Ecological Dynamics of Livebottom Ledges and Artificial Reefs on the Inner Central West Florida Shelf

Jennifer Maria Dupont
University of South Florida

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Ecological Dynamics of Livebottom Ledges and Artificial Reefs on the Inner Central West Florida Shelf

by

Jennifer Maria Dupont

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
Department of Marine Science
College of Marine Science
University of South Florida

Major Professor: Pamela Hallock Muller, Ph.D.
Walter Jaap, M.S.
Gabriel Vargo, Ph.D.
David Mann, Ph.D.
John Ogden, Ph.D.

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Dedication

This is dedicated to my parents, Lars and Marianne Dupont. Thank you for your love, support, and inspiration. I am the luckiest daughter ever and I hope that I have made you proud.
Acknowledgements

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Ecological Dynamics of Livebottom Ledges and Artificial Reefs on the Inner Central West Florida Shelf

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ABSTRACT

The West Florida Shelf (WFS) is one of the largest and most diversely-used continental shelf/slope systems in the world. The presence of paleoshorelines and scarped hardbottom outcrops (up to 4 m in relief) along the inner shelf (10-30 m depth) provide important habitat for a variety of infaunal, epifaunal, and fish assemblages that contribute to the productivity of the region. This dissertation will present a comprehensive overview of the geological, physical, and chemical settings of the inner West Florida Shelf, with particular focus on biological and ecological community dynamics of epibenthic macroinvertebrates, algae, and fish assemblages. Baseline and comparative data sets are presented in the form of historic and modern species lists, with focus on seasonal and intra-annual variations. Quantitative effects of disturbances (e.g., hurricanes, thermal stresses, and red tides) and subsequent recovery rates are discussed as they periodically perturb inner-shelf systems and can have significant effects on community structure. Benefits of and recommendations for using artificial reefs as restoration tools along the inner shelf, as mitigation for future disturbances, are presented.
1. Overview of the Inner Central West Florida Shelf

1.1. Introduction

The West Florida Shelf (WFS) is one of the largest and most productive continental shelf/slope systems in the world. It covers 170,000 km$^2$ and extends more than 200 km west from the intertidal zone to the 200 m isobath across a very gentle slope ($<<1^\circ$) of ancient limestone platforms (Okey et al. 2004). The WFS is characterized by a range of seafloor morphologies, gradients, sediment types, biotic communities, reefal structures, and paleo sea-level indicators. Due to the importance of continental shelf resources to the State of Florida, including the prolific finfish and shellfish fisheries, offshore petroleum and natural gas exploration, and tourism industries, the WFS has been the subject of numerous studies that address the unique physical oceanographic regimes, chemical influences, and geologic features of the dynamic area.

Despite the robust collection of WFS works, there is a large gap in knowledge of spatial distributions of benthic fauna and flora (epifaunal and infaunal), and temporal changes in these communities. This is surprising considering that a number of the prolific finfish that populate the WFS (and which are the main targets of economically-important commercial and recreational fisheries) utilize virtually every portion of the broad continental shelf at some point in their life history. For example, gag grouper, *Mycteroperca microlepis*, (one of the most valuable finfishes in the southeastern United States and a ubiquitous staple at Florida seafood restaurants), aggregate and spawn in
deep (>70 m) shelf waters (Coleman et al. 1996). Following spawning, females move into shallower waters (<30 m) while males drift off into deeper waters (McGovern et al. 1998). The larvae drift inshore and postlarvae recruit to seagrasses, mangrove creeks, and coastal estuaries and lagoons where they remain for 3-5 months. They then move offshore to reefs and ledges along the WFS (Ross and Moser 1995) where the long-lived, slow-growing, protogynous hermaphrodites mature between year 5 and 6 to repeat the process.

*Mycteroperca microlepis* is one of a number of economically-important fish species that spend time traversing the ledges of the inner WFS. Through various life stages, they rely on limestone outcrops that support diverse livebottom (reef-like) communities and demersal fish assemblages, and which occupy approximately 50% of the inner WFS (Locker et al. 2003; Obrochta et al. 2003; Hine et al. 2008). Although tropical reef development is absent along the inner WFS (Jaap 1984), the extensive systems of scarped hardbottom provide habitat (up to 4m relief) and support an association of hardy corals and other biota. The hardbottoms also provide structure, protection, and abundant food sources for demersal and pelagic fish species that inhabit the areas. Shallow inner WFS livebottom ledges are biotic oases along the otherwise monotonous, quartz-sand dominated inner WFS. Scientists, managers, conservationists, and fishermen need to understand the spatial and temporal dynamics that operate in these areas, as they are inextricably linked to the productivity of the region.

Disturbances, including hurricanes, thermal stresses, and harmful algal blooms, frequently affect areas along the WFS, which are already marginal with respect to a number of first-order determinants for reef assemblages including temperature, nutrient,
light, and aragonite saturation regimes. Acute disturbances, combined with chronic marginal conditions, are important community-structuring forces along the WFS livebottom ledges. Baseline conditions for WFS benthic and fish assemblages must be defined, especially as reefs continue to be stressed by global change including ocean acidification and rising sea level.

In this introductory chapter, I will present a review of the general geological, physical, and chemical processes that influence the biological assemblages of the WFS, with particular focus on inner shelf areas (10-30 m depth) along central west Florida. The studies on natural ledges and artificial reefs (15-20 m depth) presented in this paper were initiated in response to a massive red tide (*Karenia brevis*) and associated hypoxic/anoxic event in 2005 that affected approximately 5,600 km² of benthic communities and fish assemblages along the inner west central Florida shelf (FWRI 2005), causing substantive economic losses in the area. Mass mortalities of invertebrates, fish, and marine mammals, along with adverse human effects (e.g., respiratory issues), quickly raised interest in understanding the dynamics and effects of the harmful algal bloom events that regularly affect the area with varying severity. Interest in mitigating the harmful algal blooms has peaked significantly in response to the massive 2005 red tide, and a number of studies and experiments are currently under way seeking to eliminate these “problem blooms”. The real problem is, however, that there are few studies that quantitatively document the effects of red-tide events and the subsequent recovery processes that take place along the WFS. Vargo et al. (1987) showed that red tides have the potential of contributing greatly to the primary production and annual carbon input along the WFS, and may be essential in ensuring the continued productivity
of the region. In addition, although natural disturbances such as red tides can be detrimental to individuals and communities at large spatial scales (10-1000 km), new substratum becomes available at smaller temporal and spatial scales (Connell 1978). Patches of opportunity are opened for renewal, development, and community succession (Holling 1996) and the current diversity of scarped hardbottoms, and their associated fish assemblages, may depend on the red-tide events.

In the chapters that follow this introduction, I will present a data set on the seasonal dynamics of shallow inner WFS livebottom ledges (abiotic and biotic data). I will quantify the impacts of the 2005 red-tide event on artificial reef communities (epibenthic and demersal fish), and discuss the use of artificial reefs as restoration and conservation tools along the WFS in context of future disturbances including, but not limited to, red tides.

1.2. Geological Setting

There is a robust body of knowledge on the formation and current geological setting of the extensive WFS and I refer readers to review sources including papers in Marine Geology’s Special Issue #200 (2003) and Hine et al. (2008), which provide a comprehensive set of papers that discuss shelf origin, sand ridges, transverse bars, sediment distribution, and many other topics in great detail.

The west-central coast of Florida, extending from Anclote Key in the north to Cape Romano in the south, is an estuarine, barrier island, inner shelf system of marked contrasts, contradictions, and significant characteristics (Hine et al. 2003). I will focus on describing areas along the central west Florida Shelf extending from offshore (~40 km)
Clearwater Beach south to approximately 50 km west of the mouth of Tampa Bay (Fig. 1.1), since sites along this area are discussed in future chapters.

Figure 1.1. Offshore (40-50 km) sites surveyed extending from Clearwater Beach south to the mouth of Tampa Bay. FWRI11, MT, and Station B are natural hardbottom ledges and the GNGS sites are a set of artificial reefs deployed in 2001.

The central WFS is situated between the siliciclastic sand-dominated northwest shelf off the Florida Panhandle, which is significantly influenced by rivers and river deltas, and a carbonate-dominated shelf off the southwest Florida Peninsula, which is characterized by reefs, inner shelf carbonate muds, outer shelf skeletal sands, and lithified submerged calcarenitic (oolitic/skeletal grainstones) paleoshorelines (Hine and Locker 2006). The central WFS is a vast transition zone that has been starved of both siliclastic and carbonate sediments, and is therefore characterized by extensive outcrops of karstified-deformed, biologically-eroded Neogene-Quaternary limestone surfaces. The
outcrops occupy approximately 50% of the shelf seaward of 5 km (Locker et al. 2003) and support a diverse benthic community covering a surface that has sinkholes, elevated terraces, rock ledges, and scarps (Hine and Locker 2006). The outcrops can provide as much as 4 m of relief and are veritable oases of biotic productivity (i.e., epibenthic and fish assemblages) surrounded by mobile sediment.

The surficial sedimentary pattern has been reported to consist of a nearshore band of fine-grained, quartz-rich (>75% quartz) sand, shifting offshore into coarse-grained, carbonate-rich (>75% CaCO3) sand and gravel (Doyle and Sparks 1980), although patchy distributions of other sediment types are common along the central inner WFS (Brooks et al. 2003). The complex and patchy distribution of sediments represents multiple sediment sources. The shallow inner shelf areas (10-30 m depth) that are the focus of the rest of this dissertation are dominated by fine-grain, quartz-rich sands which form a thin veneer (<3 m) over the karstic limestone surface (Doyle and Sparks 1980; Holmes 1981). Biogenically-derived carbonate sediments, primarily of the mollusk-rich foramol assemblage characteristic of non-tropical carbonate systems, are also present in association with hardbottom outcrops. The carbonate component reflects the influence of the living assemblages along the WFS (Brooks et al. 2003). In addition, phosphorite-rich sands that exist as a thin veneer on a majority of the hardbottoms are likely the product of the reworking of underlying phosphate-rich strata. Input rates of all the sources to the surface sediment are unknown although it is unlikely that they are very high as evidenced by the thin and patchy sediment cover (Brooks et al. 2003)

The distribution of hardbottom outcrops and movement of sediments are important aspects in determining where WFS livebottoms can develop. Though there are
a number of abiotic factors that affect the distribution and abundance of benthic invertebrates (i.e., temperature, salinity, turbidity, currents, wave shock, and dispersal barriers), the availability of suitable substrate is the single most important factor in offshore areas along the WFS where abiotic parameters are less variable as compared to nearshore areas (Collard and D’Assaro 1973; Lyons and Collard 1974). Although temperature and salinity fluctuations tend to be limiting in estuarine environments, such parameters become more constant in offshore areas, where bottom substrate and overlying water mass characteristics become critical factors. The availability of suitable substrate (in the form of emergent hardbottom) may be particularly important for larval stages of corals, which depend on the ability of the larvae to identify a suitable substratum for settlement where they can metamorphose and grow colonies (Richmond 1997). Bare substratum may occasionally be generated (i.e., by shifting sediments) and the frequency and duration of exposure of suitable substrate is one limiting factor in epibenthic macroinvertebrate recruitment and colonization. Biological community structuring forces (i.e., predation, competition, physiological tolerance, and population attributes) are also essential in determining the abundance and distribution of benthic invertebrates.

Brooks et al. (2003) studied the patterns and control of surface sediment distribution along the west-central Florida inner shelf and determined that the patchy distribution of sediments indicates that a majority of the sand grains reside in close proximity to where they were originally deposited (e.g., phosphorite-rich sand is consistently found surrounding hardbottoms and the source is attributed to the underlying phosphatic limestone). Typical large-scale sediment distribution mechanisms (storms
and tides) do not appear to regularly influence the regional distribution of sediment. The distribution pattern is more a reflection of sediment source than the mechanism of transport (Brooks et al. 2003). Small-scale, periodic events that mobilize and redistribute sediment (e.g., storms and tides) along the WFS have been reported by Twichell et al. (2003) and are locally important in distributing sediments. These events could be expected to periodically expose or cover local low-relief hardbottom outcrops, affecting the sessile and slower-moving flora and fauna that inhabit the areas (e.g., corals, Porifera, algae, echinoderms, etc.). The small-scale disturbance events are discussed in conjunction with larger-scale disturbances such as hurricanes and red-tide events in Chapter 2.

1.3. Physical Oceanography

The west Florida coast is a low-energy coast with mean annual wave heights of 10-25 cm (Tanner 1960) and tidal ranges < 1 m (Davis 1989). As discussed above, these processes are incapable of regional-scale sediment redistribution. Circulation along the WFS is very complex, driven to different degrees by winds, tides, and buoyancy fluxes, and is also influenced by the prominent GOM circulation feature to 1000 m depth, the Loop Current (He and Weisberg 2003). The Loop Current connects the Yucatan Current to the Florida Current via its northern, clockwise flow into the GOM. Variability in the Loop Current and spin-off eddies have been studied and modeled extensively (Hurlburt and Thompson 1980; He and Weisberg 2003) and may be important factors in determining the ecological diversity of benthic and fish communities throughout the Gulf of Mexico (GOM). Along the eastern GOM, variations in the Loop Current and the
separation of anticyclonic eddies or rings can strongly influence benthic habitats in terms of larval and nutrient supply (Richards et al. 1993).

Tidal currents are relatively weak along the WFS (He and Weisberg 2002) and subtidal sea level and current variations are correlated with synoptic-scale wind variations (Mitchum and Sturges 1982). Monthly mean currents mid-shelf suggest a seasonal cycle with along-shore flows oriented southeast in the spring and northwest in fall (He and Weisberg 2002). The southeastward spring component advects river waters, including from the Mississippi River, forming a low salinity tongue that often carries a chlorophyll plume southward along the WFS.

There appears to be a distinct separation between shelf-break currents (controlled by the Loop Current) and the inner-shelf currents (controlled by local winds), although the unique geometry of the WFS does lend itself to intermittent Loop Current intrusions into shallower isobaths, shoreward of the shelf break (He and Weisberg 2003). These types of intrusions, during upwelling-favorable winds, contribute deep, nutrient-rich waters to areas of the WFS and have been implicated in stimulating blooms of harmful algae such as *Karenia brevis* (see biological section below). He and Weisberg (2003) speculate that bottom topography and coastline geometry are important in generating regions of convergence and divergence along the WFS, and may create upwelling centers. The Florida Big Bend region (where the shelf break is 20 m deeper thereby requiring less upwelling for the deep waters to broach the shallower shelf) is one area that may serve as a communication center between deep GOM waters and the WFS (He and Weisberg 2003). There are numerous other areas that could also contribute to mean seasonal upwelling, greatly influencing nutrient concentrations and productivity all along the WFS.
1.4. Chemical Oceanography

The GOM is traditionally classified as an oligotrophic system (El-Sayed et al. 1972; Biggs 1992), although Muller-Karger et al. (1991) did show, via satellite measurements, that strong seasonal changes in shelf production occur along the WFS. There is evidence, however, that although the open-ocean, pelagic GOM is oligotrophic, the waters that overlie the shallow inner WFS are not. The intermediate nutrient conditions are discussed further in Chapter 2.

Gilbes et al. (2002) attempted to statistically explain cross-shelf and along-shelf differences in nutrients, suspended sediments, and optical properties (diffuse attenuation coefficients) as they related to phytoplankton production and the development of a seasonal plume. They sampled along a transect (3 stations: nearshore, mid-shelf, and offshore) leading southwest from the mouth of Tampa Bay, and combined the results with data from the northwestern GOM. Although their results were obtained from only one cruise, some general trends were presented. Nearshore stations along the WFS were characterized by high nutrient concentrations, low salinities, high suspended sediments, and high diffuse attenuation coefficients. These stations reflected the influence of river discharge from the nearshore, coastal areas. On middle-shelf and offshore stations, an increase in salinity was accompanied by a decrease in nutrients, suspended sediments, and diffuse attenuation coefficients, along with surface pigments, indicating that these areas are less influenced by river inputs. The stations southwest of Tampa Bay (situated closest to those sites discussed in this dissertation) were characterized by \( \text{NH}_4^+ \) concentrations between 0.0 and 0.3 \( \mu \text{M} \), \( \text{NO}_2^- + \text{NO}_3^- \) levels between 0.2 and 0.4 \( \mu \text{M} \), dissolved organic nitrogen (DON) between 6.0 and 9.0 \( \mu \text{M} \), total dissolved nitrogen
(TDN) between 6.0 and 10.0 µM, total particulate nitrogen (TPN) between 1.0 and 2.0 µM, PO₄ between 0.05 and 0.12 µM, dissolved organic phosphorous (DOP) between 0.10 to 0.17 µM, total dissolved phosphorous (TDP) between 0.15 and 0.25 µM, total particulate phosphorous (TPP) between 0.2 and 0.4 µM, and Si at 0.0 µM (Gilbes et al. 2002).

Nitrogen, not phosphorous, is generally the limiting nutrient along the WFS as the shallow shelf is situated in a broad phosphatic province. Normal background nitrate levels in the GOM are <0.1 µM although the combination of upwelling-favorable west winds and the complex physical oceanographic dynamics along the WFS, have caused significant increases in nitrate concentrations (up to 3.31 µM in near-bottom stocks) along the 20 m isobath from the Big Bend area to southeastern regions (Walsh et al. 2003). Nitrogen limitations can also be lifted through actions of diazotrophs such as Trichodesmium (Lenes et al. 2001) and the effects of such blooms are discussed in the biological section below. The effects on benthic communities and fish populations, as well as on phytoplankton assemblages, vary from year to year but can be significant in structuring WFS biotic assemblages.

1.5. Biological Oceanography

1.5.1. Faunal Zones

Much of the WFS may be considered ecotonal between the temperate Carolinian and tropical Caribbean (or West Indian) zoogeographic benthic invertebrate provinces (Hedgpeth 1957; Lyons and Collard 1974), meaning that hardy constituents of both occur across the WFS. One of the primary sources of detailed, exploratory information into WFS biological diversity is compiled in a series of reports titled “Memoirs of the
Project Hourglass was a 28-month program conducted between August 1965 and November 1967. The systematic sampling (fixed locations, gear, and interval) of the Hourglass cruises was designed to provide extensive biological information on organisms in offshore waters in the GOM. Stations were sampled on a monthly basis in an hourglass pattern west of Egmont Key and Sanibel Island in depths of approximately 7, 20, 40, 60, and 80 m. Dredging, exploratory trapping, fishing, night-lighting, plankton and nekton tows, water sampling, Secchi disk measurements, and red-tide sampling were among the techniques used to sample the WFS during the Hourglass cruises.

Lyons and Collard (1974) used the data from >700 dredge and trawl tows from the Hourglass cruises, supplemented with a number of additional collections and SCUBA observations, to tentatively delineate faunal variation zones along the WFS. I say “tentatively” as there are no clear-cut faunal boundaries in the eastern GOM, particularly in offshore deeper waters where temperature and salinity extremes factor less into benthic invertebrate distributional limits as compared to nearshore (estuaries and bays) areas. Substrate is the single most important variable in the distribution of GOM invertebrates. Lyons and Collard (1974) suggest five zones along the WFS based on the degree of faunal change (Figure 1.2). The shoreward zone (0-10 m) extends from the land-water interface to the mean depth where rocky outcrops become important substrate elements. Salinities fluctuate in response to runoff from nearby rivers and bays, and nutrient concentrations are generally higher than those of the rest of the GOM. This zone includes areas such as the Ten Thousand Islands where mangroves and seagrass beds transition into the offshore rocky outcrops. Both tropical and temperate species can be
found in this zone, although the latter tend to be more common. *Astrangia poculata*, an ephemeral coral species that encrusts molluscan shells and shell fragments, occurs in the shoreward zone. Coastal Barrier Islands, the Big Bend, and the Cape San Blas areas are subdivisions of the shoreward zone.

![Figure 1.2](image.jpg)

Figure 1.2. Faunal zone delineations of the WFS (not to scale) as proposed by Lyons and Collard (1974). Chapters 2-5 will concentrate areas along the inner shelf zone (10-30 m).

The second faunal zone is the shallow inner shelf zone (10-30 m depth) where rock substrate allows establishment of a number of tropical species including scleractinians, mollusks, and crustaceans that are common in the shallower waters of the
Florida Keys. Sediments along the shallow shelf are composed primarily of quartz sands with percentages of biogenically derived carbonates increasing seaward. A number of coral genera, including *Stephanocoenia*, *Siderastrea*, *Cladocora*, *Solenastrea*, and *Oculina*, are often observed along the shallow inner shelf. These shallow inner shelf communities are the focus of this paper and historic data from these depths/areas are chosen to represent the historic communities in comparative studies with modern surveys.

The middle shelf I (30-60 m depth) is separated from the shallow shelf by the widespread presence of carbonate sediments and an overlying mass of offshore, blue water. Widespread outcrops, including those of the Florida Middle Grounds, support diverse communities of Loggerhead sponges, corals, and tropical algae. The middle shelf II (60-140 m depth) sediments are almost entirely carbonate, composed of coralline algae, bryozoan and molluscan fragments, with planktic foraminiferal tests beginning to contribute to sediment composition. The sessile epifauna is mainly composed of scattered poriferans, bryozoans, ascidians, and alcyonarians attached to small rocks and shells, along with *Agaricia* spp. assemblages, whose light requirements tend to limit them to approximately 80 m depth. This zone is frequently impacted by the Loop Current.

The last zone is the deep shelf (140-200 m), which overlaps greatly with the middle shelf II. Species diversity tends to decrease with depth and Pequegnat (1970) noted a number of brachyurans most common in depths corresponding to the deep shelf zone. Beyond 200 m, the molluscan-dominated calcareous sands give way to planktonic foraminiferal sands and coccolith muds (calcareous oozes) as the continental slope drops steeply (200-3200 m) to the floor of the GOM.
Like the benthic macroinvertebrate faunal assemblages, the fish assemblages along the WFS are rich, including both Caribbean (tropical) species and warm-temperate (subtropical) species, with the majority of species along the central WFS belonging to the latter group (Springer and Woodburn 1960; Briggs 1973). The mobility of fish species renders faunal zone designation nearly impossible, although Darovec (1995) used similarities in inverse cluster analyses from two different types of sampling gear and two different years to demonstrate the possibility that depth-related fish community structures may exist along the WFS. His work suggests that nearshore/estuarine and middle/offshore shelf fishes may have more restricted ranges whereas shallow inner shelf fishes are more widely dispersed among stations. Further analyses of abiotic parameters indicate that salinity and temperature ranges generally decreases with increasing depth. Darovec (1995) concludes that there is evidence to support the hypothesis that depth, through its effect on bottom temperature and salinity, may be responsible for some of the fish distributions observed by the Hourglass study. This evidence does not, however, preclude support for other hypotheses.

The longitudinal faunal zones of Lyon and Collard (1974) are cross-cut by latitudinal zoogeographic divisions. I propose that the inner WFS can be divided into three latitudinal zones. The first, most southerly zone, is a tropical stenopic zone that extends from the Straits of Florida-Dry Tortugas to the Content Keys (24° 45’ N). Coral genera including *Acropora*, *Diploria*, and *Colpophyllia* are iconic presences in these coral-reef communities. The second zone, the transition zone, extends from the Content Keys to Naples, FL (26° 05’ N). Determining the exact extent of the transition zone is difficult, as it is characterized by the gradual overlap of both tropical and subtropical
flora and fauna; discharges from adjacent rivers (Caloosahatchee River and San Carlos Bay estuary) often affect the development of epibenthic communities. The remaining northern extent of the WFS is a warm temperate-subtropical zone that includes the rocky outcrops and hardbottom communities that are the focus of this dissertation.

1.5.2. The 2005 Red Tide

During summer of 2005, a persistent red tide (harmful algal bloom) and subsequent hypoxic/anoxic conditions negatively affected epibenthic hard-bottom communities in the GOM off west central Florida (Heil 2006). The event was the impetus behind the in-depth temporal and spatial analyses of WFS shallow inner shelf assemblages presented in this paper. The results serve as baseline indices (natural reefs) and potential avenues for mitigation (artificial reefs) in future events. Catastrophic events like the 2005 red tide have been documented since 1881, and observed for an even longer period of time. In 1881, Ernest Ingersoll of the U.S. Fish Commission described the waters of the GOM during the 1878 red tide as “brownish, discolored…thick and glutinous…they lay in streaks drifting with the tide. Everywhere throughout this whole extent of coast [of Florida], except in the mouths of rivers and in shallow bayous, all the forms of sea-life died as if stricken with a plague fatal alike to all, and were drifted upon the beaches in long windrows so dense that near human habitations, men were obliged to unite in burying them to prevent pestilential stench…” (Ingersoll 1881).

The organism responsible for the Florida red tide was originally identified as Gymnodinium brevis (Davis 1948; Steidinger 1975) but was later changed to Karenia brevis (Daubyerg et al. 2000). Numerous questions still exist regarding the physical, chemical, and biological factors that lie behind the red tide blooms and subsequent mass
mortalities of benthic animals and plants, fishes, and marine mammals. One of the best documented red tides occurred in the mid-eastern GOM during the summer of 1971.

Qualitative observations before, during, and after the 1971 event provided insight into effects of a red tide bloom (Smith 1975). After the red tide dissipated in September 1971, researchers assessed the impact on reef fish communities. They estimated that 80-90% of resident reef fish species perished in the event. On inshore reefs (13-18m), fewer than 26% of reef fishes survived the red tide (Smith 1975). Smith reported that invertebrate populations sustained even higher mortality than fish populations. Echinoderms, gastropod mollusks, decapod crustaceans, scleractinian corals, polychaetes, and poriferans all declined drastically (based on qualitative observations). These observations indicate that red tides have the potential to greatly affect community structure and functioning throughout the affected areas.

