

Ecological impacts of the 2005 red tide on artificial reef epibenthic macroinvertebrate and fish communities in the eastern Gulf of Mexico

Jennifer M. Dupont*, Pamela Hallock, Walter C. Jaap

University of South Florida College of Marine Science, 140 7th Avenue South, St. Petersburg, Florida 33701, USA

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 <25 m 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. Ongoing monitoring 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 structures of artificial reefs 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 2 yr; 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. Substantial recovery of the benthos occurred in 2 yr, which was more rapid than predicted in previous studies.

KEY WORDS: Disturbance recovery · Assemblage succession · Red tide · Artificial reefs · West Florida shelf

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Effects of red tide have been documented along the west Florida shelf since 1844 (Ingersoll 1881). Since these early effects included fish kills, toxic shellfish, and sick and dying birds, they have been attributed to *Karenia brevis* blooms (Rounsefell & Nelson 1966). These red tides have varied in location, size, duration, and intensity, and exposure to the brevetoxins affects 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, and several factors have been suggested to play a role, including eutrophication (Brand & Compton 2007), upwelling and current regime (Tester & Steidinger 1997), and iron fertilization (Walsh et al. 2006). Minor *K. brevis* blooms (<10⁵ cells l⁻¹ as defined by the Florida

Fish and Wildlife Research Institute [FWRI], St. Petersburg) of limited duration and associated fish kills may be an annual, natural phenomenon in coastal waters of the Gulf of Mexico (Steidinger & Ingle 1972, Walsh et al. 2006), although occasionally large blooms (>10⁵ 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 to 18 m depth) resident fish species perished. Echinoderms, gastropod mollusks, decapod crustaceans, scleractinian corals, polychaetes, and sponges sustained even

*Email: jdupont@mail.usf.edu

higher mortalities. Major red tides might result in near-extirpation of shallow-water live-bottom biota, requiring 5 yr or more for benthic communities to recover to pre-red tide conditions (Smith 1975, 1979).

With respect to the infaunal benthos, Simon & 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 losses. Only 5 of the 22 most abundant species remained on the intertidal flat after the 1971 event. Repopulation of the polychaete fauna and re-establishment of the benthic community following the natural defaunation were quantified and modeled in subsequent years (Dauer & Simon 1976, Simon & Dauer 1977). Recovery rates of infaunal communities in Tampa Bay were much faster than those predicted by Smith (1975) for eastern Gulf of Mexico live-bottom systems.

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 lower trophic levels, acute exposure to algal toxins produces deleterious effects on zooplankton, including reduced feeding, growth, and egg production (Gill & Harris 1987, Turner & 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 the present study were to quantify the impacts of the 2005 red tide/hypoxia disturbance (Heil 2006), which persisted for >1 yr 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 2 yr 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. Our data greatly augment the limited database of community-scale

ecological impacts of red tides in the Gulf of Mexico and provide a quantitative, multi-year study of epibenthic macroinvertebrate and demersal fish community dynamics after a toxic red-tide disturbance.

MATERIALS AND METHODS

Study area characteristics. In 2001, as mitigation for construction of a natural gas pipeline, Gulfstream Natural Gas Systems (GNGS) installed artificial reef structures at 6 sites in US Federal Waters, 19 to 25 km west of Tampa Bay and in water depths of 18 to 25 m (Fig. 1). Three sites consisted of limestone boulders (>1 m diameter) haphazardly dispersed to provide some overlap and habitat structure (hereinafter referred to as 'LB sites'). Pre-fabricated 1.8 m × 2.4 m reef modules (designed by H. Hudson) were installed at the other 3 sites (RM sites). Modules, 153 in total, were constructed of limestone in a concrete matrix and dispersed among the 3 RM sites. The 6 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 the LB and RM sites. Fish assemblages at adjacent (within 10 m) low-relief live-bottom reference (Ref) sites were also monitored, but no regular benthic data were collected as the sites were often buried under sediment. Abiotic parameters

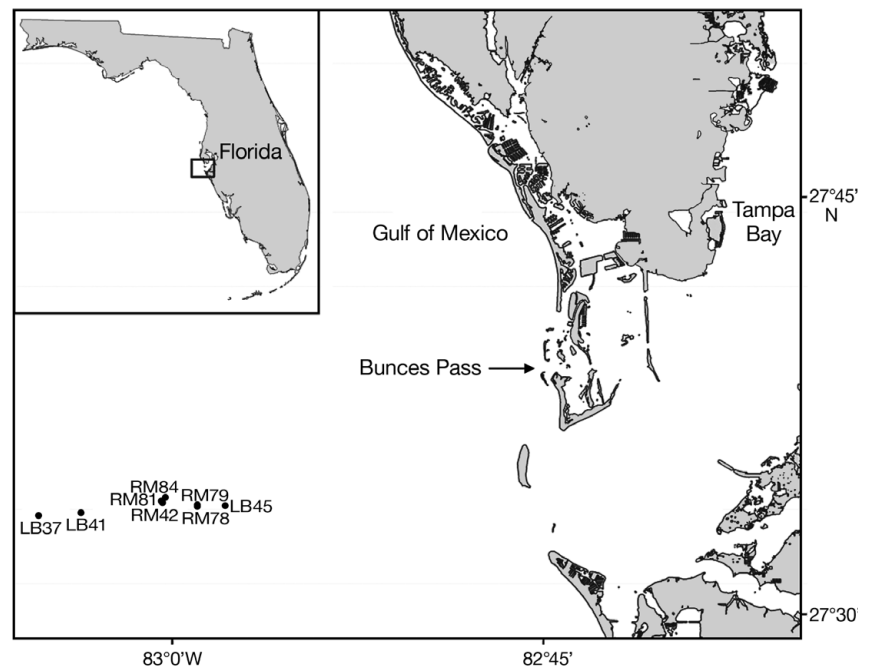


Fig. 1. Location of Gulfstream Natural Gas Systems limestone boulder (LB) and reef module (RM) sites in the eastern Gulf of Mexico. There were 3 LB sites (with 1 photostation each) and 3 RM sites (with 5 photostations in total)

