**Appendix A**, **Table A.2**). The most frequently documented species were *Calothrix*, *Lyngbya*, *Microcoleus*, and *Schizothrix*. Other species observed were *Anabaena*, *Anacystis*, *Entophysalis*, *Hormothamnion*, *Nodularia*, *Oscillatoria*, and *Porphyrosiphon.*

There is very little information available on how diversity of cyanobacteria changes along the NHBs of the east Florida coast. However, it can be fairly easily observed in both intertidal and subtidal hardbottoms, particularly during the late summer time period. Peaks in abundance of an unknown filamentous cyanobacteria species on dead intertidal worm reefs during late summer have been consistently observed (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Subtidally, it also appears that filamentous cyanobacteria (likely *Lyngbya* sp.) may bloom during the summer time period. Peaks in abundance may be enhanced during this time period when late summer upwelling events provide excess nutrients to these shallow waters (McCarthy, 2005).

Cyanobacteria reproduce asexually and possibly via parasexual processes. Asexually, filamentous forms reproduce by trichome fragmentation, or by formation of special hormogonia (distinct reproductive segments of the trichomes). Hormogonia display gliding motions and gradually develop into new trichomes (World Health Organization, 1999). They also contain akinetes, which are modified vegetative cells that can remain dormant for long periods of time until environmental conditions are favorable to the germination of the new filaments. While there is no evidence of sexual reproduction, cyanobacteria may reproduce parasexually via transformation and conjugation (like bacteria).

3.2 SUMMARY

NHB areas off Florida's east coast provide critical substrate for the settlement, growth, and production of macroalgae and filamentous cyanobacteria. Some important functions of macroalgal communities are to 1) provide oxygen through respiration processes, 2) aid in nutrient cycling, and 3) provide food and shelter for numerous species of herbivorous fishes, invertebrates, and juvenile green turtles. For example, the chemical content and architecture of *Laurencia* sp. function as important cues for spiny lobster postlarval settlement and subsequent juvenile shelter selection. Both use the architecture of, and the food present on, *Laurencia* in selecting habitat (Herrnkind and Butler, 1986). Other macroalgal species such as the ubiquitous calcareous *Halimeda* also contribute three-dimensional structure for many species while alive, as well as calcium carbonate sands after they die and decompose. In particular, in the Florida Keys the contribution of *Halimeda* is widely evident where the process of deposition and sedimentation enrich local substrata, promoting the growth and productivity of other macroalgal and invertebrate species (Wiman and McKendree, 1975).

There have been several noted invasive magroalgal species encountered along Florida's NHB. Generally, Williams and Smith (2007) report that there currently are 277 species of macroalgae that have been introduced at the global scale due to human activities. Those with opportunistic life history characteristics make them more likely to become invasive species under certain conditions (i.e., siphonous greens like *Caulerpa* spp.) and consequently warrant a higher level of monitoring (Williams and Smith, 2007). Generally, most macroalgae are nitrogen-limited, and when land-based runoff creates high nutrient levels, macroalgal proliferation can increase. Under these conditions, some non-native as well as native species can become invasive monocultures that smother corals and other invertebrates, limiting availability light and creating anoxic conditions. LaPointe et al. (2005) investigated N sources predominantly responsible for an invasive species outbreak (*Caulerpa brachypus*) and the exponential production of a native species (*Codium isthmocladum*) that became harmful algal blooms in Palm Beach and Broward County. Through "signature" analysis of nitrogen, they determined the greatest source of available and assimilable nitrogen was from land-based sewerage systems.

Macroalgae can be classified according to morphological and functional adaptations and are divided into six main groups: 1) sheet (foliose), 2) filamentous, 3) coarsely-branched), 4) thick-leathery, 5) jointed-calcareous, and 6) crustose.

While no one particular alga would completely align with the definition of keystone species, there are a handful of species within the macroalgal community that are both abundant on NHB and play an important role among the grazers. Ten genera (*Caulerpa, Ceramium, Codium, Dictyota, Gelidium, Graciliaria, Laurencia, Padina, Ulva, Bryopsis*) recurred in NHB studies for all six counties examined. *Ceramium*, *Ulva*, *Dictyota*, *Hypnea*, *Laurencia*, *Gelidium*, *Caulerpa*, and *Jania* were found in the foraging samples of herbivores, and were documented in studies in at least five of the six counties. Some general patterns observed for macroalgae in different NHB regions (counties) were 1) no calcareous green (including *Halimeda*) species were found in Brevard County, 2) fewer *Caulerpa* species were present north of Sebastian Inlet (Brevard County) when compared to NHB in counties south of this area, 3) a higher number of red algal species in northern NHB counties (Indian River and Brevard), and 4) relatively few species of brown algae in northern NHB.

While there are not a great deal of comparable macroalgal data from along the east Florida coast, biomass appears to be relatively higher in the northern east Florida coast NHB counties than in the southern ones. While the specific reasons for this have not been experimentally tested, the trend may be due to latitudinal differences in nutrients (possibly a function of oligotrophic waters of the Florida Current), wave dynamics, and abundance and diversity of grazing fishes and invertebrates. Finally, cyanobacteria can be commonly encountered along the east Florida NHB, although there is not much known about how diversity changes with depth and latitude. Ongoing research at two major institutions on the east Florida coast is exploring community interactions involving cyanobacteria and sessile organisms in subtropical ecosystems.

Macroalgae from the filamentous and thick-leathery functional form groups represented more than 50% of the macroalgae documented from studies conducted on east-Florida NHB. Ninety-seven macroalgal species were identified as having filamentous functional forms. This group included 24 green, 9 brown, and 64 red algae. Commonly encountered thick-leathery group (thick blades and branches with differentiated internal anatomy heavily corticated, and thick body walls) species included *Sargassum, Lobophora, Gracilaria, Turbinaria, Padina, Stypopodium,* and *Udotea*. In contrast, there were 31 species from the sheet functional form group that included 8 green (*Ulva* sp.), 22 brown (*Dictyopteris delicatula* and *Dictyota* sp.), and 1 red (*Nitophyllum puncatum*) macroalgal species. There were 75 macroalgal species within the coarsely-branched group, which was dominated by red and green algae with typical genera of *Acanthophora, Laurencia, Liagora, Udotea, Caulerpa*, and *Penicillus*. Common species from the jointed-calcareous group (articulated, calcareous, and upright) include *Halimeda, Galaxaura, Jania,* and *Amphiroa*. Within this group, macroalgae on the hardbottom in Brevard/Indian River Counties showed no *Halimeda* north of Sebastian Inlet, relatively few *Caulerpa* species, and no calcareous greens when compared to NHB in counties south of this area. Finally, crustose group members such as *Peyssonnelia* could be encountered but are not well-documented in Florida NHB.

Generally, there appears to be greater numbers of annual species in intertidal and shallow subtidal waters along the east Florida coast than in deeper (>31 m) waters off the Florida coast, where most of the documented macroalgal species are considered perennial. Some patterns elicited among the functional form groups encountered along the east Florida coast are 1) resilience among many species in the sheet and filamentous groups, and 2) resistant species in the thick-leathery group. In the shallower, harsher NHB, most macroalgae in the filamentous functional group exhibit high tolerance for changes in sedimentation and will commonly turf to persist in stressful environmental conditions. Dense turfs of filamentous algae are common in lower shallow intertidal waters, and this morphological adaptation helps these species persist and grow under intense grazing pressure and/or high-energy beach conditions. In contrast, the sheet group tends to be opportunistic (***r*** strategy), settle, and grow quickly, be eurytopic in nature, and incur high levels of physical damage from grazing and sedimentation activities.

Regardless of general life history strategy, most macroalgae along the east Florida NHB are capable of sexual and asexual reproduction; however, the latter remains less costly. The degree of dispersal of fragments or reproductive propagules from parent sources is unknown for species along the coast but is likely to be highly variable. Recent research suggests dispersal distances may be greater from the source than predicted for many rocky intertidal species. Finally, there is essentially no information available on seasonal recruitment patterns for any algal species along the east Florida coast.

Chapter 4
Invertebrates

4.1 INTRODUCTION

There is a high diversity and abundance of sessile and motile invertebrate species associated with NHBs along the east Florida coast (see **Appendix B**, **Table B.1**). A total of 533 species of invertebrates has been identified from NHB along the east Florida coast. On a large scale, the diversity and abundance at any particular location varies dramatically based on latitude, depth, and, often, season. Variability in these community and population measures within a specific area can be high because of changes in features of the substrate itself, local hydrodynamics, and other biotic and abiotic factors. Often, the highest community biomasses occur in hardbottom areas with higher abundances of sessile invertebrate species (some may be considered foundational or keystone contributors to the community) that enhance local shelter. Higher biomasses of macroalgae that occur in the more northern hardbottoms along the east Florida coast likely serve the same purpose. In some cases, these hardbottom-enhancing species may also significantly contribute to local food webs (i.e., *Phragmatopoma lapidosa*). Therefore, changes in the abundance of these foundational species, whether natural or anthropogenic, will likely have profound effects on local invertebrate and vertebrate diversity and abundance.

The approach of this chapter is to give an overview of the sessile and motile invertebrate communities associated with east Florida NHBs. Invertebrate community changes with latitude, depth, and season will be discussed, where possible, based on available data and personal research experiences. The chapter will additionally discuss the ecological function and life history and reproductive characteristics of each taxonomic group in the context of how they may affect distribution and abundance in the study region.

4.2 SESSILE SPECIES

4.2.1 Polychaetes

4.2.1.1 Diversity and Trophic Function

Diversity and abundance of polychaetes along NHBs from the east Florida coast is high (**Appendix B**, **Table B.1**) with 87 worm species being found along the coast. Nelson (1989) and Coastal Science Associates, Inc. (2000) observed 49 and 53 polychaete species, respectively, on hardbottoms in Indian River County, while Rudolph (1977) identified 85 species from Palm Beach County hardbottoms.

Little is known about the ecological function of most polychaete species along the east Florida coast, but they are probably very important in local food webs as both consumers and prey. Most polychaetes are suspension feeders, although some are deposit feeders and carnivores. They are most likely very important food sources for various fish and invertebrate species, although no research has addressed this in the study region.

Most available research on polychaetes has focused on various aspects of the reef-building polychaete *Phragmatopoma lapidosa*, also known as *P. caudata* (Kirtley, 1994) and/or *P. l. lapidosa* (Pawlik, 1988). This species is clearly a keystone contributor to the biological diversity of hardbottoms along the Florida coast. The relief provided by these "worm reefs" supports a higher diversity and abundance of marine species than that of neighboring sand or hardbottom habitats (**Figure 4.1**). In particular, worm reefs are considered important sources of food and shelter for juvenile green turtles (*Chelonia mydas*) (Wershoven and Wershoven, 1989; Ehrhart et al., 1996; Holloway-Adkins, 2001). Prior studies have also identified that the reefs provide shelter for over 423 invertebrate species (Gore et al., 1978; Nelson, 1988, 1989; Nelson and Demetriades, 1992) and over 200 fish species (Gilmore, 1977; Gilmore et al., 1981; Lindeman, 1997a; Lindeman and Snyder, 1999). The importance of worm reefs in providing food and shelter for juvenile and adult fishes of commercial value resulted in their designation as EFH/HAPC by the

NMFS. In addition, worm reefs are important for the maintenance, propagation, and persistence of beaches and barrier islands by primarily retaining sediments (Kirtley, 1966, 1967; Multer and Milliman, 1967; Gram, 1968; Kirtley and Tanner, 1968; Mehta, 1973; Kirtley, 1974).

Figure 4.1. Intertidal worm rock at Bathtub Reef, Stuart, Martin County, Florida. *Photo by D. McCarthy*.

While *P. lapidosa* is important in enhancing shelter in hardbottoms, they may also be important within food webs along the east Florida coast (**Figure 4.2**). It is apparent that various decapods (Gore et al., 1978) and gastropods (Watanabe, 2002; Watanabe and Young, 2006) will prey on *P. lapidosa*. It is likely, though not confirmed, that some fish species such as parrotfish may feed on them as well. Further, the rock-boring urchin *Echinometra lucunter* clearly bores into worm reef and limestone, causing worm mortality along hardbottoms in St. Lucie County (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). However, these biotic forms of mortality probably do not affect *P. lapidosa* abundance and distribution at the same level that seasonal natural disturbances such as high wave energy and sand scouring/burial (McCarthy, 2001).

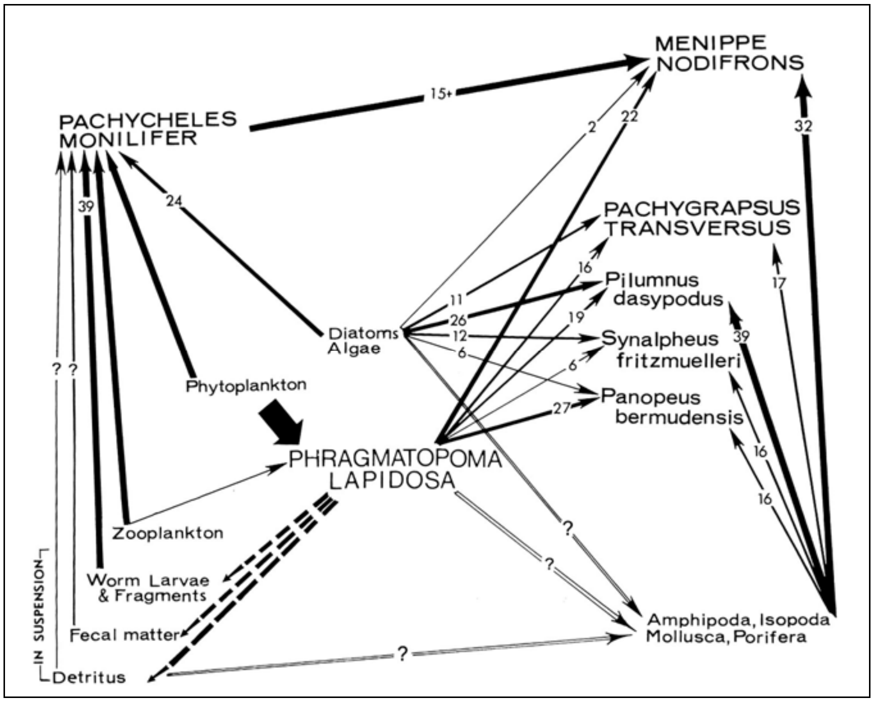


Figure 4.2. The trophic subweb postulated for the six most abundant species of decapod crustaceans on central Florida sabellariid worm reefs. The numbers on the lines indicate the percent of observed prey material noted in the gut contents from all combined individuals of a species. Trophic lines without numbers, or with question marks, are interpolated from our field observations or from records in the literature. Dashed lines indicate production from *Phragmatopoma lapidosa* (From: Gore et al., 1978).

4.2.1.2 Latitudinal and Cross-shelf Distribution

Figure 4.3. Close up of the anterior end of the reef-building polychaete *Phragmatopoma lapidosa* (*caudata*). *Photo by D. McCarthy*.

There is no information currently available on how diversity and abundance of most polychaetes change with latitude and depth along east Florida coast NHBs. Inconsistent sampling methods for the few available studies make comparisons invalid. While Rudolph (1977) found nearly twice as many polychaetes as Nelson (1989), the later author suggests that increased sampling in Indian River County is likely to reveal more species than the 49 encountered in his study. Further, both of these studies focused only on species encountered within a depth of 2 to 4 m. There are no known comparative ecological studies of polychaete assemblages with increasing depth along the coast. The best available research for the east Florida coast has been conducted on *Phragmatopoma lapidosa* (Family Sabellariidae) (**Figure 4.3**). *P. lapidosa* grasps sediment grains from the water column by its oral tentacles, coats them with a proteinaceous cement, and then implants them into tubes with their opercular paleae (Kirtley, 1966). Numerous individuals make tubes that then form vast hardbottom reefs in intertidal and shallow (generally highest abundances occur in <4 m) subtidal waters from Cape Canaveral to Key Biscayne in Florida (about 650 km) and further south to Santa Catarina, Brazil (Kirtley, 1994) (**Figures 4.4** and **4.5**). Within Florida, there appears to be higher abundances of this species towards the northern half of the east Florida hardbottom area (USFWS, 1999), with peak abundance possibly occurring within the Stuart to Vero Beach area. This may be because this region has the optimal range of sediment sizes, hydrodynamics, and sea water temperature. For example, juvenile worms most often use small, dark grains of heavy minerals, while adults tend to use larger, light-colored sand grains (Kirtley, 1966; Eckelbarger, 1976). In Stuart, McCarthy (2008) has observed the percentage of total intertidal worm reef occupying the hardbottom at Bathtub Reef to vary between <10% and >45% during his 6-year study (**Figure 4.6**). Northern limits of *P. lapidosa* may be controlled by the cooler sea water temperatures that occur towards Cape Canaveral. Eckelbarger (1976) observed significantly higher mortality (LD_{50}) of *P. lapidosa* at temperatures below 15.5ºC and above 29.5ºC. Temperatures to the north of St. Lucie County can be as low as 7ºC (Smith, 1981). To the south, McCarthy et al. (2008) suggests that *P. lapidosa* may have lower abundance in south Florida and throughout most of the Caribbean because of lack of availability of small sediment sizes for new recruits to build tubes.

Figure 4.4. Close up of the anterior tube of an individual *Phragmatopoma lapidosa* (*caudata*). *Photo by D. McCarthy*.

Figure 4.5. Honeycomb structure created by thousands of *Phragmatopoma lapidosa* (*caudata*). *Photo by D. McCarthy*.

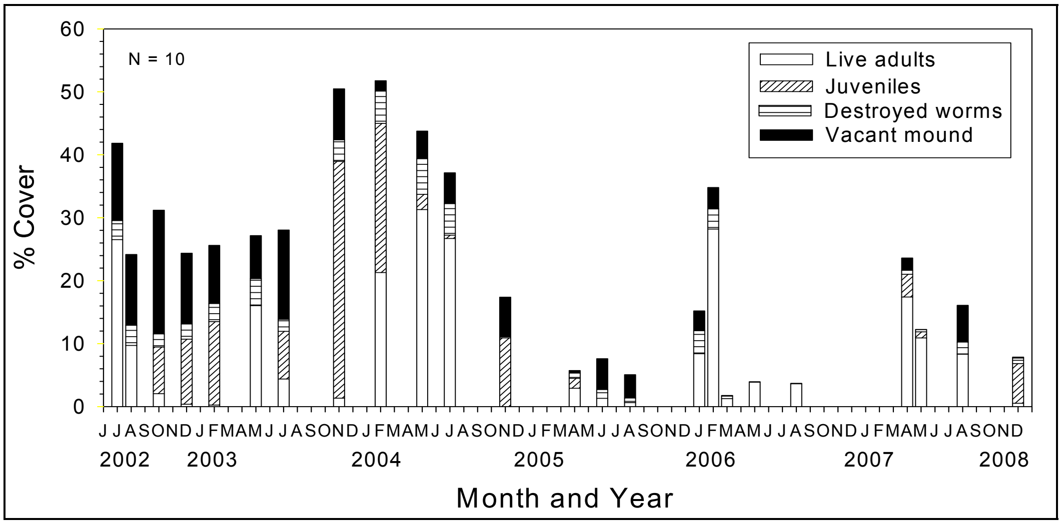


Figure 4.6. Monthly mean percentage cover of live adults, juveniles, destroyed worms, and vacant mounds for *Phragmatopoma lapidosa* on Bathtub Reef, Stuart, Martin County, Florida (McCarthy, 2008).

4.2.1.3 Reproduction and Life History

There is a wide range of reproductive and life history strategies for the polychaetes that have been identified along the east Florida coast. Most polychaetes become reproductive within a year of settlement and probably do not live more than 3 years (Giangrande, 1997). They are primarily known to reproduce sexually and have external fertilization; however, there is little known about seasonal spawning patterns of polychaetes in the study region. Among polychaetes in general, some spawn throughout the year, while others are seasonal reproducers. Regardless, most produce trochophore larvae that live in the plankton from weeks to months, depending on the species (Pernet et al., 2002). Consequently, larval dispersal varies based on species (Giangrande, 1997). Very little is known about seasonal recruitment patterns for most polychaetes along the east Florida coast.

Like many polychaetes, *P. lapidosa* are dioecious worms that externally spawn gametes into the water, where fertilization results in larvae that drift in the plankton for 2 to 20 weeks (Eckelbarger, 1976; Pawlik and Mense, 1994). Laboratory studies (Pawlik et al., 1991; McCarthy et al., 2002) suggest that competent larvae position themselves deep in the water column and consequently may be more likely to be transported inshore during seaward-directed winds that result in near-bottom return flow. This larval behavior may also serve to limit dispersal among *P. lapidosa* populations within its rather large range. A molecular study by Drake et al. (2007) suggested that *P. lapidosa* sampled in Florida (Miami) and those sampled in the Caribbean (Puerto Rico and Virgin Islands) may be two distinct populations. Combined, these data support that *P. lapidosa* may have limited dispersal along the Florida coast. Future research is needed to establish whether there are important Florida populations that provide larvae to other Florida populations.

It has been well documented that *P. lapidosa* require hard substrates for settlement and will repeatedly “test” substrates before settling on the preferred one (Eckelbarger, 1976; Pawlik, 1988). Behavioral preferences for moderate amounts of current have been quantified in laboratory studies with *P. californica* (Pawlik et al., 1991; Pawlik and Butman, 1993). Further, it is well known that *P. lapidosa* often settle and metamorphose in response to contact with the tubes of adult worms (Eckelbarger, 1976; Krueger, 1976). Chromatographic analysis of the organic content of the tubes of the closely related *Phragmatopoma californica* revealed that a mixture of free fatty acids was responsible for inducing settlement (Pawlik, 1986). Additionally, laboratory and field experiments by Jensen and Morse (1990) indicated that *P. californica* larvae also respond to butylated hydroxytoluene (BHT), which they suggest mimics the activity of an unidentified, cross-linked dihydroxyphenylalanine residue used to construct the tubes. Laboratory larval settlement responses of *P. californica* have been found to be identical to those of *P. lapidosa* (Pawlik, 1988).

Recruitment occurs throughout most of the year for *P. lapidosa* but peaks during fall and winter (McCarthy, 2001). Among five intertidal locations along the Florida coast (Satellite Beach, Stuart, Coral Cove, Palm Beach, Boynton Beach), it appears that *P. lapidosa* recruit at the highest levels in Stuart, followed by Satellite Beach. McCarthy (2001) suggested that subtidal recruitment may be highest during seasons with increased wave activity. Overall, worm reefs appear to go through predictable patterns of annual change (McCarthy, 2001). These changes include high recruitment in early autumn through winter, rapid reef growth (approximately 0.5 cm/day) resulting in maximum structure in spring and summer (**Figures 4.7** and **4.8**), and decay by early autumn (**Figure 4.9**). McCarthy (2001) noted that sublethal disturbance may cue spawning from mid-winter through early fall. Based on the annual cycle of reef growth and decline, it seems that physical processes rather than predator/prey relationships within the food web are more likely to limit the abundance and diversity of flora and fauna on worm reefs (Applied Biology, Inc., 1979; McCarthy, 2001). When these data are integrated with those of Lindeman (1997a), they reveal important links between the seasonal cycle of sabellariid reef expansion and degradation, and the occupation of those reefs by juvenile and adult organisms.

Figure 4.7. *Phragmatopoma lapidosa* (*caudata*) recruits recovered after 5 weeks deployment in intertidal hardbottom off Boynton Beach, Florida. Recruitment plates were 9 cm by 9 cm. *Photo by D. McCarthy*.

Figure 4.8. High worm reef cover and wave activity at groynes at Palm Beach, Florida. *Photo by D. McCarthy*.

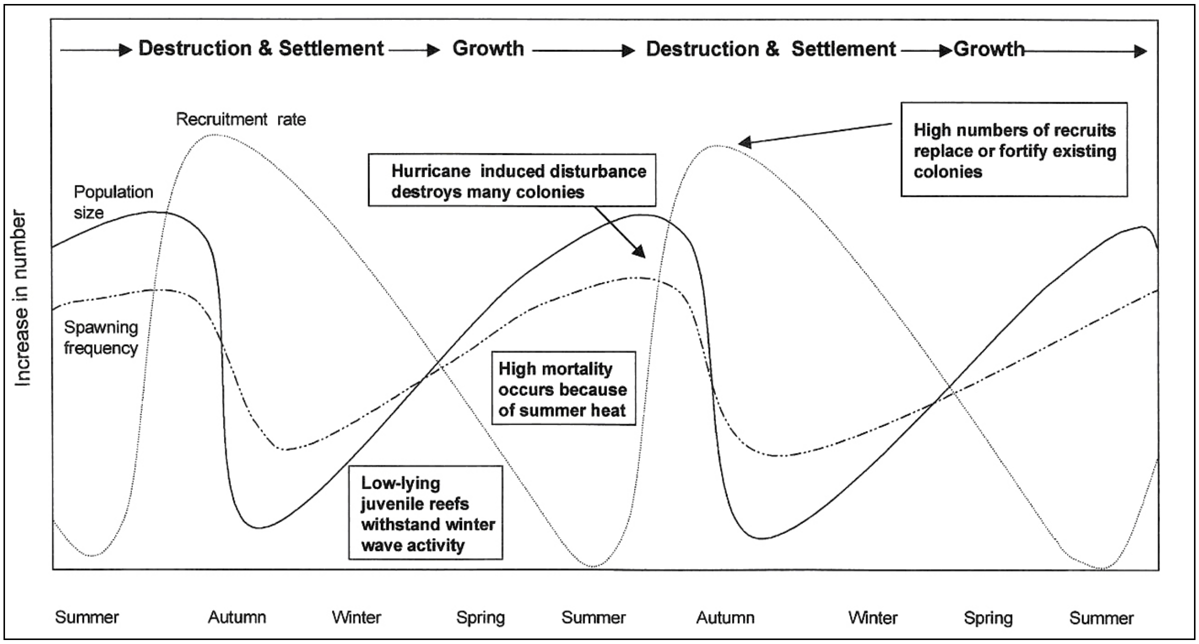


Figure 4.9. Seasonal reproductive and life history trends of *Phragmatopoma lapidosa* in the Boynton Beach area as illustrated by McCarthy (2001).

McCarthy (2001) studied the recruitment of sessile organisms in the intertidal and subtidal (3 to 4 m) zones at Boynton Beach, Florida from June 1997 to January 2000. He reported 23 sessile species recruiting to his settlement plates, with *P. lapidosa* being most commonly encountered (**Table 4.1**). The recruitment rate of some 7 to 11 species m^{-2} d^{-1} occurred in both zones and was highest in summer and early fall. Although recruitment generally occurred at both depth zones, it was higher in the subtidal zone compared to the intertidal zone. McCarthy (2001) suggested that while high numbers of species may recruit into these habitats, most probably do not survive to adulthood, possibly due to a combination of factors. First, there was likely high mortality of recruits that could not tolerate frequently-occurring physical factors such as sand scouring and smothering. Second, high rates of *P. lapidosa* recruitment were observed to limit growth of sessile organisms, often growing over them. Finally, he also suggested that predation may not be as important in explaining recruit mortality in these two zones as the two previously-mentioned reasons.

4.2.2 Anthozoans

4.2.2.1 Diversity and Trophic Function

Anthozoans are fairly abundant and diverse (54 species identified) along all NHBs from the east Florida coast (**Appendix B**, **Table B.1**). Most species provide shelter for various organisms via their external features. A number of invertebrates and fishes take refuge in the shelter created by corals. Consequently, when abundant, they are very important shelter-enhancing invertebrates that contribute to increased local biodiversity. For example, in the Florida Keys, 517 fish and 2,059 invertebrate species have been identified in coral reef habitats (Causey et al., 2002). Further, anthozoans such as gorgonians and some hard corals can serve as food sources for reef residents such as gastropods, bristle worms, and parrotfish (Birkland, 1974; Kinzie, 1974; Birkland and Gregory, 1975; Preston and Preston, 1975; Harvell and Suchanek, 1983; Lasker, 1985; Rotjan and Lewis, 2005) but are not likely to be very important on a large scale (O'Neal and Pawlik, 2002).

Table 4.1. Species recruitment into intertidal (I) and subtidal (S) habitats from June 1997 through January 2000 in Boynton Beach, Florida. Light blue areas indicate simultaneous settlement into intertidal and subtidal habitats. Pink shading indicates habitat lost to sand cover (From: McCarthy, 2001).

Species	1997										1998														1999												2000	
	Jun		Jul		Aug		Sep		Nov		Jan		Feb		Apr		Jun		Jul		Sep		Oct		Jan		Mar		May		Jun		Aug		Sep		Jan	
Zone	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S
Anomia simplex	a	p	p	p	a	a	a	p	a	a	a	a	a	a	a	p	a	p	a	p	a	p	a	p	a	p	a	a	a	a	a	a	a	a	a	a	a	a
Pinctada imbricata	a	p	p	p	p	p	p	p	a	p	a	a	a	a	p	p	a	p	p	p	p	p	a	p	a	p	a	p	p	a	a	a	p	a	p	a	a	a
Hipporina americana	a	p	a	p	a	a	p	p	a	a	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	a	a	a	a	a	a	a	a	a
Canopeum reticulum	a	p	a	a	a	p	p	p	p	p	a	p	a	p	p	p	a	p	a	a	a	p	p	p	a	p	a	p	a	a	a	a	a	a	p	a	p	a
Balanus eburneus	a	a	a	p	a	a	p	p	p	a	a	p	a	p	a	a	a	a	a	a	a	p	a	p	a	a	a	a	a	a	a	a	p	a	p	a	a	a
Chthalamus fragilis	p	a	p	a	p	a	p	a	p	p	a	a	a	p	a	a	p	a	p	p	p	a	p	a	a	a	a	p	a	a	p	a	p	a	a	a	a	a
Cliona sp.	a	a	a	a	a	a	a	a	p	p	a	p	a	p	a	p	p	p	a	p	p	p	a	p	a	p	a	a	a	a	a	a	a	a	a	a	a	a
Phragmatopoma lapidosa	a	a	p	a	p	a	p	a	p	a	p	p	p	p	p	p	p	a	a	a	p	p	p	p	p	p	p	p	p	a	p	a	p	a	p	a	p	a
Watersipora subviodea	a	p	a	p	a	a	a	a	a	p	a	p	a	p	p	p	a	p	a	p	a	a	a	p	p	p	p	p	p	a	p	a	a	a	a	a	p	a
Didemnum sp.	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	a	p	p	p	a	p	a	a	a	a	a	a	a	a	a	a
Diplosoma sp.	a	p	a	p	a	p	a	p	p	p	p	p	p	p	p	p	p	p	a	p	a	p	a	p	p	p	p	p	a	a	a	a	a	a	p	a	p	a
Balanus amphitrite	a	a	a	a	a	a	p	a	a	p	a	p	a	a	a	p	a	p	a	p	a	p	a	p	a	p	a	a	p	a	a	a	a	a	a	a	a	a
Brachiodontes citrinus	a	p	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Phallusia nigra	a	p	a	a	a	a	a	p	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Botryllus sp.	a	a	a	a	a	a	p	p	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Bugula sp.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Hydroides dianthus	a	p	a	p	a	a	a	a	a	a	a	p	a	a	a	p	a	a	a	p	a	p	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Terebellid sp.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Actinia bermudensis	a	p	a	a	a	a	a	a	p	p	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Siderastrea radians	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Unknown blue sponge	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Vermicularia sp.	a	a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Turbicellaora avicularis			a	a	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a	p	a	p	a	a	a	p	a	a	a	a	a	a	a	a	a	a	a	a
Species number at each habitat	1	11	4	8	4	4	8	9	8	9	2	10	2	9	6	13	5	9	2	12	4	14	3	14	4	11	3	9	4	0	3	0	4	0	5	0	4	0
Species number at both	0		2		1		5		5		2		2		5		2		2		3		2		4		3		0		0		0		0		0	
Total see number	12		10		8		12		12		10		9		14		12		12		15		15		11		9		4		3		4		5		4	

a = absent; p = present.
Subtidal species *Cthalamus fragilis* was more intertidal than subtitled and experienced significant, predation; *Balanus eburneus* recruited to both intertidal and subtital; Upper intertidal species (*Vermicularia* sp.) and intertidal.

4.2.2.2 Latitudinal and Cross-shelf Distribution

The diversity and abundance of anthozoans changes dramatically with latitude, and to a lesser extent with depth, along the east Florida coast NHBs. Throughout tidal pools in the intertidal and very shallow subtidal zones along the entire coast, there are few of these animals present. The species that can be encountered include the starlet coral *Siderastrea* spp. (**Figure 4.10**), two species of zoanthids (*Palythoa caribaeorum* and *Zoanthus pulchellus*) (**Figure 4.11**), and several species of solitary anemones (*Bunodosoma caveranta*, *Actinia bermudnesis*, *Diadumene leucolena*). These are species that generally have a higher tolerance for the fluctuations in salinity and temperature that occur in these habitats (Muthiga and Szmant, 1987; Lirman et al., 2002). *P. caribaeorum* is also known to be a very fast growing highly aggressive competitor for space among coral species (Suchanek and Green, 1981). Progressing into the shallow subtidal area these species probably are more abundant, although there are no available data to support this statement. Generally, anthozoans are not very abundant within the 0 to 4 m depth range.

Figure 4.10. An intertidal colony of the scleractinian *Siderastrea* sp. in Palm Beach, Florida. *Photo by D. McCarthy.*

Figure 4.11. The zooanthid *Zoanthus pulchellus* and various other sessile invertebrates (and green algae) on intertidal hardbottom in Palm Beach, Florida. *Photo by D. McCarthy.*

Anthozoan diversity in the subtidal hardbottom changes most significantly with latitude. However, there are very few studies of anthozoan communities in water depths less than 4 m. North of Martin County, there are generally fewer hard corals. Besides small *Siderastrea* spp., the most frequently encountered hard corals are the *Oculina* species (*O. varicosa* and *O. diffusa*). The latter two species become fairly abundant in water depths in excess of 6 m (Reed et al., 1982; D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). However, there are occasional occurrences of *Cladocora arbuscula* and grouped polyps of *Phyllangia americana* and *Astrangia* spp. (Brooke and Young, 2005). It is in the deeper NHB that *Oculina* spp. are likely most important in contributing significant shelter for invertebrate and vertebrate species (Reed, 1982; Reed et al., 1982; Reed and Mikkelsen, 1987). The shelter value of the much deeper (70 to 152 m) *O. varicosa* reefs has been recognized and has resulted in their being listed as an HAPC by the SAFMC (NMFS, 2007). In terms of soft corals within NHB, two species of gorgonians (*Leptogorgia virgulata* and *Leptogorgia hebes*) and one species of telestacean (*Carijoa* [*Telesto*] *riisei*) are fairly common in the 4 to 6 m depth range. Progressing southward, diversity and abundance of anthozoans, particularly scleractinians, increase on subtidal hardbottoms (Southeast Florida Coral Reef Evaluation and Monitoring Project [SFCREMP], 2007; J. Beal, Florida Fish and Wildlife Conservation Commission [FWC], pers. comm.). In Martin County, the St. Lucie Inlet Reef appears to be the northernmost extent of several of the reef-building corals (i.e., *Diploria* and *Montastraea* spp.) that are known important biodiversity contributors within the Caribbean region. Additionally, a high number of octocoral species (~15 spp; J. Beal, FWC, pers. comm.) are encountered at this latitude. Consequently, this reef was recently designated for protection as part of the St. Lucie Inlet Preserve State Park because of the diversity and abundance of corals and other shelter-enhancing invertebrate species (polychaetes, sponges, tunicates, algae) present.

Both diversity and abundance of stony coral species on NHB increase southward from Martin County (**Appendix B, Table B.1**; SFCREMP, 2007). A synthesis of available reports revealed that 7, 22, 24, and 32 stony coral species were identified in NHB in St. Lucie, Martin, Palm Beach, and Broward Counties, respectively. The SFCREMP (which encompasses sites in Martin, Palm Beach, Broward, and Dade Counties) also documented an increase in stony coral diversity towards Dade County, although observed species numbers are low because of the scientific approach used. In their study, the highest diversity of corals among shallower sites (17 to 19 species) occurred in Dade and Broward Counties compared to Palm Beach and Martin Counties (8 to 9 species) (SFCREMP, 2007). They also observed that seven species of stony corals (*Dichocoenia stokesii*, *Diploria clivosa*, *Millepora alcicornis*, *Montastraea cavernosa*, *Porites astreoides*, *Siderastrea siderea*, and *Solenastrea bournoni*) were present in all four counties from Martin to Dade County (SECREMP, 2007). However, it should be noted that in order to compare all four locations, only the shallowest sites (8 m in Palm Beach, Broward, and Dade; 5 m in Martin County) were used, which is outside the designated NHB depth range. In shallower hard bottoms (<7 m), Prekel at al. (2007, 2008) and Coastal Planning & Engineering, Inc. (2006) recorded 19 stony coral species on NHB in Broward County, observing that *Siderastrea siderea* was most common (81.3% of observations of corals), followed by *Porites porites*, *Dichocoenia stokesii, Phyllangia americana*, and *Porites astreoides* (accounting for between 1.1% to 4.9% of observations). Also, in Broward County, hardbottom areas have been observed at the 4 m depth and deeper, with fairly high percent cover of the scleractinian *Acropora cervicornis* (Moyer et al., 2003; Vargas-Angel et al., 2003; SFCREMP, 2007). The tree-like morphology of this coral offers important shelter value to motile invertebrates and vertebrates. Consequently, in 2006 this species (along with *A. palmata*) was designated by the National Oceanic and Atmospheric Administration (NOAA) as threatened under the ESA because of its significant decline and subsequent risk of extinction within this Florida-Caribbean region.

The diversity and abundance of octocoral species on NHB likely increases southward from St. Lucie County, although there is not a great amount of data that clearly identifies whether species were observed within NHB or deeper (**Appendix B, Table B.1**). In this study, a synthesis of available reports revealed that 3, 12, 14, and 14 octocoral species were identified in NHB in St. Lucie, Martin, Palm Beach, and Broward Counties, respectively. However, over 40 octocoral species have been identified in hard bottom habitats up to 8 m in depth from Palm Beach to Dade Counties (Jaap, 1984; Vare, 1991).

4.2.2.3 Reproduction and Life History

Sexual vs. Asexual Reproduction

There is high diversity in reproductive methods among anthozoan species found along east Florida. Most species can reproduce and/or propagate both sexually and asexually (see Fautin, 2002 for a review of cnidarian reproduction). However, the relative importance of these forms of reproduction in maintaining population numbers varies with the species and sometimes is unclear. Asexual reproduction via longitudinal fission appears to be the dominant form of vegetative proliferation among sea anemones (Shick, 1991). This may not be important for most colonial scleractinians relative to sexual reproduction, but it has been suggested to be the dominant form of reproduction for *Acropora cervicornis*, whereby propagation occurs when branches break off during a storm and new colonies form (NOAA Fisheries, 2008). There is less information available on gorgonians, but it has been suggested that *Plexaura* may reproduce via parthenogenesis, whereby eggs develop without the aid of fertilization (Brazeau and Lasker, 1989). This species may also asexually reproduce when branches break during storms (Lasker, 1984).

Seasonal Spawning Patterns

There have not been many studies documenting seasonal reproductive patterns for anthozoans along the Florida coast, but it is likely that many species spawn at the same times as their Caribbean counterparts. Some species are known to externally fertilize, while others brood their larvae. A number of the scleractinian species in the region have been noted to spawn during late summer. To the north, *Oculina* spp. spawns during late summer, producing planula that can settle in 3 weeks (Brooke and Young, 2005). While not confirmed for Florida, *Leptogorgia* spp. and *Pseudoplexaura porosa* may spawn seasonally during this time period as well (Beasley et al., 1997; Kapela and Lasker, 1999). In southeast Florida, the reef building corals *Montastraea annularis*, *M. cavernosa*, *Acropora cervicornis*, and *A. palmata* (Szmant-Froelich, 1986; Vargas-Angel et al., 2006) also spawn during this time period. In Martin County, it has been suggested that *Montastraea* and *Diploria* colonies do not spawn because they are at the northern limit of their distribution and do not have the energetic reserves to produce gametes (J. Beal, FWC, pers. comm.).

In contrast to seasonal spawning, some anthozoans may spawn for most of the year. *Siderastrea radians* and *Porites astreoides* brood larvae during an extended season and reach the ability to reproduce at smaller sizes than species such as *Diploria* spp. and *M. cavernosa* (Soong, 1991, 1993). *S. radians* may be encountered throughout the east Florida coast in intertidal and shallow subtidal hardbottoms because of its strong tolerances to environmental fluctuations and continuous reproductive capability, which allow for it to be able to take advantage of available space created by natural and anthropogenic disturbances throughout the year.

Larval Transport and Recruitment

Little is known about larval transport and recruitment for anthozoans along the east Florida coast. The amount of time that larvae can be in the plankton varies from days to months. Some species of zoanthids have larvae that are well-known for being far dispersed in the plankton. However, while they may survive there for as long as 22 weeks, their ability to metamorphose may be lost after 11 weeks (Ryland, 1997). Brooke (2002) suggests that larvae of the ivory bush coral (*Oculina varicosa*) not only have the potential to be transported between the deep reef tracts but may also contribute to nearshore shallow water populations during summer upwelling events. In contrast, the staghorn coral *Acropora cervicornis* likely has low dispersal and hence gene flow, which suggests that this endangered species require local source populations for their recovery (Vollmer and Palumbi, 2007).

Generally, the few studies of hardbottom recruitment along the east Florida coast have observed infrequent and sporadic seasonal recruitment of anthozoans. Yoshioka (1996) studied recruitment of several gorgonian species on the Atlantic coast of Panama, observing limited yet highly variable seasonal recruitment. Both Cummings (1994) and McCarthy (2001) observed seasonal recruitment of sessile invertebrates to hardbottoms (4 to 8 m depths) in southeast Florida and encountered only one scleractinian species (*S. radians*). McCarthy (2001) sampled plates frequently in Boynton Beach for ~2.5 years, encountering this species only once out of over 1,200 settlement plates sampled. Cummings (1994) additionally observed the anthozoans *Carijoa* (*Telesto*) *riisei*, *Bunodosoma granuliferum*, and *Palythoa mamillosa*, while McCarthy encountered only the actiniarian *Actinia bermudensis*. Consequently, it appears that anthozoan recruitment is low in these habitats and may not provide rapid recovery and/or maintenance of coral populations after natural or anthropogenic disturbance events. Such recovery may be further reduced by cyanobacteria and macroalgal blooms, which can prohibit coral recruitment and appear to be more frequent along the east Florida coast in recent years (Paul et al., 2005; Ritson-Williams et al., 2005; Kuffner et al., 2006).

4.2.3 Sponges

4.2.3.1 Diversity and Trophic Function

Sponges are fairly abundant and diverse (50 species identified) on all NHBs along the east Florida coast (**Appendix B**, **Table B.1**). Most species provide shelter for various organisms via internal spaces as well as their external features. Amphipods, crabs, shrimp, nemertines, polychaetes, molluscs, and brittle stars all take refuge in sponges (Wulff, 2006; D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Consequently, when abundant, sponges are important shelter-enhancing invertebrates that can contribute to increased local biodiversity. Sponges may also serve as an important food source for many of the angelfishes, filefishes, trunkfishes, cowfishes, and butterflyfishes that are particularly common in southeast Florida (Pawlik, 1998). As filter feeders, they also may be important in removing nutrients (e.g., carbon, nitrogen, oxygen) from the water column and thus significantly impact pelagic ecosystems (Peterson et al., 2007; see Bell, 2008 for a review). Finally, some sponges can have a detrimental effect. For instance, the rock-boring pionid (formerly clionid) species can aid in the fragmentation and disintegration of coral heads (Glynn, 1997; Zilberberg et al., 2006). The rate of this type of coral disturbance may be accelerated by heavy storms, hurricanes, and any other source of physical stress (Tunnicliffe, 1981; Highsmith, 1982; Rutzler, 2002). Such bioerosion by sponges results in the production of reef sediment, which can affect the structural integrity of coral (Rutzler, 1975; Glynn, 1997). Further, the proliferation of clionid sponges has been linked to organic pollution and temperature increases (Rose and Risk, 1985; Holmes, 1997; Rutzler, 2002). For example, Ward-Paige et al. (2005) suggested that sewage contamination in the Florida reef tract results in increases in bioeroding sponges that shift the carbonate balance from one of reef construction (accretion) to that of reef destruction (erosion).

4.2.3.2 Latitudinal and Cross-shelf Distribution

The diversity of sponges probably increases with latitude and depth along the NHBs along the east Florida coast. However, abundance patterns are unclear for most species, with little quantitative information being available for the 0 to 4 m depth range. Within the 5 to 8 m depth range, mean percent cover of sponges is highly variable, ranging between 0.14% and 10.29% in the survey areas (SFCREMP, 2007). Within the lower intertidal and shallow subtidal zones, the most conspicuous sponge is the rock-boring sponge *Pione lampa* (formerly *Cliona lampa*) (**Figure 4.12**). It probably continues on to deeper depths where other rock boring sponges such as *Pione delitrix* can be encountered. SFCREMP (2008) observed *P. delitrix* at the 5 to 8 m depth range for the four locations it studied along the east Florida coast. There were no latitudinal trends with this species, with total colony areas varying between 3.2 and 32.16 cm^2/m^2.

Figure 4.12. An intertidal colony of the rock-boring sponge *Pione (Cliona) lampa* in Stuart, Florida.
Photo by D. McCarthy.

4.2.3.3 Reproduction and Life History

Sponges can reproduce sexually and asexually, although the relative importance of these strategies in population maintenance is often unclear. Asexual reproduction (i.e., fragmentation, budding) may be important for a number of the shallower sponge species because of the high frequency of lethal and sublethal disturbances that result from high wave energy and sand scouring. Some more vertically-oriented sponges common off east Florida such as *Aplysina* spp. (**Figure 4.13**) and *Iotrochota birotulata* may propagate exclusively by asexual fragmentation (Wulff, 1991). Schönberg (2002) suggests that *P. lampa* can produce gemmules (normally found in freshwater species) that can resist sand burial, heat, and desiccation and ensure survival in these harsh habitats. Additionally, gemmules may be scattered and dispersed during periods of increased wave activity along the coast.

Sexually, fertilization in most sponges is internal, with embryos being either brooded or shed immediately into the water column. In both cases, the resultant larvae either swim in the water column or crawl away on the substrate (Maldonado and Bergquist, 2002). For species with planktonic larvae, most appear to be short-lived lecithotrophs living in the plankton from a few hours to several days (Lindquist et al., 1997; Bergquist, 2002).

Figure 4.13. The demosponge *Aplysina fistularia* on hardbottom off Palm Beach, Florida. *Photo by D. McCarthy.*

There is very little information on seasonal spawning, dispersal, and recruitment patterns of sponges along the Florida coast. Cummings (1994) often encountered the rock-boring sponge *Pione* (formerly *Cliona*) *lampa* during her recruitment study in 2 m of water off Boca Raton. She less frequently encountered *Chondrilla nucula*, *Spongia* sp., *Demapsamma* sp., and one unknown species.

4.2.4 Hydrozoans

4.2.4.1 Diversity and Trophic Function

Various hydrozoans can be abundant along all NHBs along the east Florida coast but are generally lower in diversity (12 species identified) compared to some of the other sessile invertebrates discussed (**Appendix B**, **Table B.1**; **Figure 4.14**). Some species may provide limited shelter for some small organisms, but most probably do not. With their relatively small biomass and nematocyst defense capability, it is unlikely, that they are an important part of the food web, although this is not known.

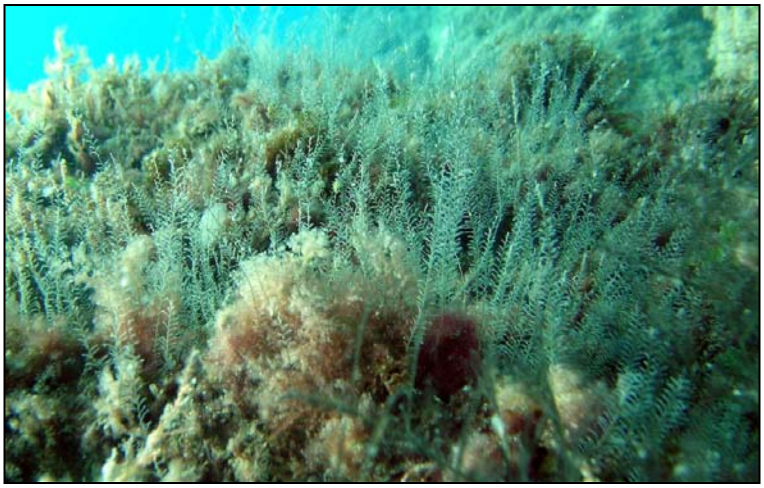


Figure 4.14. Colonial hydrozoans on a mitigation reef in Juno Beach, Florida. *Photo by D. McCarthy.*

4.2.4.2 Latitudinal and Cross-shelf Distribution

It is unknown how the diversity and abundance of hydrozoans change with latitude and depth along east Florida coast NHBs. SFCREMP (2007) encountered the fire coral *Millepora alcicornis* at a depth of 5 m at the St. Lucie Reef but not at any of the other shallower water sites (all other sites were ~8 m) in southeast Florida. However, *M. alcicornis* was fairly abundant at deeper sites surveyed. There are few known hydroid species within the intertidal zone, but generally several that are common within the shallow subtidal zone. Some of the more commonly occurring hydroid species along the coast include *Thyroscyphus ramosus*, *Campanularia* sp., *Eudendrium ramosum*, *Lytocarpus philipinus*, *Pennaria* sp., and *Sertularella* sp.

4.2.4.3 Reproduction and Life History

Hydrozoans are primarily colonial organisms that have life cycles that may include polyps, medusae, or both. Reproduction can occur via asexual and/or sexual reproduction. Generally, clonal reproduction by budding is most common among the solitary A-form polyps (Ruppert et al., 2004). Offspring that may drift in the plankton (or creep along the sea floor bottom) include asexually produced medusae or planula larvae that are formed via sexual reproduction (external or internal fertilization) of medusae or polyps (Ruppert et al., 2004). Hydrozoan larvae are generally short-lived in the plankton. For instance, *Mitrocomella polydiademata* are ready to settle 3 to 5 days after fertilization (Martin and Koss, 2002). Consequently, there probably is very limited dispersal among offspring from their parents.

There is very little information on seasonal spawning and recruitment patterns of hydrozoans along the Florida coast. If local species are like temperate hydrozoans, they may reproduce asexually throughout the year but sexually on a seasonal basis (Coma et al., 1996). Cummings (1994) observed recruitment of *Thyroscyphus marginatus*, *Eudendrium* spp., *Lytocarpus philipinus*, *Pennaria* sp., and *Gymnangium* spp. throughout the year. In contrast, Walton Smith et al. (1950) observed very low recruitment of hydroids in the Key Biscayne area. The most common identifiable hydroid in that study was *Tubularia* sp.

4.2.5 Tunicates and Bryozoans

4.2.5.1 Diversity and Trophic Function

Tunicates and bryozoans are fairly abundant and diverse (93 bryozoan species) along all NHBs along the east Florida coast (**Appendix B**, **Table B.1**). Most occur in colonies (branching or encrusting forms), although there are some solitary forms of tunicates that are abundant (i.e., *Phallusia*, *Mogula*). Both groups are particularly abundant under ledges and within crevices. Most species probably do not provide very large shelter enhancement to the habitat, but some do provide shelter to smaller species such as amphipods, crabs, shrimp, nemertines, polychaetes, molluscs, and brittle stars that may take refuge along the edge of colonies or within some branching forms (i.e., *Bugula* spp.) (Voultsiadou et al., 2007; D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). It is unlikely that many of the tunicates are important in the diet for any hardbottom predator, as many produce secondary metabolites that deter at least fish predators (Pisut and Pawlik, 2002; Odate and Pawlik, 2007). Bryozoans may be more susceptible to predation, although they have morphological defenses to deter predators as well (Harvell, 1992; Ruppert et al., 2004).

4.2.5.2 Latitudinal and Cross-shelf Distribution

There is not a great deal of information available on how the diversity and abundance of tunicates and bryozoans change with latitude and depth along the east Florida coast NHBs. The most conspicuous animals of these types found in tide pools of the lower intertidal zones and shallow subtidal habitats are the colonial tunicates *Botryllus planus* (**Figure 4.15**), *Botrylloides nigrum*, *Didemnum* spp. (probably most common), and the bryozoan *Watersipora subvoidea*. Progressing into the shallow subtidal area, diversity may slightly increase but abundance appears to remain fairly low. Essentially all bryozoans remain within crevices and under ledges, while several species of tunicate can be found on top of hardbottoms. Some common tunicate species encountered subtidally include *Eudistoma* sp., *Diplostoma* sp., *Distaplia* sp., *Mogula* sp., and *Phallusia* (*Ascidia*) *niagra*, with the latter species clearly more abundant from St. Lucie southward (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.).

4.2.5.3 Reproduction and Life History

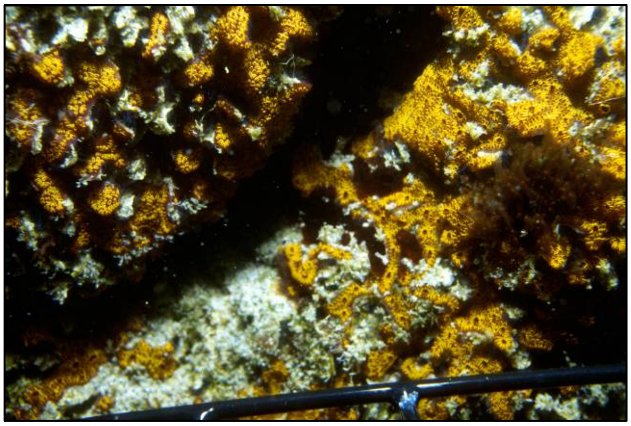


Figure 4.15. *Botryllus* sp. overgrowing dead worm rock at Boynton Beach, Florida. *Photo by D. McCarthy.*

Most tunicates and bryozoans along the east Florida coast have colonial forms and can reproduce asexually and sexually. Asexually, most tunicates and bryozoans proliferate via budding (Ruppert et al., 2004). In the case of bryozoans, their success at occupying space may be largely related to their capacity for colonial growth via budding (Seed and Hughes, 1992), and this may be the case for tunicates as well. Sexually, individuals in both groups are hermaphrodites that, depending on the species, fertilize internally or externally. While a few families of tunicates have direct development, in most cases lecithotrophic larvae are produced that live in the plankton for a few minutes to a few hours (Clooney et al., 2002). Consequently, their dispersal distance from parent populations should not be very great. Bryozoan larvae may be either planktotrophic or lecithotrophic, but also have a very short planktonic period (Temkin and Zimmer, 2002).

There is very little available information on seasonal spawning and recruitment patterns of tunicates and bryozoans in the study region. In Boynton Beach, the colonial ascidians *Didemnum* sp. and *Diplosoma* sp. and the bryozoans *Canopeum reticulum* and *Watersipora subzoidea* appear to recruit throughout most of the year (McCarthy, 2001). In the same study, *Bugula* sp., *Phallusia niagra*, and *Botryllus* sp. sporadically recruited just a few times during the 2.8-year study.

4.2.6 Molluscs (Sessile)

4.2.6.1 Diversity and Trophic Function

A number of mollusc species occur on NHBs along the east Florida coast (**Tables 4.1** to **4.4**; **Appendix B**, **Table B.1**). The sessile forms include primarily bivalves but also two species of vermetid gastropods. Most bivalves are found under ledges and within crevices in somewhat low abundance. The vermetid gastropods occur primarily in the upper intertidal zone (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Both groups of molluscs can contribute to enhancing shelter on hardbottoms and may benefit generally smaller invertebrates (i.e., sipunculans, xanthid crabs, shrimp) and possibly a few small or juvenile fish species. They are likely preyed on by invertebrates and fishes, but no data are available on their trophic importance along the east Florida coast.

4.2.6.2 Latitudinal and Cross-shelf Distribution

It is unclear how the diversity and abundance of molluscs change with latitude and depth along the NHBs along the east Florida coast. The most conspicuous molluscs are found in the upper intertidal zones. These are the vermetid gastropod *Petaloconchus nigricans* and *P. varians*, which can form vast networks of tubes (10 to 15 cm thickness) that provide significant shelter for a number of invertebrates (xanthid crabs, sipunculans, polychaetes, and nemertines) and fishes (blennies, gobies, toadfishes). Eight species of bivalves occur at the intertidal worm reef at Stuart: *Barbatia dominensis*, *Isognomon radiatus*, *Musculus lateralis*, *Ostrea equestris*, *Sphenia antillensis*, *Anomia* sp., *Pteria* sp., and *Pinctada imbricata* (McCarthy, 2008). To the north in St. Lucie County, Reed and Mikkelsen (1987) identified 40 bivalve species associated with the scleractinian coral *Oculina varicosa* at 5.5 m depth. Cummings (1994) and McCarthy (2001) combined identified *Isognomon radiatus*, *Ostrea equestris*, *Anomia simplex*, *Pteria* sp., *Brachiodontes citrinus*, and *Pinctada imbricata* on settlement plates in the 4 to 8 m depth range.

Table 4.2. Abundance of associated macroinvertebrates collected from sabellariid worm reef (Stations 9 and 10 combined) at the St. Lucie Power Plant from April 1976 through April 1979 (From: Applied Biology, Inc., 1979).

Species	1976			1977				1978				1979	
	Apr	Jul	Oct	Jan	Apr	Jul	Oct	Jan	Apr	Jul	Oct	Jan	Apr
MOLLUSCA													
Gastropoda													
Anachis avara						75	5		3	1			
Anachis floridana				2		15	16	1		11			
Anachis lafresnayi						1				1			
Astraea tuber						1				1			
Barleeia tincta						26				1			
Cypraea sp.												1	
Erato maugeriae							1						
Fissurella barbadensis					1	2							
Lamellaria perspicua												1	2
Lucapinella limatula						2							
Mitrella argus				4		36	9					5	
Nudibranchia sp.							1						
Phidiana ?lynceus									1				2
Pisania tinctus						1				1			
Thais haemastoma floridana		1			1								
Thais rustica												3	
Tricolia affinis pterocladica						1							
Bivalvia													
Barbatia domingensis													1
Isognomon radiatus						1							
Musculus lateralis						1							
Ostrea equestris						4							
Sphenia antillensis			1		1				1				1
ARTHROPODA													
Pycnogonida													
Tanystylum sp.							2						
Stomatopoda													
Gonodactylus bredini						1							1
Gonodactylus sp.													
Isopoda													
Accalathura crenulata													1
Anthuridae sp.											1		
Asellota sp.							1						
Dynamenella sp.			1			1			1	2			
Excorallana sexticornis		11		5	10	51	9	14	5	56	4		42
Mesanthura decorata		1	4		2	2			3	6			
Paranthura infundibulata		1	1		2	1		1	5				
Sphaeroma walkeri		6	1	27	70	12	1	3	4	41	7		18

Table 4.3. Molluscs recorded during a survey of a newly constructed artificial reef structure in the nearshore (~8 m depth) area off Boca Raton, Florida (Adapted from: Cummings, 1994). ● denotes species presence.

Scientific Name	December 1988-January 1989	July 1989-August 1989	July 1990
Class Gastropoda			
Order Neogastropoda			
Anachis floridana		●	●
Thais rustica	●	●	●
Iselica fenestrata	●		
Class Bivalvia			
Order Pterioida			
Isognomon radiatus	●	●	●
Ostrea equestris	●	●	
Ostrea sp.			●
Pinctada imbricata	●		

Table 4.4. Data summary for molluscs collected from 41 colonies of the scleractinian coral *Oculina varicosa* on four reefs off the east Florida coast (From: Reed and Mikkelsen, 1987). Numbers in parentheses = total species. Density = number of individuals/100 g coral dry weight. Skeletal volume determined by water displacement. Percent dead coral based on dry weight.

	Water Depth			
	6 m	27 m	42 m	80 m
Molluscs				
Number of individuals	2,027	61	594	2,450
Average number of individuals/coral	145	15	46	245
Average density	29.3	9.1	3.8	14.7
Gastropod species	(155) 59	9	67	89
Bivalve species	(68) 40	15	24	46
Total species	(230) 101	25	91	140
Mean number of species/coral	18	9	18	42
H' Diversity	2.97	4.24	5.13	4.79
H (Brillouin)	2.87	3.55	4.81	4.66
E (Equitability)	0.44	0.92	0.79	0.67
DI (Dominance)	54.4	13.1	15.8	23.9
Corals				
Number of coral samples	14	4	13	10
Colony dry weight (g)	196-1,207	147-204	526-2,715	279-2,658
Skeletal volume (mL)	97-723	53-110	260-1,431	149-1,544
Percent colony dead	0-62.8	5.7-40.0	3.4-43.2	27.5-87.9

4.2.6.3 Reproduction and Life History

Vermetid gastropods and bivalves are sexually reproducing invertebrates. Vermetid gastropods are protandrous hermaphrodites that internally fertilize, producing lecithotrophic larvae with a short, free-swimming/crawling phase. Bivalves usually have separate sexes and either spawn externally or brood larvae. Their embryos may end up in the plankton, while others may directly develop (Zardus and Martel, 2002). However, most bivalves produce veliger larvae that swim in the plankton for 3 to 4 weeks. Depending on the species, larvae can be planktotrophic or lecithotrophic.

Little is known on seasonal spawning and recruitment patterns of these species along the Florida coast. In Boynton Beach, *Vermicularia* sp. and *Brachiodontes* sp. recruitment appears highly sporadic (McCarthy, 2001). In the same area, *Pinctada imbricata* recruited seasonally, with peak recruitment occurring during the fall (McCarthy, 2001). Larvae from bivalves generally are longer-lived in the plankton than many invertebrates and may have somewhat longer dispersal among offspring from their parents.

4.2.7 Barnacles

4.2.7.1 Diversity and Trophic Function

Barnacles are encountered throughout intertidal, and to a lesser extent, subtidal hardbottoms along the east Florida coast. There are nine species found along the coast (**Appendix B**, **Table B.1**). They are active suspension feeders that use cirri to move water and feed. When in large numbers, they can provide hardbottom shelter enhancement (usually in the upper intertidal zone) and serve as a food source for some fishes (i.e., sheepshead) and some larger decapods (stone crabs) and gastropods (oyster drills). However, they are not likely to be very important on a large scale due to their generally low abundance.

4.2.7.2 Latitudinal and Cross-shelf Distribution

There is not a great deal of information on how diversity and abundance of barnacles change with latitude and depth along the east Florida coast NHBs. The most conspicuous barnacle, the volcano barnacle (*Tetraclita squamosa stalactifera*), is very prominent along the coast at the upper intertidal zone, where the competitive *P. lapidosa* does not often occur (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.) (**Figure 4.16**). Multer and Milliman (1967) also suggested that *T. s. stalactifera* compete for space with *P. lapidosa* in this zone. McCarthy (2001) suggests that *P. lapidosa* consistently recruits in large numbers and out-competes other recruit species such as barnacles by growing over them. When *P. lapidosa* is not present, a number of other barnacle species may often be present in these habitats. The barnacle *Balanus tintinnabulum antillensis* was observed attached to cocinoid rock underlying the worm-built structure on Hutchinson Island (Camp et al., 1977) and on an artificial reef in Boca Raton (Cummings, 1994). The invasive barnacle *Megabalanus cocopoma* was identified on intertidal hard bottom in Stuart (McCarthy, 2006). McCarthy (2001) observed the following barnacle species on intertidal and subtidal hard bottoms in Boynton Beach: *Balanus eburneus*, *B. amphitrite*, and *Chthamalus fragilis*. Further to the south in the Key Biscayne area, additional barnacles encountered are *Balanus improvisus* and *Chthamalus stellatus* (Walton Smith et al., 1950). Considering relatively high dispersal ability, most of these species probably occur throughout intertidal and shallow subtidal hardbottoms along the east Florida coast.

