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Only the Strong Will Survive: Red Tides as Community-Structuring Forces in the Eastern Gulf of Mexico

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Abstract

A harmful algal bloom (red tide) and associated anoxic/hypoxic event in 2005 resulted in massive fish kills and collapse of epibenthic communities in depths less than 25 m along the central west Florida shelf. An ongoing collaborative monitoring study involving University of South Florida and Florida Aquarium science divers provided a focused time series (2005 to 2007) of natural hardbottom/ledge community succession after the red tide disturbance. Coral species, including *Oculina diffusa, Solenastrea hyades, Stephanocoenia intersepta,* and *Siderastrea spp.,* appear to have bleached during the red tide disturbance, but recovered soon thereafter. Successional stages of fish communities tend to follow a predictable progression and revert to a pre-red tide state. This is in contrast to MacArthur-Wilson mechanisms which have been used to describe species diversity of patch or discontinuous habitats as a balance between immigration and extinction rates (equilibrium). Regular occurrence of red tides, along with fluctuating sea temperatures, turbidity, hurricanes, and other disturbances in the eastern Gulf of Mexico, may prevent communities from reaching a dynamic equilibrium. These results corroborate previous predictions that the fluctuating nature of the shallow eastern Gulf of Mexico may limit the effective species pool of colonists.

Keywords: benthic, MacArthur-Wilson equilibrium, succession, West Florida Shelf

Introduction

During summer of 2005, epibenthic hard-bottom communities in the Gulf of Mexico off west central Florida were negatively affected by a persistent red tide (harmful algal bloom) and subsequent hypoxic/anoxic conditions (CA Heil, pers. comm., 2006). Such catastrophic events have been documented since 1881, and observed for an even longer period of time. The organism responsible for the Florida red tide has been identified as *Karenia brevis* (Davis, 1948; Steidinger, 1975), but 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. Given the near-annual regularity of minor and major bloom events (Walsh et al., 2006), surprisingly few studies have investigated the effects of red tides on benthic invertebrate and demersal fish communities on the west Florida shelf. One of the best-documented red tides occurred in the mid-eastern Gulf of Mexico during the summer of 1971. Observations before, during, and after the 1971 event provided insight into effects of a red tide bloom (Smith, 1975; Smith, 1979). 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 (13-18 m), an estimated 74% of the species were killed (Smith, 1975). Smith reported that invertebrate populations sustained even higher mortality than fish populations. Echinoderms, gastropod mollusks, decapod crustaceans, scleractinian corals, polychaetes, and sponges all declined drastically (based on qualitative observations).

Some biotic groups appeared to recolonize relatively rapidly (e.g., benthic algae and certain fishes), while others (*e.g.*, scleractinian corals and echinoderms) took several years to recruit. The post-impact recolonization study by Smith (1975) was instrumental in overturning previously held notions that the effects of red tides are negligible and short-lived, with only temporary effects on inshore and nearshore fisheries. His study asserted that major red tides might result in the near-extirpation of shallow-water reef biotas, requiring up to a decade or more for benthic communities to reestablish to pre-red tide conditions.

Decadal scale recovery rates of benthic as predicted by Smith (1975) are cause for concern in the Gulf of Mexico, whose oligotrophic waters support diverse, and very lucrative, commercial and recreational fisheries. In 2000, the commercial fish and shellfish harvest from the five U.S. Gulf states was estimated to be 772 million kg (approximately 20% of the total domestic landings in the United States) and valued at over $900 million (GulfBase.org). The recreational fishery is also significant as 40% of domestic landings come from the Gulf states, excluding Texas (O'Bannon, 2001). The productivity of coastal waters is due to the benthic-pelagic coupling (Marcus and Boero, 1998) in the form of biogeochemical cycling (the turnover of nutrients in form of living matter or its decomposed constituents), and the importance of fit, functioning benthic communities to the overall health of Gulf of Mexico fisheries cannot be overstated. It is essential, therefore, that we understand the population and community dynamics in the region in terms of the species present along the inner west Florida shelf as well as the ecological impacts and subsequent recovery rates of benthic invertebrate and demersal fish communities after a catastrophic disturbance such as the 2005 red tide and associated anoxic event.