The GOM physical circulation patterns vary annually and seasonally and there are numerous hypotheses for their contributions to Karenia brevis initiation, transport, and advection/dispersion. The inherent seasonal and annual variability of the Loop Current has been implicated in the initiation of certain red tides. The number and strength of Loop Current meanders varies annually and the eddies and warm filaments associated with the meanders could have entrained within them nutrients and K. brevis cells that are then transported nearshore (Murphy et al. 1975; Tester and Steidinger 1997) where increased nutrient concentration sustain the Karenia brevis growth. Another hypothesis is that nutrient-rich water from the Mississippi River becomes entrained in the Loop Current as a result of seasonal variations in its northward penetration in the GOM (Huh et al. 1981; Gilbes et al. 1996; He and Weisberg 2003). The waters are transported along the WFS
where, again, nutrient limitations are lifted as a result of nearshore/coastal nutrient concentrations.

A third hypothesis that may have specifically applied to the initiation of the 2005 *K. brevis* bloom is the Saharan dust/Iron fertilization/*Trichodesmium* hypothesis (Lenes et al. 2001; Walsh et al. 2003; Walsh et al. 2006). Aeolian dust containing Fe is blown across the Atlantic from the Saharan desert during the summer months. *Trichodesmium* cyanobacteria are Fe-limited diazotrophs that inhabit the offshore oligotrophic waters of the GOM; once their Fe levels are met, they fix atmospheric nitrogen into biologically available forms such as nitrite and nitrate, rendering them usable to dinoflagellates including *K. brevis*. Walsh et al. (2006) discussed the mechanisms involved in the hypothesis and concluded that the amount of nitrogen fixed by the cyanobacteria was sufficient to have sustained the 2005 red tide. The model carried with it a number of stipulations and further investigation is needed to confirm the experimental conditions.

*Karenia brevis* has physiological adaptations that allows it to out-compete other phytoplankton once it emerges from its initiation depth (if that mechanism is indeed responsible for bloom initiation). *Karenia brevis* is positively phototactic so it congregates at the surface and subsurface waters during the day but disperses downward towards higher nutrient levels at night. *Karenia brevis* is low-light adapted and can utilize blue and green light for photosynthesis, which gives it a competitive advantage at low light levels. During times of increased irradiance in surface waters, *K. brevis* is equipped with “sunscreens” in the form of xanthophylls that may help protect it from increased UV light, which is harmful to other phytoplankton. *Karenia brevis* is auxotrophic and uses both dissolved inorganic nitrogen (DIN) and dissolved organic
nitrogen (DON) sources such as urea and uric acid that are excreted by zooplankton and fish. Diatoms and *K. brevis* both have low $K_s$ values, but diatoms have much higher growth rates, therefore they outcompete *K. brevis* at times of high inorganic nitrogen loading, but *K. brevis*’s ability to utilize organic nitrogen gives it a competitive advantage at times when ratios of DIN:DON are low.

A number of physical and climatological conditions were implicated in the development of hypoxic/anoxic waters at depth during the 2005 red-tide event, exacerbating biotic mortalities and evacuations (Heil 2006; personal observation). The summer of 2005 was extremely warm and the thermocline was very shallow in the GOM, with significant water column stratification. There were a number of major hurricanes that swept through the area, temporarily mixing the stratified water column that could have brought *K. brevis* cells in the bottom waters to the surface, where the supply of both DON and DIN (from the *Trichodesmium* bloom) and inherent physiological advantages of *K. brevis* over diatoms enabled the development of a large-scale bloom. *Karenia brevis* cells that remained caught beneath the strongly established thermocline contributed two-fold to the increase in organic matter as: (1) the phytoplankton cells themselves, upon death, fell to the bottom and the organic matter was oxidized by bacteria, and (2) the organisms affected by the brevetoxin died and contributed to the organic matter and subsequent oxygen depletion. The events resulted in the creation of a zone of benthic anoxia that extended from Pinellas County south to Sarasota (FWRI 2005). Throughout the water column, the rain of organic matter from the phytoplankton and dead fish was oxidized, with a hydrogen sulfide layer forming at the top of the thermocline at approximately 6 m (personal observation). Stratification of the water
column persisted throughout the summer and into the winter months; associated anoxic conditions extirpated much of the living, sessile biota and many slower moving fish and invertebrates. Mobile species evacuated shallow inner shelf areas in favor of deeper waters, where both *K. brevis* and bottom-water anoxia were absent.

The red-tide event of 2005 provided an opportunity for a quantitative study of the responses of the benthic invertebrate community and demersal fish assemblage to a major red tide disturbance. At the same time, I began to amass a comprehensive database on shallow inner WFS species diversity and relative abundances using both historic studies and modern surveys. The marginality of modern-day reef assemblages, combined with work on artificial reefs along the WFS, inspired thoughts and analyses on the use of artificial reefs as recruitment enhancement tools along the WFS, in areas frequently impacted by disturbance such as red tides and hurricanes. These data are presented and discussed in subsequent chapters of this dissertation.

1.6. Overview of Dissertation

The main body of this document is composed of three chapters that are either published, in review, or pending submission for publication. Each chapter is treated as an independent scientific contribution containing its respective figures and tables. All references for the entire document are grouped at the end of the dissertation. A conclusion chapter summarizes and compares the information (natural ledges and artificial reef assemblages) and outlines the relevance and usefulness of the data in future conservation and management projects along the WFS. Chapter summaries are as follows:
• Chapter 2 examines the components and dynamics of marginal reef/livebottom assemblages along the WFS.

• Chapter 3 presents a refereed paper published in the *Coastal Management Journal* (Dupont 2008) that discusses the effectiveness of a set of artificial reefs deployed along the WFS.

• Chapter 4 discusses the results of a focused (2005 to 2007) monitoring study of recruitment and succession on artificial reef structures before and after the red-tide disturbance.

• Chapter 5 compares aspects of the natural ledge and artificial reef communities and discusses the use of low-relief artificial reefs as recruitment enhancement tools to increase resiliency of livebottom assemblages along the marginal WFS.
2. Central West Florida Shelf Natural Ledge Dynamics

2.1 Abstract

The West Florida Shelf (WFS) is one of the largest, most productive, and heavily-used continental shelf/slope systems in the world. The WFS is home to some of the most valuable commercial and recreational finfishes in the southeastern United States. Shallow inner WFS livebottom assemblages (10-30 m depth) support a number of finfish life stages by providing structure and protection from predators, benthic primary production, and a variety of food sources (associated crustaceans, mollusks, gastropods, and smaller fish). Livebottom assemblages (including scleractinian corals, macroalgae, poriferans, and echinoderms) along the WFS occur in transitional environmental conditions between subtropical/tropical Caribbean and temperate Carolinian zoogeographic provinces. Temperature, nutrient, and light regimes are highly variable and the livebottom and fish assemblages are further stressed by periodic, acute disturbances including harmful algal blooms (red tides) and hurricanes. This paper assesses the spatial and temporal (seasonal) trends of epibenthic macroinvertebrates, juvenile corals, macroalgae, and demersal fish species over a two-year time period following a red-tide disturbance at two livebottom reefs along the shallow inner WFS. Data from modern surveys are combined with historic data from similar depths to generate comprehensive species lists. The goal is to provide baseline data on the essential communities that can be used to assess future
disturbance impacts and recovery rates, particularly in the face of global environmental change.

2.2 Introduction

The West Florida Shelf (WFS) is one of the largest and most productive continental shelf/slope systems in the world. Due to the importance of continental shelf resources to the State of Florida, including the prolific finfish and shellfish fisheries, offshore petroleum and natural gas exploration, and tourism industries, the WFS has been the subject of numerous studies that address the unique physical oceanographic regimes, chemical influences (from the Mississippi River and the numerous rivers/estuaries that drain into the GOM), and the dynamic geologic features (see Chapter 1 and references therein). However, a more detailed search into the biological attributes of the WFS, specifically community ecology studies, turns up far fewer papers. In general, the existing biological papers fit into two categories. The first includes papers that address specific taxa or populations including, among others, Echinodermata (Hill and Lawrence 2003; Cobb and Lawrence 2005), zooplankton (Huntley and Boyd 1984; Kleppel et al. 1996), phytoplankton, including harmful algae blooms (HABs--Vargo et al. 1987; Tester and Steidinger 1997; Lenes et al. 2001; Walsh et al. 2006), viral and bacterial assemblages (Hewson et al. 2006), and characteristics and life cycles of individual fish species such as Epinephelus morio (Richardson and Gold 1997), Sardinella aurita (Kinsey et al. 1994), and Mycteroperca microlepis (Fitzhugh et al. 2001). The second category of biological articles focuses primarily on either deep-water or mid-shelf reef communities including Pulley Ridge (Jarrett et al. 2005; Hine et al. 2008) and the Florida
Middle Grounds (Cheney and Dyer 1974; Hine et al. 2008), along with a few nearshore (<10 m depth) seagrass community studies (Dawes and Tamasko 1988; Zieman et al. 1989).

While the above studies, combined with the extensive research on physical, chemical, and geological features, have contributed greatly to our understanding of WFS dynamics, there is a dearth of data describing shallow inner shelf (10-30 m depth) epibenthic macroinvertebrate and fish communities on the WFS. The broad nature of the gently-sloping WFS allowed for the extensive, lateral movement of the shoreline during sea-level cycles, and led to the development of diverse distributions of paleoshorelines and shallow-water hardbottoms (Hine et al. 2008). Geologic works (Locker et al. 2003; Obrochta et al. 2003; Hine et al. 2008) have shown that along the west-central Florida coast, at least 50% of the inner shelf seaward of 5 km consists of hardbottom, or lithified seafloor. Hardbottoms are common in shallow carbonate and siliclastic marine settings, but are generally poorly described and documented (Obrochta et al. 2003). Although tropical reef development is absent along the inner WFS (Jaap 1984), most likely limited by excess nutrients and the associated high bioerosion rates (Hallock and Schlager 1986; Hallock 1988), the extensive systems of scarped hardbottom provide relief (up to 4m) and important habitat that support an association of hardy corals and other biota. Much of the WFS may be considered ecotonal between the temperate Carolinian and tropical Caribbean (or West Indian) zoogeographic benthic invertebrate provinces (Hedgpeth 1957; Lyons and Collard 1974), meaning that hardy constituents of both occur across the WFS.
While the body of literature on physical and geological characteristics of the WFS has grown in recent years and numerous hardbottom areas have been mapped (Locker et al. 2003; Obrochta et al. 2003; Hine et al. 2008), there is little information on the abundance and diversity of the epibenthos (livebottom) and demersal fish assemblages that inhabit the WFS ledges on the inner shallow shelf, and even less information on temporal (seasonal and interannual) changes in community structure. Jaap (1984) described the inner WFS habitats as critical habitats that should be provided with rational management due to their association with extensive fisheries of the eastern Gulf of Mexico including numerous important grouper and snapper species. As demands on the WFS resources increase, including proposed offshore oil and natural gas exploration and production, detailed information on the life histories and ecology of marine organisms that inhabit these areas is essential to resource management.

This paper first will summarize available information from historic work on epibenthic communities and demersal fish assemblages along the inner WFS. Then it will present seasonal data from monthly sampling of two hardbottom areas along the WFS over a two-year period. The larger goal is to provide baseline information on ecological attributes of the WFS, which can be used in future works that assess impacts from disturbances that are common in the GOM, including hurricanes, tropical storms, winter cold events, HABs, and hypoxic/anoxic events, as well as potential offshore petroleum exploration projects.
2.3 Historic Data

One of the primary sources of detailed, exploratory information for WFS biological diversity is compiled in a series of reports titled “Memoirs of the Hourglass Cruises” (FWRI 2005). Project Hourglass was a 28-month program conducted between August 1965 and November 1967. The systematic sampling (fixed locations, gear, and interval) of the Hourglass cruises was designed to provide extensive biological information on organisms in offshore waters in the GOM. Stations were sampled on a monthly basis in an hourglass pattern west of Egmont Key and Sanibel Island in depths of approximately 7, 20, 40, 60, and 80 m. Dredging, exploratory trapping, fishing, night-lighting, plankton and nekton tows, water sampling, Secchi disk measurements, and red-tide sampling were among the techniques used to sample the WFS during the Hourglass cruises. The full suite of Hourglass data are available online; in this paper I will focus on Station B epibenthic and fish communities as the depth and location are most similar to my surveys of natural ledges (discussed in this chapter) and artificial reefs (Chapters 3 and 4) along the WFS. The coordinates for the my natural ledge sites, Station B, and the artificial reefs are shown in Table 2.1 and a map of their locations with respect to one another is presented in Figure 2.1.

Table 2.1. Coordinates of sites sampled 1965-1967 (Station B), 2005-2007 (Artificial Reefs), and 2006-2007 (FWRI1 and MT)

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>FWRI1</td>
<td>27 54' 47.16&quot;N</td>
<td>83 06' 19.80&quot;W</td>
</tr>
<tr>
<td>Mastedon Tabletop (MT)</td>
<td>27 54' 48.95&quot;N</td>
<td>83 06' 21.24&quot;W</td>
</tr>
<tr>
<td>Clearwater Wreck (CW)</td>
<td>27 54' 06.48&quot;N</td>
<td>83 06' 29.16&quot;W</td>
</tr>
<tr>
<td>Station B (Hourglass Program)</td>
<td>27 37&quot;N</td>
<td>83 07'W</td>
</tr>
<tr>
<td>Artificial Reefs</td>
<td>27 34'N</td>
<td>83 05'W</td>
</tr>
</tbody>
</table>
A number of other reports and manuscripts have utilized the information gathered during Project Hourglass, and have contributed subsequent information to descriptions of WFS biology. Interestingly, the majority of these works were produced in response to proposed outer continental shelf oil exploration and production activities in the eastern GOM during the 1970’s and 1980’s. Local stakeholders, including the scientific community, and Federal agencies such as the Minerals Management Service initiated studies of eastern GOM ecosystems, recognizing that there was a scarcity of basic environmental information for the area and that the increased demand for domestic energy sources, combined with the distinct possibility that oil might exist beneath the WFS, could open certain tracts for lease (a possibility that is again under consideration today). Basic works on the biological/faunal zones of the WFS (Lyons and Collard 1974; Lyons and Camp 1982) have designated five faunal zones: the shoreward zone (0-10 m depth), the shallow inner shelf (10-30 m), the middle shelf I (30-60 m), the middle shelf II (60-140 m), and the deep shelf (140-200 m).
This paper will focus on sites within the shallow inner shelf (10-30 m) faunal zone (Fig. 2.1) where the presence of rock substrate supports a number of tropical biota including scleractinians, codiaceans, mollusks, and crustaceans that are common in the shallower waters of the Florida Keys. Sediments along the shallow shelf are composed primarily of quartz sands with percentages of biogenically derived carbonates increasing seaward. The benthic communities are diverse and generally concentrated on the shoreward-facing (lee) side of the scarped hardbottom (Obrochta et al. 2003). *Halimeda* spp. meadows cover the upper flat hardbottoms proximal to the scarp (Fig 2.2) while red calcareous algae, boring mollusks (*Lithophaga* spp.), boring poriferans (*Cliona* spp.) and echinoderms occupy both upper flat and scarped surfaces (Obrochta et al. 2003). A
number of other benthic flora and fauna have also been documented on the shallow inner WFS (Dawes and Lawrence 1990).

Figure 2.2. Examples of hardbottom ledge communities along the shallow inner west Florida shelf.

Though numerous works have been published on WFS faunal zones, the majority have used data from one source: The Hourglass Cruises. The Hourglass Cruises were comprehensive in both spatial and temporal sampling scales and the benthic collection methods (otter trawl and box dredge), providing valuable perspective on faunal zones along the WFS. However, the data collected during the Hourglass Cruises are now over 40 years old, and a methodological review reveals limitations that influence data interpretation. The otter trawl and box dredge data are binary (presence/absence) for most taxa, and are insensitive to relative abundance patterns. Equal weighting of rare and common species also contribute to biases in station/site descriptions. The continued characterization of important resources along the WFS requires robust sampling methods and modern data sets. My goal in this chapter is to present quantitative approaches to characterizing areas along the shallow inner central WFS. The methods can then be
expanded, in conjunction with technologic advances such as submersibles and ROVs, to
shelf-wide community surveys.

2.4 Background and Rationale for Current Study

This chapter focuses on sites located in the inner shallow central WFS (10-30 m
depth) faunal zone of Lyons and Collard (1974) and Lyons and Camp (1982). Monthly
surveys of epibenthic community and fish assemblage data were conducted from
February 2006 through December 2007, representing almost two years of data. The
study was initiated in response to a massive Karenia brevis bloom (red tide) that persisted
in the area during the majority of 2005 (Heil 2006). Reports of mass benthic mortalities,
along with in situ dissolved oxygen measurements and K.brevis cell counts (FWRI 2005),
confirmed that the development of an intense thermocline, combined with the rain of
decomposing organic matter from the algal bloom, led to the development of
hypoxic/anoxic conditions and mass mortalities in patches of bottom waters along the
WFS. Reports indicated that deeper, offshore areas (>30 m) were relatively unaffected
by the K. brevis and anoxia, while shallower areas displayed mass die-offs of
scleractinian corals, poriferans, echinoderms, mollusks, and crustaceans, as well as a
number of fish species. Previous reports (Smith 1975; 1979) have qualitatively assessed
the impacts and recovery rates of both epibenthic macroinvertebrates and fish
assemblages in response to red tide events. These studies, while informative, lack an
attention to quantitative details on shallow shelf community composition (species
diversity and abundances) as well as temporal (seasonal) fluctuations, particularly in the
case of epibenthic macroinvertebrates.
My study began in February 2006 as a combined effort between University of South Florida (USF), Florida Aquarium (FLAQ), and FWRI scientists and divers to document the benthic mortalities associated with the 2005 *K. brevis* bloom and hypoxic/anoxic bottom-water conditions. Although the *K. brevis* bloom dissipated in late 2005, sampling was not begun until February 2006 due to logistical and weather-related issues. Despite the lack of quantitative information before, during, and immediately after the *K. brevis* bloom and associated hypoxia/anoxia, a two-year data study was initiated to assess post-disturbance conditions and to track the recovery of epibenthic macroinvertebrate and fish species. Quantitative assessments of red-tide effects are presented in Chapter 4, from a set of artificial reefs deployed along the shallow inner shelf.

2.5 Methods

2.5.1. Site Characteristics

Sampling effort was focused at two sites, FWRI1 and Mastedon Tabletop (MT) (Table 2.1). FWRI1 and MT were chosen for a variety of reasons. First, they were located approximately 40 km west of Clearwater, Florida, at 18-20 m depth, and were situated along the shallow inner WFS (10-30 m depth). Second, while they were located north of the Hourglass Program Station B, they were situated at approximately the same longitude (and depth), thereby allowing for qualitative comparisons between historic and modern surveys. Third, both FWRI1 and MT had been sampled during an FWRI red-tide sampling cruise from August 10-12, 2005. Water samples and *in situ* diver-collected data confirmed the presence of medium to high concentrations of *K. brevis* cells in surface waters (>100,000 cells L\(^{-1}\)), hypoxic (<2 mg L\(^{-1}\)) bottom waters, and benthic mortalities,
indicating that both sites were affected by the red-tide bloom. Fourth, both sites had
typical WFS hardbottom features, including up to 2 m of scarped hardbottom, undercut
by bioerosional forces (Obrochta et al. 2003), and provided suitable substrate for
epibenthic macroinvertebrate and fish associations. Fifth, the sites were located in close
proximity to one another and were easily accessed by boat from Clearwater, FL,
providing access to sample the sites on a monthly basis.

2.5.2. Benthic Community Data
During each sampling, one of the two sites (MT or FWRI1) was chosen as the
target site. The captain of the boat navigated precisely to the coordinates and a buoy was
dropped marking the site. The anchor was then deployed in close proximity to the buoy
and divers descended down the anchor line to the site. This precise navigation was
necessary through the first year (2006). During the second year of sampling (2007), a
temperature logger was deployed at each of the three sites. The logger was attached to a
cinderblock along with a sub-surface buoy situated five meters from the bottom, allowing
for exact location of the study site. Upon reaching the bottom, diver teams began to
survey the fish assemblage utilizing the Bohnsack and Bannerot (1986) method described
below while I conducted photographic benthic transect surveys.

Three 15 m transect lines that trended ledge-parallel (northwest to southeast) were
surveyed at random distances from one another (random number of fin-kicks chosen a
priori). Photographs were captured at each 0.5 m mark along the transect line using a
Canon Powershot A550 with the camera set to the underwater scene for best contrast.
The camera was kept at a fixed distance of 50 cm from the bottom, providing a total of
thirty 48 cm x 38 cm photographs per transect. The distance ensured that there was
maximum coverage of the transect with no overlap between photos, and enabled the identification of many organisms to genus and species levels during the post-processing analysis of images.

Substrate and biological cover attributes of the benthic photographic transects were assessed using point-count analysis (e.g., Curtis 1968; Bohnsack 1979; Carlton & Done 1995; Jaap and McField 2001; Jaap et al. 2003). Twenty randomly generated points were superimposed on each image in Coral Point Count v.3.4 (Kohler & Gill 2006), and the benthic component under each point was identified to provide an estimate of benthic cover (Hackett 2002). Seven major biological and substrate categories (Coral, Porifera, Macroalgae, Dead Coral with Algae, Bleached Coral, Bare Substrate, and Other Living Fauna) were included in the assessment, with subcategories (including specific coral and algal species) also being identified when possible. One advantage of the program, Coral Point Count v.3.4, is that subcategories are linked to a major category, thereby providing researchers with the ability to describe organisms to species level when possible, without sacrificing the description in the major category. This capability is especially important when analyzing photos in the eastern GOM, where seasonal visibility can vary, often precluding accurate identification of organisms to species level. The data are reported as percent cover (% cover) values, and are averaged over the three transects (n=3) for each sampling. This was the maximum number of transects possible, while remaining within dive limits.

Adult coral species were identified in all photographs for comparison with 1965-1967 coral data, in terms of species richness (simple presence/absence enumeration). Juvenile corals were also easily seen in the photographs and included in the analyses, as
very little is known about the spawning and recruitment patterns of the hardy coral
species that inhabit the hardbottom outcrops on the WFS. A criterion of minimum size
was used to distinguish sexually-produced juvenile corals from adult coral and isolated
fragments (Miller et al. 2000; Irizarry-Soto 2006). Because the majority of the adult
corals on the WFS ledges were small (<20 cm), including species such as Siderastrea
radians and Stephanocoenia intersepta, isolated colonies less than 2 cm in diameter were
considered sexually-produced juveniles (Irizarry-Soto 2006). Although numerous
juveniles were observed in photos, the inherent properties of new recruits (i.e., small size,
propensity for burial under sediment) make true quantitative reports through photo
documentation very difficult. Instead of counting individual recruits, as is often done in
situ using quadrats, the simple presence/absence of juveniles in photos was recorded as a
percentage of photos containing juveniles per 15 m transect (i.e., the number of photos
with at least one juvenile/30 pictures). This allowed me to observe general patterns of
recruitment on a 2-year time scale, with particular focus on the seasonal influences on
coral spawning and recruitment in the eastern GOM.

The monthly variations of the seven major categories and juvenile photo-transect
percentages were plotted as boxplots displaying interquartile ranges, medians, means, and
outliers. These data reveal insight into seasonal trends and sample distributions of major
component categories over the two-year period. The major benthic component data were
right-skewed and subsequently transformed using a Log(x+1) transformation. One-way
Analysis of Variance (ANOVA) was used to test for significant seasonal differences in
the major categories followed by the Tukey’s post-hoc multiple comparison procedure to
determine pair-wise differences. A Principal Components Analysis (PCA) was used to
reduce the dimensionality of the data, determine important gradients, and spatially
display the data.

2.5.3. Fish Assemblage Data
During each sampling trip, 2-4 research divers conducted fish surveys in
accordance with the Bohnsack-Bannerot fish count protocol (Bohnsack and Bannerot
1986). The Bohnsack method provides standard quantitative data on reef-fish
assemblage structure over a variety of habitats in an efficient and effective manner.
Observers position themselves on the center point of the census area, and wait for three
minutes prior to recording. The waiting period allows for the dampening of any
disturbance and fishes can acclimate to diver presence. Divers attempt to count all
individuals and species of fish in an imaginary 5 m radius cylinder extending from the
bottom to the surface. New species are listed while rotating in one direction and scanning
the field of view. The observer remains stationary except for rotation. Five minutes was
chosen as an optimum counting time because it allows for most fish to habituate to the
diver, but minimizes the time for mobile species outside the cylinder to accumulate. The
observers were usually able to conduct between 3 and 5 surveys per dive, yielding from
6-20 fish surveys per dive. A number of these surveys did, however, have to be
eliminated from use in the study as the observers were either practicing fish-identification
skills or did not pass the GOM fish identification test administered before the dives. Due
to the mobile nature of the fish and the close proximity of the two sites, the data were
analyzed as a group, with no differentiation between FWRI1 and MT data. The grouping
of data yielded a database that was more chronologically consistent than if the two sites
had been analyzed separately. Species numbers and assemblage composition from the
2006-2007 data were compared to lists from comparable depths (Station B) of the Hourglass Cruises. Data were also compared to artificial reef sites situated in comparable depths/locations in the GOM (Chapter 3).

Fish species abundance data from the 2006-2007 surveys (pooled) were entered into a matrix worksheet and an Anderson-Darling test was used to test for normality within samplings. The Anderson-Darling test p-values indicated that, at $\alpha >0.02$, there is evidence that most samples did not follow a normal distribution. Therefore, non-parametric multivariate analyses were conducted using the Primer-ETM (Clarke & Warwick 2001) package of software applications to analyze assemblage-wide changes/differences among samplings. Abundance data were square-root transformed to focus attention on patterns within the whole assemblage, mixing contributions from both common and rare species (Clarke & Warwick 1994). Multivariate distances were calculated using the Bray-Curtis similarity coefficient (Bray & Curtis 1957) and plotted using a non-metric multi-dimensional scaling (MDS) ordination. The MDS finds a non-parametric monotonic relationship between dissimilarities in the item-item matrix and the Euclidean distance between the items, and plots the location of each item in low-dimensional space. MDS ordination stress levels $<0.15$ signify a useful representation (i.e., configuration closely represents the rank order of dissimilarities in the original triangular matrix), while stress levels $>0.20$ signify a random arrangement of samples, bearing little resemblance to the original ranks (Clarke 1993). Factors were added to the original data to view and determine optimal spatial arrangements among groups. Factors included site, year (2006 or 2007), season, and sampling. Second-level procedures (Clarke & Warwick 2001), including Analysis of Similarity (ANOSIM) and Similarity
Percentages (SIMPER) tests, were used to test for significant differences in fish
assemblage structure between those samples/groups that appeared to separate spatially in
the MDS.