(temperature and Secchi depth) and habitat characteristics (rugosity and depth) were recorded during each of the 5 fish censuses (described below under 'Fish communities').

In addition to the regular sampling of abiotic parameters during each fish census, scientists from the FWRI 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 west 24 km from Bunces Pass and passed through areas located 5 to 7 km north of the GNGS artificial reef sites. 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.

Benthic communities. Eight 1.0 m² photostations were digitally photographed in March 2005 (prior to the red tide), August 2005 (during the red-tide event), July 2006 (6 mo after the dissipation of the red tide), and March 2007 (2 yr after the initial sampling time). Three of the photostations were located at LB sites and 5 at RM sites (Fig. 1). 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 4 photos were processed with Canvas™ to create a seamless 1.0 m² mosaic that was used for analysis (Fig. 2). The 8 photostations were chosen because they had been photographed prior to the red-tide event. Because of the small sample size, 10 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 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 2 types of artificial reefs during each sampling period, and the photostations were deemed sufficiently representative of the relatively uniform benthic community development.

Substrate and biological cover attributes of the benthic photostations were assessed using point-count analysis (e.g. Curtis 1968, Bohnsack 1979, Carleton & Done 1995, Jaap & McField 2001, Jaap et al. 2003). One hundred random 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). 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 higher taxon and their respective 'bleached' or 'dead' counterparts, e.g. the coral *Cladocora arbuscula* (LeSueur, 1821), the urchin *Arbacia lixula* (Linnaeus, 1758), and the phylum Porifera. We categorized normal-appearing *C. arbuscula* as coral that did not display any signs of bleaching, whereas the bleached category includes all corals displaying partial or full bleaching. Normal-appearing Porifera included *Cliona* sp. along with other unconfirmed sponge species, 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 (i.e. August 2005 mosaics were compared to March 2005 mosaics to determine locations of previously healthy animals). The remaining 14 categories consist of: *Leptogorgia virgulata* (Lamarck, 1815), *Astrophyton muricatum* (Lamarck, 1816), ascidians, rock/rubble, unknown, and 9 algal categories. Algae were divided into 5 distinguishable algal genera or species (*Acetabularia* spp., *Halimeda* spp., *Caulerpa mexicana*, *Caulerpa prolifera*, and *Caulerpa racemosa*) and 4 general algal classifications. General categories include rhodophytes (e.g. *Eucheuma* spp. and *Gracilaria* spp.) and chlorophytes (e.g. *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 Primer6™ (Clarke & Warwick 2001) non-parametric software package, as data displayed significant non-normality. Point-count values were square-root-transformed to draw information from across the whole

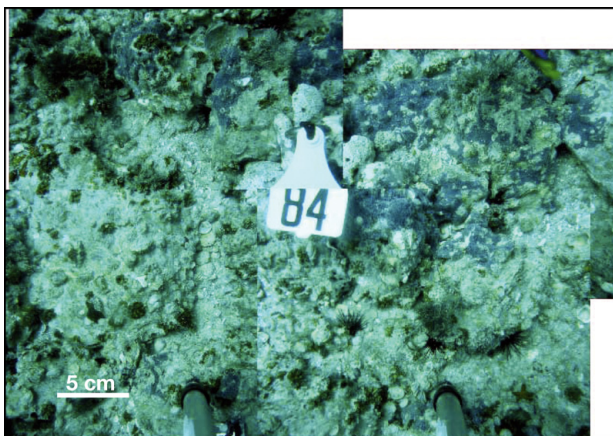


Fig. 2. Example of 1 m² photo-mosaic from Stn RM84 (~17 m depth). Four photos were combined to produce composite images that were used in point-count analyses

assemblage (Clarke & Green 1988). 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 indicate a useful representation (i.e. configuration closely represents the rank order of dissimilarities in the original triangular matrix), while stress levels >0.20 indicate a random arrangement of samples, bearing little resemblance to the original ranks (Clarke 1993). Second-level procedures (Clarke & Warwick 2001) were used to test for significant differences in benthic community structure among those samples/groups that separated spatially in the MDS. An analysis of similarity (ANOSIM) was run to detect significant community differences among sampling times. ANOSIM is analogous to the multivariate analysis of variance (MANOVA) but is used preferentially in the present paper because the probability distribution of counts could not be normalized by any transformation due to the dominance of zero values.

Data for all 8 photostations were grouped together ($n = 8$) for each of the 4 survey periods, as a 2-way ANOSIM revealed no differences between the benthic communities at the 2 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 2 conditions of (1) contributing significantly to the average dissimilarity between time periods and (2) contributing consistently (small standard deviation) to the average dissimilarity.