The goals of this paper are two-fold. First, we aim to qualitatively describe the epibenthic and demersal fish communities on two natural hardbottom/ledge communities on the inner west Florida shelf, defined by Hine et al. (2003) as those areas landward of the 30 m isobath. Though there have been numerous papers published on the geological origin and characteristics of areas along inner shelf areas (Harrison et al., 2003; Twichell et al., 2003; Hine et al., 2003) as well as the physical oceanographic features that dominate (Nummedal et al., 1977; He and Weisberg, 2002; Liu and Weisberg, 2005), there have been relatively few descriptions of species that inhabit these areas. The lack of community-scale benthic descriptions makes it very difficult for scientists and managers to understand the impacts that acute stresses, such as the 2005 red tide event, have on natural ledge/hardbottom areas. This paper lays the groundwork for future quantitative, comparative studies by presenting a baseline species list from natural hardbottom habitats during a two-year study period that commenced shortly after the dissipation of the red tide. Although the seasonal/annual variability and quantitative statistics are not discussed, our second goal in the paper is to begin to speculate on the role of *Karenia brevis* as a potential community-structuring force on the west Florida shelf. The regular occurrence of minor and major red tide blooms (and the development of anoxic waters at depth) may play an important role in limiting the diversity of inner shelf communities. Qualitative observations and speculative discussions are presented in this paper, with quantitative analyses to follow in future publications.

Methods

Study Site Descriptions

The west central coast of Florida shelf is an estuarine, barrier island, inner shelf system of marked contrasts and contradictions (Hine et al., 2003). The coastal/shelf system is both wave and tide-dominated, relatively sediment-starved yet receives large inputs of sand from the Tampa Bay estuary, and is generally considered to be a low wave-energy system with indications of intermittent high wave-energy such as overwash fans and tidal cut inlets (Hine et al., 2003). A strong topographic influence is conferred on the region east of the 30 m isobath (representing the past 8,000 years of coastal and shelf evolution as evidenced by sea-level curves). The area is underlain by the Neogene limestone of a formerly active carbonate platform, with sediments rich in carbonate components and exposed hardbottom areas that occupy approximately 50% of the inner shelf. Ledges or scarps up to 4 m in relief are superimposed on the platform and tend shore-parallel (Obrochta et al., 2003). Two sites, Mastedon Tabletop (MT) and Fish and Wildlife Research Institute #1 (FWRI1) were chosen for monitoring after the dissipation of the 2005 red tide, as they had been severely affected by the anoxic conditions that developed during the event (Fish and Wildlife Research Institute, St. Petersburg, pers. comm.). GPS coordinates and site characteristics are displayed in Table 1. The two sites have the typical limestone outcroppings set in sandy substrate areas as described by Obrochta et al. (2003).

Table 1. Site Locations and Characteristics

Site	GPS Coordinates	Depth (m)
MT	27º90.20´ 83º10.79´	19.8
FWRI 1	27º91.31´ 83º10.55´	19.5

Benthic Data Collection

The project commenced in February 2006, approximately three months after the dissipation of the *Karenia brevis* bloom, and sampling was conducted on a monthly basis (weather permitting) through the next 22 months. A team of 4-6 divers entered the water upon reaching the site GPS coordinates. The divers navigated to a sub-surface buoy attached to a cinderblock, with attached temperature profiler that marked the site location. Three 15-m transect lines were laid on the bottom in a random fashion using headings determined *a priori* on board the vessel emanating at the marker. Digital photographs were acquired every 0.5 m along the transect line, at a consistent distance of 0.5 m from the bottom. The sampling strategy afforded the single benthic data collector enough time to attain maximum spatial coverage while remaining well within dive limits.

Substrate and biological cover attributes of the benthic photostations were assessed using point-count analysis (Curtis, 1968; Bohnsack, 1979; Carlton and Done, 1995; Jaap and McField, 2001; Jaap et al., 2003;). Twenty 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). Species were identified where possible, especially among the scleractinian corals and other sessile macroinvertebrates. Algae were identified to genus and, if possible, to species levels. General classifications of the algae were used if genera or species could not be determined in the photographs. These classifications include Rhodophyta (e.g, *Eucheuma* and *Gracilaria spp.*), Chlorophyta (e.g., *Udotea sp.*) and Phaeophyta (e.g., *Sargassum sp.*); if identification proved impossible due to poor quality of photograph, excess sedimentation, etc., the algae were grouped into Macroalgae and Turf Algae categories. Qualitative species lists were generated with assistance from past publications (Dawes and Lawrence, 1990) and are presented in this paper. Future work will focus on quantitative assessment of benthic component cover. The lists presented here are not meant to be comprehensive, as the data were collected through photographic analyses, thereby excluding cryptic species from appearing in the analyses.