Figure 4.16. The volcano barnacle *Tetraclita squamosa stalactifera* and various other sessile invertebrates on intertidal hardbottom in Palm Beach, Florida. *Photo by D. McCarthy.*

4.2.7.3 Reproduction and Life History

Most barnacles are simultaneous hermaphrodites that externally fertilize eggs within their mantle cavities. Eggs are brooded there, hatch out into the plankton, and become nauplius larvae that are carried with currents until they settle as cyprids. Many cyprids may preferentially settle on conspecifics, cuing in on chemical and topographical features of the adults (Ruppert et al., 2004). Generally, there is perceived to be high initial post-settlement mortality, with surviving barnacles probably living 1 to 10 years, depending on various abiotic and biotic factors (Ruppert et al., 2004).

Little is known about seasonal reproductive patterns of most barnacles along the east Florida coast, although some species may have similar patterns as counterparts within the region. McCarthy (2001) observed barnacle recruitment on intertidal and subtidal (4 to 5 m) hardbottom habitats in Boynton Beach. In the intertidal zone, all three barnacle species encountered (*Balanus eburneus, B. amphitrite,* and *Chthamalus fragilis*) recruited seasonally, with peak recruitment occurring during the summer time period (May to August). *C. fragilis* recruited more intertidally rather than subtidally and generally was the most abundant barnacle recruiter during the study. *B. eburneus* was the only barnacle species that recruited equally to both intertidal and subtidal habitats. In contrast, *B. amphitrite* was the most abundant subtidally, recruiting throughout the year, while *B. eburneus* and *C. fragilis* had sporadic recruitment patterns. The study also suggested that there may be significant post-settlement mortality by mobile predators (i.e., crabs and fishes) for *C. fragilis* in subtidal habitats but not for any of the other barnacle species. In southeast Florida, *B. amphitrite* and *B. improvisus* had similar seasonal peaks in recruitment as those found by McCarthy (2001) but were also found to recruit more continuously throughout the year (Walton Smith et al., 1950). Interestingly, *Tetraclita* spp. were essentially non-existent in both studies yet are often the most abundant adult barnacles along the coast. A possible explanation for this may be that settlement plates in both studies were not placed high enough in the intertidal zone to observe recruitment of this species. Larval behavioral preferences may have positioned such competent larvae so that they were transported only to these upper reaches of the intertidal zone where most adults are found.

4.3 MOTILE SPECIES

4.3.1 Crustaceans

4.3.1.1 Diversity and Trophic Function

The structure provided by east Florida coast NHBs supports a high diversity and abundance of crabs, stomatopods, shrimp, lobsters, isopods, and amphipods (**Appendix B**, **Table B.1**). Sabellariid reefs, in particular, support an even higher diversity and abundance of these crustaceans than neighboring sand or hardbottom habitats. Van Montfrans (1981) reported that the majority of decapods along the east Florida coast can be regarded as tropical in origin, as can be seen by their associations with southern latitude coral reefs. Furthermore, *Phragmatopoma* worm rock reefs are an important habitat for tropical marine decapods (**Figure 4.17**), especially in the high energy surf zone, where corals tend not to prevail at the more northern latitudes.

Trophically, crustaceans are important in food webs along the east Florida coast as major prey for other invertebrates and fishes. They can also be important as predators of various invertebrates and small fishes (USFWS, 1999). Gore et al. (1978) postulated a possible food sub-web for sabellariid colonies on the east Florida coast based on the gut contents of six common species collected. The worms form the basis of the food sub-web on which some species of reef-dwelling crabs forage (**Figure 4.2**).

Figure 4.17. Tidal spray crab (*Plagiusa depressa*) in Palm Beach, Florida. *Photo by D. McCarthy.*

4.3.1.2 Latitudinal and Cross-shelf Distribution

The most quantitative research with any invertebrate group along the Florida coast has been done with crustaceans. While most of this research was done over 20 years ago, the combined results provide the bulk of what is known about the hardbottom community ecology along the east Florida coast.

Decapods

Camp et al. (1977) studied the nearshore ecology at Hutchinson Island, Florida (September 1971 to July 1974). Sampling occurred during the day on five stations at depths of 7 to 11 m on sand and sand shell substrate. Three nearshore zones included 1) the shallow beach terrace, 2) crest of shallow off shore shoal, and 3) a deeper "trough" zone between them. More than 170 species of arthropods (of which 113 were included in quantitative analysis) were recorded. Species recruitment curves never reached asymptote over the 2 years because of high species turnover rate and some poor grab efficiencies. Some 25 to 36 arthropods found only at the intertidal worm reef were unique to that habitat, with 13 others also found offshore (**Table 4.5**). Highest densities of organisms were encountered from July to September, and lowest densities occurred January to March. The crabs *Pachycheles monilifer* (porcellanid crab) and *Pachygraphsus transverses* (grapsid crab) were numerically dominant, but in terms of biomass, *Menippe nodifrons* (xanthid crab) was dominant. *M. nodifrons* was observed physically altering the reef by breaking off pieces, crushing them to expose the worms, and feeding on them. Shared species occurred infrequently or in low abundance offshore, indicating a distinct difference between worm reef and offshore faunas. Consequently, species associated with worm rock habitat were unique to that habitat compared to that offshore (**Table 4.5**).

In a nearby study, Applied Biology, Inc. (1979) monitored a worm reef at the Florida Power & Light Company St. Lucie Power Plant from April 1976 to April 1979. Most of the sabellariid-associated fauna in this study were crustaceans, molluscs, and echinoderms. Species encountered, in order of abundance, were *Menippe nodifrons*, *Pachycheles monilifer, Excorallana sexticornis*, and *Sphaeroma walki* (isopods) and *Pachygrapsus transverses* (**Tables 4.2**, **4.6**, and **4.7**). The number of associated species collected was highest in July when water temperatures peaked and reef size was largest. Numbers and diversity of organisms was lowest in October to January, when water temperatures were decreasing and reef size was the smallest.

Gore et al. (1978) investigated latitudinal changes in crustaceans in a 2-year study of four worm reef sites on the central east Florida coast from St. Lucie Inlet north to Sebastian Inlet (1974 to 1975). A total of 96 species of decapod and stomatopod crustaceans representing 52 genera and 22 families was identified. Two surveys occurred, with sampling conducted both on the worm reef itself and in areas adjacent to the reef. Specifically associated with the worm reef were 24 common species, of which the first 11 species comprised 90% and the next 13 species comprised 4% to 7% of the collected samples. The remaining 3% (27 species) were considered uncommon (**Table 4.8**). The six most common species (80% of the samples) were the porcellanid crab *Pachycheles monilifer*, the grapsid crab *Pachygraphsus transverses*, the aphid pistol shrimp *Synalphus fritzmuelleri*, and the xanthid crabs *Menippe nodifrons*, *Pilumnus dasypodus*, and *Panopeus bermudensis*. *P. monilifer* and *M. nodifrons* are restricted to worm reefs along the east coast of Florida. The abundance of the dominant species was relatively similar at all sites, but the less dominant species varied among sites (**Table 4.9**). This variability is also indicated in that about 20 species appeared to be common to Gore et al. (1978) surveys (**Table 4.5**) and about 31 species more occur in Gore et al. (1978) that are not listed in Camp et al. (1977). Furthermore, species richness was highest at St. Lucie Inlet south, intermediate (53%) towards the north from Walton Rocks to Fort Pierce Inlet, and lowest (13%) at Sebastian Inlet north.

Table 4.5. Comparison of worm reef arthropods found in the vicinity of Hutchinson Island, Florida with arthropod species found offshore in the same area (From: Camp et al., 1977). ● denotes species presence.

Species Found Only at Worm Reef	Rank	Species Found at Worm Reef and Offshore Sites	Stations				
			I	II	III*	IV	V
			Depths (m)				
			8.4	11.2	7.1	10.9	10.9
Balanus tintinnabulum antillensis		*Tanystylum orbiculare*	●	●			
Paranthura infundibulata		*Balanus trigonus* (on *Plagiusa depressa)*	●	●	●	●	●
Sphaeroma walkeri		*Gonodactylus bredini*	●	●		●	●
Bopyridae sp. D (on *Petrolisthes armatus)*		*Periclimenes americanus*	●	●		●	●
Alpheus malleator		*Alpheus formosus*		●			
A. nuttingi		*A. normanni*	●	●		●	●
A. thomasi		*Synalpheus* sp. B	●				
Synalpheus fritz muelleri		*Paguroidea* sp.	●	●		●	●
Synalpheus sp. A		*Paguristes hummi*	●	●		●	●
Calcinus tibicen		*Epialtus* sp.	●	●			
Paguristes tortugae		*Mithrax forceps*	●	●			
Pagurus brevidactylus		*Mithrax* sp.	●	●			
Megalobrachium poeyi		*Pitho lherminieri*	●	●			
Pachycheles monilifer	2						
Petrolisthes armatus							
P. galathinus							
Microphrys bicornutus							
Mithrax coryphe							
Eurypanopeus abbreviatus							
Menippe nodifrons	1						
Panopeus bermudensis							
Pilumnus dasypodus							
Xantho denticulatus							
Pachygrapsus transversus	2						
Plagusia depressa							

Yellow shading indicates species in common with Gore et al., 1978 study.
* Station III had no hard substrate.

Table 4.6. Abundance of associated decapods collected from sabellariid worm reef (Stations 9 and 10 combined) at the St. Lucie Power Plant from April 1976 through April 1979 (From: Applied Biology, Inc., 1979).

Species	1976			1977				1978				1979	
	Apr	Jul	Oct	Jan	Apr	Jul	Oct	Jan	Apr	Jul	Oct	Jan	Apr
Alpheus formosus	1			2		1	6	5	1	1			3
Alpheus malleator							2						
Alpheus normanni											1		
Alpheus nuttingi						1	4		3				
Alpheus thomasi			2				2						
Alpheus sp. *A*					1								
Alpheus sp.								2				2	
Calcinus tibicen						1							
Epialtus sp.							1						
Eriphia gonagra													
Hippolytidae sp.													1
Lysmata intermedia				2			1						
Lysmata wurdemanni											1		
Lysmata wurdemanni?													
Majidae sp.													1
Menippe mercenaria	2	4	3			3	3	1		6	6	2	
Menippe nodi frons	26	11	172	27	19	114	198	159	19	58	99	93	35
Microphrys bicornutus						1							
Pachycheles monolifer	107	101	42	3	66	71	39	86	74	36	1	15	69
Pachygrapsus transversus	23	5	28	4	4	22	23	8	4	10	14	13	32
Pagurus carolinensis		1			1	4	3				1		2
Panopeus bermudensis		1	2		3	6		2	2	16		2	
Pelia mutica				1									
Petrolisthes armatus			1	1			1		1				
Petrolisthes galathinus							1	2					
Pilumnus dasypodus				2		19	11	14	10	22	3	3	3
Pilumnus sp.		2	1		2								2
Pitho lherminieri										2			
Pi tho sp.								1					
Plagusia depressa					1						1		
Synalpheus fritzmuelleri		6	6	2	2	3	74	15	4	13	1	1	2
Synalpheus townsendi							1						
Synalpheus sp.						1							
Upogebia affinis										1			
Xantho denticulatus						2			1	1			
Xanthidae sp.							1						3

Table 4.7. Comparison of associated decapod and stomatopod crustaceans from studies at Walton Rocks and the St. Lucie Power Plant (From: Applied Biology, Inc., 1979).

	Florida Department of Natural Resources Within 2 km South of St. Lucie Power Plant June 1975	Smithsonian Institution Fort Pierce Bureau[b] Walton Rocks		Applied Biology, Inc. St. Lucie Power Plant		
		1974	1975	April 1976 through January 1977	April 1977 through January 1978	April 1978 through January 1979
Number of genera	22	15	11	12	18	14
Number of species	30	20	13	15	29	18
Diversity (d)	---	1.88	1.62	1.88	2.3	2.28
Equitability (e)	---	0.1	0.31	0.33	0.24	0.39

[a] Camp et al., 1977.

[b] Gore et al., 1978 and R.H. Gore, pers. comm.

Table 4.8. The 51 most recurrent species of decapod and stomatopod crustaceans encountered from sabellariid worm reefs in the Indian River region of Florida, 1974 to 1975 (From: Gore et al., 1978).

Taxon	St. Lucie		Walton Rocks		Fort Pierce		Sebastian	Abundance		60% to 80% Spawning
	1974	1975	1974	1975	1974	1975	1974*			
1. *Pachycheles monilifer*	127		163		256		None	C	MC	Year round
2. Menippe nodifrons	98		216		107		22	C	MC	May-Aug
3. Synalpheus fritzmuelleri	54		64		42		None	C	MC	Year round
4. Pachygrapsus transversus	51		48		56		66	C	MC	Year round
5. Pilumnus dasypodus	17		15		64		None	C	MC	May-Aug
6. Pitho lherminieri	14		4		None		None	C		
7. Mithrax coryphe	14		2		6		None	C		
8. Gonodactylus bredini	11		4		None		None	C		
9. Pilumnus sayi	9		None		18		None	C		Jan-Aug
10. Petrolisthes galathinus	8		1		14		None	C		Jan-Aug
11. *Alpheus formosus*	8		None		8		None	C		Jan-Jul
12. Pagurus carolinensis	8		1		1		None	C		May-Aug?
13. Xantho denticulatus	7		3		None		None	C		
14. Gonodactylus oerstedii	7		None		None		None	C		
15. Menippe mercenaria	6		20		24		3	C		
16. Synalpheus sp. A	6		None		4		None	C		
17. Epialtus bituberculatus	6		None		10		None	C		Jan-Aug
18. Alpheus nuttingi	5		4		9		None	C		Nov-Aug
19. Microphrys bicornutus	4		None		4		None	C		
20. Plagusia depressa	3		2		1		1	C		May-Aug?
21. Panopeus bermudensis	2		15		44		4	C	MC	May-Oct
22. Alpheus thomasi	2		4		2		None	C		Jan-Aug?
23. Synalphells minlls	2		None		7		None	C		
24. Synalpheus townsendi	2		2		3		None	C		Jan-Aug
25. Uhlias limbatus	2		None		None		None	UC		
26. Processa fimbriata	2		None		1		None	UC		
27. Metalpheus rostratipes	1		2		None		None	UC		
28. Lysmata intermedia	1		None		1		None	UC		
29. Petrolisthes armatus	1		1		1		None	UC		
30. Alpheus normanni	1		None		None		None	UC		
31. Epialtus dilatatus	1		None		None		None	UC		
32. Alpheus paracrinitus	1		None		None		None	UC		
33. Megalobrachium soriatum	1		None		None		None	UC		
34. Mithrax acuticornis	1		None		None		None	UC		
35. Neopontonides beaufortensis	1		None		None		None	UC		
36. Mithrax pleuracanthus	1		None		None		None	UC		
37. Upogebia affinis	1		None		None		None	UC		
38. Platyactaea setigera	1		None		None		None	UC		
39. Micropanope granulimanus	1		None		None		None	UC		
40. Mithrax hispidus	None		2		None		None	UC		
41. Alpheus armillatus	None		1		4		None	UC		
42. Periclimenes americanus	None		1		1		None	UC		
43. Eurypanopeus dissimilis	None		1		None		None	UC		
44. Lysmata wurdemanni	None		None		1		None	UC		
45. Synalpheus brevicarpus	None		None		1		None	UC		
46. Alpheus bouvieri	None		None		1		1	UC		
47. Paguristes tortugae	None		None		1		None	UC		
48. Eurypanopeus abbreviatus	None		None		1		None	UC		
49. Alpheus heterochaelis	None		None		1		None	UC		
50. Panopeus occidentalis	None		None		None		5	UC		
51. Panopeus herbstii	None		None		None		1	UC		

* Sebastian Inlet station not sampled in 1975. C = common (97%); MC = most common (80%); UC = Uncommon (3%).

Table 4.9. Species richness of decapod and stomatopod crustaceans collected from sabellariid worm reefs in the Indian River region of Florida, 1974 to 1975 (From: Gore et al., 1978).

St. Lucie	Walton Rocks	Fort Pierce	Sebastian*
Most species rich	49% common with St. Lucie	56% common with St. Lucie	13% common with St. Lucie
39 species	19 of 39 species	22 of 39 species	5 of 39 species

* Sebastian Inlet station not sampled in 1975.

Encompassing a larger geographical area along the Florida coast, van Montfrans (1981) studied decapod crustaceans associated with worm rock at five sites from Miami north to Cape Canaveral. There were a few species that accounted for the majority of individuals inhabiting intertidal and subtidal zones (**Tables 4.10** and **4.11**). The 4 most abundant of 15 species identified in the intertidal zone included *Pachygrapsus transvenus, Menippe nodifrons, Panopeus bermudensis*, and *Pilumnus lacteus.* In the subtidal zone, the 4 most abundant of 10 species included *Synalpheus fritznuelleri, Pilumnus dasypodus, Menippe nodifrons,* and *Petrolisthes galathinus.* Furthermore, species common to both subtidal and intertidal habitats included *Menippe nodifrons, Panopeus bermudensis, Pachygrapsus transverses, Petrolisthes armatus,* and *Pilumnus lacteus.* In terms of cross-shelf distribution, the diversity and abundance of decapods tended to increase with depth. In terms of latitudinal distribution in the subtidal zone, total numbers were highest at Deerfield Beach (610) but decreased towards the north at Hutchinson Island (394), Fort Pierce (202), and Satellite Beach (71). Moreover, total numbers decreased south of Deerfield Beach at Miami (296) (**Table 4.12**). Towards the southern two study sites (Miami and Deerfield Beach), *Pilumnus dasypodus, Petrolisthes galathinus,* and *Synalpheus fritznuelleri* were dominant, although their order of dominance varied. In the central two study sites (Hutchinson Island and Fort Pierce) the dominant species mix consisted of *Menippe nodifrons* (which occurs subtidally and intertidally)*, Synalpheus fritznuelleri, Pachycheles monilifer*, and *Petrolisthes galathinus.* At the most northern study site (Satellite Beach), the species mix changed to the following three dominant species: *Menippe nodifrons, Pachygrapsus transvenus,* and *Petrolisthes armatus.* Many tropical species (Families: Alpheidae, Palaemonidae, Hippolytidae, Stenopodidae, Paguridae, Palinuridae, Porcellanidae, Xanthidae, Grapsidae, and Majidae) decrease in numbers and species from south to north, probably due to higher variability in sea surface temperature near Cape Canaveral versus Miami, and may be displaced further offshore in the north (van Montfrans, 1981).

Table 4.10. Rank analysis of intertidal decapods from the east Florida coast (From: van Montfrans, 1981).

Species	Bio1. Index (3-pt. System)	Frequency as One of Top Three Species in Nine Samples	Frequency in Nine Samples	Total Number Collected	Greater Numbers Occurring in a Sample	Overall Density/ 1,000 m of Reef Sampled
Pachygrapsus transvenus	26	9	9	324	97	1.969
Menippe nodifrons	11	5	5	113	91	0.687
Panopeus bermudensis	4	3	4	23	17	0.140
Pilumnus lacteus	4	2	2	11	10	0.067
Alpheus bouvieri	2	1	3	7	3	0.043
Clibinarius tricolor	2	1	2	3	2	0.018
Eriphia gonagra	2	1	2	3	2	0.018
Paguristes tortugae	2	1	1	2	2	0.012
Pagurus carolinensis	2	1	1	20	20	0.121
Petrolisthes armatus	2	2	4	10	6	0.061
Alpheus malleator	l	1	1	1	1	0.006
Cyclograpsus integer	1	1	1	2	2	0.012
Eurypanopeus abbreviatus	1	1	1	2	2	0.012
Menippe mercenaria	1	1	4	5	2	0.030
Plagiusa depressa	1	1	2	3	2	0.018

Species highlighted in yellow occur in both intertidal and subtidal habitats.

Table 4.11. Rank analysis of the dominant subtidal decapods from the east Florida coast (From: van Montfrans, 1981).

Species	Bio1. Index (3-pt. System)	Frequency as One of Top Three Species in Nine Samples	Frequency in Nine Samples	Total Number Collected	Greater Number Occurring in a Sample	Overall Density/ 1,000 m of Reef Sampled
Synalpheus fritznuelleri	11	6	7	443	131	1.727
Pilumnus dasypodus	10	5	6	255	84	0.994
Menippe nodifrons	9	4	7	330	241	1. 287
Petrolisthes galathinus	6	3	4	399	308	1. 556
Panopeus bermudensis	5	2	6	131	65	0.51
Pachycheles monilifer	5	3	6	101	56	0.218
Pachygrapsus transversus	5	2	5	34	15	0.132
Petrolisthes armatus	1	1	7	27	6	0.105
Pilumnus lacteus	1	1	3	87	62	0.339
Lysmata wurdemianni	1	1	2	11	7	0.027

Species highlighted in yellow occur in both intertidal and subtidal habitats.

Table 4.12. Total number of the three most common subtidal decapod species at stations along the east Florida coast (Adapted from: van Montfrans, 1981).

Station A Dade Miami		Station B Broward Deerfield Beach		Station E St. Lucie Hutchinson Island		Station C St. Lucie Fort Pierce		Station D Brevard Satellite Beach	
Pilumnus dasypodus	106	*Petrolisthes galathinus*	328	*Menippe nodifrons*	247	*Pachycheles monilifer*	71	*Menippe nodifrons*	44
Petrolisthes galathinus	103	*Synalpheus fritznuelleri*	165	*Synalpheus fritznuelleri*	137	*Petrolisthes galathinus*	71	*Pachygrapsus transvenus*	20
Synalpheus fritznuelleri	87	*Pilumnus dasypodus*	117	*Pachycheles monilifer*	10	*Synalpheus fritznuelleri*	60	*Petrolisthes armatus*	7
Totals	**296**		**610**		**394**		**202**		**71**
All common to the subtidal zone		All common to the subtidal zone		*M. nodifrons* common to both zones		All common to the subtidal zone		All common to both subtidal and intertidal zones	
Southern sites				Middle sites				Northern range	

Species highlighted in yellow occur in both intertidal and subtidal habitats.

Reed et al. (1982) studied the composition of decapod crustaceans and the total number of individuals per species on east Florida oculinid coral reefs. A total of 50 species was identified with four locations of varying depth being examined: Fort Pierce Inlet (6 m), north of Fort Pierce (27 m), south of Fort Pierce (42 m), and offshore east of Fort Pierce Inlet (80 m depth). Species showed strong clustering by station with a gradual decrease in density as depth increased (**Table 4.13**). At the 6-m depth, there were discrete species clusters that were considerably different from all the other stations. Stations at 42- and 80-m depths showed little species differences. Species composition was relatively stable at each depth, and there were no dramatic seasonal overturns of assemblages. However, there was a degree of trophic portioning between the shallow station (Fort Pierce: 6 m), which was numerically dominated by the filter-feeding porcellanid crab *Megalobrachium soriatum*, and the 27-m station, which was dominated by the carnivorous *Pagurus carolinensis*. Four species that were found at all study sites included *Megalobrachium soriatum* and *Synalpheus townsendi* (**Tables 4.13** and **4.14**).

Table 4.13. Numerical abundance of decapod species at *Oculina varicosa* coral reef stations at depths of 6, 27, 42, and 80 m (Adapted from: Reed et al., 1982).

Number Abundance	6 m Fort Pierce Inlet	27 m North of Fort Pierce	42 m South of Fort Pierce St. Lucie Inlet	80 m Offshore East of Fort Pierce
1	*Megalobrachium soriatum*	*Pagurus carolinensis*	*Pagurus carolinensis*	*Pagurus carolinensis*
2	*Pachycles monilifer*	*Megalobrachium soriatum*	*Megalobrachium soriatum*	*Megalobrachium soriatum*
3	*Mithrax forceps*	*Synalpheus townsendi*	*Pagurus piercei*	*Pagurus piercei*
4	*Thor manningi*	*Mithrax forceps*	*Synalpheus townsendi*	*Synalpheus townsendi*
5	*Synalpheus fritzmuelleri*	*Pelia mutica*	*Periclimenes iridescens*	*Galathea rostrata*
6	*Synalpheus* cf. *townsendi*	*Stenorhynchus seticornis*		*Micropanope scuptipes*
7		*Micropanope nuttingi*		*Thor manningi*
8		*Paguristes tortugae*		*Pseudomedaeus distinctus*
9				*Pseudomedaeus agassizii*
10				*Nematopaguroides pusillus*
11				*Euchirograpsus americanus*

Table 4.14. Percent occurrence of decapod species at *Oculina varicosa* coral reef stations at depths of 6, 27, 42, and 80 m (Adapted from: Reed et al., 1982).

Percent Occurrence	6 m Fort Pierce Inlet	27 m North of Fort Pierce	42 m South of Fort Pierce St. Lucie Inlet	80 m Offshore East of Fort Pierce
~100		*Pagurus carolinensis* *Megalobrachium soriatum*	*Pagurus carolinensis*	*Pagurus piercei* *Synalpheus townsendi* *Galathea rostrata*
~90	*Megalobrachium soriatum* *Mithrax forceps*		*Pagurus piercei*	*Pagurus carolinensis* *Micropanope scuptipes*
~80	*Pachycles monilifer*		*Synalpheus townsendi*	
~70		*Synalpheus townsendi*	*Periclimenes iridescens*	*Thor manningi* *Pseudomedaeus distinctus* *Nematopaguroides pusillus*
~60	*Thor manningi* *Synalpheus fritzmuelleri*		*Megalobrachium soriatum*	*Megalobrachium soriatum* *Euchirograpsus americanus*
~50	*Synalpheus* cf. *townsendi*	*Mithrax forceps* *Pelia mutica* *Stenorhynchus seticornis* *Micropanope nuttingi* *Paguristes tortugae*		*Pseudomedaeus agassizii*
≤40	Rest	Rest		Rest

Crustacean species found on 6-m oculinid corals include *Epialtus* spp., *Pagurus* spp., and *Synalpheus* spp. (which is often associated with sponges and algae) (Reed et al., 1982). Also, there were 14 species that appeared to be shared between oculinid and sabellariid worm reefs mentioned in Gore et al. (1978). Furthermore, Reed et al. (1982) reported that on oculinid reefs, *Pachycheles monolifer* and *Synalpheus fritzmuelleri* were abundant*, Pagurus carolinensis* was common, and that *Syalpheus minus*, *S. townsendi*, and *Megalobrachium soraitum* were rare on sabellariid reefs. Species common on the sabellariid reefs but rare on oculinid reefs included *Pilumnus dasypodus*, *Petrolisthes galathinus*, *Epialtus* sp., *Alpheus formosus*, and *Synalpheus* cf. *fritzmulleri*.

The gradient in species assemblages was attributed to a gradient of environmental factors across the shelf (**Table 4.15**). At a depth of 6 m, the environment is characterized as having variable wave surge and sedimentation. The temperature was about 25°C and varied less relative to other sites, which accounted in part for the highest diversity of species – 11 endemic and uniquely associated with this depth. At 42 m, temperature was more variable, averaging about 18°C, with relatively less wave energy and sedimentation. As a result, diversity and number of endemic species was relatively low but individual numbers were highest. At the 80-m depth, the physical parameters were similar to those at the 42-m station, but there were relatively high numbers of species and endemic species but lowest individual numbers of each species. Temperature changes caused by upwelling events that occur periodically were considered to be an important factor controlling the community structure on these oculinid reefs.

Table 4.15. Physical parameters measured between 1976 and 1979 at *Oculina varicosa* coral reef stations at depths of 6, 27, 42, and 80 m. Range (mean and ± 1 standard deviation) (From: Reed et al*.,* 1982).

Parameter	6 m Fort Pierce Inlet	27 m North of Fort Pierce	42 m South of Fort Pierce St. Lucie Inlet	80 m Offshore East of Fort Pierce
Salinity (%)	28.2-36.4 (32.5 ± 3.4)	No data available	35.9-36.2 (only 2 values)	35.7-36.4 (36.0 ± 0.2)
Temperature (°C)	13.7-31.0 (24.6 ± 3.1)		8.0-27.8 (18.4 ± 2.7)	7.4-26.7 (16.2 ± 3.7)
Current (cm/sec)	0-70.5 (8.9 ± 2.1)		0-49.5 (8.7 ± 2.4)	0-58.5 (8.6 ± 1.7)
Visibility (m)	0-9 (3 ± 2)		0-21 (9 ± 5)	0-25 (9 ± 5)
Sedimentation (mg/cm^2/day)	137-1,640 (846 ± 593)		No data available	15-78 (53 ± 34)

Further south along the coast, Cummings (1994) reported the presence of six species of crustaceans associated with the colonization of a newly constructed artificial reef structure in the nearshore (~8 m depth) area off Boca Raton, Florida (April 1988 to July 1990). Decapod species observed from December to January 1988 included *Eurypanopeus abbreviatus* and *Percnon gibbesi.* From July to August 1989, *Mithrax forceps*, *Pagurus carolinensis*, and *Percnon gibbesi* were identified. In addition to these species, Sultzman (1990, 1997) encountered penaeid shrimp and blue crabs in the nearshore areas along the Florida coast.

Isopods and Amphipods

Nelson and Demetriades (1992) sampled worm rock from rock jetties at Sebastian Inlet, Florida, for a period of 1 year (April 1984 to March 1985) at daytime low tides. They collected six isopod species, of which *Paradella dianae* (53,000/m^2) and *Sphaeroma walkeri* (35,000/m^2) represented 98% of the total number of 6,136 isopods present (**Table 4.16**). Two peaks in abundance occurred for both species during the year (February-March and August-October). Recruitment was year-round (both species), and growth was bimodal for *P. dianae* (mode 1.1 to 1.5 mm size class in all months; 2.7 to 3.1 mm some months; shifted smaller [2.3 to 2.7 mm] or larger [3.1 to 3.5 mm]) and bimodal and skewed unimodal for *Sphaeroma walkeri* (some months mode 0.85 to 1.75 mm size class; shifted smaller [1.75 to 2.65 mm] or larger [2.65 to 3.55 mm] some months). Total monthly isopod density was negatively correlated with percent algal coverage on worm reef, and *S. walkeri* density was negatively correlated with air and water temperature on the north jetty site (which received more sunlight) but not on the south jetty site. *Pardella danae* density was not significantly correlated with physical parameters. Filamentous algal coverage by species such as *Enteromorpha* sp. tended to restrict access to suitable crevices in the worm rock. Nelson and Demetriades (1992) also collected 10 amphipod species, of which *Hyale perieri* (22,000/m^2), *Elasmopus pectinicrus* (10,000/m^2), and *Ampithoe pollex* (4,000/m^2) represented 91% of the total number of 3,801 amphipods (**Table 4.16**). Maximum abundance was observed to occur in late summer and early spring for *Hyale perieri* and was negatively correlated with salinity*.* For *E. pectinicrus*, a single maximum occurred during October to November, and abundance for *A. pollex* appeared to be lowest during November to January and was positively correlated with air temperature.

S. walkeri is more widely distributed than *P. danae* along the east Florida coast (Camp et al., 1977). Carlton and Iverson (1981) described its natural history and indicate that distribution is temperature-limited at a minimum surface winter isotherm of 15°C, which is typical at Sebastian Inlet (December to January). *P. danae* is typically cryptic in its habitat and found under stones, in empty barnacle tests, under chitons, in empty worm rock tubes, or in crevices of worm rock.

Table 4.16. Abundance of isopods and amphipods from sabellariid worm rock with percentage of contribution of species to total abundance of each order at Sebastian Inlet, Florida, April 1984-March 1985 (From: Nelson and Demetriades, 1992).

Species	Abundance	Percentage of Relative Abundance
Isopoda		
Paradella dianae	4,244	69.0
Sphaeroma walkeri	1,757	28.7
Paranthura infundibulata	79	1.3
Jaeropsis sp. nov.[1]	39	0.7
Excorallana spp.[2]	19	0.3
Amphipoda		
Hyale perieri	2,189	57.5
Elasmopus pectinicrus	966	25.4
Ampithoe pollex	396	10.4
Corophium acutum	145	3.8
Ericthonius sp.	55	1.4
Jassa cf. falcata	21	0.5
Ampithoe longimana	18	0.5
Stenothoe georgiana	11	0.3
Podocerus brasiliensis	2	0.1
Cymadusa compta	1	0.1

[1] Undescribed species, T.E. Bowman, personal communication.

[2] Includes two species, one of which is probably *Excorallana sexlicornis*. Positive identifications could not be made because few fully differentiated males were present (T.E. Bowman, personal communication).

4.3.1.3 Reproduction and Life History

Most crustaceans have separate sexes and reproduce sexually. Depending on the species, fertilization can be internal or external, with eggs being either shed directly into the sea or brooded by the females (most common with crabs and shrimp). In either case, most crustaceans produce larvae (nauplius or zoea) that eventually end up as part of the plankton. They can be lecithotrophic or planktotrophic and can be in the plankton from a few weeks (i.e., xanthid crabs, penaeid shrimp) to almost a year (i.e., spiny lobster) (Lyons et al., 1981; Young and Chia, 1987; Florida Wildlife Research Institute [FWRI], 2007a). In contrast, isopods, amphipods, and other pericarids lack larval stages. Their young emerge as miniature versions of the adults. Consequently, there is a wide range of dispersal capabilities among crustaceans. Upon recruitment, some become reproductive quickly and are short-lived like the amphipods and isopods (Nelson and Demetriades, 1992), while others, such as stone crabs (Lindberg and Marshal, 1984; Bert, 1992; FWRI, 2007b) and spiny lobster (Lyons et al., 1981), may live several years.

General reproduction and life history are fairly well known for such groups as penaeid shrimp and blue crabs. Penaeid shrimp have a short life span of about 1.5 years and spawn offshore in deeper waters (FWRI, 2006). The larvae develop in the plankton and move back into the salt marshes and tidal creeks. Blue crabs *(Callinectes sapidus)* have a life span of about 4 years, reaching sexual maturity in 1 year (Tagatz, 1968a). Females mate once in their lifetime during March to July or October to December (Tagatz, 1968a,b). After mating in the upper reaches of estuaries, females migrate to the mouth of the estuary and nearshore areas to spawn (FWRI, 2007c). Zoea drift in continental shelf waters for as long as 30 to 45 days (FWRI, 2007c), but this can vary by species and with temperature.

The Cuban stone crab *(Menippe nodifrons*) spawns from May to August (Gore et al., 1978), and the megalope stage is attainable within 16 to 17 days at 30°C in the laboratory, versus 28 to 37 days at 20°C (Scotto, 1979). Cuban stone crabs are closely allied to their commercial exploited counterpart *Menippe mercenaria,* which also has abbreviated zoeal stages (five or atypically six), depending on the ambient water temperature (Scotto, 1979). Ong and Costlow (1970) suggested 30°C was the optimum survival temperature for *M. mercenaria* larvae, with optimum salinity of 30 to 35 ppt (megalopal stage was reached in 14 days, first crab in 21 days, with 60% to 72% larval survival rate). Highest survival rate with *M. nodifrons* (15%) occurred at 20°C (megalopal stage was reached in 28 to 34 days, first crab in 45 to 49 days, but this can be prolonged; megalopal stage reached in ~37 days, first crab in ~52 days, with the atypical sixth zoeal stage). Stone crabs may live as long as 7 years (FWRI, 2006). Andryszak and Gore (1981) reported in their study of larval development of the deep water xanthid *Micropanope sculptipes* that it had four larval stages, like the majority of xanthid species. As a result, species with fewer larval stages would indicate that they spend less time as part of the plankton.

Spiny lobsters (*Panulirus argus*) spawn in late spring and early summer on the outer reefs and offshore (**Table 4.17**). The larvae (phyllosoma) live offshore for 6 to 12 months and are solitary, observing a diurnal vertical migration pattern (occurring shallower at night and deeper during the day). Post-larval (puerulus) recruitment occurs year-round, and the larvae move from the open ocean towards nearshore, moving in the surface 1 m of water. Movement is aided by wind-driven surface currents and/or flood tides at night following the new moon. When they are >15 to 20 mm carapace length (CL), they move into crevices and nocturnally feed on invertebrates, mainly molluscs (depth <5 m). As growth increases to 20 to 50 mm CL (7 to 10 months), they move to deeper water (depths of 10 to 20 m), 50 to 80 mm CL (1 year) (depths of 100 to 500 m), and >80 mm CL (15+ years) (depths of 500 to 1,000 m). Typically, 1-year-old subadults are found in 3- to 10-m water depths. Most crustacean larvae are subsequently returned to estuarine and nearshore areas by tides and wind-driven currents, which may cause some unexpected upwelling events (Pitts and Smith, 1997; Pitts, 1999).

Along the east Florida coast, some crustaceans spawn year-round, while others do so only seasonally (**Tables 4.8** and **4.17**). Notable year-round spawners are *Pachycheles monifer, P. transversus,* and *Synalpheus fritzmuelleri.* Ovigerous females of *P. dianae* and *S. walkerii* reported by Nelson and Demetriades (1992) were present year-round, so they probably spawn year-round as well. In contrast, *Menippe nodifrons*, *Pilumnus* spp., *Pagurus* sp., *Petrolisthes galathinus*, and *Alpheus* spp*.* appear to spawn seasonally during the spring or summer time period.

Reed et al. (1982) suggested that recruitment of *Oculina* coral reefs in shallow areas (6 m depth) along the east Florida coast may occur from two directions, the surrounding algae-sponge habitat and adjacent sabellariid worm reefs. The authors provided examples for species colonization that may occur from inshore to offshore, and vice versa: 1) *Pachycheles monilifer*, which was dominant on sabellariid worm reefs, was also restricted to 6-m depth on oculinid reefs; 2) *Megalobrachium soriatum*, which was the second most common species on oculinid reefs and rare on worm reef according to Gore et al. (1978), was found at all oculinid stations (6-, 27-, 42-, and 80-m depths); 3) the following species were observed on both sabellariid worm reef and 6-m oculinid reef but not at the deeper stations: *Synalpheus fritzmuelleri*, *Pilumnus dasypodus*, *Petrolisthes galathinus*, *Alpheus formosus*, and *Epialtus* sp.; and finally, but considered least likely, 4) colonization could occur as the larvae settle out of the plankton from offshore at 80-m depths moving shoreward, and the perseverance of various species would be controlled by selective elimination as a result of periodic cold water upwelling events. Recruitment of dominant isopods associated with worm rock occurred in most months (Nelson and Demetriades, 1992).

Table 4.17. Summary of the life history characteristics of the ontogenetic stages of spiny lobster (*Panulirus argus*) (Adapted from: http://bio.fsu.edu/~herrnlab/Life_History_Table.pdf).

Life Stage	Phyllosoma	Puerulus	Algal phase	Post-algal	Juvenile	Adult
Size	1 to 10 mm	5 to 6 mm CL	6 to 20 mm CL	20 to 50 mm CL	50 to 80 mm CL	>80 mm CL
Duration	6 to 9 months	1 to 2 weeks	2 to 3 months	7 to 10 months	1 year	15+ years
Color	Transparent body	Transparent body	Cryptic: banded disruptive	Semi-cryptic: spotted	Semi-cryptic: spotted	Semi-cryptic: spotted
Habitat	Open ocean	Offshore moving inshore	Macroalgae, seagrass	Bays, hardbottom sponges, holes	Bays, hardbottom patch reefs, amid seagrass holes	Offshore reefs
Food	Soft-bodied zooplankton	Non-feeding stage	Generalist: invertebrates (especially molluscs)	Same	Same	Same
Forage grounds	Upper 200 m	Non-feeding stage	Macroalgal patches	Grass beds, rocks	Grass beds, rocks	Grass beds, reefs
Home range	Unknown	Not available	<5 m	10 to 20 m	100 to 500 m	500 to 1,000 m
Predators	Pelagic fishes	Coastal fishes, jellyfishes	Small fishes, crabs, octopus	Fishes, crabs, octopus	Octopus, large fishes, stingrays, man	Large Goliath grouper, sharks, man
Antipredation strategy	Sparseness	Fast-moving, crypsis	Camoflage, shelter use	Shelter use, aggregation	Shelter use, aggregation, cooperative defense	Large size, shelter use aggregation, cooperative defense
Activity	Diurnal vertical migration	Nocturnal	Nocturnal only	Nocturnal only	Nocturnal crepuscular (diurnal at mass migration)	Nocturnal crepuscular (diurnal at mass migration and reproductive season
Sociality	Solitary	Solitary	Solitary, asocial	Gregarious (forage as individuals)	Gregarious (forage as individuals)	Semi-gregarious (forage as individuals)

CL = Carapace length.

4.3.2 Gastropods and Other Molluscs

4.3.2.1 Diversity and Trophic Function

There is a high diversity and abundance of gastropods on hardbottoms along the east Florida coast. Reed and Mikkelsen (1987) studied the molluscan community associated with the scleractinian coral *Oculina varicosa* at four sites of varying depth. They identified 230 species-level taxa, including 155 gastropods, 68 bivalves, 1 scaphopod, 5 polyplacophorans, and 1 cephalopod (**Table 4.4** and **Appendix B**, **Table B.2**). The observed taxa utilized four modes of existence: motile species (47%), symbiotic (32%), epilithic (18%), and endolithic (3%). There may be as many as 40 gastropod species that are rare and endemic to small nearshore reaches of Florida coastline (USFWS, 1999), specifically beach-rock outcrops along Palm Beach and Martin Counties (Petuch, 1988).

Gastropods are likely very important in food webs along the east Florida coast. They are important as predators of various invertebrates and small fishes (McGraw and Gunter, 1972, Carriker, 1978; Reed and Mikkelsen, 1987; Watanabe and Young, 2006). Watanabe and Young (2006) indicated that the main predators of *P. lapidosa* were the dog whelk *Stramonita haemastoma* and decapod crustaceans (Gore et al., 1978), although they also observed low numbers of the non-shell-boring gastropods *Pollina tinca* (Buccinidae) and *Leucozonia nassa* (Fasciolaridae) feeding on *P. lapidosa. Stramonita haemostoma* traditionally feeds on oysters, however, at Walton Rocks had developed a much longer proboscis to feed on worms than conspecifics that fed on bivalves (Watanabe, 2002). Boring gastropods feed by scraping the surface of shells and also by applying secretions that dissolve the shell, or by injecting toxins (McGraw and Gunter, 1972; Carriker, 1978). Additionally, gastropods can be a major prey item for other invertebrates such as the stone crab *Menippe mercenaria* occasionally observed on worm reefs, portunid crabs (Butler, 1985; Richardson and Brown, 1992), spiny lobsters (*Panulirus argus*) (Sultzman, 1990), blue crabs (FWRI, 2007c), and other snails such as *Pisania tincta* (Buccinidae) (Watanabe, 2002), as well as fishes (puffers, sheepshead, black sea bass, porgies, yellowtail snapper) (South Carolina Marine Resources Research Institute and Duke University Marine Laboratory, 1982; Cummings, 1994; USFWS, 1999).

4.3.2.2 Latitudinal and Cross-shelf Distribution

There is not much information on how gastropod diversity and abundance change with latitude and depth along the east Florida coast. Petuch (1987) reported that *Cerithium lindae*, *Nerita lindae*, and *Modulus papei* and two unnamed periwinkle species were associated with these nearshore habitats. Furthermore, it is possible to find *Thias rustica*, *T. deltoidea*, and *T. floridana* (also *Purpura patula*) along the east Florida coast. Two species of prickly winkle (*Tectarius antonii* and *T. nodulosus*), as well as the abundant *Cenchrus muricatus*, occur along Florida. *Aplysia* increases in abundance and number of species moving south towards the Keys. *Nerites* and *Siphonarias* are tropical, and few are encountered that survive the cold winter months. Petuch (1987) mentions endemic intertidal species, including several new species of small gastropods, some of which include *Nerita lindae* and *Cerithium lindae* from Martin, Palm Beach, and Broward Counties and some yet unnamed findings. In the rocky intertidal zone along Palm Beach County, it is possible to find *Nerita peleronta*, *N. versicolor*, *N. tesselata*, *N. fulgurans*, and *N. lindae* (E. Petuch, Florida Atlantic University, pers. comm.).

Applied Biology, Inc. (1979) monitored a sabellariid worm reef at the St. Lucie Power Plant (April 1976 to April 1979) and found 17 gastropod and 5 bivalve species associated with the reef. The four most common species of gastropods included *Anachis avara*, *Mitrella argus*, *Anachis floridana*, and *Barleeia tincta* (**Table 4.2**). As with other fauna observed, the number of gastropod species collected was highest in July when water temperatures peaked and reef size was largest (July 1977). Numbers and diversity of organisms were lowest from October to January when water temperatures were decreasing and reef size was the smallest. McCarthy (unpublished) noted the presence of *Stramonita haemostoma* (dog whelk) and *Aplysia dactylomela* (spotted sea hare) in observations at Bathtub Reef (2002 to 2003). *S. haemostoma* was significantly abundant all over the worm reef, but only during fall and early winter.

Reed and Mikkelsen (1987) conducted studies of molluscs on the east Florida coast associated with *Oculina variosa* coral reef at four sites and depths (inner shelf 6 m, mid-shelf 27 m, outer shelf 42 m, and shelf edge 80 m). At the 6-m depth, *Parviturboides interruptus* was the most abundant species, representing 54% of specimens. In comparison, all other stations were dominated by at least five species that made up 50% of the specimens observed. *Chione grus* was dominant at 27 m (13%), *Lithophaga bisculata* was dominant at 42 m (16%), and *Costoanachis lafresnayi* was dominant at 80 m (24%) (**Figure 4.18**).

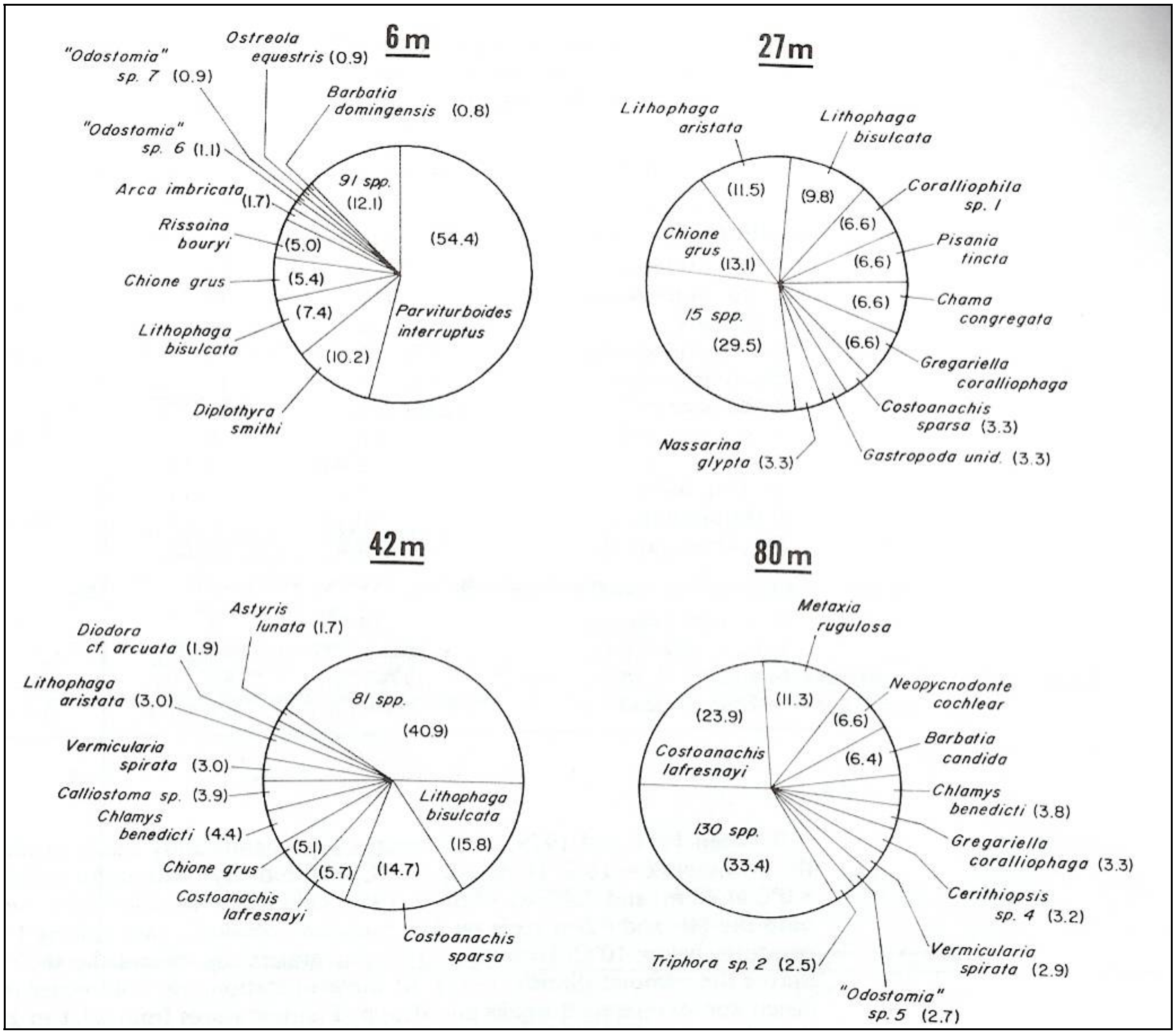


Figure 4.18. Species composition at each of four *Oculina* stations (From: Reed and Mikkelsen, 1987). Numbers in parentheses are percent of total individuals for each station.

In addition, three distinct species groupings were determined. One species group common to the 6-m depth was dominated by *Parviturboides interruptus*, *Diplothyra smithii*, *Rissoina bouryi*, and two species of *Odostomia*. The second, at 80-m depth, was dominated by *Metaxia rugulosa*, *Calliostoma roseolum*, and two other species of *Odostomia*. Finally, a third species grouping consisting of species common throughout the shelf was dominated by *Lithophaga bisculata*, *Calliostoma sparsa*, and *Fargoa bushiana*. The density of organisms at 6 m was significantly similar to that at the 80 m depth station but was significantly higher than that encountered at the 42 m depth (**Table 4.4**). Seasonal variations in community composition were minimal at 80 m because of high similarity of within-station fauna and low fluctuations in ordination scores. Also, at depths greater than 6 m, seasonal fluctuations in numbers of individuals and species were not as pronounced. At 6-m sites, these parameters varied according to temperature cycles, with a peak in numbers and species in June. This was due primarily to high densities of *Parviturboides interruptus*, *Chione grus*, and *Diplothyra smithii* and influx of rare species, respectively.

Cold water upwelling and cooler average temperatures may have accounted for more eurythermic tropical, temperate, and boreal species at the shelf edge (80 m) than on the inner shelf (6 m). Regarding trophic structure, species assemblages at 80 m were distinct from those at 6 m, in that specimens collected from the 6-m depth were predominantly herbivores and detritovores. Those collected from 80-m depths were predominantly carnivorous species. Habitat structure at the 80-m depth consisted of more dead and living coral than the other sites and, as a result, provided more space for epilithic molluscs and epizooiic (sponges, tunicates, and hydroids) and carnivorous species to colonize. At the 6-m depth, more boring endolithic species of molluscs prevailed, with densities five times that compared to the 42- or 80-m stations (**Appendix B**, **Table B.3**).

4.3.2.3 Reproduction and Life History

Gastropod species sexually reproduce but can be dioecious or hermaphroditic. Fertilization can be internal or external, producing offspring that develop directly or indirectly. In direct development, offspring often are encapsulated in egg cases that are attached to the seafloor. Juveniles hatch out of the cases as miniature adults. In indirect development, a trochophore (only archaeogastropods such as limpets, nerites, and turbans) or veliger larva (most other gastropods) is produced. In the latter case, veligers can be lecithotrophic and short-lived (days to weeks) in the plankton or planktotrophic and long-lived (up to 3 months) in the plankton.

Little is known about seasonal spawning and recruitment patterns of gastropods along the Florida coast. These larvae are among the most abundant nearshore zooplankton, but their occurrence is likely to be both local and brief, and information about larval ecology is limited (Reed and Mikkelsen, 1987; Johnson and Allen, 2005). However, community persistence seems to be influenced strongly by physical factors such as the stability and sustainability of adequate substrate, reduced wave energy, and/or severe storm surf (Woodley et al., 1981; Sousa, 1984), as well as adequate food supply. Also, habitat that is not prone to severe desiccation like intertidal habitats (as a result of low tides and high temperature maxima) can support more snails (Newell, 1979). In addition, Watanabe (2002) noted that low abundance of encrusting flora and fauna, presence of filamentous algae, and smooth worm reef mounds (dead worm reef) tended to increase stress and mortality to intertidal invertebrates, leading to a reduction in food supply for the snails. The physical environment is markedly different between inner and outer shelf reefs. At the 6-m depth, there were more waves, sedimentation, light, and constant temperature conditions that favored algal growth and herbivores. At a depth of 80 m, temperature fluctuations are as much as 13°C in 48 hours, and Reed and Mikkelsen (1987) speculated that recruitment of molluscan larvae from species pools outside of the *Oculina* reefs may be greater at the shelf edge reefs than at the inner shelf because they are closer to the warm Florida Current, which supplies tropical species of larvae from the south year-round. Moreover, outer shelf reefs are close to the deep, cool counter-current from the north that flows through the Florida Straits. The latter supplies temperate and boreal species to the shelf edge reefs. Larval distribution is probably greatly affected by numerous upwelling events caused by wind stress and tides (Pitts and Smith, 1997; Pitts, 1999; McCarthy, 2005).

Watanabe (2002) conducted studies on the dog whelk *Stramonita haemostoma* occurring at Marineland (rock boulders) and Bathtub Reef (worm rock) along the east Florida coast (1999 to 2001). Usually, spawning occurs from April to August (Butler, 1985). However, this can be affected by diet. Watanabe (2002) found that snails feeding on their normal diet of oysters reproduced earlier (May to August) compared to those feeding on *P. lapidosa* (July to September). Data from Marineland indicated that *S. haemostoma* is capable of producing from 226 to 270 egg capsules per snail, and as many as one to six clutches over the summer, with some individuals spawning multiple times. Egg capsules contain larvae that hatch into veligers after 10 to 27 days and then become part of the plankton for several months (Scheltema, 1971; Dobberteen and Pechenik, 1987). Each egg capsule can contain from 836 to 1,766 larvae (Watanabe, 2002). In general, the life span of these gastropods is about 5 years, with seasonally-induced settlement throughout their range (Gunter, 1979; Butler, 1985). However, the production of snails was lower on the Bathtub Reef worm reef (life span of 1 year) compared to rock boulders at Marineland (significantly longer). The community of snails on worm rock consisted of a new single cohort generated each year (recruited September to October) that completely died off by July to August, after 9 to 10 months. In addition, *P. lapidosa* recruitment and demise occurred in the same time frame (September to October and July to August, respectively) (McCarthy, 2001; Watanabe, 2002). No reproduction occurred on the worm rock at Bathtub Reef; however, at Marineland, the snail community was more persistent, with multiple cohorts (new recruits arriving from October to November) and reproduction and survival through fall and summer. Watanabe (2002) postulated that this may be due to availability of food throughout the year and the ability to survive harsh summer heat and weather conditions. Consequently, this was reflected in snail density, which was lower at Bathtub Reef (0.6 to 5.5 individuals/m^2/yr), representing a single cohort each year, compared to other locals with multiple cohorts per year, i.e., Marineland (16.1 ± 19.8 individuals/m^2/yr), Louisiana oyster beds (2.9 to 37.9 individuals/m^2/yr) (Brown and Richardson, 1987), and Gulf (2.7 to 27 individuals/m^2/yr) (Butler, 1985).

In southeast Florida, Cummings (1994) studied the recruitment and community development associated with a newly constructed artificial reef (April 1988 to July 1990) off Boca Raton, Florida. A total of 64 invertebrate species was recorded during the study, of which three were gastropod species and four were bivalve species (**Table 4.3**). Invertebrate species diversity was significantly higher in July 1990 than in December 1988 to January 1989. However, the seasonality of invertebrates was not confirmed because of a temporary and unexpected burial of four of six sampling locations. Generally, the invertebrate community never seemed to reach an equilibrium and stayed in an early stage of development because of frequent physical disturbance.

4.3.3 Echinoderms

4.3.3.1 Diversity and Trophic Function

Echinoderms can be abundant along some east Florida coast NHBs. While echinoids are often most visible out on reefs, there are a number of holothurians, ophiuroids, asteroids, and crinoids that can be encountered along the coast (**Appendix B**, **Table B.1**). Overall, most echinoderms do not provide significant shelter for higher numbers of species. Some exceptions to this may occur with small animals such as shrimp, mysids, copepods, porcellanid crabs, brittle stars, blennies, gobies, and pearlfish (Randall et al., 1964: Schoppe, 1991). However, some echinoderm species may be very important herbivores that influence abundance or diversity of macroalgae that in turn affects the amount of either 1) shelter or food for other species, and/or 2) space availability for recruitment of other sessile organisms such as stony corals (see Duffy and Hay, 2001 for a review). In the more northern sections of east Florida NHB, the echinoid *Echinometra lucunter* is very abundant and significantly reduces biomass of macroalgae and cyanobacteria (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Such removal of macroalgae and cyanobacteria may be important in providing recruitment opportunities for sessile invertebrate such as *Oculina* and *Siderastrea*. Recent observations of removal of macroalgae by urchins were documented during monitoring of the Indian River County Ambersand mitigation reef. Observations indicated an 8-fold increase in urchin populations on the mitigation artificial reef between 2006 and 2008 where removal of macroalgae and mud cover increased recruitment opportunities for the scleractinian *Oculina* (Miller and Kosmynin, 2008; Coastal Eco-Group Inc., 2009). Other echinoderms such as some holothurians and brittle stars are deposit-feeders that may convert detrital food sources into macroorgansim biomass that is available to higher trophic levels and enhance sediment resuspension and nutrient exchange with the water column (Bertness, 2007).

Echinoderms can be important as a food sources to key species in a number of marine ecosystem food webs (see Duffy and Hay, 2001 for a review) but have not been studied in this sense along the east Florida coast. It is very likely that sea urchins are important prey components of food webs as there are several predators found along the coast that are relatively abundant and known to prey on sea urchins. Examples of these predators include spiny lobsters, spider crabs, grunts, jacks, wrasses, triggerfishes, and birds (Abbott et al., 1974; Hendler, 1977).

4.3.3.2 Latitudinal and Cross-shelf Distribution

How abundance and diversity of echinoderms change along east Florida coast NHBs is unclear for most of this group. The clearest patterns occur with echinoids, with a much higher biomass of echinoids occurring towards the northern half of the east Florida reef tract. To the north of Palm Beach County, nearshore reefs can have fairly high densities of the rock-boring urchins *Echinometra lucunter* (**Figure 4.19**) and *Arbacia punctulata*. McCarthy (2001 and unpublished data) observed densities varying between 2 and 16 urchins/m^2 at several locations off Vero Beach. Approximately 80% were *E. lucunter*, 19% *A. punctulata*, and 1% the pencil urchin *Eucidaris tribuloides*. *Echinometra lucunter* also is found in tidal pools in the intertidal and in the very shallow subtidal zone along the entire coast. In this region, there may be an increase in abundance of *A. punctulata* with depth. This may be explained by the colder temperature tolerances of this species, as it is found much further north on the eastern coast than any of the other species (Hendler et al., 1995). The echinoid *Tripneustes ventricosus* also has been recorded as far north as Indian River County but generally occurs in low densities (C. Miller, Coastal Eco-Group, Inc., and D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Progressing southward, in Martin County, several other species may be encountered on NHBs. These include *Diadema antillarum*, *Lytechinus variegatus*, and *T. ventricosus*. Of these three species, *D. antillarum* is more normally encountered on coral reefs and hardbottoms, whereas the other two are more common on seagrass habitats. *D. antillarum* have been observed throughout the east Florida coast but appear to be most abundant at the St. Lucie Reef (SFCREMP, 2007). Generally, south of Martin County, echinoid biomass decreases significantly, with only occasional observations of *E. tribuloides* and even rarer encounters with *D. antillarum* (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.).

Figure 4.19. The rock-boring urchin *Echinometra lucunter* on shallow hardbottom habitat in Vero Beach, Florida.
Photo by D. McCarthy.

Very little is known about the holothurians along the Florida coast. The most conspicuous sea cucumbers are holothuroids. *Holothuria grisea* is most abundant in the intertidal and shallow subtidal zones along the east Florida coast (**Figure 4.20**) (Hendler et al., 1995). It can be found within cracks and crevices within worm rock or associated hardbottoms. It appears to occur in highest densities from Martin County and northward, although this has not been experimentally confirmed. The diversity of holothurians probably increases with depth. J. Beal (FWC, pers. comm.) identified five holothurians at the St. Lucie Reef in Martin County.

Figure 4.20. The sea cucumber *Holothuria grisea* on shallow hardbottom habitat in Ambersands Beach, Florida.
Photo by D. McCarthy.

Very little is known about the brittle stars and crinoids that occur along the east coast. There are probably a number of brittle star species that may be in high abundance along the coast, as they are somewhat easily encountered upon dissection of worm rock (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). They also can be observed in the deeper subtidal hardbottoms from Palm Beach County southward. In contrast, crinoids probably are not that abundant but have been encountered in some areas. For instance, the crinoids *Davidaster rubiginosa* and *Nemaster grandis* have been identified in a depth of ~6 m at the St. Lucie Reef (J. Beal, FWC, pers. comm.).

4.3.3.3 Reproduction and Life History

All of the echinoderm species found along east Florida reproduce sexually. Most are slow egg producers (Eckelbarger, 1994) that seasonally spawn. While some do brood their young and have crawl-away larvae, many broadcast spawn, where fertilization results in either planktotrophic or lecithotrophic larvae. Larval time spent in the plankton varies from a few hours to months. After settlement and metamorphosis, many probably live for several years (Ruppert et al., 2004).

While there is some information available on seasonal spawning patterns of echinoderms along the east Florida coast, there is little known on their dispersal and recruitment patterns. *E. lucunter* probably spawns during late summer/early fall, whereas *A. punctulata* spawns during late spring/early summer (Serafy, 1979). *L. variegatus* has two spawning periods---one during late spring and a second smaller peak in fall (McCarthy and Young, 2002). *D. antillarum* spawning periods appear somewhat variable throughout the Caribbean populations studied but often have a well-defined lunar rhythm (Hendler et al., 1995). At Walton Rocks, Fort Pierce, the sea cucumber *H. grisea* occurs in low abundance during winter, when the animals may migrate offshore (Hendler et al., 1995). While most echinoderms found in our area produce planktonic larvae that may spend several months in the plankton before settling and recruiting to hardbottoms, there may be high dispersal and connectivity among echinoderm populations in the Florida-Caribbean region. There is no substantial research that has documented recruitment patterns for any echinoderm species along the east Florida coast. However, studies of echinoderms generally reveal recruitment to be low, if not sporadic, during the course of a single year.

