

Final Report

Project Number: SWG05_028

FWC Agreement No.: 06013

Project Title: Ecological Effects of Harmful Algal Blooms on Fish and Wildlife Communities Associated with Submerged Aquatic Vegetation

Project Director: Damon Gannon, PhD

Project Assistants: Deborah Fauquier, Elizabeth Berens, Sandra Camilleri, Janet Gannon, Jason Allen, and Randall Wells

Dates Covered by Report: July 1, 2006 – June 30, 2009

Date Report Submitted: June 1, 2009

ABSTRACT

Seagrass habitats are highly productive and ecologically rich areas for estuarine fish and bird species. Among all the sources of stress to seagrass habitats, harmful algal blooms (HABs) are ranked in the highest category. HABs are a source of ecological disturbance that are thought to alter water quality (physical and chemical), species composition, and patterns of primary productivity in seagrass meadows. We investigated the extent to which red tide affected the local abundance and habitat use of individual species and the composition of the fish and avian communities utilizing submerged aquatic vegetation habitats in Sarasota Bay. Data were obtained by conducting seasonal surveys of (1) fishes, (2) birds, (3) *K. brevis* cell counts, and (4) water quality (dissolved oxygen, salinity, temperature, turbidity) during red tide and non-red tide conditions. Summer and winter surveys funded by this grant were conducted between July 1, 2006 and March 20, 2009. These data were supplemented by fish surveys conducted from June 2004 to March 2006 and daily *K. brevis* cell counts made at two monitoring stations from 2003 to March 2009. The abundance and diversity of fishes decreased coincidentally with the occurrence of red tides during summer (48% decrease in overall fish abundance). Fish community structure also changed in association with the occurrence of summer red tides. During periods of high *K. brevis* concentrations in summer, low dissolved oxygen concentrations appeared to compound the effects of the red tide on fish abundance. Abundance and diversity of fishes associated with the seagrass community rebounded by 2008 following the major red tide disturbances of 2005 and 2006. The occurrence of red tide did not have a significant effect on the overall abundance of birds, however it was associated with decreases in diversity (Shannon-Weaver index, summer) and species richness (summer and winter). Decreases in diversity, combined with non-significant increases in overall abundance, suggest that a small number of bird species are drawn to the easy prey made available by red tide (i.e., dead or debilitated fish).

INTRODUCTION

Seagrass habitats are highly productive and ecologically rich areas for wildlife (Heck et al. 2003). Florida's *Comprehensive Wildlife Conservation Strategy* lists submerged aquatic vegetation (i.e., seagrass) as a priority habitat with a statewide threat status of "Very High" and a condition of "Poor and Declining". Among all the sources of stress to seagrass, harmful algal blooms (HABs) are ranked in the highest category. HABs are a source of ecological disturbance that are thought to alter water quality (physical and chemical), species composition, and patterns of primary productivity in seagrass meadows.

Globally over the past 30 years, HABs have been becoming more frequent and widespread (Van Dolah 2000). In Florida, the most prevalent HAB is the red tide organism, *Karenia brevis*, a dinoflagellate that produces brevetoxins (Baden et al. 1989; Kirkpatrick et al. 2004). Brevetoxins are neurotoxins that can cause acute respiratory and neurological symptoms including death in marine mammals, sea turtles, birds, and fishes (Gunter et al. 1948; Steidinger *et al.*, 1973; Bossart et al. 1998; Foote et al. 1998; Landsberg & Steidinger 1998; Kreuder et al. 2002; Flewelling et al. 2005; reviewed by Landsberg et al. 2009). HABs can also increase biochemical oxygen demand, resulting in hypoxia or anoxia, and causing fish to die or abandon habitat (Smith 1975; Paerl & Pinckney 1996; Paerl et al. 1999; Eby & Crowder 2002, 2004).

Prior to this study, the ecological impact of HABs on wildlife communities was not well documented. Red tides are well known to cause episodes of high mortality among marine vertebrates. However, little information existed on whether red tides have significant effects at either the population or community level (Landsberg et al. 2009).

This study aimed to determine how red tide influences mortality, recruitment, growth rates, body conditions, abundance, and community composition of fishes and sea birds utilizing seagrass habitats in Sarasota Bay, FL. It is impossible to develop effective management strategies when the exact nature of a problem is not understood. This project documented the population- and community-level effects of *K. brevis* blooms on fishes and birds inhabiting seagrass habitats of Sarasota Bay. We tested the following hypotheses:

1. Occurrence of red tide is associated with changes in local abundance of fishes and birds in seagrass habitats;
2. Red tide causes a change in the composition of the fish and bird communities associated with seagrass;
3. Changes in community composition are related to differences in behaviors among species;
4. Red tide is associated with changes in mean sizes of individual fishes;
5. Decreases in local abundance of fish are greatest when red tide is accompanied by hypoxia.

METHODS

General Approach and Study Area

To understand how red tide affects the fish and bird communities found in seagrass habitats of Florida's southwest coast, we conducted seasonal (summer and winter) surveys of (1) live fishes, (2) live birds, (3) *K. brevis* cell counts, and (4) water quality (dissolved oxygen, salinity, temperature). All four types of data were collected

simultaneously at a minimum of 20 sampling sites per field season ($\times 2$ field seasons per year $\times 3$ years = 120 samples). Additional bird, water quality, and *K. brevis* surveys were conducted at another 40 sampling sites per field season. *K. brevis* cell counts and water quality were also monitored every other week at 10 fixed stations, distributed throughout our study area (including all Gulf passes). Supplementing the sampling described here, Mote Marine Laboratory's Phytoplankton Ecology Program also monitors *K. brevis* cell counts daily at two sites in Sarasota Bay: New Pass and City Island Grass Flats. In addition to the work on seagrass communities supported by this grant, we conducted parallel research in four other habitat types (sandflat, mangrove fringe, open bay, and nearshore Gulf) from June 2004 to March 2008.

The study area encompassed the estuarine waters from Anna Maria Sound (27.5528° N / 82.7423° W) southward to Phillippi Creek (27.27096° N / 82.53757° W), including the waters of Sarasota, Palma Sola, and Roberts Bays (Figure 1). Selection of sampling sites for bird and fish surveys used a random sampling system developed with GIS, relational databases, and visual basic programming. Potential seagrass habitat to be sampled in the study area was identified from digitized polygons obtained from FWC's biennial seagrass surveys. A sampling grid having 200×200 -m resolution was overlaid on the seagrass polygons in our study area. Grid cells to be sampled were chosen at random using a custom Visual Basic program. Sampling sites were located at the centroids of each grid cell and were located in the field with a WAAS-enabled GPS unit (Garmin GPS Map 162).