2.5.4. Abiotic Data
Abiotic parameters, including salinity and Secchi disk depths, were measured
sporadically throughout the study and average values are reported in this paper.
Consistent bottom temperature data were collected beginning in mid-February 2007.
Temperature loggers were deployed throughout the year from February to November at
three sites, FWRI1, MT, and CW. The loggers were affixed to a cinder block with a sub-
surface buoy and were deployed for periods of 1 to 3 months, at which time they were
swapped out and taken back to the lab for data download. The loggers were set to record
temperature data at either 5 or 10 minute intervals. The data are presented in this paper,
and represent one of the first high-resolution benthic temperature databases for the central
shallow inner WFS.

Secchi depths were converted into light attenuation coefficients (k-values) and
percent surface light reaching bottom at 17 m depth was calculated using the Beer-
Lambert Law: \( \frac{I_x}{I_0} = e^{-kz} \).

2.6 Results
2.6.1. Historic Data
Historic data from the Hourglass Program Station B are summarized in this paper
in the form of species lists (Tables 2.2 through 2.5) and used as qualitative comparative
baselines to my surveys, which are also included in the tables. Coral species are listed in
Table 2.2, echinoderms in Table 2.3, benthic algae in Table 2.4, representing those
epibenthic flora and fauna that were readily identified in digital photo-transect surveys. Although a number of other Hourglass reports were generated on various taxa (not presented here), this paper will focus on benthic species lists that either: (1) fit into one of the seven benthic major categories (e.g., corals and macroalgae) or (2) are epibenthic macroinvertebrates that may have fallen into the “Other Living Fauna” category, but are easily distinguished in photographs (e.g., Echinodermata). Table 2.5 lists fish species from all studies.
Table 2.2. Coral species recorded at shallow hardbottom sites on the inner west Florida shelf. Data are compiled from three data sets and species presence is denoted by the corresponding number: (1) 1965-1967 (Hourglass Program), (2) 2006-2007 (Natural Reef Ledges) and (3) 2005-2007 (Artificial Reefs). Reproductive modes are also listed. N/K=Not known.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reproduction</th>
<th>Data Set</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cladocora arbuscula</em></td>
<td>N/K</td>
<td>1,2,3</td>
</tr>
<tr>
<td>(LeSueur, 1821)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phyllangia americana</em></td>
<td>N/K</td>
<td>1,2,3</td>
</tr>
<tr>
<td>Milne-Edwards &amp; Haime, 1849</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Solenastrea hyades</em></td>
<td>Broadcast</td>
<td>1,2</td>
</tr>
<tr>
<td>(Dana, 1846)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Manicina areolata</em></td>
<td>Brooding</td>
<td>1</td>
</tr>
<tr>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Siderastrea radians</em></td>
<td>Brooding</td>
<td>1,2,3</td>
</tr>
<tr>
<td>(Pallas, 1766)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oculina robusta</em></td>
<td>Broadcast</td>
<td>1,2</td>
</tr>
<tr>
<td>(Pourtalès, 1871)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stephanocoenia intersepta</em></td>
<td>Broadcast</td>
<td>1,2</td>
</tr>
<tr>
<td>(Esper, 1795)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Scolymia lacera</em></td>
<td>Brooding</td>
<td>1</td>
</tr>
<tr>
<td>(Pallas, 1766)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Balanophyllia floridana</em></td>
<td>N/K</td>
<td>1</td>
</tr>
<tr>
<td>De Pourtalès, 1868</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Porites divaricata</em></td>
<td>Brooding</td>
<td>1</td>
</tr>
<tr>
<td>LeSueur, 1821</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Millepora alcicornis</em></td>
<td>Budding</td>
<td>1</td>
</tr>
<tr>
<td>Linnaeus, 1758</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Astrangia poculata</em></td>
<td>N/K</td>
<td>1</td>
</tr>
<tr>
<td>(Ellis &amp; Solander, 1786)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Isophyllia sinuosa</em></td>
<td>Brooding</td>
<td>1</td>
</tr>
<tr>
<td>(Ellis &amp; Solander, 1786)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Occurred at ≤10% frequency in the Hourglass Program*
Table 2.3. Echinoderm species recorded on shallow hardbottom sites on the inner WFS. Data are compiled from three data sets and species presence is denoted by the corresponding number: (1) 1965-1967 (Hourglass Program), (2) 2006-2007 (Natural Reef Ledges) and (3) 2005-2007 (Artificial Reefs).

<table>
<thead>
<tr>
<th>Echinodermata</th>
<th>Data Set</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arbacia punctulata</em> (Lamarck, 1816)</td>
<td>1,2,3</td>
</tr>
<tr>
<td><em>Lytechinus variegatus</em> (Lamarck, 1816)</td>
<td>1,2</td>
</tr>
<tr>
<td><em>Clypeaster prostratus</em> Ravenel, 1848</td>
<td>1*</td>
</tr>
<tr>
<td><em>Clypeaster subdepressus</em> (Gray, 1825)</td>
<td>1</td>
</tr>
<tr>
<td><em>Mellita quinquiesperforata</em> (Leske, 1778)</td>
<td>1</td>
</tr>
<tr>
<td><em>Encope aberrans</em> Martens, 1867</td>
<td>1*</td>
</tr>
<tr>
<td><em>Encope michelini</em> Agassiz, 1841</td>
<td>1</td>
</tr>
<tr>
<td><em>Plagiobrissus grandis</em> (Gmelin, 1788)</td>
<td>1*</td>
</tr>
</tbody>
</table>

Occurred at ≤10% frequency in the Hourglass Program
Table 2.4. Benthic algae species recorded on shallow hardbottom sites on the inner WFS. Data are compiled from three data sets and species presence is denoted by the corresponding number: (1) 1965-1967 (Hourglass Program), (2) 2006-2007 (Natural Reef Ledges) and (3) 2005-2007 (Artificial Reefs).

<table>
<thead>
<tr>
<th>Benthic Algae</th>
<th>Data Set</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cyanophyta</strong></td>
<td></td>
</tr>
<tr>
<td><em>Calothrix confervicola</em></td>
<td>1*</td>
</tr>
<tr>
<td>C. Agardh 1824</td>
<td></td>
</tr>
<tr>
<td><em>Lyngbya bergei</em></td>
<td>1*</td>
</tr>
<tr>
<td>Kellerman 1893</td>
<td></td>
</tr>
<tr>
<td><em>L. confervoides</em></td>
<td>1</td>
</tr>
<tr>
<td>Umezaki (1961)</td>
<td></td>
</tr>
<tr>
<td><strong>Chlorophyta</strong></td>
<td></td>
</tr>
<tr>
<td><em>Avrainvillea levis</em></td>
<td>1*</td>
</tr>
<tr>
<td>Howe 1905</td>
<td></td>
</tr>
<tr>
<td>A. longicaulis</td>
<td>1</td>
</tr>
<tr>
<td>G.Murray &amp; Boodle</td>
<td></td>
</tr>
<tr>
<td><em>Anadyomene stellata</em></td>
<td>1*</td>
</tr>
<tr>
<td>C. Agardh 1822</td>
<td></td>
</tr>
<tr>
<td><em>Caulerpa mexicana</em></td>
<td>1,2,3</td>
</tr>
<tr>
<td>Küntzig ex Sonder 1849</td>
<td></td>
</tr>
<tr>
<td><em>C. paspaloides</em></td>
<td>1</td>
</tr>
<tr>
<td>Weber-van Bosse 1898</td>
<td></td>
</tr>
<tr>
<td><em>C. peltata</em></td>
<td>1*</td>
</tr>
<tr>
<td>(Weber-van Bosse) Reinke 1900</td>
<td></td>
</tr>
<tr>
<td><em>C. prolifera</em></td>
<td>1*,2,3</td>
</tr>
<tr>
<td>Lamouroux 1809</td>
<td></td>
</tr>
<tr>
<td><em>C. sertularioides</em></td>
<td>1,2,3</td>
</tr>
<tr>
<td>Howe 1905</td>
<td></td>
</tr>
<tr>
<td><em>Codium isthmocladum</em></td>
<td>1,2,3</td>
</tr>
<tr>
<td>Vicker 1905</td>
<td></td>
</tr>
<tr>
<td><em>C.i. subsp. clavatum</em></td>
<td>1</td>
</tr>
<tr>
<td>Vicker 1905</td>
<td></td>
</tr>
<tr>
<td><em>C. repens</em></td>
<td>1</td>
</tr>
<tr>
<td>P. and H. Crouan Ex Vickers</td>
<td></td>
</tr>
<tr>
<td><em>Cystodictyon pavonium</em></td>
<td>1*</td>
</tr>
<tr>
<td>Lambert</td>
<td></td>
</tr>
<tr>
<td><em>Halimeda discoidea</em></td>
<td>1,2,3</td>
</tr>
<tr>
<td>Decaisne</td>
<td></td>
</tr>
<tr>
<td><em>H. opuntia</em></td>
<td>1*</td>
</tr>
<tr>
<td>(Linnaeus)</td>
<td></td>
</tr>
<tr>
<td><em>Pseudotetraspora antillarum</em></td>
<td>1*</td>
</tr>
<tr>
<td>Howe 1905</td>
<td></td>
</tr>
</tbody>
</table>
Udotea conglutinata 1,2,3
J. V. F. Lamouroux 1812

U. cyanthiformis 1*
J. V. F. Lamouroux 1812

U. flabellum 1,2,3
Howe

Valonia macrophysa 1*
C. Aghardh 1823

Phaeophyta

Cladosiphon occidentalis 1*
Kylin

Colpomenia sinuosa 1
Derbes and Solier

Dictyopteris delicatula 1*
J.V. Lamouroux 1809

D. membranacea 1*
Batters

Dictyota dichotoma 1,2,3
Nizamuddin 1981

D. divaricata 1*
J.V. Lamouroux 1809

Ectocarpus elachistaeformis 1*
Heydrich (1892)

Giffordia sp. 1*
G. Hamel

Rosenvingea intricata 1
Børgesen

R. sanctae-cruis 1*
Børgesen

Sargassum filipendula 1,2,3
Grunow 1916

S.f.v.montagnei 1,2,3
Steidinger & Van Breedveld 1969

S. natans 1,2,3
Gaillon 1828

Sporochnus bolleanus
C.Agardh 1824 1
S. pedunculatus 1
Lucas 1936

Rhodophyta

Acrochaetum antillarum 1*
Farlow, W. G. 1876
A. flexuosum 1*
Naegeli 1858
A. thurettii 1*
Born
Agardhiella ramosissima 1
Schmitz (1896)
A. tenera 1
Schmitz (1896)
Amphiroa rigida v. antillana 1*
Lamouroux 1816
Asterocytis ramosa 1*
Tanaka 1944
Botryocladia occidentalis 1
Kylin
Brongniartella mueronata 1*
H Woods 1897
Callithamnion halliae 1*
Collins, Holden & Setchell 1900
Ceramium fastigiatum 1
Celan & Serbanescu 1959
C. leptozonum 1*
Howe 1918
C. rubrum 1*
Hudson
Champia parvula 1,2,3
Harvey
Chondria floridana 1
M.A. Howe
C. tenuissima 1*
C. Agardh 1817
Chrysymenia enteromorpha 1
Harvey (1853)
C. ventricosa 1*
J. Agardh (1842)
Crouania attenuata 1*
J. Agardh, 1842
Dasya collinsiana 1*
M. Howe
D. corymbifera 1
J. Agardh 1841
D. pedicellata 1
C. Agardh 1824
D. rigidula 1*
Ardissone 1878
Digenia simplex 1*
Wulfen 1803
Erythrocladia sp. 1*
Rosenvinge 1909
Eucheuma acanthocladum 1,2,3
J. Agardh 1847
E. isiforme 1,2,3
J. Agardh 1847
Fosliella atlantica 1
Harvey 1836
Gracilaria armata 1*
Greville 1830
G. blodgetii 1
Harvey 1853
G. cervicornis 1*
J. Agardh 1852
G. cylindrica 1
Børgeesen 1920
G. debilis 1
Børgeesen
G. ferox 1
J. Agardh 1852
G. foliifera 1
Børgeesen 1932
G.f.v. angustissima 1
Taylor
G. mammillaris 1
M.A. Howe 1918
G. sjoeestedtii 1*
Kylin
G. verrucosa 1
Papenfuss 1950
Halymenia agardhi 1*
C. A. Agardh 1817
H. bermudensis 1*
Collins and Harvey
H. floresia 1
C. A. Agardh
H. gelinaria 1
Collins & Howe 1916
H. pseudofloresia 1
Collins and Howe
Jania adherens 1
Lamouroux 1816
J. capillacea 1*
Harvey 1853
Laurencia gemmifera
Harvey 1853
L. intricata 1 *
Lamouroux
L. obtusa 1 *
Lamouroux
L. poitei 1
Howe
Lithothamnium incertum 1
Dakwix 1854
L. occidentale 1
Lemoine 1917
Lomentaria baileyana 1
Farlow
Peyssonnelia rubra 1 *
J. Decaisne 1841
Polysiphonia hapalacantha 1 *
Harvey 1853
P. subtilissima 1 *
Mont 1840
Spyridia filamentosa 1
Harvey
Wrightiella blodgettii 1 *
Schmitz
Wurdemannia miniata 1
Feldmann & Hamel 1952

Angiospermae
Halophila baillonis 1
Aschers 1874
Thalassium testudinum 1
Keough 1986

*Occurred at ≤10% frequency in the Hourglass Program
Table 2.5. Fish species recorded on shallow hardbottom sites on the inner WFS. Data are compiled from three data sets and species presence is denoted by the corresponding number: (1) 1965-1967 (Hourglass Program), (2) 2006-2007 (Natural Reef Ledges) and (3) 2005-2007 (Artificial Reefs).

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Data Set</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abudefduf saxatilis</td>
<td>Sergeant major</td>
<td>3</td>
</tr>
<tr>
<td>Acanthostracion quadricornis</td>
<td>Cowfish/boxfish</td>
<td>1,3</td>
</tr>
<tr>
<td>Acanthurus chirurgus</td>
<td>Doctorfish tang</td>
<td>2</td>
</tr>
<tr>
<td>Anisotremus surinamensissi</td>
<td>Black margate</td>
<td>2</td>
</tr>
<tr>
<td>Anisotremus virginicus</td>
<td>Porkfish</td>
<td>3</td>
</tr>
<tr>
<td>Antennarius ocellatus</td>
<td>Ocellated frogfish</td>
<td>1</td>
</tr>
<tr>
<td>Apogon quadrisquamatus</td>
<td>Sawcheek cardinalfish</td>
<td>1</td>
</tr>
<tr>
<td>Archosargus probatocephalus</td>
<td>Sheephead</td>
<td>2,3</td>
</tr>
<tr>
<td>Arius felis</td>
<td>Hardhead catfish</td>
<td>1</td>
</tr>
<tr>
<td>Balistes capriscus</td>
<td>Grey triggerfish</td>
<td>1,2,3</td>
</tr>
<tr>
<td>Bothus roebi</td>
<td>Twospot flounder</td>
<td>1</td>
</tr>
<tr>
<td>Calamus bajonado</td>
<td>Jolthead</td>
<td>3</td>
</tr>
<tr>
<td>Calamus penna</td>
<td>Sheephead porgy</td>
<td>2,3</td>
</tr>
<tr>
<td>Calamus spp.</td>
<td>Porgy</td>
<td>1,2,3</td>
</tr>
<tr>
<td>Caranx cryos</td>
<td>Blue Runner</td>
<td>2,3</td>
</tr>
<tr>
<td>Caranx ruber</td>
<td>Barjack</td>
<td>2,3</td>
</tr>
<tr>
<td>Centropristis ocyurus</td>
<td>Bank seabass</td>
<td>1</td>
</tr>
<tr>
<td>Centropristis striata</td>
<td>Black seabass</td>
<td>1,2,3</td>
</tr>
<tr>
<td>Chaetodipterus faber</td>
<td>Atlantic spadefish</td>
<td>1,3</td>
</tr>
<tr>
<td>Chaetodon ocellatus</td>
<td>Spotfin butterflyfish</td>
<td>2</td>
</tr>
<tr>
<td>Chaetodon sedentarius</td>
<td>Reef butterflyfish</td>
<td>3</td>
</tr>
<tr>
<td>Chaetodon striatus</td>
<td>Banded butterflyfish</td>
<td>2</td>
</tr>
<tr>
<td>Chasmodes saburrae</td>
<td>Florida blenny</td>
<td>3</td>
</tr>
<tr>
<td>Chilomycterus schoepfi</td>
<td>Striped burrfish</td>
<td>1</td>
</tr>
<tr>
<td>Citharinthys macrops</td>
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<td>Nurse shark</td>
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<td>Scientific Name</td>
<td>Common Name</td>
<td>Category</td>
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<tr>
<td>---------------------------------------</td>
<td>------------------------------</td>
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<tr>
<td>Gobiosoma macrodon</td>
<td>Tiger goby</td>
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<td>Blackedge moray</td>
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<td>Gymnothorax saxicola</td>
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<td>French Grunt</td>
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<td>Haemulon plumieri</td>
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<td>Halichoeres maculipinna</td>
<td>Clown wrasse</td>
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<td>Pancake batfish</td>
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<td>Queen angelfish</td>
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</tr>
<tr>
<td>Holacanthus townsendi</td>
<td>Townsend angelfish</td>
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<tr>
<td>Holocentrus adscensionis</td>
<td>Squirrelfish</td>
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<tr>
<td>Hypoplectrus unicolor</td>
<td>Butter Hamlet</td>
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<tr>
<td>Kryptolepis sp.</td>
<td>Chub</td>
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<td>Lutjanus griseus</td>
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<td>Mycteroperca phenax</td>
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<td>Nicholsina usta</td>
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<td>Ocyurus chrysurus</td>
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<td>Ogocephalus radiatus</td>
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<tr>
<td>Ophidion spp.</td>
<td>Cusk-eel</td>
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<tr>
<td>Opisstonema oglinum</td>
<td>Threadfin herring</td>
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<td>Opsanus pardus</td>
<td>Leopard toadfish</td>
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<td>Orthopristis chrysoptera</td>
<td>Pigfish</td>
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<td>Seaweed blenny</td>
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<td>Paralichthys albigutta</td>
<td>Gulf flounder</td>
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<td>Paralichthys lethostigma</td>
<td>Southern Flounder</td>
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<td>Pareques umbrosus</td>
<td>Cubbyu</td>
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<tr>
<td>Pomacanthus arcuatus</td>
<td>Grey Angelfish</td>
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<td>Pomacanthus paru</td>
<td>French angelfish</td>
<td>3</td>
</tr>
<tr>
<td>Porichthys electrodon</td>
<td>Atlantic midshipman</td>
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<tr>
<td>Prionotus longispinosus</td>
<td>Bigeye searobin</td>
<td>1</td>
</tr>
<tr>
<td>Prionotus martis</td>
<td>Barred searobin</td>
<td>1</td>
</tr>
<tr>
<td>Prionotus ophryas</td>
<td>Bandtail searobin</td>
<td>1</td>
</tr>
</tbody>
</table>
**Prionotus roseus**    Bluespotted searobin    1  
**Prionotus tribulus**  Bighead searobin  1  
**Pristigenys alta**     Short bigeye    1  
**Ptereleotris calliura** Blue goby  2,3  
**Rhinobatos lentiginosus** Atlantic guitarfish  1  
**Rhomboptilus aurorubens** Vermilion snapper 1  
**Rypticus maculatus**  Whitespotted soapfish 1,2,3  
**Rypticus saponaceus**  Greater soapfish 1  
**Sardinella aurita**    Spanish sardine 1,3  
**Scartella cristata**  Molly miller 3  
**Scomberomorus maculates**  Spanish mackerel 2,3  
**Scorpaena brasiliensis**  Barbfish 1  
**Scorpaena calcarata**  Smooth-head scorpionfish 1  
**Seriola dumerili**  Greater amberjack 2,3  
**Serranus subligarius**  Belted sandfish 2,3  
**Serranus tigrinus**  Harlequin bass 2  
  Sp.?  Filefish 1,2,3  
  Sp.?  Orange blenny 3  
  Sp.?  White goby 2,3  
**Sphoeroides spengleri**  Bandtail puffer 1,2,3  
**Sphyraena barracuda**  Great barracuda 2,3  
**Stegastes leucostictus**  Beaugregory 2,3  
**Stegastes variabilis**  Cocoa damsel 2,3  
**Syacium papillosum**  Dusky flounder 1  
**Symphurus urospilus**  Spottail tonguefish 1  
**Synodus foetens**  Inshore lizardfish 1,2,3  
**Synodus intermedius**  Sand diver 1,2  
**Thalassoma bifasciatum**  Bluehead wrasse 3  
**Trachinocephalus** spp.  Snakefish 1  

### 2.6.2. Benthic Community Data

Seven major categories (Coral, Porifera, Macroalgae, Dead Coral with Algae, Bleached Coral, Bare Substrate, and Other Living Fauna) were identified in the digital photo transects. Juvenile corals are considered as an eighth major category for a number of the analyses. Boxplots of the eight categories are displayed in Figures 2.3 through 2.5 and 2.7 through 2.11. The data are displayed in two panels on each graph, each
corresponding to percent cover of the category at one of the two study sites, FWRI1 or MT. Note that the y-scale changes in each graph.

Average transect coral cover (Fig. 2.3) varied from a low of 1.3% (July 2006, MT) to a high of 6.1% (June 2007, FWRI1). The data in the boxplots represent three replicates per sampling time, with ranges of coral cover varying within sampling times from as high as 7% (April 2006, MT) to as low as 0.23% (July 2006, MT). Adult coral species were identified and compared (presence/absence) to a list of species collected at Station B during the Hourglass cruises (Table 2.2). Seven species, four of which were observed infrequently (≤ 10% of the time) at Station B, were not detected in photographs from the modern surveys.

Percent cover of both macroalgae (Fig. 2.4) and bare substrate (Fig. 2.5) were highly variable. Regression analysis revealed a significantly (p<0.05) negative correlation, with months of high macroalgal cover (e.g., May) corresponding to low percentages of bare substrate (Fig. 2.6).
Figure 2.3. Boxplot of percent coral cover at FWRII and MT from February 2006 to December 2007. The bars represent the interquartile ranges, sample means are designated by a diamond and medians by a horizontal line.
Figure 2.4 Boxplot of macroalgal cover at FWRI1 and MT from February 2006 to December 2007.

Figure 2.5. Boxplot of bare substrate cover at FWRI1 and MT from February 2006 to December 2007.
Juvenile corals were detected in photo-transects in all sampling times (Fig. 2.7). Percentages of transects with juvenile corals varied from 9.6% (May 2007, MT) to a high of 47% (June 2007, FWRI1). Poriferans (2.8) also displayed major ranges and seasonal changes in average percent cover with a low of 0.0% (May 2006, FWRI1) and a high of 7.1% (FWRI1, November 2007). The remaining categories (Other Living Fauna, Dead Coral with Algae, and Bleached Coral; Figs. 2.9 to 2.11) contributed very little to overall percent WFS cover (<2.5% during all samplings).
Figure 2.7. Boxplot of percentage of transect photos in which juvenile corals were identified at FWRI1 and MT from February 2006 to December 2007.
Figure 2.8. Boxplot of Porifera cover at FWRI1 and MT from February 2006 to December 2007.

Figure 2.9. Boxplot of other living fauna cover at FWRI1 and MT from February 2006 to December 2007.
Figure 2.10. Boxplot of dead coral with algae cover at FWRI1 and MT from February 2006 to December 2007.

Figure 2.11. Boxplot of bleached coral cover at FWRI1 and MT from February 2006 to December 2007.
One-way ANOVAs revealed that only four of the eight categories displayed significant seasonal changes (Table 2.6). Macroalgae and Bare Substrate cover values in fall were significantly different (F=10.6 and F=9.9, respectively; p=0) from both spring and winter values. Porifera percent cover values were significantly lower in the spring (F=7.7; p=0) than fall. Juvenile coral presence percentages were significantly lower (F=10.5; p=0) in the spring as compared to all other seasons.

Table 2.6. ANOVA and Tukey’s post-hoc comparison results for the 4 categories that displayed significant seasonal differences. Results from the Tukey’s test first list the category’s determining season followed by the season(s) that it differs significantly from.

<table>
<thead>
<tr>
<th>Category</th>
<th>ANOVA Results</th>
<th>Differing Seasons (Tukey’s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macroalgal Cover</td>
<td>F=10.6; p=0</td>
<td>Fall – Spring &amp; Winter</td>
</tr>
<tr>
<td>Bare Substrate Cover</td>
<td>F=9.9; p=0</td>
<td>Fall – Spring &amp; Winter</td>
</tr>
<tr>
<td>Coral Juvenile Presence</td>
<td>F=10.5; p=0</td>
<td>Spring – Summer, Fall, &amp; Winter</td>
</tr>
<tr>
<td>Porifera Cover</td>
<td>F=9.9; p=0</td>
<td>Spring – Fall</td>
</tr>
</tbody>
</table>

A PCA (Fig. 2.12) of the eight categories (including juvenile corals) indicates that the first component is positively related to percent cover of poriferans, bare substrate, and juvenile coral counts and negatively related to the percent cover of macroalgae. The second principal component is positively related to coral percent cover and negatively to dead coral with algae. The first two components (eigenvalues of 2.7 and 1.2, respectively) cumulatively explain about 50% of the total variance, indicating that a number of other factors (or components) are involved in WFS benthic community dynamics.
Figure 2.12. Principal Components Analysis of Log (x+1) transformed data from seven major categories plus juvenile corals. Eigen values for the first two components are 2.7 and 1.2, respectively, and cumulatively explain approximately 50% of the variance.