4.4 SUMMARY

4.4.1 Diversity

There is a high diversity and abundance of sessile and motile invertebrate species associated with NHBs along the east Florida coast (**Appendix B**, **Table B.1**). A total of 534 species of invertebrates has been identified along the east Florida coast, and there are likely to be more. The diversity of sessile species is greatest for cnidarians (~21%), bryozoans (~29%), and sponges (~19%). At generally lower diversities, tunicates, polychaetes, and bivalves are commonly encountered in these habitats as well. In contrast, some sessile taxonomic groups may not be represented with as high a diversity but can occur in very high biomass. A premier example is the sabellariid polychaete *P. lapidosa*, which can be very abundant along the more mid- to northern sections of the Florida coast.

The most diverse and generally abundant motile invertebrates are arthropods (~47%) and polychaetes (~28%). There are over 100 species of crustaceans that are extremely abundant, especially on worm reef-dominated hardbottoms. These include crabs, stomatopods, shrimp, lobsters, isopods, and amphipods. There are over 87 reported polychaete species that are likely to be very abundant, although more research is needed to confirm this. There are also fairly high numbers of gastropods, flat worms, ribbon worms, and echinoderms on these habitats. While less diverse, to the north along the east Florida coast there is generally high biomass of echinoderms such as the sea urchins *E. lucunter* and *A. punctulata.* While these are some generally-observed trends, some groups such as brittle stars are probably fairly diverse and abundant but have not been extensively studied.

4.4.2 Trophic Patterns and Functional Groups

The two premier ecological functional roles of invertebrates along the east Florida coast are as 1) shelter-enhancing organisms that increase local diversity of fishes and invertebrates, and 2) either predators or prey in local food webs. Generally, the highest community biomasses along the east Florida coast occur in hardbottom areas with higher abundances of sessile invertebrate species (some may be considered foundational or keystone contributors to the community) that enhance local shelter. Along the Florida coast, important shelter-enhancing taxonomic groups are hard and soft corals, sponges, tunicates, molluscs, barnacles, and polychaetes (i.e., *P. lapidosa*), however, their importance in this function varies dramatically with depth and latitude. In terms of contribution to local food webs, important taxonomic groups are sponges, crabs, shrimp, polychaetes, echinoderms, crabs, and shrimp. Again, their importance in this function likely varies dramatically with depth and latitude.

The range of trophic roles is very different between sessile and motile east Florida invertebrates. Most sessile invertebrates are passive consumers, either being suspension feeders (sponges, sabellariid polychaetes, barnacles, tunicates) or opportunistic carnivores (hard and soft corals, bryozoans, hydrozoans). All of these invertebrates may be fed on by motile invertebrates or fishes, but there is little information available on their role in this function. In contrast, there is more trophic diversity among motile invertebrates. Most decapods and gastropods are active carnivores, although some are omnivores, herbivores, and suspension feeders. Echinoids such as *E. lucunter*, *A. punctulata*, and *D. antillarum* are important herbivores in the areas where they occur. These motile groups are also likely to be fed on by motile invertebrates or fishes, but there is little information available on their role in this function.

4.4.3 Latitudinal and Cross-shelf Distribution

On a large scale, the diversity and abundance of invertebrates along the east Florida coast varies dramatically based on latitude, depth, and, often, season. Variability in these community and population measures can be very high because of changes in features of the substrate itself, local hydrodynamics, and other biotic and abiotic factors. However, while there is not a good quantitative comparison of community assemblages along the coast, there are some general trends that appear to occur.

Sessile invertebrate communities change noticeably with latitude and depth along the Florida coast. In intertidal hardbottoms to the north, dominant invertebrates are bryozoans, sabellariid polychaetes, sea anemones, and tunicates, although they generally do not occur in high biomass. In the more mid-sections of the east Florida coast, there is generally an increase in abundance of *P. lapidosa*, both intertidally and subtidally to approximately 4 m depth. Throughout tidal pools in these intertidal areas, *Siderastrea* spp., two species of zoanthids, and several species of solitary anemones can be encountered. Within the lower intertidal and shallow subtidal zones, the most conspicuous sponge is the rock-boring sponge *Pione* (formerly *Cliona*) *lampa*. In the more northern counties (Brevard and Indian River Counties) that have subtidal hardbottom, sponges, two species of gorgonians (*Leptogorgia virgulata* and *Leptogorgia hebes*), and one species of telestacean (*Carijoa* (*Telesto*) *riisei*) can be encountered. In this area, the most significant hard corals are *Siderastrea* spp. and the *Oculina* species. The latter two species become fairly abundant in excess of 6 m (Reed et al., 1982; D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). However, there are occasional occurrences of *Cladocora arbuscula* and grouped polyps of *Phyllangia americana* and *Astrangia* spp. (Brooke and Young, 2005; CSA International, Inc., 2008; Coastal Eco-Group Inc., 2008, 2009). Progressing southward along the coast, the diversity and abundance of anthozoans, particularly scleractinians, increases on subtidal hardbottoms (SFCREMP, 2007; J. Beal, FWC, pers. comm.). Within Martin County, the St. Lucie Inlet Reef appears to be the northernmost extent of several of the reef-building corals that are important biodiversity contributors within the Caribbean region. Within the 5 to 8 m depth range, mean percent cover of sponges is highly variable in samples, ranging between 0.14% and 10.29% (SFCREMP, 2007). In Broward County, a large percentage of the coral community in the excess of 3 to 7 m depth range is composed of the scleractinian *Acropora cervicornis* (Moyer et al., 2003; Vargas-Angel et al., 2003; SFCREMP, 2007).

4.4.4 Reproduction and Life History

A wide range of reproductive strategies is seen among the invertebrates encountered along the east Florida coast NHB. Most sessile organisms can reproduce asexually and sexually, while the majority of motile invertebrates are sexual reproducers. Both sessile and motile invertebrates tend to be short-lived (particularly in intertidal and very shallow subtidal waters), with a capability to reproduce continuously or semi-continuously.

Almost all sessile invertebrates can reproduce asexually and sexually, although the relative importance of these modes in maintaining the population is often unclear. Sponges, cnidarians, bryozoans, and colonial tunicates are all important shelter-enhancing Florida invertebrates that have these reproductive capabilities. In some cases, such as with the scleractinian *A. cervicornis*, it is known that they primarily proliferate via asexual reproduction. Asexual reproduction may be very important for a number of shelter-enhancing invertebrate species in the shallower hardbottoms, where there is generally high disturbance. Noticeable sessile invertebrates that reproduce primarily via sexual reproduction are mostly polychaetes, bivalves, gastropods, and echinoderms. In particular, the reef-building polychaete *P. lapidosa* reproduces entirely via sexual reproduction, as do the vermetid gastropods in the genus *Petaloconchus.*

Sexually reproducing sessile and motile invertebrates generally have seasonal spawning patterns, although many have the capability to spawn throughout most of the year. Seasonal spawning peaks often occur during the spring or summer time period for most of the invertebrates along the coast. However, the ability to continuously spawn is perceived to be an adaptation to take advantage of space made available by natural disturbances (McCarthy, 2001). For most sessile invertebrates, spawning is external and results in planktonic larvae, although there are instances of brooding and crawl-away young.

4.4.5 Dispersal and Connectivity

There is generally very little known regarding dispersal and connectivity of invertebrates along the east Florida coast. Considering known general reproductive capabilities of the various taxonomic groups, there is likely to be fairly low dispersal for many species, particularly the sessile ones. Tunicates, hydrozoans, some gastropods, amphipods, and isopods are likely to have the most limited dispersal capability. Sponges and hard and soft corals may be at an intermediate level of dispersal, while crustaceans, polychaetes, echinoderms, and bivalves generally should have higher dispersal and connectivity. However, several studies suggest that even some of these groups (i.e., *Phragmatopoma, Acropora*) may have fairly limited dispersal.

4.4.6 Recruitment and Cross-shelf Habitat Use

There is very limited information on seasonal recruitment patterns for invertebrates along the east Florida coast. There is essentially no information on cross-shelf habitat use. McCarthy (2001) studied the recruitment of sessile organisms in the intertidal and subtidal (3 to 4 m) zones at Boynton Beach, Florida from June 1997 to January 2000. He reported 23 species of sessile organisms recruiting to his settlement plates, with *P. lapidosa* being most commonly encountered (**Table 4.1**). The recruitment rate of some 7 to 11 species m^2/day occurred in both zones and was highest in summer and early fall. Although recruitment generally occurred at both depth zones, it was higher in the subtidal zone compared to the intertidal zone. McCarthy (2001) suggested that while high numbers of species may recruit into these habitats, most probably do not survive to adulthood. This may be due to a combination of factors. First, there was likely high mortality of recruits that could not tolerate physical factors that were very frequent, such as sand scouring and smothering. Second, high rates of *P. lapidosa* recruitment were observed to limit growth of sessile organisms, often growing over them. Finally, he also suggested that predation may not be as important in explaining recruit mortality in these two zones as the two previously-mentioned reasons. Overall, he suggested that worm reef-dominated hardbottoms appear to go through predictable patterns of annual change. These changes include high recruitment in early autumn through winter, rapid reef growth (approximately 0.5 cm/day) resulting in maximum structure in spring and summer, and decay by early autumn (**Figure 4.9**). When these data are integrated with those of Lindeman (1997a), they reveal important links between the seasonal cycle of sabellariid reef expansion and degradation and the occupation of those reefs by juvenile and adult organisms.

4.4.7 Economic and Recreational Value

Invertebrates significantly contribute to the economic and recreational value of NHBs along the east Florida coast. Sessile invertebrates such as *P. lapidosa* and a number of coral and sponge species provide high aesthetic value to NHBs as well as important shelter to many invertebrate and fish species of commercial and recreational value. Many of these species simply would not exist were it not for these foundational invertebrate species. Invertebrates also contribute to nearshore value via their significant role in the food web that again likely supports many commercially- and recreationally-important fish species. Finally, some invertebrates (e.g., spiny lobster) add value to the habitat as they are of direct commercial and recreational interest to the public.

4.4.8 The Importance of Hardbottom to Invertebrates

The presence of hardbottom is absolutely necessary for most of the invertebrates encountered along the east Florida coast. Sessile invertebrates such as corals, sponges, polychaetes, bryozoans, and tunicates are simply not found in neighboring sand bottom areas. Of these species, the lack of community contributors such as sabellariids and corals would likely result in the absence of most motile invertebrate and many fish species.

Chapter 5
Fish Assemblages

5.1 INTRODUCTION

NHB fish assemblages of mainland Florida can vary in diversity and total abundances. Very little journal literature exists on these assemblages. However, enough information is available from the gray literature and the scant research literature to allow fundamental evaluation of these often discrete, narrow habitat patches along east Florida that aggregate shallow reef organisms.

Gilmore (1977) and Gilmore et al. (1981) discussed surf zone reefs and offshore reefs in terms of fishes and habitat features. In surf zone reefs in depths of 0 to 2 m, 105 fish species were documented. A total of 192 fish species from NHB areas within a depth range of 0 to 4 m was compiled from new data or the literature (Lindeman, 1997a). The number has increased (Lindeman and Snyder, 1999; Baron et al., 2004) but has not been comprehensively revisited. Despite approximately three decades of monitoring of the juvenile-dominated and sometimes speciose NHB habitat (**Figure 5.1**), total species richness estimation is constrained by the paucity of published fish research in this habitat area. In addition, the existing fish species numbers may be low due to an absence of research on the diminutive, cryptic fish fauna, including gobiids, blenniids, and labrisomids. Ackerman and Bellwood (2000) and Robertson and Smith-Vaniz (2008) identified several problems regarding the underestimation of species diversity when cryptic ichthyofauna are chronically undersampled.

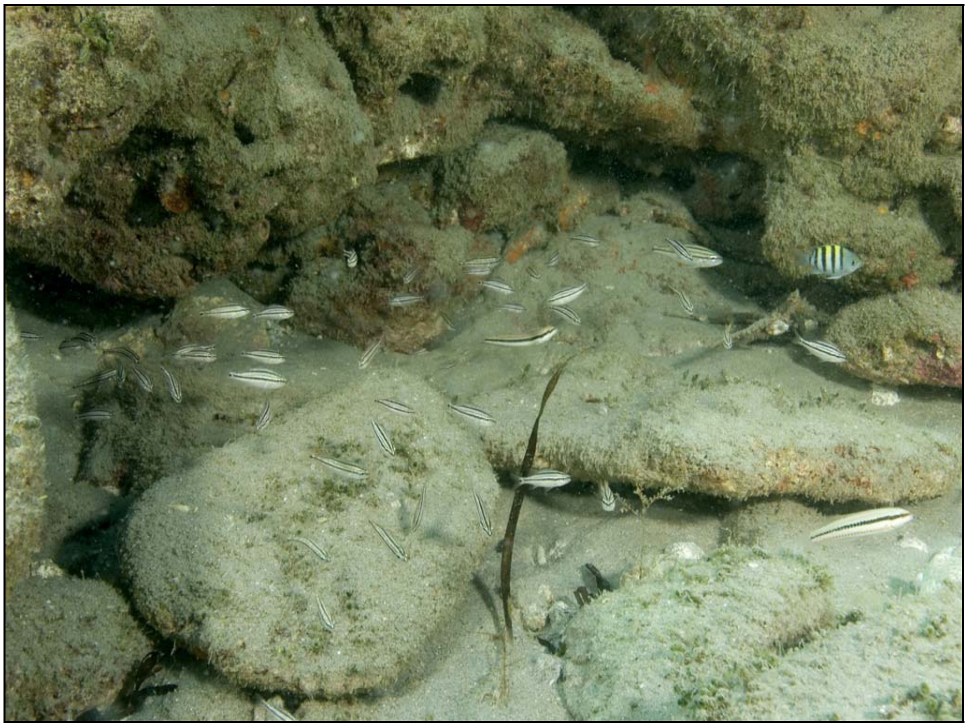


Figure 5.1. Multispecies school of juvenile fishes including four species and three families (grunts, wrasses, and damselfishes) in association with nearshore hardbottom structure. *Photo by D. Snyder.*

Of the species recorded from NHB, the great majority of abundance and frequency records involve approximately 20 to 30 species; however, assemblage composition varies latitudinally and seasonally. The species are largely within approximately 10 families and include labrids, pomacentrids, haemulids, and carangids as prominent components (Lindeman and Snyder, 1999; Baron et al., 2004). To deal with this diversity, we identified four focal group categories based on groupings that share substantial habitat use and trophic attributes (**Table 5.1**):

Demersal Carnivores: A diverse array of demersal piscivores, invertivores, and planktivores including grunts (Haemulidae), snappers (Lutjanidae), wrasses (Labridae), squirrelfishes (Holocentridae), drums (Sciaenidae), cardinalfishes (Apogonidae), sweepers (Pempheridae), and over 15 other families, including some blenniids and labrisomids. Grunts typically are the most abundant and diverse fish fauna on NHB structure of mainland east Florida, with 11 species recorded and over 80% of total individual abundance in available studies. Since new larval recruits feed on plankton, grunt early life stages can also be abundant planktivores on subsets of the shallow reef. This group also includes notable nearshore fishery species as adults or during developmental periods before maturation.

Cryptic Hardbottom Residents: The gobies, blennies, sand stargazers, clingfishes, and related forms (Blenniidae, Labrisomidae, Clinidae, Chaenopsidae, Dactyloscopidae, Gobiesocidae) include at least 25 species recorded from shallow hardbottom. Almost all of the cryptic, attached fishes have specialized morphological adaptations for NHB residency and a structure-attached life history after settlement. Though they typically perch on hardbottom, these species are trophically diverse. The gobiids and some blennies are herbivorous, but notable and mobile carnivores, including several families of eels, are also within this group (**Table 5.1**).

Coastal Pelagics: Includes transient, water-column dwelling piscivores such as jacks, mackerels (often in large schools), and sharks (Carangidae, Scombridae, and Carcharhinidae) and small, schooling bait species including the planktivorous herring, anchovies, scads, and mullets (Clupeidae, Engraulidae, Carangidae, and Mugilidae, respectively), approximately 25 species in total.

Herbivores and Omnivores: Includes approximately 20 species of damselfishes (Pomacentridae), parrotfishes (Scaridae), doctorfishes (Acanthuridae), chubs (Kyphosidae), porgies (Sparidae), and some species of filefishes (Monacanthidae) and spiny puffers (Diodontidae). The site-associated blennies (Blenniidae) are also herbivorous. Several of these species occur in very high abundance and may be of trophic significance in the uptake and energetic conversion of macroalgae and other items.

Table 5.1. Focal groups of fishes based on trophic and habitat use attributes.

Groups	Approximate Number of Families and Species	Example Families and Genera
Demersal carnivores	30 families; 10 species	Haemulidae (grunts, *Haemulon* and *Anisotremus*); Labridae (wrasses, *Halichoeres*); Sciaenidae (drums, *Pareques* and *Bairdiella*); Lutjanidae (snappers, *Lutjanus*)
Cryptic hardbottom residents	8 families; 30 species	Gobiidae (gobies, *Coryphopterus*); Labrisomidae (scaled blennies, *Labrisomus*); Apogonidae (cardinalfishes, *Apogon*); Muraenidae (moray eels, *Muraena*)
Coastal pelagics	10 families; 25 species	Carangidae (jacks, *Caranx*); Clupeidae (herring, *Harengula*); Scombridae (mackerels, *Scomberomorus maculatus*)
Herbivores	7 families; 20 species	Pomacentridae (damselfishes, *Stegastes* and *Abudefduf*); Kyphosidae (chubs, *Kyphosus*); Scaridae (parrotfishes, *Sparisoma*); Acanthuridae (surgeonfishes, *Acanthurus*); Sparidae (porgies; *Diplodus*)

For each focal group, prominent biological features are summarized with emphasis on spawning activities, shelter use characteristics, and trophic functioning in association with NHB, IHB, and shallow OHB. We do not refer to these as guilds; these groups are too diffuse and are used solely to simplify the taxonomic and ecological complexity of the fishes examined. Guilds often attempt to separate species groups according to only one primary functional category (e.g., feeding guilds or habitat associations [Appeldoorn and Lindeman, 1985; Elliot et al., 2007]), and we are not that restrictive in this case.

An additional fish assemblage occurring largely over adjacent sand plain habitats, the surf zone fish assemblage, can co-occur with NHB and IHB structure and organisms, e.g., via trans-habitat feeding migrations. There is a small literature on the species characteristics of shallow sand plain and surf zone habitats of east Florida, including Gilmore et al. (1981), Peters and Nelson (1987), and Gorecki (2007). There are significant differences in the taxonomic and ecological species compositions of adjacent surf zone and NHB fish assemblages in east Florida. For example, different sciaenid faunas (croakers and drums) occur between NHB and sand plain areas (Gilmore et al., 1981). For the family Sciaenidae, the most ecologically and economically significant species associate with sand habitats more often than reef habitats. There are also important species and process interactions between surf zone and NHB fishes (e.g., in some sites, Spanish mackerel and pompano are often caught by fishers over NHB or near the edges of NHB and sand). Ontogenetic foraging events, particularly from NHB habitats over adjacent sand plain habitats, may become important as cohorts of hundreds of surviving and maturing juveniles of grunt, wrasse, and other species migrate increasingly away from the NHB to seek more prey and habitats associated with mature stages (Randall, 1967; Parrish, 1989), often but not always in deeper water.

Based on the demonstrated or potential value of NHB areas as both nurseries and spawning sites for economically valuable species, these habitats were determined to support highly important ecological functions; a primary NMFS criterion for EFH-HAPC designation under the federal Sustainable Fisheries Act (1996). The mandate of the Sustainable Fisheries Act to conserve significant habitats drove substantial convergences between fishery management and habitat management in some areas of the country (SAFMC, 1998; Fluharty, 2000; Lindeman et al., 2000). The Federal EFH-HAPC designation has administrative significance for all species of haemulids, lutjanids, and serranids managed under the SAFMC Snapper Grouper Fishery Management Plan; this includes over 40 species, many of which are significant components of Florida's approximately $6 billion per annum recreational salt water fisheries. At least 15 of these managed species occur on NHB, typically as juveniles or earlier life stages.

5.2 DEMERSAL CARNIVORES

5.2.1 Focal Families and Species

This category includes demersal invertivores, piscivores, and planktivores that are not site-attached to hardbottom structure (**Table 5.1**). Many families are represented in NHB habitats, with some species also having significant roles on deeper and structurally different hardbottom habitats after emigrating following settlement and maturation (**Figure 5.2**). Families include the grunts (Haemulidae, 11 species recorded from NHB), wrasses (Labridae, 11 species), snappers (Lutjanidae, 6 species), squirrelfishes (Holocentridae, 3 species), drums (Sciaenidae, 6 species), groupers (Serranidae, 9 species), threadfins (Polydactylidae, 2 species), sweepers (Pempheridae, 1 species), lizardfishes (Synodontidae, 3 species), and over 15 other families.

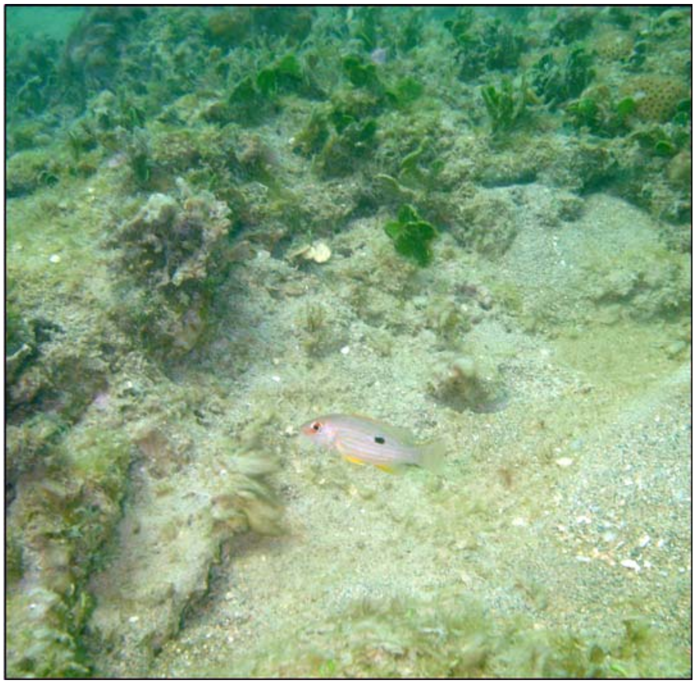


Figure 5.2. Early juvenile lane snapper (*Lutjanus synagris*) associating with algal-rock-sand interface, 3 to 4 m, John U. Lloyd State Park, Broward County, Florida. Note rapid metamorphosis compared to haemulids. *Photo by L. Jordan.*

Over 80% of the individual abundances in the NHB fish assemblage in both northern Palm Beach County and central Broward County were represented by species of grunts and margates (Lindeman and Snyder, 1999; Baron et al., 2004). Diverse and widely distributed, the 18 species of the genera *Haemulon* and *Anisotremus* (Haemulidae, Percoidei) comprise one of the most ecologically and economically important groups of reef fishes in the Western Atlantic (15 and 3 species, respectively) due to their high abundance and trophic importance as predators and prey across diverse cross-shelf habitats. There are 12 haemulid genera in the Western Hemisphere, and these taxa occupy a spectrum of habitats from riverine to deep reef (Lindeman and Toxey, 2003). Many of the reef species typically use nearshore habitats during settlement and early juvenile maturation periods and utilize offshore reefs during older life stages.

Some demersal carnivore species are significant in recreational or commercial fisheries. Their species-specific usage patterns of NHB may range from 1) habitat use primarily during early life stages, to 2) adults using NHB or adjacent areas for feeding. These species include snappers and groupers in the former category and pompano (*Trachinotus carolinus*) and sheepshead (*Archosargus probatocephalus*) in the latter group. Commonly under-recognized as NHB users, some of the most sought-after inshore gamefish species are caught on NHB habitats throughout several NHB areas of the project region, including tarpon (*Megalops atlanticus*), red drum (*Sciaenops ocellatus*), snook (*Centropomus undecimalis*), and sea trout (*Cynoscion* spp.), the majority capable of feeding on both fishes and invertebrates. Larger demersal carnivores of shallow hardbottom include sharks (**Figure 5.3**).

Figure 5.3. Resting nurse shark, *Ginglymostoma cirratum*, a generalized feeder on bottom invertebrates, 3 m depth, Palm Beach, Florida.
Photo by D. Snyder.

One demersal carnivore, striped croaker (*Bairdiella sanctaeluciae*), is listed as a species of special concern by state and federal agencies because its distribution in U.S. waters is limited to eastern Florida. This species occurs over NHB and OHB from Jupiter to Melbourne, Florida and can be locally abundant on NHB (Gilmore and Snelson, 1992) and shallow water artificial reefs (Continental Shelf Associates, Inc., 2006; Coastal Eco-Group Inc., 2009).

5.2.2 Shelter Use

5.2.2.1 Spawning Sites and Larval Transport

Spawning in many fish families that use shallow hardbottom is still poorly known. Some of the species in this category spawn in aggregations, but many spawn in pairs (Thresher, 1984). Snapper species (Lutjanidae) form spawning aggregations in southern Florida and Cuba that can potentially generate propagules that settle in eastern mainland Florida (Lindeman et al., 2000; Paris et al., 2005), but they do not spawn directly on shallow hardbottom. On the other end of the life history scale are families that greatly limit their dispersal such as jawfishes (Opistognathidae), which brood eggs in their mouths. Predicatively understanding local and meso-scale physical oceanography as well as behavioral processes will be critical to addressing such dispersal issues further. Whether the species has life history traits that predispose it to wide dispersal or local retention, larval transport is also poorly known in terms of empirical studies. Some useful information is available from studies focusing on receipt in east Florida of upstream snapper larvae from known snapper spawning aggregations in Cuba. Coupled biophysical modeling for several demersal snapper species found on east Florida NHB suggests advection rates of lutjanid larvae (lane snapper, *Lutjanus synagris*, and gray snapper, *L. griseus*) from Cuba to east Florida are relatively low (Paris et al., 2005).

Despite their abundance, information on reproduction in grunts is limited (García-Cagide et al., 2001). Fishermen have reported potential spawning aggregations, but this information requires validation (Claro and Lindeman, 2003), and spawning has not been observed in any Western Atlantic haemulids. There is little evidence that any species of *Haemulon* would spawn in association with NHB. Black margate could be an exception in deeper NHB or IHB areas, especially near channels, since this species can grow to maturity in very shallow water and there is indirect evidence that it may spawn in nearshore channels. The potential spawning of other haemulid species in deeper IHB or shallow OHB is not precluded, especially given the unusual early life history details discussed below.

Considerable evidence suggests that larvae of *Haemulon* and *Anisotremus* do not commonly leave insular or continental shelves, may associate with the bottom in transient manners within a week after hatching, and undergo a slow epibenthic metamorphosis that extends well past settlement (Lindeman et al., 2001). The evidence includes post-settlement planktivory (Helfman et al., 1982), a slow morphological metamorphosis away from larval characteristics (translucence, incomplete fin development) that continues for weeks post-settlement (Lindeman, 1986; Lindeman and Richards, 2005), and the absence of haemulid larvae from offshore ichthyoplankton surveys (Richards, 1984; Sponaugle et al., 2003). This suggests that larval dispersal may be constrained by behaviors and positioning that appear to not favor advection by flow fields.

Retention on the shelf in shallow water coupled with such early settlement, possibly involving multiple bottom-association events prior to conventional “settlement,” is a relatively uncommon early life history strategy (Lindeman et al., 2001). The typical settlement pattern for many percoid and other important groups of families involves direct settlement with a rapid metamorphosis (one to several days). Grunts, a basal-intermediate percoid family, have a slower and different demersal metamorphosis process from many other species and families.

5.2.2.2 Settlement and Early Associations with Shelter

Settlement and early habitat use of the species in the demersal carnivore group are not well known; however, general patterns that characterize certain taxa provide some insight. Most groupers are very secretive at settlement and are rarely observed during visual surveys. Another characteristic of groupers and several other species including snappers is settlement on inshore seagrass meadows. Individuals of these species will, as they grow, migrate to NHB habitats. Lane snapper and mahogany snapper (*Lutjanus mahogoni*) are two lutjanid species that appear to settle directly on NHB (lane snapper also will settle in seagrass meadows).

Grunts and margates (*Haemulon* and *Anisotremus* species) settle by 7 to 10 mm standard length (SL) at the least. These are small settlement sizes compared to most reef fish families, and grunts possess an unusual epibenthic larval stage as part of a highly extended metamorphosis that proceeds well past settlement (**Figure 5.4**). Understanding of the dense newly settled schools that grunts can form has been complicated by a sequence of two post-settlement pigment patterns (newly settled and early juvenile) that most species possess during an extended epibenthic metamorphosis (Lindeman, 1986; Lindeman et al., 2001) (**Figure 5.5**).

Few speciose genera of Western Atlantic reef fishes show such extended morphological and ecological metamorphoses at settlement. The newly settled pattern between 7 and 15 mm SL shows transitional attributes of both larval and early juvenile pigmentation and continuation of planktivory into post-settlement stages (**Figure 5.4**); delayed metamorphoses are not present in larval recruits of many other percoid fishes. Grunts are among the most common settlers in many differing shallow coastal habitats (McFarland et al., 1985; Shulman and Ogden, 1987; Lindeman and Snyder, 1999; Baron et al., 2004) and are the most common settler on shallow hardbottom of east mainland Florida of all the families in the huge perciform suborder Percoidei. Evolutionarily, the only families that are similarly abundant are in the very different suborder Labroidei (e.g., damselfishes and wrasses) (Kaufman and Liem, 1982).

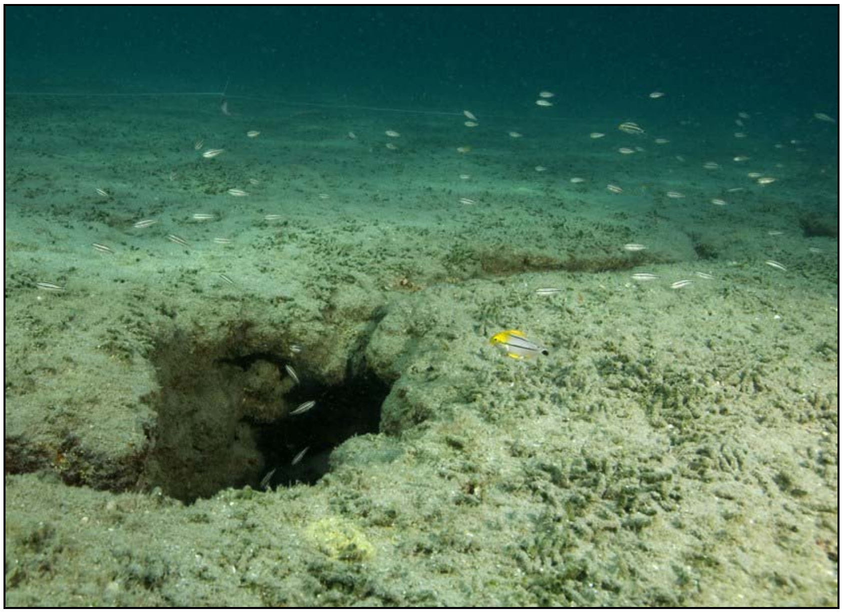
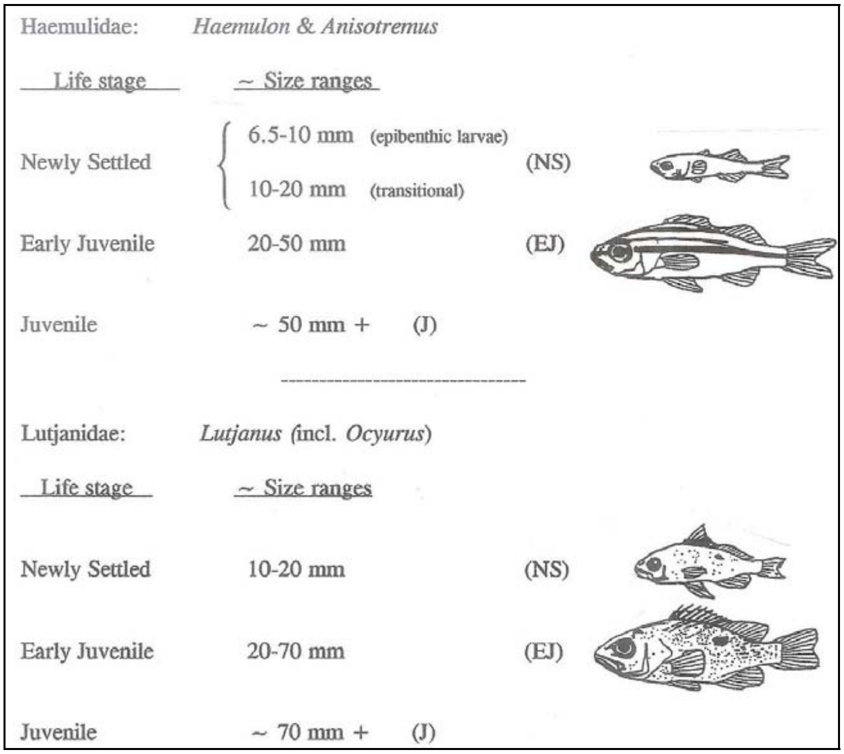


Figure 5.4. Newly settled grunts in the transitional epibenthic planktivore stage (approximately 12 to 20 mm standard length) after settlement and before adoption of demersal feeding (by the late early juvenile stage), Palm Beach, Palm Beach County, Florida. *Photo by D. Snyder.*



Haemulidae: *Haemulon & Anisotremus*

Life stage	~ Size ranges	
Newly Settled	6.5-10 mm (epibenthic larvae) 10-20 mm (transitional)	(NS)
Early Juvenile	20-50 mm	(EJ)
Juvenile	~ 50 mm +	(J)

Lutjanidae: *Lutjanus* (incl. *Ocyurus*)

Life stage	~ Size ranges	
Newly Settled	10-20 mm	(NS)
Early Juvenile	20-70 mm	(EJ)
Juvenile	~ 70 mm +	(J)

Figure 5.5. Early life stages of primary reef-associating genera of haemulids and lutjanids of the western Atlantic. Life stage designations and size ranges (mm standard length) based on morphological and ecological information from Starck, 1970; Lindeman, 1986; Richards, 1994; and Lindeman and Richards, 2005. Representative figures are of newly settled and early juvenile stages of smallmouth grunt (*Haemulon chrysargyreum*) and mutton snapper (*Lutjanus analis*).

Sweepers (*Pempheris schomburgkii*) and drums (*Pareques* spp., *Bairdiella sanctaeluciae*, and *Odontoscion dentex*), like the grunts and margates, settle in groups near vertical ledges where they are readily observed. The common wrasses such as slippery dick, puddingwife (*Halichoeres radiatus*), and clown wrasse may exhibit a very different pattern of settlement: presumably settling and burying themselves in sand bottom, remaining there for at least 5 days before emerging to take up residence on the reef (Victor, 1991).

5.2.2.3 Juvenile and Adult Habitat Use

On hardbottom from 0 to 7 m deep (mean depth of 3.9 m) in Broward County, 84% of all fishes and over 90% of all juvenile fishes surveyed were species of *Haemulon* (Baron et al., 2004). This study covered areas with wide eastward hardbottom strata crossing among NHB, IHB, and shallow OHB depth zones, in contrast to many NHB areas in northern Palm Beach County. Four of the top six most abundant species in transects were grunts, along with *H. bivittatus* and *Stegastes variabilis* (Baron et al., 2004). The most abundant grunt was “Unidentified *Haemulon* sp.” with over 8,000 individuals, with a mean total length (TL) of 2.6 cm for transect counts.

In surveys at Coral Cove County Park and Carlin Park in northern Palm Beach County, and Ocean Ridge in southern Palm Beach County, 7 of the top 12 most abundant species from the three sites were grunts and margates, in order: sailors choice (*Haemulon parra*), black margate (*Anisotremus surinamensis*), porkfish (*A. virginicus*), tomtate (*H. aurolineatum*), unidentified *Haemulon* spp., French grunt (*H. flavolineatum*), and smallmouth grunt (*H. chrysargyreum*). In all species, the most abundant life stages were early juvenile and juvenile stages, newly settled stages, and adults. Adult abundances were significantly different from pooled early life history stages in all species tested (**Figure 5.6**).

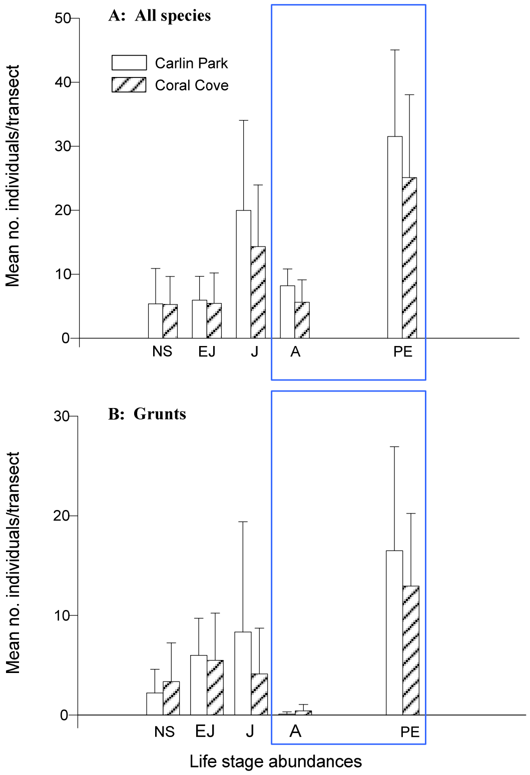


Figure 5.6. Comparisons of abundances of life history stages at two sites in northern Palm Beach County (From: Lindeman and Snyder, 1999). Boxes note comparisons between adult stages and all sub-adult stages pooled. A: All species pooled. B: Only grunts (species of *Haemulon* and *Anisotremus*) pooled. NS = newly settled; EJ = early juvenile; J = juvenile; PE = pooled early stages.

5.2.3 Trophic Patterns

There are no fish feeding studies from shallow hardbottom habitats in the project region. The most detailed examination of food habits of Caribbean reef and coastal pelagic fishes is Randall (1967). His study areas were in the U.S. Virgin Islands and Puerto Rico. These are insular systems with both similarities and differences in the seascapes that these animals move across compared to east Florida. The grunts and margates of the genera *Haemulon* and *Anisotremus* show a wide array of invertivory. Some species are planktivorous as adults (*H. striatum*), others are very specialized for feeding on hard-shelled invertebrates (*H. macrostomum*), while the majority of species are relatively generalized feeders on both soft- and hard-invertebrate prey, often from either softbottom or hardbottom environments (Randall, 1967; Sierra, 2001).

Most species are primarily demersal invertivores, as well as some important demersal piscivores and planktivores. Over 50 species of NHB fishes consume invertebrates as a primary dietary component. Eleven species of wrasse illustrate a pattern similar to grunts and other families: invertebrates from many diverse taxa are consumed by differing congeners with low to high levels of specialization within the genus. For example, many wrasse species (genus *Halichoeres*) feed on “shelled invertebrates” in the northeast Caribbean, though specific dietary compositions can vary (Randall, 1967; Randall’s data tabulated by taxa in Sierra, 2001). The dominant labrid in both the Jupiter and Fort Lauderdale studies was the slippery dick (*H. bivittatus*). This species feeds on crabs, urchins, annelids, and gastropods (Randall, 1967) and is an opportunistic feeder. Other labrids, such as the clown wrasse, *H. maculipinna*, feed primarily on soft annelids (Randall, 1967). As mentioned elsewhere, these comparative patterns are largely predictive without empirical feeding information from the project region.

Additional invertivores on NHB habitats include snake eels (Ophichthidae), one species of moray eel (chain moray, *Echidna catenata*), and squirrelfishes (Holocentridae), which feed on crabs, shrimp, and molluscs. Smaller serranids (*Serranus* spp.) and reef drums including *Pareques lanceolatus* and *P. punctatus* prey upon shrimp, echinoids, and annelids. Several species of goatfishes (Mullidae) and some labrisomid species prey upon swimming crabs and ophiuroids. Juvenile stages of most snapper species feed on crabs and shrimp and with growth switch to fishes. The boxfishes (Ostraciidae) broadly feed on sponges, sipunculids, tunicates, and crustaceans. Spiny puffers (Diodontidae) feed on gastropods, echinoids, and crabs (Randall, 1967).

Piscivorous families on NHB include the lizardfishes (Synodontidae) and older groupers and snappers. Most species of moray eels are also piscivores, but these are considered under cryptic hardbottom residents. These species consume a high diversity and abundance of smaller prey fishes above or adjacent to reef structure. Common prey items include juvenile stages of grunts, wrasses, and herring (Randall, 1967).

Demersal planktivory by older juveniles and adults is present among cardinalfishes (Apogonidae), sweepers (Pempheridae), and species such as yellowtail snapper. The apogonids reside in crevices during the day and feed on the larvae of shrimp, crabs, and annelids in the northeast Caribbean (Randall, 1967). Based also on the work of Randall (1967) and Gladfelter (1979), the copper sweeper (*Pempheris schomburgkii*) also resides near crevices and overhangs where it feeds on annelid larvae and other plankton. Large schools of newly settled individuals are commonly observed. They appear to possess an extended epibenthic larval period similar to grunts. Less common yellowtail snapper feed on a variety of plankton in the water column above the surface of hardbottom structure.

5.2.4 Developmental Patterns and Cross-shelf Habitat Use

The great diversity of families and species of demersal invertivore groups and the absence of habitat use literature from east Florida NHB constrains broad summary, as does geographic variation. However, the available information suggests over 30 species of haemulids, labrids, lutjanids, sciaenids, serranids, and others typically redistribute across the shelf during development, often into deeper waters.

The degree to which maturing juveniles on discrete NHB patches can successfully emigrate to deeper water reef structure is unexamined. Based on the data and evidence from other studies, some species assumedly should attempt to emigrate away at a certain age. We assume this process is gradual and involves exploratory behavior that may be associated with nocturnal sand plain feeding migrations in some species (e.g., snappers, grunts). The advent of small telemetric tags used in conjunction with a coordinated set of cross-shelf receiving stations could help resolve this issue for some species.

5.2.5 Latitudinal Distribution

Information from multiple sites is limited and comparisons are complicated by variable relative abundances of NHB, IHB, and connected OHB habitats among the counties (**Table 2.1**), the very different geomorphologies and oceanographic conditions latitudinally, and by the differing depths examined in the existing studies.

Some differences among ichthyofaunal assemblages are seemingly present between the southern and northern areas of mainland southeast and east-central Florida in terms of the most abundant species. Baron et al. (2004) found one black margate, *Anisotremus surinamensis,* out of >72,000 individuals from 164 families recorded in Fort Lauderdale in the summer of 2001. To the north, Lindeman and Snyder (1999) found 636 *A. surinamensis* out of 10,491 individuals censused, 6% of the overall assemblage. *A. surinamensis* in the Jupiter area ranked seventh in individual abundance of over 80 species recorded.

In the same studies, Baron et al. (2004) found 43 sailors choice, *Haemulon parra,* out of 72,000 fish recorded; most were older juveniles with mean lengths between 15 and 17.5 cm. A total of 58,000 grunts ranging from 1 to 7 cm TL (mean of approximately 2.6 cm), >80% of the total number of species recorded, was identified as *Haemulon* sp. in the Broward research. *H. parra* in the Jupiter area ranked first in abundance of all species. Lindeman and Snyder (1999) found 1,326 *H. parra* individuals, primarily early juvenile and newly settled stages, 13% of all fishes recorded in 2 years. There is a similar difference between south and north abundances in the hairy blenny, *Labrisomus nuchipinnis*; a dominant cryptic hardbottom resident species of the Jupiter area and sites to the north (Gilmore, 1977; Gilmore et al., 1981; Lindeman and Snyder, 1999) that was uncommon in Broward surveys (Baron et al., 2004).

Given the high number of species and families and the substantial physiographic transitions between Miami and Cape Canaveral, there have to be some species whose distribution and abundance patterns consistently differ between the northern and southern areas of the project region. Absent further empirical information from more equivalent depth settings, the early comparisons of latitudinal variation above will remain somewhat tenuous until more studies become available.

5.3 CRYPTIC HARDBOTTOM RESIDENTS

5.3.1 Focal Families and Species

Shelter association and trophic diversity are high among cryptic hardbottom resident species. For example, five primary cryptic resident families (gobiids, labrisomids, clinids, blenniids, and chaenopsids) and their over 25 phylogenetically similar species show feeding patterns that vary from herbivory (all gobiids and some common blennies) to invertivory (cardinalfishes, squirrelfishes) and piscivory (eels).

5.3.2 Shelter Use

5.3.2.1 Spawning and Larval Transport

Little is known of the spawning and larval biology of cryptic hardbottom resident species in east Florida. The available evidence suggests that most cryptic NHB-associated species can build nests. Compared to some other nest layers at these depths (e.g., damselfishes), the nests of most cryptic residents of NHB-IHB habitats are typically more cryptic, often under overhangs or deep in small holes and crevices. The molly miller (*Scartella cristata*) will deposit eggs in empty barnacle shells or abandoned worm holes (Breder and Rosen, 1966). Direct assessment of spawning biology is limited. Indirect evidence includes color patterns associated only with courtship and spawning (**Figure 5.7**). Gobies, blennies, and associated cryptic resident taxa tend nests of eggs.

Figure 5.7. Spawning coloration in male hairy blenny (*Labrisomus nuchipinnis*), with female in background, 2 m depth, Pecks Lake Reef, southern Martin County, Florida. *Photo by T. Gibson.*

There is considerable information from some congeneric gobiids and blenniids from the Pacific coast of North America (or confamilials). In these species, often residing in tidepools and rocky subtidal and intertidal habitats, the available evidence suggests larval dispersal patterns are frequently limited (Gunderson et al., 2008). Larval retention is a primary early life history characteristic of many rocky intertidal species (Marliave, 1986; Strathmann et al., 2002; Broitman et al., 2008; Gunderson et al., 2008).

5.3.2.2 Settlement and Early Habitat Associations

Early development and settlement is also poorly known in the cryptic residents of shallow hardbottom of east Florida. Breitburg (1991) documented features of demersal schooling before settlement in the naked goby. Developmental studies of many species detail how the pectoral fins are modified and fused into ventral, cup-like structures that allow direct attachment to NHB structure in high wave energy environments. These structures are formed by the time the age at which settlement can occur is reached.

5.3.2.3 Juvenile and Adult Habitat Use

Figure 5.8. A cryptic hardbottom resident, spotted moray eel (*Gymnothorax moringa*), depth 2 m, MacArthur Beach State Park, Palm Beach County, Florida. *Photo by D. Snyder.*

Cryptic resident species do not appear to migrate further offshore with development, displaying no cross-shelf ontogenetic migrations. They are life-long residents of the NHB, IHB, or shallow OHB structure on which they settle, and display feeding modes from herbivory to probable piscivory (**Figure 5.8**). Nine species of gobies and blennies were recorded as “restricted to the nearshore” in Baron et al. (2004): four labrisomid species, four gobiids, and one blenniid species; this number represents 45% of all the species they estimated to be nearshore-restricted.

Hairy blenny was the largest and most abundant cryptic hardbottom resident in the Jupiter surveys, with 806 individuals recorded out of 10,491 individuals censused, 8% of the overall individual total (Lindeman and Snyder, 1999). Hairy blenny ranked fifth in individual abundance of over 80 species recorded. Hairy blenny was also the most abundant cryptic hardbottom species on Ambersand mitigation reef surveys, Indian River County, representing 30% of the individuals censused on artificial reefs and natural nearshore hardbottom over 3 years of annual monitoring (Coastal Eco-Group Inc., 2009). Baron et al. (2004) recorded no hairy blennies on transect and point-counts in Fort Lauderdale, though the species was recorded in qualitative roving diver surveys. They found the bridled goby, *Coryphopterus glaucofraenum,* and the rosy blenny, *Malacoctenus macropus*, at 2 to 5 cm size ranges to be the most abundant cryptic resident species.

Other cryptic taxa observed on NHB include moray eels (Muranenidae), snake eels (Ophichthidae), soapfishes (Serranidae), and cardinalfishes (Apogonidae). Juveniles and adults from these groups are generally solitary, dwelling under ledges and in crevices provided by NHB, IHB, or OHB. All of these taxa are predatory and generally leave their hiding places to forage at night. Baron et al. (2004) recorded spotted moray, purplemouth moray, and goldentail moray offshore Fort Lauderdale; spotted snake eel also occurred within their study area. In Jupiter, Lindeman and Snyder (1999) observed all of these eels except the purplemouth moray, but also reported the chain moray (*Echidna catenata*).

Cardinalfishes (apogonids) were more diverse and abundant in visual samples recorded in Fort Lauderdale (Baron et al., 2004) in data from 0 to 7 m. Two genera and six species were reported, with twospot cardinalfish (*Apogon pseudomaculatus*) and flamefish (*Apogon maculatus*) represented by the most individuals. Cardinalfishes were less commonly seen in Jupiter censuses; flamefish was the only species recorded. Greater soapfish (*Rypticus saponaceous*) is the most commonly observed soapfish in the region and was infrequently seen by Baron et al. (2004) and Lindeman and Snyder (1999).

5.3.3 Trophic Patterns

Highly diverse feeding patterns exist among cryptic hardbottom fish species. Herbivory, invertivory, planktivory, and piscivory are all known for the small fishes that attach to NHB structure, often out of human sight. Randall (1967) found that “all gobiids” and two common blenny species (*Scartella cristata* and *Parablennius marmoreus*) fed primarily on algae in the U.S. Virgin Islands and Puerto Rico.

Labrisomids such as the very common hairy blenny, a generalized invertivore in Randall (1967), probably can also feed upon late stage larvae of some reef-associated fishes such as grunts (R.G. Gilmore, Jr., Estuarine, Coastal, and Ocean Science, Inc., Vero Beach, FL, pers. comm.). First-ever food habit studies on these and other NHB species would be of great value, as knowledge of the trophic structure of this east Florida fish subassemblage is depauperate.

5.3.4 Latitudinal Distribution

As was the case for grunts, there is a contrast between the southern and northern sites surveyed in Baron et al. (2004) and Lindeman and Snyder (1999). No hairy blennies were recorded on transect and point-counts in Fort Lauderdale, though the species was recorded in qualitative roving diver surveys (Baron et al., 2004). In contrast, hairy blenny was the largest and most abundant cryptic hardbottom resident in the Jupiter surveys to the north, with 806 individuals recorded out of 10,491 individuals censused, 8% of the overall individual total (Lindeman and Snyder, 1999). Hairy blenny ranked fifth in individual abundance of over 80 species recorded.

By definition, the visual methods used by Baron et al. (2004) and Lindeman and Snyder (1999) will not fully account for all cryptic species present in the area. Accordingly, other cryptic taxa were seldom observed and therefore contribute little information to support analyses of latitudinal patterns. Nevertheless, some basic patterns may be described for the soapfishes and cardinalfishes. For soapfishes it appears that the whitespotted soapfish is more common north of Broward County and the greater soapfish is more prevalent from Palm Beach County southward. As mentioned above, the cardinalfishes were much more diverse in the southern area samples, and observations on OHB indicate that cardinalfish species drop out with increasing latitude to about Jupiter; from this area north, twospot cardinalfish and flamefish are the most commonly-observed species on OHB and NHB.

5.4 COASTAL PELAGICS

5.4.1 Focal Families and Species

Though typically transient, coastal pelagic fish species can interact with NHB in manners that have local trophic impacts. Their roles as both predators and prey can be seasonally significant. We therefore consider coastal pelagic species as a transient subcomponent of the larger NHB-associated ichthyofauna. The species in the coastal pelagic functional group are water-column dwelling, often schooling fishes that are typically moving. These species usually do not reside on NHB for extended periods of time.

The diverse taxa of the coastal pelagic group includes

- small, schooling herring, anchovies, scads, mullets, and halfbeaks (Clupeidae, Engraulidae, Carangidae, Mugilidae, and Hemiramphidae, respectively), prey to many NHB resident and transient species;
- large, schooling mackerels, bluefish, and pompanos (Scombridae, Pomatomidae, and Carangidae, respectively) in cooler months, predators on many nearshore fishes and prey to anglers; and
- the largest apex marine predators of coastal Florida, several shark species such as nurse, requiem, and hammerhead (Ginglymostomatidae, Carcharhinidae, and Sphyrnidae, respectively), some of which are commonly solitary, whereas others can form schools. Many of these species, including blacktip (*Carcharhinus limbatus*), blacknose (*C. acronotus*), bull (*C. leucas*), spinner (*C. brevipinna*), tiger (*Galeocerdo cuvier*), and lemon (*Negaprion brevirostris*) sharks, are federally managed (NMFS, 1999).

5.4.2 Shelter Use

5.4.2.1 Spawning and Larval Transport

Some of these species have little or no association with particular bottom types while spawning. Structural components of the water column, such as temperature gradients, may have more of a habitat influence than bottom type (Kingsford et al., 2002). Several clupeids have been observed with developing or ripe ovaries in nearshore waters of Palm Beach County, particularly Spanish sardine (*Sardinella aurita*), false pilchard (*Harengula clupeola*), and scaled sardine (*H. jaguana*) (D. Snyder, CSA International, Inc., pers observ.). Bigeye scad (*Selar crumenophthalmus*) also has been collected with ripe ovaries in nearshore waters adjacent to NHB (Continental Shelf Associates, Inc., 1992).

Although there is little direct evidence of coastal pelagic species spawning over or adjacent to NHB, when depth preferences and behavior are considered, it could occur in some species. For example, Atlantic thread herring (*Opisthonema oglinum*), Spanish sardine, and round scad (*Decapterus punctatus*) would probably spawn in deeper offshore waters, whereas the false pilchard, scaled sardine, and redear sardine (*Harengula humeralis*) are more likely to spawn in shallow habitats such as NHB (e.g., Martinez and Houde, 1975). Another group that spawns in shallow coastal waters and has been observed over NHB, IHB, and OHB off Palm Beach (the northern limit of its distributional range) are the halfbeaks (*Hemiramphus brasiliensis*) and (*H. balao*) (Berkeley and Houde, 1978; McBride et al., 2003).

5.4.2.2 Settlement and Early Habitat Associations

Many coastal pelagic species do not appear to possess a discrete, bottom-associated settlement event associated with NHB. However, schools of late-stage larvae of some herring and jack species can occur nearshore. Some herring and anchovy species, including species such as the thread herring (*Opisthonema oglinum*) and *Anchoa* spp., can form schools of elongate, translucent late-stage larvae in the water-column above NHB and IHB structure.

Jacks are a diverse family with many representatives associating with NHB, IHB and OHB. Early life stages of many of the jacks, including *Caranx* spp., bigeye scad, and round scad, associate with drifting flotsam and *Sargassum* and utilize nearshore environments, including NHB, following strong easterly winds. Others, particularly Atlantic bumper, associate with large jellyfishes and are similarly transported from the open ocean into NHB areas.

As mentioned above, most jacks species, including scads (*Selar crumenophthalmus*; *Decapterus* spp.), crevalles (*Caranx* spp.), amberjacks (*Seriola* spp.), Atlantic bumper, and rainbow runner (*Elagatis bipinnulata*), settle and associate with flotsam and *Sargassum*. Individuals from another group of jacks, consisting of Florida pompano (*Trachinotus carolinus*), permit (*T. falcatus*), and palometa (*T. goodei*), settle in very shallow coastal water (Fields, 1962) and will opportunistically shelter in tide pools formed by NHB, such as in Brevard County NHB (Continental Shelf Associates, Inc., 2005c).

Baron et al. (2004) observed seven species from five genera of jacks. In their surveys of NHB and OHB, the bar jack (*Caranx ruber*) accounted for most of the observations and ranged from 3 to 25 cm TL. To the north, yellow jack (*C. bartholomaei*) was the most commonly observed carangid on NHB (Lindeman and Snyder, 1999).

5.4.2.3 Juvenile and Adult Habitat Use

Clupeid and engraulid records from all survey methods in the Fort Lauderdale and Jupiter study areas are absent or very low, respectively. Only Spanish sardine and unidentified engraulids were recorded from Jupiter NHB transects (scaled sardine was also found over open sand, near NHB). Based on roving diver surveys and on-water boat observations, the diversity and abundance of highly motile, surface-associated herring and anchovy species in association with NHB is underestimated by transect and point-count methods. Continental Shelf Associates, Inc. (1992) collected juvenile bigeye scad in mixed schools of juvenile clupeids associated with NHB in Jupiter and Palm Beach.

Transect counts of jacks (carangids) at Fort Lauderdale sites found bar jack, yellow jack, and blue runner (*Caranx crysos*) at minimum sizes of 3, 7, and 7 cm TL, respectively. Mean lengths surveyed for these species were 8, 15, and 14 cm SL, respectively (Baron et al., 2004). Many of these individuals were juvenile stages, with bar jack in association with shallow hardbottom structure at post-settlement stages. Juveniles of these species were also recorded in the Jupiter surveys where divers observed post-settlement behavior in yellow jack at 3 cm. Schools of thousands of scombrids and bluefish are often fished in IHB but have not been censused.

An exceptional example of a coastal pelagic schooling species in association with shallow hardbottom exists at the Peck’s Lake reef system in southern Martin County, where a semi-continuous gradient of worm-rock encrusted hardbottom extends from NHB through OHB depths and is used by a massive seasonal adult aggregation of Spanish mackerel (*Scomberomorus maculatus*). This aggregation has been highly predictable in the late fall through winter (October to late March) and heavily fished for well over a decade. There is little direct information on what the aggregating mechanism is; perhaps it is feeding. There is no evidence of spawning in the Peck’s Lake system, with spawning probably occurring later in spring and further offshore. The area is characterized by expansive NHB and IHB reefs, some with high (2 m) and convoluted relief, many with substantial *P. lapidosa* habitat structure, most of it the remaining framework of dead colonies. Unlike many NHB systems, hardbottom extends to approximately 8 m depths offshore.

Before the highly touted and exploited Spanish mackerel fishery at Peck's Lake reef, there was a massive seasonal aggregation of mackerel and bluefish inside the Lake Worth Lagoon, 45 km to the south. These fish entered Lake Worth usually during March and April, presumably on their way back north following the regular southerly migration triggered by the passage of winter cold fronts. This subpopulation was fished regularly by hundreds of small commercial hook-and-line fishermen, maintained consistency for years, and was considered a limitless resource. The aggregation began to diminish by the mid-1970’s with the growth of the commercial fishery, and also because of water quality degradation in the lagoon from increased dredge-and-fill activity in the lake and the expansion of the Port of Palm Beach (T. Twyford, West Palm Beach Fishing Club, West Palm Beach, FL, pers. comm.). When the fishery evolved beyond hook-and-line fishers, big net boats with roller rigs, spotter planes, and run-around gill nets heavily fished mackerel up and down the east Florida coast. The fishery begin to rebound through tighter gear restrictions and quota limitations, then the net ban in 1995 further boosted mackerel recovery. It appears that since the net ban, Spanish mackerel have been able to stay in the Pecks Lake area for long stretches with less disturbance from the current heavy hook-and-line fishing than from the run-around nets used before the net ban. Run-around nets also took other coastal pelagic species that associate with NHB, including ladyfish (*Elops saurus*) and jack crevalle (*Caranx hippos*).

There are reports of a sizable aggregation of small Gulf kingfish (*Menticirrhus littoralis*) near Jap Rock in Boca Raton that occurs February/March; it is not as large as the Peck’s Lake aggregation and receives less fishing pressure (T. Gibson, Outdoor Life Magazine, pers. comm.). King mackerel (*Scomberomorus cavalla*) form similar aggregations at various sites further out on the shelf and shelf edge, as do the little tunny (*Euthynnus alletteratus*), but aggregations of neither species maintain as long as the Spanish mackerel do at Pecks Lake (D. Snyder, CSA International, Inc., pers. comm.). There are a few other predictable Spanish mackerel aggregations that also occur seasonally in Florida Bay and on Florida's southwest coast in the winter (T. Twyford, West Palm Beach Fishing Club, West Palm Beach, FL, pers. comm.).

Each year in the fall, adult and subadult striped mullet (*Mugil cephalus*) mass migrate along the coast of southeastern Florida. Although not directly associating with NHB, the large schools of mullet pass near and over hardbottom areas during their migration.

Adult bull sharks were observed at Coral Cove in northern Palm Beach County during July 2004 (Continental Shelf Associates, Inc., 2005b). Large schools of blacktip and spinner sharks migrate along the east Florida coast during winter and early spring (D. Snyder, CSA International, Inc., pers. observ.). Groups of individuals from larger schools will associate with NHB temporarily (for a few days or weeks) during the migration. Large individuals of great hammerhead (*Sphyrna mokkaran*) are occasionally observed following the migrating blacktips (D. Snyder, CSA International, Inc., pers. observ.).

5.4.3 Trophic Patterns

Many coastal pelagic species are prominent piscivores, typically transient but capable of substantial localized predation in deeper NHB through OHB habitats. Prominent piscivorous species include the jacks, mackerels, cobia, and requiem sharks. Many piscivorous species also can feed on invertebrates. In Randall (1967), approximately half of the species of jacks fed on bottom macroinvertebrates, including shrimp, cephalopods, and crabs, while the gut contents of the other half of the species indicated they were piscivorous. The most abundant species in both the Jupiter and Fort Lauderdale surveys were the yellow jack and bar jack, species recorded to feed on invertebrates and fishes and only fishes, respectively.

The piscivorous coastal pelagic subgroup includes some gamefish species that are preyed upon by seasonal aggregations of marine mammals (dolphins) that gather in coastal NHB through OHB environments in the fall and winter to feed on Spanish mackerel, bluefish, and cobia. These same species are also targeted by recreational anglers. The mackerel and bluefish are on the seasonal southern boundary of their fall migration to warmer water prior to late spring spawning off east Florida. Sharks are also routinely fished and sighted by anglers and surfers in deeper NHB and OHB areas; these species include nurse, blacktip, spinner, bull, lemon, sandbar (*C. plumbeus*), sharpnose (*Rhizoprionodon terraenovae*), and tiger sharks.

Primary plantivorous coastal pelagic species include the Spanish sardine, round scad, bigeye scad, and thread herring (*Opisthonema oglinum*). In the northeast Caribbean, thread herring fed on copepods and also the planktonic stages of annelids and crustaceans (Randall, 1967).

5.4.4 Latitudinal Distribution

Observations of coastal pelagic species utilizing NHB in Fort Lauderdale (Baron et al., 2004) and Jupiter (Lindeman and Snyder, 1999) were limited to the jacks previously discussed. Differences in the numbers and kinds of coastal pelagic species between these two studies are difficult to explain because the visual sampling methods used do not adequately sample such highly migratory species.

Some of the most prominent and seasonally periodic coastal pelagic species are warm temperate migrants from cooler, Carolinian waters of the South Atlantic Bight. Examples of seasonal transient schoolers that range from the shelf edge through NHB structure include bluefish (*Pomatomus saltatrix*) and Spanish mackerel. These species can probably be significant predators on OHB through deeper NHB habitats in the northern study area when large schools migrate off east-central Florida in fall months. However, these species typically do not go as far south as the NHB in Broward and Miami-Dade Counties.