Water Quality Measurements and *Karenia brevis* Cell Counts

Water quality parameters (temperature, salinity, and dissolved oxygen concentration) were measured within 30 cm of the surface and 30 cm of the bottom at each bird and fish sampling station using YSI 85 multiprobes. *Karenia brevis* cell concentrations (cells/l) were measured from samples of surface water collected at (1) fish survey stations, (2) bird survey stations, and (3) at 10 fixed monitoring stations that were sampled twice per month. These *K. brevis* counts were also supplemented by daily cell counts made at two fixed monitoring stations (New Pass and City Island Grass Flats) by Mote Marine Laboratory's Phytoplankton Ecology Program (funded by separate sources). Sample collection and processing was identical for all of the *K. brevis* sampling regimes. Samples of water taken within 10 cm of the surface were collected in scintillation vials. Water samples were immediately preserved in Utermohl's solution and stored in the dark at room temperature. Cell counts were performed in the laboratory using an inverted Olympus CK40 microscope. Protocols for water collection, preservation, and *K. brevis* enumeration followed the methods of Lund et al. (1958), Sournia (1978), and Sellner et al. (2003).

Sampling periods were designated as "red tide" or "non-red tide" based on *Karenia brevis* cell counts. The study area was considered to be under red tide conditions when *K. brevis* concentrations exceeded 100,000 cells/liter anywhere in the study area (from any of the 4 *K. brevis* sampling regimes) on that day or any time during the previous 30 days (Gannon et al. 2009). One hundred thousand cells/liter was chosen as the threshold as this value is thought to be the level at which fish kills begin to occur (Quick and Henderson 1975, Landsberg and Steidinger 1998, Gannon et al. 2009). This 100,000 cells/liter threshold has been used as an approximate guide to "fish killing

potential,” but it should be noted that it does not take into account the potential for persistence of toxins in the food web (See Naar et al. 2007 and Fire et al. 2008), nor does it consider the proportions of inter- and extracellular concentrations of brevetoxin (see Pierce et al. 2001 and Naar et al. 2007).

Bird Sampling

Boat-based point surveys were conducted by two observers for 5-minute observation periods. Observers scanned 360 degrees around the boat, identified individual birds to species, and recorded location and behavioral activity. Foraging activity was noted and prey species were identified visually when possible. Relative abundance was calculated by sightings per unit effort (SPUE), or the number of individual birds sighted within the 5-minute sampling period.

Fish Sampling

Fish surveys were carried out with a 183-m purse seine net. The methods used are similar to those used by the Fishery Independent Monitoring Program of the Florida Fish and Wildlife Conservation Commission (Wessel & Winner 2003). The mesh size was 2.5-cm (diamond), made from No. 7 nylon twine. The net was symmetrical (no bunt), and was 6.6 meters deep. The cork line was 1.3-cm twisted polypropylene line with SB10 “can” floats spaced every 45 cm. The footrope was a doubled, 39-kg lead-cored line. The purse rings were 10.2-cm stainless steel alpine clips attached to 91-cm of 9.5-mm braided polypropylene line, which were fastened to the footrope at 2.8-m intervals. The lead tom weight weighed 68 kg. The purseline was 366 m of 18-mm, non-

rotating, 12-strand braided polytron. This purse seine captured fish from the surface to the benthos when used in water depths between 0.4 and 4.0 meters (Sarasota Bay's maximum depth = 4 m). All fish and invertebrates captured in the net were identified to species and counted, and up to 100 individuals from each species were measured from every deployment of the net. Relative densities of fish were expressed as catch per unit effort (CPUE), or the number of fish captured in each standardized deployment of the net.

Analyses

Differences in the overall densities of fishes (CPUE) and birds (SPUE) between seasons and between red tide and non-red tide periods were assessed with t-tests.

Differences in mean lengths of pinfish between red tide and non-red tide periods were assessed with Kolmogorov-Smirnov tests.

Changes in diversity of the bird and fish communities associated with the occurrence of red tide were assessed by the Shannon-Weaver diversity index (Shannon & Weaver 1949). Differences between red tide and non-red tide periods regarding Shannon-Weaver diversity indices were assessed using two-sample t-tests (Hutcheson 1970).

Classification and regression tree (CART) analysis was used to explore relationships between a dependent variable (either overall fish CPUE or fish species richness) and five independent variables (water depth, water temperature, dissolved oxygen concentration, salinity, and *Karenia brevis* cell count), separately for winter and summer. The CART method tests the global null hypothesis of independence between the dependent variable and each of the environmental variables (Urban 2002). CART is

useful for identifying physiological or ecological threshold values and for identifying critical values of environmental parameters for the purposes of setting regulatory limits. Here we applied a CART analysis to determine whether there were any threshold values in water quality parameters or in *K. brevis* cell counts associated with abrupt changes in fish abundance or diversity. We ran the CART analysis using the “Party” library in the R software environment (version 2.6.1, R Development Core Team; Hothorn et al 2006). P-values were calculated using a quadratic test statistic.

To determine whether red tide was associated with a change in the composition of the fish community, we performed one-way MANOVAs with fixed effects in Statistica (version 5.5, StatSoft, Inc.). All fish captured were assigned to a guild based on their vertical distribution in the water column and their feeding habits, as follows: 1) demersal herbivore, 2) demersal invertivore, 3) demersal omnivore, 4) demersal piscivore, 5) detritivore, 6) pelagic filter feeder, 7) pelagic invertivore, 8) pelagic omnivore, and 9) pelagic piscivore. Assignments to guilds were based on the literature including Robins et al. (1999) and Hoese & Moore (1998). Species included in each guild are listed in appendix 2. The dependent variables used in the MANOVAs were the CPUEs for each of the nine trophic guilds, and the independent variable was a binary indicating whether the sample was collected during red tide or non-red tide conditions.

We used canonical correspondence analysis (CCA) to investigate the relationship between community structure and environmental features, as well as the degree of similarity in guild composition of seine samples during red tide and non-red tide periods (ter Braak & Verdonschot 1995, Guisan & Zimmermann 2000, McCune & Grace 2002). The potential homogenizing effect of guilds that were rare in the seagrass habitat during

both sampling periods (red tide and non-red tide) were minimized by including only those guilds that were present in more than 10% of seine sets in at least one sampling period (red tide or non-red tide period). Stations at which no fish were captured were also excluded from analysis. Fish assemblage data, calculated from the CPUEs of each guild, were used to calculate a Bray-Curtis similarity matrix. CCA results were displayed as triplots in which seine samples, guilds, and environmental features were plotted in two-dimensional ordination space defined by CCA axes 1 and 2. The association of environmental variables with the axes is represented by how parallel each variable's vector is to the axis. The distance between individual seine samples reflects their degree of similarity regarding guild composition. The distance between guilds on the triplot indicates their degree of similarity regarding the range of environmental conditions under which they were found. The plotted positions of individual seine samples relative to the environmental vectors are indicative of the environmental conditions at the time of sampling. Likewise, the position of each guild relative to the environmental vectors indicates the environmental conditions under which the guild is normally found. CCA was performed using PC Ord (version 4.34, MjM Software). A $\log(x+1)$ transformation was applied to all CPUE and *K. brevis* cell count data prior to analysis.

RESULTS

Mote Marine Laboratory has conducted coordinated surveys of (1) water quality (2005-present), (2) *K. brevis* concentrations (2005-2009), (3) relative abundance and species composition of birds (2006-2009), and (4) relative abundance and species composition of fishes (2004-2009) in 5 distinct habitats within the Sarasota Bay region.