Fish communities. Censuses of the fish communities were conducted in summer 2005 (June, prior to bloom), winter 2005 (November 2005 to January 2006), summer 2006 (July and August), winter 2006 (December 2006 to March 2007), and summer 2007 (June 2007) at randomly chosen LB, RM, and Ref stations. Censuses were conducted using a modified Bohnsack visual fish-census method (Bohnsack & 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 min. Ten surveys were conducted at LB, RM, and Ref sites during each sampling period (30 in total). These data are summarized in 5 separate GNGS reports (GNGS 2005a, 2005b, 2006a, 2006b, 2007). These reports rely on information collected by research divers on SCUBA and no backup identification (e.g. voucher

specimens, photos) was collected. A comprehensive species list is not presented, due to inherent issues with *in situ* fish identification and the possibility that certain species may have been misidentified. Instead, we discuss the trends in discriminating species that contributed substantially and consistently to changes in fish assemblages before and after the red-tide event.

Species-richness values were plotted to depict temporal trends before, during, and after the red-tide event at the 3 types of habitat (LB, RM, and Ref). Abundance data were fourth-root-transformed to focus attention on patterns within the whole community, mixing contributions from both common and rare species (Clarke & Warwick 1994). ANOSIM tests were performed within each sampling time to determine whether fish assemblages were significantly different between LB, RM, and Ref sites. The 3 types of habitat differed significantly from one another in terms of fish-community structure, so subsequent analyses were performed on data separated by habitat.

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. tomtate *Haemulon aurolineatum*) are seasonally schooling species that can skew statistical analyses with abundance values 3 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 & Ray (1986), McEachran & Fechhelm (1998), and Froese & Pauly (2005), as well as the 5 GNGS reports (GNGS 2005a, 2005b, 2006a, 2006b, 2007).

RESULTS

Study-area characteristics

Depths at the sites ranged from 16.9 to 19.5 m (Table 1); rugosity was greatest at the LB sites (1.53) and least at the Ref 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 measurements ranged from 7.3 to 17.6 m, with considerable variability.

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

Table 1. Abiotic and habitat characterization data summary presented as mean values (\pm SE). Data were recorded during each of the 5 fish censuses. LB = limestone boulder sites, RM = reef module sites, na = not applicable, RI = rugosity index, WD = water depth

Site and year	Temperature ($^{\circ}$ C)		Secchi depth (m)	
	Summer	Winter	Summer	Winter
LB (WD = 19.5 \pm 1.1 m, RI = 1.53 \pm 0.04)				
2005	26.5 \pm 0.5	22.2 \pm 1.0	13.9 \pm 0.5	9.0 \pm 0.7
2006	29.1 \pm 0.3	18.2 \pm 0.7	17.6 \pm 2.1	12.6 \pm 0.8
2007	26.7 \pm 0.8	na	10.5 \pm 0.7	na
RM (WD = 16.9 \pm 0.2 m, RI = 1.36 \pm 0.08)				
2005	27.3 \pm 0.1	22.8 \pm 0.8	10.9 \pm 0.4	7.3 \pm 0.3
2006	29.6 \pm 0.2	18.2 \pm 0.6	9.6 \pm 0.3	12.3 \pm 0.4
2007	26.3 \pm 0.5	na	9.4 \pm 0.7	na
Reference (WD = 18.5 \pm 0.9 m, RI = 1.13 \pm 0.03)				
2005	26.9 \pm 0.2	20.7 \pm 1.2	8.5 \pm 0.4	9.8 \pm 0.5
2006	29.4 \pm 0.4	18.1 \pm 0.4	12.9 \pm 1.7	12.8 \pm 0.7
2007	25.9 \pm 0.5	na	9.8 \pm 0.6	na

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, water quality and chlorophyll levels were recorded during an FWRI cruise along a transect just north of the GNGS artificial reefs (Fig. 3). Dissolved oxygen levels 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

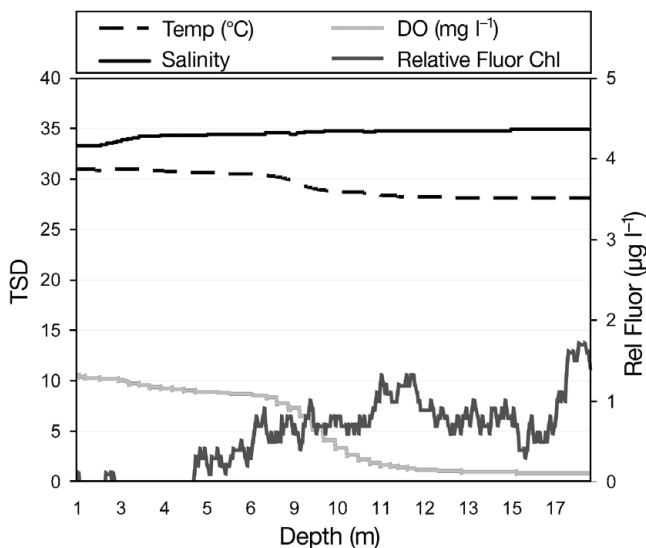


Fig. 3 Environmental parameters taken along a 24 km east-west transect positioned 5 to 7 km north of the Gulfstream Natural Gas Systems artificial reefs. Data are plotted on a non-metric depth scale to display the trend of all 4 parameters. DO = dissolved oxygen, Relative Fluor Chl = relative fluorescence of chlorophyll, Temp = temperature, TSD = temperature, salinity, and dissolved oxygen

chlorophyll increased to 1.7 μ g l^{-1} at offshore sites. These FWRI data are representative of conditions that prevailed along areas of the central west 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 August 2005, thereby negatively affecting both benthic macroinvertebrate and fish communities.