2.6.3. Fish Assemblage Data
There were a total of 47 fish species observed over the 22-month study period at FWRI1 and MT. Hourglass Program collections enumerated 59 species at natural ledge Station B over the 28-month sampling period between 1965 and 1967. I also observed 71 species at a set of artificial reefs (Chapter 3), located near Station B in comparable depths. The complete list of species (113 total) is shown in Table 2.5. The mobile nature of fish makes it difficult to quantify spatial and temporal changes in assemblage structure. No transformations were able to make the data conform to normality so non-parametric multivariate procedures were used to yield insights into some of the changes in assemblage structure in the 22-month data set from the pooled FWRI1 and MT data (justification for pooling provided in methods section).
The 2-D non-metric MDS ordination of fish data is shown in Figure 2.13. The 2-D stress level (=0.2) configuration signifies that the spatial arrangement of the MDS may be a near random arrangement of samples, bearing little resemblance to the original ranks (Clarke 1993). However, when the data are viewed in a 3-dimensional MDS graph by season factor, the stress level decreases to 0.14. The 3-D version is not presented here due to the complicated visualization of group-separation that it provides. The 3-D MDS does indicate that there is spatial separation amongst the groups and renders second-level seasonal procedures valid. Seasonal differences among fish assemblages are confirmed by an ANOSIM Global R=0.3 (p=.001). ANOSIM and SIMPER pair-wise comparison results are shown for those seasons that differed significantly in their fish assemblage (Table 2.7).
Summer fish assemblages differed from the other three seasons, and the same top four species (*Halichoeres bivittatus*, *Diplectrum formosum*, *Haemulon plumierii*, *Serranus subligarius*) were implicated in the dissimilarities. Abundances of *D. formosum* continuously decreased from winter through spring to summer, and then increased again in the fall. *Halichoeres bivittatus* abundances responded in the exact opposite manner through the seasons (first increasing from winter to spring to summer, then decreasing in the fall). No other linked trends were observed in the species data, although *H. plumierii* and *S. subligarius* did display opposite trends in abundance between the winter to summer samplings and the summer to fall samplings. Seasonal
trends were generally less clear and therefore less quantifiable among fish assemblages as compared to the benthic community data.

Table 2.7. ANOSIM analysis and SIMPER pair-wise comparisons of fish assemblages during fall, winter, spring, and summer samplings. Only those seasons that differed significantly from one another (ANOSIM $R>0.3$; $p<0.05$) are shown. The SIMPER results list the four top species contributing to the dissimilarity between the two seasons. Their relative abundance change (+/-) is also listed.

<table>
<thead>
<tr>
<th>Seasons</th>
<th>ANOSIM Results</th>
<th>SIMPER Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter &amp; Summer</td>
<td>$R=0.4$; $p=.001$</td>
<td><em>Halichoeres bivittatus</em> (+)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Diplectrum formosum</em> (-)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Haemulon plumieri</em> (-)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Serranus subligarius</em> (+)</td>
</tr>
<tr>
<td>Spring &amp; Summer</td>
<td>$R=0.7$; $p=.001$</td>
<td><em>Halichoeres bivittatus</em> (+)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Diplectrum formosum</em> (-)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Haemulon plumieri</em> (+)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Serranus subligarius</em> (+)</td>
</tr>
<tr>
<td>Summer &amp; Fall</td>
<td>$R=0.4$; $p=.001$</td>
<td><em>Halichoeres bivittatus</em> (-)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Diplectrum formosum</em> (+)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Haemulon plumieri</em> (+)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Serranus subligarius</em> (-)</td>
</tr>
</tbody>
</table>

2.6.4. Abiotic Data

Bottom temperature was measured from March to November 2007. Ten-day averages were plotted for FWRII (Fig. 2.14). Temperature trends at MT were similar as the sites are located in close proximity. Maximum daily fluctuations were observed at FWRII during March with a one-day increase in temperature from 17.5°C to 19.6 ºC (Fig. 2.15). The greatest monthly increase in temperature occurred over the month of May as temperatures at the bottom rose from 21.1 ºC to 24.8 ºC. The greatest temperature decrease occurred in November as temperatures dropped from 25.7 ºC to 21.3 ºC.
Figure 2.14. Ten-day average bottom temperature data at FWRI1 from March to December 2007.
Average salinity over the 2-year study period at FWRI1, MT, and CW was 34.3 at the surface and 34.0 at the bottom. Light attenuation coefficients (k-values) calculated from Secchi depths varied from a minimum of 0.07 in April to a maximum of 0.21 in August, with an average k of 0.16. These correspond to percent surface light reaching a depth of 17 m depth between 2.7% and 33%, with an average of 6.4%. A number of phytoplankton species were observed in water samples collected at the three study sites, but only September 2006 samples contained any *Karenia* spp. (low cell counts<30,000 cells/liter), indicating that harmful algal blooms were not affecting the areas during my study.
2.7 Discussion

2.7.1. Benthic Communities

Livebottom communities have both seasonal and non-seasonal components to their structure. The assessment of seasonality is influenced by the type of data available and by practical limitations on sampling adequacy. The degree of seasonal environmental variation along WFS livebottom ledges depends on depth, latitude, and proximity to the shelf edge. Past studies have shown that seasonal species richness/abundance variation is generally greater at shallow, inner-shelf benthic communities as compared to mid-shelf or outer-shelf areas (MMS 1985). Seasonal biotic variations detected in historic studies (primarily from the Hourglass Cruises) were proposed to reflect seasonal abundance patterns of different algal groups, which are prolific along the WFS (Table 2.4). The majority of species in Table 2.4 represent collection and microscopic analyses from the Hourglass Cruise collections, which are optimal methods for studying algal diversity. I identified algal species, when possible, from the digital photographs, but in general they were placed in a general “Macroalgae” category.

Results from the Macroalgae (Fig. 2.4) and Bare Substrate (Fig. 2.5) boxplots and one-way ANOVAs from the 2006-2007 data (Table 2.6) corroborate historic seasonal hypotheses as significant seasonal differences were observed in both the Macroalgae and Bare Substrate categories. The two categories were negatively correlated (Fig. 2.6); high values of one category (i.e., high macroalgal cover in the spring or bare substrate in the fall) corresponded to low cover values of the other category. Macroalgae tended to dominate in the spring months (April and May). Anomalously high percent cover of macroalgae in the late winter of 2006 (February, ~67%) are due to the abundant growth
of “slimy” unidentifiable alga or cyanobacterium that covered the subtrata (Fig. 2.16). The growth had disappeared by the April and May 2006 samplings, replaced by fleshy macroalgal species. The slimy growth was absent during the February 2007 sampling. The prolific growth of the unidentified microorganism may have been opportunistic after the dissipation of the red tide, when other competing species had perished as a result of the *K. brevis* bloom. Follow-up work after a future red-tide event might yield more insight into the algae/cyanobacteria dynamics in benthic WFS communities.

Figure 2.16. Photograph depicting conditions at FWRI1 in February 2006. Anomalously high percent cover of the “Macroalgae” category was attributed to this unidentified algal growth. The growth had disappeared by the April 2006 sampling. The coral in the picture is *Solenastrea hyades*.

Two other categories also displayed significant seasonal differences. Percent cover of Porifera (including clionids and *Dysidea*. spp.) was significantly lower in the spring as compared to fall values (Fig. 2.8; Table 2.6). Poriferans appear to be particularly sensitive to red-tide disturbances (Chapter 4) such as the event that occurred
during the majority of 2005, and dissipated a few months prior to the commencement of this study. Low percent cover of poriferans in the spring of 2006 could be attributed to mass mortalities during the 2005 red tide. Populations began to recover in late 2006 and into 2007. By the fall 2007 samplings, average cover at both sites hovered between 5% and 7%. The majority of seasonal differences in cover of poriferans could be attributed to red-tide effects as well as the “masking” effects that fleshy macroalgae might have in the digital photographs taken in the spring.

Table 2.2 displays the list of 12 scleractinian and 1 milleporid corals identified at Station B (1965-1976), FWRI1 and MT (2006-2007), and GOM artificial reefs (2005-2007). Although 13 corals were identified in the Hourglass Program, 4 of these were sampled infrequently over the 28-month period (Millepora alcicornis, Porites divaricata, Isophyllia sinuosa, and Astrangia poculata) and understandably do not appear in my digital photographs. There is further evidence that two additional species (Manicina areolata and Scolymia lacera) may no longer be present along shallow inner WFS ledges (W. Jaap pers. comm.). The only other species observed at Station B and not in my data set is Balanophyllia floridana. The different collection techniques are implicated in the discrepancies. Benthic-dredging techniques utilized in the historic work will tend to collect more species than digital photo transects, leading to the appearance of a more diverse coral community.

Percentage of transect photos in which juvenile corals were identified was the last major category to differ seasonally (Fig. 2.7). Percentages were lower in the spring as compared to other seasons, probably because high macroalgal cover during spring months effectively masked the recruits. Trends in juvenile corals are discussed further in
the section below, as the importance of recruitment processes to the resilience and survival of livebottom ledges, and those fish species that inhabit them, along the WFS can not be overemphasized.

There appeared to be significant spatial variability in the benthic data along the WFS ledges as evidenced by large ranges in percent cover within sampling times. Randomly-placed transects were used instead of permanently-fixed stations to maximize spatial coverage. However, it is important to note that ledges along the WFS are livebottom areas, meaning that their biotic cover is patchy in nature as compared to “traditional” coral reefs. The difference in percent cover of the major categories varied immensely from transect to transect during certain samplings, indicating that a greater sampling effort (more random transects) would benefit future studies seeking to quantify livebottom communities along the WFS.

2.7.2. Juvenile Coral Recruitment
Over the last few decades, studies on reproduction and ecology of reef corals have elucidated the sensitivity of these processes to natural and anthropogenic stresses (Hughes 1994; Wolanski et al. 2003; Bellwood et al. 2004). The recruitment of sexual and asexual individuals plays a major role in the dynamics of reef ecosystems and can ultimately play a role in both the short and long-term recovery (or decline) of a reef system. Much more study of coral larvae and recruitment is needed on WFS livebottom habitats, including origins/reservoirs, spatial and temporal recruitment scales, and juvenile survival rates, as there is little known about these processes.

In the Caribbean, several studies have shown that reef topography, depth gradient, oceanographic and environmental processes, as well larval dispersion (i.e., life histories),
contribute to the abundance, survivorship and distribution of coral recruits (Bak and Engel 1979; Chiappone and Sullivan 1996; Edmunds et al. 2004). There are a number of upstream sources of larvae to the WFS, resulting from the inherent interconnectivity of the GOM via the Loop Current and its associated eddies and spin-offs (Berger et al. 1996; Sahl et al. 1997; Walker et al. 1997; Nowlin et al. 1998). Lugo-Fernandez et al. (2001) demonstrated that the Flower Garden Banks (FGB) in the northern GOM contain a repository of coral species that may function as a regional source of larvae. More likely, larvae come from other coral-inhabited ledges along the WFS.

Although adult forms of corals are relatively easy to identify in digital photographs, it is very difficult to distinguish juvenile coral species. Photo-quadrats and transects are not optimal methods for recruitment studies, and tend to underestimate the number of juveniles as compared to in situ visual survey methods (Edmunds et al. 1998). Therefore, I made no attempt to identify the individual coral species in the photographs. Instead, monthly juvenile distributions were assessed as a function of the average percentage of photographs in the transects (n=3) that contained at least one juvenile coral (<2 cm in size).

The sizes of the juveniles varied from approximately 2 mm in diameter up to the 2 cm limit, as smaller juveniles were indistinguishable in the photographs. Juvenile corals were present in all three 15 m transects during all sampling times at both FWRI1 and MT, although an analysis of photographs from November and June indicate that juvenile coral sizes in June photographs were, on average, larger than November sizes. Many GOM and Caribbean coral species spawn after a full moon or in concert with maximum water temperatures from July through September (Szmant 1986; de Graaf et al. 1999). Since
most coral larvae are competent within 3-10 days and competence periods can last as long as 120 days (Fadalllah 1983; Wilson and Harrison 1998), settling of some larvae along WFS ledges could begin immediately after spawning as early as July, particularly for brooding species whose larvae tend to settle in close proximity to the adult colonies. Larval settling could last through January for the larvae that travel long distances (i.e., from the FGB). Given the general growth rate of 12 mm yr\(^{-1}\) for small corals (Bak and Engel 1979; Van Moorsel 1988), it is plausible that detection of juveniles in photographs could occur within 2-3 months of spawning, which corresponds to the November sampling (assuming that settling of larvae occurred some time around August). Smaller size classes of recruits (between 2 and 4 mm) in November samples as compared to June (8 to 10 mm) corroborate these recruitment time scales and correspond to the peak spawning times of a number of the brooding and broadcast-spawning species.

The lower numbers of juveniles in the spring months coincided with times of increased macroalgal cover (Figs. 2.4 and 2.7), particularly in May when macroalgal cover exceeded 60% at both sites. Accordingly, the cover of bare substrate decreased in the month of May and increased again towards the end of the year (Fig. 2.5). The growth of macroalgae could obscure the juvenile corals, again indicating that photographic methods have limited resolution, especially in areas where seasonal changes in benthic cover are substantial.

The percentage of photos containing juvenile corals has a similar range at both sites although there are differences during certain samplings (Fig. 2.7). The random placement of transects and the small number of transects limits data resolution. More
detailed analyses of juvenile patterns were precluded by the methodology, although the data did unveil some interesting ideas and hypotheses which are discussed below.

Rezak et al. (1990) proposed that the installation of thousands of oil and gas platforms along the northwest and central shelf of the GOM could provide stepping stones for corals to advance eastward across the Gulf, extending their range through areas where substrate had previously been unsuitable for settling and growth. The natural ledges along the WFS, with their limestone outcrops, function as stepping stones in their own right, as they provide suitable substrate for the larvae of hardy coral species that originate in coral repositories such as the FGB, the Florida Middle Grounds, and other ledges along the WFS. WFS natural ledges are an essential link in the GOM basin-wide system connecting Caribbean coral larvae entrained in Loop Current rings (Biggs 1992) to the FGB and on to the rest of the southeastern GOM (Lugo-Fernandez et al. 2001).

It is important to note that the basin-wide larval interconnectivity studies are not limited to just coral larvae. Lee et al. (1992) demonstrated that eddies also remove and displace fish larvae in the Florida Current, affecting Florida Keys’ species, particularly those that spawn in the water column. The mechanisms that prevail in the GOM have basin-wide implications for all larval organisms. The availability of substrate and habitat, as well as suitable environmental conditions and biological forces (e.g., predation and competition), are the keys to successfully recruiting new, sexually-produced larvae. Lugo-Fernandez et al. (2001) proposed that the strategic placement of artificial structures along the dispersing routes from the FGB could strengthen coral strongholds, and decrease the distance between sources of coral larvae in the GOM. Dupont (2008; see Chapter 3 of this dissertation) evaluated a set of artificial reefs designed to mimic natural
WFS ledge relief deployed in approximately 20 m depth in previously unsuitable (sand over limestone) habitat. Within 4-5 years of deployment, a robust epibenthic community of corals (smaller species such as *Cladocora arbuscula* and *Phyllangia americana*), poriferans, echinoderms, ascidians, and algae had developed on the artificial substrate. Seventy-one species of fish (demersal and pelagic) were found to be associated with the structures, providing evidence that artificial reef placement in the GOM may be an effective way to boost larval survival between upstream and downstream sources and sinks.

Lugo-Fernandez et al. (2001) suggest that if coral populations of the FGB continue to thrive, they could contribute to the long-term recovery of damaged reefs of the southern GOM (Tunnel 1992) and the Florida Keys (Porter and Meir 1992) or perhaps become a coral refuge or repository. Larval supply, recruitment, and survival are important steps for resisting phase shifts to degraded alternate states and provide valuable information on the reproductive success of species (Bellwood et al. 2004). An understanding of coral recruitment patterns and juvenile survival over time are essential to understanding ecological and physical processes that control population growth, distributions, and variability of community structures in time and space. It will also help us better understand how these systems fare after a natural or anthropogenic disturbance event.

### 2.7.3. Fish Assemblages

Fish assemblage data are notoriously difficult to collect and analyze, particularly when resources, manpower, and logistics prevent the collection of large, statistically robust data sets. The Bohnsack method (Bohnsack and Bannerot 1986) was chosen for
its ability to collect standard quantitative data on reef-fish assemblage structure over a
variety of habitats in an efficient and effective manner. However, statistical robustness of
the data depends on large sample sizes which, due to logistical issues (e.g., time and
personnel constraints, dive limits), were often impossible to collect in my study.
Therefore, the data presented in this paper represent an overview of shallow inner shelf
fish assemblages but are by no means comprehensive.

A total of 47 fish species were observed over the 22-month study period at
FWRII and MT. Hourglass Program collections enumerated 59 species at natural ledge
Station B over the 28-month sampling period between 1965 and 1967 (Table 2.5). Only
12 of the species were observed in both the historic study and my study. Sampling
techniques likely account for these observed differences. During the Hourglass Program,
a flat trawl and a balloon trawl were dragged along the bottom for 15-30 minute
intervals. The resulting collections represent a community heavily skewed to demersal
species such as flounders (e.g., Bothus robins, Cycloplectus fimbriata, Etropus crossotus,
Etropus rimusus, and Syacium papillosum) and searobins (e.g., Prionotus spp.), while
Bohnsack surveys tend to account for pelagic species, along with demersals. Although
the sampling techniques were very different, the combination of survey data yield a more
comprehensive species list for shallow inner WFS ledges. The list can function as an
ecological baseline for scientists and marine managers.

Additional data from artificial reefs (designated with a number “3”) at comparable
depths/locations are also displayed in Table 2.5. Seventy-one species were observed at
artificial reefs with 24 exclusively observed at the artificial reefs. The majority of the 24
additional species are tropical/subtropical species and include various angelfish (e.g.,
Holacanthus ciliaris, Holacanthus townsendi, Pomacanthus arcuatus, and Pomacanthus paru) and smaller tropicals (e.g., Calamus bajonado, Chaetodon sedentarius, Thalassoma bifasciatum, Hypoplecetus uniclor, Scartella cristata, and Chasmodes saburrae). The artificial reefs are located south of FWR11 and MT (Fig. 2.1) and experience warmer water temperatures, as evidenced by average temperatures in March 2007 of 19.1°C and other consistently warmer months.

A multidimensional scaling ordination of samplings at FWR11 and MT, relating their respective fish assemblages (Fig. 2.13), tentatively groups the samples by season. An ANOSIM test was employed to test for significant seasonal differences. Results indicate that the fish assemblage during the summer differed from all other seasons (Table 2.7). Abundances of Halichoeres bivittatus, Diplectrum formosum, Haemulon plumierii, and Serranus subligarius were consistently the top four contributors to seasonal dissimilarities. The reproductive habits, low population doubling times, mobility, and resiliency of these species may contribute to seasonal differences, as they quickly evacuate and re-populate areas in response to changing environmental conditions and biological forces (e.g., aggregate spawning, food supply, or predator to prey ratios).

Halichoeres bivittatus are protogynous hermaphrodites that form leks (mating arenas) while spawning; peak spawning occurs in May or June (Allsop and West 2003). Haemulon plumierii peak spawning activity has also been reported in May (Murie and Parkyn 1999), although spawning has also been shown to occur year-round in this species, particularly in its southernmost distribution (Munro et al. 1973). Diplectrum formosum and S. subligarius are synchronously hermaphroditic, with short population doubling times (<15 months), hence are highly resilient (Froese and Pauly 2008). Benthic
invertebrates (mollusks, crabs, worms, shrimp, gastropods, and crustaceans) and other smaller fishes tend to be the major food source for the four discriminating species. These four species may move from ledge to ledge along the WFS, following optimal environmental conditions and food sources as they become available and avoiding stressful environmental conditions such as hypoxia as they occur.

Future work on fish assemblages along the WFS ledges should incorporate a number of sampling methods and collection gears. The combination of data from three studies in comparable depths within a small, geographic area revealed a diverse (113 species) fish community. Further studies are needed to quantify populations of fishes and determine their spatial and temporal distributions. Smaller, non-commercial species (including the majority of those enumerated in this paper) may be important sources of food for the commercially-important species that utilize natural ledges along the WFS throughout their life cycles. Managers and conservationists should consider these areas as inherently important to sustaining the economically-important fisheries of the eastern GOM.

2.7.4. Marginal West Florida Shelf Assemblages and Disturbance

In this section, I discuss the inherent marginal or transitional conditions of the eastern GOM and the effects of regular disturbances as they pertain to the development of livebottom assemblages along the WFS ledges. Marginal reef assemblages reflect the effects of steady-state or long-term average environmental limitations (Guinnotte et al. 2003). The WFS ledges are situated where first-order determinants of global reef distribution (temperature, salinity, nutrients, light, and aragonite saturation state) are marginal (Kleypas et al. 1999).
The definition of “marginal” with respect to coral reefs has been discussed in depth and Guinnotte et al. (2003) suggest that marginality may be defined in three ways: a) in a purely statistical sense, identifying the subset of reef communities or conditions that are near the extreme of a particular suite of environmental variables or community conditions; b) in terms of organism and community condition (cover, composition, diversity, health) or metabolism; c) on the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms. Hardbottom outcrops and their associated livebottom assemblages along the shallow inner WFS can be defined as marginal under the second and third definitions.

Under the second definition it is apparent that although WFS livebottom assemblages are home to an abundance of benthic flora and fauna including scleractinian corals and calcifying algae such as *Halimeda* spp, they are by no means comparable to accretional coral reefs where high cover and diversity of zooxanthellate, scleractinian corals with hydrocorals and reef-associated calcifying algae epitomize the definition of a non-marginal reef community (Guinnotte et al. 2003). Under the third definition, there is ample evidence that a number of first-order determinants (e.g., temperature, nutrients, salinity, light, and aragonite saturation state) defined by Kleypas et al. (1999) are at or near minimum or maximum limits for coral-reef development along the eastern GOM.

Guinnotte et al. (2003) defined high-temperature, thermally stressed areas as those experiencing temperatures >31.1°C. Temperatures >31.1 °C were sustained for about a month between mid-August and mid-September at FWRI1 and MT in 2007. Increased
temperatures correspond to increased metabolic rates (Nichol 1967) and as a result, organisms inhabiting these areas may be particularly sensitive to the development of hypoxic conditions during severe red-tide events. Those areas exposed to temperatures <18 ºC, especially for long periods of time, were also defined as thermally stressed by Guinnotte et al. (2003). Bottom temperatures at FWRI1 and MT were <18 ºC for the first 2 weeks in March 2007, and were also near this range throughout most of February. These results indicate that the inner WFS ledges experience marginal temperature conditions for reef development. Salinity ranges at the sites are, however, within normal reef limits, although about 2 ppt lower than typical for Florida Keys reefs, which could negatively affect the aragonite saturation state (discussed below).

Nutrient concentrations along the WFS are also marginal for reef growth. Kleypas et al. (1999) averaged values across reef locations and found that 90% of reef locations have <0.60 µmol L⁻¹ nitrate and <0.20 µmol L⁻¹ phosphate. Ambient nitrate concentrations during non-bloom periods within 5 km of the WFS coast are <0.5 µmol L⁻¹. Nitrate limitations along the WFS can, however, be alleviated when diazotrophs (Trichodesmium spp.) bloom in response to iron-laden Saharan dust events (Lenes et al. 2001). Approximately 50-100% of the dissolved organic nitrogen (DON) excreted by the Trichodesmium is in the form of amino acids, which help mitigate nitrogen limitation for other members of the phytoplankton community and the microbial loop, including Karenia brevis (red tide). Moreover, Florida is a phosphatic province and phosphorous species are rarely limiting, indicating that livebottom communities are near marginal nutrient limits in non-bloom conditions and can become inundated with nitrogen during
blooms, along with increased carbon input (Vargo et al. 1987). In addition algae blooms can have a shading effect (Okey et al. 2004).

Hallock and Schlager (1986) discussed the importance of water transparency and light intensity at depth as they pertain to coral-reef development and growth. Branching corals require approximately 60% of surface light, head corals require about 20%, and plate corals require 4%. Percentage of light reaching livebottom assemblages along the shallow inner WFS (17 m depth) over my 22-month study averaged 6.4%, with a maximum of 33% and a minimum of 2.3%. The WFS assemblages are exposed to variable light intensities, with optimal light for photosynthesis occurring during the spring, when macroalgal cover increases, and lower light intensities dominating in the fall.

Aragonite saturation, the last of the first-order determinants of reef distribution as defined by Kleypas et al. (1999), covaries with temperature and salinity, from maximum values near the equator to minimum values outside the 20°-30° latitude belt. FWRII and MT are situated between 27° and 28° latitude, and therefore near the lower aragonite saturation limits but not outside of them. The lower salinity (~2 ppt < Florida Keys reefs) likely decreases aragonite saturation and thereby contributes to marginality for scleractinian corals among the WFS livebottom communities.

West Florida Shelf hardbottom communities are, for the most part, exposed to conditions that are above the “lower limits” of salinity, light, and aragonite saturation for reefs, yet these are not reef-forming areas. This suggests that other factors prevent these communities from building reefs. The first possibility is that second-order determinants play an important role in limiting reef growth in this region. Second-order determinants include biological variables (i.e., species diversity and larval sources) and hydrodynamics.
(i.e., wave and tide action, sediment movement) which act on a regional scale (Kleypas et al. 1999). Larval availability, recruitment, and survival do not seem to be limiting factors in the development of livebottom communities, as long as suitable settling substrate is available. Hydrodynamic influences are very limited along the shallow inner WFS as these ledges are situated at sufficient depths to avoid strong wave or tide action and resulting sediment movement. The patchy sediment distribution and close proximity of sediment types to their source, suggests that storms are not responsible for the large-scale sediment redistribution on the west central inner Florida shelf, but may be locally important (Brooks et al. 2003). Small-scale, periodic mobilization and redistribution of sediment by storms has been shown by Twichell et al. (2003). However, it does not appear that second-order determinants are the primary causes of the lack of reefs along the WFS.