5.5 HERBIVORES AND OMNIVORES

5.5.1 Focal Families and Species

Many schooling herbivores common to Caribbean reefs occur in association with NHB and include the surgeonfishes (Acanthuridae), parrotfishes (Scaridae), porgies (Sparidae), and chubs (Kyphosidae); most of these families are represented largely by juvenile life stages, but also frequently occur as adults (Lindeman and Snyder, 1999; Baron et al., 2004). Non-schooling herbivores on NHB include the damselfishes (five species), filefishes (Monacanthidae), spiny puffers (Diodontidae), presumably all gobiids, and several blenniids (Randall, 1967).

Herbivorous fishes may be defined as browsers on macroscopic algae and grazers on turfing algae (e.g., Choat et al., 2002; Floeter et al., 2005). In NHB environments, herbivores represented few species, but these can be locally abundant. Browsers are represented by the chubs (*Kyphosus sectatrix* and *K. incisor*) and adult porgies (*Diplodus* spp.). The chubs will also feed in surface waters on drifting *Sargassum* algae. Grazers are represented by surgeonfishes (*Acanthurus* spp.) and parrotfishes (primarily *S. rubripinne*).

There can be substantial ontogenetic variation in feeding among some species. For example, the silver porgy (*Diplodus argenteus*), a very abundant sparid on NHB, is probably omnivorous like its closely related congener, the spottail pinfish, *D. holbrooki.* The latter species was found to eat both algae and macroinvertebrates by Hay and Sutherland (1988) in a study of rocky jetty-type structures in Murell's Inlet, South Carolina. Carr and Adams (1972) documented that *D. holbrooki* fed on ectoparasites and were therefore considered to be cleaners. Juveniles of *D. argenteus* have been observed cleaning larger fishes in NHB environments (D. Snyder, CSA International, Inc., pers. observ.).

5.5.2 Shelter Use

5.5.2.1 Spawning Areas and Larval Transport

Nearshore spawning in most motile and site-associated herbivores is not well known. There is considerable information from other locations and typically deeper, more coralline habitats for damselfishes. At least four damselfish species (sergeant major [*Abudefduf saxatilis*], cocoa damselfish [*Stegastes variabilis*], dusky damselfish [*S*. *adustus*], and beaugregory [*S*. *leucostictus*]) can spawn directly on NHB surface to build their egg nests (**Figure 5.9**). These species can clear algae from the substrata and lay adhesive demersal eggs directly onto the rock surface.

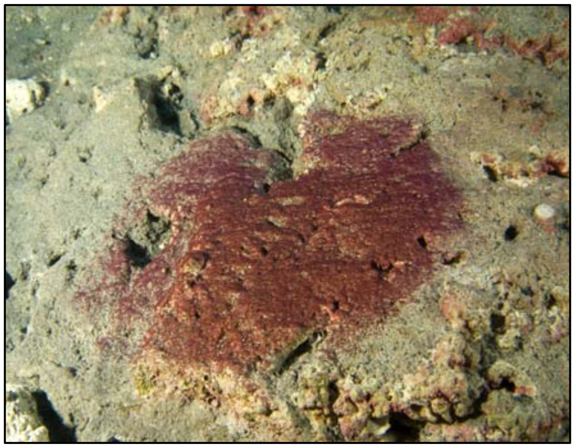


Figure 5.9. Example of nest of the sergeant major (*Abudefduf saxatilis*) on hardbottom, 20 m depth, Jupiter, Palm Beach County, Florida.
Photo by D. Snyder.

It is difficult to summarize the use of NHB habitat for spawning in non-nesting species of herbivorous fishes since research information is very limited. Many species exhibit larger adult populations on deeper reefs, but the complexity is amplified in areas of the study region where NHB is not discrete, but is instead part of a continuous IHB through OHB habitat gradient. Other prominent taxa that can potentially spawn in association with NHB include porgies (Sparidae).

Many other herbivores that use NHB are primarily represented by early life stages and typically do not spawn in association with NHB, though they may spawn in association with OHB. This includes some species of scarids and acanthurids.

5.5.2.2 Settlement and Early Associations with Shelter

At least 20 species of herbivorous fishes settle on NHB. The more abundant of these include some of the most well known reef fishes of the Caribbean: sergeant major, cocoa damselfish, redfin and bucktooth parrotfishes (*Sparisoma rubripinne* and *S. radians*, in northern and southern sites, respectively), and doctorfish and ocean surgeonfish (*Acanthurus chirurgus* and *A. bahianus*, respectively). Seasonal recruitment pulses of these and other herbivores may simultaneously influence algal assemblage composition and provide a prey base for larger piscivores.

Herbivorous species of damselfishes and surgeonfishes have displayed substantial temporal variation in larval recruitment studies in other regions, and these patterns have been used to argue that coral reef fishes represent non-equilibrium systems (Sale, 1991). Notably, these studies are typically from deeper and more coralline habitats. It is logical to also treat NHB habitats as non-equilibrium systems that are highly mediated by disturbances that impact algal and herbivore abundance in unstudied manners.

Most of species of scarids (parrotfishes) settle on NHB or IHB. Baron et al. (2004) recorded stoplight (*Sparisoma viride*) and bucktooth parrotfishes as small as 2 cm and six other species including *Scarus* spp. and bluelip parrotfish (*Cryptotomus roseus*) as small as 3 cm, strongly suggesting that these individuals settled on NHB or OHB in their study area. Lindeman and Snyder (1999) observed newly settled silver porgy that settled predictably in relatively high numbers during late winter and early spring. Damselfishes and chubs do not appear to have particularly distinct settlement seasons but were sporadically observed as newly settled individuals.

5.5.2.3 Juvenile and Adult Habitat

Shelter use characteristics of herbivores largely involve daytime site associations and social behaviors that can be considered in terms of either site-associated species or wide-ranging, often schooling species. The primary site-associated herbivores include at least two different groups: the damselfishes, which can enforce relatively sizeable territories to maintain algal feeding sites, and species of gobiids and blenniids. The feeding of the latter group is less known than in damselfishes, but is assumed to be associated with short-distance benthic browsing movements. More motile and gregarious species also feed on NHB macroalgae, including surgeonfishes, parrotfishes, and chubs. These species can form sizable schools that effectively remove macroalgal cover on deeper reefs.

The numerical contribution of herbivores to the assemblages characterized by Baron et al. (2004) in Fort Lauderdale and Lindeman and Snyder (1999) in Jupiter differed in terms of overall diversity and abundance of dominant taxa. Censuses conducted in Jupiter (Lindeman and Snyder, 1999) revealed that 26% of the individuals observed were herbivores, numerically dominated by (in rank order of abundance) silver porgy, cocoa damselfish, ocean surgeon, doctorfish, redfin parrotfish, redtail parrotfish (*S. chrysopterum*), and juvenile parrotfish (*Sparisoma* spp.). The diversity of herbivores, especially the parrotfishes, was higher in the southern area studied by Baron et al. (2004). They observed 17 herbivore species, including damselfishes, porgies, surgeonfishes, parrotfishes, and chubs; this group was dominated numerically by bucktooth parrotfish. Parrotfishes represented 2% of the individual abundances recorded in transects by Baron et al. (2004). Lindeman and Snyder (1999) found higher abundances of chubs, porgies, and cocoa damselfishes in Jupiter.

5.5.3 Trophic Patterns

Early life stages of schooling herbivores frequently occur in association with NHB and include the surgeonfishes (Acanthuridae), parrotfishes (Scaridae), chubs (Kyphosidae), and porgies (Sparidae) (**Figure 5.10**). Available evidence suggests that all the species of the three former families are almost wholly herbivorous (Randall, 1967; Sierra, 2001), but the porgies are not. The seasonally abundant silver porgy, *D. argenteus*, fed on algae, gastropods, and crabs in the northeast Caribbean and is omnivorous (Randall, 1967). Non-schooling herbivores that are residents on NHB include the damselfishes (five species), some species of filefishes, one species of spiny puffer, several blenniids, and perhaps all of the gobiids (Randall, 1967).

Figure 5.10. Early juvenile stages of reef herbivores including surgeonfishes, damselfishes, and parrotfishes on nearshore hardbottom, 3 m depth, Palm Beach, Palm Beach County, Florida. *Photo by D. Snyder.*

There are few or no feeding studies on these families from east Florida hardbottom habitats. In the northeast Caribbean, all species of *Stegastes* are omnivorous, with some annelids and crustaceans as well as algae seen in their gut contents. Beaugregory and threespot damselfish (*Stegastes planifrons*) were found to have the most algae in their diet per volume (Randall, 1967). Sergeant major also is omnivorous, feeding on algae, anthozoans, and crustaceans. Based on Randall (1967), omnivores include 1) species of filefishes that feed on hydrozoans, algae, gorgonians, and zooantharians, and 2) the sharpnose puffer, *Canthigaster rostrata*, which feeds on plants, sponges, echinoids, and molluscs.

Hay and Sutherland (1988) state that in warm temperate, rocky nearshore habitats, well-lit areas are algae-dominated and shaded areas are the realm of invertebrates. In east Florida, we cannot falsify this since well-lit open areas of NHB can be dominated by algae (though *P. lapidosa* encrustations can also dominate in some locations). This is presumably one reason that from a distance, the ichthyofauna on the well-lit crests of shallow hardbottom can appear to be dominated by herbivores (chubs, porgies, damselfishes), while many invertivores are located near-bottom, associated with microhabitats away from the most well-lit and open areas.

5.5.4 Developmental Patterns and Cross-shelf Habitat Use

Resident herbivores such as damselfishes and cryptic hardbottom species do not engage in ontogenetic habitat shifts. Some schooling species (surgeonfishes, parrotfishes, or chubs) represented largely by juveniles on NHB may migrate away from NHB to deeper structural habitats with maturation, but definitive information is unavailable. The ability to successfully make such migrations will correlate in complex manners with the degree to which cross-shelf habitat corridors are available and also drivers associated with potential ontogenetic shifts in food needs.

5.5.5 Latitudinal Distribution

There are complex similarities and differences in the presence and abundance of herbivores between the two sites for which quantitative data are available. Cocoa damselfish was the most abundant pomacentrid in both studies, however, the closely-related beaugregory was much more abundant at the southern site. Sergeant major were abundant in both areas (Lindeman and Snyder, 1999; Baron et al., 2004).

The silver porgy (represented primarily by juveniles, which are not herbivorous) was the second-most abundant species at the northern Jupiter sites but was not a significant component of the Fort Lauderdale assemblage (Lindeman and Snyder, 1999; Baron et al., 2004). More parrotfish species were found in the Fort Lauderdale study, probably due to the wider depth distributions of the surveys. Floeter et al. (2005) documented a negative correlation between diversity and density of herbivorous fishes with latitude, thus the low numbers of herbivorous species observed on NHB may reflect a larger-scale pattern.

5.6 SUMMARY

5.6.1 Species Richness

During the present study, it was possible to revisit and expand upon the most recent fish species lists for NHB of mainland east Florida. Based on new and old information, including the work of Baron et al. (2004) and Herrema (1974), over 250 species of fishes are now recorded from NHB (**Appendix C**, **Table C.1**). This list documents species records and spatial and temporal attributes for all fish species recorded from NHB. Similarities with many shallow coral reef assemblages are present (Banks et al., 2008). Differences between NHB fish assemblages and hermatypic reef assemblages in OHB depth ranges can involve the higher relative proportion of early life history stages on NHB structures, a juvenile-dominated assemblage (Lindeman and Snyder, 1999; Baron et al., 2004).

The current working number of species is 257 (**Appendix C**, **Table C.1**) from 68 families. The previous list of fish species recorded from 0 to 4 m NHB totaled 192 species (Lindeman, 1997a). Primary additions to that estimate derive from the Baron et al. (2004) study in the southern project area in depths to 7 m, which added several dozen species to the list of records, many of which are uncommon or not found in 0 to 4 m NHB in the northern project region. This pattern suggests that there is a southern NHB ichthyofauna and a less diverse northern fauna, particularly north of the deflection of the Gulf Stream offshore. We also characterized fundamental ecological attributes of these species (**Appendix C**, **Table C.1**). Species assessments of trophic patterns, residency, size classes, life stages, and the components within from this table (e.g., higher percentages of piscivores and planktivores compared to herbivores) are ongoing.

5.6.2 Spawning

A wide range of spawning patterns is seen among the fishes of east Florida shallow hardbottom. Nesting is undertaken in differing manners by species of fishes from quite different families. Damselfishes, locally abundant herbivores, can influence subtidal fish distributions on 1-m scales by their aggressive territoriality. Some of the species recorded from NHB build and protect nests in which they grow their young, sometimes at monthly intervals (Thresher, 1984). Several very different families, including the site-attached labrisomids, blennies, and gobies (potentially important predators of small fishes and invertebrates), also build nests in cryptic manners on NHB structure, often laterally or upside-down on inverted microhabitats. Though understudied, we estimate that over 30 fish species spawn in association with NHB. Most motile species do not spawn on NHB, though there probably are exceptions. In addition, some coastal pelagics spawn on or near NHB (Continental Shelf Associates, Inc., 1992).

5.6.3 Settlement and Early Associations with Habitat

Directed studies of fish settlement in NHB through OHB depths are lacking in the mainland east Florida study region. Patterns of settlement can be inferred from the larger, assemblage studies. In some species of grunts, there is evidence of potentially substantial variation in larval recruitment among years (Lindeman and Snyder, 1999; Jordan et al., 2004; Continental Shelf Associates, 2006; Coastal Eco-Group Inc., 2008). However, estimates of temporal patterns in fish settlement in the region (from seasonal to interannual) are currently based on very limited information.

Information on the use of the water column by settlement-stage larvae is lacking. Larval occurrence of some taxa in surf zone areas has been examined in other areas but not in this study region (Ruple, 1984; Jahn and Lavenberg, 1986). Low or high relief hardbottom could be a visual cue for settling larvae, but other sensory systems, particularly hearing and olfaction, can also be important (Kingsford et al., 2002). Larval fishes, including many clupeids, engraulids, and atherinids (Sponaugle et al., 2003), can form assemblages over shallow coral reefs but are unstudied over NHB or IHB. Sponaugle et al. (2003) found that shallow, near-reef larval fish assemblages differed from offshore collections. A significant aspect of this was the higher nearshore frequency of haemulid larvae.

Are nearshore fish larvae spending substantial time in the water column near NHB before settling there? This is possible for some taxa (e.g., clupeioids) but cannot be confirmed without more empirical support. For many species in South Florida, transport of larvae to NHB or OHB settlement areas may occur via cross-shelf oceanographic transport mechanisms resulting from diverse meso-scale phenomena in south and east Florida (Lee et al., 1995; Limouzy-Paris et al., 1997).

5.6.4 Developmental Patterns and Cross-shelf Habitat Use

Substantial stretches of NHB exist in portions of Broward, Palm Beach, Martin, St. Lucie, Indian River, and Brevard Counties (26°20' to 27°15' N) and elsewhere (Perkins et al., 1997; **Table 2.1**, present study). Although these areas are typically separated by kilometers of sand, there are some areas where there is a semi-continuous hardbottom gradient from the beach into depths exceeding 6 m. Offshore, many mid-shelf areas (5- to 20-m depths) are also dominated by expanses of sand, despite the variable occurrence of several mid-shelf reefs. Therefore, in many shallow areas, there are no natural habitats in the same or adjacent nearshore areas that can support equivalent abundances of early life stages of fishes and the invertebrates they largely feed on. Absences of nursery structure can logically result in increased predation and lowered growth. In newly settled and juvenile stages, such conditions could foster demographic bottlenecks that ultimately result in lowered local population sizes (Jones, 1991).

Empirical information is highly limited on the amount of connectivity between shallow patches of hardbottom and deeper reefs for fishes and invertebrates of east Florida. The limited available information suggests that diverse fish species that can ontogenetically migrate into deeper water use NHB during early life stages (Gilmore et al., 1981; Vare, 1991; Lindeman and Snyder, 1999; Baron et al., 2004). If the NHB in use is close enough to IHB or OHB, some of these species, depending on many changing biophysical drivers (e.g., predation, growth, larval recruitment) could migrate ontogenetically into deeper habitats. Answers to the question, "How close is *close enough*?" will vary by species, site, and time. For fishes, tagging studies would be useful using species on highly segregated, NHB-depth reefs in comparison to fishes tagged on NHB structure that is not restricted to depths <4 m but extends as emergent structure into depths of >6 m.

NHB can be not only spatially patchy for shallow organisms, it can also be temporally patchy due to natural burial events. Natural burial events are typically associated with rapid sediment redistributions in association with high wind and/or wave events. These events and partial or complete NHB burial are more common in the winter. In the absence of some storm-induced burial of subpatches or patches of habitat, NHB can be subject to very high wave energy and substantial scouring of surfaces, especially in the intertidal and immediate subtidal. Many organisms assumedly would associate with shelter as possible during these events, perhaps moving into the deepest NHB or IHB or nearby sand area available and returning post-event, if feasible. Information on organismal responses to high wind and wave events is needed and will assist in discerning larger patterns of cross-shelf distribution.

Are there substantive reasons to not consider the fishes associated with NHB a reef fish assemblage? A useful discussion on this topic in the literature occurred regarding benchline criteria for both taxonomic and ecological definitions of "what reef fishes are" (Bellwood and Sorbini, 1996; Bellwood, 1998; Robertson, 1998a,b). Bellwood (1998) concluded that reef fish assemblages ultimately occur in association with too many non-coral reef structures and recommended instead the term *fishes on coral reefs*. Robertson identified various challenges to a unifying taxonomic structure. He defined reef fishes as "species that live *on consolidated substrata that form coral and inorganic reefs.*" He described inorganic reefs, including rocky shores, as follows: "… the inorganic bedrock provides large and small physical structure that fishes use as habitat features…". In addition, all of the 10 consensus families of reef fishes in Bellwood (1998) are represented in association with NHB of east Florida. Earlier sections detail the long-standing geological literature on the reef attributes of NHB (e.g., **Chapters 1** and **2**). These lines of evidence suggest there are few, if any, reasons to conclude that the fishes of NHB of mainland east Florida do not constitute a reef fish assemblage.

5.6.5 Trophic Patterns and Functional Groups

There are no feeding studies of fishes from shallow hardbottom habitats in the project region. The most detailed examination of food habits of Caribbean reef and coastal pelagic fishes remains Randall (1967). His study areas were in the U.S. Virgin Islands and Puerto Rico. In the last decade, a series of detailed studies of feeding and habitat use of grunts and snappers has occurred in Curacao and other Caribbean islands (e.g, Nagelkerken et al., 2000; Dorenbosch et al., 2004). The older and newer trophic studies are largely from insular systems with potential differences in seascapes and landscapes in comparison to continental, mainland shelf areas such as east Florida (Robins, 1991). Based largely on studies from insular areas, the grunts and margates of the genera *Haemulon* and *Anisotremus* show a wide array of invertivory. Some species are planktivorous as adults (*H. striatum*), others are very specialized for feeding on hard-shelled invertebrates (*H. macrostomum*), while the majority of species are relatively generalized feeders on both soft- and hard-invertebrate prey, often from either softbottom or hardbottom environments (Randall, 1967; Sierra, 2001).

Most NHB species are demersal invertivores; however, assemblages also include important demersal piscivores and planktivores. Over 50 species of NHB fishes consume invertebrates as a primary dietary component. Eleven species of wrasse exihibit a pattern similar to grunts and other families: invertebrates from many diverse taxa are consumed by differing congeners with low to high levels of specialization within the genus. For example, many wrasse species (genus *Halichoeres*) feed on “shelled invertebrates” in the northeast Caribbean, though specific dietary compositions can vary (Randall, 1967; Randall’s data tabulated by taxa in Sierra, 2001). The dominant labrid in both the Jupiter and Fort Lauderdale studies was the slippery dick (*H. bivittatus*). This species feeds on crabs, urchins, annelids, and gastropods (Randall, 1967) and is an opportunistic feeder. Other labrids, such as the clown wrasse, *H. maculipinna*, primarily feed on soft annelids (Randall, 1967). As mentioned elsewhere, these comparative patterns are largely predictive without empirical feeding information from the project region.

Although the NHB assemblage is juvenile-dominated, a well-developed food web exists, with all of the trophic categories of Bellwood’s (1998) “consensus reef fish families” represented, including diverse herbivores and piscivores on juvenile fishes. Following from Randall (1967) and Bohnsack and Harper (1988), we characterized fish species according to the following trophic categories: herbivore, planktivore, detritivore, invertivore, and piscivore. This categorization scheme aids assessment of potential functional groups to better understand trophic relationships among NHB, IHB, and OHB assemblages. When the full spectrum of ontogenetic dietary shifts is considered for most species, many are omnivorous (e.g., planktivory to invertivory to piscivory from species as diverse as labrisomids and lutjanids). The degree of feeding variation within individual genera can be high, and it is very important to recognize that feeding patterns can vary geographically based not only on variable within-species behavior but based also on geography-dependent food availability (Turingan et al., 1995) and inter-annual variations in food availability (Sierra, 2001).

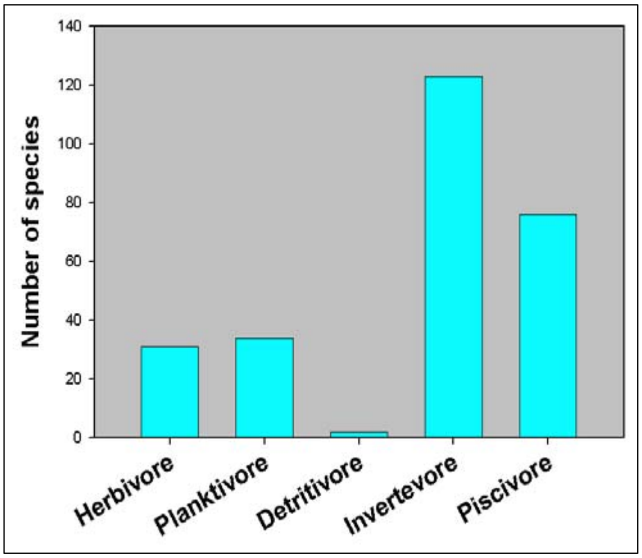


Figure 5.11. Relative adult trophic composition as measured by numbers of species per functional grouping.

The most prevalent trophic component among species was invertebrate feeding (**Figure 5.11**). Invertivory was four times more common among species than herbivory or planktivory. Randall categorized the diversity of invertivores according to 1) sessile animal feeders (e.g., sergeant major feeding on *Zooanthus*), 2) “shelled” invertivores (e.g., most *Halichoeres* species of wrasses), and 3) generalized invertebrate predators. The latter group was by far the biggest and included eels, squirrelfishes, snappers, species of basslets (*Serrranus*), some drums (sciaenids), goatfishes (mullids), pompanos (*Trachinotus* spp.), clown wrasse (*H. maculipinna*), and some labrisomids, including the hairy blenny. Specialized invertebrate feeding can occur as well, as in the preference for echinoids in older black margates. Early juvenile stages of porkfish, *Anisotremus virginicus*, and porgies, *Diplodus* spp., can serve as cleaners of invertebrate ectoparasites.

Piscivory ranked almost twice as high as herbivory and planktivory (**Figure 5.11**) but is inflated by the presence on the list of many piscivorous pelagic species that uncommonly associate with NHB. Prominent piscivores include lizardfshes (synodontids), jacks, snappers, muraenid and ophichthid eels (*Gymnothorax* and *Ophichthus* spp.), mackerels, and sharks. Many diverse piscivores feed on invertebrates as well (e.g., tarpon, nurse sharks) (Randall, 1967).

Herbivores were represented by juvenile stages of many common schooling herbivore species of Caribbean reefs and included the surgeonfishes (three species of *Acanthurus*), parrotfishes (especially redfish parrotfish), silver porgy (*Diplodus*), and chubs (*Kyphosus incisor* and *K. sectatrix*) (**Appendix C**, **Table C.1**). Less mobile herbivores include the damselfishes (five species). Omnivorous species of filefishes and puffers, all gobiids, and several blennioids are also herbivorous (Randall, 1967).

Planktivorous fishes of shallow hardbottom are diverse and include over 10 species of herring and anchovies (clupeids and engraulids), scads (*Decapterus* spp. and *Selar crumenophthalmus*), and a variety of demersal fishes including species of apogonids, blackbar soldierfish (*Myripristis jacobus*), and small demersal schools of copper sweeper (*Pempheris schomburgkii*). Some locally abundant NHB species, including thread herring (*Opisthonema oglinum*) and copper sweeper, were found by Randall (1967) to feed heavily on polychaete larvae (23% of total volume, 23 specimens and 27%, 19 specimens, respectively) in the northeast insular Caribbean. Substantial planktivory also occured in species of drums (*Pareques* spp. and *Odontoscion dentex*), sergeant major, bluehead wrasse, and juvenile stages of haemulids and carangids (Randall, 1967). The species-specific and collective impacts of these planktivores upon the seasonal dynamics of worm reef formation by *P. lapidosa* larvae deserve study.

5.6.6 Latitudinal Variations in Shallow Hardbottom Fish Assemblages

Some differences among ichthyofaunal assemblages are present between the southern and northern areas of mainland southeast and east-central Florida in terms of the most abundant species and habitat structure (e.g., earlier examples in present chapter; **Appendix C**, **Table C.1**). Factors influencing these potential differences include 1) differences in the quantity or structure of shallow hardbottom of southeast Florida compared to east central Florida and 2) major, long term differences between southern and northern sites in presence/absence or abundance of locally prominent species. The available NHB areal data shows higher cover in some areas compared to others (**Table 2.1**). In the second case, there are not easy numeric or image-based answers. In terms of assemblages, the differences could be based on true differences in fish assemblages between southeast Florida and east-central Florida or sampling artifacts, differing physical regimes, larval recruitment variation, post-settlement growth and mortality variation, or combinations of these factors.

There are significant differences in abundance between three of the most abundant species in the Jupiter area in comparison to the Fort Lauderdale area. Only one black margate out of >72,000 individuals was recorded in Fort Lauderdale (Baron et al., 2004), while 636 black margates out of 10,491 individuals were censused in Lindeman and Snyder (1999). Also, 43 sailors choice were recorded in Baron et al. (2004) with mean lengths above 15 cm, while 1,326 *H. parra* individuals were recorded in Lindeman and Snyder (1999), primarily early juvenile stages below 5 cm. The hairy blenny was the most abundant cryptic hardbottom fish species in the Jupiter surveys, with 806 individuals recorded in transect surveys, 8% of the overall individual total (Lindeman and Snyder, 1999). Though the hairy blenny was recorded in qualitative roving diver surveys, none were recorded in transect and point-counts in Fort Lauderdale (Baron et al., 2004).

Potential explanations for such marked difference in dominant species within the 100-km north-south distance between these studies may include temporal recruitment variations, NHB structural differences between survey areas, species reaching their biogeographic distributional limits between these sites, and other factors. The Fort Lauderdale study occurred during several summer months in 2001, while the Jupiter study occurred between 1994 and 1996. Recruitment in haemulids can vary across temporal scales (McFarland et al., 1985; Jordan et al., 2004), and the possibility that the patterns reflect differences in interannual larval recruitment in the 6 years between these survey snapshots cannot be excluded.

NHB structural differences probably exist between these areas as described above, but many of the more prominent species appear to be relatively opportunistic in their use of differing NHB and IHB microhabitat structure. At least three of the prominent species (black margate, sailors choice, and hairy blenny) with apparent major distributional differences here are listed by Gilmore and Hastings (1983) as species whose Florida distributions are restricted to east Florida, not occurring in the Gulf of Mexico as congeners do. More research is required to parse the multiple factors and examine the above alternatives to better understand these and other north-to-south differences in fish assemblage pattern.

Chapter 6
Marine Turtles

6.1 INTRODUCTION

Much of what is known about marine turtles in Florida is from their nesting habits on sandy beaches. More recently, acknowledgment has been made regarding the importance of NHB as important habitat for juvenile and subadult species of marine turtles. Green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and hawksbill (*Eretmochelys imbricata*) turtles utilize NHB as developmental habitat in waters around Florida. These species have fundamental developmental requirements that are supplied by nearshore hardbottom (e.g., food, shelter, predator avoidance). Data from mark and recapture studies indicate that turtles may revisit or take up long-term residency on nearshore reefs (Holloway-Adkins, in prep.). Impacts of coastal development on marine turtles include pollution, dredge and fill projects, shoreline hardening, and commercial and recreational fishing activities. This document explores the use of nearshore waters by adult marine turtles and their hatchlings; however, particular focus is directed towards the use of NHB as developmental habitat for juvenile stages of marine turtles.

6.1.1 Adult Marine Turtles

Nearshore waters act as important corridors during the life history stage of nesting adult females and emerging marine turtle hatchlings. The terrestrial encounter with sandy beaches for nesting represents but a brief moment in the life history of all marine turtles; however, due to the ease of accessibility, it has been the most studied. Populations of adult female marine turtles use nearshore waters to access adjacent beaches during turtle nesting seasons. Depending on the species, nesting in Florida can begin as early as February for leatherback turtles *(Dermochelys coriacea)* and end as late as November for green turtles.

NHB exists adjacent to many of the prime nesting beaches on the east Florida coast. Rocks are exposed during low tide events on some of these beaches; however, no historical evidence exists indicating NHB rock impedes marine turtle nesting in these areas. Turtles have been observed climbing over exposed rocks while entering and exiting the surf during nesting events (**Figure 6.1**).

Figure 6.1. Adult female green turtles (in foreground and distance) crossing the nearshore hardbottom structure after nesting in Coral Cove Park, Palm Beach County, Florida. *Photo by D. Snyder.*

6.1.2 Hatchling Marine Turtles

A generalized conceptual model of ontogenetic habitat stages for marine turtles was constructed by Musick and Limpus (1997) that describes the functional role of oceanic and neritic habitats in the life history of marine turtles (**Figure 6.2**). The life cycle for most marine turtle species begins on a subtropical or tropical beach. Marine turtles hatch from eggs inside clutches of eggs laid and incubated in warm summer sands. Newly hatched turtles emerge from the nest and make their way across the sand and into the ocean. Turtles that hatch from Florida's Atlantic beaches are believed to spend the next 3 to 11 years (highly variable among species) in the pelagic environment, riding eddies and other circulatory systems within the North Atlantic Gyre (**Figure 6.3**). Juvenile green turtles enter neritic habitats at around 20 to 25 cm straight carapace length (SCL). Data from age-at-size models indicate their age to be approximately 3 to 5 years (Witherington et al., 2006a). Loggerheads are rarely encountered in nearshore environments until approximately 45 cm SCL. Their time at large is estimated to be between 6.5 and 11.5 years (Bjorndal et al., 2000).

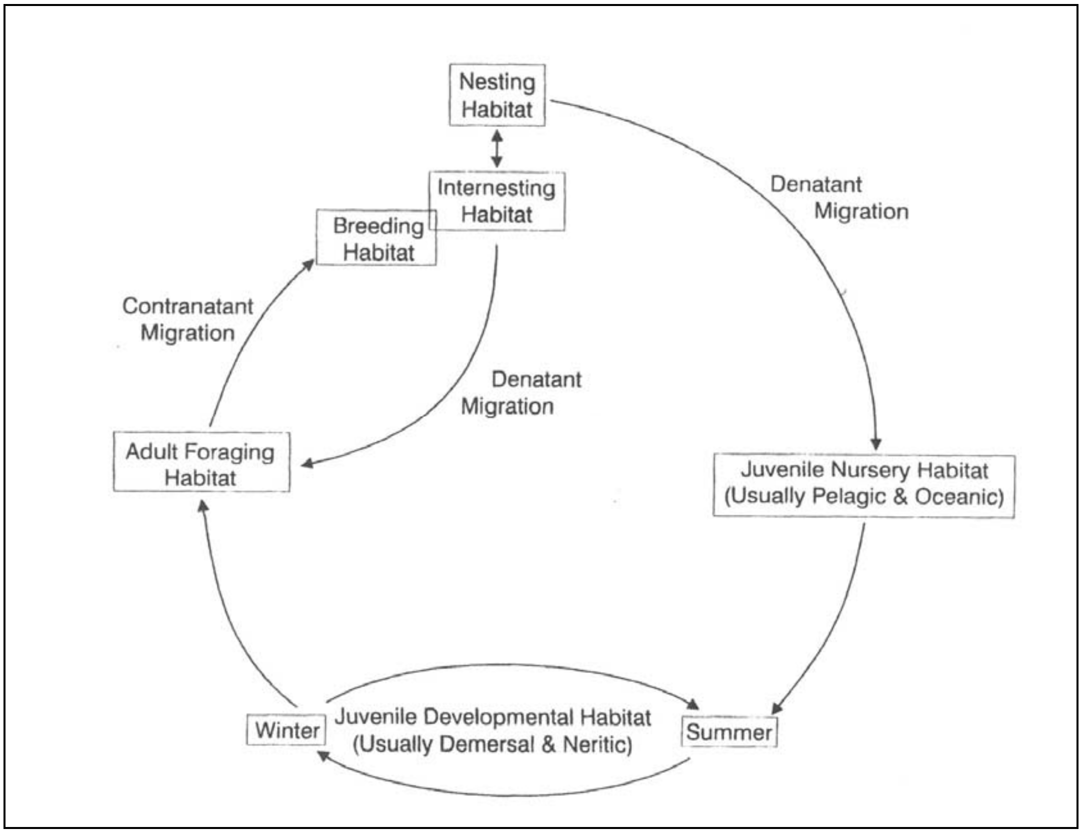


Figure 6.2. Conceptual model of ontogenetic habitat stages in marine turtles (From: Musick and Limpus, 1997).

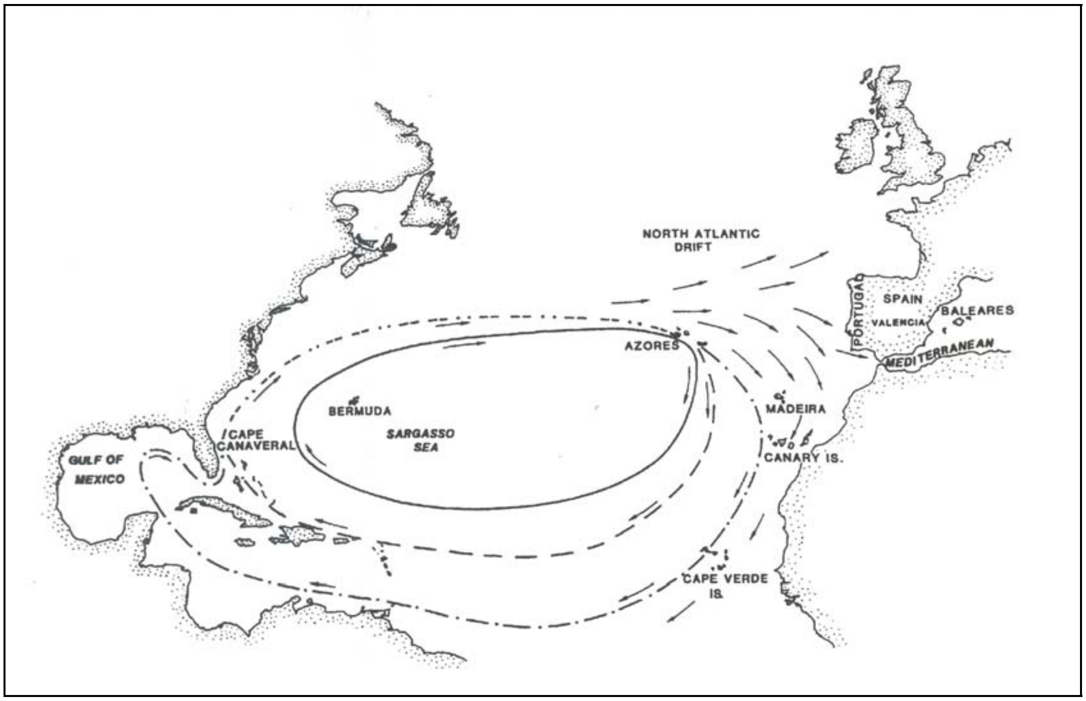


Figure 6.3. North Atlantic Gyre with potential oceanic transport routes for juvenile marine turtles (From: Musick and Limpus, 1997).

More recently, adjacent hardbottom habitats have been recognized as juvenile developmental habitat (Wershoven and Wershoven, 1992a; Bresette et al., 1998; Ehrhart et al., 2001; Holloway-Adkins et al., 2002; Jones et al., 2004; Makowski et al., 2006b; Garrido, 2007). Few data exist on populations of marine turtles utilizing NHB as developmental habitat, and not enough data are available to clearly establish long-term patterns in the distribution and abundance of marine turtles associated with NHB on the east Florida coast. Data herein are predominantly from non-peer reviewed articles, reports, and personal communications and observations, though more information is beginning to enter the peer-review literature. **Table 6.1** lists marine turtle species and their presence in or around NHB and indicates areas that are still in question.

6.1.3 Predators

Many predators prey upon hatchlings even before they leave the nest. Frequently, ghost crabs, beetles, worms, and other invertebrates invade the nest before hatchlings emerge to the surface of the sand. Raccoons, coyotes, and vultures are capable of destroying nests and consuming eggs and hatchlings. If a hatchling survives exiting the nest, reaches the surface, and makes its way to the sea, a ghost crab, sea bird, or a raccoon may consume it. Once in the water, the long journey out to meet the Florida Current is wrought with more predators that are capable of making a meal of a small hatchling turtle. Interestingly, Whelan and Wyneken (2007) found no significant differences between predation levels of hatchlings migrating from nearshore waters over either sand or hardbottom nearshore waters; however, higher hatchling predation levels were documented for animals that migrated over the more predator-rich hardbottom habitat. As marine turtles mature, their largest threat comes in the form of discarded anthropogenic debris that turtles may ingest (Bjorndal et al., 1994) or become entangled in and drown. Impacts from commercial fishing activities (e.g., drowning in shrimp trawler nets, long-line fishing gear, and gill nets) pose the greatest threats to loggerhead and Kemp's ridley (*Lepidochelys kempii*) turtles.

Table 6.1. Role (functions) of nearshore hardbottom (NHB) (and reference to offshore hardbottom [OHB]) in marine turtle life history stages.

Species	Life Stage	NHB	OHB	Diet	Shelter	Corridor	Relative Occurrence
Green turtle (*Chelonia mydas*)	hatchling	no	no	n/a	no	yes	n/a
	post	no	no	omnivorous	no	yes	n/a
	juvenile	yes	yes	omnivorous - herbivorous	yes	yes	n/a
	subadult	no	no	herbivorous	no	possible	occasional
	adult	no	no	herbivorous	OHB – nesting?	yes	occasional
Loggerhead turtle (*Caretta caretta*)	hatchling	no	no	n/a	no	yes	frequent
	post	no	no	omnivorous	no	yes	occasional
	juvenile	yes	yes	carnivorous	possible	probably not	rare
	subadult	yes	yes	carnivorous	possible	possible	occasional
	adult	yes	yes	carnivorous	OHB – nesting	yes	occasional
Hawksbill turtle (*Eretmochelys imbricata*)	hatchling	no	no	n/a	no	possible	rare
	post	no	no	omnivorous	no	no	rare
	juvenile	yes	yes	spongivorous	yes	possible	occasional
	subadult	yes	yes	spongivorous	yes	possible	occasional
	adult	no	no	spongivorous	OHB – nesting?	possible	occasional
Leatherback turtle (*Dermochelys coriacea*)	hatchling	no	no	n/a	no	yes	frequent
	post	no	no	jellyfishes	no	no	n/a
	juvenile	no	no	jellyfishes	no	no	no
	subadult	no	no	jellyfishes	no	no	no
	adult	yes	yes	jellyfishes	no	possible	occasional

n/a = Not available.

6.1.4 Water Depth

Visual transect surveys to determine turtle density distribution along NHB were conducted by Inwater Research Group, Inc. (2005) in St. Lucie and Martin Counties. Transects were surveyed for turtles inshore (200 m from shore, 3 m water depth) and offshore (400 m from shore, 4 m water depth) waters. Inwater Research Group, Inc. found that loggerhead turtles were similarly distributed across inshore and offshore surveys. However, green turtle densities were twice as high inshore as offshore. It is possible that loggerheads select deeper reef and sand bottom habitats to forage and rest. Their food resources are available in both habitat types. Visual transect surveys conducted in Brevard (Holloway-Adkins and Provancha, 2005) and Indian River (Inwater Research Group, Inc., 2004) Counties indicate the density of juvenile green turtles is higher in shallow nearshore waters. High catch-per-unit-effort (CPUE) rates are associated with the shallower reefs in 1.5 to 2.5 m water depths, closest to shore in Brevard and Indian River Counties (unpublished data).

6.1.5 Seasonality

Transect survey data indicate that marine turtles are present year-round at all of the NHB study sites (Inwater Research Group, Inc., 2004, 2005; Holloway-Adkins, 2005). Seasonal data from tangle net capture methods are normally restricted to summer months when ocean conditions are relatively calm. Tangle nets, however, are used to capture turtles entrained into the intake canals at the St. Lucie Power Plant in St. Lucie County. Seasonal data from the plant show a high number of very small size-class juvenile green turtles (potential new ocean recruits) are present each winter (Bresette et al., 1998).

6.2 SPECIES OVERVIEWS

Five of the seven circumglobally distributed marine turtles species have been observed in or adjacent to NHB of mainland east Florida. Largely depending on the time of year or latitude of observation, the most frequently observed turtles commonly are green, loggerhead, and hawksbill turtles. In deep offshore waters (>20 m), fishermen have reported frequent sightings of loggerhead turtles and occasional sightings of leatherback turtles.

A small number of studies have investigated marine turtles in nearshore waters on the east Florida coast (**Figure 6.4**, **Table 6.2**). Two relatively long-term studies (i.e., 19+ years) have been conducted on marine turtles associated with NHB on the east Florida coast. Ehrhart et al. (2003) has researched marine turtles on sabellariid worm reefs near Sebastian Inlet in Indian River County, in summer, since 1989. A long-term study of marine turtles entrained from offshore cool-water intake pipes at the St. Lucie Power Plant in St. Lucie County has been documented since 1976 (Bresette et al., 1998; Ecological Associates, Inc., 2000).

Shorter or more recent studies have been conducted in Brevard County (Holloway-Adkins and Provancha, 2005), Palm Beach County (Makowski et al., 2006b) (L. Wood, Palm Beach Zoo, unpublished data), and Broward County (Wershoven and Wershoven, 1992a). Additional studies utilizing passive observation techniques to describe and/or assess marine turtle populations over NHB have been used in Indian River County (Inwater Research Group, Inc., 2004), St. Lucie and Martin Counties (Inwater Research Group, Inc., 2005), Palm Beach County (Jones et al., 2004; Garrido, 2007) and Broward County (Makowski et al., 2006a). Wood's (2006) study is the first and only study to focus on hawksbill turtles on the east coast of Florida.

There are few studies that utilize tangle net capture methods in NHB, but this method standardizes CPUE so comparisons among studies can be made. CPUE is based on the length of the net or nets used, the amount of time the net is in the water, and the number of turtles captured during that time. CPUE data indicate higher capture numbers per effort in Indian River County (**Table 6.3**).

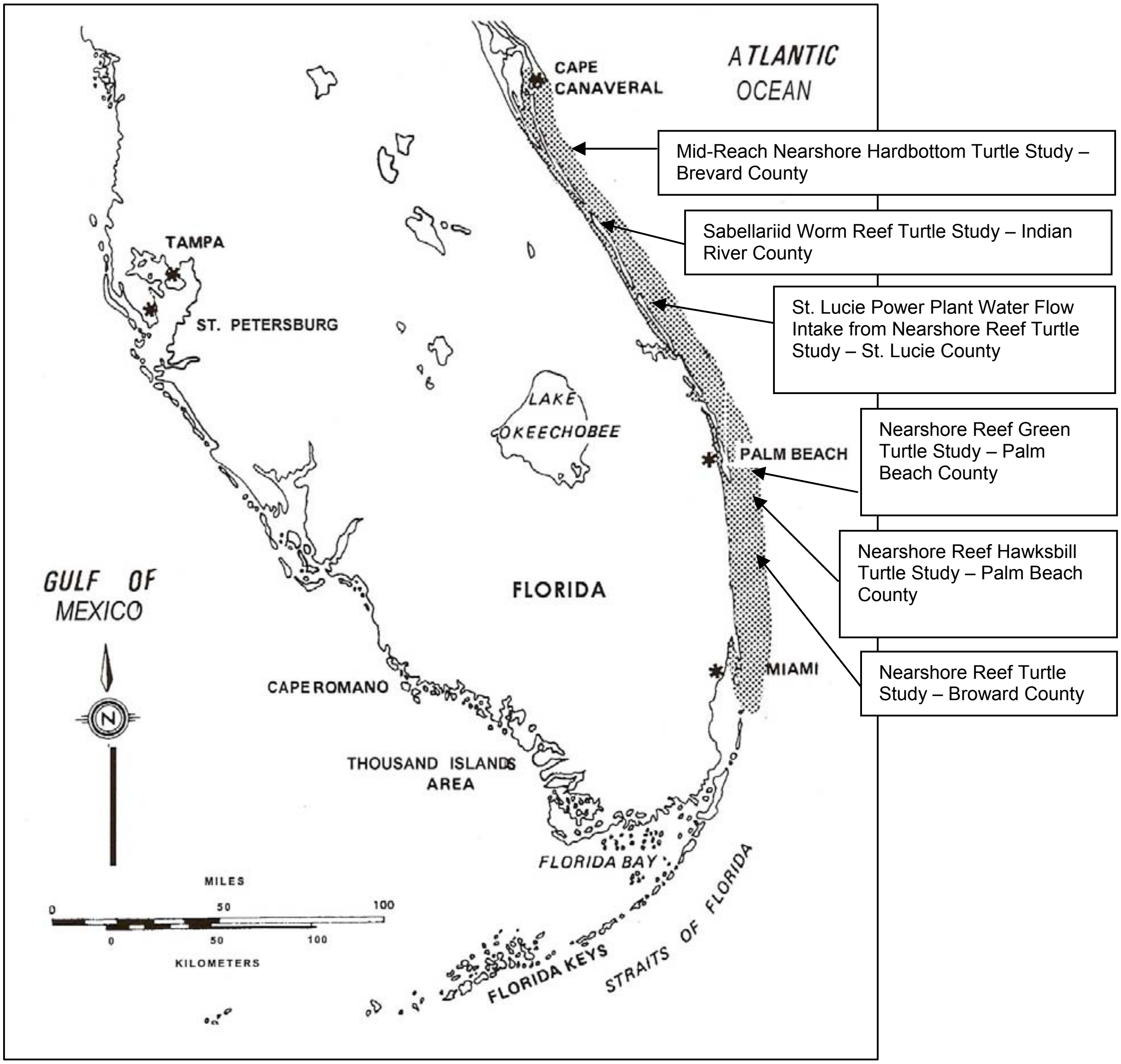


Figure 6.4. General locations of study areas for marine turtles in coastal areas superimposed over distribution of reef-building sabellariid worms along mainland east Florida (Modified from: Zale and Merrifield, 1989).

Table 6.2. Marine turtle mark and recapture population studies conducted over nearshore hardbottom.

Marine Turtle Study	Location (County)	Capture Method	Time of Year	Duration	Permit Holder (Current)	Species
Mid-Reach	Brevard	Tangle nets	Mostly summer	2004 to Present	Holloway-Adkins	Cm, Cc
Indian River County	Indian River	Tangle nets	Summer	1989 to Present	Ehrhart	Cm, Cc, Ei
St. Lucie Power Plant	St. Lucie	Entrainment and nets	Year-round	1976 to Present	Bresette	Cm, Cc, Ei, Dc, Lk
Little Breakers Reef	Palm Beach	Night SCUBA diving	Summer and Fall	2003 to 2004	Wyneken	Cm
Breakers Reef	Palm Beach	SCUBA diving	Year-round	2004 to Present	Wood	Ei
Broward County	Broward	SCUBA diving	Year-round	1987	Wershoven	Cm, Cc, Ei

Cm = *Chelonia mydas*; Cc = *Caretta caretta*; Ei = *Eretmochelys imbricata*; Dc = *Dermochelys coriacea*; Lk = *Lepidochelys kempii*.

Table 6.3. Catch-per-unit-effort (CPUE) for marine turtle population studies conducted with tangle net capture methods adjacent to nearshore hardbottom habitats on the east coast of Florida.

Location	CPUE	Year	N
Worm reefs, Indian River County, Florida (Data from Ehrhart et al., 2001)	38.86	2000	98
Worm reefs, Indian River County, Florida (Data from Ehrhart et al., 1996)	6.28	1989 to 1995	190
Nearshore reefs, Brevard County, Florida	3.52	2003 to 2004	20
Nearshore reefs, Brevard County, Florida	1.25	2005	9

Most adult female marine turtle species travel several hundred kilometers from foraging grounds to nesting beaches to lay eggs (Hirth, 1997). Nesting populations of turtles are believed to use nearshore waters predominantly as a corridor to the adjacent nesting beach, and green and loggerhead turtles have been observed mating close to shore (K. Holloway-Adkins, ECB, pers. observ.). However, adult loggerhead and green turtles have been frequently observed using OHB as rest areas during the nesting season in relatively large numbers, especially on reefs adjacent to Palm Beach County (Mortimer, 1995). There is no evidence to suggest that turtles laying subsequent clutches on east Florida beaches are foraging in adjacent waters during this period.

High and low relief in NHB offers sheltered rest areas for marine turtles (**Figure 6.5**). Divers frequently observe loggerhead turtles resting under ledges and in shallow depressions on the reef (K. Holloway-Adkins, ECB, pers. observ.). Juvenile green turtles are easily captured, as they also rest under low relief areas and in shallow depressions in the reef (Makowski, 2004). Over 100 hawksbill turtles have been hand-captured from reefs in shallow (~2 m) and deep water (>18 m; Wood, 2006). Hawksbill turtles were more frequently captured on deeper reef areas, and all recaptured turtles were captured from deep reefs (L. Wood, Palm Beach Zoo, pers. comm.).

Figure 6.5. Loggerhead (*Caretta caretta*) resting on offshore hardbottom, Breakers Reef, Palm Beach County, Florida. *Photo by S. Hurley.*

6.2.1 Green Turtles

Juvenile green turtles are speculated to spend the first few years of their life in the pelagic (oceanic) zone, feeding on a variety of invertebrates and plants, and drifting with *Sargassum* racks along converging fronts (Carr and Meylan, 1980). However, efforts to confirm this hypothesis have been difficult (Witherington et al., 2006a). It appears that after approximately 2 to 5 years (at approximately 20 to 25 cm), green turtles move into shallow coastal and estuarine waters (Hirth, 1997; Musick and Limpus, 1997) (**Figure 6.6**).

Figure 6.6. Juvenile green turtle (*Chelonia mydas*) over nearshore hardbottom in Palm Beach, Palm Beach County, Florida. *Photo by D. Snyder.*

At present, green turtles are the most frequently observed marine turtle species found associated with NHB from Brevard to Broward Counties. The presence of juvenile green turtles during surveys conducted during each season and observations of individual animals year-round suggest some animals continuously use NHB for several years. Where shallow NHB (intertidal and shallow subtidal waters) exists, juvenile green turtle densities were observed to be higher than they were in deeper, subtidal areas in Brevard (Holloway-Adkins, 2006), Indian River (Ehrhart et al., 2001), St. Lucie (Inwater Research Group, Inc., 2005), and Martin (Inwater Research Group, Inc., 2005) Counties. In areas where intertidal hardbottom was non-existent (Palm Beach and Broward Counties), juvenile green turtles utilized the first line of shallow reefs that paralleled the shore (Wershoven and Wershoven, 1992a; Makowski, 2004; Garrido, 2007).

Ecological Associates, Inc. (2000) reported a substantial increase in the number of juvenile green turtles captured annually at the St. Lucie Power Plant after 1992, and their speculations as to why this has occurred include cooler water temperatures in northern regions, increased reef area providing a more abundant foraging resource, or an overall increase in the population of juvenile green turtles. None of these reasons have been substantiated to date; however, since their report (Ecological Associates, Inc., 2000), the relative abundance of green turtles has still remained high on NHB.

Mitochondrial DNA analysis conducted by Bagley (2003) and by Bass and Witzell (2000) indicate green turtles using NHB foraging grounds on the east coast of Florida showed high levels of genetic diversity. Bagley (2003) found 14 different haplotypes for green turtles captured over nearshore reefs in Indian River County. Haplotypes were from a mixed stock of nesting beaches from Florida, Mexico, Costa Rica, and Aves Island.

Many researchers remark that the health condition of turtles captured or observed on NHB reefs typically is good and/or better than that of turtle populations residing in the Indian River and Mosquito Lagoon waters. Few animals from NHB study sites are afflicted with fleshy tumors (manifestations of fibropapillomatosis, or FP disease). None of the turtles captured in NHB waters in Brevard County have shown signs of the disease (Holloway-Adkins, 2005). Garrido (2007) did not sight any turtles on Palm Beach County reefs with the disease.

Foraging sample analysis for turtles in Brevard, Indian River, Palm Beach, and Broward Counties indicate that a large percentage of the juvenile green turtle diet consists of red algae, with lower percentages of the diet from green and brown algae (**Table 6.4**). Relatively small amounts of invertebrate and inorganic food items (e.g., sand, shell, rock) were also found in foraging samples, and some samples contained pieces of plastic or other discarded marine debris.

Juvenile green turtles have frequently been sighted in Palm Beach County, resting under ledges on shallow NHB (Jones et al., 2004). They were easily captured by Makowski (2004) while tucked under and around ledges west of Breakers Reef and on low relief areas and shallow depressions in the reef.

6.2.2 Loggerhead Turtles

Large juvenile loggerhead turtles recruit from oceanic environments into shallow coastal waters at >45 cm SCL (Witherington et al., 2006b). Loggerheads frequently have been captured during trawl events in areas north of the NHB region (i.e., Port Canaveral Inlet and shipping channel) (Schmid, 1995). They have also frequently been captured in the adjacent Indian River Lagoon system (Bresette et al., 2000). However, researchers infrequently sight or capture small size-class loggerheads in Brevard and Indian River County over shallow NHB habitats (Ehrhart et al., 2001; Holloway-Adkins and Provancha, 2005). Additionally, in St. Lucie County, juvenile loggerheads are systematically captured from the cool-water intake canals located in NHB (Ecological Associates, Inc., 2000). Juvenile loggerheads have been frequently observed foraging and resting on OHB in Palm Beach County (Mortimer, 1995).

Loggerheads are considered to be omnivores. They forage on a wide variety of invertebrates, including salps, molluscs, and crustaceans. They tend to feed on more sessile organisms, many of which bury in soft bottom or sandy areas of reef and estuarine habitats.

Table 6.4. Macroalgal species present in foraging samples from various population studies conducted on marine turtles on nearshore hardbottom habitat. ● denotes species presence.

Macroalgal Forage Species	Gilbert (2005) – Indian River	Holloway-Adkins (2001) – Indian River	Holloway-Adkins (2005) – Brevard County	Jones et al. (2004) – Palm Beach	Makowski (2004) – Palm Beach	Wershoven and Wershoven (1992b) – Broward
Acanthophora muscoides					●	
Acanthophora spicifera	●	●		●		
Agardhiella subulata			●	●		
Amphiroa rigida		●				
Asteromenia (Fauchea peltata)		●				
Bostrichia sp.		●				
Botryocladia occidentalis		●				
Botryocladia sp.	●					
Bryocladia cuspidata		●	●			
Bryothamnion seaforthii	●	●				●
Bryothamnion sp.					●	●
Caulerpa mexicana		●				
Caulerpa microphysa	●					
Caulerpa peltata				●		
Caulerpa prolifera	●	●	●			
Caulerpa racemosa	●	●				
Caulerpa taxifolia		●				
Centroceras clavulatum		●	●			
Ceramium sp.	●	●	●	●		
Chaetomorpha linum			●			
Chaetomorpha sp.	●	●	●			
Chondria dasyphylla			●			
Chondria sp.	●	●	●			
Chondrocanthus acicularis			●	●		
Cladophora catenata		●				
Cladophora sp.			●	●	●	
Codium sp.		●				
Dascycladus vermicularis					●	
Dasya pedicillata		●				
Dasya sp.	●					
Dictyopteris delicatula		●				
Dictyopteris sp.	●				●	●
Dictyospareia sp.	●					
Dictyota sp.	●	●			●	
Dudresyna crassa			●			
Erythrotrichia carnea				●		
Eucheuma nudum		●				
Gelidiaceae						●
Gelidiella sp.						●
Gelidium americanum		●	●	●		
Gelidium pusillum		●	●			
Gelidium sp.	●		●			●
Gracilaria armata		●				

Table 6.4. (Continued).

Macroalgal Forage Species	Gilbert (2005) – Indian River	Holloway-Adkins (2001) – Indian River	Holloway-Adkins (2005) – Brevard County	Jones et al. (2004) – Palm Beach	Makowski (2004) – Palm Beach	Wershoven and Wershoven (1992b) – Broward
Gracilaria blodgettii		●				
Gracilaria mammillaris	●	●	●		●	
Gracilaria sp.			●	●		●
Gracilaria tikvahiae		●				
Gracilaria verrucosa		●				
Halimeda discoidea	●					
Halimeda sp.						●
Halymenia floresia		●				
Hypnea cervicornis		●				
Hypnea cornuta		●				
Hypnea musciformis		●				
Hypnea sp.	●	●	●			●
Hypnea spinella		●				
Hypnea valentiae			●			
Jania adherens		●	●			
Jania sp.	●				●	
Laurencia corallopsis				●		
Laurencia gemmifera				●		
Laurencia poiteaui	●	●				
Laurencia sp.			●			
Liagora sp.	●					
Lomentaria baileyana		●				
Neomeris annulata				●		
Nitophyllum punctatum				●		
Padina profunda		●		●		
Padina sp.	●		●			
Polysiphonia sp.	●					
Polysiphonia subtilissima		●				
Pterocladia sp.						●
Rhizoclonium sp.					●	
Rhodymenia sp.	●					
Sargassum sp.	●	●				
Schizothrix arenaria				●		
Schizothrix calcicola				●		
Scinaia complanata		●		●		
Scinaia sp.	●					
Siphonocladus tropicus					●	
Solieria sp.	●	●				
Spyridia filamentosa		●				
Ulva sp. (*Enteromorpha chaetomorphoides*)		●				
Ulva sp. (*Enteromorpha* sp.)	●	●			●	
Ulva lactuca			●			
Ulva sp.	●	●	●			

6.2.3 Hawksbill Turtles

Except for stranding data and sightings by SCUBA divers, little is known about the distribution of hawksbill turtles on NHB. Wood (2006) began studying *E. imbricata* on reefs off Palm Beach County in 2004 and has captured over 100 hawksbills in water depths as shallow as 2 m and on deep reefs (>18 m) by SCUBA diving capture methods (L. Wood, in prep.). Based on SCL measurements (35.7 to 83.9 cm; mean 57.0 cm), this population is primarily composed of relatively large juvenile and subadult animals (**Figure 6.7**). Preliminary DNA analyses indicate a majority of these turtles are representative of Mexican stocks. Though not systematically studied until recently, SCUBA divers have reported an abundance of hawksbills in the area for decades (N. Rouse [deceased Divemaster, The Scuba Club, Inc., West Palm Beach, FL], personal dive logs; L. Wood, Palm Beach Zoo, pers. comm.).

Hawksbills are generally considered spongivores. However, a number of studies have shown their diet to be more varied than originally thought, and can include macroalgae, soft and hard corals, tunicates, jellyfishes and other small invertebrates that may or may not be associated with the sponges they commonly consume (Mayor et al., 1998; Leon, 2000; Leon and Bjorndal, 2002). Feeding observations conducted by L. Wood (Palm Beach Zoo, pers. comm.) reveal that hawksbills actively select and consume pieces and/or portions of sponges. This feeding behavior may play an important role in shaping the coral reef community and promoting the recolonization of sponges (Leon and Bjorndal, 2002). Jackson (1997) concluded that hawksbill turtles are keystone-like species in coral reefs systems.

Hawksbill turtles are frequently approachable. They can be found out in the open, as well as under ledges or resting near reef structures (coral heads, barrel sponges, etc.).

Figure 6.7. Juvenile hawksbill turtle (*Eretmochelys imbricata*) foraging on a tunicate wedged between the rocks on Nursery Reef, Pompano Beach, Florida (6 m water depth). A queen angelfish (*Pomacanthus* sp.) and gray angelfish (*Holacanthus* sp.) stood by, collecting scraps dropped by the hawksbill. *Photo by K. Holloway-Adkins.*

6.3 DISTURBANCE EVENTS AND TURTLES

6.3.1 Shoreline Project Disturbances

Juvenile green turtle abundance declined during surveys conducted between pre- and post-construction Broward County beach nourishment activities (Makowski and Kruempel, 2007). In one segment of the project area, green turtle abundance declined by 29.8% from pre-construction levels. In another segment, a 10.0% decline in turtle abundance was reported. Overall abundance level changes, however, were not statistically significant, and Prekel et al. (2007) suggest declines in abundance may be correlated with a temporary reduction in available macroalgae food resources. Third year post-nourishment biological monitoring surveys revealed that algae preferred by juvenile green turtles (based on foraging analysis from Wershoven and Wershoven, 1988 and Makowski et al., 2006a) were more abundant at 36-months post-construction. There appeared to be a temporary absence of turtles in the vicinity of a newly nourished section of beach in Indian River County in 2004. However, turtles returned to shallow subtidal areas shortly after water clarity was restored (K. Holloway-Adkins, ECB, pers. observ.). High turbidity levels from suspended sediments did not appear to affect foraging by juvenile green turtles, but excessive turbidity likely affects macroalgal food resources.

6.3.2 Red Tide Disturbances

Beginning in November 2007, red tide lingered onshore and offshore the east Florida coast for several weeks. FWRI (St. Petersburg) confirmed that red tide created from the dinoflagellate *Karenia brevis*, which originally bloomed off the west coast of Florida, was responsible for a major fish kill and several turtle deaths and sickness in Brevard and Volusia Counties. Over 30 juvenile green turtles were negatively affected by red tide events off the Brevard County coast (FWC personnel, pers. comm.). Many of the turtles that washed ashore during this event were transported to nearby rehabilitation facilities, and a few died. Loggerhead turtles succumbed to red tide toxicity and did not recover as well or as quickly as green turtles (M. Bauer, Volusia County Marine Science Center, pers. comm.). Many loggerhead turtles washed up dead or were transported live to facilities but did not recover.

6.4 SUMMARY

Data indicate that predominantly green and hawksbill turtles are the most frequently encountered species and the ones that assume relatively long-term residency on NHB. These data and observations suggest that the developmental life stages of juvenile green and hawksbill turtles, in particular, are intimately tied to the NHB habitat. The mean population size and size-class range suggest that the smaller mean size turtles (20 to 42 cm) are obligately tied to certain habitats within the NHB. At the very least, we are beginning to understand that juvenile green turtles are more susceptible to the debilitating fibropapillomatosis disease, which has been documented to occur in extremely high levels (50% or greater) in estuaries, bays, and sounds around the world (Herbst and Klein, 1995). Nevertheless, juvenile green turtles may not be obligately tied to NHB, but rather it might be to their advantage to have access to NHB for habitat.