The activities supported by this grant included field research in the seagrass habitat from July 1, 2006-March 27, 2009.

A total of 454 bird survey stations (Table 1) and 186 fish/bird stations (Table 2) were sampled in seagrass habitats from July 1, 2006-March 27, 2009 (this grant). An additional 80 purse seine sets were made in seagrass habitats between June 2004 and March 2006. *Karenia brevis* cell count water samples were collected from 482 seagrass stations between July 1, 2006 and March 20, 2009: 186 during fish surveys (Fig. 1), 228 during bird surveys, and 68 during dedicated red tide surveys. From July 2005 to March 2009, an additional 763 *K. brevis* cell count samples were also collected in other habitats of Sarasota Bay, for a total of 1,245 samples. In addition, Mote Marine Laboratory's Phytoplankton Ecology Program conducted cell counts from water samples collected every week day at monitoring stations in New Pass and City Island Grass Flats from Jan 1, 2003 to March 30, 2009 (Fig. 2).

Using the definition outlined in the Methods section, the periods from January 22, 2005 to December 31, 2005 and from August 10, 2006 to February 15, 2007 were designated as "red tide periods." The final two years of the study were free of red tide (from February 15, 2007 through the end of the study on March 27, 2009). This is the longest period that red tide has been absent from the Sarasota Bay study area since our surveys began in 2004.

Bird surveys were conducted in the seagrass habitats of Sarasota Bay during summer and winter fields seasons from June 2006 to September 2008 aboard two research platforms, R/V Lorry and R/V Flip (Data from the winter of 2008/2009 are still being processed, as that field season ended in late March.). R/V Lorry conducted

dedicated bird surveys. R/V Flip, the fish sampling vessel, was used as a vessel of opportunity to collect data on birds during fish sampling trips. A total of 8,285 individual birds from 39 species were counted at 454 stations surveyed by R/V Lorry (Table 1). The average sightings per unit effort (SPUE) was 18.47 ± 27.10 birds per station across all seasons for R/V Lorry (n=454 stations) and 20.93 ± 37.71 birds per station for R/V Flip (n=146 stations). Overall bird densities, as measured from R/V Lorry, were higher in the winter than they were in the summer. The most abundant bird species were laughing gulls (*Larus atricilla*), double-crested cormorants (*Phalacrocorax auritus*), brown pelicans (*Pelecanus occidentalis*) and sandwich terns (*Sterna sandvicensis*). Certain bird species were only counted in the summer seasons including anhingas (*Anhinga anhinga*), black-crowned night herons (*Nycticorax nycticorax*) and yellow-crowned night herons (*Nyctanassa violacea*). Bird species present only during the winter seasons included migrating species such as the American oystercatcher (*Haematopus palliatus*), American white pelican (*Pelecanus erythrorhynchos*), Common loon (*Gavia immer*), pied-billed grebe (*Podilymbus podiceps*), red-breasted merganser (*Mergus serrator*), as well as non-migrating green herons (*Butorides virescens*), herring gulls (*Larus argentatus*) and ring-billed gulls (*Larus delawarensis*).

Between June 2004 and March 2009, we conducted 939 purse seine sets in 5 habitats of the Sarasota Bay region. Of these, 266 sets were made in the seagrass habitat yielding 162,043 fish from 104 species (this grant funded the 186 sets made from July 1, 2006-March 20, 2009) (Table 2). Of the 266 sets made in the seagrass habitat between June 2004 March 2009, 61 were conducted during red tide periods and resulted in the capture of 35,606 fish from 56 species (Table 2). There was one seagrass station at

which no fish were caught, which occurred during the summer 2005 red tide period. Overall fish densities in seagrass were lower in the winter than in the summer (Fig. 3). However, the lowest mean seasonal CPUE occurred during the summer of 2005, which coincided with the most prolonged and severe red tide event of the study. The highest mean CPUE occurred during the summer of 2008, after nearly two years in which red tide conditions were absent from the study area (Fig. 3).

Fish densities were higher in the seagrass during summer than during winter (t-test, $P < 0.05$) (Fig. 3). During summers, fish CPUEs were significantly lower during red tide periods in comparison to non-red tide periods ($t = 4.06$, $df = 44$, $P < 0.05$). However, during winter there was no significant difference in fish densities between red tide and non-red tide periods ($t = 0.04$, $df = 28$, $P = 0.96$) (Figs. 3, 4). There were no significant differences in overall density of birds between red tide and non-red tide periods in winter, summer, or with all seasons combined (t tests, $P \geq 0.14$), although mean SPUE was higher during red tide periods (Fig. 5). Pinfish caught during red tide were significantly smaller than those caught during non-red tide periods in the months of August and March (Table 6).

Fish species richness was higher in summer than in winter and higher during non-red tide periods than red tide periods (Table 2). Shannon-Weaver diversity indices for fish differed between red tide and non-red tide periods during summer, but not during winter (Table 3). During summer, every fish trophic guild, with the exception of guild 6 (pelagic filter feeders), had a lower CPUE during red tide periods than during non-red tide periods. In contrast, in winter, only guild 2 (demersal invertivores) had a lower CPUE during red tide periods, in comparison to non-red tide periods (Table 4). In

summer, bird diversity was lower during red tide than non-red tide periods (Table 5). The sample size of bird surveys conducted during red tide periods in winter was too low to make a definitive statement about changes in bird diversity related to red tide in winter.

Canonical correspondence analysis of fish catches during summer indicated clear differences between the fish communities found in seagrass during red tide periods and those found during non-red tide periods (Fig. 6). *Karenia brevis* was plotted on the CCA triplot near the center of the distribution of purse seine samples collected during red tide.

Consistent with the analyses above, CART analysis showed that the effect of red tide on the fish community was stronger during summer than it was during winter (Figs. 7-10). Of the potential predictor variables tested (dissolved oxygen, temperature, depth, salinity, and *K. brevis* cell count), *K. brevis* cell count had the greatest influence on CPUE and species richness. Overall CPUE (all species) was significantly lower when *K. brevis* cell count exceeded 33,000 cells/liter (Fig. 7). For purse seine samples made when *K. brevis* cell count exceeded 33,000 cells/liter, dissolved oxygen concentration also had a significant impact on CPUE; dissolved oxygen concentrations <4.32 mg/l were associated with significantly lower catches (Fig. 7). Of the potential predictor variables investigated, only *K. brevis* concentration appeared to have a significant association with species richness; sets made where cell counts were <31,000 cells/liter yielded significantly more species than did those made where cell counts were higher (Fig. 8). For our winter data, water temperature and salinity were the only factors having a significant association with CPUE, and none of the variables investigated had a clear influence on species richness (Fig. 10).