Another possibility is that the combination of thermal stress, abundant nutrients, and times of lowered light levels may cumulatively and synergistically prevent coral reef development. A third suggestion, specific to WFS hardbottoms, is that the chronic stresses imposed by the lower limits of certain first-order determinants, combined with acute disturbances such as red tides and storm/hurricane events, may restrict reef development, limiting livebottom species to those that are hardy, weedy (quick to recruit or migrate back after a disturbance), and tolerant of persistent chronic and repeated acute disturbances.

The spatial scale of acute disturbance affects ecosystem resilience (Sousa 1985), along with factors such as the frequency and duration of the disturbance (Nystrom et al. 2000). Estimates from FWRI indicate that approximately 5600 square kilometers of
benthic communities may have been affected by the 2005 red tide and the hypoxic/anoxic conditions (FWRI 2005). Table 2.8 places red tide events and associated hypoxic/anoxic conditions into context with other natural disturbances’ spatial extent, frequency, and duration. It also describes the level within the ecosystem that is most affected (individual, population, community, or ecosystem) and the primary disturbance mechanism(s).

Although natural disturbances such as red tides and hurricanes can be detrimental to communities at large spatial scales (10-1000 km), new substratum becomes available at various temporal and spatial scales (Connell 1978), increasing the chance of recruitment and survival at the individual/population level. Patches of opportunity are opened up for renewal, development, and evolution as a result of periodic disturbances (Holling 1996).

Regional conditions that are marginal between temperate and tropical provinces along with chronic and acute disturbances in the eastern GOM influence community structure on livebottom ledges. The episodic occurrence of severe red tides, in conjunction with other stochastic factors such as fluctuating sea temperatures, turbidity, and hurricanes, likely prevents the development of coral reef assemblages. Should the frequency and severity of disturbances decrease, different community structures might develop, possibly a more “coral reef-like” community. At present, hardbottom ledges, with their marginal environments, select for hardy species that can either survive the persistent marginal conditions and intermittent large-scale acute disturbances (e.g., *Solenastrea hyades* corals which temporarily retract their polyps or bleach in response to a disturbance, but quickly recover after the disturbance has been alleviated) and/or whose r-selected reproductive characteristics enable them to quickly recruit to available substrate and utilize open niches (e.g., *Diplectrum formosum* and *Serranus subligarius*).
Table 2.8. Natural disturbances acting on WFS livebottom areas. The “level influenced” column specifies whether benthic (B) or fish (F) levels are most influenced by the respective disturbance process.

<table>
<thead>
<tr>
<th>Process</th>
<th>Spatial Extent</th>
<th>Frequency</th>
<th>Duration</th>
<th>Level Influenced</th>
<th>Mechanism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predation and grazing</td>
<td>1 m</td>
<td>Days-Months</td>
<td>Minute-Days</td>
<td>Individuals (B,F)</td>
<td>Mortality</td>
</tr>
<tr>
<td>Bioerosion</td>
<td>1-10 m</td>
<td>Months-Years</td>
<td>Days-Weeks</td>
<td>Individuals (B)</td>
<td>Creation and collapse of scarped hardbottom</td>
</tr>
<tr>
<td>Bleaching/Disease</td>
<td>1 m</td>
<td>Months-Years</td>
<td>Days-Weeks</td>
<td>Communities (B)</td>
<td>Physiological weakening, mortality</td>
</tr>
<tr>
<td>Storm events</td>
<td>1-10^2 km</td>
<td>Months</td>
<td>Hours</td>
<td>Individuals (B) Populations (B)</td>
<td>Sediment movement-burial and exposure</td>
</tr>
<tr>
<td>Hurricanes</td>
<td>10-10^3 km</td>
<td>Months-Decades</td>
<td>Days</td>
<td>Communities (B)</td>
<td>Physical disturbance</td>
</tr>
<tr>
<td>Seasonality (temperature, light, etc.)</td>
<td>Regional</td>
<td>Annual</td>
<td>Months</td>
<td>Individuals (B,F) Populations (B,F)</td>
<td>Light limitation, algal blooms, energetics</td>
</tr>
<tr>
<td>Red tides</td>
<td>10-10^3 km</td>
<td>Months-Years</td>
<td>Months</td>
<td>Individuals (B) Populations (F)</td>
<td>Brevetoxin effects</td>
</tr>
<tr>
<td>Severe red tides resulting in anoxia</td>
<td>10-10^3 km</td>
<td>Years-Decades</td>
<td>Months-Years</td>
<td>Communities (B,F) Populations (B,F)</td>
<td>Brevetoxin and anoxic effects – exposure of bare substratum</td>
</tr>
<tr>
<td>Sea-level or temperature change</td>
<td>Global</td>
<td>10^4 - 10^5 years</td>
<td>10^3 - 10^4 years</td>
<td>Communities (B,F) Ecosystems (B,F)</td>
<td>Chronic stress – thermal, light, aragonite saturation etc.</td>
</tr>
</tbody>
</table>

Kleypas et al. (2001) suggest that future aragonite saturation state reductions will gradually lead to less carbonate accumulation, slower coral extension rates and weaker skeletons, and possibly to reduced cementation and reef structure stabilization. This
suggests that non-framebuilding communities will become more common. They also postulate that if these areas are exposed to episodic extremes (i.e., thermal stresses, nutrient pulses), increases in mortality could be expected to occur. The livebottom assemblages of the WFS may represent the future state of western Atlantic/Caribbean coral reefs that are currently at or near their marginal limits. The good news is that WFS ledge organisms, as individuals and populations, appear to have acclimated to intermittent episodic disturbances, giving some hope to the survival of other communities that reach the “tipping point” over to non-framebuilding reefs, after some period of acclimatization and selection.

Recruitment of sexually or asexually-produced individuals is very important to the recovery of livebottom and coral-reef assemblages after a disturbance. Recruitment enhancement plans, such as the placement of artificial reefs along the WFS, should be seriously considered as a mechanism to enhance both epibenthic and fish communities along the natural ledges. Enhancing communities from the benthos up will increase productivity at the upper trophic levels, ensuring the preservation of important commercial and recreational fisheries in the eastern GOM. The importance of benthic communities to the overall productivity of the WFS should not be ignored or, worse yet, negatively affected by activities at the surface or in the pelagic zone. Appropriate considerations for livebottom areas, which occupy >50% of the shallow inner WFS, must be incorporated into any construction, management, and conservation plans.
3. Artificial Reefs as Restoration Tools: A Case Study on the West Florida Shelf

3.1 Abstract

Artificial reefs are one of a number of tools that should be considered by scientists and managers when planning coastal zone restoration and/or mitigation projects. In this paper, the details of one project from the West Florida Shelf are presented. Two types of artificial reefs were used to mitigate pipeline construction impacts on natural hardbottom ledges in the eastern Gulf of Mexico. The project’s primary objective was to avoid the paradigm of building artificial reefs as fish attraction devices, and to instead implement a design that would mimic, not augment, natural hardbottom conditions. Fish assemblage parameters (species richness and commercial fish abundances) were compared between the artificial habitats and natural hardbottom reference sites. Results indicate that species richness trends are similar among artificial and natural reefs, while certain commercial fish abundances are significantly higher on the artificial reefs. Recommendations for future restoration/mitigation projects using artificial reefs are discussed.
3.2 Introduction

The modern era of artificial reef-building is barely a half-century old, but its brief history has included extraordinary advancements in structural designs, technologies, and techniques, as well as changes in uses, stakeholder interests, management schemes, and evaluation criteria. Artificial reefs are defined as one or more objects of natural or human origin that are purposefully submerged to influence biological, physical, or socio-economic processes related to marine resources (Jensen 1997; Seaman 2000). Artificial reefs have been used most prominently for fisheries harvest enhancement though they have been employed globally in a variety of other coastal management schemes including aquaculture in the Adriatic Sea (Fabi et al. 1989), enhancement of recreational diving and tourism opportunities throughout the United States (Milon 1991; Ditton et al. 1999), habitat rehabilitation in the Maldives (Clark and Edwards 1994), and prevention of trawling in Europe (Reilini 2000).

One of the more recent applications of artificial reefs has been for environmental mitigation purposes, especially in coastal areas where physical damage by storms, exposure to toxic phytoplankton blooms, destructive fishing practices, construction and dredging projects, and chemical pollutant contamination are among a few of the many natural and anthropogenic causes of habitat degradation. In the restoration of ecosystems after such damage, especially where physical structure provides added benefits (e.g., habitat or shelter) to the ecosystem, artificial reefs represent one potentially useful restoration tool (Pickering et al. 1998). Physical structure in an ecosystem can be achieved in a number of ways, and definitive progress has been made since the early 1900s when artificial reefs were built as “a hit-or-miss dumping operation of unsightly
scrap material” (Dean 1983) such as tires and car bodies. While numerous studies have reported on the effectiveness of artificial reefs in aggregating fish (Randall 1963; Buchanan 1973; Stone et al. 1979), relatively few studies discuss the design, location, planning, and evaluation of artificial reefs (Bohnsack et al. 1994) in relation to specific project objectives such as mimicking natural habitat for mitigation purposes or enhancing targeted species and their supporting community structures. It is increasingly becoming recognized that this is one of the major areas where further work is needed: determining the relative benefits of different designs for production purposes (Bohnsack and Sutherland 1985; Seaman and Sprague 1991; Pickering and Whitmarsh 1997) and in meeting stated project objectives.

In this paper, a detailed overview of one mitigation/restoration project on the central West Florida Shelf in the eastern Gulf of Mexico will be presented. The goal of the paper is to discuss the pertinent information of an artificial reef study as defined by Baine (2001) including details on the project’s objectives, reef site, environmental conditions, design, monitoring, results and performance evaluation, and legal framework. Conclusions will be drawn regarding the success of the design and planning of the particular set of artificial reefs in fulfilling management goals and objectives, and explanations will be given for observed failures in project execution. Recommendations for future mitigation/restoration projects using artificial reefs in the Gulf of Mexico, and in coastal areas worldwide, will be discussed.
3.3 Artificial Reef Project Background and Objective

In 2001, Gulfstream Natural Gas System, L.L.C. (heretofore referred to as GNGS) constructed a 90-cm diameter pipeline across the Gulf of Mexico (GOM) to transport natural gas from plants in Mississippi and Alabama to markets in central and southern Florida. Under the Federal Mitigation Plan, GNGS was required to measure, mitigate, and monitor construction impacts to hard/live bottom benthic habitats in the GOM. The overall objective of the mitigation sites was to mimic the natural habitats (fish and benthic communities) that were either directly impacted by pipeline construction activities or indirectly affected by increased water column turbidity and sedimentation. A secondary objective was to evaluate the efficacy of two different reef designs in achieving the primary goal.

3.4 Artificial Reef Site Description

Compensatory mitigation for livebottom impacts caused by pipeline construction included the installation of six artificial reef sites on the seafloor (16-20 m depth) in Federal Waters, 19-25 km west of the mouth of Tampa Bay, FL (coordinates of sites have not been publicized to ensure that natural community development occurs without the impacts of recreational diving and fishing activities). Three of the six sites were created by dispersing approximately 13,000 metric tons of limestone boulders (>1 m diameter) in 150 m x 150 m areas. These will be referred to as limestone boulder (LB) sites. Three additional sites consisted of grouped placement of pre-fabricated 1.8 m wide x 2.7 m long x 1.8 m tall reef modules (Fig. 3.1; designed by H. Hudson, U.S. patent #5215406) constructed of limestone in a concrete matrix in 150 m x 150 m areas. A total of 153
modules were dispersed among the three sites and will be referred to as reef module (RM) sites. All six artificial reef sites were deployed near natural livebottom areas and on sand bottom that did not exceed a thickness of 0.6 m.

Figure 3.1. Artificial reef module designed by H. Hudson (U.S. patent #5215406) and constructed of limestone in a concrete matrix (each module occupies 8.7 m³). The cavity passes through the entire length of the module. Three groups of 17 modules were placed at each of the three Reef Module (RM) artificial reef habitats.

Ten Reference (R), or control, sites were established in close proximity to the artificial reefs, in unimpacted livebottom areas. These sites were monitored consistently along with the artificial reefs sites and the data will be used for comparative analyses as no comparative, quantitative community data are available from the impacted sites prior to the advent of construction activities. The project’s lack of pre-construction data should be noted and remedied in future mitigation efforts. Consistent measurements of abiotic parameters, habitat characteristics, and biotic data should be performed prior to construction activities for a sufficient duration of time (length of time will vary among
projects and should be determined prior to start of project) as these data allow for effective evaluation of a project’s progress towards achieving the stated objective.

3.5 Environmental Conditions

Seasonal (summer and winter) abiotic parameters (temperature and Secchi depth), and habitat characteristics (rugosity and depth) were measured and the results are displayed in Table 3.1. Surface roughness and vertical complexity were measured using a Rugosity Index calculated as the ratio of a fixed length of chain (9.6 m) to the linear distance traversed by the chain. Rugosity measurements were significantly different among all three habitat types (Kruskal-Wallis H=24.3, p=0.001) with LB sites consistently displaying highest surface roughness and R sites the lowest. All other abiotic parameters were not significantly different among the sites within the respective sampling.
Table 3.1. Abiotic and habitat characterization data summary presented as mean (n=10) values (± S.E). Data were recorded during each of the 5 sampling times.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Limestone Boulders (LB)</th>
<th>Reef Modules (RM)</th>
<th>Reference Stations (R)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water Depth (m)</td>
<td>19.5 (1.1)</td>
<td>16.9 (0.2)</td>
<td>18.5 (0.9)</td>
</tr>
<tr>
<td>Rugosity Index</td>
<td>1.53 (0.04)</td>
<td>1.36 (0.08)</td>
<td>1.13 (0.03)</td>
</tr>
<tr>
<td>Water Temperature (ºC)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer 2005</td>
<td>26.5 (0.5)</td>
<td>27.3 (0.1)</td>
<td>26.9 (0.2)</td>
</tr>
<tr>
<td>Winter 2005</td>
<td>22.2 (1.0)</td>
<td>22.8 (0.7)</td>
<td>20.7 (1.2)</td>
</tr>
<tr>
<td>Summer 2006</td>
<td>29.1 (0.3)</td>
<td>29.6 (0.2)</td>
<td>29.4 (0.4)</td>
</tr>
<tr>
<td>Winter 2006</td>
<td>18.2 (0.7)</td>
<td>18.2 (0.6)</td>
<td>18.1 (0.4)</td>
</tr>
<tr>
<td>Summer 2007</td>
<td>26.7 (0.8)</td>
<td>26.3 (0.5)</td>
<td>25.9 (0.5)</td>
</tr>
<tr>
<td>Secchi Depth (m)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer 2005</td>
<td>13.9 (0.5)</td>
<td>10.9 (0.4)</td>
<td>8.5 (0.4)</td>
</tr>
<tr>
<td>Winter 2005</td>
<td>9.0 (0.7)</td>
<td>7.3 (0.3)</td>
<td>9.8 (0.5)</td>
</tr>
<tr>
<td>Summer 2006</td>
<td>17.6 (2.1)</td>
<td>9.6 (0.3)</td>
<td>12.9 (1.7)</td>
</tr>
<tr>
<td>Winter 2006</td>
<td>12.6 (0.8)</td>
<td>12.3 (0.4)</td>
<td>12.8 (0.7)</td>
</tr>
<tr>
<td>Summer 2007</td>
<td>10.5 (0.7)</td>
<td>9.4 (0.7)</td>
<td>9.8 (0.6)</td>
</tr>
</tbody>
</table>

aData are adapted from 5 GNGS reports (GNGS, 2005a; GNGS, 2005b; GNGS 2006a; GNGS 2006b; GNGS, 2007)

3.6 Artificial Reef Size and Design

The influence of artificial reef size and structure on species abundance and richness is an ongoing debate, as is the debate over whether increases in artificial reef fish biomass are a result of simple attraction to the structure versus new production (Pickering and Whitmarsh 1997). Results from numerous studies indicate that larger reefs, with greater habitat heterogeneity, tend to attract a greater number of persistent species and a higher biomass (Campos and Gamboa 1989; Bohnsack et al. 1994; Moffitt et al. 1989; Pickering and Whitmarsh 1997). Bohnsack et al. (1994) attributed the higher biomass densities on large reefs to larger but fewer individuals which out-competed or preyed
upon smaller individuals (including juveniles). They suggested that larger reefs may be better for aggregating large adult fishes, whereas smaller reefs are better for overall recruitment, as significantly higher settler mortality was observed at the larger reefs due to increased competition and predation from larger resident populations and larger individual fish (Bohnsack et al., 1994).

The GNGS reefs are all large artificial reefs, as compared to reefs in the Bohnsack et al. (1994) study and other work (Rounsefell 1972). The GNGS reefs were designed to mitigate pipeline effects in an equivalently-sized area, and provide habitat for adult fishes that may have been displaced due to construction activities. The six GNGS reefs each covered a similar spatial area (22,500 m²), but the design and layout of the reefs (LB and RM) were very different, allowing for statistical comparisons between species colonization trends and assessment of the efficacy of the two different reef types in mimicking natural trends. The LB sites were created by lowering approximately 13,600 metric tons of boulders (>1 m diameter) into the 22,500 m² areas. The boulders were strategically overlapped and stacked during deployment to provide various swim-through holes, crevices, and sheltered areas. The boulders were spread contiguously throughout the area, as opposed to the RM sites which consisted of the ordered placement of 51 modules per site (three groups of 17 modules), with approximately eight meters separating each module. Areas in between modules consisted of bare, unconsolidated substrate. Each module occupied 8.7 m³ and was designed with one crevice cut into the limestone at the top of the concrete matrix that extended through the entire module (Fig. 3.1).
The LB site design is more representative of natural substrates in the GOM (and other hardbottom or reef areas) which are comprised of various rock types with different physical relief, modified by the provision of secondary substrate (Pickering and Whitmarsh 1997). Small and large crevices are dispersed throughout the area and different orientations of the physical structure alter water flow regimes in the area. Though LB sites displayed greater structural complexity (Table 3.1), both the LB and RM sites were designed as low vertical relief (<3 m) artificial habitats to mimic the relief of the natural inner continental shelf which consists of 50% exposed hardbottom, superimposed with ledges or scarps up to 4 m in relief (Hine et al. 2003). It is important to note that, in this particular case study, the objective was not to enhance fishery harvests, but instead to mitigate losses to natural habitat through restoration of equivalent fish and benthic invertebrate populations. The use of low vertical relief designs in the GNGS work is not typical of other coastal artificial projects whose main objective is to attract and aggregate fish for fishing purposes through use of large, heterogeneous artificial reefs.

3.7 Monitoring Methods

GNGS collected data on epibenthic and fish communities as part of the monitoring portion of the Federal Mitigation Plan. This paper will focus on fish assemblage data, with further emphasis on commercial species, as reef fish abundances and diversities demonstrate a significant dependence on available habitat (Sale 1978; Moffitt et al. 1989; Pratt 1994). A qualitative overview of epibenthic macroinvertebrate and macroalgal communities are given in this paper and will be discussed in detail in
future publications, as their contributions to artificial reef performance evaluation is very significant.

Ten point-count censuses of the fish communities were conducted at each of the three habitat types (LB, RM, and R) in Summer 2005 (June), Winter 2005 (November 2005-January 2006), Summer 2006 (July-August), Winter 2006 (December 2006-March 2007), and Summer 2007 (June 2007). Censuses were conducted using the Bohnsack Point Count Method (Bohnsack and Bannerot 1986; Bohnsack et al. 1994). The data are summarized in five separate GNGS reports (GNGS 2005a; GNGS 2005b; GNGS 2006a; GNGS 2006b; GNGS 2007), but the author was granted access to the individual excel data files to further analyze temporal and spatial trends through inter-sampling and inter-habitat statistical analyses.

Total fish assemblage data were averaged (n=10) within each of the three habitats during the five sampling times. Species richness values were compared to determine whether temporal changes in fish assemblages followed similar patterns at the artificial reefs and reference sites.

Commercially important species were analyzed separately due to their importance to Gulf of Mexico fisheries management, conservation, and economy. Commercially important species were identified using The Gulf of Mexico Fishery Council (2005) commercial fishing species list. Temporal trends were ignored as the data were pooled with respect to habitat (n=50) with the goal of determining whether artificial reef sites differed significantly from reference sites. Analysis of Variance (ANOVA) followed by Tukey’s post hoc comparison tests were used to test for significant differences among each commercial fish species’ abundance means over the three types of habitat.
3.8 Results and Performance Evaluation

A total of 71 fish species were observed at the artificial reefs and reference sites over the course of the study. An index of species richness values at each of the three habitat types is shown in Figure 3.2. The data are part of a larger study that assesses the impacts of a massive *Karenia brevis* (red tide) bloom that passed through the GNGS areas shortly after the Summer 2005 sampling (Heil 2006; Dupont Chapter 4). Although the macroinvertebrate and fish communities at the artificial reefs and adjacent natural, reference sites were negatively affected by both the dinoflagellate toxin as well as the development of a bottom anoxic layer, the *K. brevis* bloom did provide a literal “blank slate” for comparing recolonization and recruitment patterns of communities at the artificial and reference sites. These comparative data are very useful in assessing and evaluating the artificial reefs’ efficacy in achieving the GNGS project’s primary goal: mimicking natural reef biotic composition and patterns. The secondary objective can also be accomplished as the two types of artificial reefs (LB and RM) can be statistically compared to the reference sites and to one another.
Figure 3.2. Species richness trends over the five samplings: Summer 2005 (S05), Winter 2005 (W05), Summer 2006 (S06), Winter 2006 (W06), and Summer 2007 (S07). The data are part of a larger study that assessed the effects of a *Karenia brevis* (red tide) bloom that passed through the area immediately after the Winter 2005 sampling, extirpating a majority of the benthos and altering the fish assemblage. Recovery trajectories of species richness at the three habitat types (RM – Reef Modules, LB – Limestone Boulders, and Ref – Reference) are very similar.

Fish species richness trends were very similar as declines of 50-65% were observed between the Summer 2005 and Winter 2005 samplings at LB, RM, and R sites (Figure 3.2). The number of species recovered to 80-124% of their original values by the Summer 2007 sampling, with similar recovery trajectories displayed at all three habitat types. The similarities between species richness patterns is a promising observation, as the LB and RM recovery trajectories appear to effectively mimic the R sites. LB sites did display consistently higher species numbers and abundances as compared to RM and R
sites during all samplings. These trends could be explained by the greater habitat heterogeneity and vertical relief inherent within the LB site design (Table 3.1). The high concentration of boulders in the LB areas (in contrast to the equally spaced groups of modules at RM sites), coupled with the presence of numerous protected areas and swim-through holes due to boulder overlap and stacking, would be expected to cater to a more diverse fish community as opposed to the lower relief, less spatially complex nature of the RM and R sites. Vertical relief within a structure varies turbulence patterns, water flow, sedimentary regimes (Pickering and Whitmarsh 1997) and larval settlement patterns, all of which promote a diverse community structure. The structural complexity of reefs, particularly the presence and variety of crevices (Luckhurst and Luckhurst 1978; Anderson et al. 1989), the proximity of neighboring modules, and the provision of secondary biotic space through bio-fouling (Palmer-Zwahlen and Aseltine 1994) have been shown to contribute significantly to species composition, colonization patterns, and biological productivity of reefs. It should, however, be noted that other studies have shown that certain fish do prefer less complex structures (Risk 1972; Sale and Douglas 1984) and if management plans call for the restoration or enhancement of these particular target species, rather than the overall fish assemblage, then vertical relief should be varied accordingly.

Of the 71 observed fish species, 12 are listed as commercially important or protected species according to The Gulf of Mexico Fishery Council (2005). These species are: *Mycteroperca microlepis* (Gag grouper), *Mycteroperca bonaci* (Black grouper), *Mycteroperca phenax* (Scamp grouper), *Epinephelus itajara* (Goliath grouper), *Epinephelus morio* (Red grouper), *Seriola dumerili* (Greater amberjack), *Balistes*
capriscus (Grey triggerfish), Lachnolaimus maximus (Hogfish), Lutjanus synagris (Lane snapper), Lutjanus griseus (Mangrove/Grey snapper), Scomberomorus maculates (Spanish mackerel), and Ocyurus chrysurus (Yellowtail snapper). ANOVA analyses and post hoc tests indicated that only five species’ abundances (M. microlepis, M. phenax, L. griseus, B capriscus, and L. maximus) were significantly higher (ANOVA F >12, p<.0001) at one or both of the artificial reef habitat types. The five species’ sampling distributions at the three habitat types, including median, interquartile range, upper and lower limits, and outliers, are plotted in Figure 3.3. The remaining seven species were observed infrequently, and the data were consistently classified as outliers with no significant differences observed among the three habitats. Several of the species that showed no variation in abundances among habitats (e.g., S. dumerili, S. maculates, O. chrysurus) are pelagic, migratory species that display less site fidelity and dependence on benthic habitats. These species are expected to benefit less from the placement of artificial reefs as compared to demersal, philopatric, habitat-limited, territorial, and/or reef-dependent species (Pickering and Whitmarsh 1997).
Figure 3.3. Sampling distribution plots (including median, interquartile range, upper and lower limits, and outliers) of the five commercially important fish species whose abundances were significantly higher (ANOVA F > 12.0, p < .0001) at the artificial reef habitat types (RM and LB) as compared to the natural hardbottom/reference (R) habitats. An additional seven commercial species displayed no significant differences among habitats.