To date, only one area has been assigned critical habitat status for green and hawksbill turtles (Culebra, Puerto Rico). At present, marine turtle nesting beaches have been afforded more protection than developmental habitat for turtles. While beaches are important, the intermediate life stage (juvenile) might well be the most key component to the persistence and recovery of marine turtles (Bjorndal and Bolten, 2003). Until recently, we have attempted conservation of marine turtles with a focus on the individual species. A more effective approach may be to gain better insight into the functional roles of different life-history stages of marine turtles and adopt an approach that more strongly emphasizes ecosystem management with respect to all the habitats in which these animals are encountered (Costanza et al., 1997; Jackson et al., 2001; Bjorndal and Bolten, 2003).

Section 3

Functional Attributes of Nearshore Hardbottom and Mitigation Alternatives

Chapter 7
Functional Ecological Attributes of Shallow Hardbottom

7.1 INTRODUCTION

The overarching goal of this synthesis is to identify and provide supporting evidence of the important functional attributes of NHB, IHB, and shallow OHB. In this chapter, information in the preceding **Chapters 3** through **6** on species and assemblage composition, interactions, and diversity will be examined in relation to the following priority issues:

1. What are specific ecological functions of NHB?
2. What can happen to the coastal ecosystem (broader than NHB) when NHB is lost due to nourishment?
3. Is OHB habitat able to ecologically compensate for the loss of NHB?
4. If the NHB habitat has specific properties and functions that cannot be compensated for by existing OHB habitat, what are the best mitigation alternatives for the loss of natural NHB?

Richardson and Poloczanska (2008) examined traditional research approaches using functional groupings and individual species, preferring the latter. We recognize important roles for both approaches, depending on the starting objectives, and, given our objectives, will use both approaches according to topic. Advanced methods of examining functional roles using, for example, biological traits analysis (Bremner, 2008) may be of use in collective examination of NHB and deeper assemblages.

The total number of reliably recorded species of invertebrates, fishes, algae, and other fauna from hardbottom from depths of 0 to approximately 4 m is at least 1,050 species along the mainland east Florida coast (**Chapters 3**, **4**, **5**, and **6**). A total of 523 invertebrate species has been recorded to date. Among the most important invertebrates in terms of abundance and ecological function is the tube-building sabellariid polychaete worm *Phragmatopoma lapidosa*, which engineers structure utilized by at least 200 species of decapod crustaceans alone (Gore et al., 1978), many with direct or secondary trophic links to recreationally important fish species. However, the presence and significance of *P. lapidosa* declines south of Palm Beach County. The array of other significant invertebrates is large and includes *Pione* spp., *Siderastrea* spp., *Menippe nodifrons*, *Pachygrapsus* spp., *Petrolisthes* spp., *Echinometra lucunter*, and *Synalpheus* spp. The total number of fish species recorded is 257; several records await confirmation. The fish assemblage of NHB throughout the project region is a juvenile-dominated reef fish assemblage including grunts, damselfishes, wrasses, porgies, blennies, snappers, and other families of reef-associated fishes.

The energetic functioning of NHB systems is in part driven by diverse macroalgal assemblages that include 275 species. The total number of algae and cyanobacteria recorded includes 277 identified species, with 341 total types and species, including unidentified species (**Table 7.1**). Of these, the rhodophytes (red algae) were most diverse, with 153 identified species. The most important species in terms of abundance and ecological function include *Laurencia poiteaui, Caulerpa prolifera, Dictyota* sp., *Caulerpa sertularioides,* and *Caulerpa racemosa*.

Table 7.1. Total numbers of family, genera, and species of macroalgae associated with nearshore hardbottom habitat from studies along the east Florida coast (see **Appendix A**, **Table A.1**).

Group Division	Family	Genera	Species
Algae			
Chlorophyta	10	20	59
Rhodophyta	30	62	153
Phaeophyta	9	15	48
Total algae	49	97	260
Cyanobacteria	8	11	17

Total number of species = 277; Total overall = 341 (includes unidentified types).

7.2 ECOLOGICAL FUNCTIONAL GROUPING

To structure the ecological complexity within shallow hardbottom, we organized the high diversity of species by identifying functional groupings that characterize the use of shelter and trophic resources and comparing patterns among primary functional groups, taxa, and other system components. Knowledge of the parts and processes that compose the functional attributes of shallow reef habitats in mainland east Florida is needed for management, but such efforts are frequently confounded by the morass of terminological holes involving the term *function* (Jax, 2005; **Chapter 1**, present study).

Many studies have historically focused on two basic categories of functional attributes: 1) structure-shelter and 2) feeding (trophic support). These groups can be useful as organizing steps in more detailed and measurable functional analyses such as traits analyses. Based on the literature on NHB and the literature on functions and functional groups, we identified at least 12 nominal functional group categories in **Chapters 1** through **6** that apply to NHB, IHB, and shallow OHB assemblages:

- Structure-shelter associated functional groupings. Examples include groups of species sharing one or more of the following attributes and associating with shallow hardbottom:
  - Habitat engineering functions (keystone framework builder);
  - Nesting and spawning site usage of NHB through OHB;
  - Structure as attachment resource for sessile organisms;
  - Settlement and post-settlement nursery areas; and
  - Juvenile and adult patterns of cross-shelf distributions.

- Trophic functional groupings. Food capture patterns, larger energetic fluxes and physical dynamics drive food web dynamics (e.g., inter-community nutrient exchange functions of carnivores and herbivores on NHB and OHB [Parrish, 1989]), such as the following:
  - Herbivory;
  - Carnivory;
  - Autotrophy;
  - Detritivory and omnivory; and
  - Cleaning symbioses.

These 10 categories do not contradict the functional analysis framework associated with mitigation planning employed by the UMAM protocol (Continental Shelf Associates, Inc. et al., 2006). We also recognize that these are not entirely discrete groupings; there can be overlap among group processes and members, and also other attributes to emphasize. However, when synthetically evaluated for algae, invertebrates, fishes, and turtles, these groupings provide an heuristic structure that includes a majority of fundamental processes and functions of NHB, IHB, and shallow OHB.

7.2.1 Structure-Shelter Associated Functional Groupings

Habitat and structure-associated processes influence most aspects of the life cycle of all shallow hardbottom organisms. The details of how spatial and structural habitat attributes influence plant and animal distributions have rarely been studied for shallow hardbottom systems of the region. Attributes of the nearshore seascape of mainland east Florida that are fundamental to nearshore marine habitats and their spatial relationships include the following:

- NHB habitats are often separated from deeper hardbottom by several or many kilometers of relatively flat sand expanses;
- North of Government Cut, Dade County, seagrass beds and mangroves are seen only in the lee of barrier islands and not in direct proximity to shallow hardbottom. These vegetated habitats occur inside the inlets of the study area and are typically not in direct proximity with shallow hardbottom as in the Florida Keys and Caribbean. Therefore, NHB is the only physical structure with raised relief (0.5 to 3.0 m emergent height) in shallow waters of mainland east Florida (sand bedforms may have relief of ≤0.5 m);
- These nearshore areas are disturbance-mediated by depth and latitude. For example, higher energy nearshore wave environment exists north of the Bahamas wave shadow where more temperate coastal conditions also become more apparent and individual species adaptation to wider ranges of physical conditions is important;
- Diversities of motile invertebrates correlate positively with the presence of *P. lapidosa*, while sessile organisms generally correlate negatively with the presence of *P. lapidosa*; and
- The fish assemblages of shallow hardbottom in mainland east Florida are juvenile-dominated by species characteristic of coral reef fish assemblages.

7.2.1.1 Habitat Engineers

In terms of functional group considerations there is a prominent keystone component of hardbottom habitats along the Florida coast in the form of the habitat engineering polychaete *P. lapidosa* and the carbonate structures they rapidly build, commonly known as worm reefs or work rock. Worms of this sabellariid species select sediments from the water column and glue sand together to make sand tubes, forming substantial reefs in intertidal and shallow (<4 m) subtidal hardbottoms from Cape Canaveral to Key Biscayne in Florida. Their distribution continues southward to Santa Catarina, Brazil (Kirtley, 1994). Other representatives from their family (over 100 species) build extensive reefs that can be found in many locations throughout the world (reviewed by Kirtley, 1994; Pandolfi et al., 1998).

In Florida, the structure provided by *P. lapidosa* worm reefs on top of coquina shellrock is a substantial contributor to biological diversity, supporting higher diversities and abundances of species, including hundreds of species of invertebrates (Gore et al., 1978; Nelson, 1989), than neighboring sand habitats and hardbottom without *P. lapidosa* colonization. Eight federally-listed and 15 state-listed species are associated with nearshore reefs off east Florida (USFWS, 1999). Additionally, green, hawksbill, and loggerhead turtles, primarily represented by juvenile and subadult stages, are recorded in association with shallow hardbottom habitats. In particular, worm reefs are important sources of food and shelter for juvenile green turtles (Wershoven and Wershoven, 1989; Ehrhart, 1992; Ehrhart et al., 1996; Holloway-Adkins, 2001; Makowski et al., 2006b).

Worm reefs can also be important in the maintenance and persistence of beaches and barrier islands by retention of sediment, reduction of wave energy, grain sorting, and the progradation of beaches (Gram, 1965; Kirtley, 1966, 1967; Multer and Milliman, 1967; Kirtley and Tanner, 1968; Mehta, 1973; Kirtley, 1974; Pandolfi et al., 1998). *P. lapidosa* qualifies as a habitat engineer under criteria in Jones et al. (1994) and Coleman and Williams (2003) and has fast accretion rates (~0.5 cm per 24-hour period), with the potential to quickly create new structure with many microhabitat features, particularly subsequent to settlement events.

7.2.1.2 Nesting and Spawning Sites

Because many nearshore areas are expanses of sand in the absence of hardbottom, NHB may have substantial value as reference points for spawning activities of inshore fishes. Many fishes require three-dimensional structure as a reference point for coarse-scale aggregation and fine-scale behavior during spawning (Thresher, 1984). New information suggests that over 30 species may spawn directly on (nests) or near these reefs. Some are of substantial economic value; these include snook (*Centropomus undecimalis*), bigeye scad (*Selar crumenophthalmus*), and several herring species (*Harengula* spp.). Others, including small, cryptic species, especially blennies (*Labrisomus nuchipinnis, Malacoctenus triangulatus*, *Parablennius marmoreus*, and *Scartella cristata*) and damselfishes (*Abudefduf saxatilis* and *Stegastes* spp.) that deposit eggs directly on substratum, are common on NHB.

Most species of invertebrates are broadcast spawners or they release gametes or larvae directly on or above shallow hardbottom. This particularly applies for the vast majority of sessile invertebrates in the project region, suggesting that at least 400 to 450 invertebrate species reproduce in association with shallow hardbottom. Reproduction in over 200 algal species also occurs in association with shallow hardbottom.

7.2.1.3 Structure for Attachment

The hard substrata associated with NHB is essential in providing a point of attachment for many sessile animals and algae. Without the substrate, organisms such as worm rock, sponges, crabs, many algal species, site-associated fish species, and others simply would not have the resources to exist in these subtidal areas. Along the east Florida coast, hardbottom facilitates worm rock recruitment, which in turn provides shelter for many motile invertebrates and fishes (Kirtley, 1966, 1974: Gore et al., 1978; USFWS, 1999; McCarthy, 2001). Shelter is created not only by the external structure made by the worms but by the internal structure as well. The mounds created by *P. lapidosa* are relatively soft, and remarkable numbers of some invertebrates can be found within the worm rock, as some species of crabs, bivalves, and other worms are able to burrow in the rock to take shelter (Gore et al., 1978; Van Montfrans, 1981; Nelson and Demetriades, 1992). Other species such as snapping shrimp and sea cucumbers are seen using previously made crevices or holes. Overall, shelter inside the worm rock hosts flat worms, ribbon worms, sipunculans, many crustaceans, bivalves, and gastropods that would not exist in similar diversities or individual abundances in simple coquina rock hardbottom habitats.

Hay and Sutherland (1988) emphasized the role of light in structuring rocky marine communities in the southeast U.S., with well-lit structure often dominated by algae and unlit areas by invertebrates. This pattern may generically apply to shallow hardbottom of mainland east Florida, but it is not yet tested. The high diversities of algae would not exist without substrate for over 200 species to attach to. A variety of opportunities for intertidal and subtidal research into rocky intertidal processes involving invertebrates, algae, and their interactions remain relatively unexamined in association with shallow hardbottom of east Florida.

In addition to providing essential functions for numerous fishery species, bioerosion of hardbottom provides a source of new microhabitat and sand on the continental shelf (Riggs et al., 1985). Boring and burrowing shrimp and bivalves chemically or mechanically excavate holes, eventually weakening the rock; clionid sponges and rock-boring urchins do this as well. This habitat engineering manifests itself in differing ways. For example, crabs bore into worm mounds, and the synergistic effect of these boring organisms is high when coupled with natural disturbances such as wave activity. These all contribute to worm reef degradation and an increase in structural complexity by late summer/early fall. This process also enhances the structural complexity of hardbottom outcrops, promoting diversity of reef microhabitat structure.

7.2.1.4 Settlement and Post-settlement Nursery Areas

Invertebrates

It is probable that most of the motile invertebrates that settle on intertidal and shallow hardbottom along the coast ultimately die in the same areas that they settle. Many species that thrive in these shallow habitats (*P. lapidosa*, *Pione lampa*, and *Siderastrea radians*) become sexually mature very young and reproduce continuously (Soong, 1993; McCarthy, 2001; Schönberg, 2002; McCarthy et al., 2003). Most research on gastropods and crustaceans suggests that animals settle there and live a maximum of 2 to 3 years because of the ephemeral nature of these habitats (Gore et al., 1978; McCarthy, 2001; Watanabe, 2002; Watanabe and Young, 2006). For example, the oyster drill *Stramonita (Thais) haemostoma* has a population size distribution that gets progressively larger from fall to winter (but never as big as their oyster drill counterparts within the Indian River Lagoon) until seasonal disturbance results in high mortality by late summer (Watanabe, 2002; Watanabe and Young, 2006). However, they have adapted by becoming reproductively active faster than their lagoonal counterparts so that they can lay eggs before they die and produce a new cohort seemingly to maintain the population. Consequently, these new recruits settle in high numbers and shift the population distribution size back to smaller modal sizes.

High mortality of *P. lapidosa* mounds is common in some NHB areas of east-central Florida and increases during the summer as a result of the effects of several disturbance agents (McCarthy, 2001). In the early summer, some individuals at the tops of intertidal mounds perish, leaving the tops susceptible to decay and colonization by other sessile organisms. It is likely that this mortality is caused by desiccation and/or heat stress from extreme summer temperatures. By the late summer and early autumn, wave activity from hurricanes results in maximum physical disturbance to sabellariid reefs. A large percentage of both intertidal and subtidal reefs are severely damaged at this time. Intertidal worms are more susceptible to physical destruction of their colonies, whereas subtidal worms get smothered by sand but the sand reef remains intact. In addition, post-hurricane deposition of muddy sediment can kill attached invertebrates and prevent settlement (CSA International, Inc., 2007; Miller and Kosmynin, 2008).

Almost simultaneously with peaks in lethal disturbance, however, larvae of *P. lapidosa* arrive in large numbers to renew the reef by massive recruitment in cracks, atop, or on edges of adult mounds (McCarthy, 2001). Generally, recruitment occurs at the highest levels in the intertidal versus subtidal zone (**Figure 7.1**). McCarthy (2001) suggests that subtidal recruitment may be enhanced during periods of increased wave activity. Preliminary results from an ongoing study suggest that among five intertidal locations along a 218-km stretch of east Florida (Satellite Beach, Stuart, Coral Cove, Palm Beach, Boynton Beach), during the years from 2006 to present, *P. lapidosa* recruited at the highest levels in Stuart, followed by Satellite Beach. However, at all five locations, peak larval recruitment appears to occur during the fall-winter time periods. Consequently, recruitment during this time results in new low-lying reefs that are highly resilient and will eventually restore the structure of the reefs. As disturbance lowers adult abundance and creates new settlement space, new individuals potentially can arrive in sufficient numbers to restore the populations. Therefore, local populations may remain at fairly high abundances year after year while experiencing moderately high mortality from various agents of disturbance (McCarthy, 2001; **Figure 7.1**), a pattern seen in some intertidal organisms in the Pacific U.S. When this *P. lapidosa* colonization information is integrated with those of other researchers (Gilmore, 1977; Gilmore et al., 1981; Lindeman and Snyder, 1999), links are suggested between the seasonal cycle of sabellariid reef expansion and degradation, and the occupation of those reefs by juveniles and adults of other organisms.

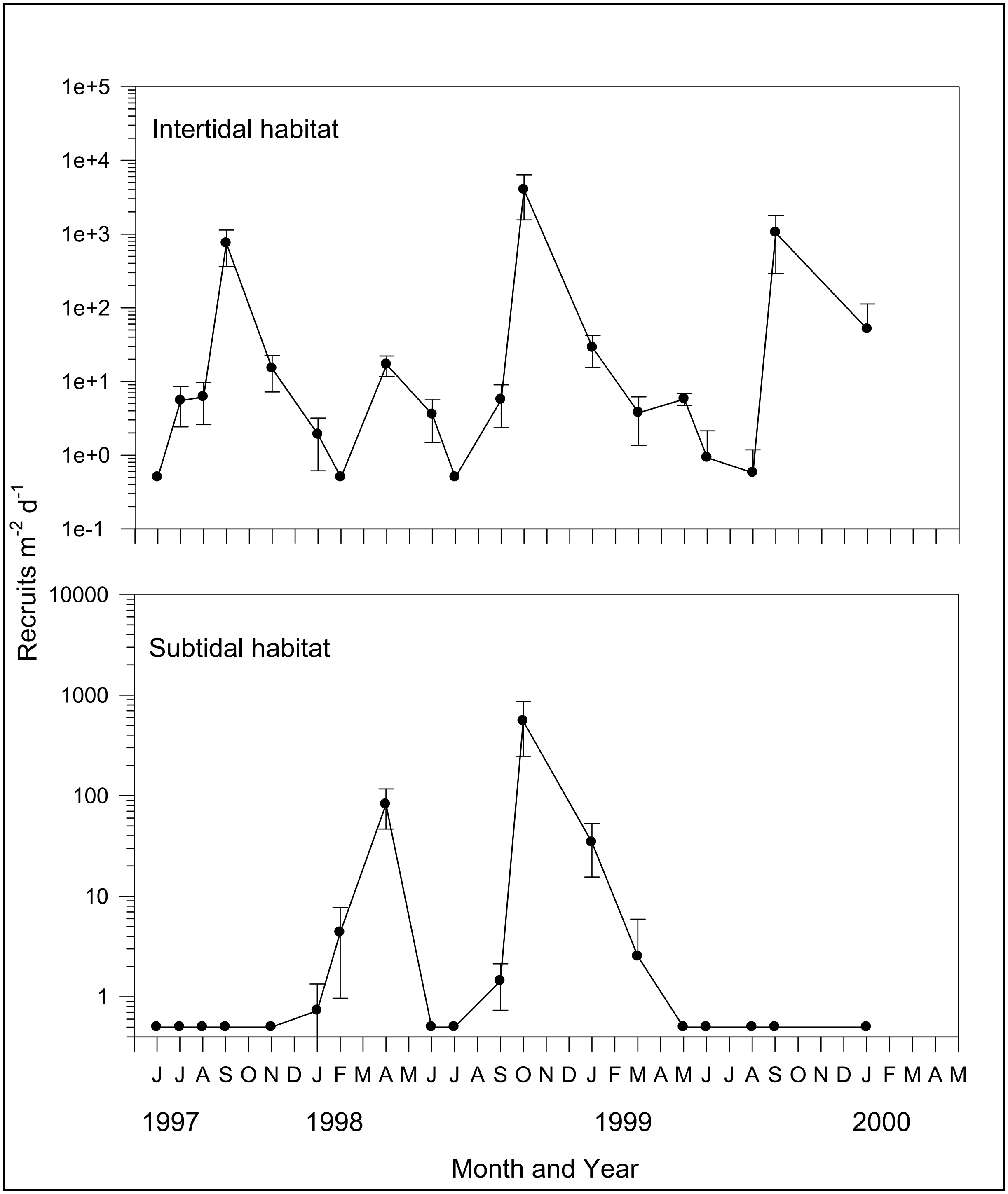


Figure 7.1. Seasonal larval recruitment of the sabellariid worm *Phragmatopoma lapidosa* in intertidal and subtidal nearshore hardbottom habitats off Boynton Beach, Palm Beach County, Florida. Mean values (± standard deviation) of recruitment are plotted on log scales. All subtidal sites covered with sand after May 1999 (From: McCarthy, 2001).

Some biological information on ephemeral exposure of NHB is available in regards to short-term *P. lapidosa* tolerance to sand covering. These worms typically have some tolerance to limited sand covering for short periods of time, up to 72 hours in various studies (Main and Nelson, 1988; Sloan and Irlandi, 2007). After this time period, most individual worms die. Mortality occurs earlier during warmer periods. Scleractinian corals (e.g., *Siderastrea radians*) have been recorded growing on seasonally buried NHB (V. Kosmynin, FDEP Bureau of Beaches and Coastal Systems, pers. comm.). Care should be exercised in averaging NHB exposure over multiple years for beach nourishment projects. The majority of beaches and nearshore sedimentary systems have been exposed to several renourishments or have been indirectly affected by long-shore drift. To best capture natural situations and away-from-nourishment effects, photoimagery is best taken right before dredge and fill events when aerial resources are available and visibility allows (V. Kosmynin, FDEP Bureau of Beaches and Coastal Systems, pers. comm.).

On hardbottom deeper than 4 m, the degree of disturbance is likely less; there is evidence that this may correlate with the presence of longer-lived invertebrate species (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). There appears to be a higher number of sessile species that take longer to become sexually mature and reproduce seasonally. It is unclear how much movement there is of motile invertebrates among hardbottoms within this depth range. However, spiny lobster clearly move long distances among hardbottom habitats, as seen in the Florida Keys and Bahamas (Kanciruk and Herrnkind, 1978) (see **Section 7.2.1.5**).

Fishes

In terms of ecological function, several lines of evidence suggest that NHB reefs may serve as significant settlement areas in shallow marine waters from Broward through Brevard Counties. The following summary of fishes is based on information available for mainland southeast and east central Florida (Gilmore et al., 1981; Lindeman, 1997a; Lindeman and Snyder, 1999; Baron et al., 2004), with some papers including life stage-specific abundance data. Pooled early life stages can represent over 80% of the total individuals at sites censused (**Figure 5.6**). Eight of the top 10 most abundant species were consistently represented by early stages. Use of hardbottom habitats was recorded for newly settled stages of more than 20 species. Some species have characteristic settlement microhabitats in which they can differentially aggregate while undergoing transformation from epibenthic larvae into demersal juvenile stages. Microhabitat adaptation in newly settled drums (*Pareques* spp., Sciaenidae) can involve the occurrence of triangularity, for example in the frontal and lateral profiles of individual larvae, the crevices between rock and coarse sand they typically utilize, and the outer boundary shapes of schools that settlers can form (**Figure 7.2**).

Figure 7.2. Newly settled drums (*Pareques* species) commonly associate with ledges and triangular cavities at the base of shallow hardbottom structures, such as in this photograph taken from 2 m depth, Singer Island, Palm Beach County, Florida. *Photo by D. Snyder.*

The presence of more juvenile stages than adults does not guarantee a habitat is a valuable nursery (Adams et al., 2006). Rapid decays in the benthic or planktonic survival of early stages of marine fishes are common demographic patterns (Shulman and Ogden, 1987; Jones, 1991), ensuring that if distributions are homogeneous, all habitats will have more early stages than adults. Settlement and early life stage utilization of shallow hardbottom has been studied in more detail in recent years, in part due to artificial reef placement in IHB and OHB depths. Despite substantial sampling efforts in deeper waters, many species of grunts are not encountered as early stages in midshelf or deepter reef habitats (e.g., Jordan et al., 2004). Adults are often infrequent or absent from the shallow habitats. There is considerable evidence for habitat segregation among life stages of some species, with the earliest stages of many species of grunts and snappers often using the shallower habitats (Starck, 1970; Dennis, 1992; Lindeman et al., 1998; Jordan et al., 2004). Similar ontogenetic differences in both distribution and abundance exist for diverse species from other families that utilize NHB habitats. Based on available information, we estimate that at least 40 fish species utilize NHB as a primary or secondary larval settlement area, many (but not all) with seasonal peaks in warmer months (Lindeman and Snyder, 1999; Baron et al., 2004).

In mainland east Florida, NHB may also serve as intermediate nursery habitat for late juveniles emigrating out of estuaries (Vare, 1991; Lindeman and Snyder, 1999). This appears to also apply to some fishes from hardbottom to the north. Nearshore and inner shelf hardbottom areas north of Cape Canaveral can also serve as important settlement and nursery habitat for immigrating larvae of coastal fish species. Powell and Robbins (1998) collected larvae from 22 reef-associated families adjacent to hardbottom habitat in Onslow Bay, North Carolina. Tomtate (*Haemulon aurolineatum*), white grunt (*H. plumieri*), snappers (including vermilion snapper, *Rhomboplites aurorubens*), black sea bass (*Centropristis striata*), bank sea bass (*C. ocyurus*), sand perch (*Diplectrum formosum*), spottail pinfish (*Diplodus holbrooki*), and whitebone porgy (*Calamus leucosteus*) were commonly collected (SAFMC, in prep.). These species may have been spawned in Onslow Bay in somewhat deeper water and recruited locally to nearshore hardbottom (Powell and Robbins, 1998; SAFMC, in prep.).

7.2.1.5 Juvenile and Adult Cross-shelf Distributions

The vast majority of invertebrate species do not migrate or shift habitats from shallow hardbottom. Some motile exceptions may include portunid crabs, spiny lobster, and squids, but there is not a great deal of invertebrate migration between NHB and neighboring habitats. The polychaete *P. lapidosa* generally has higher abundance intertidally than subtidally along east Florida hardbottoms (**Figure 7.1**). It is moderately abundant in subtidal NHB and somewhat common in IHB. Generally, *P. lapidosa* is in very low abundance or not encountered in nearshore OHB along the east Florida coast.

Spiny lobster, primarily known from NHB in Indian River and St. Lucie Counties, clearly move long distances from shallow to deep habitats, as seen in the Florida Keys and Bahamas (Kanciruk and Herrnkind, 1978). Spiny lobsters have been observed moving along 4 m reef at Boynton in chains of ~15 (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Within that area of the coast, there were probably hundreds on the move heading northward. Mass migrations (referred to as “crawls” by locals) by large numbers of spiny lobsters occurs typically in late summer early fall along the coast of southeast Florida. Single-file lines of individual lobsters move presumably from offshore areas toward the shore where they seek cover around any structured object (natural or artificial). Kanciruk and Herrnkind (1978) determined that mass migration in the Bahamas was triggered by the onset of cold fronts. At least one mass migration in 1980 off Palm Beach, Florida was associated with a cold water upwelling event (D. Snyder, CSA International, Inc., pers. observ.).

Damselfishes and cryptic hardbottom fish species do not engage in ontogenetic habitat shifts. Juveniles of schooling species (surgeonfishes, parrotfishes, chubs) may migrate away from NHB to deeper structural habitats with maturation, but depth-specific information is largely unavailable among these habitats. The ability to successfully make such migrations will correlate in complex manners with the degree to which cross-shelf habitat corridors are available and, also, drivers associated with potential ontogenetic shifts in food needs. Cryptic resident species do not appear to migrate further offshore with development, displaying no cross-shelf ontogenetic migrations. They are life-long residents of the NHB, IHB, or shallow OHB structure that they settle on and display feeding modes from herbivory to probable piscivory. A variety of other species (e.g., wrasses, grunts, snappers, sciaenids, mullids, *S. rubripinne*) may sample other habitats with age and eventually emigrate; presumably survival will be very dependent on the habitat and predator seascape, both while traveling and eventually on entering new habitat.

Juvenile marine turtles off Florida coastal waters are predominantly found associated with NHB habitats. Recapture data and tracking information from population studies suggest that turtles spend several years in neritic habitats (Ehrhart et al., 2001; Makowski et al., 2006b). Juvenile green turtles have been recaptured on the same NHB reef locations more than 9 years later (Ehrhart, unpubl. data). Studies in NHB habitat indicate that juvenile green turtles grow slower in NHB versus estuarine habitats (Kubis, 2003); however, the costs of slow growth may be offset by relatively lower predation levels due to higher structural complexity offering better protection from predators.

7.2.2 Trophic Functional Groupings

7.2.2.1 Herbivory

Invertebrate herbivory on macro- and micro-algae may be high among the diverse array of plants associated with shallow hardbottom. In various temperate rocky intertidal studies, over 50 species of shallow hardbottom or rocky intertidal invertebrates have been reported to feed on macro- and microalgae (**Appendix D**, **Table D.1**). Some of the same macroalgal genera are found on Florida NHB (*Acanthophora*, *Bryopsis*, *Ceramium*, *Chondria*, *Codium*, *Dictyota*, and *Sargassum*) and are likely grazed on by fish and invertebrate herbivores. Vertebrate grazing analyses from juvenile green turtle foraging samples (Holloway-Adkins, 2001) and herbivorous fishes (Randall, 1967) indicate *Ceramium* sp., *Ulva* sp., *Polysiphonia* sp., *Lyngbya* sp., *Centroceras* sp., and *Dictyota* sp., are primary food items for these animals (**Appendix D**, **Tables D.2** and **D.3**).

Along east Florida hardbottom there are a number of echinoids that may be important herbivores. The most significant are *Echinometra lucunter, Tripneustes ventricosus*, and *Arbacia punctulata*. They are generally most abundant to the north of Palm Beach County at depths in excess of 1 m and occur in highly variable densities that can range as high as ~25 individuals /m^2 and likely exert substantial herbivory affects on marcoalgae and sessile invertebrates in the areas where they occur. Other echinoids such as *Diadema antillarum, Lytechinus variegatus*, and *Eucidaris tribuloides* are herbivores but probably do not exert the same influence over macroalgal communities because of their generally low abundance.

Many reef fish herbivores occur in association with NHB and include the surgeonfishes (Acanthuridae), parrotfishes (Scaridae), porgies (Sparidae), and chubs (Kyphosidae); most of these families are represented largely by juvenile life stages on NHB, but can occur as adults (Lindeman and Snyder, 1999; Baron et al., 2004). Non-schooling herbivores on NHB include the damselfishes (five species), filefishes (Monacanthidae), spiny puffers (Diodontidae), presumably all gobiids, and several blennids (Randall, 1967). In NHB environments, herbivores represented relatively few fish species (**Figure 5.11**), but these can be locally abundant and may have some impacts on macroalgal biomass, though this is unstudied.

There can be substantial ontogenetic variation in feeding among some species. For example, the silver porgy (*Diplodus argenteus*), a very abundant sparid on NHB, is probably omnivorous like its closely related congener, the spottail pinfish (*D. holbrooki*). The latter species was found to eat both algae and macroinvertebrates by Hay and Sutherland (1988) in a study of rocky jetty-type structures in Murell's Inlet, South Carolina. Carr and Adams (1972) documented that *D. holbrooki* fed upon ectoparasites and were therefore considered to be cleaners. Juveniles of *D. argenteus* have been observed cleaning larger fishes in NHB environments (D. Snyder, CSA International, Inc., pers. observ.).

Juvenile green turtles preferentially feed on several algal species from a larger pool of available algae (**Appendix D**, **Table D.3**). High wave energy not only strongly influences the production of macroalgae, but also can reduce grazer accessibility, especially in intertidal and shallow subtidal sections of NHB and IHB. This species may be more abundant where competition from herbivorous fish and invertebrate species is reduced (e.g., the northern project region with cooler waters). Macroalgal resources, in turn, may be more abundant for several reasons, including cooler water temperatures, higher nutrient levels, and, potentially, a lower abundance and diversity of grazers.

7.2.2.2 Carnivory

Invertivory

Crustaceans are often very important predators upon invertebrates within shallow hardbottom food webs along the east Florida coast. Some crustaceans can also feed on small fishes. Gore et al. (1978) postulated a possible food web for sabellariid colonies on the east Florida coast where the worms form the basis of the food web on which many species of reef-dwelling crabs forage (**Figure 7.3**).

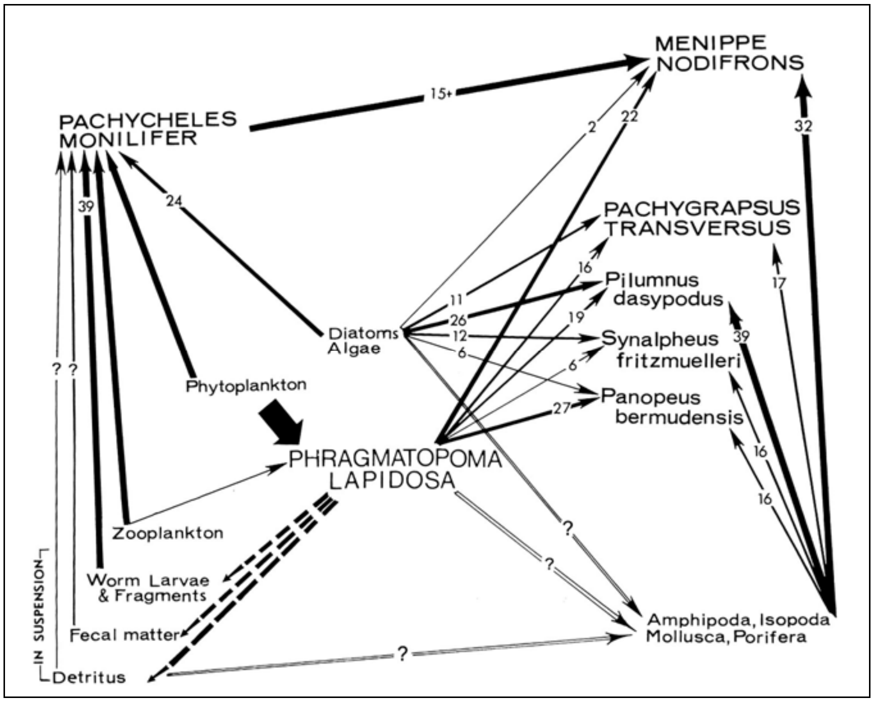


Figure 7.3. Food web among six common decapod crustaceans from worm reefs. Numbers on lines indicate the percent of observed prey material in the guts of all individuals examined per species. Dashed lines indicate production from worm reef (*Phragmatopoma lapidosa*) (From: Gore et al., 1978).

There is a high diversity and abundance of infaunal invertebrates within soft sediments adjacent to east Florida NHB. Within the intertidal and shallow subtidal zones, there are various crustaceans, molluscs, bivalves, and polychaetes that can be very abundant. Mole crabs (*Emerita talpoida*) and various *Donax* spp. are often most conspicuous. However, several species of polychaetes such as *Nephtys bucera* and *Scolelepis squamata* are common in these habitats as well. Progressing into deeper sand bottom areas (~3 m water depths), the polychaetes *Dispio uncinata* and *Paraonis* sp. and the bivalve *Tellina* sp. are very dominant. However, amphipods, caridean shrimp, portunid crabs, gastropods, and bivalves can also be encountered. Some threatened coastal bird species feed on intertidal invertebrates and can exchange energy between the upper beachface and the NHB, or the coastal ocean and NHB. Species include herons, egrets, plovers, brown pelicans, and others (Bishop et al., 2006).

Many demersal fish species may migrate further into adjacent sand areas in search of food as they mature, and they can exchange large amounts of nutrients in these often nocturnal migrations (Parrish, 1989). Meyer et al. (1983) provides a specific example of intercommunity energy exchange and growth impacts for grunts in the U.S. Virgin Islands. Older life stages of grunts and other species on NHB may be engaging in sand feeding migrations at night, exchanging energy between reef and softbottom environments. In addition, coastal pelagics can transport energy into and out of the system via transient usage of NHB and IHB structure.

The majority of the approximately 200 fish species recorded from NHB through OHB in east Florida feed on invertebrates, first as zooplanktivorous larvae and via an explosion of diversity in invertebrate consumption with maturation among reef fishes (**Figure 7.4**). There are often large variations in prey composition among differing life stages. Detailed studies on trophic ecological process of shallow invertebrates and fishes of Florida NHB are lacking, therefore constraining analyses.

Figure 7.4. Gray triggerfish, *Balistes capriscus*, pursuing invertebrate prey, Breakers Reef, approximately 6 m depth, Palm Beach, Florida. *Photo by D. Snyder.*

Planktivory and Suspension Feeding

A number of sessile invertebrates encountered along east Florida hardbottoms are suspension feeders. Within the intertidal sections of the NHB, *P. lapidosa* and several barnacle species are the most commonly encountered. From subtidal NHB to OHB, *P. lapidosa* can be abundant in shallower depths, but a number of sponge and tunicate species become more prevalent. Additional suspension feeders encountered in these habitats are sabellid and serpulid polychaetes, several species of bivalves, and decapods such as porcellanid crabs.

At least 30 fish species associated with NHB can be classifed as planktivorous. Common planktivores found on NHB including herrings (*Harengula* spp., *Opisthonema oglinum*), sardines (*Sardinella aurita*), and scads (*Decapterus* spp., *Selar crumenophthalmus*) tend to form large schools and frequently move within local areas. Many fishes are planktivorous as newly settled or early juvenile individuals (haemulids, reef sciaenids) but change diets with ontogeny. Silver porgy and spottail pinfish are examples of species that shift from planktivory as young to omnivory as adults (Carr and Adams, 1972). Grunts such as French grunt and tomtate are obligate planktivores as newly settled individuals but gradually switch to demersal carnivory as they grow. Observations on NHB in Palm Beach County indicate that larger juveniles of the these species will opportunistically feed on plankton when directional currents are strong and presumably carrying greater quantities of plankton over the NHB. Given the high proportion of early stage fishes found on NHB, planktivory represents an important trophic element of the local system that is subsidized by the import of plankton from the broader scale coastal waters. At present nothing is known regarding the diversity, composition, or temporal occurrence of the planktonic prey base in NHB environments.

7.2.2.3 Autotrophy

Cyanobacteria and macroalgae, the primary producers in marine ecosystems, convert sunlight and nutrients into assimilable energy used by primary consumers. These photosynthetic cohorts specialize in the ability to convert abiotic material (carbon) and light into food. Macroalgae utilize both nutrients and carbon dioxide and are able to fix nitrogen, and many species of cyanobacteria also can fix nitrogen (Vermaas, 2001). Primary animal autotrophs in this system are the zooxanthellae-bearing sceleractinians. In addition to autotrophic production, these species have multiple ecological functions as shelter and direct food resources (Banks et al., 2008). While primary production is the foundation of the trophic food pyramid, the importance of maintaining balanced trophic levels in marine systems, especially coral reefs, is high (e.g., Paddack et al., 2006). Overgrowth of coral reefs by macroalgae due to increased nutrient input or a significant reduction of primary consumers by overfishing can have large, well-documented impacts on coastal food webs (Jackson et al., 2001).

There may be a generally higher biomass of macroalgae in the more northern sections of hardbottom along the east Florida coast. The exact reasons for this trend are unclear. The Florida Current may contribute to this trend because its coastal influence decreases towards the north. Consequently, there are cooler waters and possibly higher upwelled nutrients in the more northern hardbottom areas along the coast. More nutrients may provide important resources to increase algal biomass. Additionally, towards the south there may be a higher diversity and abundance of herbivorous fishes that may affect macroalgal production in those areas, thus creating space for otherwise substrate-limited organisms (i.e., corals). These and other alternatives are ripe for empirical investigation.

7.2.2.4 Detritivory and Omnivory

Many detritivores in association with NHB are omnivorous. In marine food webs, detritivores play important roles as recyclers in ecosystem energy flow and biogeochemical cycles. A number of motile invertebrates found on shallow hardbottom are known to feed on detritus, although no known studies have specifically investigated invertebrate detritivory on NHB. Most known invertebrate detritivores found on Florida NHB are polychaetes or crustaceans, although some gastropods and echinoderms are likely to feed on detritus as well. The Gore et al. (1978) trophic web for worm reef areas suggested that the highly abundant crustacean *Pachycheles monilifer* was abundant in shallow hardbottom habitats because of its omnivorous diet that includes detritus in suspension. They also suggested that various amphipods, isopods, molluscs, and sponges gain nutrition from suspended detritus.

There are a number of motile invertebrates and some fish species on NHB that can be considered omnivores. Most omnivorous invertebrates are crustaceans, and several are very abundant. A number of xanthid, portunid, and hermit crabs and shrimp can be omnivorous. Slipper, spiny, and spotted spiny lobster are omnivores that are also common in subtidal NHB, IHB, and OHB. Some molluscs (e.g., a few gastropods and cephalopods) can be omnivorous as well. As adults, omnivorous species of fishes include chubs (*Kyphosus* species), filefishes and puffers, all gobiids, and several blennioids. When whole ontogeny is considered, some species are relatively omnivorous, feeding on plankton not only as larvae but sometimes for a week or more after settlement (e.g., haemulids, some sciaenids, pempherids).

7.2.2.5 Cleaning Symbioses

Cleaning behavior is defined as the removal by a cleaning organism of ectoparasites or injured tissue from a host or client organism. In marine environments, shrimp and fishes are the primary taxa that engage in cleaning behavior. Despite the many examples of cleaning behavior, only a few species are obligate cleaners, whereas most of the facultative cleaners do so only as juveniles (e.g., Hobson, 1971; Poulin and Grutter, 1996; Sazima et al., 1999). Hobson believed that only certain individuals of some species clean and that cleaning behavior is widespread among small species that pick organisms from the substrate or water column.

Figure 7.5. A juvenile French angelfish (*Pomacanthus paru*) cleaning an adult gray triggerfish (*Balistes capriscus*) in 4 m depth off Palm Beach, Palm Beach County, Florida. *Photo by D. Snyder.*

Examples of fish species recorded from shallow hardbottom that act as facultative cleaners include the young of leatherjack (*Oligoplites saurus*) (Lucas and Benkert, 1983), spottail pinfish (*Diplodus holbrooki*) (Carr and Adams, 1972), porkfish (*Anisotremus virginicus*) (Longley and Hildebrand, 1941), angelfishes (*Pomacanthus* spp. and *Holacanthus* spp.) (Brockmann and Hailman, 1976), and the wrasses (Feitoza et al., 2002). Cleaning behavior can frequently be observed on NHB, with cleaners including juvenile angelfishes, wrasses, gobies, porkfish, and silver porgy (D. Snyder, CSA International, Inc., pers. observ.). **Figure 7.5** shows a juvenile angelfish cleaning a gray triggerfish on NHB near Palm Beach, Florida. Baron et al. (2004) included nine species of known cleaners during their Broward County study. Lindeman and Snyder (1999) encountered six known cleaning species in the Jupiter area. Shrimp known to be cleaners, including *Stenopus hispidus*, *S. scutelous*, *Lysmata* spp., and *Periclimenes pedersoni*, do inhabit NHB (D. Snyder [CSA International, Inc.] and D. McCarthy [Jacksonville University, Jacksonville, FL], pers. comm.); however, none were recorded during the sampling programs discussed in **Chapter 4**.

7.3 LATITUDINAL COMPARISONS

Sessile invertebrate communities change noticeably with latitude along the east Florida coast. In intertidal hardbottoms to the north, dominant invertebrates are bryozoans, sabellariid polychaetes, sea anemones, and tunicates (**Chapter 4**). North of Palm Beach County, there is an increase in abundance of *P. lapidosa*, both intertidally and subtidally. Throughout tidal pools within intertidal areas of these latitudes, the starlet coral *Siderastrea radians,* two species of zoanthids, and several species of solitary anemones can be encountered. Within the lower intertidal and shallow subtidal zones, the most conspicuous sponge is the rock-boring sponge *Pione lampa*. In the more northern counties that have subtidal hardbottom (i.e., Brevard and Indian River), sponges, two species of gorgonians (*Leptogorgia virgulata* and *L. hebes*), and one species of telestacean (*Carijoa* [*Telesto*] *riisei*) can be encountered. In this area, the most significant hard corals are *Siderastrea* and the *Oculina* species. However, there are occasional occurrences of *Cladocora arbuscula*, and grouped polyps of *Phyllangia* and *Astrangia* spp. (Brooke and Young, 2005). Within Martin County, the St. Lucie Inlet Reef appears to be the northernmost extent of several of the reef-building corals that are known biodiversity contributors.

To the south, the diversity and abundance of anthozoans increase on subtidal hardbottoms (SFCREMP, 2007; Beal, unpublished data). The geological origins of Broward's NHB have some different characteristics than northern areas (Moyer et al., 2003; Banks et al., 2008). Unlike counties to the north, Broward County possesses a nearshore ridge complex inside the inner reef line that has a complicated array of depth strata. The shallowest prominent scleractinians in the 3 to 7 m depth range include *Solenastrea bournoni*, *Diploria clivosa*, *Dichocoenia stokesii*, and the staghorn coral, *Acropora cervicornis* (Moyer et al., 2003; Vargas-Angel et al., 2003; SFCREMP, 2007). The potential biological significance of these latitudinal differences for shallow hardbottom communities has not been formally evaluated for any invertebrate species to date.

Differences among ichthyofaunal assemblages are suggested between the southern and northern areas of mainland southeast and east-central Florida in terms of the most abundant species (**Chapter 5**), but information remains relatively limited. Causes of the differences can include 1) differing amounts and types of shallow hardbottom among sections of southeast Florida and east-central Florida and 2) differences in northern geographic distributional boundaries among some highly abundant species.

There are notable differences in abundance between three of the most abundant species in the Jupiter area in comparison to the Fort Lauderdale area. Only one black margate out of >72,000 individuals was recorded in Fort Lauderdale (Baron et al., 2004), while 636 black margates out of 10,491 individuals were censused in Lindeman and Snyder (1999). Also, 43 sailors choice, *Haemulon parra,* were recorded in Baron et al. (2004), while 1,326 *H. parra* individuals were recorded in Lindeman and Snyder (1999). The hairy blenny was the most abundant cryptic hardbottom species in the Jupiter surveys, 8% of the overall individual total (Lindeman and Snyder, 1999); none were recorded in transect and point-counts in Fort Lauderdale (Baron et al., 2004). Numbers of the abundant porgies, *Diplodus* spp., were also much lower. Seasonality of sampling will be important as comparative information is examined further.

The latitudinal distribution of marine turtles associated with NHB is unclear at this time. General patterns, however, indicate that loggerhead turtles are sparsely present in northern NHB (Brevard and Indian River Counties) and moderately present on deeper reefs in southern NHB (Palm Beach County). Visual transect survey data indicate that juvenile green turtles are more abundant in intertidal and shallow subtidal areas than in deeper subtidal areas, and hawksbill turtles are infrequently encountered north of Palm Beach County.

7.4 DISTURBANCE ECOLOGY

Disturbance has been defined in several ways (see Sousa, 2001 for a review). It is often defined as damage or mortality that is caused by some external agent or force. This agent can be either physical (e.g., wave activity) or biological (e.g., predation) (Sousa, 2001). Disturbance may be lethal, resulting in the death of the animal, or it may a sublethal stress that reduces the potential for growth or reproduction of an organism. Obviously, any disturbance can affect reproduction if it kills the animal before it has the chance to reproduce. Sublethal disturbance can also influence reproduction by affecting the available energy an animal has for reproduction. Several correlative studies on marine invertebrates have shown negative relationships between fecundity and external stress factors such as sedimentation, wave activity, and turbidity (Kojis and Quinn, 1984; Jokiel, 1985; Rinkevich and Loya, 1987; Tomascik and Sander, 1987; Szmant and Gassman, 1990; Van Veghel and Bak, 1993; Ward, 1995).

Nonlethal disturbance might affect gamete production by diverting energy to regeneration of body parts (Lawrence and Vasquez, 1996). Such disturbance is known to occur to individuals by a variety of mechanisms, including unsuccessful predation attempts, trampling by humans or other animals, or the impact of objects propelled by waves (see Sousa, 2001 for a review). Stress caused by changes in several environmental factors has been implicated in numerous studies of spawning and/or gametogenic synchrony in marine invertebrates (Young, 1945; see Giese and Kanatani, 1987 for a review). Several studies of nonlethal disturbance have revealed that polychaetes regenerating damaged or lost body parts have lower fecundity and increased time to maturity than their undamaged counterparts (Hill and Grassle, 1981; Hill et al., 1982; Zajac, 1985).

Nonlethal disturbance could also affect the frequency of spawning of animals and plants. Barry (1989) suggested that disturbance might affect seasonal spawning patterns of *Phragmatopoma californica* because lethal disturbance generally breaks tubes, facilitating a known spawning response. Young (1945) observed increased spawning frequency with increased stress on the byssal threads of the mussel *Mytilus edulis*.

Spawning in individuals of detached mounds of *P. lapidosa* rolling around in the surf zone has been observed (J. Pawlik, University of North Carolina, Wilmington, NC, pers. comm.) Additionally, stress caused by changes in water pressure, desiccation, temperature, wave action, and salinity have been implicated in numerous studies of spawning and/or gametogenic synchrony of populations of marine invertebrates (see Giese and Kanatani, 1987 for a review). Differences in disturbance between habitats could affect fecundity differences between intertidal and subtidal individuals. Disturbance events that result in mortality can be very important in affecting the community of sessile organisms in a given area. On one end of the spectrum, high intensity and/or frequent disturbances such as wave activity can result in either no individuals in an area or very low numbers and diversities of organisms. In such cases, only the most morphologically adapted organisms such as limpets or chitons may be present. Moderate levels of disturbance may serve to mediate the effects of competition and result in the highest diversity of organisms (Levin and Paine, 1974). Such frequent disturbances may reduce the effectiveness of some opportunistic species from utilizing all available substrate space. The availability of such available space can then be colonized by other species if they can tolerate the level of disturbance in the area. In locations with lower intensity or less frequent disturbances, there is a tendency for lower diversity because a competitive dominant occupies most of the available substrate. During these competitive interactions, the size of substrate spaces created by disturbance is also important in terms of the type of organisms that occupy the space, and the time that it takes for the space to become fully utilized (see Sousa, 2001 for a review). Generally, larger “patches” of substrate space tend to be occupied more by sexually (versus asexually) reproducing species. These patches often take longer to become fully re-colonized. However, the time of colonization by sexual reproducers depends on how often these species spawn and the number of larvae they produce. In contrast, smaller patches tend to be colonized more quickly by asexually reproducing species (tunicates, corals, macroalgae) if they are present on the fringes of the patch.

7.5 OBLIGATE AND FACULTATIVE HABITAT USE

Certain species such as *P. lapidosa* may be limited to NHB (some in IHB) because of the need for substrate to settle and on the turbulent hydrodynamic regime that aids tube building and feeding that is primarily found in these depths. Most other invertebrate species can be found on NHB, IHB, and OHB, although their proportions likely vary. A number of those invertebrates that take shelter within or eat worm rock may be considered obligate to *P. lapidosa*, but further empirical evidence is required. Hardbottom substrata provide attachment sites for most species of macroalgae. Many of these species probably have an obligate association with shallow hardbottom for shelter and position-maintenance. Many algal species also have adaptive chemical defenses against herbivores (**Table 7.2**).

The species list for the entire NHB ichthyofaunal assemblage shows substantial similarities with many shallow coral reef species assemblages. Differences between NHB fish assemblages and reef assemblages in OHB depth ranges often involve the higher relative proportion of early life history stages on NHB structures, a juvenile-dominated assemblage. This suggests potentially important roles for differing ontogenetic species in shallow hardbottom systems (Werner and Gilliam, 1984; Livingston, 1988), a useful concept for some applications involving the spatial ecology of species whose behaviors, habitats, and functional roles can change several times post-settlement. While NHB may be considered facultative habitat for juvenile green turtles because turtles can use alternate systems for growth (e.g., the Indian River Lagoon), it raises the question of what is the most essential or effective habitat for this life stage. The promotion of the potentially debilitating disease fibropapillomatosis (or FP) has been attributed to environmental cofactors present within lagoon/estuarine systems. The occurrence of FP is substantially higher in estuarine environments, making the Indian River Lagoon, overall, a less-than-ideal water quality habitat for turtles. Tracking data from several sources indicate that most sub-adult green turtles (approximately 70 cm SCL; D. Bagley, in prep.) relocate and move into seagrass beds, where they forage. Some important nutritional aspects that are components of marine turtle developmental phases may drive their selection of certain habitats. Little is known about hawksbill turtles in NHB habitats; however, their unique diet of sponges will limit their foraging range to more tropical regions in areas where NHB provides suitable substrate for sponge settlement.

When newly settled and juvenile life stages are considered, questions of habitat dependence (an obligate attribute) and habitat opportunism (a facultative attribute) often focus on habitats used at settlement or associated life stages. Tests of dependence require consistent evidence that at least one life stage is restricted only to the habitat in question. For example, in the Dry Tortugas area of the Florida Keys, gray snapper settle in grass habitats in strictly euhaline waters and use a variety of other high-salinity habitats through maturity (Starck, 1970). Gray snapper can possibly migrate to Florida Bay from the Dry Tortugas, but because all demersal size classes occur in the euhaline, Dry Tortugas area, estuary dependence as a species paradigm is potentially excluded (Lindeman et al., 2000). Experimental manipulations could be of value in further examining the alternatives.

For NHB-associated fishes, existing information can exclude many motile species as having an obligate association with shallow hardbottom. However, there are species such as the striped croaker, and some goby and blenny species, that can have very high associations with shallow hardbottom (and shallow artificial reefs). In these species, experimental studies could possibly parse the degree of habitat dependency. Importantly, obligate associations with specific habitats (and foods) are relatively uncommon for many motile, shallow fish species anyway; individual marine organisms still have an immediate need for the structure or food a facultative habitat provides. Therefore many habitats, though used facultatively, still have measurable and potentially essential value as aggregators of the shelter and food resources that the early life stages of many species require.

Table 7.2. Macroalgal species found on Florida's Atlantic nearshore hardbottom habitat with known secondary metabolites proposed to aid in defense against herbivores. Table constructed primarily from data in Paul and Alstyne (1992) and Diaz et al. (2006).

Species		
Asparagopsis (Falkenbergia hillebrandii)	*Dictyota indica*	*Laurencia papillosa*
Avrainvillea sp.	*Dictyota pinnatifida*	*Laurencia poiteaui*
Bryocladia cuspidata	*Dictyota* sp.	*Laurencia* sp.
Bryopsis pennata	*Dictyota volubilis*	*Lobophora (Pocockiella variegata)*
Bryopsis plumosa	*Galaxaura cylindrica*	*Lyngbya* sp.
Bryopsis sp.	*Galaxaura marginata*	*Neomeris annulata*
Bryothamnion seaforthii	*Galaxaura rugosa*	*Neomeris* sp.
Bryothamnion sp.	*Galaxaura* sp.	*Padina gymnospora*
Bryothamnion triquetrum	*Gelidiella* sp.	*Padina profunda*
Caulerpa brachypus	*Gelidium americanum*	*Padina sanctae-crucis*
Caulerpa cupressoides	*Gelidium crinale*	*Padina vickersiae*
Caulerpa fastigiata	*Gelidium pusillum*	*Padina* sp.
Caulerpa isthmocladium	*Gelidium* sp.	*Penicillus dumelosus*
Caulerpa mexicana	*Grateloupia filicina*	*Penicillus* sp.
Caulerpa microphysa	*Halimeda discoidea*	*Polysiphonia binneyi**
Caulerpa peltata	*Halimeda incrassata*	*Polysiphonia denudata**
Caulerpa prolifera	*Halimeda* sp.	*Polysiphonia macrocarpa**
Caulerpa racemosa	*Halimeda tuna*	*Polysiphonia* sp.*
Caulerpa sertularoides	*Halymenia agardhii*	*Polysiphonia sphaerocarpa**
Caulerpa sertularoides farlowii	*Halymenia floresia*	*Polysiphonia subtilissima**
Caulerpa sp.	*Halymenia floridana*	*Sargassum cymosum*
Caulerpa taxifolia	*Halymenia* sp.	*Sargassum filipendula*
Chaetomorpha aerea	*Hincksia (Giffordia conifera)*	*Sargassum filipendula var. montagnei*
Chaetomorpha brachygona	*Hincksia (Giffordia duchassaigniana)*	*Sargassum fluitans*
Chaetomorpha media	*Hincksia (Giffordia mitchelliae)*	*Sargassum natans*
Chaetomorpha sp.	*Hincksia (Giffordia rallsiae)*	*Sargassum polyceratium*
Codium decorticatum	*Hypnea cervicornis***	*Sargassum* sp.
Codium interextum	*Hypnea cornuta***	*Stypopodium zonale*
Codium isthmocladum	*Hypnea musciformis***	*Udotea conglutinate*
Codium repens	*Hypnea* sp.**	*Udotea flabellum*
Codium sp.	*Hypnea spinella***	*Udotea* sp.
Codium taylori	*Jania adherens*	*Ulva (Enteromorpha chaetomorphoides)**
Cryptonemia crenulata	*Jania capillacea*	*Ulva (Enteromorpha compressa)**
Cryptonemia luxurians	*Jania rubens*	*Ulva (Enteromorpha flexuosa paradoxa)**
Dictyota bartayresii	*Jania* sp.	*Ulva (Enteromorpha flexuosa)**
Dictyota cervicornis	*Laurencia corallopsis*	*Ulva (Enteromorpha prolifera)**
Dictyota dentata	*Laurencia gemmifera*	*Ulva (Enteromorpha* sp.*)**
Dictyota dichotoma	*Laurencia intricate*	*Ulva lactuca**
Dictyota dichotoma v. menstrualis	*Laurencia microcladia*	*Ulva* sp.*
Dictyota divaricata	*Laurencia obtuse*	

* Inducible defenses that operate quickly, from seconds to minutes. ** Defense under question.

7.6 POPULATION CONNECTIVITY AND MAINTENANCE

For sessile invertebrates, there appears to be a trend towards limited dispersal of larvae or juveniles along the east Florida coast, but empirical information is limited. Of those species that reproduce sexually and asexually, many seem to propagate more via asexual reproduction. The scleractinian *Acropora cervicornis* is suggested to primarily reproduce when storm activity breaks its branches and individual pieces attach to the hardbottom (www.nmfs.noaa.gov/pr/species/invertebrates/staghorn.html). Recent molecular research supports this idea, as there appears to be restricted gene flow among Caribbean populations (Vollmer and Palumbi, 2007). Similar storm-induced asexual reproduction may influence reproduction in some sponges (*Pione* spp. and possibly *Aplysina* spp.) (Schönberg, 2002; M. Maldonado, Centros de Estudios Avanzados (CSIC), Girona, Spain, pers. comm.).

In terms of sexually reproducing invertebrates, there is a tendency towards shorter planktonic periods, and larval behaviors that work in concert with local currents, which may restrict dispersal of some of these species (McCarthy, 2001; Vollmer and Palumbi, 2007). For example, *P. lapidosa* larvae can be ready to settle 2 weeks after fertilization (Eckelbarger, 1976; Pawlik and Mense, 1994). They likely position themselves deeper within the water column, which may allow for local retention (McCarthy, 2001; McCarthy et al., 2002). Florida populations genetically compared to those in the Caribbean appear different, suggesting limited genetic exchange (Drake et al., 2007). Finally, the ubiquitous shallow water scleractinian *Siderastrea radians* broods its young, likely resulting in lower dispersal of offspring from parent populations (Soong, 1993).

A tremendous amount of new review, empirical, and modeling information is coming to bear on long-vexing issues of population connectivity. Considerable information has amassed regarding a variety of biotic and abiotic factors that contribute to retention in larvae. Retention on levels that challenge long-held views regarding long distance dispersal is now becoming commonplace (Jones et al., 1999; Cowen et al., 2000, 2006; Sponaugle et al., 2002; Paris et al., 2005; Cowen et al., 2006; Jones et al., 2008). Though many differences exist, there are similarities between mainland east Florida shallow hardbottom habitats and rocky intertidal habitats of the U.S. Pacific coast at some scales of examination.

Gunderson et al. (2008) proposed several broad categories of dispersal based on work with rocky intertidal Pacific fauna that have utility in examining potential dispersal and connectivity patterns in mainland east Florida. Their categories included 1) highly open connectivity among patchy populations and broad dispersal; 2) mesoscale dispersal structured by physics and resulting in several metapopulation sub-structures; 3) diffusive dispersal with stepping-stone metapopulations; and 4) non-dispersing networks of closed populations.

Efforts are underway to examine life history and empirical information on prominent invertebrate and fish species and functional groupings in the present study in order to assign select species or families of primary groups to appropriate connectivity categories. Nesting fish species with short larval periods (damselfishes), as well as species with limited pelagic larval periods (e.g., grunts, drums), show attributes of populations that could currently be placed in either the second or third dispersal category of Gunderson et al. (2008), through mesoscale details of east Florida differ. In terms of many taxa, these connectivity patterns may change markedly above and below the deflection of the Florida Current. Future research on these issues could be highly informative.

Chapter 8
Mitigating Shallow Hardbottom Impacts

An application of this synthesis report will be in the development of approaches to supplement current efforts to optimize the mitigation of unavoidable impacts. In this chapter, we examine fundamental theory and practice, and how mitigation is currently applied in nearshore waters of mainland east Florida. We also address Issue 4 (**Chapter 1**, **Section 1.1**), which is the question: if NHB has specific properties and functions that cannot be compensated for by existing OHB habitat, what are the best mitigation alternatives for the loss of NHB?

To investigate the background issues and Issue 4, we used biological information from prior assemblage-specific chapters in **Section 2** to examine preliminary scenarios of what happens to organisms during and subsequent to a dredge and fill burial at the fill site and how those stressors and effects may or may not cascade into local impacts at organismal and population scales. We also examine information regarding latitudinal differences in mitigation planning and implementation. It appears that only with such information aiding the front end of mitigation can the amounts and types of measurable compensation for lost services be fully evaluated.

8.1 STRESSORS AND EFFECTS

Recent methodological developments within the field of environmental assessment may aid evaluations of issues related to mitigation. Use of stressor and response characterizations within comparative ecological risk assessment frameworks is tractable. Full-experimental studies are often done in ecotoxicology, but synoptic, heuristic studies at scales that can slide from organismal to local population biology levels are feasible if the structured quantities of information assembled throughout **Sections 2** and **3** are used. Whichever specific approaches are used, considerations of cumulative effects are necessary in comprehensive stressor and effect characterizations (Vestal and Rieser, 1995; Lindeman, 1997b).

8.1.1 Ecological Assessment Frameworks

We used simultaneous evaluations of stressors, effects, and their potential co-occurrence with flexible protocols to help ensure comprehensive evaluations of effects (U.S. Environmental Protection Agency [USEPA], 1992; Harwell et al., 1995). This framework for assessing environmental effects of human activities was formalized by the USEPA in 1992 as comparative ecological risk assessment (CERA), and a number of approaches have developed. These approaches can be applied in iterative manners and by use of group-based protocols.