DISCUSSION

Two major red tides occurred in the study area between January 1, 2005 and March 20, 2009, with *Karenia brevis* densities peaking at over 10^7 cells l^{-1} . These red tides corresponded with decreases in fish abundance and diversity, decrease in average lengths of pinfish, and changes in fish community structure during the summer months. The effects during winter were less severe. Fish species richness during red tide periods was significantly lower than during non-red tide periods in both seasons, and the Shannon-Weaver diversity index was significantly lower during red tides in summer. Members of guild 6 (pelagic filter feeders, primarily clupeids) appeared not to suffer the declines in abundance that the other guilds experienced. Low dissolved oxygen appeared to compound the effects of red tide regarding reductions in overall fish abundance.

Overall bird densities were higher during red tides than they were during non-red tide periods in summer and winter. However, species richness and Shannon-Weaver diversity indices were lower during red tides in both seasons. This indicates that a few species became numerically dominant during red tides, probably as they were attracted by easy prey (i.e., dead or debilitated fish). It is worth noting that many birds appeared to become physically impaired during these red tide events. During red tides, we observed laughing gulls, brown pelicans, and an osprey flying into fixed objects.

Many factors can affect reproduction, mortality, recruitment, and habitat use of fishes, so it can be difficult to identify the specific cause of a decline in fish abundance from observational field studies. However, the fact that nearly every species showed the same pattern of changes in abundance (with the exception of clupeids, guild 6) suggests a large-scale environmental perturbation was the underlying cause. The numbers of fish

kills increased during red tides (Florida Fish Kill Database, Gannon et al. 2009). Ninety-six percent of fish kills that occurred in our study area between 2004 and 2007 did so when the study area was classified as being under red tide conditions, and all fish kills attributed to red tide in the State's Fish Kill Database occurred during periods in which we classified the study areas as being under red tide conditions (Florida Fish Kill Database, Gannon et al. 2009). The fish kills associated with these red tide events, especially those in 2005, were massive and likely involved millions of fishes (observations made by the authors). During the entire red tide event of 2005, the town of Longboat Key, one of five municipalities bordering the study area, removed 121 tons of dead fish from its beaches and residential canals (Cooper 2005). Fishes collected from the Sarasota Bay study area during these red tide periods had high brevetoxin concentrations in their tissues (Fire 2006 and Fire et al. 2008). Thus, the overwhelming weight of evidence is consistent with the hypothesis that *K. brevis* red tides were a major causative factor contributing to the changes in fish abundance, diversity, and community structure.

Distinct differences were found between red tide and non-red tide periods regarding the structure of the fish community. In the CCA analyses, differentiation between the communities present during red tide and non-red tide conditions corresponded with the environmental vector representing *Karenia brevis* cell count (Fig. 6). Of all the factors measured, (water temperature, dissolved oxygen concentration, salinity, depth, and *K. brevis* density), *K. brevis* concentration had the most significant effect on overall fish density and species richness during summer. (Figs. 7 & 8).

Dissolved oxygen concentration also had a significant effect on fish densities when *K. brevis* cell counts exceeded 33,000 cells per liter.

The changes in fish abundance and community structure that we documented could have been caused by mortality and/or emigration. Our sampling methods were unable to discriminate between these two potential mechanisms. However, the occurrence of extremely large fish kills and high PbTx concentrations in fish tissues (Fire 2006, Fire et al. 2008) suggests brevetoxin-induced mortality was a significant factor underlying the community-level changes. Brevetoxins are known to be lethal to fishes (Steidinger et al. 1973, Baden & Mende 1982, reviewed by Landsberg 2002 and Landsberg et al. 2009) and have also recently been demonstrated to accumulate in tissues of living specimens (Flewelling et al. 2005, Naar et al. 2007, Fire et al. 2008). Brevetoxins can be detected in fish tissues more than a year following red tides (Naar et al. 2007) and were found in fish tissues several months following these particular red tide events in Sarasota Bay (Fire et al. 2008), indicating that they remain in the food web for substantial periods of time.

Our CART analyses suggested that changes in fish abundance and in species richness might have occurred at *Karenia brevis* cell densities much lower than 10^5 cells l^{-1} (Figures 7&8), which is the threshold density generally considered to induce fish kills (Quick and Henderson 1975, Landsberg & Steidinger 1998). This would suggest that either fish kills occurred at cell densities lower than the 10^5 cells l^{-1} threshold or that fish detected and avoided low-density *K. brevis* blooms. If fishes were displaced within the study area, fish densities would have increased in remaining refuges, similar to the habitat compression response fishes show to hypoxia (Eby & Crowder 2002, Eby et al.

2005). However, we found no evidence of habitat compression at the scale of our study. It is possible that fishes may have abandoned the study area entirely in search of regions that were less affected by red tide, but this seems unlikely because the spatial extent of these red tides far exceeded that of the study area (Hu et al. 2006), meaning they would have had to move hundreds of km to escape the red tide. The hypothesis that fishes emigrated away from areas afflicted by red tide also assumes that they can detect and avoid *K. brevis* blooms or brevetoxin itself, which has not been demonstrated experimentally. Thus the hypothesis that the observed changes in fish abundance were caused by brevetoxin-induced mortality is supported by our data and by the published literature, whereas the alternative hypothesis that the changes resulted from fish emigrating to other areas has less support but cannot yet be ruled out as a possible mechanism. It should be noted that potential time lags between bloom occurrence and sample collection call for caution to be exercised when interpreting the cell count thresholds identified by the CART analyses.

There are two potential mechanisms by which fish can be exposed to PbTx: direct exposure to free toxins dissolved in the water (released by lysed cells, Pierce et al. 2001) and exposure via the food web. Experiments with filter-feeding striped mullet (*Mugil cephalus*) indicated that the route of exposure, in addition to the form and concentration of PbTx, is important in determining the lethality of PbTx to fishes (Naar et al. 2007). Free PbTx was more lethal than equivalent concentrations of the same forms of the toxin contained within intact *Karenia brevis* cells that were consumed by the mullet. Once brevetoxins have been released by lysed cells, they can persist in the environment for extended periods. For example, Fire et al. (2008) discovered brevetoxins more than two

months following a *K. brevis* bloom and Naar et al. (2007) detected brevetoxins more than a year post bloom. Thus, *K. brevis* cell count is a crude measure of a fish's potential exposure to PbTx. We were forced to use *K. brevis* cell count as a proxy for PbTx exposure because making accurate measurements of both free- and intracellular-PbTx levels in field samples is nearly impossible using current techniques (at least with the sample sizes that are necessary for statistically robust analyses). The unarmored *K. brevis* cells break open very easily, so the process of sample collection and preparation may cause the concentration of free PbTx to be overestimated and that of intracellular PbTx to be underestimated. A simple, rapid method of simultaneously assessing the concentrations of brevetoxins that are free in the water and contained within living *K. brevis* cells would undoubtedly improve our understanding of the relative importance of the major PbTx vectors. Despite these limitations, we were still able to detect relationships between *K. brevis* cell counts and fish abundance.

Due to their frequency and severity, Florida red tides are likely to have an important influence on the structural dynamics of estuarine and nearshore communities in this region. HABs in general appear to be increasing in frequency and severity in many regions of the world (Anderson 1989, Smayda 1990, Hallegraeff 1993, Van Dolah 2000). *Karenia brevis* red tides occur nearly every year in the Sarasota Bay region, and Brand and Compton (2007) suggested that *K. brevis* blooms are increasing in frequency and severity in southwest Florida. Thus the influence of red tides on fish abundance, diversity, and species composition may be increasing.