The five species that preferred the artificial reefs (Fig. 3.3) are euryphagic carnivores, with a number of them feeding on benthic invertebrates and smaller fishes. The epibenthic communities on the artificial reefs were typically dominated (percent cover values > 60%) by algal species including cyanophytes and other filamentous algae, as well as rhodophytes (Gracilaria and Eucheuma spp), chlorophytes (Caulerpa mexicana, C. racemosa, Halimeda spp., and Udotea spp.), and other undistinguishable macroalgae. Sessile and slow-moving macroinvertebrates included scleractinian corals.

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(Cladocora arbuscula and Phyllangia americana), poriferans (Cliona spp.), and Echinoderms (Diadema antillarum and Astrophyton muricatum) which, along with bare substrate (rubble), accounted for the majority of the remaining benthic percent cover on the artificial reefs. The reference (R) sites, in contrast, were relatively devoid or sparsely colonized by epibenthic invertebrates and macroalgae.

Although mobile invertebrates, including mollusks, gastropods, and crustaceans, were not enumerated in the study, it is assumed that a diverse sessile macroinvertebrate and algal community on the artificial reefs could provide secondary substrate and shelter for mobile invertebrate fauna, hence enhancing food source availability for both carnivorous and herbivorous fish species. The preferential association of the five commercial species, as well as many of the other non-commercial fishes, with the vertical relief and substrate provided by the artificial reefs (particularly the LB sites) can be attributed to: 1) the provision of shelter and habitat (attractive to both juvenile and adult stages), and 2) the development of secondary substrate and epibenthic invertebrate communities that provide food sources.

The results from the fish assemblages indicate that the artificial reefs were effective in mimicking the natural hardbottom areas in the GOM in terms of species-richness trends and abundances of most commercial fish species. The GNGS artificial reefs were built as low relief structures to increase the environmental carrying capacity and biomass of the previously vacant areas, while maintaining and mimicking the integrity of natural hardbottom areas in the GOM as a means of environmental mitigation (i.e., avoiding the paradigm of artificial reefs as pure fish attraction devices).
3.9 Ecological and Legal Framework

The GNGS reefs were successful in fulfilling the project objectives due to a number of opportune situational conditions, within both the ecological and legal/management contexts. From an ecological standpoint, the abiotic conditions of the uncolonized substrates in the GOM are ideal for artificial reef placement and recruitment of thriving epibenthic and fish communities. The LB and RM sites were chosen in areas with less than 0.6 m of unconsolidated substrate (mostly fine quartz and biogenic sands), underlain with calcitic or dolomitic limestone (Obrochta et al. 2003) to minimize sinking of the artificial reef habitats. The depths of the reefs (>16 m) were sufficient to avoid displacement or movement due to wave and wind action during tropical storms and hurricanes as reported by divers that examined the reefs after a series of severe hurricanes passed through the GOM in 2004 and 2005. The complicated physical oceanographic dynamics of the region (wind and wave forces, tidal currents, Loop Current eddy intrusions, tropical storms, Tampa Bay influences, etc.) connect the GNGS sites to areas throughout the GOM as well as coastal and nearshore Florida state waters, in terms of larval supply, anthropogenic influences, nutrient supply, fluctuations in temperature, salinity, dissolved oxygen, and other important abiotic parameters that affect the health of ecosystems. The proximity of the GNGS artificial reefs to natural hardbottom areas provided an initial supply of adult fish that quickly colonized the areas, but future diversity patterns may vary considerably given the dynamics of the region, and should continue to be investigated.

From a legal or policy stance, the deployment of artificial reefs is often dependent on a complex array of permits and authorizations with the outcome a compromise
between the mandates and agendas of numerous local, national, and international agencies (Pickering et al. 1998). The ability to award a permit or lease and the conditions attached to the award, depend on how the proposed project fits within the legislative and policy frameworks governing the actions of the agencies involved and the use of coastal areas (Pickering et al. 1998). Three permits, with subsequent modifications, were issued to GNGS for construction and operation of the pipeline. Permits for Federal waters were issued by the U.S. Army Corps of Engineers and Minerals Management Service. The Florida Department of Environmental Protection issued a permit for operations in Florida State waters. Extensive discussion, collaboration, and compromise among agencies was required but the resulting permits, and subsequent modifications, ensured that proper construction, operation, mitigation, and monitoring activities ensued in the GOM and along the West Florida Shelf. The site placement of the GNGS reefs (i.e., in Federal waters and at sufficiently deep depths) avoided many of the issues that usually accompany deployment of artificial reefs in coastal areas including provisions for the safety of navigation, cables and pipelines, coastal defense, and development control (Pickering et al. 1998). The issue of regulation of fishing and diving activities on the GNGS reefs has been avoided, because the coordinates for the sites are not available to recreational anglers, dive charters, or the general public, thereby allowing the artificial reef sites to be monitored without the influence of anthropogenic pressures.

3.10 Conclusion

Coastal managers along the West Florida Shelf, and other coastal areas worldwide, should consider artificial reefs to be one of a number of available management tools in
future mitigation and restoration projects, although it is essential that projects be evaluated on a case-by-case basis so that coastal managers define and execute a plan that fits their specific area’s environmental, economic, and social needs as well as the available resources. Case studies of various artificial reef projects are important in elucidating planning schemes, personnel and agency structures, resource needs, management, monitoring, and enforcement techniques that make certain projects successful, where others fail. Baine (2001) attributed the failure of most artificial reefs in meeting project objectives to seven major issues: siting, size, stability, cost, inadequate monitoring, unmanaged local use, and the influence of external climatic factors. Of these seven proposed causes of failure, only the influence of external climatic factors is beyond the scope of general planning and management. The other six factors are essential components to a coastal management scheme that employs the use of artificial reefs, and it is essential that managers consider and evaluate these in detail.
4. Ecological Impacts of the 2005 Red Tide on Artificial Reef Epibenthic Macroinvertebrate and Fish Communities in the Eastern Gulf of Mexico

4.1 Abstract

A harmful algal bloom (red tide) and associated anoxic/hypoxic event in 2005 resulted in massive fish kills and comparable mortality of epibenthic communities in depths less than 25 meters along the central west Florida shelf. There is a robust body of information on the etiology of red tide and human health issues; however, there is virtually no quantitative information on the effects of red tide on epibenthic macroinvertebrate and demersal fish communities. An ongoing monitoring study of recruitment and succession on artificial reef structures provided a focused time series (2005 to 2007) before and after the red tide disturbance. Radical changes in community structure were observed after the red tide. Scleractinian corals, poriferans, and echinoderms were among the epibenthos most affected. Fish species richness declined by >50%, with significant reductions in the abundances of most species. Successional stages were monitored over the next two years; stages tended to follow a predictable progression and revert to a pre-red tide state, corroborating previous predictions that the frequency of disturbance events in the shallow eastern Gulf of Mexico may limit the effective species pool of colonists. The data indicate that recovery times may be shorter than predicted in previous studies.
4.2 Introduction

Blooms of the toxic dinoflagellate *Karenia brevis* have been documented along the west Florida shelf since the late 1800’s (Ingersoll 1881). These red tides have varied in location, size, duration and intensity, and exposure to the brevetoxins has been shown to affect vertebrates’ (fish, marine mammals, and humans) central nervous systems by alteration of sodium channels (Kirkpatrick et al. 2004). There is no single known cause of the red tides, though several factors have been suggested to play a role, including eutrophication (Dixon and Steidinger 2004; Brand and Compton 2007), upwelling and current regime (Tester and Steidinger 1997) and iron fertilization (Walsh et al. 2006).

Minor *K. brevis* blooms (< $10^5$ cells L$^{-1}$ as defined by the Florida Fish and Wildlife Research Institute, St. Petersburg) of limited duration and associated fish kills may be an annual, natural phenomenon in coastal waters of the Gulf of Mexico (Steidinger and Ingle 1972; Walsh et al. 2006), although occasionally large blooms (> $10^5$ cells L$^{-1}$) cause mass mortalities of fish, marine mammals, and other marine life (Landsberg 2002; Flewelling et al. 2005).

Given the prevalence of minor and major bloom events, surprisingly few studies have investigated the effects of red tides on benthic invertebrate and demersal fish communities on the west Florida shelf. In a qualitative study of the impacts of the 1971 red tide, Smith (1979) reported that 77% of shallow-water (12-18 m) resident fish perished. Echinoderms, gastropod mollusks, decapod crustaceans, scleractinian corals, polychaetes, and poriferans sustained even higher mortalities. Post-impact recolonization studies by Smith (1975, 1979) indicated that major red tides might result in near-
extirpation of shallow-water livebottom biotas, requiring a decade or more for benthic communities to recover to pre-red tide conditions.

With respect to the infaunal benthos, Simon and Dauer (1972) conducted a quantitative study of communities in the northern Tampa Bay estuary, also during the 1971 red tide event. They compared the community structure before and after the red tide and quantified the sustained losses. Only 5 of the 22 most abundant species remained on the intertidal flat after the 1971 event. Repopulation of the polychaete fauna and reestablishment of the benthic community following the natural defaunation were quantified and modeled in the subsequent years (Dauer and Simon 1976; Simon and Dauer 1977). Recovery rates of infaunal communities in Tampa Bay were much faster than those predicted by Smith (1975) for eastern Gulf of Mexico livebottom systems.

The studies outlined above represent the majority of the information available on the ecological effects of red tides on benthic and demersal communities in the eastern Gulf of Mexico. Typically, studies on harmful algal blooms have focused on the acute effects of algal toxins, rather than ecological impacts of chronic exposure to algal toxins (Van Dolah et al. 2001). At the lower trophic levels, acute exposure to algal toxins has been shown to produce deleterious effects on zooplankton, including reduced feeding, growth, and egg production (Gill and Harris 1987; Turner and Tester 1997). It is virtually unknown how chronic exposure to algal toxins may impact population dynamics of other lower trophic level species, and how changes in these dynamics may ultimately affect important commercial and recreational fish populations over time-scales spanning years to decades (Van Dolah et al. 2001).
The objectives of this study were to quantify the impacts of the 2005 red tide/hypoxia disturbance (Heil 2006), which persisted for over one year along the west Florida shelf, on artificial reef epibenthic macroinvertebrate and fish communities. We also monitored successional stages of and temporal changes to the communities for two years post-event. The artificial reef communities were chosen due to the availability of a ‘before-impact’ database that provided us with an important ecological baseline. The unique baseline is used to assess the immediate red tide impact and examine recovery trajectories of benthic and fish communities in a specific habitat area. These data can be used in future quantification of seasonal and annual changes that result from natural or anthropogenic disturbances. Data greatly augment the limited database of community-scale ecological impacts of red tides in the Gulf of Mexico and represent the first quantitative, multi-year study of epibenthic macroinvertebrate and demersal fish community dynamics after a toxic red-tide disturbance.

4.3. Methods

4.3.1. Study Area Characteristics

In 2001, as mitigation for construction of a natural gas pipeline, Gulfstream Natural Gas Systems (GNGS) installed artificial reef structures at six sites in U.S. Federal Waters, 19–25 km west of Tampa Bay and in water depths of 18–25 m (Fig. 4.1). Three sites consisted of limestone boulders (>1 m diameter) haphazardly dispersed to provide some overlap and habitat structure (hereafter referred to as “LB sites”). Pre-fabricated 1.8 m x 2.4 m reef modules (H. Hudson™) were installed at the other three sites (hereafter referred to as RM sites). A total of 153 modules were constructed of limestone in a concrete matrix and dispersed among the three sites. The six mitigation sites were
deployed on sand bottom that did not exceed a thickness of 0.6 m. Under the Federal Mitigation Plan, GNGS was required to monitor the development of benthic and fish communities at these LB and RM sites, as well as at three adjacent undisturbed Reference (control) sites (hereafter referred to as “R sites”). Abiotic parameters (temperature and Secchi depth) and habitat characteristics (rugosity and depth) were recorded during each of the five fish censuses (described below).

Figure 4.1. The location of GNGS Limestone Boulder (LB) and Reef Module (RM) sites in the eastern Gulf of Mexico. Reference (R) sites were located in close proximity.
In addition to the regular sampling of abiotic parameters during each fish census, scientists from the Florida Fish and Wildlife Research Institute (FWRI) in St. Petersburg, FL sampled temperature, salinity, dissolved oxygen, and relative fluorescence along an east-west transect during the peak of the red tide bloom in August 2005 (FWRI unpubl. data). The cruise track extended out 24 km from Bunces Pass and passed through areas located 5-7 km north of the GNGS artificial reef sites. Satellite images (MODIS and SeaWiFS) were examined along the west Florida shelf, but the presence of clouds precluded determining whether a unified water mass extended throughout the 5-7 km area. The FWRI data are presented as representative of the parameters that were observed at depth during the height of the 2005 red tide bloom in the general area of the GNGS artificial reefs.

4.3.2. Benthic Communities

Eight 1 m² photostations were digitally photographed in March 2005 (prior to the red tide), August 2005 (during the red tide event), July 2006, and March 2007. Three of the photostations were located at LB sites and five at RM sites. The center of each photostation was marked with a 0.67 m-long stainless steel rod and a uniquely numbered plastic tag. Photographs were captured using an Olympus 5060 series digital camera encased in an underwater housing. The camera was attached to an apparatus that maintained a 50 cm distance from the substratum. Four photographs were taken adjacent to the center of the photostation, each capturing an area of 0.25 m². The four photos were processed with Canvas™ to create a seamless 1.0 m² mosaic that was used for analysis (Fig. 4.2). The eight photostations were chosen as they had been photographed prior to the red tide event. Because of the small sample size, ten random 0.25 m quadrats were
photographed throughout each of the artificial reef sites (LB and RM) during August 2005, July 2006, and March 2007 samplings to provide a statistical assessment of spatial differences at each of the reefs, and to assess whether the small number of photostations could accurately portray the community that developed at each of the sites. There were no significant differences among quadrats within each of the two types of artificial reefs during each sampling, and the photostations were deemed sufficiently representative of the relatively uniform benthic community development.

Figure 4.2. Example of 1 m² photo-mosaic from station #84 (~17 m). Four photos were combined to produce composite images that were used in point-count analyses.

Substrate and biological cover attributes of the benthic photostations were assessed using point-count analysis (e.g., Curtis 1968; Bohnsack 1979; Carlton and Done 1995; Jaap and McField 2001; Jaap et al. 2003). One hundred random points were superimposed on each image in Coral Point Count v.3.4 (Kohler and Gill 2006), and the
benthic component under each point was identified to provide an estimate of benthic
cover (Hackett 2002). Twenty biological and substrate categories were included in the
assessment. Important species were identified where possible. Six of the categories
included a particular species or phylum (the coral, \textit{Cladocora arbuscula} [LeSueur 1821],
the urchin, \textit{Arbacia lixula} [Linnaeus 1758], the phylum Porifera) and their respective
“bleached” or “dead” counterparts. Normal-appearing \textit{C. arbuscula} did not display any
signs of bleaching, whereas the bleached category includes all corals displaying partial or
full bleaching. Normal-appearing Porifera included \textit{Cliona} spp. while the dead/diseased
Porifera category refers to organisms whose position in the photostation mosaics
corresponded to those of their healthy counterparts in earlier mosaics (\textit{i.e.}, August 2005
mosaics were compared to March 2005 mosaics to determine locations of previously
healthy animals). The remaining 14 categories consist of \textit{Leptogorgia virgulata} [Lamarck 1815],
\textit{Astrophyton muricatum} [Lamarck 1816], ascidians, rock/rubble, unknown, and
nine algal categories. Algae were divided into five distinguishable algal genera or species
\textit{(Acetabularia spp., Halimeda spp., Caulerpa mexicana, C. prolifera, and C. racemosa)}
and 4 general algal classifications. General classifications include rhodophytes (\textit{e.g.},
\textit{Eucheuma} and \textit{Gracilaria} spp.) and chlorophytes (\textit{e.g.}, \textit{Udotea} spp.); if identification
proved impossible due to poor quality of photograph, excess sedimentation, etc., the
algae were grouped into macroalgae and turf algae/cyanophyte categories.

Multivariate analyses were conducted using the Primer-E™ (Clarke and Warwick
2001) package of non-parametric software applications, as data displayed significant non-
normality. Point-count values were square-root transformed to draw information from
across the whole assemblage (Clarke and Green 1988). Multivariate distances were
calculated using the Bray-Curtis similarity coefficient (Bray and Curtis 1957) and plotted using a non-metric multi-dimensional scaling (MDS) ordination. The MDS finds a non-parametric monotonic relationship between dissimilarities in the item-item matrix and the Euclidean distance between the items, and plots the location of each item in low-dimensional space. MDS ordination stress levels <0.15 signify a useful representation (i.e., configuration closely represents the rank order of dissimilarities in the original triangular matrix), while stress levels >0.20 signify a random arrangement of samples, bearing little resemblance to the original ranks (Clarke 1993). Second level procedures (Clarke and Warwick 2001) were used to test for significant differences in benthic community structure between those samples/groups that separated spatially in the MDS. An analysis of similarity (ANOSIM) test was run to detect significant community differences among sampling times. The ANOSIM is analogous to the multivariate analysis of variance (MANOVA) but is used preferentially in this paper because the probability distribution of counts could not be normalized by any transformation due to the dominance of zero values.

Data for all eight photostations were grouped together \( n = 8 \) for each of the four survey periods, as a two-way ANOSIM revealed no differences between the benthic communities at the two types of artificial structures (LB and RM) within sampling times. The similarity percentages (SIMPER) procedure was utilized to detect the biological or substrate categories that contributed significantly to changes in cover between surveys. Discriminating categories satisfy the two conditions of (1) contributing significantly to the average dissimilarity between time periods and (2) contributing consistently (small standard deviation) to the average dissimilarity.
4.3.3. Fish Communities

Censuses of the fish communities were conducted in summer 2005 (June), winter 2005 (November 2005-January 2006), summer 2006 (July-August), winter 2006 (December 2006-March 2007), and summer 2007 (June 2007) at randomly chosen LB, RM, and R sampling stations. Censuses were conducted using a modified Bohnsack visual fish-census method (Bohnsack and Bannerot 1986; Bohnsack et al. 1994), with observers’ fish identification skills evaluated prior to the surveys. Once in the water, the divers rotated and counted fish within a 5 m radius cylinder extending from the surface to bottom for 5 minutes. Ten surveys were conducted at LB, RM, and R sites during each sampling period (30 total). These data are summarized in five separate GNGS reports (GNGS 2005a, 2005b, 2006a, 2006b, and 2007).

Species-richness values were plotted to depict temporal trends before, during, and after the red-tide event at the three types of habitat (LB, RM, and R). Abundance data were fourth-root transformed to focus attention on patterns within the whole community, mixing contributions from both common and rare species (Clarke and Warwick 1994). ANOSIM tests were performed within each sampling time to determine whether fish assemblages were significantly different between LB, RM, and R sites. The three types of habitat differed significantly from one another in terms of fish-community structure, so subsequent analyses were performed on separated data.

Multivariate tests included ANOSIM and SIMPER analyses. For certain analyses, fish species were classified according to their predominant habitat: pelagic or demersal. For analysis purposes, those fish that are not considered demersal, but feed on benthic organisms, were included in the demersal category. These distinctions were important as
certain pelagic species (e.g., *Haemulon auroleineatum*) are seasonally schooling species that can skew statistical analyses with abundance values three orders of magnitude higher during summer samplings. Separate analyses were performed with these species removed from the data set to assess the influence of other rarer species. Habitat classifications were based upon species descriptions from Robins and Ray (1986), McEachran and Fechhelm (1998), Froese and Pauly (2005), as well as the five GNGS reports.

### 4.4 Results

#### 4.4.1 Study Area Characteristics

Mean depth, temperature, and Secchi depths at the sites during each sampling time are displayed in Table 4.1. Depths at the sites ranged from 16.9 to 19.5 m; rugosity was greatest at the LB sites (1.53) and least at the R sites (1.13). Seawater temperatures ranged from 18.1°C in the winter to 29.6°C in the summer, within the nominal values for the area (Joyce & Williams 1969). Secchi depth measurement ranged from 7.3 m to 17.6 m, with considerable variability to the measurements.
Table 4.1. Abiotic and habitat characterization data summary presented as mean values (± S.E). Data were recorded during each of the five fish censuses.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Limestone Boulders (LB)</th>
<th>Reef Modules (RM)</th>
<th>Reference (R)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water Depth (m)</td>
<td>19.5 (1.1)</td>
<td>16.9 (0.2)</td>
<td>18.5 (0.9)</td>
</tr>
<tr>
<td>Rugosity Index</td>
<td>1.53 (0.04)</td>
<td>1.36 (0.08)</td>
<td>1.13 (0.03)</td>
</tr>
<tr>
<td>Water Temperature (ºC)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer 2005</td>
<td>26.5 (0.5)</td>
<td>27.3 (0.1)</td>
<td>26.9 (0.2)</td>
</tr>
<tr>
<td>Winter 2005</td>
<td>22.2 (1.0)</td>
<td>22.8 (0.7)</td>
<td>20.7 (1.2)</td>
</tr>
<tr>
<td>Summer 2006</td>
<td>29.1 (0.3)</td>
<td>29.6 (0.2)</td>
<td>29.4 (0.4)</td>
</tr>
<tr>
<td>Winter 2006</td>
<td>18.2 (0.7)</td>
<td>18.2 (0.6)</td>
<td>18.1 (0.4)</td>
</tr>
<tr>
<td>Summer 2007</td>
<td>26.7 (0.8)</td>
<td>26.3 (0.5)</td>
<td>25.9 (0.5)</td>
</tr>
<tr>
<td>Secchi Depth (m)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer 2005</td>
<td>13.9 (0.5)</td>
<td>10.9 (0.4)</td>
<td>8.5 (0.4)</td>
</tr>
<tr>
<td>Winter 2005</td>
<td>9.0 (0.7)</td>
<td>7.3 (0.3)</td>
<td>9.8 (0.5)</td>
</tr>
<tr>
<td>Summer 2006</td>
<td>17.6 (2.1)</td>
<td>9.6 (0.3)</td>
<td>12.9 (1.7)</td>
</tr>
<tr>
<td>Winter 2006</td>
<td>12.6 (0.8)</td>
<td>12.3 (0.4)</td>
<td>12.8 (0.7)</td>
</tr>
<tr>
<td>Summer 2007</td>
<td>10.5 (0.7)</td>
<td>9.4 (0.7)</td>
<td>9.8 (0.6)</td>
</tr>
</tbody>
</table>

aData are adapted from: GNGS 2005a, 2005b, 2006a, 2006b, and 2007

The extended temporal and spatial scale of the 2005 Karenia brevis bloom prompted a focused sampling effort by the FWRI in August 2005. Water samples from areas west of Tampa Bay indicated that medium to high concentrations (>10^5 cells L^-1) of K. brevis were present in both the surface waters and at depth in areas within the 30 m isobath (FWRI unpubl. data). On August 3, 2005, a cruise transect passed through areas in close proximity to the GNGS artificial reefs and the depth-correlated parameters are shown in Figure 4.3. Dissolved oxygen levels (mg L^-1) decreased at depth at the offshore sites, declining from >9 mg L^-1 at depths <5 m to 0.8 mg L^-1 at depths > 17 m. Relative fluorescence of chlorophyll increased at offshore sites up to 1.7 µg L^-1. FWRI data are representative of conditions that prevailed along areas of the west-central Florida shelf.
where high concentrations of *K. brevis* occurred during 2005. Diver observations indicate that similar hypoxic/anoxic conditions were present at depth at GNGS reefs during the August 2005 sampling time, thereby negatively affecting both benthic macroinvertebrate and fish communities.

![Environmental parameters taken along a 24 kilometer east-west transect positioned 5-7 kilometers north of the Gulfstream Natural Gas Systems artificial reefs](image)

**Figure 4.3.** Environmental parameters taken along a 24 kilometer east-west transect positioned 5-7 kilometers north of the Gulfstream Natural Gas Systems artificial reefs.

### 4.4.2. Benthic Communities

The close proximity and similar abiotic conditions at the GNGS artificial reefs led to the development of relatively uniform epibenthic communities, despite the difference in substrate type at LB and RM sites. A two-way ANOSIM was run between the habitat types within the sampling times and confirmed that there were no significant differences in benthic community structure at the LB and RM sites. The benthic data (n=3 at LB sites and n=5 at RM sites) were pooled for subsequent analyses.
A non-metric MDS plot spatially grouped the samples according to similarities in benthic composition (Fig. 4.4). Samples grouped relatively well into four distinct groupings, corresponding to the four sampling times. Samples are overlain with the dendrogram similarity results (40% and 60% intervals). Arrows depict the temporal trajectory of benthic community succession. The trajectory proceeds in a clockwise circle with the initial March 2005 samples grouped at the bottom of the MDS. The August 2005 samples (taken during the peak of the red tide) group farthest to the left, July 2006 samples grouped towards the top right, and March 2007 samples are
interspersed between the July 2006 and March 2005 samples, as the community proceeded to return to the baseline state.

An ANOSIM indicates that, when analyzed in chronological order, the benthic compositions differed significantly between March 2005 and August 2005 (ANOSIM R = 0.8, p = 0.2%), between August 2005 and July 2006 (ANOSIM R = 0.8, p = 0.2%), and between August 2005 and March 2007 (ANOSIM R = 0.9, p = 0.1%). Table 4.2 lists the major components contributing to differences, as well as their average changes in percent cover. Percent cover and condition of poriferans tended to have a strong influence on temporal trends, as they contributed to significant community differences in all three temporal pairings. Poriferans were negatively affected by the August 2005 red tide; percent cover of dead Porifera increased by 6.5% between March 2005 and August 2005. *Cladocora arbuscula*, the only scleractinian coral enumerated in the photographs, was also severely affected by the red tide; percent cover of bleached *C.arbuscula* increased by 6.1%, with an accompanying 5.1% percent cover decrease in normal *C.arbuscula* between March 2005 and August 2005. During post red-tide samplings (July 2006 and March 2007), the predominant contributors to community differences were algal taxa. Turf-algae cover increased 28% by July 2006 and increased by an additional 7.0% by March 2007. Percent cover of various rhodophytes and chlorophytes increased by March 2007, with an accompanying decrease in the rock/rubble category as the algae encroached upon the vacated spaces. Declines in the dead Porifera category were observed in the last two samplings, but there is a noticeable lack of recovery of the normal Porifera category. Percent cover of normal (non-bleached) *C. arbuscula* increased
during both the July 2006 (+0.6%) and March 2007 (+8.0%) samplings, with many of the colonies regaining their symbiotic zooxanthellae.