Prior to examining mitigation issues in detail, we assembled a preliminary CERA to identify some of the effects for which a mitigation reef might have to compensate. We simultaneously evaluated information on the specific stressors introduced by an anthropogenic event, the biological responses of the organisms and life stages in question, and the ultimate effects at individual and population levels. Subsequently, information on stressors and effects was integrated based on spatial and temporal patterns of co-occurrence for prominent species groups. Due to the inherent complexity of characterizing stressors, effects, and their co-occurrence, full-scale ecological risk assessments are large projects, typically requiring a team of experts. Mechanics for executing a full CERA are detailed in the above references.

8.1.2 Stressors, Responses, and Effects

At least three fundamental categories of stressors can be identified in beach dredge and fill projects: turbidity, sedimentation (burial), and direct mechanical impacts. In the case of dredge and fill projects of mainland east Florida, sediments are excavated from areas offshore, fill is pumped into the supratidal and intertidal zones, a sand dike is built, and the fill is bulldozed into a broad beach. Most involve the excavation and dumping of from 500,000 to 1,500,00 yd^3 of sediments per project. Follow-up projects are usually incorporated into the original engineering design at 5- to 10-year intervals. Excavation typically occurs at one or more mid-shelf "borrow sites" that have been identified through geotechnical surveys as possessing beach-compatible sediments. Diverse spatial and temporal issues involving turbidity and sedimentation exist, including the abrasive effects of near-bottom sediment movements (V. Kosmynin, Bureau of Coastal Systems, FDEP, Tallahassee, FL, pers. comm.). The ratio of fines (silts and clays) to larger sediments is one of many multi-scale issues of particular environmental interest.

In the present study, species of representative fishes, invertebrates, and algae were considered in terms of differential life stage-specific responses and effects (e.g., the ontogenetic species of Livingston, 1980, 1988). It is not possible to characterize stressor effects and responses of every life stage of key species in association with dredge burial of their shelter and food resources. Considerable evidence suggests that survivorship of early life stages is a primary determinant of ultimate adult population sizes of reef organisms (Sale, 1991 and many other papers on marine invertebrates and fishes). Therefore, early demersal life stages, numerically dominant for many fish and invertebrate species (**Sections 2** and **3**), were emphasized in evaluations of potential responses.

Table 8.1 shows multiple potential responses by physiological and behavioral systems (Olla et al., 1974; modified from Eisler, 1979). Many response categories can be associated with stressors arising from a natural or anthropogenic habitat burial event at short or extended temporal scales (Cech et al., 1998). Fish and invertebrate organ systems exist typically in states of relative homeostasis. Disturbance events create or amplify existing stressors. Organ- and behavior-scale systems can be challenged in discrete manners that, in combination, can rapidly degrade the fitness of cohorts of early life stages.

Table 8.1. Representative response categories in early stages of marine invertebrates or fishes when challenged by stressors from habitat burial (Modified from: Eisler, 1974; Olla et al., 1974).

Response Category	Potential Response
Sensory Capacities	Phototaxis Geotaxis Chemotaxis Chemoreception Temperature preference Tactile inhibition Lateral line sensitivity
Rhythmic Activities	Reproductive cycle Daily activity cycle
Motor Activities	Avoidance Attraction Substrate association Equilibrium Swimming preference Spontaneous locomotor activities
Physiological Responses	Respiration Feeding Pigmentation development Morphological development
Motivation and Learning Phenomena	Feeding Conditioned avoidance response
Migration Behaviors	Subdaily feeding migrations Ontogenetic habitat shifts
Intraspecific Behaviors	Visual attraction Aggregation and schooling
Interspecific Behaviors	Aggression and territoriality Predation vulnerability

In terms of the spatial distribution of stressors from dredge and fill activities, three overlapping cross-shelf strata are applicable: nearshore (0 to 4 m depth), intermediate (4 to 6 m), and shallow offshore (6 to 10 m). The mechanical conditions under which many beach engineering operations occur can preclude direct assessment. For example, visual assessment of direct dumping of dredge fill on hardbottom reefs is not possible, often for weeks post-project, due to elevated turbidities at and adjacent to the project site. This situation also applies to direct assessment of the interface of the dredge head and substrate during excavation of fill offshore and habitat scale effects of fill burial inshore.

Although effects of elevated turbidity on the health of organisms are poorly known in many marine environments (Rogers, 1990; Wilber and Clarke, 2001), some information is available. Offshore and inshore, the introduction of unusually high concentrations of silts and clays may exceed the tolerance thresholds of organisms in both direct (death) and indirect (lowered growth or lowered egg production) manners. A relatively short period of dredge-induced turbidity caused an abrupt decrease in growth in two species of hard corals and may have had long term impacts on coral reproduction, including the important *Montastraea annularis* (Telesnicki and Goldberg, 1995). This species is found on shallow hardbottom of Broward County and also is an important component of mid-shelf reef structure. Telesnicki and Goldberg (1995) also demonstrated negative effects of sediment loads on hard corals at turbidity levels below the maximum allowed by the State during dredging. Well-adapted invertebrates such as sabellariid worms that encrust shallow rocks can undergo partial or complete mortality in burial exceeding 3 days (Sloan and Irlandi, 2007) and by the elimination of attachment substrata for future cohorts of larvae.

In addition to characterizing effects and consequences at organismal and population scales, discriminating natural background variation from stressor-induced effects is also important across the shelf. Natural stressors can be significant in both winter and summer seasons. Long-term estimates of average turbidity values under natural conditions are lacking. In systems with substantial natural background disturbances, e.g., NHB of the northern project area, impact questions ideally should consider what additional stress loads beyond the natural background disturbance regime can generate measurable declines in primary metrics of NHB condition. On the other hand, perhaps the additional anthropogenic stress load is negligible with the pre-existing natural disturbance load. The problem is that it is not only a matter of “quantity” – days of high wind/wave energy or the frequency of natural vs. anthropogenic burial of NHB, but, in addition, “quality” – the durability of offshore vs. shallow sediments that are being displaced by dredges and storms, respectively. This physical complexity is multiplied by the physiological stressor-effect relationships of key species (e.g., **Table 8.1**). **Figure 8.1** provides a schematic overview of some of the key biological process (growth rates, fecundity, mortality) in terms of their response to dredging scenarios in addition to natural background turbidity fluctuations. Importantly, these biological processes are related so that sublethal, lowered growth in a cohort can potentially lower fecundity at a later age (**Figure 8.1**). As with most multivariate, non-linear systems, conclusions regarding impacts will often be driven by site-specific aspects of the area in question and the breadth of species and life history stages considered.

Along with hurricanes in summer, natural high-turbidity conditions in southeast Florida also result from fall through late winter wind events, often associated with fronts. For many species of fishes, this is apparently a period of less significance to settlement stages. Spring through fall dredge burials of hardbottom eliminate the habitat that marine fish and invertebrate larvae utilize right before or during their peak periods of settlement to bottom structures. For motile species, the assumption that most or all fishes and invertebrates on NHB habitats can simply swim away is tenuous when applied to newly settled and early juvenile life stages in a dredge-induced sedimentation event (e.g., see tables in **Sections 8.1.2.1** and **8.1.2.2**).

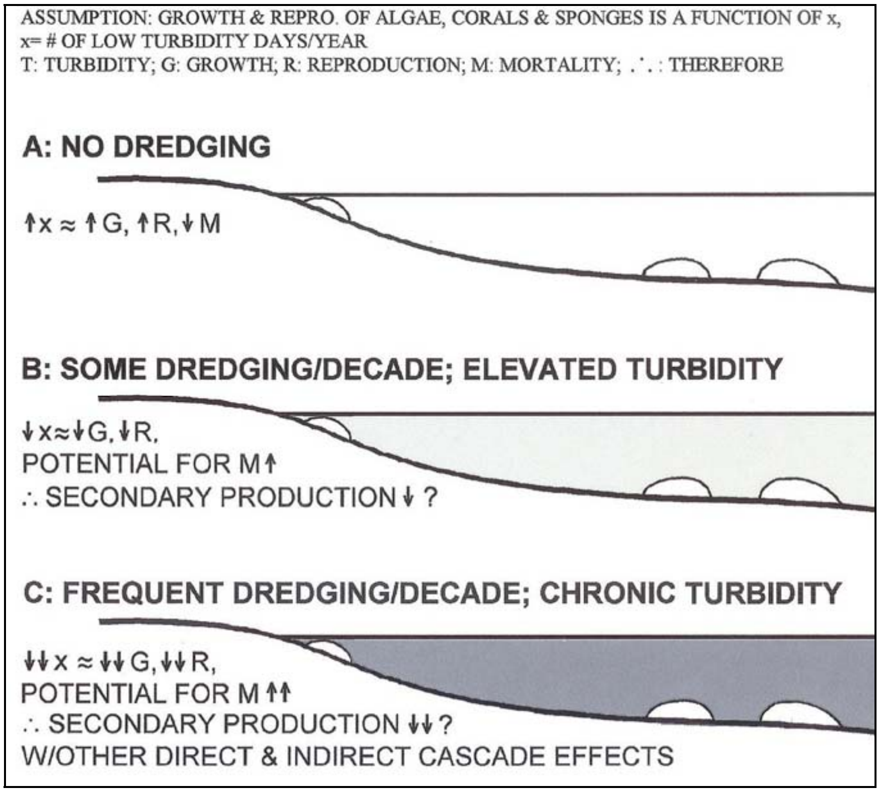


Figure 8.1. Three scenarios of cross-shelf turbidity and sedimentation effects (direct and indirect) for systems subjected to A) no dredging, B) some dredging, and C) semi-continuous dredging (e.g., north-central Jupiter Island). These scenarios assume substantial natural turbidity from storm events and represent effects of fill in addition to background turbidity levels.

Early stages of fishes and invertebrates appear to be adapted to sheltering in hardbottom microhabitat crevices of all types and locations during wind and wave events and may survive such events. However, this assumes that the dredge fill sediments are coarse enough to not constantly resuspend. Laboratory and field investigations suggest that native beach sediments will settle to the bottom faster and resist resuspension more effectively than the high amounts of fine skeletal sediments transported to the fill sites from dredging of high carbonate sediments native to low-energy environments offshore (Wanless and Maier, 2007). Intermediate or long term information on changes in nearshore water clarity and other important physiological variables for fishes, invertebrates and algae are not available over the last decades.

In a natural wind event, water turbidity stressors are probably near the same scale as in a full dredge and fill project. However, most natural wind events do not result in the complete burial of all hard bottom structure. Organisms that are adapted to survive natural wind and wave disturbance events rely on shelter; dredging projects steadily eliminate all of the shelter, unlike most storm events. There is clear evidence that hurricanes and tropical storms can move sediments in such volume that entire NHB tracts are buried. The additive or multiplicative affects of smaller wind/wave events versus major storm or dredge and fill events of less frequency suggest hypothetical and logical possibilities (**Figure 8.1**) but little empirics. If a precautionary approach to ecosystem-based management is being applied (e.g., National Research Council, 1999 and dozens of journal articles on coastal management and fisheries science), the collective impacts of dredge and fill projects cannot be negated simply by assumptions that major knowledge gaps (i.e., large topics with little published research) mean the array of potential stressors are benign in the long term (Peterson and Bishop, 2005). In addition, the recreational values and ecosystem services provided by these habitats within an overall degraded coastal system are in no way free from continued degradation as well.

In addition to natural turbidity and sedimentation events discussed above, there are influential and potentially synergistic effects from the discharge of freshwater through south Florida's flood control system that create major turbidity plumes near inlets. During the wet season (May through October), normal discharges are less than 50 m^3/sec, but following hurricanes can reach 400 m^3/sec (Hu and Wan, 2006). High volume discharges are most prevalent near the St. Lucie Inlet in Martin County, because the St. Lucie River is the seaward discharge point for water released from Lake Okeechobee. Smaller volumes of freshwater are discharged from other inlets including Port Everglades in Broward County, Lake Worth and Jupiter Inlets in Palm Beach County, Fort Pierce Inlet in St. Lucie County, and Sebastian Inlet in Indian River County. In addition to influencing light penetration, turbidity, and salinity, freshwater discharges can carry contaminants, harmful algae, and excess nutrients.

8.1.2.1 Invertebrates

Stressors associated with sedimentation, turbidity, and mechanical impacts can affect co-occurring invertebrates on scales ranging from individual physiology through, potentially, local population structure (**Table 8.2**). Increased turbidity associated with dredging may cause sublethal impacts to sessile invertebrates that may include withdrawal into crevices or body cavities, and possibly termination of feeding. Similarly, motile invertebrates such as small crabs and shrimp may withdraw into crevices and be functionally prohibited from feeding because of not being able to seek food. With an increase in the scale of dredging, most of these organisms (regardless of the ability to move) would perish, or at the very least be severely physically and/or physiologically stressed. In the later case, such stress would likely reduce survival and reproductive ability (**Table 8.2**). Not only does this high mortality affect population numbers, it also likely affects trophic interactions (Nelson, 1989).

Table 8.2. Invertebrate predictors of responses to dredge and fill burial: 1) organismal responses, and 2) assemblage-scale responses. Scenarios are for the fill site only.

1) Organismal Responses			
Scale of Effect	Sessile	Mobile on Bottom	Highly Mobile
Behavioral responses (min to hr)	- Withdraw in crevices or within body cavity - Terminate feeding	- May withdraw in crevices - Terminate feeding	- Flee
Physiological responses	- Asphyxiation/death - Gill filament damage - Filter feeding shutdown - Other organ damage	- Asphyxiation/death - Gill filament damage - Other organ damage - Predation in flight	
Affected invertebrate classes and life stages (All = all life stages)	Demospongiae, All Turbellaria, All Anthozoa, All Polychaeta, All Hydrozoa, All Stenolaemata, All Anopla, All Gymnolaemata, All Enopla, All Gastropoda, All Bivalvia, All Crionoidea, All Polyplacophora, All Ascidiacea, All Archaeogastropoda, All Entoprocta, All	Echinoidea, All Gastropoda, All Crustacea, All Merostomata, All Stelleroidea, All Holothuroidea, All	Squid spp. (Teuthida)
Behavioral responses (>1 day to 1 week)	No survival	Very low survival probability	Attempt to disperse to other hardbottom habitat
Flight access to other hardbottom	Impossible	Rarely	Site-dependent
Predicted local population mortality	High, 95% to 100%	High, 90% to 100% Sublethal impacts on any survivors	Unknown
Population connectivity	Highly variable	Variable	

Table 8.2. (Continued).

<table>
<tr><th colspan="4">2) Assemblage Responses and Potential Local Population Implications</th></tr>
<tr><th></th><th>Sessile</th><th>Mobile on Bottom</th><th>Highly Mobile</th></tr>
<tr><td>Without mitigation</td><td>Will cease to exist</td><td>Will not exist or with greatly reduced numbers</td><td>Will flee to other structural habitats, fate unknown</td></tr>
<tr><td colspan="4"><i>With resource mitigation</i>
<u>Mitigation for Shelter</u>
In large part depends on recruitment capability of invertebrates. The recruitment of sessile shelter-enhancing invertebrates will significantly affect survival of motile invertebrate species. There will be very few older motile adults that will migrate into the affected area.
<u>Mitigation for Food Resources</u>
If they can settle, most suspension feeding invertebrates should not be adversely affected. However, the slow recovery of crevice dwelling species (small crabs, shrimp, worms) may affect prey availability for many motile invertebrate predators and fishes.
<u>Water Quality</u>
Degradation in water quality via immediate and chronic turbidity issues may affect fitness and/or survival of suspension feeders. It may also affect predator-prey interactions.</td></tr>
<tr><td colspan="4"><i>Food web and community-scale trophic impacts</i>
<u>Before</u>
Community is highly diverse, consisting of a mix of opportunistic and rare species. Food web consists of suspension feeders, herbivores, omnivores, and various levels of carnivores.
<u>After</u>
Low diverse community that consists of more opportunistic species and even fewer less abundant species such as corals and sponges. The reduction of shelter-enhancing sessile species will reduce the number of smaller carnivore trophic levels and is likely to affect higher trophic levels within the community.</td></tr>
</table>

The loss of the high biomass of invertebrates (crabs, shrimp, worms, gastropods, bivalves) found within and near shelter-enhancing invertebrates (i.e., *Phragmatopoma* worms) and/or macroalgae can significantly modify in the nearshore food web. Before a dredging event, the community can be diverse, consisting of a mix of opportunistic and uncommon species. In this condition, the food web consists of suspension feeders, herbivores, omnivores, and various levels of carnivores. However, after a dredging event that results in high mortality and habitat elimination, there is likely to be a less diverse community consisting of more opportunistic species and fewer uncommon species such as corals. Reduced shelter enhancement (via fewer sessile species) will reduce the number of smaller carnivore trophic levels, with possible effects to the higher trophic levels within the community.

Mitigation efforts to restore hardbottom habitats in large part depend on recruitment capability of invertebrates. The recruitment of sessile shelter-enhancing invertebrates will significantly affect recruitment and survival of motile invertebrate species. There will be very few older motile adults that will migrate into the area of impact. If they settle, most suspension-feeding invertebrates should not be adversely affected. However, the slow recovery of crevice-dwelling species (small crabs, shrimp, worms) may affect prey availability for many motile invertebrate predators and some fishes. Severe degradation in water quality (most likely via chronic turbidity) may affect fitness and/or survival of suspension feeders. It may also affect predator-prey interactions because of reductions in visibility. Significantly, mitigation planning should also consider that worm rock structures are most abundant in intertidal and subtidal NHB and substantially less adapted for IHB and OHB depths in east Florida (**Chapter 4**).

8.1.2.2 Fishes

The diversity of potential effects at the individual level is high. For example, seven differing sensory system variables and at least five other variables associated with motor activity and water-column positioning can be affected by dredge burials of resident fish habitats (**Table 8.1**). Effects can be direct or indirect and operate over the short-term, long-term, or both (**Table 8.3**). Indirect effects at the individual level can cumulatively translate into population-level effects or not. Impacts months or years after the initial impact are difficult to measure (Cech et al., 1998).

Table 8.3. Predictors of organism-scale responses to dredge and fill burial in fishes. Scenarios are for fill site effects only.

Scale of Effect	High Site Association	Intermediate Site Association	Fully Mobile
Behavioral responses (min to hr)	- Withdraw in crevices or within body cavity - Terminate feeding	- May withdraw in crevices - Terminate feeding - Flee	- Flee - Associate with sediment plume and feeding opportunities?
Physiological responses	- Asphyxiation/death - Gill filament damage - Other organ damage	- Asphyxiation/death - Gill filament damage - Other organ damage - Predation in flight	
Affected fish families and life stages (All = all life stages)	Pomacentridae, All Gobiidae, All Muraenidae, All Blenniidae, All Apogonidae, All Gobiesocidae, All Ophichthidae, All Pempheridae, NS, J Haemulidae, NS Sciaenidaea, NS Lutjanidae, NS Chaetodontidae, NS Pomacanthidae, NS	Residents Lutjanidae, J Scaridae, J, A Labridae, J, A Serranidae, J Sciaenidae, J Acanthuridae, J Balistidae, J Pomacanthidae, J, A Transients Scorpaenidae, J, A Kyphosidae, J Chaetodontidae, A, J Pempheridae, A	Lutjanidae, A Scaridae, A Scombridae, J, A Labridae, A Sciaenidae, A Acanthuridae, A Balistidae, J Haemulidae, A Carangidae, A, J Kyphosidae, J, A Sparidae, A, J
Behavioral responses (>1 day to 1 week)	No survival	Very low survival probability	Attempt to disperse to other hardbottom habitat
Flight access to other hardbottom	Impossible	Very site-dependent	Site-dependent
Predicted local population mortality	High, 95% to 100%	High, 90% to100%. Mortality due to shelter or food resource gaps during flight periods of >1-2 days. Sublethal impacts on any survivors	Low, but taxa-specific. Some species able to relocate with relative ease, others no
Population connectivity	Nesting species with low larval durations are common	Variable	Variable

NS = Newly settled; J = Juvenile; A = Adult.

Many responses will show some species specificity, and within species, substantial ontogenetic variation. The cryptic hardbottom resident fishes and herbivorous damselfishes (including adults) and the earliest life history stages of the other fish subassemblage types are among the most susceptible to direct mortality (**Table 8.3**). Consideration of effects on fishes at these scales, and their effects on higher organizational scales, are generally absent from the literature on shallow hardbottom and beach dredging in Florida. As the majority of motile fishes using nearshore areas of southeast Florida are juveniles or younger, and life stages of many conspecifics using mid-shelf areas are typically older, the greatest direct and indirect impacts may occur at nearshore fill sites and during flight responses; however, impacts at offshore borrow sites also remain underexamined, with occasional exceptions (Wilber and Stern, 1992).

Many of the effects examined here may be pulsed through time on very patchy scales. Interactions among short- and long-term effects may also occur, adding to the complexity in evaluating stressors and responses. Examination of cumulative effects of both direct and indirect stressors is still often unattempted, yet of importance to the full understanding of anthropogenic effects. It is useful to discriminate among lethal and sublethal effects, which in turn can produce differing responses based on the time-scale evaluated. For example, identical organ systems can undergo sublethal or lethal effects (e.g., respiratory stress vs. respiratory trauma). These variations, in turn, lead to differing effects at greater exposure durations. Examples can be developed for each combination of stressor intensity and duration.

8.1.2.3 Algae

Though over 200 species of algae are recorded from NHB, the diversity of potential effects may not be as high as in other organisms. Motility and other life history attributes are not as variable, and since almost all species rest on or attach to substrate, mortality is high across all divisions of algae (**Table 8.4**). Preliminary examinations of what effects such stressors can generate at population levels suggest that long term and more meso-scale spatial frameworks may be required to fully detail dredge and fill effects on algal populations and trophically-associated invertebrates and fishes (**Figure 8.1**). Potential long term reductions in water clarity can also affect food webs and require further examination to understand effects on growth rates, predation rates, and reproductive potential for diverse taxa.

Table 8.4. Predictors of organism- and population-scale responses to dredge and fill burial in macroalgae. Scenarios are for fill site effects only.

Scale of Effect	High Site Association	Intermediate Site Association	Fully Mobile
Behavioral responses	N/A	N/A	N/A
Physiological responses	Mortality loss of photosynthesis and respiration	Loss of primary production	
Affected taxa and life stages	All Divisions Rhodophyta – SR, F, T Phaeophyta – SR, F, T Chlorophyta – SR, F, T Cyanobacteria	Fragmentation/Clonal: *Sargassum* spp. *Caulerpa* spp.	Spore fragmentation: *Sargassum* spp.
Behavioral responses	N/A	N/A	N/A
Flight access to other hardbottom	N/A	N/A	N/A
Predicted mortality	High, 75% to 100%	Highly variable, 0% to 75%. Sublethal impacts present	Low-none
Population connectivity	Quasi-closed, non-dispersing systems	Diffusive and mesoscale dispersal	Broad dispersal

F = Fragment or clonal reproduction; SR = Spore recruitment; T = Turf species.
N/A = Not available.

8.1.2.4 Turtles

NHB appears to provide intermediate life stage habitat for juvenile marine turtles, in particular green, loggerhead, and hawksbill turtles whose residency is approximated to be 2 to 5 years. Turtles may remain in the same area during this period or they may “migrate” with water temperature changes. The magnitude of site fidelity is unknown at this time, but tag and recapture data as well as tracking data indicate that turtles display some site specificity, even as juveniles (Ehrhart et al,, 1996; Bressette et al., 1998; Kubis, 2003; Makowski et al., 2006b). **Table 8.5** reflects preliminary efforts to assess the response of turtles to fill impacts given their mobility and potential responses.

Poor water quality impacts food resources for most marine turtle species (i.e., molluscs and crustaceans for loggerheads, sponges for hawksbills, macroalgae for green turtles). Mitigation should include monitoring water quality before, after, and during dredge burial and mitigation construction. Water from land-use runoff sources should receive proper treatment before reaching the shoreline; otherwise, unhealthy and deleterious conditions may occur on both short- and long-term time-scales. Degraded water quality has been suggested as a potential environmental co-factor for FP disease found in a relatively large number of juvenile green turtle populations worldwide (Herbst and Kline, 1995). The disease manifests predominantly as tumors on the eyes and fleshy parts of the body. FP can impair swimming and foraging abilities and make an animal more susceptible to predation and/or starvation or death. Internal tumors are typically lethal.

Table 8.5. Predictors of organism- and population-scale responses to dredge and fill burial for marine turtles. Scenarios are for fill site effects only.

Scale of Effect	High Site Association	Intermediate Site Association	Fully Mobile
Behavioral responses	- Flee to deeper water - Withdraw under ledges - Loss of food resources	- May withdraw under ledges, or flee in random walk response, or flee in optimal foraging response.	- Immediately flee
Physiological responses	- Increase foraging effort - Increased predator exposure	- Increased predator exposure - Slower growth rate - Stress	- Increased predation - Slower growth rate - Stress - Higher carbohydrate intake necessary for energy to migrate
Affected taxa and life stages	Green turtle - J Hawksbill - J, S Loggerhead - S Disperse until new structure present	Green turtle - J Hawksbill - J, S Loggerhead - S	Loggerhead - S
Behavioral responses	see above	see above	see above
Flight access to other hardbottom	Green turtle Loggerhead turtle Hawksbill turtle	Transient/migratory? Green turtle Loggerhead turtle Hawksbill turtle	Green turtle Loggerhead turtle Hawksbill turtle
Predicted mortality	Unknown/undocumented	Unknown/undocumented	Unknown/undocumented
Population connectivity	Quasi-closed as juveniles. Juveniles appear to disperse at certain size-classes	Juveniles appear to disperse at certain size-classes	Broad dispersal (temporary condition)

J = Juvenile; S = Subadult.

8.2 MITIGATION OF NEARSHORE HARDBOTTOM BURIAL

The process and practice of mitigation is similar to ecological restoration; the distinction between restoration and mitigation is that mitigation is invoked when the impact is known in advance, not accidental or natural as in restoration. Thus the relatively new field of restoration ecology provides much of the theoretical and applied direction for mitigation efforts (e.g., Race and Fonseca, 1996; Zedler, 2000; Falk et al., 2006; Miller and Hobbs, 2007). Most of the experience in attempting to restore habitats and ecosystems comes from terrestrial and wetland environments. The legislative framework for mitigation is also derived primarily from wetland contexts. Thus far, work in marine environments in general and NHB mitigation in particular is still in its infancy.

As discussed in **Chapter 1,** adherence to particular ecological concepts can influence the interpretation of restoration efforts. In fact, restoration projects are themselves likely to yield new insights into ecological understanding, as many are quasi-experimental. Downes et al. (2002) stated “It has been said that an ultimate test of our understanding of an ecosystem is to create or repair a habitat and its function.”

As discussed above, dredging projects designed to rebuild eroded beaches may bury expanses of NHB and increase turbidity, both acutely and chronically. Although NHB is naturally buried and uncovered seasonally and with the passage of storms, additional burial through dredging can amplify and extend the natural effects and loss of habitat within a stratum of the broader cross-shelf continuum. This is particularly true if burial affects time periods specific to the larval recruitment or movements of local fishes and invertebrates.

For projects conducted under Section 404 of the Clean Water Act or the Rivers and Harbors Act of 1890, potential impacts are treated in a three-step sequence. The first part of the sequence seeks through the analysis of alternatives to *avoid* adverse environmental impacts; if adverse impacts cannot be avoided, then all efforts to *minimize* them must be taken; and in the event that minimization is not feasible and impacts are unavoidable, then *compensatory mitigation* is required. In most beach dredging projects where hardbottom is present in the project area, compensatory mitigation is required (USFWS, 2004).

Mitigation efforts should seek to ameliorate not only the effects of direct burial and immediate habitat loss but also turbidity, including chronic turbidity. Artificial reefs can compensate only for structural habitat loss; mitigating for chronic turbidity and low water clarity (transmissivity) is not accomplished by reef placement. In this chapter, the focus is on mitigation of direct habitat loss through burial by dredge fill. To date, deploying artificial reefs has been the preferred route for compensating for unavoidable impacts to NHB (USFWS, 2004). Artificial reefs have been used for fishery management and habitat enhancement for years (Seaman, 2000; Brickhill et al., 2005), but the use of reefs for mitigation or restoration has been a more recent phenomenon (Ambrose, 1994; Miller, 2002; Reed et al., 2006). The process usually involves pre-project evaluation of expected impacts to existing NHB by utilizing aerial photographs to quantitatively map the area of hardbottom to be impacted. Expected impacts are modeled by estimating where the seaward margin of fill will distribute along the shoreline, the equilibration point following placement of sand on the beach. Once the potentially impacted area is determined, a mitigation plan is prepared, consisting of a calculated mitigation ratio, an engineering analysis, and a monitoring plan.

8.2.1 Artificial Reefs

The approach used to offset the effect of habitat burial has been to construct artificial reefs near impacted sites. Because some fishes and invertebrates will colonize hard substrate through migration of adults or settlement of larvae from the plankton, simply placing a structure on the seafloor will attract certain elements of the local fauna. As mentioned above, artificial reefs have a long and complicated history in fishery and habitat management. In addition, artificial structures have been used extensively in Europe and other coastal areas in association with beach projects (Bacchiocchi and Airoldi, 2003; Airoldi et al., 2005).

Research on the applications of artificial reefs has been extensive (e.g., Seaman and Sprague, 1991; Seaman, 2000), with legitimate claims of success, typically for offshore fishing values. Artificial reefs can become ecological traps that subject colonizing organisms to fishery exploitation (Bohnsack, 1989) or high levels of predation (Hixon and Beets, 1993), and they can be sources or sinks within particular seascapes (Crowder et al., 2000). Success is often a function of what is measured, and consensus agreement on the most critical metrics for success often is not evaluated.

Placement of reefs on sedimentary bottoms can, over time, alter sediment grain size distribution and organic matter accumulation around the reef, causing a corresponding change in associated infaunal assemblages (Davis et al., 1982; Ambrose and Anderson, 1990; Fabi et al., 2002). None of these drawbacks should preclude the use of artificial reefs as mitigation unless independent research from the proposed deployment site indicates that one or all would be influential.

A commonly posed concern with the use of artificial reefs is the potential predation risk to newly settled organisms. It is assumed that predators are more abundant or more effective on artificial reefs than they are on natural reefs. It is important to note that the field studies that demonstrated high predation were conducted on small artificial reefs, where the presence of only a few small predatory fishes can exert considerable influence on the existing community (Hixon and Beets, 1993; Eklund, 1996; Leitao et al., 2008). It is not clear how the results from studies of smaller isolated artificial reefs can be scaled to larger artificial reefs, but certainly increasing or decreasing the size or complexity of a reef could modify observed predation effects. McCarthy (2001) studied post-settlement mortality of sessile invertebrates in intertidal and subtidal hardbottom off Boynton Beach and found no predation effect for total number of species or for the majority of individual species. This suggests that sessile invertebrate mortality in intertidal and shallow subtidal hardbottom can be the result of sand scouring and wave activity in addition to capture by mobile predators such as crabs or fishes.

Because current mitigation efforts have been exclusively centered on constructing artificial reefs in shallow water, an essential step in the process is to evaluate engineering stability. Reefs placed in shallow depths to achieve like-kind mitigation will be subject to high-energy waves and dynamic sand movements. Most reefs have been built from concrete or quarried limestone boulders (**Figure 8.2**). These materials are subjected to stability tests that consider a range of wave energy impinging on proposed structures. Stability test results generally preclude deploying limestone boulders or concrete slabs in water depths less than 4 m. These depths also mark the shallow operating depths of work barges and attending tugboats.

Figure 8.2. Artificial mitigation reef and substantial algal and hydroid growth, 6 m depth, Juno Beach, Palm Beach County, Florida. *Photo by D. Snyder.*

An additional consideration is sediment overburden within proposed reef footprints. If the sediment overburden exceeds the maximum dimension of a reef unit, the entire reef unit could settle under the sand. Therefore, prior to selecting sites, considerable effort must be expended to measure sediment thickness (e.g., Deysher et al., 1998).

Because of the stability and logistic issues stated above, it is apparent that NHB cannot be mitigated for in like-kind fashion, given present technology and budgets. The solution has been to build reefs in deeper water where they are persistent and not subject to the burial and erosion that characterizes the 0 to 4 m depths (**Figure 8.2**). Reefs built of limestone boulders are higher relief with different structural features than much of the naturally occurring NHB. In addition to stability and logistic concerns, spatial arrangement of artificial reefs over the seafloor needs to be evaluated from an ecological perspective (e.g., Jordan et al., 2005; Lindberg et al., 2006). These factors must be considered when monitoring and evaluating the efficacy of mitigation reefs. Alternative modular designs are also being developed (**Figure 8.3**; Continental Shelf Associates, Inc. et al., 2006).

In assessing restoration efforts in terrestrial assemblages by reference sites, White and Walker (1997) classified the basic elements of the reference information based on proximity in space and time. Their classification, revised for NHB, is presented in **Table 8.1**. The actual impact site provides the current ecological snapshot of conditions of the impact site, but it is only a snapshot and does not give an accurate picture of processes. For example, in coastal areas the natural condition may have long ago been obscured by anthropogenic effects, leading to the question “what is natural?”(Sapp, 1999; Jackson, 2002). Temporal data from the impact site are valuable, particularly if a before-after-control-impact (BACI) approach is to be used in assessing the restoration (Osenberg et al., 2006). Data such as these would be short term, for example during the year prior to a proposed dredge and fill project. Longer term (decadal) patterns will be more elusive, as White and Walker (1997) point out that temporal data do not always allow us to directly associate physical and biological factors related to disturbance regimes. Contemporary information from different sites will provide insight on how existing processes affect species assemblage attributes and dynamics. Unfortunately, in most NHB situations the primary spatial factor is one of water depth.

Figure 8.3. Prototype mitigation reef modules made from articulated mat with integral coquina rock surface. Each block is about 30 inches x 30 inches x 12 inches (Continental Shelf Associates, Inc. et al., 2006). *Photo by D. Snyder.*

If like-kind mitigation is desired, then managers and permit applicants will have to accept that material will be lost (buried) under the sand. To some extent, this mimics the natural situation. Given the expense of constructing reefs, it is unsettling to place one in very shallow water only to have it disappear beneath a moving sand bar. However, during other seasons the reef material will likely uncover. Potentially more problematic would be public safety issues in very shallow waters as well as potential movement of reef materials onto the beach with time.

Fauna and flora that live in the intertidal sections of the NHB have to be adapted to survive through changes in a number of environmental factors. These factors not only change with season but also with state of the tide. They include seasonal and daily changes in water/air temperature, salinity, and desiccation. Additionally, organisms within this depth zone are exposed to some of the highest wave energy that occurs when seasonal storms or hurricanes affect the area.

Restoration of buried worm reefs could be better effected by using existing knowledge on behavioral preferences of *P. lapidosa* and other sessile invertebrates during settlement. For instance, it has been well documented that *P. lapidosa* repeatedly “test” substrates before settling on the preferred one (Eckelbarger, 1976; Pawlik, 1988). The recruitment of *P. lapidosa* to deployed substrates is variable but commonly higher at locations closer to the bottom and/or with moderate turbulence (D. McCarthy, Jacksonville University, Jacksonville, FL, pers. observ.). Behavioral preferences for moderate amounts of current have been quantified in laboratory studies with *P. californica* (Pawlik et al., 1991; Pawlik and Butman, 1993). Consequently, assuming adequate larval supply, there are likely to be unique combinations of hydrodynamics and substrate features that will enhance recruitment of invertebrates. A description of those features would allow coastal managers to modify artificial reefs to include those preferred features and thereby maximize larval settlement and formation of “natural” habitats.

McCarthy and Holloway-Adkins (2007) investigated whether the *P. lapidosa* will recruit on deployed sets of settlement plates in ~4 m water depth off Brevard County, Florida, an area that has little significant subtidal NHB. They also investigated whether recruitment varies with height above the seafloor bottom, orientation, or chemical coating of the settlement plates. They deployed three 100 cm x 100 cm x 70 cm ultraviolet-stabilized polyethylene propagule and larval measurement (PALM) boxes off Satellite Beach, Florida (28°09.637’ N, 80°34.951’ W) in a water depth of 4.6 m. Fifteen 10 cm x 10 cm x 1.5 cm limestone settlement plates were vertically attached on the north, east, west, and south faces of each PALM box. The PALM boxes were deployed for two time periods. The first deployment occurred on 24 May 2006, and plates were recovered on 8 July 2006. The second deployment also took place on 8 July 2006, with boxes being recovered on 5 May 2007.

They found that *P. lapidosa* recruitment varied considerably for the two time periods sampled. During the May to July 2006 time period, *P. lapidosa* was the dominant encrusting organism, recruiting in fairly high yet variable levels. Most *P. lapidosa* worms encountered on the settlement plates were alive and in a range of sizes indicating multiple cohorts of recruitment. Additionally, encrusting species such as bryozoans, hydrozoans, ascidians, and barnacles were also frequently encountered on the settlement plates. During the July 2006 to May 2007 time period, the PALM boxes were partially buried with sediment and experienced high mortality of recruits of various species of encrusting organisms. *P. lapidosa* recruitment was very low, with most of the observed recruits on the plates being bivalves and barnacles. For both time periods, there was a trend that *P. lapidosa* recruitment was lowest on plates at the rows furthest from the seafloor. Otherwise, *P. lapidosa* recruitment occurred equally on plates regardless of chemical treatment and plate orientation. In conclusion, recruitment of *P. lapidosa* did occur to artificially deployed structures off the Brevard County coast in mean water depths of approximately 4.6 m.

The variation in recruitment between sampling periods may be because of 1) differences in time the plates were deployed, and/or 2) natural seasonal fluctuations in larval availability. The general lack of significance among the experimental treatment means are probably a result of local hydrodynamic and/or turbidity conditions that consistently and dramatically fluctuate. These fluctuations likely are continually creating favorable conditions for the settlement of *P. lapidosa* larvae, regardless of the effect of plate orientation, height, and chemical treatment. Finally, it should be cautioned that *P. lapidosa* may recruit at these latitudes but may not survive at these depths because water temperatures likely reach cold temperature limits for this species (Eckelbarger, 1976; D. McCarthy, Jacksonville University, Jacksonville, FL, pers. comm.).

The use of artificial reef habitat by marine turtles is largely undocumented in the peer-reviewed literature. Jones et al. (2004) observed juvenile green turtles resting among artificial reef rocks deployed in approximately 4 to 7 m water depths in Boca Raton, Florida. Garrido (2007) observed hawksbill turtles on shallow artificial reefs in West Palm Beach, Florida. Juvenile green and adult loggerhead turtles were observed on the nearshore artificial reef during annual surveys between 2006 and 2008 (Coastal Eco-Group Inc., 2008, 2009). Properly designed artificial reefs with ledges and crevices may provide adequate shelter for resting marine turtles and provide adequate substrate to support the foraging habits of hawksbill and green turtles. However, juveniles mostly forage on shallow, narrow reefs in intertidal and shallow subtidal depths, and the placement of mitigation reefs in deeper waters may create competition. These aspects remain unstudied, to date.

Mitigation reefs provide hard substratum for the recruitment of macroalgae and invertebrate food resources for fish, turtles, and other invertebrates. Mature macroalgae have been successfully transplanted on artificial reef surfaces (Ohno et al., 1990). Holloway-Adkins and McCarthy (2007) conducted experiments to test macroalgal recruitment on subtidally deployed structures off Brevard County where hardbottom is absent. The experiment involved examining levels of recruitment on different substrate types that might be used in artificial reef construction in 4.6 m water depth. While characteristics of limestone (light coloration, porosity, and texture) make it ideal substrata for macroalgae (Dawes, 1998), no significant differences in macroalgal recruitment on experimentally tested settlement plates were found (Holloway-Adkins and McCarthy, 2007). Six of 15 red algae and three of five green algae documented by Continental Shelf Associates, Inc. (2005a) on adjacent NHB recruited on the settlement plates. Eleven macroalgae and seven invertebrate species found in the foraging samples of green turtles recruited on the deployed settlement plates (Holloway-Adkins and McCarthy, 2007). Monitoring of mitigative artificial reefs in Broward County revealed overall macroalgal species richness was as high, or sometimes higher, as the natural NHB reefs during post-construction monitoring periods (Prekel et al., 2007). Species richness of green turtle-preferred macroalgae after 36 months was also similar to what was found on natural NHB. However, higher quantities of macroalgae were documented on the natural reefs than on the artificial reefs (Prekel et al., 2007).

The deployment of mitigation reefs prior to dredge and fill projects could, ideally, provide a more timely compensation of functional loss through the continuous existence of hardbottom structure that would provide shelter and recruitment habitat during and after project construction. The timing of mitigation deployment, both seasonally and pre-construction, could potentially influence initial recruitment success. Deployment of mitigation reef structures 6 months to 1 year prior to project initiation could allow for more adequate dispersal of macroalgal spores and fragments, as well as invertebrate larvae from existing hardbottom. There have been relatively few attempts to mitigate losses of NHB along the east Florida coast until recently. In 2004, the USFWS (2004) reviewed permit applications from southeastern Florida (Indian River to Dade Counties) for projects where compensatory mitigation was recommended or required to offset impacts to hardbottom habitats. They selected 26 projects from USACE regulatory division permits and planning division civil works projects. This review revealed that 217 acres of hardbottom was expected to be impacted. Approximately 113 acres of artificial or natural materials were to be deployed as replacement habitat; this total included 43 acres completed and 70 acres for projects not yet completed (USFWS, 2004). The impacts in these examples were caused by filling, sedimentation, dredging for beach nourishment, and port expansion (**Table 8.6**). The anticipated impacts of pending projects were also related to beach nourishment and port expansion.

Table 8.6. Summary of compensatory mitigation for completed projects in southeast Florida between 1985 and 2004 (Adapted from: U.S. Fish and Wildlife Service, 2004).

Project Type Name/Corps'	Florida County	Avoid and Minimize	Reduced Impacts (acres)	Recommended Acres	Required Acres	Constructed Acres	Location	Type (in/out of kind)	Material (Acreage)
Beach Renourishment									
Indian River County, Sectors 1&2 (200091872)	Indian River	Yes	7.2	10.5	5.2		Offsite	In	Limestone
Fort Pierce Shore Protection (Federal project)	St. Lucie	Yes	N/A	5.0	5.0	5.0	Onsite	In	Limestone
Martin County Renourishment (199501665)	Martin	Yes	.38	N/A	1.4	5.0	Onsite	Out	Concrete
Jupiter/Carlin Park Shore Protection (199900902)	Palm Beach	Yes	N/A	4.0	4.0	4.0	Offsite	In and Out	Limestone (3.25) Concrete (0.75)
Jupiter Inlet Sand Bypassing	Palm Beach	No	N/A	2.32	N/A	1.16	Offsite	In	Limestone
Juno Beach Shore Protection (1997066559)	Palm Beach	Yes	Reduced fill and length	4.47	4.47	2.22	Onsite and Offsite	In	Limestone
Phipps Park Shore Protection	Palm Beach	Yes	N/A	3.1	N/A	N/A	Onsite	In	Limestone
Ocean Ridge Shore Protection (199301576)	Palm Beach	Yes	5.9	4.55	4.55	4.55	Onsite and Offsite	In and Out	Limestone (2.1) Concrete (2.0)
North Boca Raton Shore Protection	Palm Beach	Yes	0.2	N/A	0.16	0.16	Offsite	In	Limestone (0.07) Modules (0.09)
South Boca Raton Shore Protection (199401196)	Palm Beach	Yes	N/A	2.38	2.38	3.0	Offsite	In	Limestone
Broward County Shore Protection (19990554)	Broward	Yes	22	13.5	7.6	8.9	Onsite	In	Limestone
Bal Harbor BEC&HP (Federal project)	Miami-Dade	N/A	N/A	0.8	N/A	0.48	Offsite	In	Limestone (0.26) Modules (0.22)
Sunny Isles BEC&HP (Federal project)	Miami-Dade	Yes	N/A	3.13	3.13	0.33	Onsite and Offsite	In	Limestone (0.19) Modules (0.14)
63rd Street BEC&HP (Federal project)	Miami-Dade	Yes	N/A	0.08	0.08	0	Offsite	In	Limestone

Table 8.6. (Continued).

Project Type Name/Corps'	Florida County	Avoid and Minimize	Reduced Impacts (acres)	Recommended Acres	Required Acres	Constructed Acres	Location	Type (in/out of kind)	Material (Acreage)
Surfside and Miami Beach BEC&HP (Federal project)	Miami-Dade	Yes	0.005	0.07	0.07	0.07	Offsite	In	Limestone
Total	**--**	**--**	**13.69**	**36.58**	**30.44**	**25.97**	**--**	**--**	**--**
Navigation Improvements									
Fort Pierce Deepening	St. Lucie	Yes	2.25	15.0	4.0	4.0	Offsite	Out	Concrete 4.0
Hillsboro Inlet Navigation Improvement (199301995)	Broward	Yes	1.25	0.8	0.8	0	Onsite	In	Limestone 0
Miami Harbor Deepening	Miami-Dade	No	0	N/A	13.5	13.5	Onsite	In	Limestone N/A Modules 0.6
Total	**--**	**--**	**3.5**	**15.8**	**18.3**	**17.5**	**--**	**--**	**--**
Combined Totals (Beach/Nav)	--	--	**17.19**	**52.38**	**48.74**	**43.47**	--	--	**--**

N/A = Not available.

For 18 completed projects, USFWS (2004) identified approximately 103 acres of direct impact to hardbottom habitat. Of this, 15 acres were related to port channel expansion, 49 acres were covered during beach nourishment projects, 25 acres were due to long-term sedimentation from pipeline leaks or rupture, and 14 acres were related to pipeline or anchor cable placement. An additional 10 acres of indirect impact to NHB was projected from short-term turbidity and sedimentation at Ocean Ridge and Indian River County beach nourishment projects.

Another 10 proposed projects were expected to directly impact about 114 acres of hardbottom habitat. Eighty-three acres are expected to be impacted from proposed port expansion, 18 acres are expected to be impacted from dredge filling, 12 acres are expected to be impacted by the deployment of liquid natural gas pipelines, and 1 acre is expected to be impacted from sedimentation (USFWS, 2004). Since the 2004 USFWS report was released, there have been changes to some of the projected projects. For example, Brevard County Mid-Reach will impact approximately 3 acres of hard bottom, not 22 acres (Continental Shelf Associates, Inc. et al., 2006). For 15 of the 18 completed projects, compensatory mitigation was recommended, and the total acreage was 69 of the 103 acres directly impacted by these projects (**Table 8.6**). For the proposed projects, mitigation was recommended for 6 of the 10 proposed projects. These six projects will account for 82 acres of the 100 acres expected to be directly impacted.

8.2.2 Monitoring

Monitoring of mitigation performance or success is an important part of the entire process. Great sums of money are spent with current mitigation programs, and it is imperative to gain an understanding of successful applications to better guide future attempts. Monitoring mitigation projects is similar in approach to environmental impact monitoring, but there are important differences. The two monitoring types are similar in that most situations do not lend themselves to elegant experimental designs. Impact or mitigation locations are rarely replicated, and suitable control areas are often hard to find. Currently, there are several issues to consider when establishing a particular monitoring of restoration or mitigation program:

- Setting goals;
- Framing hypotheses; and
- Study design.

Establishing the goals of the monitoring program should be the first priority once the impact acreage has been scaled to corresponding mitigation acreage. Intuitively, the goals for NHB would be to restore the functional attributes of the impacted habitat to the level of an adjacent natural reference area. In reviews of past restoration projects, particularly in wetland and terrestrial contexts, clear statements of the project goals often were not included (Race and Fonseca, 1996; Hackney, 2000; Redmond, 2000). Setting goals will influence most of the other elements of the process. For example, if the goal is to restore functional aspects of the impacted assemblage, then the focus should be on reestablishing functional groups or clusters of focal species. Osenberg et al. (2006) distinguished between endpoint and effect-size based goals, pointing out that both approaches have merits. Endpoints provide a basis for comparison and efficacy, whereas the effect size is necessary to understand how well the mitigation performed.

Again, the conceptual foundation of ecology comes into play, and interpretation of various concepts such as community structure, function, and succession will be important in setting and evaluating goals (Palmer et al., 1997). Application of various community ecology theories in restoration efforts will depend on species present and characteristics of the natural environment. In the nearshore environment where assemblages would be less biologically predictable and driven by chance colonization and recruitment, conventional succession theory may be of little use.

Framing scientific and statistical hypotheses in accordance with standard practice in ecology (falsificationist approach) relative to restoration projects presents a logical paradox (McDonald and Erickson, 1994; Underwood, 1996; Downes et al., 2002). In the conventional approach, the researcher frames a null hypothesis, such as: there is no difference in mean species richness between the control and impact sites. Data are collected and evaluated using a statistical test for the hypothesis that is rejected if an arbitrarily selected *p*-value for the test is reached. As Underwood (1990) pointed out:

“It is sometimes considered appropriate to phrase the statistical definition of recovery as some measure in the disturbed area not being significantly different from that in control areas. This has been fossilized in legislation in some aspects of environmental management (USEPA, 1985). This is inappropriate because sloppy, imprecise sampling leads to declaring recovery is complete when it is not. If the confidence interval(s) around the mean measure in the disturbed area or in the control areas (or both) is (are) large, they will not differ significantly in any test—even if the mean values are nothing like each other.”

Statistical methods exist that remedy these logical issues; these methods are called bioequivalence by McDonald and Erickson (1994). With this approach, the researcher defines, in advance, a minimum measure. For example, 90% of the fish species richness (or 80% of the biomass of epibiota) found in control areas would represent recovery in the mitigated habitat (e.g., McDonald and Erickson, 1994; Cole and McBride, 2004). This quantitatively defined endpoint must be exceeded before the habitat is considered restored. Thus, with this method the null hypothesis is that the mitigation site is not equivalent to the control site. Bioequivalence gets around the logical problem, and the formal hypothesis tested is ratio of variables between the restored and reference sites. Following this approach, inadequate sampling will cause the test to retain the null hypothesis of no equivalence, even if the mean measure does exceed the criterion for recovery. Furthermore, the burden of proof is now with the responsible party.

In the past, most deployments were made with engineering considerations mentioned above and have not lent themselves to elegant experimental designs. Researchers are forced to use approaches that deal with lack of replication, arbitrary placement of materials, and other violations of conventional experimental treatments. For this reason, the various forms of BACI designs are most appropriate (Osenberg and Schmitt, 1996; Stewart-Oaten and Bence, 2001; Osenberg et al., 2006). In addition, control site selection is a problem in many areas where NHB is impacted. The ideal control site is not a pristine and unaffected site against which to compare the mitigation reef. Control sites are those selected to represent the habitat that is being mitigated for, including any current anthropogenic influences. They are not randomly selected from a population of such sites. Equivalence tests described above can be used with BACI designs (Downes et al., 2002).

A variation of the BACI design is to restore only part of an impacted area and compare the restored site (artificial reef) to the “unrestored control sites” as well as a natural control site over time (Downes et al., 2002). This will allow researchers to judge the direction of change, as well as the relative degree of change. Downes et al. (2002) indicated that three distinct treatments are needed:

1. degraded location(s) that need restoration;
2. similar degraded site(s) that will not be restored; and
3. site(s) that represent the target state.

A critical element of study designs is identifying response variables and using those variables to evaluate success. McCoy and Mushinsky (2002) described success as “an acceptably small difference between the structure and/or function of a restored system and that of a reference system.” When convergence of community structure is the goal in evaluating restoration success for artificial reef deployments in NHB mitigation, this definition could be incorporated into an equivalency statement. As mentioned above and by others (Underwood, 1990; Downes et al., 2002), the challenge is determining the response variable(s) and setting the level of equivalency.

8.3 CONCLUSIONS

8.3.1 Regional and Organism-specific Issues

- Mitigation of NHB impacts by using artificial reefs can often provide adequate replacement of lost structural habitat and therefore some ecological functions.
- Not all reef designs and deployments will be successful in all situations; site-specific factors must be considered. Different approaches and designs will be required for different locations in southeast Florida and east-central Florida.
- For worm reef areas, ensuring successful local larval recruitment events is essential. To this end, project designers need to be sure that sediment size range is suitable to incoming recruits.
- For worm reef areas, a measure of success is not only the presence of worm reef but duration: it should persist through 1 year with new recruits being encountered in the second year. More importantly, there should be some of the dominant crustaceans encountered within it (e.g., *Pachycheles monilifer* [porcellanid crab], *Pachygraphsus transverses* [grapsid crab], *Menippe nodifrons* [xanthid crab], and *Synalphus fritzmuelleri* [snapping shrimp]).
- In deeper or more southern areas of the project region, the presence of specific sponge and anthozoan species can be used to judge success of artificial mitigation reefs.
- In shallow mitigation to the mid- and north sections of the project region, reef deployment should minimize impact to the yearly recruitment cycles of the habitat engineering worm reef.
- In terms of Issue 4: Can NHB functions be replaced with artificial reefs in IHB or OHB depths? Probably not in large part for IHB and less for OHB, due to the depth limits on the habitat engineering worm species *P. lapidosa,* and the associated assemblage of many dozens of species that *P. lapidosa* structures support in areas from Brevard County to mid-Palm Beach County.
- Artificial reef mitigation does not appear to remove or provide compensatory mitigation for the direct and indirect physiological and potential population scale impacts of turbidity and sediment resuspension.
- If possible, materials should be used for artificial reef construction that support algae and worm rock to the north, and more sponges and corals to the south.
- Over 275 species of algae associate with NHB, and most are subject to high mortality on sites that are filled. Mitigation reefs can provide new attachment sites for algae. Algal growth on mitigation reefs should correlate with water clarity.
- Pre-construction deployment of mitigation reefs (6 months to 1 year prior) in regards to seasonal recruitment patterns of focal reef organisms (i.e., sabellariid worms, prominent fish species, macroalgae) may potentially accelerate functional compensation of habitat loss and should be a priority in project planning.

8.3.2 Monitoring Issues

- A single approach for scaling mitigation is needed early in the project. Although competing models can be effective, using two different (non-complementary) approaches on the same project can lead to confusion.
- Clear goals for mitigation should be established.
- Comparisons of biotic attributes between natural and artificial reefs should be framed using equivalency approaches when feasible.
- Study designs should be flexible and adaptive given the typical lack of natural controls or replication.

Chapter 9
Summary

Synthesis of available information on shallow hardbottom structure and distribution, organismal biology and assemblage scale drivers, and stressors and mitigation responses are presented within **Sections 1**, **2**, and **3**, respectively. Although many research gaps are present, substantial amounts of information can be assembled relative to shallow hardbottom ecological functions in terms of latitudinal and depth variation in areas within the study region. We will summarize primary findings on assemblages of algae, invertebrates, fishes, and turtles. We will then summarize information on ecological functions of shallow hardbottom, stressors and responses, and mitigation alternatives.

In the context of the three sections we will also consider the four original issues: 1) What are specific ecological functions of NHB?, 2) What is happening to the coastal ecosystem (broader than NHB) when this NHB is lost due to nourishment?, 3) Is OHB able to compensate for the loss of NHB?, and 4) If the NHB habitat has specific properties and functions that cannot be compensated for by existing OHB habitat, what are the best mitigation alternatives for the loss of natural NHB? Issue 1 and portions of Issues 2 and 3 are addressed in sections below on algal, invertebrate, fish, and turtle assemblages. Additional components of Issues 2, 3, and 4 are subsequently addressed in sections below on ecological functions. Issue 4 is addressed in the section on mitigation with support from other sections. A paucity of depth-specific data exists for a majority of taxa in the region and continues to limit some summary statements about core differences among NHB, IHB, and OHB.

9.1 ALGAL, INVERTEBRATE, FISH, AND TURTLE ASSEMBLAGES

Shallow hardbottom habitats of southeast and east central Florida support a sometimes diverse, juvenile-dominated reef assemblage of invertebrates, fishes, and marine turtles. There are also many species of algae that can dominate cover. In total, at least 1,050 algal, invertebrate, and fish species are now recorded from NHB habitats of mainland east Florida. The physical environment is subject to wind and wave disturbance of sometimes high levels at intermediate temporal and spatial scales. Hardbottom patches occur in many areal sizes, frequencies, and depths and are the predominant shallow water habitat off mainland Florida's beaches. These patches are the only natural structural habitat, outside of sand plain features, on the ocean side of all the inlets from Government Cut north to at least Port Canaveral; commonly considered habitats such as seagrass beds and mangroves do not occur outside of the inlets along this reach. Patchily distributed NHB, IHB, and OHB areas can aggregate many diverse organisms and can be of local significance within the nearshore shelf seascape.

9.1.1 Algae

The total number of recorded algal taxa, identified and unidentified, is approximately 340, including 277 known species. Potentially dominant genera are *Ceramium, Dictyota, Hypnea, Laurencia, Gelidium, Caulerpa*, *Jania*, and *Ulva*, depending on subregions and other factors. While no one macroalgal species can be considered a keystone in the NHB, a handful of species appear to repeatedly surface in our examination of abundant and frequently utilized macroalgae. *Halimeda* spp. also aid in sand production.

Sunlight converted into macroalgal tissue is directly consumed by as many as 20 genera of invertebrates, at least 14 genera of fishes, and the juvenile stage of the endangered green turtle, *Chelonia mydas*. Algae are a dominant driver of the food web and also contribute to shelter used by dozens of species of invertebrates and fishes. All algal species contribute to oxygen and nutrient production. In terms of functional form groups, jointed-calcareous algae are most responsible for sediment enrichment and sand building.

The abundance and diversity of macroalgae on NHB vary substantially with changes in latitude from Cape Canaveral to Miami Beach. Proximity to relatively warm, oligotrophic Florida Current waters is a primary factor influencing macroalgal species distribution on NHB. Several other factors that influence distribution include small and large scale hydrodynamics, different substrate types (e.g., worm reefs, limestone, coral reefs), water depth, light penetration (due to water clarity), sand scouring and burial, wave energy, fish and invertebrate grazing pressure, and the various life history strategies of different macroalgae (Lobban and Harrison, 1994). Some observations on the distribution of algae on NHB are 1) overall biomass appears comparatively higher in northern NHB regions (i.e., Indian River and Brevard Counties), 2) species with more grazer-resistant properties (e.g., phaeophytes, calcareous and crustose rhodophytes) are more diverse and abundant in southern NHB regions, and 3) cyanobacteria are commonly encountered on all NHB. However, caution is advised in drawing conclusions from these observations since they have yet to be thoroughly and rigorously tested. A more thorough understanding of the functional role of macroalgae and cyanobacteria would include measuring: a) resilience under disturbance events (e.g., hurricanes), b) abundance and diversity at macro- and micro-level scales, c) temporal variability, and d) role of grazers in controlling productivity.

9.1.2 Invertebrates

Over 533 species of invertebrates have been identified along the east Florida coast. The diversity of sessile species is greatest for cnidarians (~21%), bryozoans (~29%) and sponges (~19%). Some sessile taxonomic groups may not be represented with such high diversity but can occur in very high biomass. A primary example is the sabellariid polychaete *Phragmatopoma lapidosa*, which can be very abundant along the mid- to north sections of the project area and is a habitat engineer that creates structure supporting high diversities of many other invertebrates.

Sessile invertebrate communities change noticeably with latitude and depth. In intertidal hardbottom to the north, dominant invertebrates are sabellariid polychaetes, bryozoans, sea anemones, and tunicates, although the latter three groups generally do not occur in high biomass. Throughout intertidal areas, in addition to *P. lapidosa,* the hard coral *Siderastrea* spp.*,* two species of zoanthids, and several species of solitary anemones can be encountered. Within the lower intertidal and shallow subtidal zones, the most conspicuous sponge is the rock-boring sponge *Pione* (formerly *Cliona) lampa*. In the more centrally located sections of the east Florida coast, there is generally an increase in abundance of *P. lapidosa* both intertidally and subtidally to water depths of approximately 4 m. Within Martin County, the St. Lucie Inlet Reef appears to be the northernmost extent of several of the reef-building corals that are important biodiversity contributors within the Caribbean region. The biomass of hard and soft corals and sponges, while variable and generally low, tends to increase to the south.

The most diverse and generally abundant motile invertebrates are arthropods and polychaetes, which represent 47% and 28%, respectively, of the total number of motile invertebrate species. Over 100 species of crustaceans are extremely abundant, especially on worm reef-dominated hardbottoms. These include crabs, stomatopods, shrimp, isopods, and amphipods. There are over 87 reported polychaete species that are likely to be very abundant, although more research is needed to confirm this. There are also fairly high numbers of gastropods, flat worms, ribbon worms, and echinoderms on these habitats. While less diverse, there generally are intermediate numbers of echinoderms such as sea urchins to the north of the coast*.* Some groups such as brittle stars are probably fairly diverse and abundant but have not been extensively studied.

Primary ecological functional roles of invertebrates along the east Florida coast include 1) shelter-enhancing organisms that increase local diversity of fishes and invertebrates, and 2) predators or prey in local food webs. Generally, the highest community biomasses along the mainland east Florida coast occur in hardbottom areas with higher abundances of sessile invertebrate species (some may be considered foundational or keystone contributors to the community) that enhance local shelter. Along the Florida coast, important shelter-enhancing taxonomic groups are hard and soft corals, sponges, tunicates, molluscs, barnacles, and polychaetes (i.e., *P. lapidosa*). However, their importance in this function may vary dramatically with depth and latitude. In terms of contribution to local food webs, important taxonomic groups are sponges, crabs, shrimp, polychaetes, echinoderms, crabs, and shrimp.

The loss of NHB would result in a significant reduction of a high biomass of invertebrates (sponges, corals, crabs, shrimp, worms, gastropods, bivalves) that could significantly change the nearshore food web. Before a dredging event, the nearshore community can be fairly diverse, consisting of a number of common and longer-lived (often uncommon) species. In this situation, the diversity contributes to a nearshore food web that consists of suspension feeders, herbivores, omnivores, and various levels of carnivores. However, after a dredging event occurs that results in high mortality and habitat elimination, there is likely to be a less diverse community consisting of more opportunistic species, and fewer rare species such as corals. Further, conditions where there is significant reduction in shelter enhancement (via fewer sessile species) in these areas could reduce the number of smaller carnivore trophic levels and have possible adverse effects on the higher trophic levels within the community. Natural recovery of hardbottom habitats would depend on both re-exposure of substrate as well as recruitment capability of sessile shelter-enhancing invertebrates which in turn likely affect associated motile invertebrate species. Although it requires further investigation, it appears that very few older adult motile invertebrates would migrate into the area of impact. Consequently, habitat recovery requires ample larval supply and recruitment of shelter-enhancing species to facilitate what could be a slow recovery of many associated motile invertebrates. The slow recovery of crevice-dwelling species (small crabs, shrimp, worms) may in turn affect prey availability for many motile invertebrate predators and some fishes. Further, severe degradation in water quality (most likely via chronic turbidity) may affect fitness and/or survival of suspension feeders. It may also affect predator-prey interactions because of reductions in visibility.