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 2-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). Samples grouped relatively well into 4 distinct sampling times. Samples are overlaid with the dendrogram similarity results (40 and 60% intervals). Arrows depict the temporal trajectory of benthic community development/succession. The trajectory proceeds with the initial March 2005 samples grouped at the bottom of the MDS, August 2005 samples (taken during the peak of the red tide) grouped 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 they return to the baseline state.

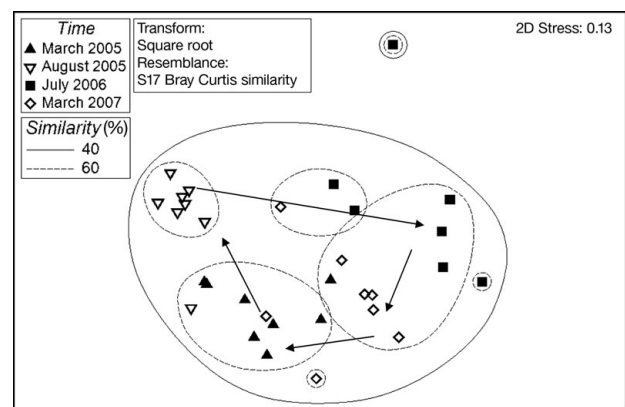


Fig. 4. Multidimensional scaling ordination of 1 m² benthic quadrats at limestone boulder and reef module sites during the 4 sampling periods. Theoretical temporal trajectory of community response is shown (→). July 2006 data point at the top of the figure is an outlier, primarily due to the station's high percent cover of turf algae

An ANOSIM indicated that, when analyzed in chronological order, the benthic community composition differed significantly between March 2005 and August 2005 (ANOSIM: $R = 0.8$, $p = 0.002$), between August 2005 and July 2006 (ANOSIM: $R = 0.8$, $p = 0.2\%$), and between August 2005 and March 2007 (ANOSIM: $R = 0.9$, $p = 0.001$). Percent cover and condition of poriferans tended to have a strong influence on temporal trends, as they contributed to significant community differences in all 3 temporal pairings (Table 2). 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% decrease in percent cover in normal *C. arbuscula* between March 2005 and August 2005. However, large, healthy colonies >10 cm in diameter were observed in July 2006 and March 2007. After the red tide, the predominant contributors to community differences were algal

Table 2. Results from the similarity percentages (SIMPER) test to determine discriminating benthic categories for pairs of sampling times that differed significantly (analysis of similarity, ANOSIM: $R \geq 0.5$, $p \leq 0.005$). Discriminating categories satisfy the conditions of contributing significantly and consistently to the average dissimilarity

Sampling times	Benthic category	Average cover change (%)
Mar 2005 and Aug 2005	Dead Porifera	+6.5
	Bleached <i>Cladocora arbuscula</i>	+6.1
	Normal <i>C. arbuscula</i>	-5.1
	Normal Porifera	-3.3
Aug 2005 and Jul 2006	Turf algae	+28.0
	Rock/rubble	-19.0
	Dead Porifera	-6.3
	<i>Caulerpa mexicana</i> (<i>C. arbuscula</i>) ^a	+5.3 (+0.6)
Aug 2005 and Mar 2007	Rhodophytes	+10.0
	Turf algae	+7.0
	Chlorophytes	+7.0
	Dead Porifera	-6.5
	(<i>C. arbuscula</i>) ^a	(+8)
Mar 2005 and Mar 2007 ^b	Rhodophytes	+3.6
	Turf algae	+2.5
	Chlorophytes	+3.2
	Rock/rubble	-3.4

^a*C. 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

^bSampling times were not significantly different; data are included to illustrate annual differences (over 2 yr sampling period)

taxa (July 2006 and March 2007). 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 during the last 2 sampling events, but there was a noticeable lack of recovery of the normal Porifera category. Percent cover of normal (non-bleached) *C. arbuscula* increased during both July 2006 (+0.6%) and March 2007 (+8.0%), with many of the colonies regaining their symbiotic zooxanthellae.

Fish communities

Observers reported 71 species/types of fish at the LB, RM, and Ref sites combined. There were significant differences in fish communities (diversity and abundance) among the LB, RM, and Ref sites (2-way ANOSIM among habitats within sampling times). Subsequent analyses were performed within individual habitat types ($n = 10$). Numbers of species present at the 2 artificial-reef habitat types and the reference sites were substantially lower immediately after the red-tide event (Fig. 5). Prior to the red-tide event, the highest number of fish species was observed at LB sites, with Ref 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 Ref sites. Species richness trended upward in all sites from summer 2006 through

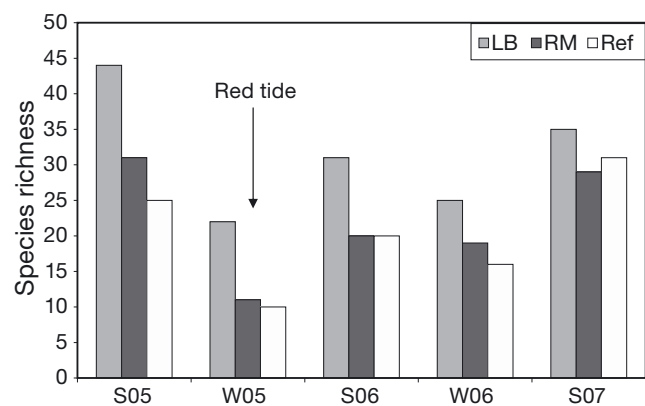


Fig. 5. Temporal changes in total fish species richness at the limestone boulder (LB), reef module (RM), and reference (Ref) sites. The summer 2005 (S05) census was conducted prior to the red-tide event; winter 2005 (W05) data were collected during and immediately after the event. Summer 2006 (S06) data collections spanned a time period between 6 and 8 mo after the dissipation of the red-tide event, winter 2006 (W06) occurred 1 yr post-event, and summer 2007 (S07) was the final sampling time in the 2 yr data set

summer 2007, with RM and Ref sites reaching their original (summer 2005) levels by summer 2007.