Table 4.2. Results from the SIMPER test to determine discriminating benthic categories for pairs of sampling times that differed significantly (ANOSIM $R \geq 0.5$, $p \leq 0.5\%$). Discriminating categories satisfy the conditions of contributing significantly and consistently to the average dissimilarity. The average percent cover change of each category is shown in the last column.

<table>
<thead>
<tr>
<th>Sampling Times (% Dissimilarity)</th>
<th>Benthic Categories</th>
<th>Average Percent Cover Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 2005 &amp; August 2005</td>
<td>Dead Porifera</td>
<td>+6.5</td>
</tr>
<tr>
<td></td>
<td>Bleached <em>C. arbuscula</em></td>
<td>+6.1</td>
</tr>
<tr>
<td></td>
<td>Normal <em>C. arbuscula</em></td>
<td>-5.1</td>
</tr>
<tr>
<td></td>
<td>Normal Porifera</td>
<td>-3.3</td>
</tr>
<tr>
<td>August 2005 &amp; July 2006</td>
<td>Turf Algae</td>
<td>+28</td>
</tr>
<tr>
<td></td>
<td>Rock/Rubble</td>
<td>-19</td>
</tr>
<tr>
<td></td>
<td>Dead Porifera</td>
<td>-6.3</td>
</tr>
<tr>
<td></td>
<td><em>C. mexicanus</em></td>
<td>+5.3</td>
</tr>
<tr>
<td></td>
<td><em>(C. arbuscula)</em></td>
<td>(+0.6)</td>
</tr>
<tr>
<td>August 2005 &amp; March 2007</td>
<td>Rhodophytes</td>
<td>+10</td>
</tr>
<tr>
<td></td>
<td>Turf Algae</td>
<td>+7</td>
</tr>
<tr>
<td></td>
<td>Chlorophytes</td>
<td>+7</td>
</tr>
<tr>
<td></td>
<td>Dead Porifera</td>
<td>-6.5</td>
</tr>
<tr>
<td></td>
<td><em>(C. arbuscula)</em></td>
<td>(+8)</td>
</tr>
</tbody>
</table>

*Cladocora arbuscula* values are displayed, though they are not among the top 4 discriminating species, due to their importance as potential bioindicators of stress during red-tide events.

4.4.3. Fish Communities

Table 4.3 provides the fish species list (71 species total) for all samplings from summer 2005 to summer 2007 at the GNGS LB, RM, and R sites. Primary habitat (demersal or pelagic) is listed for each species, and commercially important species are identified (Gulf of Mexico Fishery Management Council 2004). In some cases, divers identified fish only by common names that could not be matched with species (i.e.,
filefish and wrasse). These were rare species, whose contributions to overall community assemblage are considered to be non-significant.

Table 4.3. List of the 71 fish species observed during census activities from March 2005 to March 2007 at GNGS artificial reef sites including limestone boulder (LB), reef module (RM), and reference sites. Commercial importance and primary habitat are noted.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Commercially Important</th>
<th>Primary Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Spadefish</td>
<td><em>Chaetodipterus faber</em></td>
<td></td>
<td>Pelagic</td>
</tr>
<tr>
<td></td>
<td>(Broussonet, 1782)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bandtail Puffer</td>
<td><em>Sphoeroides splengeri</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Bloch, 1785)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barjack</td>
<td><em>Caranx ruber</em></td>
<td></td>
<td>Pelagic</td>
</tr>
<tr>
<td></td>
<td>(Bloch, 1793)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beaugregory</td>
<td><em>Stegastes leucostictus</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Muller &amp; Troschel, 1848)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belted Sandfish</td>
<td><em>Serranus subligarius</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Cope, 1870)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black Grouper</td>
<td><em>Mycteroperca bonaci</em></td>
<td>Yes</td>
<td>Pelagic/Benthic</td>
</tr>
<tr>
<td></td>
<td>(Poey, 1860)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black Seabass</td>
<td><em>Centropristis striata</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue Angelfish</td>
<td><em>Holacanthurus bermudensis</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Goode, 1876)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue Goby</td>
<td><em>Ptereleotris calliura</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Jordan &amp; Gilbert, 1882)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bluehead Wrasse</td>
<td><em>Thalassoma bifasciatum</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Bloch, 1791)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue Runner</td>
<td><em>Caranx crysos</em></td>
<td></td>
<td>Pelagic</td>
</tr>
<tr>
<td></td>
<td>(Mitchell, 1815)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Butter Hamlet</td>
<td><em>HypopLECTrus unicolor</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Walbaum, 1792)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chub</td>
<td><em>Khyphus sectatrix</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clown Wrasse</td>
<td><em>Halichoeres maculipinna</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Muller &amp; Troschel, 1848)</td>
<td></td>
<td></td>
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<tr>
<td>Cocoa Damsel</td>
<td><em>Stegastes variabilis</em></td>
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<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Castelnau, 1855)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cubbyu</td>
<td><em>Pareques umbrosus</em></td>
<td></td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Jordan &amp; Eigenmann, 1889)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish Name</td>
<td>Scientific Name</td>
<td>Habitat</td>
<td>Notes</td>
</tr>
<tr>
<td>---------------------------</td>
<td>-------------------------------------</td>
<td>--------------------------</td>
<td>---------------------------------</td>
</tr>
<tr>
<td>Emerald Parrotfish</td>
<td><em>Nicolsina usta</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Valenciennes, 1840)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Filefish</td>
<td><em>Sp.?</em></td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td>Florida Blenny</td>
<td><em>Chasmodes saburrae</em></td>
<td>Benthic</td>
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</tr>
<tr>
<td></td>
<td>Jordan &amp; Gilbert, 1882</td>
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<td></td>
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<tr>
<td>French Angelfish</td>
<td><em>Pomacanthus paru</em></td>
<td>Benthic</td>
<td></td>
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<tr>
<td></td>
<td>(Bloch, 1787)</td>
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<td></td>
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<tr>
<td>French Grunt</td>
<td><em>Haemulon flavolineatum</em></td>
<td>Benthic</td>
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<td></td>
<td>(Desmarest, 1823)</td>
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</tr>
<tr>
<td>Gag Grouper</td>
<td><em>Mycteroperca microlepis</em></td>
<td>Yes</td>
<td>Pelagic/Benthic</td>
</tr>
<tr>
<td></td>
<td>(Goode &amp; Bean, 1879)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Goliath Grouper</td>
<td><em>Epinephelus itajara</em></td>
<td>Protected</td>
<td>Pelagic/Benthic</td>
</tr>
<tr>
<td></td>
<td>(Lichtenstein, 1822)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great Barracuda</td>
<td><em>Sphyraena barracuda</em></td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Edwards, 1771)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greater Amberjack</td>
<td><em>Seriola dumerili</em></td>
<td>Yes</td>
<td>Pelagic</td>
</tr>
<tr>
<td></td>
<td>(Risso, 1810)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grey Angelfish</td>
<td><em>Pomacanthus arcuatus</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grey Triggerfish</td>
<td><em>Balistes capriscus</em></td>
<td>Yes</td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Gmelin, 1951)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulf Flounder</td>
<td><em>Paralichthys albignotta</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Jordan &amp; Gilbert, 1882)</td>
<td></td>
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<tr>
<td>Hogfish</td>
<td><em>Lachnolaimus maximus</em></td>
<td>Yes</td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Walbaum, 1792)</td>
<td></td>
<td></td>
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<tr>
<td>Inshore Lizardfish</td>
<td><em>Synodus foetens</em></td>
<td>Benthic</td>
<td></td>
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<tr>
<td></td>
<td>(Linnaeus, 1766)</td>
<td></td>
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<tr>
<td>Jackknife Fish</td>
<td><em>Equetus lanceolatus</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jolthead</td>
<td><em>Calamus bajonado</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Bloch &amp; Schneider, 1801)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lane Snapper</td>
<td><em>Lutjanus synagris</em></td>
<td>Yes</td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leopard Toadfish</td>
<td><em>Opsanus pardus</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Goode &amp; Bean, 1880)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mangrove/Grey Snapper</td>
<td><em>Lutjanus griseus</em></td>
<td>Yes</td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molly Miller</td>
<td><em>Scartella cristata</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Linnaeus, 1758)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nurse Shark</td>
<td><em>Ginglynostoma cirratum</em></td>
<td>Yes</td>
<td>Benthic</td>
</tr>
<tr>
<td></td>
<td>(Bonnaterre, 1788)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orange Blenny</td>
<td><em>Sp.?</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Scientific Name</td>
<td>Habitat</td>
<td></td>
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<tr>
<td>----------------------</td>
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<tr>
<td>Pigfish</td>
<td>Orthopristis chrysoptera (Linnaeus, 1766)</td>
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<td></td>
</tr>
<tr>
<td>Pinfish</td>
<td>Lagodon rhomboides (Linnaeus, 1766)</td>
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</tr>
<tr>
<td>Porgy</td>
<td>Calamus sp.</td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>Porkfish</td>
<td>Anisotremus virginicus (Linnaeus, 1758)</td>
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<td></td>
</tr>
<tr>
<td>Queen Angelfish</td>
<td>Holacanthis ciliaris (Linnaeus, 1758)</td>
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<td></td>
</tr>
<tr>
<td>Red Grouper</td>
<td>Epinephelus morio (Valenciennes, 1828)</td>
<td>Yes Pelagic/Benthic</td>
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</tr>
<tr>
<td>Reef Butterflyfish</td>
<td>Chaetodon sedentarius (Poey, 1860)</td>
<td>Benthic</td>
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</tr>
<tr>
<td>Round Scad</td>
<td>Decapterus punctatus (Cuvier, 1829)</td>
<td>Pelagic/Benthic</td>
<td></td>
</tr>
<tr>
<td>Sand Perch</td>
<td>Diplectrum formosum (Linnaeus, 1766)</td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>Scaled Sardine</td>
<td>Harengula jaguana Poey, 1865</td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td>Scamp Grouper</td>
<td>Mycteroperca phenax (Jordan &amp; Swain, 1884)</td>
<td>Yes Pelagic/Benthic</td>
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</tr>
<tr>
<td>Scrawled Cowfish</td>
<td>Acanthostracion quadricornis (Linnaeus, 1758)</td>
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<td></td>
</tr>
<tr>
<td>Seahorse</td>
<td>Hippocampus sp.</td>
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<td></td>
</tr>
<tr>
<td>Seaweed Blenny</td>
<td>Parablennius marmoreus (Poey, 1876)</td>
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<td></td>
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<tr>
<td>Sergeant Major</td>
<td>Abudeifuf saxatilis (Linnaeus, 1758)</td>
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</tr>
<tr>
<td>Sheepshead</td>
<td>Archosargus probatocephalus (Walbaum, 1792)</td>
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</tr>
<tr>
<td>Sheepshead Porgy</td>
<td>Calamus penna (Valenciennes, 1830)</td>
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<td></td>
</tr>
<tr>
<td>Slippery Dick</td>
<td>Halichoeres bivittatus (Bloch, 1791)</td>
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<td></td>
</tr>
<tr>
<td>Southern Flounder</td>
<td>Paralichthys lethostigma (Linnaeus, 1758)</td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>Spanish Mackerel</td>
<td>Scomberomorus maculates (Mitchell, 1815)</td>
<td>Yes Pelagic</td>
<td></td>
</tr>
<tr>
<td>Spanish Sardine</td>
<td>Sardinella aurita Valenciennes, 1847</td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td>Spot-fin Porcupinefish</td>
<td>Diodon hystrix Linnaeus, 1758</td>
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<tr>
<td>Fish Name</td>
<td>Scientific Name</td>
<td>Habitat Type</td>
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</tr>
<tr>
<td>---------------------------</td>
<td>-------------------------------------</td>
<td>--------------</td>
<td></td>
</tr>
<tr>
<td>Spottail Pinfish</td>
<td><em>Diplodus holbrooki</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>(Bean, 1878)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spotted Drum</td>
<td><em>Equetus punctatus</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>(Bloch &amp; Schneider, 1801)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Squirrelfish</td>
<td><em>Holocentrus adscensionis</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>(Osbeck, 1765)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Threadfin Herring</td>
<td><em>Opissthomema oglinum</em></td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td>(Lesueur, 1818)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tomtate</td>
<td><em>Haemulon aurolineatum</em></td>
<td>Pelagic</td>
<td></td>
</tr>
<tr>
<td>Cuvier, 1830</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Townsend Angelfish</td>
<td><em>Holacanthus townsendi</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>(Nichols &amp; Mowbray, 1914)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White Goby</td>
<td><em>Sp.?</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>White Grunt</td>
<td><em>Haemulon plumieri</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>(Lacapede, 1801)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whitespotted Soapfish</td>
<td><em>Rypticus maculates</em></td>
<td>Pelagic/Benthic</td>
<td></td>
</tr>
<tr>
<td>Holbrook, 1855</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Goatfish</td>
<td><em>Mulloidichthys martinicus</em></td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td>Cuvier, 1829</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellowtail Snapper</td>
<td><em>Ocyurus chrysurus</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>(Bloch, 1791)</td>
<td></td>
<td>Benthic</td>
<td></td>
</tr>
</tbody>
</table>

A two-way ANOSIM among habitats within sampling times indicated that there were significant differences in fish communities (diversity and abundance) among the LB, RM, and R sites. Subsequent analyses were performed within individual habitat types (n=10). Numbers of species present at the two artificial reef habitat types and the reference sites were substantially lower immediately after the red tide event (Fig. 4.5). Prior to the red tide event, the highest number of fish species was observed at LB sites, with R sites having the lowest number. Immediately after the red tide, all sites exhibited a sharp decline in species numbers: 50% for LB sites, 65% for RM sites, and 60% for R sites. Diversity trended upward in all sites from Summer 2006 through Summer 2007,
with RM and R sites reaching their original (Summer 2005) levels by the Summer 2007 sampling.

Significant temporal changes in fish assemblages were determined by an ANOSIM test (Table 4.4). Sites and samplings that display significant differences are denoted by an “S” while those that are similar are deemed non-significant and denoted by an “N”. Further analyses (SIMPER) were run on the significant samples to determine species that contributed to the dissimilarity; average changes in individual species abundances were calculated (Table 4.5).

Table 4.4. Matrix of significant (S) and non-significant (N) temporal fish-assemblage trends at LB, RM, and R sites, respectively. Summer 2005 (S05) sampling occurred prior to the peak of the red-tide event. Summer 2007 (S07) represents the final sampling in the focused two-year time series.

<table>
<thead>
<tr>
<th></th>
<th>S05</th>
<th>W05</th>
<th>S06</th>
<th>W06</th>
</tr>
</thead>
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<td>S05</td>
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<td></td>
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<tr>
<td>W05</td>
<td>SSS</td>
<td></td>
<td></td>
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<tr>
<td>S06</td>
<td>SNS</td>
<td>NSN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W06</td>
<td>NNN</td>
<td>NSN</td>
<td>NNN</td>
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</tr>
<tr>
<td>S07</td>
<td>SSS</td>
<td>SSS</td>
<td>NNN</td>
<td>SSS</td>
</tr>
</tbody>
</table>
Table 4.5. Results from SIMPER analyses performed on significantly different assemblages (determined by ANOSIM in Table 4.4 above) to determine discriminating species and their average change (+/-) in abundance between time periods. AP = Archosargus probatocephalus, SS = Serranus subligarius, SV = Stegastes variabilis, MP = Mycteroperca phenax, LM = Lachnolaimus maximus, CS = Chasmodes saburrae, HB = Halichoeres bivittatus, CC = Caranx crysos, DF = Diplectrum formosum, HP = Haemulon plumierii, CX = Calamus sp., CB = Calamus bajonado, LR = Lagodon rhomboides.

<table>
<thead>
<tr>
<th>Sampling Times</th>
<th>R</th>
<th>P (%)</th>
<th>Discriminating Species</th>
<th>(Average Change)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summer 2005 &amp; Winter 2005</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>0.7</td>
<td>0.1</td>
<td>^AP (+2), SS (-8), SV (-2)</td>
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</tr>
<tr>
<td>RM</td>
<td>0.6</td>
<td>0.1</td>
<td>^SS (-18), SV (-2), MP (-2)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>0.5</td>
<td>0.1</td>
<td>SS (-1), DF (+1), HP (-1)</td>
<td></td>
</tr>
<tr>
<td><strong>Summer 2005 &amp; Summer 2006</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>0.3</td>
<td>0.1</td>
<td>MP (-2), CC (+12), SS (-7)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>0.4</td>
<td>0.1</td>
<td>LR (+46), HP (+1), SS (-2)</td>
<td></td>
</tr>
<tr>
<td><strong>Summer 2005 &amp; Summer 2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>0.3</td>
<td>0.1</td>
<td>^CS (+5), CC (+13), SS (-2)</td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>0.5</td>
<td>0.1</td>
<td>^HB (+9), CS (+6), DF (-10)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>0.6</td>
<td>0.1</td>
<td>HB (+9), CX (+3), HP (+1)</td>
<td></td>
</tr>
<tr>
<td><strong>Winter 2005 &amp; Summer 2006</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>0.5</td>
<td>0.1</td>
<td>^SV (+3), SS (+6), LM (+1)</td>
<td></td>
</tr>
<tr>
<td><strong>Winter 2005 &amp; Winter 2006</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>0.5</td>
<td>0.1</td>
<td>SV (+2), SS (+7), LM (+1)</td>
<td></td>
</tr>
<tr>
<td><strong>Winter 2005 &amp; Summer 2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>0.7</td>
<td>0.1</td>
<td>^SS (+6), CS (+5), SV (+3)</td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>0.9</td>
<td>0.1</td>
<td>^HB (+9), CS (+7), SV (+3)</td>
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<tr>
<td>R</td>
<td>0.6</td>
<td>0.1</td>
<td>HB (+9), SS (+6), CX (+1)</td>
<td></td>
</tr>
<tr>
<td><strong>Winter 2006 &amp; Summer 2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>0.5</td>
<td>0.1</td>
<td>^SS (+6), CS (+5), LM (-3)</td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>0.6</td>
<td>0.1</td>
<td>^HB (+9), CS (+6), MP (+1)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>0.4</td>
<td>0.1</td>
<td>HB (+9), CX (+4), CB (-10)</td>
<td></td>
</tr>
</tbody>
</table>

^Indicates the placement of Haemulon aurolineatum when included in the analyses.
Serranus subligarius, Stegastes variabilis, and Mycteroperca phenax abundances all declined during or immediately after the red tide event at the LB and RM sites, contributing significantly to differences between the Summer 2005 and Winter 2005 samplings. Archosargus probatocephalus abundances increased at the LB sites, indicating that although this species may have initially evacuated the area during the red tide, it was among the first to return to the LB sites immediately after its dissipation. Diplectrum formosum displayed a similar trend at R sites, as it was the only species to increase in number from Summer 2005 to Winter 2005. Fish assemblages were significantly different only at LB sites between Winter 2005 and Summer 2006, with increased abundances in the three primary discriminating species (S. variabilis, S. subligarius, and Lachnolaimus maximus). Summer 2006 and Winter 2006 samplings had similar fish assemblages, followed by a sharp increase in most species’ abundances by the Summer 2007 sampling. Only L. maximus and Calamus bajonado abundances were lower at LB and R sites, respectively.

The remaining four pairings in Table 4.5 detail the changes in abundances between Summer and Winter samplings, with various changes in fish assemblages occurring among sites. The fifth pairing in the table compares Summer 2005 data to Summer 2007 data to assess overall changes over the two-year sampling period. Both the LB and RM sites saw overall increases in Chasmodes saburrae abundances. LB sites also experienced an increase in Caranx crysos abundances whereas RM sites experienced an increase in Halichoeres bivittatus. Both sites saw declines in certain discriminating species as Serranus subligarius and Diplectrum formosum abundances decreased at LB and RM sites, respectively. All discriminating species (Halichoeres bivittatus, Calamus
and *Haemulon plumieri* increased in abundance over the two-year sampling time at the R sites.

Attempts were made to use a non-metric MDS ordination to spatially examine the fish abundance data but, unlike the benthic data where rank dissimilarities among temporal groups were significantly higher than those within samples in a group (as determined by an ANOSIM), fish data did not separate into distinct temporal groups. High stress values in the MDS ordinations (>0.2) indicated that interpretations based on the ordination are not useful as the samples are essentially randomly placed, bearing little resemblance to the original similarity ranks in the triangular matrix (Clarke 1993). Ordinations are not displayed in this paper.

### 4.5 Discussion

#### 4.5.1. Benthic Communities

Disturbance is defined by Connell (1997) as an event that damages or kills residents at a given site. Disturbances can be either acute (short-term) or chronic (long-term) with direct effects on the physical/biological environment (e.g., a storm alters community topography) or indirect effects (e.g., a disease kills corals and indirectly reduces physical/biological complexity of the community). Red tide events are classified as acute, indirect, episodic disturbances that have the ability, through exposure to brevetoxin or hypoxic/anoxic conditions, to alter community structure by negatively impacting the benthic, demersal, and water-column communities.

The spatial scale of the disturbance affects ecosystem resilience (Sousa 1985), along with factors such as the frequency and duration of the disturbance (Nystrom et al. 2000). Estimates indicate that approximately 5,600 km² of benthic communities may
have been affected by the 2005 red tide and the anoxic/hypoxic conditions (FWRI unpub. data). Although natural disturbances such as red tides can be detrimental to individuals and communities at large spatial scales (10–1000 km²), the emigration/extirpation of organisms vacates substratum, making it available at various temporal and spatial scales (Connell 1978). This provides opportunity for renewal, development, and succession of the community (Holling 1996). Recovery times after a disturbance can vary greatly among communities and within populations depending on levels of adult dispersal/encroachment and competition, larval supply, selective forces acting on the planktonic larval stages, selectivity of larvae for different types of substrate, and predation effects on larvae (Thorson 1950, 1955, 1957, 1966).

An important conclusion in Smith’s (1975) original qualitative study on the impact of a severe red-tide event on west Florida shelf communities was that major events may result in the near-extirpation of livebottom biotas and that recovery rates may be on the order of years to decades. However, the data presented in this focused two-year time period indicate that communities may recover more quickly than originally predicted, particularly on artificial reefs. The data indicate that while benthic communities were significantly impacted by the red-tide event and related anoxic bottom conditions, the two-year recovery trajectory is towards a pre-red tide community structure (Fig. 4.4). The initial, pioneering species that recruited to the sites included dense mats of cyanophytes and other small turf algae. The cyanophytes and turf algae became sub-dominant to recolonizing filamentous algae (rhodophytes such as *Gracilaria* and *Eucheuma spp.*), chlorophytes (*Caulerpa mexicana, C. racemosa, Halimeda spp., Udotea spp.*), and other macroalgae (phaeophytes and others) by March 2007.
In addition to recruiting algal communities in the one- to two-year period after the red tide, many *Cladocora arbuscula* colonies survived the stress, despite having bleached during the height of the red tide and anoxic conditions. Large, healthy colonies >10 cm in diameter were observed in July 2006 and March 2007. Because growth rates of *C. arbuscula* are on the order of 5 cm per year (W.C. Jaap, personal comm.), larger colonies must have survived the 2005 red tide. These findings are consistent with those of Rice and Hunter (1992), who found that *C. arbuscula* are among the scleractinian corals most resistant to environmental stress. The percent of rubble/bare substrate increased from July 2006 to March 2007 as the opportunistic algal species became sub-dominant and herbivorous fish populations began to recover. Small numbers (representing <3% of benthic cover) of echinoderms (primarily *Arbacia lixula*) were also present during the July 2006 and March 2007 sampling; these echinoderms could graze on algae and expose substrate. This evidence suggests that recovery from a major red tide, including hypoxia, can occur on the order of years, rather than decades.

Results from the Simon and Dauer (1977) study in Old Tampa Bay, Tampa, FL, indicated that, although a marked loss of benthic infaunal invertebrates did occur as a result of the 1971 red tide and reported anoxia, the fauna made a rapid recovery in terms of species numbers and composition within two years. These recovery rates are similar to those I observed, and both sets of data indicate that communities may recover much faster than predicted by Smith (1975), although certain populations may take much longer to fully recover. Colonization rates of certain taxa are rapid (e.g., polychaetes in infaunal communities and algal species in epifaunal communities), while other taxa appear to have longer recovery periods, greatly influenced by the time of year when a
perturbation in the community occurs (e.g., mollusks, amphipods, and other crustacea in infaunal communities, as well as Porifera and echinoderms in epifaunal communities). I agree with the assertions by Simon and Dauer (1977) that benthic community analyses are essential when assessing the effects of disturbances (anthropogenic and natural), as opposed to single taxon studies. The variety of colonization rates suggests that certain taxa may be considered “rapid response and recovery” organisms (various algae, polychaetes), while other taxa might be more useful in determining whether a community has reached an “equilibrium” level of species (mollusks and echinoderms).

The benthic-community data presented here are limited in spatial scale and are focused only on artificial reef structures. Benthic-community dynamics could be very different at natural livebottom/rocky-ledge communities in the Gulf of Mexico. Natural livebottom communities in the eastern Gulf of Mexico have much lower relief but more diverse coral assemblages (including Oculina diffusa, Solenastrea hyades, Siderastrea spp., Stephanocoenia intersepta, and others) than the artificial reefs I studied. Comparative responses of the artificial reefs and livebottom ledge communities will define whether there are differences between the two types of habitat and provide insight into the efficacy of artificial reefs as mitigation structures. Natural livebottom areas and comparative processes will be the focus of future publications.