One group of fishes, guild 6 (clupeids), stands out from all others. Whereas the abundance of most guilds declined significantly during red tide, the abundance of

clupeids did not (Table 4). The CCA results actually indicate an association between *Karenia brevis* density and the abundance of guild 6. These data suggest that clupeids may have been more tolerant of brevetoxin poisoning, were better able to metabolize brevetoxins than were other fishes, or were better able to detect and avoid patches of *K. brevis* or brevetoxin. Being able to cope with exposure to brevetoxin might allow clupeids to occupy areas or to consume food items that might not otherwise be suitable for them. Given the high mortality that we observed for most other fishes during red tides, clupeids may become a more substantial portion of the diet for piscivores, such as seabirds and bottlenose dolphins, during these disturbance events. Thus, clupeids are likely to be an important vector by which brevetoxins are transferred to upper trophic levels (Flewelling et al. 2005). During the 2005 red tide, bottlenose dolphins in the Sarasota region exhibited changes in behavior that were consistent with a dietary shift toward clupeids (Gannon et al. in press).

The clupeid results are interesting in light of the work by Walsh et al. (2009). Based on coupled biophysical models and nitrogen isotope budgets, Walsh et al. (2009) concluded that once *K. brevis* blooms are initiated, decomposing clupeids killed by the blooms contribute roughly 50% of the nutrients required to maintain large blooms (defined as $>1 \mu\text{g chl l}^{-1}$). The findings of Walsh et al. (2009), coupled with those of this study suggest that: 1) clupeids are able to cope with low- to moderate concentrations of PbTx in the environment; 2) clupeids are better able to withstand exposure to brevetoxins than are other fishes; 3) there is a threshold point at which clupeids succumb to brevetoxicosis; and 4) once the threshold at which clupeids succumb to brevetoxicosis is reached, the recycled nutrients coming from decomposing clupeids extends the

duration of the bloom. In fact, during the peak of the red tide blooms in early summer of 2005 and late summer of 2006, we observed large rafts of dead clupeids floating on the water. Given the biomass of filter feeding clupeids, relative to those of fishes at higher trophic levels, it is not surprising that Walsh et al. (2009) found evidence of clupeids playing an important role in sustaining blooms. Certainly, nutrients of other fishes contribute to bloom maintenance but since clupeids dominate the nearshore fish community in terms of biomass, they isotopic signature overwhelms those of other fishes.

Our data suggest that red tides during winter have less severe effects than do those that occur during summer. There are several possible explanations for this observation, including: (1) fish may be less susceptible to brevetoxin during winter; (2) since fish densities in seagrass tend to be low during winter, it may be more difficult to detect the influence of red tides on fish abundance or community structure during this time of year; and (3) the red tides that took place during the winters of our study were generally less severe than were those in the summer (therefore if this study was repeated during a severe winter red tide then the results may be similar to those we found in the summer). Further study would be needed to determine why the food web appeared to respond differently in different seasons.

One important finding of this study is the speed at which the fish community apparently recovers from red tide disturbance. Following the declines in abundance during the 2005 red tide, fish abundance rebounded in 2006 (prior to the 2006 red tide, which began on August 10). Despite severe red tides in 2005 and 2006, the highest fish densities were recorded in summer 2008, after nearly a two-year absence of red tide.

Our study differed from those of Smith (1975, 1979) and Warlen et al. (1998) in a number of ways. Smith (1975, 1979) studied the communities on patch reefs in the Gulf of Mexico, offshore from our study area and recorded the presence or absence of fish species at each study site using visual (SCUBA) surveys, but did not quantify density or abundance. Smith estimated that 77% of resident fish species disappeared from reefs in the 12-18 m depth range and attributed most of the mortality to indirect (hypoxia) rather than to direct (brevetoxicosis) effects of the HAB. We recorded just a 48% decrease in the mean species richness of fishes in seagrass during red tides in summer months. The differences may be related to differences in methodologies, habitat characteristics, fish species, or relative severities of the red tide events studied. Smith's study sites were in deeper waters than were the sites studied here, and were likely to be more susceptible to density stratification, which may have promoted formation of hypoxic zones. A large hypoxic zone formed offshore of our study area during the 2005 red tide (Hu et al. 2006) but it did not appear to affect our study area directly.

Warlen et al. (1998) investigated densities of fish larvae recruiting to an estuary during red tide and non-red tide conditions. The recruitment rates they recorded during the red tide event were not particularly low, although two of the nine species investigated experienced their 8-year recruitment minima during this period (Warlen et al. 1998). All of the fishes they studied were estuarine-dependent species that spawn in the ocean. Thus larval densities inside the estuary were likely affected by many ecological and oceanographic processes. In addition, responses of larvae to PbTx may differ from those of post-larval fishes.

This study is the first step in identifying how *Karenia brevis* red tides affect seagrass-associated fish and bird communities. Important questions remain to be answered regarding: (1) the importance of temporal and spatial scales of blooms; (2) the fitness consequences of red tide to individual animals; (3) differences among species regarding their responses to red tide; and (4) economic and resource management implications of red tide to fisheries. Unfortunately, very few of these topics can be adequately addressed using laboratory experiments alone. Due to the time scales involved (months to years) and the complex interactions that occur in nature, it is necessary to employ long-term observational field methods to investigate how natural communities respond to environmental stressors. Thus to achieve an adequate understanding of how HABs affect food webs, funding agencies need to make long-term commitments to consistent and continuous observational and sampling studies of marine food webs.

SCIENTIFIC & MANAGEMENT RECOMMENDATIONS

1. Develop methods to rapidly (and cheaply) quantify intra- and extracellular brevetoxin concentrations in the field. In this study, we used *K. brevis* cell concentrations as a proxy for brevetoxin exposure potential. Actual measurements of intra- and extracellular toxin concentrations would likely result in a greater understanding of how exposure to brevetoxin affects vertebrate communities, since Naar et al. (2007) showed that the route of exposure influences the lethality of a given dosage.

2. Federal, state, and local governments should consider ways to further reduce nutrient fluxes to coastal waters from non-point sources. It is not clear that reductions in nutrient concentration will have a measurable effect on the occurrence, duration, or severity of *K. brevis* blooms. However, reducing nutrient concentrations will likely reduce overall algal biomass, improving water quality. Evidence from this study suggests that dissolved oxygen concentration and *K. brevis* concentration (a proxy for brevetoxin exposure potential) operate synergistically to stress fish populations and communities (Fig. 7). Reducing nutrient availability should help mitigate one or both of these factors.

3. Expand capabilities to detect and monitor *K. brevis* blooms, and to forecast bloom formation, concentration, spatial extent, transport, and persistence.

4. Coordinate fisheries monitoring and assessment programs with HAB and water quality monitoring programs. Particular attention should be paid to matching the temporal and spatial scales of these monitoring programs (seasonality of sampling, sampling frequency, spatial resolution of sampling, extent of spatial overlap among monitoring programs, etc.).