Significant temporal changes in fish assemblages were determined by an ANOSIM test (Table 3). 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).

Belted sandfish *Serranus subligarius*, cocoa damselfish *Stegastes variabilis*, and scamp grouper *Mycteroperca phenax* abundances all declined during or immediately after the red-tide event at the LB and RM sites, contributing significantly to differences between summer 2005 and winter 2005. Sheepshead *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 the red tide. Sand perch *Diplectrum formosum* displayed a similar trend at Ref 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 3 primary discriminating species, *Stegastes variabilis*, *Serranus subligarius*, and hogfish *Lachnolaimus maximus*. Summer 2006 and winter 2006 had similar fish assemblages, followed by a sharp increase in most species' abundances by summer 2007. Only *L. maximus* and jolthead porgy *Calamus bajonado* abundances were lower at LB and Ref sites, respectively.

A variety of patterns of change were observed between the first and last sampling times at the different habitats (Table 4). Both the LB and RM sites saw overall increases in Florida blenny *Chasmodes saburrae* abundances between summer 2005 and summer 2007. LB sites also experienced an increase in blue runner *Caranx crysos* abundances whereas RM sites experienced an increase in slippery dick *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 3 discriminating species at the Ref sites, *Halichoeres bivittatus*, *Calamus* sp. (porgy of unknown species), and white grunt *Haemulon plumierii*, increased in abundance over the 2 yr sampling time. Discriminating categories satisfy the 2 conditions of (1) contributing significantly to the average dissimilarity between time periods and (2) contributing consistently (small standard deviation) to the average dissimilarity.

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

Table 3. Matrix of significant (S) and non-significant (N) temporal fish-assemblage trends at limestone boulder (LB), reef module (RM), and reference (Ref) sites, respectively, as determined by an analysis of similarity (ANOSIM) test. Summer 2005 (S05) sampling occurred prior to the peak of the red-tide event and winter 2005 (W05) after it. Summer 2007 (S07) represents the final sampling in the focused 2 yr time series. S06 = summer 2006, W06 = winter 2006

	S05	W05	S06	W06
S05	–			
W05	SSS	–		
S06	SNS	NSN	–	
W06	NNN	NSN	NNN	–
S07	SSS	SSS	NNN	SSS

Table 4. Results from similarity percentages (SIMPER) analyses performed on significantly different assemblages of fish (determined by ANOSIM in Table 3) to determine discriminating species and their average absolute change in abundance between time periods. AP = *Archosargus probatocephalus*, CB = *Calamus bajonado*, CC = *Caranx crysos*, CS = *Chasmodes saburrae*, CX = *Calamus* sp., DF = *Diplectrum formosum*, HB = *Halichoeres bivittatus*, HP = *Haemulon plumierii*, LM = *Lachnolaimus maximus*, LR = *Lagodon rhomboides*, MP = *Mycteroperca phenax*, SS = *Serranus subligarius*, SV = *Stegastes variabilis*. For other abbreviations see Table 3

Sampling times and site	R	p	Discriminating species (average change)
S05 and W05			
LB	0.7	0.001	^a AP (+2), SS (–8), SV (–2)
RM	0.6	0.001	^a SS (–18), SV (–2), MP (–2)
Ref	0.5	0.001	SS (–1), DF (+1), HP (–1)
S05 and S06			
LB	0.3	0.001	MP (–2), CC (+12), SS (–7)
Ref	0.4	0.001	LR (+46), HP (+1), SS (–2)
S05 and S07			
LB	0.3	0.001	^a CS (+5), CC (+13), SS (–2)
RM	0.5	0.001	^a HB (+9), CS (+6), DF (–10)
Ref	0.6	0.001	HB (+9), CX (+3), HP (+1)
W05 and S06			
RM	0.5	0.001	^a SV (+3), SS (+6), LM (+1)
W05 and W06			
RM	0.5	0.001	SV (+2), SS (+7), LM (+1)
W05 and S07			
LB	0.7	0.001	^a SS (+6), CS (+5), SV (+3)
RM	0.9	0.001	^a HB (+9), CS (+7), SV (+3)
Ref	0.6	0.001	HB (+9), SS (+6), CX (+1)
W06 and S07			
LB	0.5	0.001	^a SS (+6), CS (+5), LM (–3)
RM	0.6	0.001	^a HB (+9), CS (+6), MP (+1)
Ref	0.4	0.001	HB (+9), CX (+4), CB (–10)

^aIndicates the placement of *Haemulon aurolineatum* when included in the analyses. Seasonal increases in abundances of *H. aurolineatum* skewed the statistical analyses and therefore they were excluded from the SIMPER analysis

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 (not shown) are not useful as the samples are essentially randomly placed, bearing little resemblance to the original similarity ranks in the triangular matrix (Clarke 1993).