4.5.2. Fish Communities

The mobile nature of most fish species (particularly migratory or pelagic species) allows them to respond quickly to acute disturbances such as red tide events. The patchy nature of most red-tide blooms may provide areas of refuge amidst the anoxic/toxic conditions, meaning that there are four basic responses of fish species to a red-tide
disturbance: (1) they may permanently relocate (emigrate) to another area not affected by
the toxin/anoxia, (2) they may remain in an area affected by the red tide, where they
either survive the bloom conditions or they perish, (3) they may temporarily evacuate an
unsatisfactory area, but return again upon bloom dissipation, and (4) new species may
immigrate in response to the presence of newly vacated habitat in the area or to escape
the encroaching red tide bloom as it is advected along the shelf. The first three responses
likely accounted for the significant reduction in fish species richness (Fig. 4.5) observed
after the 2005 red tide. Below I discuss species that displayed the four responses outlined
above.
Figure 4.5. Temporal changes in total fish species richness at the LB, RM, and Reference sites. The Summer 2005 (S05) census was conducted prior to the red-tide event; Winter 2005 (W05) data were collected during and immediately after the event.

Eight species were recorded during the Summer 2005 sampling, which preceded the red-tide event, but were not observed in any subsequent samplings: *Kyphosus sectatrix, Holacanthus ciliaris, Harengula jaguana, Acanthostracion quadricornis, Abudefduf saxatilis, Scomberomorus maculatus, Opissthonema oglinum*, and *Ocyurus chrysurus*. Three of these (*H. jaguana, S. maculatus, and O. oglinum*) are pelagic species that may have evacuated the area during the sampling times and simply had not returned to the sites within the study period (response #1). The remaining five species are semi-sedentary demersal species that occupy a particular ledge for extended periods, if not their entire life. The absence of adults or juveniles suggests that extirpation from the
area, rather than emigration, has occurred (response #2, mortality). The failure of these five demersal species to recolonize may be a result of their low fecundity, lack of larval supply, high planktonic mortality, lack of settlement in the area, low competitive success, or any combination of the above.

Five species were observed at all sites during all sampling times, although their abundances varied greatly (response #2, survival): *Serranus subligarius, Balistes capriscus, Diplectrum formosum, Haemulon aurol ineatum*, and *Haemulon plumieri*. These species survived the red tide as remnant populations or returned soon after its dissipation as they were observed during the pre-event sampling (Summer 2005) as well as all subsequent samplings. Other surviving remnant populations at two out of three sites include *Lachnolaimus maximus* (LB and RM), *Lutjanus griseus* (LB and RM), *Archosargus probatocephalus* (LB and RM), *Synodus foetens* (LB and R), and *Calamus bajonado* (LB and R). Two of the remnant species (*L. maximus* and *L. griseus*) are mobile, commercially important species. Artificial reef sites appear to have been effective in retaining or recruiting these species after the red-tide event.

Two other commercially important species (*Epinephelus morio* and *Mycteroperca phenax*) displayed response #3, as they were present during the Summer 2005 samplings, absent during the Winter 2005 sampling, but were again present in subsequent samplings at all sites. These species may have moved offshore to escape the detrimental red tide conditions, but then returned to utilize the artificial reef habitat. Other species that displayed this response were *Chasmodes saburrae, Rypticus maculates, Stegastes variabilis*, and *Sardinella aurita*. Surprisingly, all of these species, except *S. aurita*, are classified as demersal, reef-associated and would not be expected to move from the reefs.
during unfavorable conditions, so they may have been hidden within the reef habitat and escaped notice during the fish census. All five species are highly resilient with population doubling times < 15 months (Froese and Pauly 2005), so populations could be expected to recover quickly after acute disturbances.

Six species were observed regularly after the red tide, but were not recorded during the initial Summer 2005 sampling (response #4): Holacanthus bemudensis, Thalassoma bifasciatum, Scartella cristata, Decapterus punctatus, Pareques umbroses, and Diplodus holbrookii. This suggests that they are opportunistic species with the ability to colonize new niches opened due to the emigration/extirpation of other species. Reproductive characteristics, such as protogyny and group-spawning in T. bifasciatum up-current of settling areas (Warner 1984), could make them successful colonizers after a disturbance, provided that suitable food sources and habitat are available.

Fish abundances and community composition differed significantly between the artificial reefs, with a small number of discriminating species consistently contributing to the majority of temporal dissimilarities (Table 4.5). Discriminating species were characteristically highly resilient species with population doubling times ≤ 18 months (Froese and Pauly 2005). Adults that survived the red tide and relocated to other livebottom areas produced a steady supply of planktotrophic larvae that found favorable conditions at the artificial sites and, less abundantly, at reference sites.

LB and RM sites were generally more successful in retaining or recruiting commercial fish species during and after the red tide than the Reference sites. This may be due to the higher rugosity at the artificial sites, which in turn provides greater diversity of shelter and feeding sites (Bell and Galzin 1984). Observations indicate that structures
placed in the Gulf of Mexico are effective in retaining/recruiting commercial species. Further studies including size-distribution measurements could provide insight into whether artificial structures are contributing to overall fisheries biomass or simply attracting fish that are already present in this area of the Gulf of Mexico.

4.5.3. Red Tides as a Community Structuring Force

The data presented here contribute to a quantitative database of ecological impacts of red tides and associated hypoxic/anoxic events on West Florida Shelf communities. Smith (1979) proposed that eastern Gulf of Mexico reef-fish communities develop according to predictable, rather than chance processes. In this view, ultimate stability in species richness and composition represents the attainment of a “climax” community, as opposed to a dynamic species equilibrium predicted by MacArthur and Wilson (1963). Smith attributed the development of a climax community to the inhospitable nature of the Gulf of Mexico which reduces the effective species pool of colonists. Hardy species (or species that produce hardy planktotrophic larvae) recruit (or settle) during the early stages of colonization and are difficult to displace. These characteristics, combined with observations that benthic communities in the Gulf of Mexico are not isolated “islands,” may make it difficult to apply the MacArthur-Wilson species equilibrium model to either benthic or fish communities along the inner West Florida Shelf.

My benthic data agree with Smith’s assertions, as communities progressed towards a pre-red tide state with few changes in species composition. Successional stages appear to follow a trajectory towards the pre-red tide state, corroborating Smith’s application of the intermediate disturbance hypothesis (Connell 1978). However, I
choose to forgo use of the term and concept of a “climax community.” The proposed episodic occurrence of red tides, in conjunction with other stochastic factors such as fluctuating sea temperatures, turbidity, and hurricanes, likely prevents the development of complex climax communities. Instead, the tendency to recruit equivalent species and revert to the pre-red tide state may be an intermediate stage in a prolonged multi-staged succession that never reaches a “dynamic equilibrium” as proposed by MacArthur and Wilson (1963). Should the frequency and severity of disturbances decrease, different community structures may develop. Red tides in the Gulf of Mexico have been and will continue to be important in structuring epibenthic and fish communities. Mitigation for red tides should therefore focus on the quick restoration of communities through regulation of fisheries and placement of more artificial structures, and not on the process of eliminating the *K. brevis* bloom, which is a fundamental ecological process in the eastern Gulf of Mexico.
5. Enhancement of Natural Ledge Substrate Via Deployment of Artificial Reefs Along the West Florida Shelf

5.1 Introduction

A discussion on artificial reefs often incites vigorous debate, with the core of the argument focused on the well-rehearsed “attraction versus production” argument (Bohnsack et al. 1997; Pickering and Whitmarsh 1997). On the one hand, opponents of artificial reefs have come to regard them with alarm, considering them mere fish aggregating devices (FADs) that concentrate fish populations and render them increasingly susceptible to exploitation by fishermen. On the other hand, proponents view artificial reefs as important habitat and recruitment-enhancement tools, arguing that the substrate provided by appropriately-placed structures attracts larval recruits that might not otherwise find appropriate substratum. It is clear that the attraction/production debate is central to the issue of artificial reef deployment and it must be satisfactorily addressed by local or regional scientists and managers before extensive deployment of artificial reefs can be considered as part of a restoration, mitigation, or conservation plan.

In Chapter 3, I evaluated a specific set of WFS artificial reefs deployed with the goal of mimicking natural ledge habitat. Now I shall expand on the comparisons between artificial reefs and natural ledges, using data from Chapters 2, 3 and 4. I will address the potential for future use of artificial reefs along the WFS, including their contribution to the resolution of the attraction/production debate.
5.2 Defining Current Artificial Reef Data Issues

Productivity, as it pertains to artificial reefs, relies on the assumption that artificial reefs provide additional critical habitats that increase the environmental carrying capacity and thereby the abundance and biomass of reef biota (Polovina 1994; Bortone et al. 1994). While this definition encompasses all “reef biota” without solely focusing on fish assemblages, most papers that discuss artificial reef usefulness/efficacy discuss only the associated fish assemblages, with only minor mention of benthic communities (Randall 1963; Beets 1989; Bohnsack 1989; Beets and Hixon 1994; Carr and Hixon 1997; Rilov and Benayahu 2000, among others). This has focused thinking among resource managers and scientists that artificial reefs are primarily deployed to restore, protect, enhance, concentrate, or aggregate (depending on whether you are an opponent or proponent) fish populations, and only fish populations.

Accordingly, most artificial reef opponents cite the lack of definitive data from artificial reef fish populations in their arguments against the use of artificial reefs. Topics that lack “definitive” data include: (1) discerning whether fishes that settle on or are attracted to artificial reefs would have found suitable substrate elsewhere, (2) understanding whether fish survival and growth rates are higher at artificial reefs than in natural habitat, (3) determining whether foraging success and food web efficiency is improved by artificial reefs, and (4) knowing whether other habitat was vacated by fish moving to artificial substrate (Bohnasck et al. 1994). Bohnsack (1989) proposed that proof of artificial reefs increasing production would require direct evidence such as an increased total regional catch or standing stock in some proportion to the amount of material deployed, while accounting for fishing effort, recruitment from surrounding
areas, and changes in year class strength. A comprehensive study encompassing the above parameters has not yet been attempted (and may be virtually impossible) and so the “lack of definitive data” argument continues to be employed to discourage the use of artificial reefs.

To summarize the two main problems with artificial reef studies to date: (1) they overemphasize the contributions and importance of fish populations to reef biomass calculations and underemphasize benthic community contributions and (2) they do not provide definitive data on the preferences or movements of individual fish. I shall address the first issue using data from the WFS artificial reefs, with particular emphasis on the development of a robust epibenthic community and bottom-up production effects. The second problem is a bit more esoteric and difficult to address using data from the WFS artificial reefs, as my data can not be classified as “definitive”. I will instead present reasons why this line of thinking should be dismissed in many situations, particularly in current coastal restoration and habitat conservation projects along the WFS. The results and arguments presented here can be debated and evaluated in other regions, where applicable, as certain areas may be similar to the WFS conditions while others differ drastically.

5.3 Problem #1: Rationale for Including Benthic Communities in Production Calculations

5.3.1. Artificial Reef Contributions

Pickering and Whitmarsh (1997) revealed interesting insights into the services that artificial reefs provide outside the usual realm of fishes. They state that the artificial reef (when properly constructed and deployed) potentially provides: (1) substrata for benthic fauna and, thereby, additional food and increased feeding efficiency, (2) shelter
from predation or tidal currents (Collins et al. 1991; Spanier 1996), and (3) recruitment habitat for individuals that would otherwise be lost from the population (fishes and benthic invertebrates). These three topics will be discussed as they pertain to the Gulfstream Natural Gas Systems (GNGS) artificial reefs deployed along the shallow inner WFS, west of Egmont Key (see Chapter 3 for background on construction, deployment, monitoring, and evaluation of the reefs).

5.3.2. Substrate, Benthic Fauna, and Increased Food Availability

The deployment of artificial reefs in the eastern GOM increases the biomass of sessile benthic invertebrates and macroalgae substantially when compared to surrounding quartz-dominated sand ridges and associated infaunal assemblages. Epibenthos include corals (*Cladocora arbuscula* and *Siderastrea* spp.), poriferans, echinoderms, ascidians, and mollusks. Bubbleplots displaying the assessed categories at the GNGS artificial reefs are shown in Figures 5.1 to 5.3, and represent varying abundances of the relatively diverse epibenthic community over the four sampling times. Samplings prior to a red-tide event (March 2005) displayed coral cover of up to 21% in certain quadrats. Similarly, the March 2007 samples had coral cover up to 24%. Poriferans and other living fauna (echinoderms, ascidians) also contributed greatly to percent cover values.

Macroalgal percent cover data are shown in Figure 5.4 and are negatively correlated to bare substrate cover (Fig. 5.4) in the same manner as observed along natural livebottom ledges (Fig. 5.5). It is difficult to discern whether seasonal macroalgal trends at the artificial reefs mimic those of natural livebottoms as the samplings are less highly resolved.
Figure 5.1. Percent cover of coral at GNGS artificial reefs. Data are shown for individual 1 m$^2$ photo-quadrats captured during each of the 4 sampling times (March 2005, August 2005, June 2006, and March 2007).

Figure 5.2. Percent cover of poriferans at the GNGS artificial reefs; source of data as in Fig. 5.1.
A transition from an infaunal community to an epifaunal community generally increases the area’s biomass as demonstrated by Foster et al. (1994). They compared biomass of infauna prior to artificial reef emplacement in Delaware Bay to epifaunal biomass after. They found that biomass values had increased by 148 to 895 fold in the shift from the infaunal to epifaunal communities. These enhanced biomass figures reflect the expanding available surface area for benthic biota. Trapping of plankton and other resources by the structure, increased sedimentation of suspended particles, reef waste products, and detached organisms may also contribute to increased biomass (Foster et al. 1994). Sessile invertebrates and algae serve to attract fish (Dudley and Anderson 1982; Wallace and Benke 1984) and, as gut content surveys have demonstrated, provide an essential food source (Johnson et al. 1994).
Figure 5.4. (A) Macroalgal percent cover at GNGS artificial reefs which varies inversely with (B) bare substrate cover. Samplings (March 2005, August 2005, June 2006, and March 2007) do not display seasonal trends.
Figure 5.5. (A) Macroalgal percent cover at natural ledges (FW=FWRI1 and M=Mastedon Tabletop) which vary inversely with (B) bare substrate cover.

5.3.3. Provision of Shelter

The GNGS artificial reefs, by virtue of their design (either reef modules with the cavity cut through the limestone matrix or arrangement of limestone boulders), provide shelter for macroinvertebrates and fish species. Their design, in conjunction with the development of secondary substrate which alters reef topography and heterogeneity, provides essential shelter for juveniles and adult organisms seeking refuge from predation, wave forces, and sediment movement (Hixon and Brostoff 1985; Relini et al. 1994).
However, growth on artificial reefs depends on the length of immersion. The GNGS artificial reefs were deployed in 2001, allowing for only 4-6 years of growth at the time of data collection. Therefore, the epibenthos on the artificial reefs was much less diverse (although percent cover values of biota were similar) than on the natural livebottom ledges. Only three species of corals were observed at the artificial reefs (*Cladocora arbuscula, Phyllangia americana,* and *Siderastrea radians*) as compared to the 6 species observed at natural ledges (see Chapter 2). The same held true for macroalgal species (personal observation), as the same types of fleshy macroalgae (*Sargassum* spp.) and *Halimeda* spp. were observed on all artificial reefs.

Shelter was truly provided for fish species as evidenced by the 71 species that were observed at the artificial reefs as compared to 47 species at the natural ledges. A number of the species observed at the artificial reefs were typical of more tropical regions (i.e., *Holacanthus ciliaris, Pomacanthus paru,* and *Thalassoma bifasciatum*), and the more southerly location (50 km south) and slightly warmer waters could be a factor in the higher species richness observed at the artificial reefs. Abundances of most fish species were higher at the artificial reefs; future work should make an effort to assess size-class distributions to more effectively contribute data to resolve the production versus attraction debate.

**5.3.4. Recruitment Habitat**

Larva numbers often far exceed the numbers able to settle on a reef (Sale 1980) which, with food eliminated as a direct factor (Shulman 1984), leaves habitat as the likely limiting factor for reef populations. According to Collard and D’Assaro (1973) and Lyons and Collard (1974), the availability of suitable substrate is the single most
important recruitment/community-structuring factor in offshore areas along the WFS where abiotic parameters (temperature and salinity ranges) are less variable as compared to nearshore areas. The shelter provided by a habitat type is critical for settlement and the reduction of predation mortality among newly settled juveniles (Shulman 1984; Doherty and Sale 1986). This pertains to both macroinvertebrates (e.g., corals) and fish species. Valuable commercial fish species, including *Mycteroperca microlepis*, utilize structures provided by scarped hardbottom ledges during a number of their life stages. It is plausible, and even probable, that placement of more structures like the GNGS artificial reefs, which mimic scarped ledges, would enhance juvenile and smaller-adult survival of commercially important fish species (see Chapter 3 data on commercial fish preference of artificial reef versus reference habitat), as well as invertebrates. In addition, Chapter 4 of this dissertation discusses the recruitment of juvenile corals to available substrate along natural ledges, where bare limestone substrate provides optimum settling conditions. Figure 5.6 depicts the trends in juvenile corals along the natural ledges over the samplings, and reveals that continuous recruitment may be occurring, as long as substrate is available. Placement of more artificial-reef structures along the WFS could enhance fish and other epibenthic recruitment.
5.4 Problem #2: Rationale for Dismissing “Lack of Definitive Data” Argument Against Artificial Reef Use Along the West Florida Shelf

Artificial reefs are by no means universal tools that should be deployed in all marine restoration or conservation projects. Thorough analyses of biotic and abiotic parameters must be conducted in an area before artificial reefs can be considered as one option in a suite of alternatives. Bohnsack (1989) pointed out a number of factors that should be considered contra-indicative to artificial reef deployment. The attraction hypothesis is likely to hold for locations where natural reef habitat is abundant, fishing mortality is high, recruitment is limited, and most species are pelagic, highly mobile, and non-reef dependent. Artificial reefs would be ineffective, and even deleterious, in these areas. Increased production is likely at locations isolated from natural reefs, with low fishing pressure, and dominated by habitat-limited, demersal, philopatric, territorial, and obligatory reef species (Bohnsack 1989). If sufficient data (abiotic and biotic) are available from an area and the data indicate that production, not attraction, processes will
prevail, then artificial reefs should be considered in restoration/conservation plans. Unfortunately, “sufficient” data are not the same as “definitive” data. However, as I will explain below, there are times when logical and rational decisions can be made to restore, enhance, or conserve an area without possessing truly definitive data.

The WFS, with its expansive quartz-dominated sand ridges, intermittent limestone outcrops, and associated livebottom assemblages, is a perfect candidate for artificial reef construction and deployment. The patchy distribution of natural livebottom habitats and assemblages could be enhanced by deployment of low-relief, limestone structures in areas where a thin veneer of sand overlies limestone bedrock. Optimal placement would be between, but not close to, natural ledge substrate and oriented in a northwest to southeast (ledge-parallel) direction in accordance with Bohnsack’s (1989) recommendations.

Bombace et al. (1994) further confirmed the importance of adhering to this recommendation through their work with artificial reefs in the Adriatic Sea. Catches at reefs deployed far from natural reefs showed a gradual increase in fish abundance, species richness (both mean and total) and diversity. Evidence for this was the appearance and/or the increase in catches of some hard-substrate species of fish and mollusks which were rare or completely absent in the original sand-plain habitat. The increase of these species seemed to be directly correlated to the reef dimensions in terms of volume of immersed materials and area covered. The Bombace et al. (1994) results indicate that the spatial scale of artificial reef placement along the WFS must be sufficient to yield the desired effect of increased productivity. Calculation and modeling
of optimal spatial scales are beyond the scope of this paper but should be considered in future work.

Particular attention should also be paid to ensuring that the artificial reefs are not only located at optimal distances from natural substrates, but also constructed in a manner that mimics the natural substrates. Carr and Hixon (1997) compared fish assemblages at natural and artificial reefs and found that artificial reefs with structural complexity and other abiotic and biotic features similar to those of natural reefs would best mitigate in-kind losses of reef fish populations and assemblages from natural reefs. The GNGS reefs are good examples of sound construction and deployment as they effectively mimicked natural livebottom assemblages along the shallow inner WFS. Future deployments should evaluate whether artificial reefs would be more effective oriented in a ledge-parallel (northwest to southeast direction) or ledge-perpendicular (east to west direction). A series of ledge-parallel reefs could provide stepping stones and areas of refuge for mobile species during a red-tide/hypoxic event. Deeper areas in the eastern GOM were populated by fish during the shallow-water hypoxia of 2005, and it is plausible that the placement of artificial reefs could enhance evacuation and survival in the future. Ledge-perpendicular set-ups could provide a continuous evacuation route for mobile species and direct their movement back into shallow waters after dissipation of the red tide/hypoxia. Again, economic and ecological models would be helpful in determining optimum orientations of artificial reefs.

Fishing pressure along the WFS is high. Many commercially and recreationally-targeted finfishes, including those of the valuable Grouper/Snapper complex, inhabit the area. For artificial reefs to be successful along the WFS, they must be protected from
fishing, at the very least during the early stages of recruitment, much like the GNGS reefs. When the original plans for the GNGS pipeline construction and mitigation activities were released, the route for the pipeline was published in navigation charts, but coordinates for the artificial reefs remained unpublicized. Now, after a few years of deployment, many fishermen have learned the locations of the reefs and have begun to target them but not in sufficient numbers to alter fish abundances. Pitcher and Seaman (2000) take this recommendation one step further and state unequivocally that artificial reefs should be protected as no-take areas. Variations to this theme could include opening a small number of reefs to licensed fishing so that local fishermen would understand the effects and assist in monitoring. It is essential that fishermen are educated on the uses of artificial reefs for production/enhancement purposes as they will most likely reap the benefits in the future, but only if the reefs are left alone during the initial community-development phases.

The deployment of GNGS artificial reefs led to the development (through both initial attraction and subsequent production) of a thriving reef-like habitat. Although the benthic assemblage was less diverse than natural substrate assemblages, the fish assemblage was much more diverse, as a number of tropicals and commercially-important species were frequently counted in the area. The majority of the fish species are demersal, reef-dependent species that provide bottom-up support for the pelagics and mobile species that frequent the areas. Once again, the properties of the WFS are amenable to artificial-reef deployment, consistent with Bohnsack’s (1989) recommendations.
5.5. Conclusion

The state of the Earth’s aquatic ecosystems is in turmoil. Synergistic impacts including overfishing, pollution, ocean acidification, warming, habitat destruction, and introduction of new species are transforming once complex and productive systems such as coral reefs into monotonous level bottom with limited ecological value (Jackson 2008). Action needs to be taken now to boost resiliency of all reef assemblages, as marginal environmental conditions for reef distribution become more widespread (Guinnotte et al. 2003). What role could artificial reefs play in future mitigation, restoration, and conservation activities? Pitcher and Seaman (2000) suggest that protected artificial reefs have a role to play as hedges against extinction. Artificial reefs already sustain regional commercial and local artisanal fishing in some areas (Pitcher and Seaman 2000) and their expanded use could be employed to enhance fish stocks and benthic production, restore critical habitats, and provide refugia from which recolonization can take place. This is not to imply that artificial reefs should be used in every restoration or conservation program (for reasons stated in section 5.4 above). But in areas where abiotic and biotic parameters appear conducive to deployment, resource managers and scientists should not hesitate to construct and deploy artificial reefs to meet their production goals.

There have been recent efforts to expand offshore aquaculture along the WFS, and while caged structures may effectively grow fish, they are not long-term, sustainable solutions. The impacts of aquaculture facilities on benthic communities can be very detrimental as organic matter concentrations are elevated and the potential for benthic mortality via sedimentation and hypoxia/anoxia development is high. Instead of the short-term investment in large offshore aquaculture infrastructure, resource managers and
fisheries scientists should consider a bottom-up enhancement of fish stocks via deployment of low-relief, natural substrate structures.

Pitcher and Seaman (2000) emphasize, and I concur, that for artificial reefs to produce maximum benefits, they must be afforded some type of early-stage protection in the form of designation as a Marine Protected Area (MPA) or no-take zone. The protection would allow a complex community to recruit and establish, providing major enhancement to fishery catch. There are a variety of ways to go about designating artificial reefs as MPAs, but constituents (local stakeholders) must be part of the process. Stakeholders should be educated about the utility of artificial reefs and perhaps given access and fishing rights at certain reefs, while self-enforcing no-take zones at other reefs. Although the task of enlisting the support of local stakeholders may seem daunting, there have been cases where unexpected support for no-take areas has been expressed. The task is difficult but by no means impossible and may even prove to be enjoyable once a rapport with local WFS stakeholders has been established.

Actions need to be taken as soon as possible to save existing reefs and livebottoms. These days, we should not hesitate to employ methods to restore and protect today’s depleted ecosystems even without definitive scientific evaluation (Clark 1996). The quest for robust scientific data should absolutely continue, but it should not preclude restorative actions, or else we risk losing these valuable ecosystems forever.
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About the Author

Jennifer Maria Dupont was born and raised in New York. She earned her Bachelor’s degree, Magna cum laude, in Biology with a French minor from the University of Richmond in 2003. While at the University of Richmond, she spent a semester studying and conducting research at the Duke University Marine Laboratory and Bermuda Biological Station for Research, where she became an Advanced Open Water Diver and decided to pursue a graduate degree in Marine Science.

She started her work at the University of South Florida College of Marine Science Reef Indicators Lab in August 2004, under the direction of Dr. Pamela Hallock Muller. While at USF, she worked as an environmental consultant and conducted surveys along natural gas pipeline routes and ship groundings. She also worked as a science mentor and divemaster with the SCUBAnauts, International. She was awarded her Ph.D. in Marine Science in 2009.