It is unlikely that OHB is able to compensate for the loss of NHB, particularly in the northern areas of the east Florida coast. Mitigation efforts to restore hardbottom habitats likely depend in large part on recruitment capability of shelter-enhancing species such as *P. lapidosa*. Therefore, local hydrodynamics and the type, topography, and relief of materials must be considered for artificial reefs to maximize recruitment and subsequent recovery of the habitat. For instance, in the case of *P. lapidosa*, the abundance of this species decreases significantly in water deeper than 4 m. Even within the 0 to 4 m depth range, the highest abundances occur more towards the intertidal zone. Why this occurs may be related to improved feeding and reproduction that may occur in these more turbulent shallow waters. However, the choice to settle and live there depends entirely on factors that affect larval supply. It is likely (though requires further investigation) that settling *P. lapidosa* larvae may touch bottom at deeper waters but actively postpone metamorphosis and choose to settle when they encounter shallower waters (McCarthy, 2001). Consequently, if the goal is to mitigate for loss of worm reefs (and associated organisms), then structures deployed in the OHB would not be successful unless chemical cues, hydrodynamics, or other environmental factors could be created that accurately mimic the shallower waters and induce larvae to settle. Further, if settlement does occur at these depths, growing juveniles must survive and recruitment of associated species must occur to properly mitigate for lost habitat.

9.1.3 Fishes

Based on new and old information, over 257 species of fishes are now recorded from NHB habitats. The species list for the entire ichthyofaunal assemblage shows similarities with assemblages from many shallow coral reefs (**Chapter 5**). A wide range of spawning patterns is seen among the fishes of east Florida NHB. Nesting is undertaken in differing manners by species of fishes from quite different families. Several different families, including the site-attached blennies and gobies, also build nests in cryptic manners throughout NHB structure, often laterally or upside-down in NHB microhabitats. Though understudied, we estimate that over 30 fish species spawn on NHB. Most motile species do not spawn on NHB, though there are exceptions. In addition, some coastal pelagics may spawn on or near NHB.

Although the assemblage is juvenile-dominated, a well-developed food web exists that includes most or all common reef trophic categories, including planktivores, herbivores, invertivores, and piscivores. The most prevalent trophic component among species is invertebrate feeders. Randall (1967) categorized the diversity of invertivores according to 1) sessile animal feeders (e.g., sergeant major feeding on *Zooanthus*); 2) “shelled” invertivores (e.g., most *Halichoeres* species of wrasses), and 3) generalized invertebrate predators. The latter group was by far the biggest and included eels, squirrelfishes, snappers, species of basslets (*Serrranus*), some drums (sciaenids), goatfishes (mullids), pompanos, wrasses, and some labrisomids, including the hairy blenny. Specialized invertebrate feeding can occur as well (**Chapter 5**). When the full spectrum of ontogenetic dietary shifts is considered for most species, many are omnivorous (e.g., planktivory to invertivory to piscivory), from species as diverse as labrisomids and lutjanids.

Are nearshore fish larvae spending substantial time in the water column near NHB before settling there? This is possible for some taxa, particularly clupeiforms, gerrieds, sparids and others, but currently cannot be confirmed. For many species in south Florida, transport of larvae to NHB or OHB settlement areas may occur via cross-shelf oceanographic transport mechanisms resulting from diverse meso-scale phenomena (Limouzy-Paris et al., 1997). Directed water column or bottom sampling as done in some other areas (Ruple, 1984; Jahn and Lavenberg, 1986) is needed to address this issue.

Differences among ichthyofaunal assemblages are suggested between the southern and northern areas of mainland southeast and east central Florida in terms of the most abundant species and habitat structure (**Chapter 5**). Potential explanations for substantial differences in prominent species (sailors choice, black margate, hairy blenny) within a 360 km north-south gradient may include temporal recruitment variations, NHB structural differences between the two areas, differences in survey design, species reaching their biogeographic distributional limits between the northern and southern areas, and other factors (summaries of **Chapters 5** and **7**).

Bellwood (1998) concluded that reef fish assemblages ultimately occur in association with too many non-coral reef structures and recommended the term *fishes on coral reefs*. However, Robertson (1998a,b) defined reef fishes as "species that live *on consolidated substrata that form coral and inorganic reefs.*" Inorganic reefs, including rocky shores, were described as: "… the inorganic bedrock provides large and small physical structure that fishes use as habitat features…". All of the 10 consensus families of reef fishes in Bellwood (1998) are represented in association with NHB of east Florida. This evidence suggests there are few reasons to conclude that the fishes of NHB of mainland east Florida do not constitute a reef fish assemblage.

9.1.4 Turtles

Juvenile sea turtles of three species commonly associate with shallow hardbottom of mainland east Florida: the green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and hawksbill (*Eretmochelys imbricata*) turtles. There are many interactions between turtles and an array of organisms that utilize shallow hardbottom. For example, hawksbill turtles fragment sponges when foraging, creating space and habitat for other organisms (Leon and Bjorndal, 2002) as well as increasing sponge growth through fragmentation. Juvenile stages of the endangered green turtle can associate with shallow hardbottom for years, feeding on macroalgae and using structure for shelter. And while green turtles that forage on seagrasses have been examined for their important role in the productivity and nutrient cycling of seagrass communities (Thayer et al., 1984; Aragones and Marsh, 2000; Moran and Bjorndal, 2007), the role of green turtles foraging on macroalgae in macroalgal communities has not been examined until now (K. Holloway-Adkins, ongoing research). Under conditions where substrate for the attachment and growth of macroalgae are limited and herbivory is high, grazers can potentially experience resource competition or partitioning. The mechanistic selection behavior under variable resource conditions is important to understand, especially when planning projects that potentially impact the plight of endangered species.

Conditions over many NHB sites make studying marine turtle populations difficult, and only a handful of studies have been conducted. Juvenile green turtles are the most frequently encountered species on NHB. Genetic stock studies utilizing mitochondrial DNA analysis were conducted on a subset of juvenile green turtles captured in two long-term (>10 years) population studies on NHB: Bagley (2003) in Indian River County and Bass and Witzell (2000) in St. Lucie County. Results indicate that NHB juvenile green turtle populations in these areas were a mixed genetic stock with the same genetic haplotypes as those from an array of different nesting beaches in Costa Rica, Florida, Mexico, and Aves Island (Caribbean). Juvenile hawksbill turtles have only recently been studied and are rarely encountered north of Martin County. Genetic data from turtles captured on NHB, IHB, and OHB indicate they represent a genetic stock from various Mexico nesting beaches (L. Wood, Palm Beach Zoo, pers. comm.).

Data indicate that green and hawksbill turtles predominantly are the most frequently encountered species and the ones that assume relatively long-term residency on NHB. These data and observations suggest that the developmental life stages of juvenile green and hawksbill turtles in particular are intimately tied to the NHB habitat. The mean population size and size-class range suggest that the smaller mean size turtles (20 to 42 cm CL) are obligately tied to certain habitats within the NHB.

9.2 ECOLOGICAL FUNCTIONS AND CONNECTIVITY

Many species use NHB, IHB, and OHB as settlement and early juvenile habitats. The great majority of the species are recorded from coral reefs. For fishes, NHB assemblages are largely juvenile dominated and reef-species dominated. As the only natural habitat structure for 0.5 to 5 km of sand in any direction, shallow hardbottom structural features potentially serve a variety of ecosystem functions, including settlement and nursery areas, spawning sites (for over 100 species of invertebrates and fishes), feeding stations, and socioeconomic drivers (see **Chapter 7**). The ecosystem service roles of shallow hardbottom to local resident water users (fishers, divers, surfers), their families, and the local communities along mainland east Florida remain under examined. Conceptual ecological models can be a useful way to organize the bio-physical and socioeconomic complexity of shallow coastal systems (Ogden et al., 2005). Empirical information on feeding relationships will allow construction of more resolved food webs, which should enhance the development of conceptual ecological models for shallow hardbottom areas.

It is useful to consider the larger scale that these local populations are distributed across (in part, via planktonic larval stages). Outside of ahermatypic hardbottom reefs, nearshore marine areas of mainland east Florida show no natural, high relief, three-dimensional structures that support fish, algal, and macroinvertebrate assemblages. Energetically, hardbottom areas are nutrient-rich patches in among large sand plains. Ecological functions include shelter and feeding resource provisions to over 1,050 recorded species.

Currently, the majority of NHB habitat is within a narrow, 200- to 400-m strip eastward of a major north-to-south reach of beaches from Melbourne to Miami and display a variety of structural forms. Notable exceptions with much more gradation of shallow hardbottom habitats across the shelf and into deeper areas occur in Broward and southern Indian River Counties. NHB composes less than 50% of the alongshore distance of any of the seven county shorelines in the region, where it is often separated by kilometers of flat nearshore sand expanses. Latitudinal abundance differences may be common for prominent species (**Sections 2** and **3**).

For sessile invertebrates, there appears to be a trend towards limited dispersal of larvae or juveniles along the east Florida coast. Of those species that reproduce sexually and asexually, many seem to propagate more via asexual reproduction. Recent molecular research supports this idea, as there appears to be restricted gene flow among Caribbean populations. Similar storm-induced asexual reproduction may influence reproduction in some sponges (*Pione* spp. and possibly *Aplysina* spp.).

Much new review, empirical, and modeling information is coming to bear on issues of population connectivity (**Chapter 7**). Considerable information involving similar reef organisms from other areas has been amassed regarding a variety of biotic and abiotic factors that contribute to retention in larvae (e.g., Cowen et al., 2006). Retention on levels that challenge assumptions of routine long distance dispersal is now becoming more commonplace. Though many differences exist, there are similarities among mainland east Florida shallow hardbottom habitats and rocky intertidal habitats of the U.S. Pacific coast at some scales of examination (**Sections 2** and **3**).

9.3 MITIGATION

Increasingly important and expensive questions involve the use of mitigation projects to offset impacts from large dredge and fill projects. Typically, these questions represent key steps in the finalization of permitting processes. Preliminary conclusions regarding the functional attributes of NHB and the application of that information to the evaluation of mitigation alternatives include the following:

- Mitigation of NHB impacts by utilizing artificial reefs can often provide adequate replacement of lost structural habitat and therefore some structure- and trophic-associated ecological functions.
- Not all reef designs and deployments will be successful in all situations, and site-specific factors must be considered. Different approaches and designs will be required for different locations in southeast and east central Florida.
- For worm reef areas, ensuring successful local larval recruitment events is essential. To this end, project designers need to be sure that the sediment size range is suitable to incoming recruits.
- For worm reef areas, a measure of success is not only the presence of worm reef but duration: it should persist through 1 year, with new recruits encountered in the second year. More importantly, some of the dominant crustacean species should be encountered within the worm rock.
- In terms of Issue 4, based on available information, NHB functions will not be fully replaced with artificial reefs in IHB or OHB water depths due to the depth limits on the habitat engineering worm species *P. lapidosa* and the associated assemblage of many dozens of species that *P. lapidosa* structures support in areas from Brevard County to mid-Palm Beach County.
- Artificial reef mitigation does not appear to remove or provide compensatory mitigation for the direct and indirect physiological and potential population-scale impacts of turbidity and sediment resuspension.
- Approximately 340 algal taxa are associated with NHB, and most are subject to high mortality if a site is filled. Mitigation reefs can provide new attachment sites for algae. Algal growth on mitigation reefs should correlate in part with water clarity. The most abundant species on NHB should be considered in success criteria for artificial reef mitigation progress and monitored for persistence.
- Invertebrate and fish grazers on artificial reefs placed in IHB or OHB waters may be subject to higher predation (especially in the more northern NHB regions where high-energy waves reduce the number of larger organisms in intertidal and shallow subtidal areas). Exclusion experiments on natural NHB vs. artificial mitigation reefs placed in deeper waters will reveal if mitigation reef productivity is reduced by increased grazer pressure.
- Deployment of mitigation reefs at least 6 months to 1 year prior to project construction could accelerate colonization of algae and invertebrates, as well as provide alternate habitat for animals able to escape burial.
- Placement of artificial reefs in IHB or OHB waters to mitigate for NHB dredge and burial projects should consider the possibility that where smaller size-class juvenile marine turtle populations exist, reefs placed in deeper waters may create habitat and resources suitable for larger turtles that could displace smaller individuals. Project planning should include pre- and post-monitoring criteria that include designing artificial reefs that provide adequate shelter for the existing size-class of juvenile turtle populations. Predation may also be increased on artificial reefs.
- Monitoring plans for juvenile marine turtles should include documenting both size and species, either through observer training and/or the capture and measuring of individual animals.
- Hypotheses in mitigation studies should be framed using equivalency approaches; this will also contribute to goal setting and success criteria.
- Study designs should be flexible and adaptive, given the lack of natural controls or replication.

9.4 RESEARCH NEEDS

In terms of both ecological functions of shallow hardbottom and mitigating the loss of NHB, there are fundamental questions that require basic and reliable estimation of long-term patterns. Understanding effects beyond project boundaries at larger spatial scales is important to understanding project significance. Some areas of additional work include the following:

- Latitudinal abundance differences in prominent species require more research to explain the north-to-south differences in assemblage pattern.
- What are the most useful functional categories that can be evaluated from available information for shallow hardbottom habitat/organism assemblages? Manipulative experiments could be of particular use for some questions.
- With evaluation, are such categories applicable to the shallow hardbottom system?

- A food web model for shallow hardbottom is needed for multiple purposes. Enough information to build such a model from the bottom levels up is now accessible; however, empirical trophic studies are still badly needed.
- A full conceptual ecological model (CEM) needs to be developed; this will be more efficient if a thorough food web draft is available. The information to build a larger CEM is now available for some components.
- The intermediate or long term water quality patterns and effects on shallow hardbottom from turbidity and sedimentation events, long-shore and cross-shelf, that result from dredge and fill projects (and relationships to natural turbidity) require examination (Bishop and Peterson, 2005). Without this type of information, responses to Issue 2 regarding whole ecosystem effects when NHB is buried, or Issue 3 regarding OHB compensation roles, will be not be fully resolvable.
- Experimental investigations of mitigation reefs are needed to examine extant questions about boulder reefs vs. modular reefs, depth-related issues, and performance of differing reef array designs.

Chapter 10
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Appendices

Appendix A

Table A.1. Number of macroalgal species found during studies conducted on nearshore hardbottom habitat, by county. Data include location of study (region), species found, zone of sampling, method used to collect data (i.e., natural reef or artificial reef, beach nourishment monitoring, or foraging analysis, etc.). Color-coding indicates that similar study methods were used.

County	Region	Species Count	Intertidal	Subtidal	Inshore	Offshore	PCM - T	Study Method	Season/ Year	Source
Brevard	Brevard coastline	24	√	√				Video, random point analysis	Summer 2005	Continental Shelf Associates, Inc., 2005a
	Satellite Beach	37		√				PALM boxes	Summer 2007	Holloway-Adkins and McCarthy, 2007
	Nearshore reef, Brevard County	24	√					Lavage-percent composition	2005	Holloway-Adkins, 2005
	Brevard County	22								McCarthy, unpublished
Indian River	Vero Beach	109	√	√				Transect	Summer 1974	Juett et al., 1976
	Sebastian	46	√	√				Lavage-percent composition	Summer 1998–2000	Holloway-Adkins, 2001
		28		√				Quadrat-percent composition		Gilbert, 2005
	Indian River	42								McCarthy, unpublished
St. Lucie	Hutchinson Island	119		√				Trawl/benthic grab	September 1971 - August 1974	Moffler and van Breedveld, 1979
	Fort Pierce	29	√				√		1997	Continental Shelf Associates, Inc., 1997
	Fort Pierce-SC	51								McCarthy, unpublished
Martin	St. Lucie Inlet	41	√					Transect (drift algae included)	Spring/Fall 1957-1959	Phillips, 1961
	Nearshore Mitigation Reef	9				√	√ (Post)	Video, photo transect	Summer 2001-2006	Harris, 2006; Harris et al., 2007
	Martin County	9								McCarthy, unpublished

Table A.1. (Continued).

County	Region	Species Count	Intertidal	Subtidal	Inshore	Offshore	PCM - T	Study Method	Season/ Year	Source
Palm Beach	Boca Raton artificial reef	10					√	Quadrat-percent cover	Monthly	Cummings, 1990
	Boca Raton nearshore reef	23		√				Transect	July 1987 - August 1990	Vare, 1991
	Palm Beach County	11		√				Lavage-percent composition	August - November 2003	Makowski, 2004
	Boca Raton	17		√				Grab samples	Spring 2004	Jones et al., 2004
	Artificial reefs: (1) Juno Geogrid (2) Jupiter Cloth Reef Rock (3) Jupiter Concrete (4) Jupiter Shallow Concrete (5) Coral Cove Rock	12		√			√ (Post)	Video, random point analysis	Fall 2001-2004	Continental Shelf Associates, Inc., 2005b, 2006
	Palm Beach County	26								McCarthy, unpublished
	North Jupiter	9								
	Jupiter Area	6								
	South Jupiter	6								
	Juno	8								
	MacArthur Beach	5								
Broward	Broward County	10			√			Necropsy and lavage	1992	Wershoven and Wershoven, 1992b
	Fort Lauderdale				√	√	√	AGRRA protocol, *in-situ* quadrat analysis	Summer 2001	U.S. Army Corps of Engineers, 2003a
	Lauderdale by the Sea				√	√	√			
	Pompano Beach				√	√	√			
	John U. Lloyd State Park				√	√	√			
	Dania				√	√	√			
	Hollywood/Hallandale	27 (total)			√	√	√			
	Port Everglades-Broward/Miami-Dade County	100				√	√	Transect, BEAMR quadrat, video, random point analysis	Summer/Fall 2004	Coastal Planning & Engineering, Inc., 2006
	Shoreline (Segments I, II, III)	6		√			√	Visual transect	Summer 2004	Salmon et al., 2004

Table A.2. Families, genera, and numbers of species within each genera of macroalgae and cyanobacteria documented in the studies conducted on nearshore hardbottom of the east Florida coast listed in **Table A.1**. A zero under "Number of Species" column indicates that algae were identified only to genus level.

Family	Genus	Number of Species
Chlorophyta		
Caulerpaceae	Bryopsis	2
	Caulerpa	12
Cladophoraceae	*Chaetomorpha*	3
	Cladaphora	6
	Rhizoclonium	2
Codiaceae	*Codium*	5
Dasycladaceae	*Batophora*	1
	Cymopolia	1
	Dasycladus	1
	Neomeris	1
Derbesiaceae	*Derbesia*	1
Halimedaceae	*Halimeda*	6
Siphonocladaceae	*Dictyosphaeria*	0
	Siphonocladus	1
	Ventricaria	1
Udoteaceae	*Avrainvillea*	2
	Penicillus	1
	Udotea	6
Ulvaceae	*Ulva*	6
Ulvellaceae	*Entocladia*	1
Rhodophyta		
Acanthaceae	*Acanthophora*	2
Acrochaetiaceae	*Acrochaetium*	2
Areschougiaceae	*Eucheuma*	2
Asparagaceae	*Asparagopsis*	1
Ceramiaceae	*Callithamnion*	2
	Centroceras	1
	Ceramium	9
	Crouania	1
	Griffithsia	1
	Spermothamnion	3
	Spyridia	3
	Wrangelia	2
Champiaceae	*Champia*	1
Compsopogonaceae	*Compsopogon*	1
Corallinaceae	Amphiroa	4
	Fosliella	2
	Jania	4
	Lithophyllum	0
	Titanophora	1
Corynomorphaceae	*Grateloupia*	1
Cystocloniaceae	*Hypnea*	5
Dasyaceae	*Dasya*	6
	Dasyopsis	1
	Dictyurus	1
	Heterosiphonia	2
Delesseriaceae	*Nitophyllum*	1
Dumontiaceae	*Dudresnya*	1
Erythropeltidaceae	Erythrotrichia	1

Table A.2. (Continued).

Family	Genus	Number of Species
Galaxauraceae	*Galaxaura*	4
	Scinaia	1
Gelidiaceae	*Gelidiella*	3
	Gelidiopsis	3
	Gelidium	3
	Pterocladia	2
Gigartinaceae	*Gigartina*	1
Gracilariaceae	*Gracilaria*	16
	Hydropuntia	1
Halymeniaceae	*Cryptonemia*	2
Halymeniaceae	*Halymenia*	3
Liagoraceae	*Liagora*	2
Lomentariaceae	*Lomentaria*	1
Peyssonneliaceae	*Peyssonnelia*	1
Polyphysaceae	*Acetabularia*	4
Pyraloidea	*Chondria*	8
Rhodomelaceae	*Chondrocanthus prev. Laurencia*	1
	Bostrychia	2
	Botryocladia	4
	Bryocladia	1
	Bryothamnion	2
	Digenia	1
	Laurencia	8
	Polysiphonia	5
	Herposiphonia	1
Rhodymeniaceae	*Asteromenia*	1
	Chrysymenia	2
	Rhodymenia	2
Solieriaceae	*Agardhiella*	2
	Neoagardhiella	0
	Solieria	2
Valoniaceae	*Ernodesmis*	1
	Valonia	1
Wurdemanniaceae	*Wurdemannia*	1
Phaeophyta		
Bibionidae	*Dilophus*	1
Chordariaceae	*Hydroclathrus*	1
Dictyotaceae	*Dictyopteris*	2
	Dictyota	17
	Lobophora	1
	Padina	6
	Spatoglossum	1
	Stypopodium	1
Ectocarpaceae	*Ectocarpus*	1
Pylaiellaceae	*Bachelotia*	1
Sargassaceae	*Sargassum*	7
Scarabaeoidea	*Hincksia*	4
Scytosiphonaceae	*Colpomenia*	1
	Rosenvingea	2
Sphacelariaceae	*Sphacelaria*	2

Table A.2. (Continued).

Family	Genus	Number of Species
Cyanophyta		
Chroococcaceae	*Anacystis*	4
Entophysalidaceae	*Entophysalis*	1
Euphorbiaceae	*Anabaena*	1
Nostocaceae	*Hormothamnion*	1
	Nodularia	1
Oscillatoriaceae	*Lyngbya*	0
	Microcoleus	3
	Oscillatoria	1
Phormidiaceae	*Porphyrosiphon*	1
Rivulariaceae	*Calothrix*	2
Schizotrichaceae	*Schizothrix*	2
Total Families	57	
Total Genera	108	
Total Species	277	

Table A.3. Genera and numbers of species of macroalgae and cyanobacteria identified within genera, by county, documented in the studies conducted on nearshore hardbottom of the east Florida coast listed in **Table A.1**. Genera are listed by highest frequency of occurrence among counties.

Genus	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward	Number of Counties in which Species were Present
Bryopsis	1	1	1	1	1	2	6
Caulerpa	2	9	9	2	8	6	6
Ceramium	1	4	5	3	1	5	6
Codium	1	2	5	3	4	3	6
Dictyota	2	4	7	2	3	12	6
Gelidium	2	3	2	2	2	2	6
Gracilaria	2	9	12	6	2	8	6
Laurencia	3	4	5	2	3	4	6
Padina	1	4	3	1	3	3	6
Ulva	3	5	2	4	1	1	6
Bryothamnion		2	3	2	1	3	5
Cladaphora	1	4	2	2	2		5
Dictyopteris		2	2	1	1	2	5
Gelidiopsis	2	3	1		2	1	5
Halimeda		1	2	1	4	8	5
Hypnea	1	5	5	1		4	5
Jania	1	2	4		1	3	5
Sargassum		2	5	1	1	2	5
Acanthophora		2	2		2	1	4
Agardhiella	1	2		1	1		4
Botryocladia		3	2	1		3	4
Bryocladia	1	1	1		1		4
Chaetomorpha	1	2	1	1			4
Chondria	3	4	6			1	4
Pterocladia	1	5	4			1	4
Spyridia	1	2	1			1	4
Acetabularia			1		1	3	3
Amphiroa		2	1			3	3
Bostrichia		1	1			1	3
Centroceras	1	1		1			3
Champia		1	1			1	3
Dasya		5	2			4	3
Erythrotrichia		1		1	1		3
Galaxaura		1	1			1	3
Halymenia	1	3	4				3
Heterosiphonia		1	2			1	3
Liagora		1			1	2	3
Lomentaria	1	1	1				3
Rhizoclonium		2		1	1		3

Table A.3. (Continued).

Genus	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward	Number of Counties in which Species were Present
Rhodymenia		2	2			1	3
Scinaia	1	2			1		3
Solieria	1	2	2				3
Sphacelaria		1	1	1			3
Udotea			2		2	6	3
Valonia			1		1	1	3
Acrochaetium			2	1			2
Avrainvillea					1	2	2
Calcareous green			1		1		2
Calothrix		1		1			2
Chondrocanthus (Laurencia)	1				1		2
Chrysymenia		1	1				2
Colpomenia		1	2				2
Crouania			1	1			2
Cryptonemia		2	1				2
Dascycladus					1	1	2
Eucheuma		2	3				2
Fosliella		2		1			2
Griffithsia		1		1			2
Hincksia		4	2				2
Lobophora		1	1				2
Lyngbya		1			1		2
Microcoleus		2		1			2
Neomeris					1	2	2
Nitophyllum		1			1		2
Penicillus			1		1		2
Rosenvingea		1	2				2
Schizothrix		2			2		2
Spatoglossum		1	1				2
Spermothamnion		1	2				2
Unidentified green			2		2		2
Unidentified red			1		1		2
Wrangelia	1					2	2
Anabaena		1					1
Anacystis		4					1
Asparagopsis		1					1
Asteromenia		1					1
Bachelotia			1				1
Batophora					1		1
Callithamnion		2					1
Coralline red					1		1
Corallinaceae					1		1

Table A.3. (Continued).

Genus	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward	Number of Counties in which Species were Present
Cymopolia					2		1
Dasyopsis			1				1
Derbesia		1					1
Dictyosphaeria		1					1
Dictyurus		1					1
Digenia					1		1
Dilophus			1				1
Dudresnya	1						1
Ectocarpus			1				1
Entocladia		1					1
Entophysalis		1					1
Ernodesmis						1	1
Filamentous brown					1		1
Filamentous green					1		1
Filamentous red					1		1
Gelidiaceae						1	1
Gelidiella						4	1
Gigartina		1					1
Grateloupia		1					1
Herposiphonia				1			1
Hormothamnion		1					1
Hydroclathrus			1				1
Hydropuntia						1	1
Lithophyllum						1	1
Neoagardhiella			1				1
Nodularia		1					1
Oscillatoria		1					1
Peyssonnelia		1					1
Polysiphonia				1			1
Porphyrosiphon		1					1
Siphonocladus					1		1
Stypopodium					1		1
Titanophora		1					1
Unidentified turf					1		1
Unidentified veg.			1				1
Ventricaria						1	1
Wurdemannia			1				1

Table A.4. The number of species and percent composition of sheet functional form group macroalgae in studies on nearshore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Sheet Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	3	24	12.5	Summer 2005	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	2	12	**16.7**	2001-2004	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial					Video transects, random point analysis, percent cover
Harris, 2006; Harris et al., 2007 MARTIN	Intertidal	1	9	11.1	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	13	100	**13**	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	4	109	3.7	Summer 1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	6	41	14.6	SP/Fall/1957-1959	Transects (drift algae are included t)
Vare, 1991 PALM BEACH	Intertidal	1	23	4.4	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	0	6	**0**	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	4	37	10.8	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	2	24	**8.3**	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	5	46	10.9	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	3	11	**27.3**	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	1	10	10	YR/1992	Lavage - Percent composition and lavage
Gilbert, 2005 INDIAN RIVER	Subtidal	4	28	**14.3**		Quadrat - Percent composition transects waters 3.5 to 4.0m
Cummings, 1990 PALM BEACH	Intertidal artificial reef	2	10	**20**	Monthly	Quadrat - Percent cover and species

Table A.4. (Continued).

Source	Location/Tidal Zone	Number of Sheet Species	Total Number of Species	Percent Composition	Season/Year	Study Method
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	2	27	**7.4**		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	6	119	**5.04**	September 1971-August 1974	Trawl and benthic grab samples (includes drift)
Jones et al., 2004 PALM BEACH	Subtidal	1	17	**5.9**	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal	5	29	17.2	1997	
McCarthy, unpublished BREVARD		2	22	9.1		
McCarthy, unpublished INDIAN RIVER	Intertidal	3	42	7.1		
McCarthy, unpublished ST. LUCIE	Fort Pierce	8	51	15.7		
McCarthy, unpublished MARTIN		1	9	11.1		
McCarthy, unpublished PALM BEACH	Palm Beach County	0	26	0		
McCarthy, unpublished PALM BEACH	North Jupiter	1	9	11.1		
McCarthy, unpublished PALM BEACH	South Jupiter	0	6	0		
McCarthy, unpublished PALM BEACH	Juno	1	8	12.5		
McCarthy, unpublished PALM BEACH	MacArthur Beach	0	5	0		

Table A.5. The number of species and percent composition of filamentous functional form group macroalgae in studies on nearshore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Filamentous Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	5	24	**20.8**	Summer 2005	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	0	12	**0**	2001-2004	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial					Video transects, random point analysis, percent cover
Harris et al., 2007 MARTIN	Intertidal	1	9	11.1	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	20	100	**20**	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	38	109	**34.9**	Summer 1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	14	41	34.2	SP/Fall/1957-1959	Transects (drift algae are included)
Vare, 1991 PALM BEACH	Intertidal	2	23	**8.7**	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	2	6	33.3	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	13	37	35.1	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	8	24	33.3	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	16	46	34.8	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	4	11	**36.3**	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	1	10	**10**	YR/1992	Lavage - Percent composition and necropsy
Gilbert, 2005 INDIAN RIVER	Subtidal	6	28	**21.4**		Quadrat - Percent composition transects waters 3.5 to 4.0m
Cummings, 1990 PALM BEACH	Intertidal artificial reef	1	10	**10**	Monthly	Quadrats - Percent cover and species

Table A.5. (Continued).

Source	Location/Tidal Zone	Number of Filamentous Species	Total Number of Species	Percent Composition	Season/Year	Study Method
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	7	27	**25.9**		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	35	119	**29.4**	September 1971-August 1974	Trawl and benthic grab samples (drift included)
Jones et al., 2004 PALM BEACH	Subtidal	5	17	**29.4**	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal	7	51	13.7	1997	
McCarthy, unpublished BREVARD		5	22	22.7		
McCarthy, unpublished INDIAN RIVER	Intertidal	2	42	4.8		
McCarthy, unpublished ST. LUCIE	Fort Pierce	7	51	13.7		
McCarthy, unpublished MARTIN		5	26	19.2		
McCarthy, unpublished PALM BEACH	Palm Beach County	0	9	0		
McCarthy, unpublished PALM BEACH	North Jupiter	0	6	0		
McCarthy, unpublished PALM BEACH	South Jupiter	0	8	0		
McCarthy, unpublished PALM BEACH	Juno	0	5	0		
McCarthy, unpublished PALM BEACH	MacArthur Beach	0	5	0		

Table A.6. The number of species and percent composition of coarsely-branched functional form group macroalgae in studies on nearshore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Coarsely-Branched Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	11	24	45.8	Summer 2005	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	8	12	**66.7**	2001-2004	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial					Video transects, random point analysis, percent cover
Harris et al., 2007 MARTIN	Intertidal	3	9	**33.3**	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	26	100	**26**	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	22	109	20.2	Summer 1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	8	41	19.5	SP/Fall/1957-1959	Transects (drift algae are included)
Vare, 1991 PALM BEACH	Intertidal	9	23	**39.1**	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	1	6	**16.7**	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	14	37	37.8	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	8	24	33.3	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	12	46	26	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	1	11	**9.1**	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	4	10	**40**	YR/1992	Lavage - Percent composition
Gilbert, 2005 INDIAN RIVER	Subtidal	9	28	**32.1**		Quadrat - Percent composition transects waters 3.5 to 4.0 m

Table A.6. (Continued).

Source	Location/Tidal Zone	Number of Coarsely-Branched Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Cummings, 1990 PALM BEACH	Intertidal artificial reef	3	10	**30**	Monthly	Quadrats - Percent cover and species
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	9	27	**33.3**		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	37	119	**31.1**	September 1971-August 1974	Trawl and benthic grab samples (drift included)
Jones et al., 2004 PALM BEACH	Subtidal	5	17	**29.4**	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal	9	29	31.03	1997	
McCarthy, unpublished BREVARD		11	22	50		
McCarthy, unpublished INDIAN RIVER	Intertidal	9	42	21.4		
McCarthy, unpublished ST. LUCIE	Fort Pierce	15	51	29.4		
McCarthy, unpublished MARTIN		3	9	33.3		
McCarthy, unpublished PALM BEACH	Palm Beach County	8	26	30.8		
McCarthy, unpublished PALM BEACH	North Jupiter	2	9	22.2		
McCarthy, unpublished PALM BEACH	South Jupiter	2	6	33.3		
McCarthy, unpublished PALM BEACH	Juno	3	8	37.5		
McCarthy, unpublished PALM BEACH	MacArthur Beach	1	5	20		

Table A.7. The number of species and percent composition of thick-leathery functional form group macroalgae in studies on neaershore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Thick-Leathery Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	4	24	16.7	Summer 2005	Video transects, random point analysis, percent cover analysis
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	1	12	8.3	2001-2004	Video transects, random point analysis, percent cover analysis
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial	0	12	**0**		Video transects, random point analysis, percent cover
Harris et al., 2007 MARTIN	Intertidal	4	9	**44.4**	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	24	100	24	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	18	109	**16.5**	Summer 1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	9	41	22	SP/Fall/1957-1959	Transects (drift algae are included)
Vare, 1991 PALM BEACH	Intertidal	4	23	17.4	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	3	6	**50.00**	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	5	37	13.5	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	5	24	20.8	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	11	46	23.9	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	2	11	**18.2**	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	3	10	**30.00**	YR/1992	Lavage - Percent composition and necropsy
Gilbert, 2005 INDIAN RIVER	Subtidal	7	28	**25**		Quadrat - Percent composition transects waters 3.5 to 4.0 m

Table A.7. (Continued).

Source	Location/Tidal Zone	Number of Thick-Leathery Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Cummings, 1990 PALM BEACH	Intertidal artificial reef	2	10	**20**	Monthly	Quadrats- Percent cover and species
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	3	27	11.1		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	30	119	**25.2**	September 1971-August 1974	Trawl and benthic grab samples (drift included)
Jones et al., 2004 PALM BEACH	Subtidal	4	17	23.5	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal	7	29	24.1	1997	
McCarthy, unpublished BREVARD		4	22	18.2		
McCarthy, unpublished INDIAN RIVER	Intertidal	5	42	11.9		
McCarthy, unpublished ST. LUCIE	Fort Pierce	14	51	27.5		
McCarthy, unpublished MARTIN		4	9	44.4		
McCarthy, unpublished PALM BEACH	Palm Beach County	7	26	26.9		
McCarthy, unpublished PALM BEACH	North Jupiter	1	9	11.1		
McCarthy, unpublished PALM BEACH	South Jupiter	0	6	0		
McCarthy, unpublished PALM BEACH	Juno	0	8	0		
McCarthy, unpublished PALM BEACH	MacArthur Beach	1	5	20		

Table A.8. The number of species and percent composition of jointed-calcareous functional form group macroalgae in studies on nearshore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Jointed-Calcareous Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	0	24	0	Summer 2005	Video transects, random point analysis, percent cover analysis
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	1	12	8.3	2001-2004	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial	0	12	**0**		Video transects, random point analysis, percent cover
Harris et al., 2007 MARTIN	Intertidal	0	9	**0**	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	17	100	**17**	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	7	109	6.4	Summer1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	2	41	4.9	SP/Fall/1957-1959	Transects (drift algae are included)
Vare, 1991 PALM BEACH	Intertidal	5	23	**21.7**	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	0	6	**0**	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	1	37	2.7	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	1	24	**4.2**	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	2	46	4.4	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	1	11	9.1	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	1	10	**10**	YR/1992	Lavage - Percent composition and necropsy
Gilbert, 2005 INDIAN RIVER	Subtidal	2	28	**7.1**		Quadrat - Percent composition transects waters 3.5 to 4.0 m

Table A.8. (Continued).

Source	Location/Tidal Zone	Number of Jointed-Calcareous Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Cummings, 1990 PALM BEACH	Intertidal artificial reef	2	10	**20**	monthly	Quadrats - Percent cover and species
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	5	27	18.5		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	7	119	**5.9**	September 1971-August 1974	Trawl and benthic grab samples (drift included)
Jones et al., 2004 PALM BEACH	Subtidal	0	17	**0**	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal	2	29	6.7	1997	
McCarthy, unpublished BREVARD		0	22	0		
McCarthy, unpublished INDIAN RIVER	Intertidal	1	42	2.4		
McCarthy, unpublished ST. LUCIE	Fort Pierce	4	51	7.8		
McCarthy, unpublished MARTIN		1	9	11.1		
McCarthy, unpublished PALM BEACH	Palm Beach County	6	26	23.1		
McCarthy, unpublished PALM BEACH	North Jupiter	2	9	22.22		
McCarthy, unpublished PALM BEACH	South Jupiter	1	6	16.7		
McCarthy, unpublished PALM BEACH	Juno	1	8	12.5		
McCarthy, unpublished PALM BEACH	MacArthur Beach	1	5	20		

Table A.9. The number of species and percent composition of crustose functional form group macroalgae in studies on nearshore hardbottom. Color shading indicates similar study methods were used. High and low percent composition among similar studies are in bold.

Source	Location/Tidal Zone	Number of Crustose Species	Total Number of Species	Percent Composition	Season/Year	Study Method
Continental Shelf Associates, Inc., 2005a BREVARD	Inter- and subtidal combined	0	24	0	Summer 2005	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Shallow subtidal	0	12	**0**	2001-2004	Video transects, random point analysis, percent cover
Continental Shelf Associates, Inc., 2005b PALM BEACH	Subtidal artificial	0	12	**0**		Video transects, random point analysis, percent cover
Harris et al., 2007 MARTIN	Intertidal	0	9	**0**	Summer 2001-2006	Visual transect, video and still frame
Coastal Planning & Engineering, Inc., 2006 BROWARD	Subtidal/artificial	0	100	**0**	Summer/Fall 2004	Transect, BEAMR quadrat, Video, random point
Juett et al., 1976 INDIAN RIVER	Intertidal	2	109	**1.8**	Summer 1974	Transect
Phillips, 1961 ST. LUCIE	Station 1, just north of St. Lucie Inlet on ocean side	0	41	**0**	SP/Fall/1957-1959	Transects (drift algae are included)
Vare, 1991 PALM BEACH	Intertidal	0	23	**0**	July 1987-August 1990	Transect
Salmon et al., 2004 BROWARD	Subtidal-preconstruction	0	6	**0**	2004	Visual Transect
Holloway-Adkins and McCarthy, 2007 BREVARD	Subtidal/artificial	0	37	0	Summer 2007	Percent composition on settlement plates
Holloway-Adkins, 2005 BREVARD	Intertidal	0	24	**0**	2005	Lavage - Percent composition
Holloway-Adkins, 2001 INDIAN RIVER	Intertidal	0	46	**0**	Summer 1998-2000	Lavage - Percent composition
Makowski, 2004 PALM BEACH	Subtidal	0	11	**0**	August-November 2003	Lavage - Percent composition
Wershoven and Wershoven, 1992b BROWARD	Intertidal	0	10	**0**	YR/1992	Lavage - Percent composition and necropsy
Gilbert, 2005 INDIAN RIVER	Subtidal	0	28	**0**		Quadrat - Percent composition transects waters 31/2-4 meters
Cummings, 1990 PALM BEACH	Intertidal artificial reef	0	10	**0**	Monthly	Quadrats - Percent cover and species

Table A.9. (Continued).

Source	Location/Tidal Zone	Number of Crustose Species	Total Number of Species	Percent Composition	Season/Year	Study Method
U.S. Army Corps of Engineers, 2003a BROWARD	Intertidal	5	27	**18.5**		AGRRA protocol, *in-situ* quadrat analysis
U.S. Army Corps of Engineers, 2003a BROWARD	Subtidal	(species put together)	(species put together)			AGRRA protocol, *in-situ* quadrat analysis
Moffler and van Breedveld, 1979 ST. LUCIE	Intertidal	0	119	**0**	September 1971-August 1974	Trawl and benthic grab samples (drift included)
Jones et al., 2004 PALM BEACH	Subtidal	0	17	**0**	SP/2004	Grab samples
Continental Shelf Associates, Inc., 1997 ST. LUCIE	Intertidal barrier island that separates Indian River Lagoon from Atlantic	0	29	0	1997	
McCarthy, unpublished BREVARD		0	22	0		
McCarthy, unpublished INDIAN RIVER	Intertidal	0	42	0		
McCarthy, unpublished ST. LUCIE	Fort Pierce	0	51	0		
McCarthy, unpublished MARTIN		0	9	0		
McCarthy, unpublished PALM BEACH	Palm Beach County	0	26	0		
McCarthy, unpublished PALM BEACH	North Jupiter	0	9	0		
McCarthy, unpublished PALM BEACH	South Jupiter	0	6	0		
McCarthy, unpublished PALM BEACH	Juno	0	8	0		
McCarthy, unpublished PALM BEACH	MacArthur Beach	0	5	0		

Appendix B

Table B.1. Presence/absence of invertebrates encountered in available studies of hardbottom habitats in six counties along the east Florida coast. ● denotes species identified in at least one study within noted county; blank cell denotes species not encountered in any study in noted county. Note that species are listed as identified in the respective study, and that those highlighted in yellow were not used to determine species counts for the taxonomic groups listed in **Chapter 4**.

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Polychaetes						
Anaitidae longipes		●				
Anamobaea oerstedii		●		●		
Arabella sp.		●				
Aricidea sp.		●				
Armandia agilis		●				
Axiothella sp.		●				
Brachioma nigromaculata		●		●	●	
Clymenella torquata		●				
Decamastus sp.		●				
Dispio unicata		●				
Doruilleidae sp.		●				
Euclymene sp.		●				
Eupolymnia crassicornis		●		●		
Exogone atlantica		●				
Genetyllis sp.		●				
Glycera sphyrabrancha		●				
Goniadella sp.		●				
Haplosyllis spongicola		●				
Hermodice carunculata		●				
Kefersteinia cirrata		●		●		
Leitoscoplos fragilis		●		●		
Lumbrneris sp.		●				
Macroclymene sp.		●				
Magelona sp.		●				
Marphysa sanquinea		●				
Mediomastus californiensis		●				
Megelonna sp.		●				
Myriochele oculata		●				
Naineris grubei		●				
Nematonereis hebes		●				
Nepthys squamosa		●				
Nereis falsa		●				
Nereis lamellose		●				
Nereis pelagica		●				
Notomastus sp.		●				
Odontosyllis enopla		●				
Pectinaria gouldii		●				
Peresiella sp.		●				
Pherusa inflata		●				
Phragmatopoma lapidosa (caudata)	●	●	●	●	●	●
Pista sp.	●					
Prionospio cirrifora		●				

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Prionospio cristata		●				
Prionospio fallax		●				
Prionospio pygmaea		●				
Pseudovermilia occidentalis		●				
Sabella sp. A		●				
Sabella sp. B		●				
Sabellastarte magnifica				●		
Sabellidae			●			
Saccocirrus sp.		●				
Salmacina sp.					●	
Scolepis squamata		●				
Sabellaridae Species A					●	
Serpulidae Species A					●	
Serpulidae Species B					●	
Sicyonia brevirostris		●				
Spiophanes bombyx		●				
Spiophanes missionensis		●				
Spirobranchus giganteus				●		
Terribellidae sp.					●	
Unknown species		●				
Websterinereis tridentate		●				
Anthozoans						
Acropora cervicornis						●
Acropora palmata						●
Agaricia agaricites						●
Agaricia fragilis						●
Agaricia sp.					●	
Cladocora arbuscula					●	●
Colpophyllia natans					●	●
Dendrogyra cylindrus						●
Dichocoenia stokesii				●	●	●
Diploria clivosa				●	●	●
Diploria labyrinthiformis						●
Diploria sp.					●	
Diploria strigosa			●	●	●	●
Favia fragum				●	●	●
Isophyllia sinuosa				●	●	●
Isophyllia sp.					●	
Madracis decactis				●	●	●
Meandrina meandrites				●	●	●
Montastraea annularis						●
Montastraea franksi						●
Montastraea cavernosa				●	●	●
Montastraea faveolata				●	●	●
Mycetophyllia aliciae				●	●	●
Mycetophyllia danaana						●
Oculina diffusa		●	●	●	●	●
Oculina robusta					●	●

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Oculina varicosa		●	●	●	●	●
Phyllangia americana		●	●	●	●	●
Porites astreoides				●	●	●
Porites porites				●	●	●
Porites sp.					●	
Scolymia sp.				●		
Siderastrea radians		●	●	●	●	●
Siderastrea siderea		●	●	●	●	●
Siderastrea sp.	●	●			●	
Solenastrea bournoni			●	●	●	●
Solenastrea hyades				●	●	●
Stephanocoenia intersepta				●	●	●
Bunodosoma caveranta				●	●	●
Actinia bermudnesis				●	●	●
Diadumene leucolena				●	●	●
Palythoa caribaeorum				●	●	●
Zoanthus sp.					●	●
Zoanthus pulchellus					●	●
Briareum asbestinum				●	●	●
Carijoa riisei		●		●	●	●
Erythropodium caribaeorum					●	●
Eunicea calyculata					●	●
Eunicea sp.				●	●	●
Gorgonia sp.					●	
Gorgonia ventalina				●	●	●
Leptogorgia hebes		●	●	●	●	●
Leptogorgia virgulata		●	●	●	●	●
Muricea sp.				●	●	●
Plexaura flexuosa					●	●
Plexaurella grisea				●	●	●
Plexaurella sp.				●		
Pseudopterogorgia americana					●	●
Pseudopterogorgia sp.			●	●	●	
Pterogorgia anceps				●	●	●
Pterogorgia citrina				●	●	●
Pterogorgia guadalupensis				●	●	●
Pterogorgia sp.				●	●	
Unidentified sea rod				●		
Zoanthus sp.					●	
Sponges						
Agelas conifer					●	
Agelas schmidti					●	
Agelas sp.					●	
Aiolochroia crassi					●	
Amphimedon compressa				●	●	
Anthosigmella varians			●	●		●
Aplysina cauliformis					●	
Aplysina fistularis				●	●	

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Aplysina sp					●	
c.f. Dysidea etheria						●
Calcispongidae sp.			●			
Callyspongia sp.				●	●	
Callyspongia vaginalis					●	
Chondrilla nucula					●	
Cinachyra alloclado			●		●	
Cinachyra sp.			●	●		
Cliona celata					●	
Cliona delitrix				●	●	
Cliona lampa		●	●	●	●	
Cliona lampa forma flavida					●	
Cliona lampa forma lampa					●	
Cliona sp.	●		●	●	●	
Cliona viridis					●	
Desmapsamma sp.					●	
Diplastrella sp.				●		
Encrusting sponges			●	●		
Eurospongia rosea					●	
Euryspongia rasea					●	
Geodia sp.				●		
Haliclona sp.					●	
Halicona(purple)					●	
Halicona(red)					●	
Haloclona rubens					●	
Holopsamma sp.				●		
Iotrochota birotulata					●	
Ircinia campana			●	●	●	
Ircinia fasciculata				●		
Ircinia felix				●		
Ircinia strobilina				●	●	
Ircinia variabilis			●			
Lotrochota birotulata					●	
Microciona sp.				●	●	
Microciona spinosa			●			
Monanchora unguifera					●	
Niphates digitalis					●	
Niphates erecta				●	●	
Niphates sp.				●	●	
Niphates(purple)					●	●
Plakortis angulospiculatus						●
Poecilosclerida spp.				●		
Pseudoaxinella lunaecharta			●	●	●	
Sigmadocia caerulea				●		
Spheciospongia vesparium				●	●	
Spheciospongia vesparsa					●	
Spinosella plicifera					●	
Spinosella vaginalis					●	

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Spirastrella coccinea					●	
Spongia sp.					●	
Teichaxinella sp.					●	
Tethya sp.			●		●	
Ulosa reutzleri					●	
Unidentified orange sponge				●		
Unidentified red sponge			●		●	
Unidentified sponge1	●		●		●	
Unidentified tube-type					●	
Unidentified yellow sponge				●	●	
Verongula sp.			●			
Xestospongia muta					●	
Hydrozoans						
Aglaophenia latecarinata				●		
Aglaophenia sp.					●	
Campanularia marginata					●	
Campanularia sp.					●	
Eudendrium ramosum					●	
Eudendrium sp.					●	
Feather hydroids						●
Hydroida undet. sp.					●	
Lytocarpus philippinus					●	
Millepora alcocornis				●	●	●
Millepora complanata				●		
Millepora sp.					●	
Obelina hyanlina			●			
Pennaria sp.					●	
Sertularia flowersi			●			
Sertuarella sp.					●	
Sertularella speciosa				●		
Thryroscuphus ramosus					●	
Thyroscyphus marginatus					●	
Thyryoscyphus sp.					●	
Unident. branching hydroid					●	
Unidentified hydroid	●		●			
Unidentified star-shaped					●	
Yellow branch hydroid				●		
Platyhelminthes						
Unid *Turbellaria* sp.	●					
Polycladia sp.???		●				
Nematoda						
Unidentified sp.		●				
Sipuncula						
Unidentified sp.		●				
Unidentified sp. 1		●				
Unidentified sp. 2		●				
Unidentified sp. 3		●				
Bryozoans						

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Aetea sica	●		●			
Aetea truncate	●		●			
Aeverrillia armata	●		●			
Aimulosia pusilla			●			
Aimulosia uvulifera			●			
Alcyondium polypylum			●			
Alcyonidium capronae			●			
Alderina smitti			●			
Amathia alternata	●		●			
Amathia distans			●			
Amathia vidovici	●		●			
Anguinella palmata	●		●			
Antropora leucocypha	●		●			
Bartensia minuata			●			
Beania hirtissima			●			
Beania intermedia			●			
Beania klugei	●		●			
Beania mirabilis			●			
Bellulophora bellula			●			
Bowerbankia gracilis	●		●			
Bowerbankia imbricata			●			
Bowerbankia maxima	●		●			
Bryozoan sp.			●			
Bugula minima			●			
Bugula neritina	●		●			
Bugula stolonifera	●		●	●		
Bugula turrita			●			
Bugula uniserialis			●	●		
Caulibugula pearsei			●			
Celleporella carolinensis			●			
Celleporina hassalli			●			
Crisia elongata	●		●			
Cryptosula pallasiana	●		●			
Cupuladria doma			●			
Cymulopora uniserialis			●			
Discoporella umbellata depressa			●			
Discoporella umbellate			●			
Disporella plumose			●			
Drepanophora torquata			●			
Electra bellula			●			
Escharina pesanseris			●			
Exechonella antillea			●	●		
Floridina parvicella			●			
Floridinella typical			●	●		
Hippaliosina rostrigera			●			
Hippoporina verrilli			●			
Hippothoa balanophila			●			
Membranipora arborescens			●			

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Membranipora savarii	●		●			
Membranipora triangularis			●			
Membranipora tuberculata			●			
Microporella umbracula			●			
Nolella stipata	●		●			
Parasmitina nitida			●			
Parasmitina signata			●			
Pasythea tulipifera			●			
Phylactella ais			●			
Phylactellipora aviculifera			●			
Reginella repangulata			●			
Retevirgula caribbea			●			
Savignyella lafontii	●		●			
Schizoporella cornuta	●		●			
Schizoporella rugosa			●			
Schizoporella unicornis			●			
Scrupocellaria regularis			●			
Spathipora brevicauda			●			
Stylopoma spongites			●			
Sundanella sibogae			●			
Synnatum aegyptiacum	●		●			
Thalamoporella floridana	●		●			
Trematooecia psammophila			●			
Trypostega venusta			●			
Tubulanus riceae			●			
Valkeria atlantica			●			
Vibracellina laxibasis			●			
Vittaticella contei	●		●			
Vittaticella uberrima			●			
Watersipora sp.			●	●		
Watersipora subovoidea	●		●		●	
Zoobotryon verticillatum	●		●			
Barnacles						
Tetraclita s. stalactifera	●	●	●	●	●	●
Balanus t. antillensis			●	●		
Megabalanus cocopoma		●	●	●		
Balanus eburneus	●	●	●	●	●	●
Balanus amphitrite	●	●	●	●	●	●
Chthamalus fragilis	●	●	●	●	●	●
Balanus improvisus					●	●
Chthamalus stellatus					●	●
Balanus venustus		●				
Tunicates						
Phallusia nigra				●	●	●
Mogula sp.			●			
Botryllus planus			●	●	●	●
Botrylloides nigrum			●	●	●	●
Didemnum candidum		●				

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Didemnum sp.					●	
Eudistoma capsilatum		●				
Eudistoma obscuratum						
Diplosoma macdonaldi		●				
Diplosoma sp.					●	
Distaplia bermudensis		●				
Aplidium lobatum(?)		●				
Perophora viridis		●				
Trididemnum orbiculatum		●				
Trididemnum savignii		●				
Ecteinascidea turbinata		●				
Didemnum antillensis	●	●	●	●	●	●
Echinoderms						
Echinometra lucunter	●	●	●	●	●	●
Arbacia punctulata		●	●	●		
Eucidaris tribuloides		●	●	●	●	●
Diadema antillarum			●	●	●	●
Lytechinus variagatus			●	●	●	●
Tripneustes ventriculosus		●	●	●	●	●
Holothuria grisea	●	●	●	●		
Davidaster rubiginosa				●		
Nemaster grandis				●		
Amphioholis squamata		●				
Ophiuroidea sp.		●				
Ophiothrix suensonii		●			●	
Dendrochirotida sp.		●				
Cucumariidae sp.		●				
Isostichopus badyonotus					●	
Isostichopus sp.					●	
Unidentified sp.		●				
Nemerteans						
Amphiporus ochraceous			●			
Amphiporus texanus			●			
Baseodiscus delineatus			●		●	●
Emplectonema osceolai						●
Nemertopsis bivittata			●		●	●
Prosorhochmus americanus	●					●
Prosorhochmus belizeanus					●	
Tetrastemma enteroplecta			●		●	
Tetrastemma merula			●		●	
Tetrastemma worki			●		●	
Tubulanus pellucidus			●			
Zygonemertes cocacola			●			
Zygonemertes simonae			●			
Zygonemertes virescens			●			
Crustaceans						
Metapenaeopsis goodei			●			
M. smithi			●			

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Penaeus sp.			●			
Sicyonia dorsalis			●			
Neopontonides beaufortensis			●			
Periclimenes americanus			●			
Alpheus armillatus			●			
A. bouvieri		●	●			
A. formosus			●			
A. heterochaelis			●			
A. malleator			●			
A. normanni			●			
A. nuttingi			●			
A. paracrinitl/s			●			
A. peasei			●			
A. thomasi			●			
A. viridari			●			
Metalpheus rostratipes			●			
Synalpheus brevicarpus			●			
S. cf. cl/racaoensis			●			
S. fritzmuelleri			●			●
S. minl/s			●			
S. townsendi			●			
Synalpheus sp. A			●			
Lysmata intermedia			●			
L. wurdemanni			●			
Processa fimbriata			●			
Microprosthema semilaeve			●			
Panulirus argus			●			
Upogebia aftinis			●			
Megalobrachium poeyi			●			
M. soriatum			●			
Pachycheles monilifer		●	●			●
Petrolisthes armatus			●			
P. galathinus		●	●			
Calcinus tibicen			●			
Clibanarius antillensis			●			
C. sclopetarius			●			
C. tricolor			●			
C. vittatus			●			
Paguristes tortugae			●			
Petrochirus diogenes			●			
Pagurus carolinensis			●			
P. pollicaris			●			
Lepidopa benedicti			●			
Emerita talpoida			●			
Uhlias limbatus			●			
Arenaeus cribrarius			●			
Callinectes ornatus			●			
C. similis			●			

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Cronius ruber			●			
Portunus gibbesii			●			
Platyactaea setigera			●			
Cataleptodius floridanus			●			
Eriphia gonagra			●			
Eurypanopeus abbreviatus			●		●	
E. depressus			●			
E. dissimilis			●			
Hexapanopeus angustifrons			●			
H. paulensis Rathbun			●			
Menippe mercenaria		●	●			
M. nodifrons	●	●	●			
Micropanope granulimanus			●			
Panopeus bermudensis		●	●			
P. herbstii		●				
P. occidentalis		●				
Pilumnus dasypodus			●			●
P. lacteus Stimpson			●			
P. sayi Rathbun			●			
Xantho denticulatus			●			
Pachygrapsus transverses	●	●	●			
Plagusia depressa		●	●			
Gecarcinus lateralis			●			
Ocypode quadrata			●			
Acanthonyx petiverii			●			
Chorinus heros			●			
Epialtus bituberculatus			●			
E. dilatatus			●			
Macrocoeloma subparallelum			●			
Microphrys bicornutus			●			
M. antillensis			●			
Mithrax acuticornis			●			
M. coryphe			●			
M. forceps			●		●	
M. hispidus			●			
M. pleuracanthus			●			
M. ruber			●			
M. verrucosus			●			
Pelia mutica			●			
Pitho lherminieri			●			
Podochela riisei			●			
P. sidneyi			●			
Stenorhynchus seticornis			●			
Gonodactylus bredini			●			
G. oerstedii			●			
G. spinulosus			●			
Pagurus brevidactylus			●			
Paguristes hummi			●			

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
Tanystylum orbiculare			●			
Periclimenes americanus			●			
Paradella dianae		●	●			
Sphaeroma walkeri		●	●			
Paranthura infundibulata		●	●			
Jaeropsis sp.		●	●			
Excorallana spp.		●	●			
Hyale perieri		●	●			
Elasmopus pectinicrus		●	●			
Ampithoe pollex		●	●			
Corophium acutum		●	●			
Ericthonius sp.		●	●			
Jassa cf. falcata		●	●			
Ampithoe longimana		●	●			
Stenothoe georgiana		●	●			
Podocerus brasiliensis		●	●			
Cymadusa compta		●	●		●	
Percnon gibbesi			●			
Pagurus carolinensis					●	
Mollusca						
Aplysia dactylomela				●	●	
Anachis avara				●		
Anachis floridana			●	●	●	
Anachis lafresnayi			●	●		
Arca zebra					●	
Astrea tuber			●	●	●	
Atrina ridgida				●		
Barleeia tincta			●	●		
Cerithium litteratum					●	
Chama macreroohvilla					●	
Chlamus senits)					●	
Costoanachis sp.					●	
Lima pellucid					●	
Loligo pealeii ?					●	
Cyprea sp.			●	●	●	
Erato maugeriae			●	●		
Fissurella barbadensis			●	●		
Lamellaria perspicua			●	●		
Lucapinella limatula			●	●		
Mitrella argus			●	●		
Morula didyma					●	
Nudibranchia sp.			●	●		
Octopus vulgaris					●	
Petaloconchus sp.					●	
Petaloconchus varians	●		●	●		
Phidiana lynceus			●	●		
Pisania tinctus			●	●		
Stramonita (Thais) haemostoma			●	●		

Table B.1. (Continued).

Taxon	Brevard	Indian River	St. Lucie	Martin	Palm Beach	Broward
floridana						
Thais rustica				●	●	
Tricolia affinis pterocladica			●	●		
Aplysia dactylomela				●	●	
Littorina sp.				●		
Iselica fenestrate				●	●	
Barbatia dominensis			●	●		
Isognomon radiatus			●	●		
Musculus lateralis			●	●		
Ostrea equestris	●		●		●	
Ostrea sp.					●	
Sphenia antillensis			●	●		
Anomia sp.				●	●	
Pteria sp.				●	●	
Pteria columbus					●	
Hiatella solida				●		
Octopus briareus				●		
Octopus joubini				●		
Sepioteuthis sepioidea				●	●	
Phoronida						
Unidentified species			●	●		

Studies reviewed to compile this species list were Nelson (1989), Coastal Science Associates, Inc. (2000), M. Rice, personal communication, Rudolph (1977), Gore et al. (1978), Nelson (1988), Nelson and Demetriades (1992), Watanabe (2002), Watanabe and Young (2006), McCarthy (2001). Eckelbarger (1976), Reed et al. (1982), Reed (1982), Reed and Mikkelsen (1987), SFCREMP (2007), Prekel at al. (2008), Jaap (1984), Vare (1991), J. Beal, pers. comm., McCarthy, pers. obs., Coastal Planning & Engineering, Inc. (2006), Brooke and Young (2005), Vargas-Angel et al. (2006), Brooke (2002), Cummings (1994), McCarthy (2006, 2008), Walton Smith et al. (1950), Multer and Milliman (1967), Van Montfrans (1981), Applied Biology, Inc. (1979), Petuch (1987), Coastal Science Associates, Inc. (2000), Continental Shelf Associates, Inc. (1984), Continental Shelf Associates, Inc. (2002a,b, 2003, 2004, 2005b, 2006), Department of Environmental Resources Management (1993, 1994), Harris and Lee (2006), U.S. Army Corps of Engineers (2003b), U.S. Army Corps of Engineers (2002), Kirtley (1966), Moyer et al. (2003), and Winston (1982).