DISCUSSION

Benthic communities

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 live-bottom biotas and that recovery rates may be on the order of years to decades. In contrast, we present data that indicate much shorter recovery periods (2 to 3 yr). In addition to providing evidence about shorter community recovery periods, these data are useful baselines for future studies (e.g. before-after, control-impact [BACI] work) along the west Florida shelf. They are especially timely in lieu of the 2010 Deepwater Horizon oil spill, which may have direct (e.g. oil present in close proximity to biota) or indirect (e.g. basin-wide impacts on fish and benthic larval supply and survival, development of water column hypoxia/anoxia) impacts on benthic and fish communities along the central west Florida shelf.

Smith's (1975, 1979) original work was limited in scope and based primarily on sporadic SCUBA observations and anecdotal information from dive and fishing charters in the area at the time of the red-tide event. The study was reactionary in nature (i.e. initiated after the start of the red tide), and therefore no data were presented on communities before exposure to the red tide and accompanying hypoxia/anoxia. Follow-up SCUBA surveys were conducted at 20 sites through 1974 along the west Florida shelf, but no quantitative or statistical data were collected or presented in the paper. Instead, Smith presents lists of observed species mortalities and provides only limited descriptions of ecological succession of benthic communities.

In contrast, our 2 yr study focused on regular monitoring of specific sites, with consistent photographic documentation of benthic communities before, during, and after the massive red-tide event of 2005. Our work presents evidence that communities recover more quickly than originally predicted by Smith (1975, 1979), particularly on artificial reefs. The discrepancies in recovery periods could be attributed to inherent differences between Smith's qualitative methods and our

quantitative methods. In addition, the inherent variability in the size and severity of red-tide events, with similarly variable mortality and recovery rates, could contribute to the discrepancies. The goal of the present paper, therefore, is to present 1 set of quantitative methods to measure and monitor these variations, and it provides the first statistical observations of benthic and fish community impacts, which can be used as baselines for future red-tide studies.

While benthic communities were significantly impacted by the 2005 red-tide event and related anoxic bottom conditions, the 2 yr recovery trajectory is towards a pre-red tide community structure (Fig. 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* spp. and *Euclima* 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 1 to 2 yr 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 yr^{-1} (W. C. Jaap pers. obs.), larger colonies must have survived the 2005 red tide. These findings are consistent with those of Rice & 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 July 2006 and March 2007; these echinoderms could graze on algal species and expose substrate. Our evidence suggests that recovery from a major red tide, including hypoxia, can occur on the order of years, rather than decades.

In a previous study in Old Tampa Bay, Tampa, FL, 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 2 yr (Simon & Dauer 1977). These recovery rates are similar to those we observed, and both sets of data indicate that communities may recover much faster than predicted by Smith (1975), although some populations may take much longer to fully recover. Colonization rates of some taxa are rapid (e.g. polychaetes in infaunal communities and algal species in epifaunal com-

munities), 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). We agree with the assertions by Simon & Dauer (1977) that benthic community analyses are essential when assessing the effects of disturbances (anthropogenic and natural), as opposed to single taxon studies. The differences in colonization rates suggest 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).

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, direct, 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). Approximately 5600 km² of benthic communities may have been affected by the 2005 red tide and the anoxic/hypoxic conditions (FWRI unpubl. data). Although natural disturbances such as red tides can be detrimental to individuals and communities at large spatial scales (10 to 1000 km²), substratum is made available for repopulation at various temporal and spatial scales (Connell 1978). This provides opportunity for renewal, development, and evolution 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).

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 live-bottom/rocky-ledge communities in the Gulf of Mexico. Natural live-bottom communities in the eastern Gulf of Mexico have much lower relief but more diverse coral assemblages (in-

cluding *Oculina diffusa*, *Solenastrea hyades*, *Siderastrea* spp., *Stephanocoenia intersepta*, and others) than artificial reefs. Comparative responses of the artificial reefs and live-bottom ledge communities will define whether there are differences between the 2 types of habitat and give insight into the efficacy of artificial reefs as mitigation structures. Natural live-bottom areas and comparative processes will be the focus of future publications

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 4 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 3 responses likely accounted for the significant reduction in fish species richness (Fig. 5) observed after the 2005 red tide.

Eight species were recorded during summer 2005, which preceded the red-tide event, but were not observed in any subsequent sampling times: Bermuda chub *Kyphosus sectatrix*, queen angelfish *Holacanthus ciliaris*, scaled sardine *Harengula jaguana*, scrawled cowfish *Acanthostracion quadricornis*, sergeant major *Abudefduf saxatilis*, Spanish mackerel *Scomberomorus maculatus*, Atlantic thread herring *Opisthonema oglinum*, and yellowtail snapper *Ocyurus chrysurus*. Three of these (*Harengula jaguana*, *S. maculatus*, and *Opisthonema oglinum*) are pelagic species that may have evacuated the area during the sampling times and simply have not returned to the sites (response #1). The remaining 5 species are semi-sedentary demersal species that occupy a particular ledge for extended periods, if not their entire life. The lack of observation of adults or juveniles suggests that extirpation from the area, rather than emigration, occurred (response #2, mortality). The failure of these 5 demersal species to recolonize within 2 yr 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): belted sandfish *Serranus subligarius*, grey triggerfish *Balistes capricus*, sand perch *Diplectrum formosum*, tomtate *Haemulon aurolineatum*, and white grunt *H. 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 time (summer 2005) as well as all subsequent sampling times. Other surviving remnant populations at 2 out of 3 sites included hog fish *Lachnolaimus maximus* (LB and RM), grey snapper *Lutjanus griseus* (LB and RM), sheepshead *Archosargus probatocephalus* (LB and RM), inshore lizardfish *Synodus foetens* (LB and Ref), and jolthead *Calamus bajonado* (LB and Ref). Two of the remnant species (*Lachnolaimus maximus* and *Lutjanus griseus*) are mobile, commercially/recreationally important species. Artificial reef sites appear to have been effective in retaining or recruiting these species after the red-tide event.