Fish Data Collection

Fish censuses were conducted using a modified Bohnsack Point Count Method (Bohnsack and Bannerot, 1986; Bohnsack et al., 1994), with observers' fish identification skills evaluated prior to the surveys. All divers were Florida Aquarium REEF fish data collectors and they adapted easily to the Bohnsack Point Count Method. Once in the water, the divers rotated and counted fish within a five m radius cylinder (visibility permitting) extending from the surface to bottom for five minutes. Divers recorded fish species, abundances, and approximate sizes on underwater data sheets. Between one and three surveys were conducted in different, non-overlapping locations by each diver during each dive, to provide maximum spatial coverage. The data from the two sites were pooled and a complete species list for the sites was generated and is presented in this paper.

Results

Tables 2 and 3 list the benthic and fish populations, respectively, observed during the 22-month study period. The species listed in Table 2 represent those members of the epibenthos that are conspicuous in digital photographs; cryptic species that do no appear in the photographs are not listed. A number of the components could only be identified to the genus level, indicating that digital photographic transects may not be the best method for researchers that need to identify flora and fauna to the species level.

Table 2. Benthic Fauna and Flora

Corals *Cladocora arbuscula* (LeSueur, 1821) *Oculina diffusa* (Lamarck, 1816) *Phyllangia americana* (Milne-Edwards & Haime, 1849) *Siderastrea radians* (Pallas, 1766) *Siderastrea sidereal* (Ellis and Solander, 1786) *Solenastrea hyades* (Dana, 1846) *Stephanocoenia intersepta* (Lamarck, 1816)	**Algae** Chlorophyta *Acetabularia sp.* *Caulerpa mexicana* Sonder ex Kützing *C. prolifera* (Forskål) Lamouroux *C. sertularioides* (S.G. Gmelin) Howe *Codium isthmocladum* Vickers *Halimeda discoidea* Decaisne *Penicillus sp.*
Porifera *Cliona sp.* *Chondrosia collectrix* (Schmidt, 1870) *Cinachyra alloclada* (Uliczka, 1929)	Rhodophyta *Eucheuma isiforme* (C. Agardh) *Gracilaria sp.* *Laurencia corallopsis* (Montagne) Howe
Echinodermata *Arbacia punctulata* (Lamarck, 1816) *Astrophyton muricatum* (Lamarck, 1816)	Phaeophyta *Dictyota sp.* *Sargassum filipendula* C. Agardh
Chordata *Aplidium sp.* *Eudistoma sp.*	

Table 3 lists the 47 fish species observed and enumerated during the course of the study period. These species represent members of both the pelagic and dermersal community, with certain tropical species appearing during the summer samplings, as the waters in the Gulf of Mexico warm.