Table B.2. Molluscan community composition and total number of individuals per species collected from 41 quantitative samples of *Oculina varicosa* coral on four reefs off the east Florida coast. Species characterizations (MOE, FOOD, ZOOG, Z) were taken from the literature (sources listed in footnotes) and do not reflect the results of this study unless otherwise noted. ZOOG and Z were assigned only to fully identified species. (— = data unavailable or unknown; * or † preceding species name = abundant [>100 N], or common [10-100 N] species, respectively; * or - in station columns = presence or absence, respectively, in qualitative samples.) (From: Reed and Mikkelsen, 1987).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
Class Gastropoda									
Subclass Prosobranchia									
Order Archaeogastropoda									
Scissurellidae									
Scissurella proxima (Dall, 1927)	F	D	TC	A/B/C	1	0	0	0	1
Fissurellidae									
Diodora arcuata (Sowerby, 1862)	F	H	T	A	0	0	0	4	4
†*D.* cf. *arcuata* (Sowerby, 1862)	F	H	---	---	0	0	II	16	27
D. cayenensis (Lamarck, 1822)	F	H	TN2	A	3	0	0	0	3
D. cf. *cayenensis* (Lamarck, 1822)	F	H	---	---	0	0	1	0	1
D. dysoni (Reeve, 1850)	F	H	T	B	1	0	0	0	1
D. cf. *dysoni* (Reeve, 1850)	F	H	---	---	3	0	0	0	3
D. cf. */isteri* (Orbigny, 1842)	F	H	---	---	0	0	4	0	4
D. sp.	F	H	---	---	7	0	0	1	8
Lucapinella /imatula (Reeve, 1850)	F	H	TC	A/B	1	0	0	0	I
Puncturella sp.	F	H	---	---	---	---	*	---	*
Diodorinae sp. I	F	H	---	---	0	1	1	5	7
Diodorinae sp. 2	F	H	---	---	0	0	3	4	7
Diodorinae sp. 3	F	H	---	---	0	0	0	5	5
Diodorinae sp. 4	F	H	---	---	1	0	0	0	1
Diodorinae sp. 5	F	H	---	---	0	0	1	3	4
Trochidae									
Calliostoma euglyptum (A. Adams, 1854)‖	F	H/O	TC	A	0	0	8	0	8
C. *jujubinum* (Gmelin, 1791)‖	F	D/O	TC	A/B	---	---	*	---	*
C. *pulchrum* (C.B. Adams, 1850)‖	F	D/O	TC	A/B/C	0	0	1	4	5
†C. *roseolum* (Dall, 1880)‖	F	D/O	TC	A/B/C	0	0	0	15	15
†C. sp.	F	---	---	---	1	0	23	48	72
Cyclostrematidae									
†*Arene bairdii* (Dall, 1889)	F	H	TC	B/C	0	0	0	37	37
A. sp.	F	H	---	---	0	0	0	2	2
Turbinidae									
Turbo castanea (Gmelin, 1791)	F	H	TC	A	0	0	1	0	1
Phasianellidae									
Tricolia affinis pterocladica (Robertson, 1958)	F	D/H	T	A	1	0	0	0	1
T. thalassicola (Robertson, 1958)	F	D/H	TC	A/B	0	0	5	0	5
T. sp.	F	D/H	---	---	1	0	3	0	4
Order Mesogastropoda									
Truncatellidae									
Truncatella cf. *scalaris* (Michaud, 1830)	F	?D/H	---	---	1	0	0	0	1
Rissoidae									
Alvania auberiana (Orbigny, 1842)	F	D/H	TC	A	0	0	4	3	7
Barleeia sp.	F	D/H	---	---	1	0	0	0	1
* *Rissoina bouryi* (Desjardin, 1949)	F	H	T	---	102	0	0	0	102
Caecidae									
†*Caecurn pu/chellurn* (Stimpson, 1851)	F	H	TN4	A	11	0	0	0	11
C. sp.	F	H	---	---	3	0	0	0	3
Meioceras cubitatum (Folin, 1868)	F	H	TC	A/B	0	0	3	0	3
M. nitidurn (Stimpson, 1851)	F	H	T	A	2	0	0	0	2
Vitrinellidae									
Macrornphalina palmalitoris (Pilsbry and McGinty, 1950)	F	---	T	B	---	---	*	---	*
**Parviturboides interruptus* (C.B. Adams, 1850)	F	D/H	TC	A/B	1,103	0	0	1	1,104
Cerithiopsidae									
Cerithiopsis bicolor (C.B. Adams, 1845)	?S---S	?P	T	---	0	0	2	0	2
C. flavurn (C.B. Adams, 1850)	?S---S	?P	T	---	0	0	0	7	7
C. io (Dall and Bartsch, 1911)	?S---S	?P	T	---	5	0	0	0	5
C. sp. 3	?S---S	?P	---	---	0	0	0	9	9
C. sp. 4	?S---S	?P	---	---	0	0	1	78	79
C. sp. 5	?S---S	?P	---	---	0	0	1	51	52

Table B.2. (Continued).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
C. sp. 6	?S---S	?P	---	---	0	0	2	4	6
C. sp. 7	?S---S	?P	---	---	1	0	0	0	1
C. sp. 8	?S---S	?P	---	---	1	0	0	0	1
C. sp. 9	?S---S	?P	---	---	0	0	2	0	2
C. Sp. 10	?S---S	?P	---	---	0	0	0	2	2
C. sp.	?S---S	?P	---	---	0	0	0	1	1
Seila adamsi (H.C. Lea, 1845)	?S---S	?P	TN3	A/B	0	0	6	2	8
†*S.* sp. 1	?S---S	?P	---	---	6	0	6	6	18
S. sp. 2	?S---S	?P	---	---	6	0	2	1	9
Turritellidae									
†*Vermicularia spirata* (Philippi, 1836)	E	F	TN3	A	0	0	18	71	89
Turritellidae sp.	E	F	---	---	0	0	1	0	1
Vermetidae									
Serpulorbis decussatus (Gmelin, 1791)	.E	F	TC	A	0	0	5	1	6
Vermetidae sp.	E	F	---	---	0	0	2	0	2
Architectonicidae									
Architectonica peracuta (Dall, 1889)	S---A	C	TC	B	0	0	0	3	3
†*Heliacus bisu/catus* (Orbigny, 1842)	S---A	P/?O	TC	A/B/C	0	0	0	10	10
Mathildidae									
*Mathilda barbadensis (*Dall, 1889)	F	?C	T	B	0	0	0	1	1
Triphoridae									
**Metaxia rugulosa* (C.B. Adams, 1850)	S---S	P	T	A/B	1	0	0	277	278
M. taeniolata (Dall, 1889)	?S---S	?P	M	A/B	---	---	*	*	*
Triphora cf. *lilacina* (Dall, 1889)	?S---S	?P	---	---	0	0	0	1	1
T. cf. *nigrocincta* (C.B. Adams, 1839)	?S---S	?P	---	---	1	0	0	0	1
T. sp. I	?S---S	?P	---	---	1	0	7	0	8
†*T.* sp. 2	?S---S	?P	---	---	0	0	5	61	66
T: sp. 3	?S---S	?P	---	---	0	0	1	1	2
T. sp. 4	?S---S	?P	---	---	1	0	0	0	1
T. sp. 5	?S---S	?P	---	---	0	0	1	8	9
T. sp. 6	?S---S	?P	---	---	0	0	0	3	3
T. sp. 7	?S---S	?P	---	---	0	0	0	2	2
T. sp. 8	?S---S	?P	---	---	0	0	0	1	1
T. sp. 9	?S---S	?P	---	---	0	0	0	2	2
†T. sp.	?S---S	?P	---	---	0	0	1	0	10
Pyramidellidae									
† *Fargoa bushiana* (Bartsch, 1909)	?S---M, P	?P	M3	A	15	0	8	36	59
F. dianthophila (Wells and Wells, 1961)	S---P	P	M3	A	2	0	5	1	8
†*Odostomia# somersi* (Verrill and Bush, 1900)	?S---M, P	?P	T	---	0	0	0	18	18
O. sp. 2	?S---M, P	?P	---	---	2	0	1	1	4
O. sp. 3	?S---M, P	?P	---	---	2	0	1	2	5
†*O.* sp. 4	?S---M, P	?P	---	---	0	0	4	10	14
†*O.* sp. 5	?S---M, P	?P	---	---	0	0	1	67	68
†*O.* sp. 6	?S---M, P	?P	---	---	22	0	0	0	22
†*O.* sp. 7	?S---M, P	?P	---	---	18	0	0	0	18
O. sp. 8	?S---M, P	?P	---	---	4	0	0	0	4
O. sp. 9	?S---M, P	?P	---	---	2	0	0	0	2
O. sp. 10	?S---M, P	?P	---	---	0	0	1	5	6
O. sp. 11	?S---M, P	?P	---	---	1	0	0	1	2
O. (Ivara) sp.	?S---M, P	?P	---	---	1	0	0	0	1
Peristichia sp.	?S---M, P	?P	---	---	1	0	0	0	1
Pyramidella sp.	?S---M, P	?P	---	---	---	---	*	---	*
Turbonilla cf. *pilsbryi* (Bush, 1899)	?S---M, P	?P	---	---	0	0	0	1	1
†*T.* sp. 1	?S---M, P	?P	---	---	0	0	9	14	23
†*T.* sp. 2	?S---M, P	?P	---	---	0	0	0	15	15
T. sp. 3	?S---M, P	?P	---	---	2	0	1	1	4
T. sp. 4	?S---M, P	?P	---	---	0	0	0	1	1
T. sp. 5	?S---M, P	?P	---	---	0	0	0	3	3
T. sp. 6	?S---M, P	?P	---	---	3	0	1	0	4
T. sp.	?S---M, P	?P	---	---	1	0	0	2	3
Epitoniidae									
Epitonium sp.	?S---A	?P	---	---	0	0	0	1	1
Eulimidae									
Melanella cf. *arcuata* (C.B. Adams, 1850)	S---E	P	---	---	1	0	0	5	6
†*M.sp.1*	S---E	P	---	---	6	0	0	19	25
M. sp.	S---E	P	---	---	3	0	0	0	3

Table B.2. (Continued).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
Calyptraeidae									
†*Crepidula aculeata* (Gmelin, 1791)	E	F	TC	A/B	12	0	3	0	15
C. fornicata (Linne, 1758)	E	F	TN6	A	0	0	2	0	2
†*C.* cf. *fornicata* (Linne, 1758)	E	F	---	---	2	0	9	1	12
C. plana (Say, 1822)	E	F	TN6	A	0	1	0	0	1
C. sp.	E	F	---	---	0	1	0	1	2
Capulidae									
Capulus cf. *incurvatus* (Gmelin, 1791)	S---M	F	---	---	0	0	0	1	1
Cypraeidae									
Cypraea sp.	F	C/H	---	---	---	---	*	---	*
Triviidae									
Erato maugeriae (Gray, 1832)	S---T	C	TC	A/B	---	---	*	---	*
Trivia maltbiana (Schwengel and McGinty, 1942)	S---T	C	TC	A/B	0	0	3	0	3
Velutinidae									
Lamellaria leucosphaera (Schwengel, 1942)	F	C	T	A	1	0	0	0	1
L. perspicua (Linne, 1758)	F	C	T	A/B	---	---	*	---	*
L. sp.	F	C	---	---	1	0	0	0	1
Marsenina sp.	F	C	---	---	0	0	1	0	1
?M. sp.	F	C	---	---	0	0	0	2	2
Naticidae									
†*Haliotinella patinaria* (Guppy, 1876)	F	C	T	A	0	0	0	12	12
Cymatiidae									
Cymatium sp.	F	C	---	---	---	---	*	---	*
Order Neogastropoda									
Muricidae									
Aspella senex (Dall, 1903)	F	C	TC	---	---	---	*	---	*
Favartia cellulosa (Conrad, 1846)	F	C	TC	A	---	---	*	---	*
Murexiella levicula (Dall, 1889)	F	C	TC	A	0	0	0	3	3
M. macgintyi (M. Smith, 1938)	F	C	T	A/B	0	0	1	0	1
Thais haemastoma floridana (Conrad, 1837)	F	C	TC	A	---	---	*		*
Trachypollia didyma (Schwengel, 1943)	F	C	TC	A/B	0	0	0	1	1
T. sp.	F	C	---	---	0	0	0	1	1
Coralliophilidae									
Coralliophila cf. *aberrans* (C.B. Adams, 1850)‖	S---C	O	---	---	---	---	*	---	*
C. sp. 1	S---C	O	---	---	0	4	3	0	7
C. sp. 2‖	S---C	O	---	---	0	0	0	9	9
C. Sp.	S---C	0	---	---	0	0	1	0	1
†*Latiaxis mansfieldi* (McGinty, 1940)	S---C	0	T	B	0	0	2	15	17
Buccinidae									
Antillophos adelus (Schwengel, 1942)	F	C/S	T	---	0	0	0	7	7
Colubraria lanceolata (Menke, 1828)	F	C/S	TC	A	0	0	0	1	1
C. swifti (Tryon, 1881)	F	C/S	T	A	---	---	*	---	*
Engina corinnae (Crovo, 1971)	F	C/S	T	A	0	0	4	1	5
E. turbinella (Kiener, 1835)	F	C/S	T	A	1	0	0	0	1
†*Pisania tincta* (Conrad, 1846)	F	C/S	TC	A	8	4	3	7	22
Columbellidae									
†*Astyris lunata* (Say, 1826)	F	C	TN3	A	3	0	10	1	14
Costoanachis floridana (Rehder, 1939)	F	C	TC	A	4	0	0	0	4
C. ?hotesseriana (Orbigny, 1842)	F	C	---	---	0	0	0	1	1
**C. lafresnayi* (Fischer and Bernardi, 1856)	F	C	TN5	B	0	0	34	585	619
**C. sparsa* (Reeve, 1859)	F	C	T	A/B	14	2	87	55	158
Costoanachis sp.	F	C	---	---	0	0	4	0	4
†*Nassarina glypta* (Bush, 1885)	F	C	TC	A/B	0	2	9	36	47
Steironepion minor (C. B. Adams, 1845)	F	C	TC	A/B/C	---	---	*	---	*
S. monilifera (Sowerby, 1844)	F	C	T	A/B	1	0	0	0	1
Suturoglypta iontha (Ravenel, 1861)	F	C	TC	A/B	0	0	3	0	3
Nassariidae									
Nassarius consensus (Ravenel, 1861)	F	C/S	TC	A	0	0	2	1	3
N. cf. *consensus* (Ravenel, 1861)	F	C/S	---	---	0	0	0	7	7
N. sp.	F	C/S	---	---	0	0	2	0	2
Fasciolariidae									
Fasciolaria tulipa (Linne, 1758)	F	C	TC	A	---	---	*	---	*
Latirus cariniferus (Lamarck, 1822)	F	C	T	A	---	---	*	---	*
cf. *Pleuroploca gigantea* (Kiener, 1840)	F	C	TC	A	---	---	*	---	*
Marginellidae									
Marginella lavalleeana (Orbigny, 1842)	F	?C/S	TC	A/B	2	0	0	0	2
Volvarina avena (Kiener, 1834)	F	C/S	TC	A	---	---	---	*	*
Marginellidae sp.	F	?C/S	---	---	0	1	0	0	1

Table B.2. (Continued).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
Costellariidae									
Pusia sykesi (Melvill, 1925)	F	C	T	A/B			*		*
Turridae									
Cryoturris fargoi (McGinty, 1955)	F	C	TC	A/B	---	---	---	*	*
Daphnella morra (Dall, 1881)	F	C	TC	*A/B/C*	0	0	0	1	1
Glyphoturris rugirima (Dall, 1889)	F	C	TC	*A/B/C*	0	0	0	3	3
Ithycythara auberiana (Orbigny, 1842)	F	C	T	---	0	0	2	0	2
Nannodiella melanitica (Bush, 1885)	F	C	TC	A/B	---	---	*	---	*
Pilsbryspira albomaculala (Orbigny, 1842)	F	C	T	A	---	---	*	---	*
P. jayana (C.B. Adams, 1850)	F	C	---	---	---	---	*	---	*
P. monilis (Bartsch and Rehder, 1939)	F	C	T	A	2	0	0	0	2
Splendrillia sp.	F	C	---	---	---	---	*	---	*
Subclass Opisthobranchia									
Opisthobranchia sp. I	F	---	---	---	0	0	1	0	1
Opisthobranchia sp. 2	F	---	---	---	0	0	0	1	1
Opisthobranchia sp. 3	F	---	---	---	0	0	1	0	1
Order Cephalaspidea									
Atyidae									
Atys caribaea (Orbigny, 1841)	F	?C	TC	A/B	0	0	0	1	1
Haminoea sp.	F	C	---	---	1	0	0	0	1
Retusidae									
Pyrunculus caelatus (Bush, 1885)	F	?C	TC	A/B	0	0	1	0	1
Order Ascoglossa									
Ascoglossa sp.	F	H	---	---	1	0	0	0	1
Order Notaspidea									
Pleurobranchidae									
Pleurobrachidae sp.	F	C	---	---	3	0	0	0	3
Order Thecosomata									
Cavoliniidae									
Creseis acicula (Rang, 1828)	F	F	TN	P	0	0	0	1	1
Order Nudibranchia									
Goniodorididae									
?Okenia sp.	F	C					*		*
Polyceratidae									
?Polycera Sp.	F	C	---	---	0	0	0	6	6
Dotoidae									
Doto sp.	?S---H	?P	---	---	1	0	0	0	1
Aeolidiidae									
Spurilla neapolitana ?var. *braziliana* (MacFarland, 1909)	F	C	T	---	0	0	0	1	1
Gastropoda sp. 1	F	---	---	---	0	0	0	1	1
Gastropoda sp. 3	F	---	---	---	0	0	1	1	2
Gastropoda sp.	F	---	---	---	0	2	1	1	4
Class Scaphopoda									
Order Dentaliida									
Dentaliidae									
Dentalium sp.	F	F	---	---	---	---	*	---	*
Order Gadilida									
Siphonodentaliidae									
Cadulus sp.	F	F	---	---	0	0	0	2	2
Class Polyplacophora									
Order Ischnochitonida									
Ischnochitonidae									
Ischnochiton sp.	F	H	---	---	1	0	0	0	1
Callistoplacidae									
Callistochiton sp.	F	H	---	---	0	0	0	1	1
Chaetopleuridae									
Chaetopleura apiculala (Say, 1830)	F	H	TN3	A	0	0	0	6	6
C. cf. *apiculata* (Say, 1830)	F	H	---	---	0	0	0	7	7
Order Acanthochitonida									
Acanthochitonidae									
Acanthochitona sp.	F	H	---	---	1	0	0	1	2
Class Bivalvia									
Order Nuculoida									
Nuculidae									
Nucula ?aegensis (Jeffreys, 1879)	F	D	---	---	0	0	0	1	1
N. crenulata (A. Adams, 1856)	F	D	TC	A	0	0	0	4	4

Table B.2. (Continued).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
Nuculanidae									
Portlandia minuscula (Verrill and Bush, 1897)	F	D	M3	C	0	0	0	3	3
Order Arcoida									
Arcidae									
Anadara floridana (Conrad, 1869)	E	F	TC	A	0	0	0	1	1
†_Arca imbricata_ Bruguiere, 1789	E	F	TC	A	35	2	1	0	38
A. zebra (Swainson, 1833)	E	F	TC	A	0	1	0	1	2
Arcopsis adamsi (Dall, 1886)	E	F	TC	A	0	0	0	7	7
Barbatia cancellaria (Lamarck, 1819)	E	F	TC	A	0	1	0	0	1
*_B. candida_ (Helbling, 1779)	E	F	TC	A	1	1	8	157	167
†_B. domingensis_ (Lamarck, 1819)	E	F	TC	A	16	0	0	0	16
Order Mytiloida									
Mytilidae									
†_Gregariella coralliophaga_ (Gmelin, 1791)	N	F	TC	A	6	4	8	81	99
Lioberus castaneus (Say, 1822)	E	F	T	A	---	---	*	---	*
†_Lithophaga aristata_ (Dillwyn, 1817)	N	F	TC	A/B/C	3	7	18	0	28
*_L. bisulcata_ (Orbigny, 1842)	N	F	TC	A/B	150	6	94	17	267
Modiolus cf. _modiolus squamosus_ (Beauperthuy, 1967)	E	F	---	---	---	---	*	---	*
†_Musculus lateralis_ (Say, 1822)	E	F	TC	A	8	2	3	1	14
Mytilidae sp.	E	F	---	---	0	0	0	2	2
Order Pterioida									
Pteriidae									
Pteria colymbus (Roding, 1798)	E	F	TC	A	1	0	0	3	4
Isognomonidae									
Isognomon bicolor (C.B. Adams, 1845)	E	F	T	A	1	0	0	0	1
Order Limoida									
Limidae									
Lima lima (Linne, 1758)	E	F	TC	A/B	1	0	0	0	1
Order Ostreoida									
Ostreidae									
_Ostrea permollis (_Sowerby, 1841)	E	F	TC	A	0	0	0	2	2
†_Ostreola equestris_ (Say, 1834)	E	F	TN1	A	18	0	0	6	24
†Ostreidae sp.	E	F	---	---	0	0	0	13	13
Gryphaeidae									
*_Neopycnodonte cochlear_ (Poli, 1795)	E	F	TC	A/B/C	2	0	3	161	166
Plicatulidae									
†_Plicatula gibbosa_ (Lamarck, 1801)	E	F	TC	A	0	0	0	18	18
Pectinidae									
*_Chlamys benedicti_ (Verrill and Bush, 1897)	E	F	TC	A	0	0	26	93	119
Lyropecten nodosus (Linne, 1758)	E	F	TC	A	---	---	*		*
Pectinidae sp.	E	F	---	---	0	0	0	1	1
Anomiidae									
Anomia simplex (Orbigny, 1842)	E	F	TN3	A	1	0	0	1	2
Pododesmus rudis (Broderip, 1834)	E	F	TC	A	2	0	1	4	7
Order Hippuritoida									
Chamidae									
†_Chama congregata_ (Conrad, 1833)	E	F	TC	A	1	4	10	2	17
C. _florida_ (Lamarck, 1819)	E	F	T	A/B	0	1	0	1	2
C. _lactuca_ (Dall, 1886)	E	F	TC	A	0	0	3	5	8
C. _macerophylla_ (Gmelin, 1791)	E	F	TC	A	0	1	0	1	2
C. _sarda_ (Reeve, 1847)	E	F	T	B	0	1	0	0	1
C. sp.	E	F	---	---	0	0	0	1	1
Pseudochama radians (Lamarck, 1819)	E	F	TC	A/B	2	0	0	0	2
Order Veneroida									
Lucinidae									
†_Parvilucillu mulLilineata_ (Tuomey and Holmes, 1857)	F	F	TC	A/B	0	0	0	14	14
Thyasiridae									
Thyasira flexuosa (Montagu, 1803)	F	F	B7	A/B	0	0	0	1	1
Ungulinidae									
Diplodonta punctata (Say, 1822)	F	F	TC	A/B/C	---	---	---	*	*
Diplodonta sp.	F	F	---	---	2	0	0	2	4
Leptonidae									
Montacuta sp.	S---E	F	---	---	0	0	0	1	1
Leptonidae sp.	?S---E	F	---	---	1	0	1	2	4

Table B.2. (Continued).

	MOE*	FOOD†	ZOOG‡	Z§	6 m	27 m	42 m	80 m	Total
Lasaeidae									
Aligena cf. *texasiana* (Harry, 1969)	?S---E, P	F	---	---	1	0	0	0	1
A. sp.	?S---E, P	F	---	---	1	0	0	0	1
Erycina sp.	?S---?	F	---	---	0	0	0	6	6
Kellia suborbicularis (Montagu, 1803)	F	F	B	A	0	0	2	3	5
K. ?suborbicularis (Montagu, 1803)	F?	F	---	---	2	0	0	0	2
†*K.* sp.	?S---?	F	---	---	5	0	2	4	11
Lasaeidae sp.	?S---?	F	---	---	1	0	0	6	7
Condylocardiidae									
Carditopsis smithii (Dall, 1896)	F	F	T	A	2	0	0	0	2
Crassatellidac									
Crassinella lunulata (Conrad, 1834)	F	F	TN3	A/B	0	0	3	1	4
Cardiidae									
Cerastoderma cf. *pinnatulatum* (Conrad, 1831)	F	F	---	---	1	0	0	0	1
Tellinidae									
Tellina cf. *squamifera* (Deshayes, 1855)	F	D	---	---	1	0	0	0	1
†*T.* cf. *sybaritica* (Dall, 1881)	F	D	---	---	2	0	5	6	13
T. sp.	F	D	---	---	1	0	1	0	2
Vesicomyidae									
Calyptogena sp.	F	F	---	C?	1	0	0	0	1
Veneridae									
**Chione grus* (Holmes, 1858)	F	F	TC	A	110	8	30	1	149
Cyclinella tenuis (Recluz, 1852)	F	F	TN1	A/B	7	0	0	0	7
Veneridae sp.	F	F	---	---	0	0	3	2	5
Petricolidae									
Rupellaria typica (Jonas, 1844)	N	F	TC	A	2	0	0	0	2
Order Myoida									
Myidae									
Sphenia antillensis (Dall and Simpson, 1901)	E	F	T	A	9	0	0	0	9
Gastrochaenidae									
†*Gastrochaena hians* (Gmelin, 1791)	N	F	TC	---	1	0	4	41	46
†*Rocellaria ovata* (Sowerby, 1834)	N	F	TC	---	3	0	6	12	21
Hiatellidae									
Hiatella arctica (Linne, 1767)	E	F	B	A/B/C	0	0	2	7	9
Pholadidae									
**Dip/othyra smithii (*Tryon, 1862)	N	F	TN3	A	207	0	0	0	207
Subclass Anomalodesmata									
Order Pholadomyoida									
Lyonsiidae									
Lyonsia beana (Orbigny, 1842)	E	F	TC	A	3	0	4	0	7
Bivalvia sp. 2	---				1	0	0	0	1
Bivalvia sp. 4	---				1	1	0	4	6
Bivalvia sp. 7	---				0	0	0	1	1
Bivalvia sp. 8	---				0	0	0	1	1
Bivalvia sp.	---				3	2	1	3	9
Class Cephalopoda									
Subclass Coleoidea									
Order Teuthoidea									
Ommastrephidae									
*Illex oxygoneus (*Roper, Li and Mangold, 1969)	F	C	TN3	B/C	---	---	---	*	*
Order Octopoda									
Octopodidae									
Octopus sp.	F	C	---	---	0	1	0	0	1

* Mode of existence (MOE): E = epilithic; F = free-living; N - endolithic; S = symbiotic (-A = with anthozoan; -C = with scleractinian coral; E = with echinoderm: -H = with hydroid; -M = with mollusk; -P = with polychaete; -S = with sponge; -T = with tunicate [ascidian]).

† Feeding type (FOOD): C = carnivore; D = detritivore/deposit-feeder; F = filter-feeder/suspension-feeder/mucoid entrapper; H = herbivore; 0 = corallivore; P = parasite; S = scavenger.

‡ Zoogeographical distribulion (ZOOG): B = Areticlboreal; M - temperate; T = tropicaVstenothermic; TC = IropicaVto Cape Hatteras; TN = tropical/to nonh of Cape Hatteras [I = to Virginia; 2 - to Maryland; 3 = to Massachusetts; 4 = 10 New Hampshire; 5 = to Maine; 6 = to Canada; 7 = to Greenland].

§ Depth (Z): A = shallow (0-50 m); B = shelf (50-200 m); C - deep (>200 m); P - pelagic.

║ FOOD catcagorization of these species reflects the results of gut analyses in the present study.

\# *Odostomia* is placed in quotes according to Robertson's (1978) findings that odostomoid species require biological data (e.g., on spermatophores, reproductive anatomy insufficient here for proper generic placement).

Table B.3. Decapod crustacean community composition and total number of individuals per species on east Florida *Oculina* coral reefs (From: Reed et al., 1982).

	6 m Fort Pierce Inlet	27 m North of Fort Pierce	42 m South of Fort Pierce St. Lucie Inlet	80 m Offshore East of Fort Pierce
Families	11	9	10	10
Genera	21	13	13	20
Species	30	14	16	24
Endemic Species	16	1	3	9
Mean Species	7.9	6.8	5.9	10.9
Mean Individuals	39.8	18.5	47	87.6
Mean Coral Size (g)	521.8	131.4	1,193.50	1,613.60
Percent Dead Coral	23.3	18.3	21.9	69.9
Number Samples	15	4	13	10
Dominance (D_1)	40	32	72	18
Dominance (D_2)	55	45	79	34
Species				
1. *Pagurus carolinensis*	6	24	439	160
2. *Megalobrachium soriatum*	238	9	41	22
3. *Pagurus piercei*	0	0	37	142
4. *Synalpheus townsendi*	1	8	31	112
5. *Galathea rastrata*	0	1	5	142
6. *Micropanope scuptipes*	1	1	0	137
7. *Pachycheles monilifer*	89	0	0	2
8. *Mithrax forceps*	81	8	0	0
9. *Thor manningi*	49	3	0	29
10. *Pseudomedaeus distinctus*	0	0	11	33
11. *Synalpheus fritzmuelleri*	30	0	0	0
12. *Pseudomedaeus agassizii*	0	0	10	19
13. *Nematopaguroides pusillus*	0	0	0	29
14. *Periclimenes iridescens*	2	1	25	0
15. *Synalpheus minus*	19	0	0	0
16. *Micropanope barbadensis*	0	0	0	17
17. *Synalpheus* cf. *townsendi*	15	0	1	0
18. *Pelia mutica*	4	9	1	1
19. *Euchirograpsus americanus*	1	0	0	10
20. *Stenorhynchus seticornis*	0	3	3	5
21. *Pilumnus dasypodus*	10	0	0	0
22. *Petrolisthes galathinus*	9	0	0	0
23. *Periclimenes rathbunae*	8	0	0	0
24. *Troglocarcinus corallicola*	6	0	1	0
25. *Periclimenaeus atlanticus*	6	0	0	0
26. *Domecia acanthophora*	5	0	0	0
27. *Micropanope nuttingi*	0	3	0	2
28. *Mithrax acuticornis*	0	0	1	3
29. *Paguristes tortugae*	2	2	0	0
30. *Nanoplax xanthiformis*	0	0	0	4
31. *Lobopilumnus agassizii*	2	1	0	0

Table B.3. (Continued).

	6 m Fort Pierce Inlet	27 m North of Fort Pierce	42 m South of Fort Pierce St. Lucie Inlet	80 m Offshore East of Fort Pierce
32. Synalpheus cf. *fritzmuelleri*	3	0	0	0
33. Alpheus cristulifrons	2	0	0	0
34. Gonodactylus bredini	2	0	0	0
35. Scyllarus depressus	0	0	2	0
36. Pinnixa retinens	0	0	2	0
37. Parapinnixa hendersoni	0	0	0	2
38. Porcellana sigsbeiana	1	0	0	0
39. Periclimenes americanus	1	0	0	0
40. Epialtus sp.	1	0	0	0
41. Alpheus formosus	1	0	0	0
42. Eucratopsis crassimanus	1	0	0	0
43. Thor dobkini	1	0	0	0
44. Paractaea rufopunctata nodosa	0	1	0	0
45. Stenocionops furcata	0	0	1	0
46. Periclimenes longicaudatus	0	0	0	1
47. Solenopagurus lineatus	0	0	0	1
48. Automate evermanni	0	0	0	1
49. Aplheus cf. amblyonyx	0	0	0	1
50. Pinnotheres sp.	0	0	0	1

Appendix C

Table C.1. Fish species recorded from natural nearshore hardbottom habitats in southeast and east central Florida.

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
GINGLYMOSTOMATIDAE	*Ginglymostoma cirratum*	1				●	●	●														●
CARCHARHINIDAE	*Carcharhinus brevipinna*	3					●		●							●			●			
	Carcharhinus leucas	1					●		●							●			●			
	Carcharhinus limbatus	1					●		●							●			●			
	Carcharhinus plumbeus	1					●		●							●			●			
SPHYRNIDAE	*Sphyrna mokarran*	6					●		●							●			●			
RHINOBATIDAE	*Rhinobatos lentiginosus*	5				●			●							●			●			
DASYATIDAE	*Dasyatis americana*	4				●			●							●			●			
MYLIOBATIDAE	*Aetobatus narinari*	4				●			●							●			●			
UROLOPHIDAE	*Urobatis jamaicensis*	4				●		●							●				●			
MOBULIDAE	*Manta birostris*	4		●					●							●						
ELOPIDAE	*Megalops atlanticus*	3					●		●							●			●			
MURAENIDAE	*Echidna catenata*	3				●		●							●						●	●
	Enchelycore carychroa	2						●							●						●	
	Gymnothorax funebris	1					●	●							●						●	●
	Gymnothorax moringa	1					●	●						●							●	●
	Gymnothorax vicinus	4					●	●							●						●	●
	Muraena miliaris	3					●	●						●							●	●
OPHICHTHIDAE	*Ahlia egmontis*	2					●	●						●							●	●
	Myrichthys breviceps	4					●	●							●						●	
	Myrichthys ocellatus	5					●	●							●						●	
CLUPEIDAE	*Harengula clupeola*	1		●					●				●									●
	Harengula humeralis	1		●					●				●									●
	Harengula jaguana	1		●					●				●									●
	Opisthonema oglinum	1		●					●				●									●
	Sardinella aurita	1		●					●			●										●
ENGRAULIDAE	*Anchoa cubana*	1		●					●			●										●
	Anchoa hepsetus	1		●					●			●										●
	Anchoa lyolepis	1		●					●			●										●
SYNODONTIDAE	*Synodus foetens*	4					●	●		●			●									●
	Synodus intermedius	4					●	●						●								●
GOBIESOCIDAE	*Gobiesox strumosus*	1				?		●			●											●
ATHERINIDAE	*Membras martinica*	1		●					●			●										●
	Menidia peninsulae	1		●					●			●										●

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
BELONIDAE	*Tylosurus crocodilus*	5					●	●						●	●	●			●			
HEMIRAMPHIDAE	*Hemiramphus brasiliensis*	3		●					●			●									●	
	Hyporhamphus unifasciatus	1		●					●			●									●	
HOLOCENTRIDAE	*Holocentrus adscensionis*	4					●	●		●		●	●									●
	Holocentrus rufus	3				●		●					●								●	
	Myripristis jacobus	4					●	●		●		●	●						●			
AULOSTOMIDAE	*Aulostomus maculatus*	1					●			●				●	●	●			●			
FISTULARIIDAE	*Fistularia tabacaria*	4					●			●						●			●			
SYNGNATHIDAE	*Cosmocampus albirostris*	4				●		●				●										●
	Cosmocampus elucens	4				●		●				●										●
	Scorpaena grandicornis	5					●	●			●	●	●									●
SCORPAENIDAE	*Scorpaena plumieri*	1					●	●			●	●	●									●
TRIGLIDAE	*Prionotus scitulus*	4					●	●					●								●	
DACTYLOPTERIDAE	*Dactylopterus volitans*	4				●			●						●						●	
CENTROPOMIDAE	*Centropomus undecimalis*	3					●		●					●	●				●			
SERRANIDAE	*Centropristis striata*	1					●			●	●	●	●									●
	Cephalopholis fulva	5					●			●	●	●	●					●				
	Cephalopholis cruentata	4					●			●	●	●	●					●				
	Diplectrum formosum	4					●			●	●	●	●								●	
	Epinephelus adscensionis	4					●			●	●	●	●					●				
	Epinephelus itajara	1					●	●			●	●	●									●
	Epinephelus morio	1					●	●			●	●	●									●
	Hypoplectrus puella	4				●		●			●										●	
	Hypoplectrus unicolor	4				●		●			●										●	
	Mycteroperca bonaci	3					●			●					●						●	
	Mycteroperca microlepis	1					●			●					●						●	
	Mycteroperca phenax	4					●			●					●						●	
	Rypticus maculatus	1				●																
	Rypticus saponaceus	4				●																
	Rypticus subbifrenatus	6				●																
	Serranus baldwini	4					●	●			●	●										●
	Serranus subligarius	1					●	●			●	●										●
	Serranus tigrinus	4					●	●		●	●	●										●

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
APOGONIDAE	*Apogon binotatus*	1		●				●			●	●										●
	Apogon maculatus	1		●				●			●	●										●
	Apogon pseudomaculatus	1		●				●			●	●										●
	Apogon townsendi	4		●				●			●	●										●
	Astrapogon puncticulatus	4					●	●			●	●										●
	Astrapogon stellatus	2					●	●			●	●										●
	Phaeoptyx conklini	2		●				●			●	●										●
CARANGIDAE	*Caranx bartholomaei*	1					●		●	●	●	●	●	●							●	
	Caranx crysos	1					●		●	●	●	●	●								●	
	Caranx hippos	1					●		●	●	●	●	●								●	
	Caranx latus	1					●		●	●	●	●	●								●	
	Caranx ruber	1					●		●	●	●	●	●								●	
	Chloroscombrus chrysurus	1		●					●		●	●									●	
	Decapterus punctatus	3		●					●	●	●	●	●								●	
	Elagatis bipinnulata	4					●		●				●								●	
	Oligoplites saurus	1					●		●			●	●								●	
	Selar crumenophthalmus	3		●					●	●	●	●	●								●	
	Selene setapinnis	1				●	●		●			●	●								●	
	Selene vomer	1				●	●		●			●	●								●	
	Seriola dumerili	4					●		●	●			●	●								
	Seriola rivoliana	5					●		●	●			●	●								
	Trachinotus carolinus	3				●	●		●	●			●								●	
	Trachinotus falcatus	3				●			●	●			●								●	
	Trachinotus goodei	6				●	●						●								●	
LUTJANIDAE	*Lutjanus apodus*	1					●			●	●	●	●								●	
	Lutjanus analis	1					●			●	●	●	●	●							●	
	Lutjanus griseus	1					●		●	●	●	●	●								●	
	Lutjanus jocu	1					●		●			●	●								●	
	Lutjanus mahogoni	1					●			●	●	●	●							●		
	Lutjanus synagris	1					●			●	●	●	●							●		
	Ocyurus chrysurus	1					●			●	●	●								●		
	Rhomboplites aurorubens	6					●			●	●	●								●		
LOBOTIDAE	*Lobotes surinamensis*	5					●				●	●										●

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
GERREIDAE	*Eucinostomus argenteus*	1				●				●	●	●										●
	Eucinostomus gula	1				●				●	●	●										●
	Eucinostomus jonesii	4				●				●	●	●									●	
	Eucinostomus lefroyi	4				●				●	●										●	
	Eucinostomus melanopterus	6				●				●	●	●									●	
	Gerres cinereus	1				●		●			●	●	●									●
HAEMULIDAE	*Anisotremus surinamensis*	1				●				●	●	●	●									●
	Anisotremus virginicus	1				●				●	●	●	●								●	
	Haemulon album	4				●			●		●	●	●					●				
	Haemulon aurolineatum	1				●				●	●	●	●									●
	Haemulon carbonarium	1				●				●	●	●	●								●	
	Haemulon chrysargyreum	1		●		●				●	●	●	●								●	
	Haemulon flavolineatum	1				●				●	●	●	●								●	
	Haemulon macrostomum	3				●				●	●	●	●								●	
	Haemulon melanurum	1				●				●	●	●	●					●				
	Haemulon parra	1				●				●	●	●	●									●
	Haemulon plumierii	1				●				●	●	●	●									●
	Haemulon sciurus	3				●				●	●	●	●								●	
	Haemulon striatum	4		●					●		●	●									●	
	Orthopristis chrysoptera	5				●				●	●	●	●								●	
SPARIDAE	*Archosargus probatocephalus*	1				●			●					●					●			
	Archosargus rhomboidalis	4				●			●			●	●								●	
	Calamus bajonado	1				●			●			●	●								●	
	Calamus calamus	4				●		●		●		●	●	●							●	
	Calamus penna	4				●		●		●		●	●	●							●	
	Diplodus argenteus	1	●	●		●		●		●	●	●	●	●								●
	Diplodus holbrooki	1	●	●		●		●		●	●	●	●	●								●
	Lagodon rhomboides	5				●			●				●						●			
POLYNEMIDAE	*Polydactylus virginicus*	6				●																

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
SCIAENIDAE	*Bairdiella sanctaeluciae*	1				●		●		●	●	●	●									●
	Cynoscion nebulosus	6				●	●		●				●						●			
	Equetus acuminatus	1				●		●		●												●
	Equetus umbrosus	1				●		●		●												●
	Sciaenops ocellatus	6				●	●		●				●	●					●			
	Odontoscion dentex	1				●		●		●												●
	Umbrina coroides	3				●		●														●
MULLIDAE	*Mulloidichthys martinicus*	3				●		●				●	●								●	
	Pseudupeneus maculatus	1				●		●				●	●								●	
PEMPHERIDAE	*Pempheris schomburgkii*	1		●				●			●	●										●
KYPHOSIDAE	*Kyphosus sectatrix/incisor*	1	●							●		●	●	●							●	
EPHIPPIDAE	*Chaetodipterus faber*	1				●			●	●			●	●								●
CHAETODONTIDAE	*Chaetodon capistratus*	5				●		●			●	●								●		
	Chaetodon ocellatus	3				●		●		●												●
	Chaetodon sedentarius	4				●		●			●	●								●		
	Chaetodon striatus	5				●		●		●												●
POMACANTHIDAE	*Holacanthus bermudensis*	3				●		●		●	●	●	●	●						●		
	Holacanthus ciliaris	1				●		●		●	●	●	●	●						●		
	Pomacanthus arcuatus	1				●		●		●	●	●	●	●						●		
	Pomacanthus paru	2				●		●		●	●	●	●	●						●		
POMACENTRIDAE	*Abudefduf saxatilis*	1				●		●		●	●	●	●									●
	Abudefduf taurus	1				●		●		●	●	●	●									●
	Microspathodon chrysurus	4	●							●	●	●								●		
	Stegastes adustus	5	●					●		●	●	●										●
	Stegastes diencaeus	4	●					●		●	●	●										●
	Stegastes leucostictus	1	●					●		●	●	●										●
	Stegastes partitus	2	●	●				●		●	●	●								●		
	Stegastes planifrons	4	●								●	●								●		
	Stegastes variabilis	1	●					●			●	●										●
OPISTOGNATHIDAE	*Opistognathus aurifrons*	5		●				●				●										●
	Opistognathus macrognathus	1		●				●				●										●
	Opistognathus whitehursti	4		●				●				●										●

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
MUGILIDAE	*Mugil cephalus*	3			●				●				●						●			
	Mugil curema	3			●				●				●						●			
LABRIDAE	*Bodianus rufus*	3				●		●		●	●	●								●		
	Doratonotus megalepis	1				●				●	●	●									●	
	Halichoeres bivittatus	1				●		●		●	●	●										●
	Halichoeres cyanocephalus	4				●				●	●	●									●	
	Halichoeres garnoti	4				●				●	●	●								●		
	Halichoeres maculipinna	1				●		●		●	●	●										●
	Halichoeres poeyi	1				●		●		●	●	●										●
	Halichoeres radiatus	1				●		●		●	●	●								●		
	Lachnolaimus maximus	3				●			●				●								●	
	Thalassoma bifasciatum	1				●		●		●	●	●										●
	Xyrichtys martinicensis	4				●		●		●	●	●										●
	Xyrichtys splendens	4				●		●		●	●	●										●
SCARIDAE	*Cryptotomus roseus*	4	●																			
	Scarus coelestinus	1	●					●			●	●	●	●						●		
	Scarus coeruleus	4	●					●			●	●	●	●						●		
	Scarus guacamaia	1	●					●			●	●	●	●						●		
	Scarus iseri	5	●					●		●	●	●								●		
	Scarus taeniopterus	4	●					●		●	●	●								●		
	Scarus vetula	3	●					●			●	●	●	●						●		
	Sparisoma atomarium	1	●					●			●	●								●		
	Sparisoma aurofrenatum	3	●					●		●	●	●										●
	Sparisoma chrysopterum	3	●					●		●	●	●								●		
	Sparisoma radians	4	●					●			●	●										●
	Sparisoma rubripinne	1	●					●			●	●	●	●								●
	Sparisoma viride	3	●					●			●	●	●	●								●
URANOSCOPIDAE	*Astroscopus y-graecum*	1					●	●						●								●
TRIPTERYGIIDAE	*Enneanectes pectoralis*	5				●		●			●	●										

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
LABRISOMIDAE	*Labrisomus bucciferus*	3					●	●			●	●										●
	Labrisomus gobio	1					●	●			●	●										●
	Labrisomus kalisherae	4					●	●			●	●										●
	Labrisomus nuchipinnis	1					●	●			●	●	●									●
	Malacoctenus aurolineatus	5				●		●			●	●										●
	Malacoctenus macropus	1				●		●			●	●										●
	Malacoctenus triangulatus	1				●		●														●
	Paraclinus fasciatus	4				●																
	Paraclinus marmoratus	4				●																
	Paraclinus nigripinnis	1				●																
	Starksia ocellata	1				●																
CHAENOPSIDAE	*Acanthemblemaria aspera*	4		●				●			●	●										●
	Acanthemblemaria spinosa	4		●				●			●	●										●
	Emblemaria pandionis	4		●				●			●	●										●
DACTYLOSCOPIDAE	*Dactyloscopus crossotus*	1				●																
	Platygillellus rubrocinctus	2				●																
BLENNIIDAE	*Entomacrodus nigricans*	1	●																			
	Hypleurochilus bermudensis	4	●					●			●	●										●
	Ophioblennius macclurei	4	●																			
	Parablennius marmoreus	2	●					●			●	●										●
	Scartella cristata	1	●					●			●	●										●
CALLIONYMIDAE	*Paradiplogrammus bairdi*	5				●		●			●	●										●
ELEOTRIDAE	*Erotelis smaragdus*	3				●																
GOBIIDAE	*Coryphopterus dicrus*	4				●		●			●	●										●
	Coryphopterus eidolon	5				●		●			●	●										●
	Coryphopterus glaucofraenum	3				●		●			●	●										●
	Coryphopterus personatus	4				●		●			●	●										●
	Ctenogobius saepepallens	4				●					●	●										●
	Elacatinus macrodon	5				●					●	●										●
	Elacatinus oceanops	5				●		●			●	●										●

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
GOBIIDAE (continued)	*Gnatholepis thompsoni*	4				●		●			●	●										●
	Gobiosoma grosvenori	4				●																
	Microgobius carri	4		●							●	●										●
	Nes longus	3				●					●	●										●
	Priolepis hipoliti	4				●																
PTERELEOTRIDAE	*Ptereleotris calliurus*	4		●																		
	Ptereleotris helenae	4		●																		
ACANTHURIDAE	*Acanthurus bahianus*	1	●					●		●	●	●	●	●								●
	Acanthurus chirurgus	1	●					●		●	●	●	●	●								●
	Acanthurus coeruleus	1	●					●		●	●	●	●	●								●
SPHYRAENIDAE	*Sphyraena barracuda*	1					●	●		●		●	●	●	●	●			●			
	Sphyraena guachancho	1					●	●		●		●	●									●
	Sphyraena picudilla	5					●	●		●		●	●									●
POMATOMIDAE	*Pomatomus saltatrix*	1					●		●						●				●			
	Scomberomorus maculatus	5							●					●	●				●			
SCOMBRIDAE	*Scomberomorus regalis*	3					●		●					●	●				●			
BOTHIDAE	*Bothus lunatus*	5				●		●				●	●	●								●
BALISTIDAE	*Balistes capriscus*	4				●		●		●		●	●	●							●	
	Balistes vetula	4				●				●		●	●						●			
	Canthidermis sufflamen	5				●		●		●		●	●	●							●	
FILEFISHES	*Aluterus schoepfii*	4				●		●		●		●	●	●							●	
	Aluterus scriptus	3				●		●		●		●	●	●							●	
	Cantherhines macrocerus	5				●		●		●											●	
	Cantherhines pullus	3				●		●		●											●	
	Monacanthus tuckeri	5				●		●		●		●	●									●
	Stephanolepis hispidus	1				●		●		●											●	
OSTRACIIDAE	*Acanthostracion polygonia*	4				●		●				●									●	
	Acanthostracion quadricornis	3				●		●		●												●
	Lactophrys bicaudalis	4				●		●			●											●
	Lactophrys trigonus	4				●		●		●												●
	Lactophrys triqueter	1				●		●			●											●
TETRAODONTIDAE	*Canthigaster rostrata*	3				●		●			●	●										●
	Sphoeroides spengleri	2				●		●				●										●
	Sphoeroides testudineus	5				●		●				●	●								●	

Table C.1. (Continued).

Family	68 Families; 257 spp.	Orig. Cite*	Trophic Category**					Residency			Size Classes						Life Stages					
	Species		H	Pl	D	I	P	Res	Tran	Onto	<2	2 to 10	10 to 25	25 to 50	50 to 100	>100	NS	J	A	NS & J	J & A	All
DIODONTIDAE	*Chilomycterus schoepfii*	4				●		●				●									●	
	Diodon holocanthus	4				●		●				●	●								●	
	Diodon hystrix	3				●		●				●	●								●	
Totals			31	36	2	123	74	136	57	104	130	166	100	41	18	14	0	5	#	24	72	114

* Original Citation: 1 = Gilmore, 1977; Gilmore et al., 1981. 2 = Futch and Dwinell, 1977. 3 = Lindeman, 1997a; Lindeman and Snyder, 1999. 4 = Baron et al., 2004. 5 = Continental Shelf Associates, Inc., 2006. 6 = Present study.

** H = Herbivore; Pl = Planktivore; D = Detritivore; I = Invertivore; P = Piscivore.

Appendix D

Table D.1. Examples of controlled experiments and field analyses of similar nearshore hardbottom genera/species invertebrate mesograzers.

Mesograzer Species	Artificial Diet	Foraging Items	Location/ Species Range	Study
Littorina obtusata	*Ascophyllum nodosum*	*Ascophyllum nodosum* (ungrazed beforehand)	North Atlantic	Amsler (2001)
Idotea granulose	*Ascophyllum nodosum*	*Ascophyllum nodosum*	North Atlantic	Amsler (2001)
Placida dendritica (sea slug)	---	*Codium setchellii* (Trowbridge, 1992)	SE Australia	Arrontes (1999)
Ampithoe valida	*Gracilaria* (Nicotri, 1977)	---	North Atlantic	Arrontes (1999)
Idotea baltica	*Gracilaria* (Nicotri, 1977)	---	North Atlantic/ Baltic Sea	Arrontes (1999)
Littorina littorea	*Fucus distichus* (Van Alstyne, 1990)	---	North Atlantic	Arrontes (1999)
Hyale media	*F. vesiculosus*	---	Brazil	Arrontes (1999)
Acmaea inessa	---	Kelp: *Egregia laevigata* (Setchell)	Brazil	Arrontes (1999)
Scurria scurra	---	*Lessonia nigrescens* (Munoz and Santelices, 1989)	Brazil	Arrontes (1999)
Hyale	---	*Iridaea laminarioides*	Brazil	Arrontes (1999)
Aplysia californica	*Gracilaria ferox*	---	California	Barile et al. (2004)
Mytilus californiannus	---	*Odonthalia floccose*	Oregon rocky intertidal	Bracken (2004)
Diadema antillarum (urchin)	*Dictyota pulchella, Lobophora variegate*	---	---	Mumby et al. (2006)
Ampithoe longimana	*Ulva* sp. (*Enteromorpha*), *Hypnea musciformis, Gracilaria tikvahiae.* Did not discriminate	Red, brown, green algae. Diatoms (Cousfield, 1973; Nelson, 1979b; Hay, 1987, Duffy and Hay, 1991b, 1994) detritus	Western Atlantic	Cruz-Rivera and Hay (2001)
Elasmopus levis	*Ulva* sp. (*Enteromorpha*), *Hypnea musciformis, Gracilaria tikvahiae*	---	East coast	Cruz-Rivera and Hay (2001)
Gammarus mucronatus	*Ulva* sp. (*Enteromorpha*), *Hypnea musciformis, Gracilaria tikvahiae.*	Gut content, detritus, diatoms epiphytic algae, macroalgae (Sanders, 1962; Zimmerman, 1979; Duffy and Hay, 1994)	East coast	Cruz-Rivera and Hay (2001)
Ampithoe marcuzii	---	*Sargassum filipendula*	North Carolina	Duffy (1990)
Caprella penantis	---	*Sargassum filipendula*	North Carolina	Duffy (1990)
Jassa falcate	---	*Sargassum filipendula*	North Carolina	Duffy (1990)
Erichthonius brasiliensis	*Sargassum filipendula*	---	North Carolina	Duffy (1990)
Elysia rufescens, ornata	*Bryopsis pennata*	---	Hong Kong	Cruz-Rivera and Paul (2006)
Menaethius monoceros (crab)	*Acanthophora spicifera*	---	Hong Kong	Cruz-Rivera and Paul (2006)

Table D.1. (Continued).

Mesograzer Species	Artificial Diet	Foraging Items	Location/ Species Range	Study
Ampithoe longimana	---	*Sargassum filipendula, Dictyota, Padina gymnospora, Hypnea musciformis, Chondria dasyphylla, Ulva*	North Carolina	Duffy and Hay (2000)
Ampithoe longimana	*Dictyota dichotoma, Calonitophyllum medium* (foliose) *Hypnea musciformis and Chondria dasyphylla, Sargassum filpendula*	---	North Carolina	Duffy and Hay (1991)
Limpets, coiled snails, chitons, isopods, amphipods, gastropod	---	*Halimeda opuntia, Amphiroa sp, Bryothamnion seaforthii* occur on more coral and rock. Sandy areas had *Gracilaria, Halymenia, Solieria*. Herbivore abundance correlate with patterns.	Oregon	Gaines and Lubchenca (1982)
Ilyanassa obsolete	*Ulva lactuca*	---	Hog Island Bay, Virginia	Giannotti and McGlathery (2001)
Littorina striata	No-choice lab experiments - high feeding *Ulva (Enteromorpha muscoides), Ulva rigida.* Little to no feeding on *Alsidium corallinum* and *Laurencia corrallopsis*	---	Gran Canaria (where algae was collected)	Granado and Caballero (2001)
Osilinus atratus	No-choice lab experiments - high feeding *Ulva (Enteromorpha muscoides), Ulva rigida.* Little to no feeding on *Alsidium corallinum* and *Laurencia corrallopsis*	---	Gran Canaria (where algae was collected)	Granado and Caballero (2001)
Grapsus albolineatus		Filamentous algae	Hong Kong	Kennish (1997)
Grapsus albolineatus	*Enteromorpha clathrata, Hincksia mitchelliae, Chaetomorpha antennina* (filamentous which was eaten). *Dermonema frappieri, Pterocladia tenuis, Porphyra suborbiculata, Ulva fasciata, and Endarachne Binghamiae* (foliose which wasn't eaten)	---	Hong Kong	Kennish and Williams (1997)
Viviparus viviparous	*Chatophora incrassata, Chateophora pisiformis, Cladophora, Coleochaete pulvinata, Coleochaete scutata, mougeoutia, Oedogonium, Spirogyra tenuissima, Cyanos Anabaena,* and different families of *Rivulariacea, cyanophyta (12), Bacillariophyceae*	---	Sweden	Liess and Kahlert (2007)

Table D.1. (Continued).

Mesograzer Species	Artificial Diet	Foraging Items	Location/ Species Range	Study
Littorina brevicula and *Haliotis discus*	Ecklonia cava	---	Sangju, South Korea	Molis et al. (2006)
Diadema antillarum Philippi	*Halimeda opuntia, Lobophora variegata, Sargassum* sp., *Galaxaura* sp.	---	Discovery Bay, Jamaica	Solandt and Campbell (2001)
Acmaea testudinalis	*Clathromorphum circumscription*	---	Subarctic western North Atlantic	Steneck (1982)
Molluscs (divided by radulae-type)	*Cladophora, Polysiphonia, Ulva, Porphyra, Chondrus, Gigartina, Laminaria, Fucus, Corallina, Bossiella, Lithothamnium, Clathromorphum*	---	Maryland	Steneck and Watling (1982)
Sea urchins *S. franciscanus,* *S. drobachiensis, S. purpuratus*	*Nereocystis* (liked), *Costaria,* *L. saccharina, Callophyllis flabellulata, M. fuscum, A. cribrosum A. fimbriatum* (disliked)	---	San Juan Island and Washington coast	Vadas (1977)
Strongylocentrotus purpuratus (urchin), *Lacuna porrecta, Tegula funebralis* (snails), *Idotea wosnesenskii* (isopod)	Kelps Brown algae*: Fucus gardneri and F. spiralis*	---	Boiler Bay, Oregon	Van Alstyne et al. (1999)
Ampithoe ramondi	*Bryopsis hypnoides, Centroceras clavulatum, Ceramium flaccidum, Derbesia vaucheriaeformis, Enteromorpha prolifera (Ulva), Giffordia rallsiae, Polysiphonia havanensis*	---	Washington, D.C.	Brawley and Adey (1980)

Table D.2. Summary of the most frequently found macroalgae divisions and functional form groups that were found in foraging samples of juvenile green turtles (*Chelonia mydas*) and herbivorous fishes. Turtle data are derived from studies listed in **Appendix A**, **Table A.1**, and fish data are from footnoted sources on **Table D.3**.

Number of Herbivorous Fish/Turtles	Macroalgal Species	Functional Form Group	Division
9	*Ceramium* sp.	Filamentous	Rhodophyta
9	*Ulva* sp.	Sheet	Chlorophyta
8	*Polysiphonia* sp.	Filamentous	Rhodophyta
8	*Lyngbya* sp.	Filamentous	Cyanobacteria
7	*Centroceras* sp.	Filamentous	Rhodophyta
7	*Dictyota* sp.	Sheet	Phaeophyta
6	*Amphiroa* sp.	Jointed-calcareous	Rhodophyta
6	*Coelothrix* sp.	Coarsely-branched (fish only)	Rhodophyta
6	*Herposiphonia* sp.	Coarsely-branched	Rhodophyta
6	*Hypnea* sp.	Filamentous	Rhodophyta
6	*Laurencia* sp.	Coarsely-branched	Rhodophyta
5	*Gelidium* sp.	Coarsely-branched	Rhodophyta
5	*Caulerpa* sp.	Coarsely-branched	Chlorophyta
5	*Jania* sp.	Jointed-calcareous	Rhodophyta

Table D.3. Macroalgal species in foraging samples from different population studies conducted on juvenile green turtles (*Chelonia mydas*) and herbivorous fish populations on nearshore hardbottom habitat. Data are derived from **Appendix A**, **Table A.1** and footnoted sources.

Macroalgal Species	*Chelonia mydas*	*Acanthurus*	*Scartella*	*Entomacrodus*	*Ophioblennius*	*Kyphosus*	*Holocanthus*	*Pomocanthus*	*Abudefduf*	*Microspathodon*	*Stegastes*	*Sparisoma*	*Archosargus*	*Diplodus*	*Lagodon*
Acanthophora muscoides	√				√										
Acanthophora sp.			√									√			
Acanthophora spicifera	√														
Agardhiella subulata	√														
Amphiroa fragillisma											√				
Amphiroa rigida	√														
Amphiroa sp.		√	√		√				√						
Asteromenia (Fauchea peltata)	√														
Avrainvillea sp.											√				
Bostrichia sp.	√														
Botryocladia occidentalis	√														
Botryocladia sp.	√					√									
Bryocladia cuspidata	√														
Bryopsis pennata									√						
Bryopsis sp.		√	√						√						
Bryothamnion seaforthii	√														
Bryothamnion sp.	√					√									
Callithamnion sp.					√										
Caulerpa cupressoides								√							
Caulerpa mexicana	√														
Caulerpa microphysa	√														
Caulerpa peltata	√														

Table D.3. (Continued).

Macroalgal Species	*Chelonia mydas*	*Acanthurus*	*Scartella*	*Entomacrodus*	*Ophioblennius*	*Kyphosus*	*Holocanthus*	*Pomocanthus*	*Abudefduf*	*Microspathodon*	*Stegastes*	*Sparisoma*	*Archosargus*	*Diplodus*	*Lagodon*
Caulerpa prolifera	√														
Caulerpa racemosa	√							√							
Caulerpa sertularioides								√							
Caulerpa sp.		√	√					√	√						
Caulerpa taxifolia	√							√							
Centroceras clavulatum	√							√		√					
Centroceras sp.		√							√		√	√			
Ceramium byssoideum										√					
Ceramium sp.	√	√	√			√			√		√	√	√		
Chaetomorpha linum	√														
Chaetomorpha sp.	√								√						
Champia parvula									√						
Champia sp.									√						
Chondria dasyphylla	√														
Chondria sp.	√					√			√						
Chondrocanthus acicularis	√														
Cladophora catenata	√														
Cladophora delicatula									√						
Cladophora sp.	√	√										√			
Codium isthmocladum								√							
Codium sp.	√														
Coelothrix irregularis										√	√				
Coelothrix sp.		√						√	√			√			
Colpomenia sp.								√							
Cryptonemia crenulata								√							
Dascycladus vermicularis	√														
Dasya pedicillata	√														
Dasya sp.	√														
Dictyopteris delicatula	√							√	√						
Dictyopteris plagiogramma									√						
Dictyopteris sp.	√					√		√							
Dictyospareia sp.	√	√													
Dictyota bartayresii								√			√				
Dictyota dentata									√						
Dictyota divaricata									√						
Dictyota sp.	√	√	√			√		√							
Digenia sp.						√									
Dudresyna crassa	√														
Ectocarpus sp.		√													
Enteromorpha sp.		√													
Erythrotrichia carnea	√														
Eucheuma nudum	√														
Eucheuma sp.		√				√									
Galaxaura sp.		√													
Gelidiaceae	√														
Gelidiella sp.	√					√									
Gelidium americanum	√														

Table D.3. (Continued).

Macroalgal Species	*Chelonia mydas*	*Acanthurus*	*Scartella*	*Entomacrodus*	*Ophioblennius*	*Kyphosus*	*Holocanthus*	*Pomocanthus*	*Abudefduf*	*Microspathodon*	*Stegastes*	*Sparisoma*	*Archosargus*	*Diplodus*	*Lagodon*
Gelidium pusillum	√														
Gelidium rigidulum										√					
Gelidium sp.	√	√				√						√			
Gracilaria armata	√														
Gracilaria blodgettii	√														
Gracilaria mammillaris	√														
Gracilaria sp.	√					√									
Gracilaria tikvahiae	√														
Gracilaria verrucosa	√														
Halimeda discoidea	√														
Halimeda sp.	√	√													
Halymenia florisia	√							√							
Herposiphonia sp.		√		√	√					√	√	√			
Hypnea cervicornis	√														
Hypnea cornuta	√														
Hypnea musciformis	√							√							
Hypnea sp.	√	√	√			√		√							
Hypnea spinella	√								√						
Hypnea valentiae	√														
Jania adherens	√										√				
Jania rubens									√						
Jania sp.	√	√				√			√						
Laurencia corallopsis	√														
Laurencia gemmifera	√														
Laurencia obtusa								√							
Laurencia papillosa									√						
Laurencia poiteaui	√														
Laurencia sp.	√	√	√									√			
Liagora sp.		√													
Lomentaria baileyana	√														
Neomeris annulata	√														
Nitophyllum punctatum	√														
Padina gymnospora								√							
Padina profunda	√														
Padina sp.	√					√									
Penicillus sp.								√							
Pocockiella sp.		√				√		√							
Polysiphonia sp.	√	√		√		√			√	√	√	√			
Polysiphonia subtilissima	√														
Pterocladia sp.	√														
Rhizoclonium sp.	√	√										√	√		
Rhodymenia sp.	√														
Sargassum platycarpum								√							
Sargassum sp.	√	√				√									
Scinaia complanata	√														
Scinaia sp.	√														
Siphonocladus tropicus	√														

Table D.3. (Continued).

Macroalgal Species	*Chelonia mydas*	*Acanthurus*	*Scartella*	*Entomacrodus*	*Ophioblennius*	*Kyphosus*	*Holocanthus*	*Pomocanthus*	*Abudefduf*	*Microspathodon*	*Stegastes*	*Sparisoma*	*Archosargus*	*Diplodus*	*Lagodon*
Solieria sp.	√														
Spatoglossum sp.								√							
Sphacelaria sp.						√									
Spyridia filamentosa	√							√							
Spyridia sp.		√				√									
Turbinaria sp.						√									
Ulva lactuca	√														
Ulva sp.	√	√			√			√		√	√	√	√		
Ulva sp. *(Enteromorpha chaetomorphoides)*	√														
Wrangelia argus										√					
Cyanobacteria															
Anacystis sp.		√			√					√					
Calothrix sp.									√						
Lyngbya majuscula									√						
Lyngbya sp.		√	√	√	√					√	√	√			
Microcoleus sp.		√		√						√	√				
Oscillatoria sp.		√								√					
Phormidium sp.		√			√										
Plectonema nostocorum										√					
Plectonema sp.					√										
Schizothrix arenaria	√														
Schizothrix calcicola	√														
General Categories															
Plants and algae					√[1]										
Algae							√[2]	√[2, 3]					√[7]	√[8]	√[7, 9]
Benthic algae/weeds											√[4]				
Detritus & diatoms											√[5]				
Filamentous green											√[6]				

[1] Dominici-Arosemena and Wolff, 2005.
[2] Hourigan et al., 1989.
[3] Feddern, 1968.
[4] Randall, 1967.
[5] Randall, 1965.
[6] Irvine, 1982 in Gerking ,1994.
[7] Hay and Sutherland, 1988.
[8] Carr and Adams, 1972; Pike and Lindquist, 1994; Hay and Sutherland, 1988.
[9] Motta et al., 1995.