Two other commercially/recreationally important species (red grouper *Epinephelus morio* and *Mycteroperca phenax*) displayed response #3, as they were present during summer 2005 and absent during winter 2005, but again present at subsequent sampling times 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 Florida blenny *Chasmodes saburrae*, whitespotted soapfish *Rypticus maculatus*, cocoa damselfish *Stegastes variabilis*, and Spanish sardine *Sardinella aurita*. Surprisingly, all of these species, except *Sardinella aurita*, are classified as demersal and 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. The species are all highly resilient, with population doubling times <15 mo (Froese & Pauly 2005). These populations could be expected to recover quickly after acute disturbances.

Six species were observed regularly after the red tide, but were not recorded during summer 2005 (response #4): blue angelfish *Holacanthus bermudensis*, bluehead wrasse *Thalassoma bifasciatum*, Molly Miller blenny *Scartella cristata*, round scad *Decapterus punctatus*, cubbyu *Pareques umbrosus*, and spottail pinfish *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 group-spawning and production of pelagic larvae, 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 (listed in Table 4). Discriminating species were characteristically highly resilient species with population doubling times ≤ 18 mo (Froese & Pauly 2005). Our observations suggest that it is likely that adults that survived the red tide and relocated to other live-bottom areas produced a steady supply of planktotrophic larvae. The larvae may then have found favorable conditions and settled at the artificial sites and, less abundantly, at Ref sites.

LB and RM sites were generally more successful in retaining or recruiting commercial fish species during and after the red tide than Ref 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 & 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.

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 & Wilson (1963). Smith (1975, 1979) 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.

Our benthic data agree with Smith's (1975, 1979) 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, we 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 & Wilson (1963). Should the frequency and severity of disturbances decrease, we could expect different community structures to 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 could therefore focus on the quick restoration of communities (e.g. through placement of artificial structures) and not on the process of eliminating the *Karenia brevis* bloom, which is a fundamental ecological process in the eastern Gulf of Mexico.

Anthropogenic events, such as the 2010 Deepwater Horizon oil spill, could also have significant implications for west Florida shelf communities. The data presented in the present paper can be used to assess relative recovery rates of communities that may be affected by the oil spill, and comparisons can be made between the effects of a natural event (i.e. red tide) versus a human-induced event (i.e. the Deepwater Horizon oil spill) in the area. A number of techniques are being used for direct mitigation of oil presence in the Gulf of Mexico (e.g. chemical dispersants, mechanical recovery of oil). These techniques should be combined with longer-term mitigation measures that enhance recovery and future recruitment/survival (resilience) of populations in the eastern Gulf of Mexico, such as placement of strategic artificial structures, establishment of marine protected areas, and regulation of fisheries.

Acknowledgments. We thank Gulfstream Natural Gas Systems and E. Watkins for boat and personnel support. Thanks to the Florida Fish and Wildlife Research Institute, St. Petersburg, especially R. Pigg, for their data. This work was supported by the William and Elsie Knight Endowed Fellowship and the Gulf Oceanographic Charitable Trust Endowed Fellowship to J.M.D.

LITERATURE CITED

- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Mar Ecol Prog Ser* 15:265–274
- Bohnsack J (1979) Photographic quantitative sampling of hard bottom benthic communities. *Bull Mar Sci* 29: 242–252
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech Rep NMFS 41. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington, DC
- Bohnsack JA, Harper DE, McClellan DB, Hulbeck M (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. *Bull Mar Sci* 55:796–823
- Brand LE, Compton A (2007) Long-term increase in *Karenia brevis* abundance along the Southwest Florida coast. *Harmful Algae* 6:232–252
- Bray J, Curtis J (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Carleton J, Done T (1995) Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14: 35–46
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. *Mar Ecol Prog Ser* 46:213–226
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Plymouth Marine Laboratory, Plymouth
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101–S113
- Curtis A (1968) Quantitative photography. In: Engle C (ed) *Photography for the scientist*. Academic Press, London, p 74
- Dauer DM, Simon JL (1976) Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: species equilibrium. *Oecologia* 22:99–117
- Flewelling LJ, Naar JP, Abbott JP, Baden DG and others (2005) Red tides and marine mammal mortalities. *Nature* 435:755–756
- Froese R, Pauly D (eds) (2005) FishBase. www.fishbase.org. Accessed 18 Aug 2008
- Gill CW, Harris RP (1987) Behavioral responses of the copepods *Calanus helgolandicus* and *Temora longicornis* to dinoflagellate diets. *J Mar Biol Assoc UK* 67:785–801
- GNGS (Gulfstream Natural Gas Systems) (2005a) 2005 summer fish monitoring report for federal waters. ENSR Doc. No. 07324-066-009a. GNGS, Port Manatee, FL
- GNGS (2005b) 2005 winter fish monitoring report for federal waters. ENSR Doc. No. 07324-001. GNGS, Port Manatee, FL
- GNGS (2006a) 2006 summer fish monitoring report for federal waters, 2nd annual. ENSR Doc. No. 07324-084. GNGS, Port Manatee, FL
- GNGS (2006b) 2006 winter fish monitoring report for federal waters, 2nd annual. ENSR Doc. No. 07324-105-1. GNGS, Port Manatee, FL
- GNGS (2007) 2007 summer fish monitoring report for federal waters, 3rd annual. GNGS, Port Manatee, FL
- Hackett K (2002) A comparative study of two video analysis methods to determine percent cover of stony coral species in the Florida Keys. MS thesis, University of South Florida, Saint Petersburg
- Heil CA (2006) The perfect bloom: a review of the 2005 *Karenia brevis* bloom in the Gulf of Mexico. Summer 2006 presentation. American Society of Limnology and Oceanography, Victoria, BC