5. Develop fisheries management strategies that explicitly account for the effects of *K. brevis* harmful algal blooms on fisheries resources. An adaptive strategy should be considered, whereby catch levels could be adjusted in the short-term according to red tide conditions.

6. Accelerate the development of ecosystem-based management regimes that take into account the structure of the entire food web, from primary producers to top predators. Such a strategy would require establishing management goals regarding community structure, not just benchmarks for species of obvious economic importance.

ACKNOWLEDGMENTS

This project was made possible by the collective efforts of many people with a wide variety of talents. L. Woods fabricated the hydraulic-powered net hauler. L. Fulford designed our purse seine net and B. Fulford constructed it. We are indebted to the dozens of interns and volunteers who worked hard to help us collect data in the field. NOAA's Fisheries Service (Grant Award Number NA16FL1355), Harbor Branch Oceanographic Institution's Protect Wild Dolphins Program (grant numbers PWD 2004-18 and PWD 2005-09), and Florida's Fish and Wildlife Research Institute (FWCC grant No.04089) provided additional funding for this work. This research was authorized by the Florida Fish and Wildlife Conservation Commission (Special Activity License numbers 03SR-809 and 04SR-809) and by Mote Marine Laboratory's Institutional Animal Care and Use Committee (protocol numbers 06-10-DG1 and 07-10-DG1).

LITERATURE CITED

Allen LG (1982) Seasonal abundance, composition, and productivity of the littoral zone assemblage in upper Newport Bay, California. *Fish Bull* 80:769-790

Anderson DM (1989) Toxic algal blooms and red tides: A global perspective. In: Okaichi T, Anderson DM, Nemoto T (eds) *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier, New York. p 11-16

- Baden DG and Mende TJ (1982) Toxicity of two toxins from the Florida red tide marine dinoflagellate, *Ptychodiscus brevis*. *Toxicon* 20:457-461
- Brand LE, Compton A (2007) Long-term increase in *Karenia brevis* abundance along the Southwest Florida Coast. *Harmful Algae* 6:232-252
- Cooper C (2005) Red tide costs stress LBK's Budget Plan. *Longboat Key News*, Oct. 28, 2005, p. 1
- Deegan LA, Thompson BA (1985) The ecology of fish communities in the Mississippi River deltaic plain. In: Yáñez-Arancibia A (ed) *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration*. UNAM Press, Mexico, p 35-56
- Eby LA, Crowder LB (2002) Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Can J Fish Aquat Sci* 59:952-965
- Eby LA, Crowder LB, McClellan CM, Peterson CH, Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Mar Ecol Prog Ser* 291:249-262
- Fire SE (2006) Effects of *Karenia brevis* blooms on wild coastal bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. PhD dissertation, University of California, Santa Cruz, CA
- Fire SE, Flewelling LJ, Naar J, Twiner MJ, Henry MS, Pierce RH, Gannon DP, Wang Z, Wells RS (2008) Prevalence of brevetoxins in prey fish of bottlenose dolphins in Sarasota Bay, Florida. *Mar Ecol Prog Ser* 368:283-294
- Flewelling LJ, Naar J, Abbott JP, Baden DG, Barros NB, Bossart GD, Bottein, MYD, Hammond DG, Haubold EM, Heil CA, Henry MS, Jacocks HM, Leighfield TA, Pierce RH, Pitchford TD, Rommel SA, Scott PS, Steidinger KA, Truby EW, Van Dolah FM, Landsberg JH (2005) Brevetoxicosis: Red tides and marine mammal mortalities. *Nature* 435:755-756
- Gannon, D., E. Berens, J. Gannon, S. Camilleri, V. Palubok, R. Wells, G. Kirkpatrick, M.K. Brueggen, and A. Barleycorn. 2009. Ecological Effects of *Karenia brevis* Harmful Algal Blooms on Nearshore Fish Communities in Southwest Florida. *Mar. Ecol. Prog. Ser.* 378:171-186.
- Gannon JG, Wells RS, Allen JB, Gannon DP, Hofmann S, Kirkpatrick GJ, Palubok V (In Press) Apparent sub-lethal effects of a harmful algal bloom on bottlenose dolphins in Sarasota Bay, Florida. *Mar Ecol Prog Ser*

- Guillard R (1973) Division rates. In: Stein J (ed) *Phycological methods*. Cambridge University Press, Cambridge, p 289–311
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147-186
- Gunter G, Williams RH, Davis CC, Smith FGW (1948) Catastrophic mass mortality of marine animals and coincident phytoplankton bloom on the west coast of Florida, November 1946 to August 1947. *Ecol Monogr* 18:309-324
- Hallegraeff GM (1993) A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99
- HARNNESS (2005) *Harmful Algal Research and Response: A National Environmental Science Strategy 2005-2015*. Ramsdell JS, Anderson DM, Gilbert PM (eds) Ecological Society of America, Washington, DC
- Heck KL, Hays C, Orth RJ (2003) A critical evaluation of the nursery role hypothesis for seagrass meadows. *Mar Ecol Prog Ser* 253:123-136
- Hoese HD, Moore RH (1998) *Fishes of the Gulf of Mexico, Texas, Louisiana, and Adjacent Waters*, 2nd ed. Texas A&M University Press, College Station, TX
- Hoss DE, Engel DW (1996) Environmental Effects on Fisheries. In: Vernberg FJ, Vernberg WB, Siewicki T (eds) *Sustainable Development in the Southeastern Coastal Zone: Environmental Impacts on Fisheries*. University of South Carolina Press, Columbia, South Carolina, p 171-186.
- Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: a conditional inference framework. *J Comput Graph Stat* 15:651-674.
- Houde E, Rutherford E (1993) Recent trends in estuarine fisheries: predications of fish production and yield. *Estuaries* 16: 161-176.
- Hu C, Muller-Karger FE, Swarzenski PW (2006) Hurricanes, submarine groundwater discharge, and Florida's red tides. *Geophys Res Lett* 33:L11601 (doi:10.1029/2005GL025449)
- Hutcheson K (1970) A test for comparing diversities based on the Shannon formula. *J Theor Biol* 29:151-154
- Landsberg JH (2002) The effects of harmful algal blooms on aquatic organisms. *Rev Fish Sci* 10:113-390

Landsberg, J. H., Flewelling, L. J. and Naar, J. 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. *Harmful Algae*, 8: 598-607.

Landsberg JH, Steidinger KA (1998) A historical review of *Gymnodinium breve* red tides implicated in mass mortalities of the manatee (*Trichechus manatus latirostris*) in Florida, USA. In: Reguera B, Blanco J, Fernandez ML, Wyatt T (eds) *Harmful Algae*. Xunta de Galicia and Intergovernmental Oceanographic Commission, UNESCO, p 97-100

Lund JWG, Kipling C, LeCren ED (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations of counting. *Hydrobiologia* II: 143-170

McCune B, Grace JB (2002) *Analysis of Ecological Communities*. MjM Software, Glenden Beach, Oregon, USA.