Table 3. Fish Community Components

Common Name	**Scientific Name (species author)**
Banded Butterflyfish	*Chaetodon striatus* (Linnaeus, 1758)
Bandtail Puffer	*Sphoeroides splengeri* (Bloch, 1785)
Barjack	*Caranx rubber* (Bloch, 1793)
Beaugregory	*Stegastes leucostictus* (Muller &Troschel, 1848)
Belted Sandfish	*Serranus subligarius* (Cope, 1870)
Black Margate	*Anisotremus surinamensis* (Bloch, 1791)
Black Seabass	*Centropristis striata* (Linnaeus, 1758)
Blue Angelfish	*Holacanthus bemudensis* (Goode, 1876)
Blue Goby	*Ptereleotris calliura* (Jordan & Gilbert, 1882)
Blue Runner	*Caranx crysos* (Mitchill, 1815)
Cocoa Damsel	*Stegastes variabilis* (Castelnau, 1855)
Cotton wick	*Haemulon melanurum* (Linnaeus, 1758)
Cubbyu	*Pareques umbrosus* (Jordan & Eigenmann, 1889)
Emerald Parrotfish	*Pareques umbrosus* (Jordan & Eigenmann, 1889)
Filefish	*Sp.?*
Gag Grouper	*Mycteroperca microlepis* (Goode & Bean, 1879)
Great Barracuda	*Sphyraena barracuda* (Edwards, 1771)
Greater Amberjack	*Seriola dumerili* (Risso, 1810)
Grey Triggerfish	*Balistes capriscus* Gmelin, 1951
Harlequin Bass	*Serranus tigrinus* (Bloch, 17900
Hogfish	*Lachnolaimus maximus* (Walbaum, 1792)
Inshore Lizardfish	*Synodus foetens* (Linnaeus, 1766)
Leopard Toadfish	*Opsanus pardus* (Goode & Beane, 1880)
Mangrove Snapper	*Lutjanus griseus* (Linnaeus, 1758)
Pilotfish	*Naucrates ductor* (Linnaeus, 1758)
Porgy	*Calamus sp.*
Red Grouper	*Epinephelus morio* (Valenciennes, 1828)
Round Scad	*Decapterus punctatus* (Cuvier, 1829)
Sand Diver	*Synodus intermedius* (Spix & Agassiz, 1829)
Sand Perch	*Diplectrum formosum* (Linnaeus, 1766)
Scamp Grouper	*Mycteroperca phenax* (Jordan & Swain, 1884)
Schoolmaster	*Lutjanus apodus* (Walbaum, 1792)
Seaweed Blenny	*Parablennius marmoreus* (Poey, 1876)
Sheepshead	*Archosargus probatocephalus* (Walbaum, 1792)
Sheepshead Porgy	*Calamus penna* (Valenciennes, 1830)
Slippery Dick	*Halichoeres bivittatus* (Bloch, 1791)
Spanish Mackerel	*Scomberomorus maculates* (Mitchill, 1815)
Spotfin Butterflyfish	*Chaetodon ocellatus* Bloch, 1787
Spottail Pinfish	*Diplodus holbrookii* (Bean, 1878)
Spotted Drum	*Equetus punctatus* (Bloch & Schneider, 1801)
Tomtate	*Haemulon aurolineatum* Cuvier, 1830
White Grunt	*Haemulon plumierii* (Lacapede, 1801)
Whitespotted Soapfish	*Rypticus maculates* Holbrook, 1855
Yellowfin Mojarra	*Gerres cinereus* (Walbaum, 1792)
Yellow Goatfish	*Mulloidichthys martinicus* (Cuvier, 1829)
Yellowtail Snapper	*Ocyurus chrysurus* (Bloch, 1791)
Yellow Wrasse	*Halichoeres sp.*

Discussion

The species lists presented in this paper contribute to a limited qualitative database of benthic and fish communities that develop on the natural hardbottom/limestone ledge outcroppings in the eastern Gulf of Mexico. Dawes and Lawrence (1990) observed that the limestone outcroppings are the major sites that support a macroalgal flora at depths below 10 m in the Gulf of Mexico, and contribute greatly to both biomass and energy levels, although overall the energy levels in these communities are lower and more erratic than in shallow water seagrass beds. They also observed that at certain times during the year, algal biomass on the limestone outcroppings accounted for less than 20% of the benthos (primarily during the winter and spring). The fluctuation in available biomass suggests that secondary production must be dependent on other sources such as the shallower, but more stable seagrass, communities. These observations coincide with initial quantitative assessments of herbivorous fish populations (not presented here), which appear to fluctuate on a seasonal basis, as the fish move into the shallower seagrass communities to feed during the colder months.

The seasonal emigration of fish populations, combined with the regular occurrence of acute stresses imposed on demersal fish and benthic macroinvertebrate communities, makes it difficult to apply typical dynamic equilibrium ecological models to definitions of community succession and structure. 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 proposed by MacArthur and Wilson (1963) which predicts that species richness of insular (or insular-like) areas depends upon a balance of species immigration and species extinction rates. Immigration and extinction rates are in dynamic equilibrium, resulting in continual biotic turnover in contrast to the climax-community hypothesis (stable state). 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 the 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.

Communities along the west Florida shelf are composed of species that are tolerant and resilient to regular environmental stresses imposed on them as residents of temperate, shallow-water ledge communities. Populations may be restricted to those that are most resilient and able to withstand the red tide stress, as well as the synergistic effects that result when other natural and anthropogenic stresses, i.e., hurricanes, cold-water events, overfishing, and pollution, are factored in. Future analyses will quantify seasonal variability/stability of these communities, whose productivity contribute greatly to the socioeconomics of the west-central Florida region.

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