- Holling CS (1996) Engineering resilience versus ecological resilience. In: Schulze PC (ed) *Engineering with ecological constraints*. National Academy Press, Washington, DC, p 31–43
- Ingersoll E (1881) On the fish mortality in the Gulf of Mexico. *Proceedings of the United States National Museum*, Vol 4. Bean TH (ed) Smithsonian Institution, Washington, DC
- Jaap WC, McField MD (2001) Video sampling for monitoring coral reef benthos. *Bull Biol Soc Wash* 10:269–273
- Jaap W, Porter J, Wheaton J, Beaver C and others (2003) EPA/NOAA coral reef evaluation and monitoring project executive summary 2002. Florida Fish and Wildlife Conservation Commission and The University of Georgia. Available at: http://ocean.floridamarine.org/fknms_wqpp/products/cremp/reports/exesum02.pdf
- Joyce EA, Williams J (1969) Memoirs of the hourglass cruises: rationale and pertinent data. *Fla Dep Nat Resour Mar Res Lab* 1:1–49
- Kirkpatrick B, Fleming LE, Squicciarini D, Backer LC and others (2004) Literature review of Florida red tide: implications for human health effects. *Harmful Algae* 3:99–115
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32: 1259–1269
- Landsberg JH (2002) The effects of harmful algal blooms on aquatic organisms. *Rev Fish Sci* 10:113–390
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular biogeography. *Evolution* 17:373–387
- McEachran JD, Fechhelm JD (1998) *Fishes of the Gulf of Mexico*, Vol 1. University of Texas Press, Austin, TX
- Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Rice SA, Hunter CL (1992) Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. *Bull Mar Sci* 51:429–442
- Robins CR, Ray GC (1986) *A field guide to Atlantic Coast fishes*. Houghton Mifflin, Boston, MA
- Rounsefell GA, Nelson WR (1966) Red tide research summarized to 1964 including an annotated bibliography. *Spec Sci Rep No. 535*. US Fish and Wildlife Service, Washington, DC
- Simon JL, Dauer DM (1972) A quantitative evaluation of red-tide induced mass mortalities of benthic invertebrates in Tampa Bay, Florida. *Environ Lett* 3:229–234
- Simon JL, Dauer DM (1977) Reestablishment of a benthic community following natural defaunation. In: Coull BC (ed) *Ecology of marine benthos*. University of South Carolina Press, Columbia, SC, p 139–158
- Smith GB (1975) The 1971 red tide and its impact on certain communities in the mid-eastern Gulf of Mexico. *Environ Lett* 9:141–152
- Smith G (1979) Relationship of eastern Gulf of Mexico reef-fish communities to the species equilibrium theory of insular biogeography. *J Biogeogr* 6:49–61
- Sousa WP (1985) Disturbance and patch dynamics on rocky intertidal shores. In: Pickett STA, White PS (eds) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY, p 101–124
- Steidinger KA, Ingle RM (1972) Observations on the 1971 summer red tide in Tampa Bay. *Environ Lett* 3:271–278
- Tester P, Steidinger K (1997) *Gymnodinium breve* red tide blooms: initiation, transport, and consequences of surface circulation. *Limnol Oceanogr* 42:1039–1051
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev Camb Philos Soc* 25:1–45
- Thorson G (1955) Modern aspects of marine level-bottom animal communities. *J Mar Res* 14:387–397
- Thorson G (1957) Bottom communities. In: Hedgpeth JW (ed) *Treatise on marine ecology and paleoecology*, Vol I. Ecology. The Geological Society of America, New York, NY, p 461–534
- Thorson G (1966) Some factors influencing the recruitment and establishment of marine benthic communities. *Neth J Sea Res* 3:267–293
- Turner JT, Tester PA (1997) Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. *Limnol Oceanogr* 42:1203–1214
- Van Dolah FM, Roelke D, Greene RM (2001) Health and ecological impacts of harmful algal blooms: risk assessment needs. *Hum Ecol Risk Assess* 7:1329–1345
- Walsh JJ, Jolliff JK, Darrow BP, Lenes JM and others (2006) Red tides in the Gulf of Mexico: where, when, and why? *J Geophys Res* 111:C11003 doi:10.1029/2004JC002813
- Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. *Am Sci* 72:128–136

Editorial responsibility: Romuald Lipcius, Gloucester Point, Virginia, USA

*Submitted: September 9, 2008; Accepted: July 19, 2010
Proofs received from author(s): September 9, 2010*