Naar JP, Flewelling LJ, Lenzi A, Abbott JP, Granholm A, Jacocks HM, Gannon D, Henry M, Pierce R, Baden DG, Wolny J, Landsberg JH (2007) Brevetoxins, like ciguatoxins, are potent ichthyotoxic neurotoxins that accumulate in fish. *Toxicon* 50:707-723

NOAA (National Oceanographic and Atmospheric Administration) (2006) Notice; availability of new criteria for designation of marine mammal Unusual Mortality Events (UMEs). *Federal Register* 71:75234.

Pierce RH, Henry MS, Blum P, Payne S. *Gymnodinium breve* toxins without cells: intracellular and extra-cellular toxins In: *Harmful Algal Blooms 2000*. Hallegraeff GM, et al., editors. Intergovernmental Oceanic Commission; Paris: 2001. pp. 421–424.

Quick JA, Henderson GE (1975) Effects of *Gymnodinium breve* red tide on fishes and birds: a preliminary report on behavior, anatomy, hematology, and histopathology. *Proc Gulf Coast Reg Symp Dis Aquat Anim*: 85-115.

R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available <http://www.R-project.org>.

Robins CR, Ray GC, Douglass J (1999) *Peterson Field Guides: Atlantic Coast Fishes*. Houghton Mifflin Co., Boston, MA.

Sellner KG, Doucette GJ, Kirkpatrick GJ (2003) Harmful algal blooms: causes, impacts, and detection. *J Ind Microbiol Biotechnol* 30:383-406

Shannon CE, Weaver W (1949) *The mathematical theory of communication*. Urbana IL: University of Illinois Press.

- Smayda TJ (1990) Novel and nuisance phytoplankton bloom in the sea: Evidence for a global epidemic. In: Granéli E., Sundstrom B., Edler L., Anderson DM (eds) Toxic Marine Phytoplankton. Elsevier, New York, p 29-40
- Smith GB (1975) The 1971 red tide and its impact on certain reef communities in the eastern Gulf of Mexico. *Environ Lett* 9:141-152
- Smith GB (1979) Relationship of eastern Gulf of Mexico reef-fish communities to the species equilibrium theory of insular biogeography. *J Biogeogr* 6:49–61
- Sournia A (1978) Phytoplankton Manual. Monographs on oceanographic methodology, vol. 6. UNESCO, Paris.
- Steidinger KA, Burklew M, Ingle RM (1973) The effects of *Gymnodinium breve* toxin on estuarine animals. In: Martin DF, Padilla GM (eds) Marine Pharmacognosy: Action of Marine Toxins at the Cellular Level. Academic Press, New York, NY, p 179-202
- ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat Sci* 57:255-289
- Tomas CR (ed) (1997) Identifying Marine Phytoplankton. Academic Press, San Diego, CA, 858 pp.
- Urban D, Goslee S, Pierce K, Lookingbill T (2002) Extending community ecology to landscapes. *Ecoscience* 9:200-212
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt Int Ver Theor Angew Limnol* 9:1-38
- Van Dolah FM (2000) Marine algal toxins: Origins, health effects, and their increased occurrence. *Environ Health Perspect* 108(S1):133-141
- Walsh, J.J., Weisberg, R. H., Lenes, J. M., Chen, F. R., Dieterle, D. A., Zheng, L., Carder, K. L., Vargo, G. A., Havens, J. A., Peebles, E., Hollander, D. J., He, R., Heil, C. A., Mahmoudi, B. and Landsberg, J. H. 2009. Isotopic evidence for dead fish maintenance of Florida red tides, with implications for coastal fisheries over both source regions of the West Florida shelf and within downstream waters of the South Atlantic Bight. *Progr. Oceanogr.* 80:51-73.
- Warlen SM, Tester PA, Colby DR (1998) Recruitment of larval fishes into a North Carolina estuary during a bloom of the red tide dinoflagellate, *Gymnodinium breve*. *Bull Mar Sci* 63(1):83-95
- Wessel MR, Winner BL (2003) Using a modified purse seine to collect and monitor estuarine fishes. *Gulf and Caribbean Research* 15:61-71

Table 1. Survey effort and sightings made (all species) during dedicated (R/V Lorry) and opportunistic (R/V Flip) bird surveys in seagrass habitat of Sarasota Bay, 2006-2008.

Season	Period	No. Stations	Total Birds	No. Species	SPUE	SD	RV Lorry
Summer	2006	61	1056	17	17.31	26.39	
Winter	2007	87	2153	31	24.75	43.6	
Summer	2007	106	1591	24	15.01	14.06	
Winter	2008	94	1989	27	21.16	37.29	
Summer	2008	106	1496	22	14.11	14.14	
Summer	Non-Red Tide	257	3726	29	14.5	16.12	
Summer	Red Tide	16	417	10	26.06	32.08	
Winter	Non-Red Tide	137	2753	29	20.09	33.93	
Winter	Red Tide	44	1389	26	31.57	55.49	
Season	Period	No. Stations	Total Birds	No. Species	SPUE	SD	RV Flip
Summer	2006	29	737	12	25.41	44.87	
Winter	2007	22	262	21	11.91	20.52	
Summer	2007	27	416	17	15.41	19.67	
Winter	2008	28	1107	22	39.54	91.86	
Summer	2008	40	495	16	12.38	11.63	
Summer	Non-Red Tide	82	1072	19	13.07	14.23	
Summer	Red Tide	14	576	12	41.14	61.31	
Winter	Non-Red Tide	39	1226	22	31.44	78.84	
Winter	Red Tide	11	143	17	13	26.43	

Table 2. Survey effort and catches made (all species) during purse seine surveys of fish in seagrass habitat of Sarasota Bay, 2004-2009.

Season	Period	No. Seine Sets	Total Catch	No. Species	CPUE	S.D.
Summer	2004	16	14437	57	902.31	766.9
Winter	2004-2005	21	6948	49	330.86	580.34
Summer	2005	24	6773	38	282.21	373.52
Winter	2005-2006	19	2798	29	147.26	207.46
Summer	2006	33	39405	54	1194.09	2069.43
Winter	2006-2007	24	5120	39	213.33	181.61
Summer	2007	30	20223	59	674.1	610.33
Winter	2007-2008	29	8512	49	293.52	321.73
Summer	2008	40	50610	56	1265.25	1366.98
Winter	2008-2009	30	7217	42	240.57	240.76
Summer	Non-Red Tide	104	102897	128	989.39	1033.66
Summer	Red Tide	39	28551	46	732.08	1917.04
Winter	Non-Red Tide	101	23540	70	233.07	259.67
Winter	Red Tide	22	7055	43	320.68	551.83

Table 3. (A) Number of species and Shannon-Weaver diversity index (H') of fishes in seagrass habitat for summer and winter seasons from 2004-2009. (B) Hutcheson's t-tests assessing differences in diversity index values.

A.

Year	Season	Species	H'
2004	Summer	57	1.51
2004-2005	Winter	49	1.93
2005	Summer	38	1.45
2005-2006	Winter	30	1.86
2006	Summer	54	1.79
2006-2007	Winter	39	2.02
2007	Summer	60	1.70
2007-2008	Winter	48	1.45
2008	Summer	56	1.93
2008-2009	Winter	42	1.80

B.

T-tests for differences between summer and winter diversity (Shannon-Weaver H')

Seasons	Data Comparison	Habitat	t_o	df	$t_{0.05(2), v}$	P(2-tailed)
Sum04-08	RT vs NonRT	Seagrass	40.453	60543.577	1.645	0.0000
Win0405-0809	RT vs NonRT	Seagrass	1.554	13303.134	1.645	0.1202
Sum04-08 vs. Win0405-0809	All Data	Seagrass	9.175	42297.842	1.645	0.0000
Sum04-08 vs. Win0405-0809	NONRT data only	Seagrass	4.519	32918.471	1.645	0.0000

Table 4. (A) Results of MANOVAs testing whether CPUEs of fish trophic guilds during red tide periods differed from those of non-red tide periods. Separate tests were run for summers, winters, and all seasons combined. (B) p-values of Tukey's HSD post hoc test comparing CPUEs for each trophic guild during red tide conditions to those of non-red tide conditions.

	MANOVA by Red Tide Period		
	All Seasons	Summers Only	Winters Only
	Sum04 - Win0809	Sum04 - Sum08	Win0405 - Win0809
Wilks' Lambda	0.839217186	0.594154656	0.882801414
Rao's R	6.842380524	12.97820663	2.433889627
df 1	7	7	6
df 2	250	133	110
p	<0.01	<0.01	0.03
B.			
p-values of Tukey's HSD			
G_1	<0.01	<0.01	0.28
G_2	<0.01	<0.01	0.02
G_3	<0.01	<0.01	0.18
G_4	<0.01	<0.01	0.18
G_6	0.99	0.81	0.52
G_8	0.12	0.03	NA
G_9	<0.01	<0.01	0.39

Table 5. (A) Number of species and Shannon-Weaver diversity index (H_1') of birds in seagrass habitat for summer and winter seasons from 2006-2009. (B) t-tests assessing differences in diversity index values.

Year	Season	Species	H_1'
2006	Summer	17	1.88
2007	Winter	31	2.74
2007	Summer	24	2.22
2008	Winter	27	2.45
2008	Summer	22	2.11
RT	Summer	10	1.49
NonRT	Summer	29	2.17
RT	Winter	29	2.83
NonRT	Winter	30	2.51

T-tests for differences between summer and winter diversity

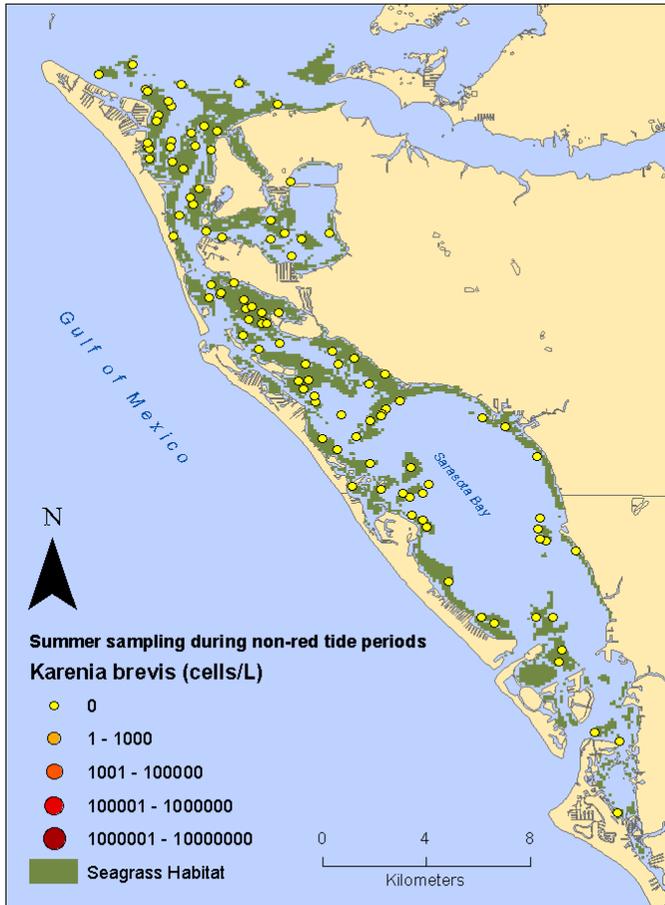
Data	t	df	p (2 tailed)
Sum 06-08 RT vs NonRT	7.38	1321	0.0001

Table 6. Kolmogorov-Smirnov tests comparing length-frequency distributions of pinfish caught during red tide periods to those caught during non-red tide periods for each month surveyed.

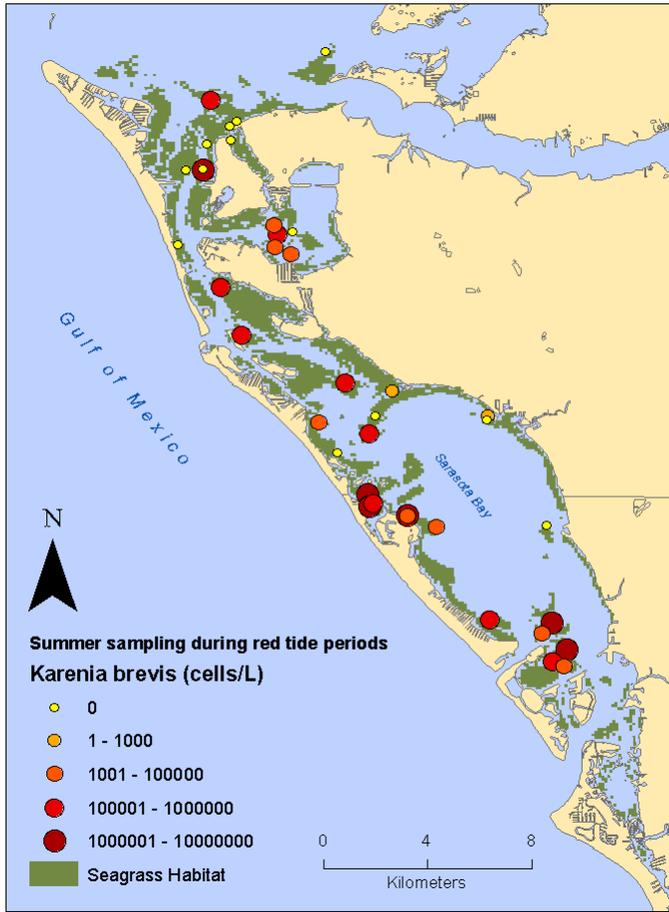
Month	D	P
JUN	0.2143	0.490
JUL	0.0714	1.000
AUG	0.3929	0.019
SEPT	0.1071	0.995
JAN	0.1786	0.720
FEB	0.1071	0.995
MAR	0.3929	0.019

Figure 1. *Karenia brevis* concentrations (cells/liter) measured from water samples collected by R/V Flip at fish sampling stations in the seagrass habitat (1 of 4 *K. brevis* sampling regimes).

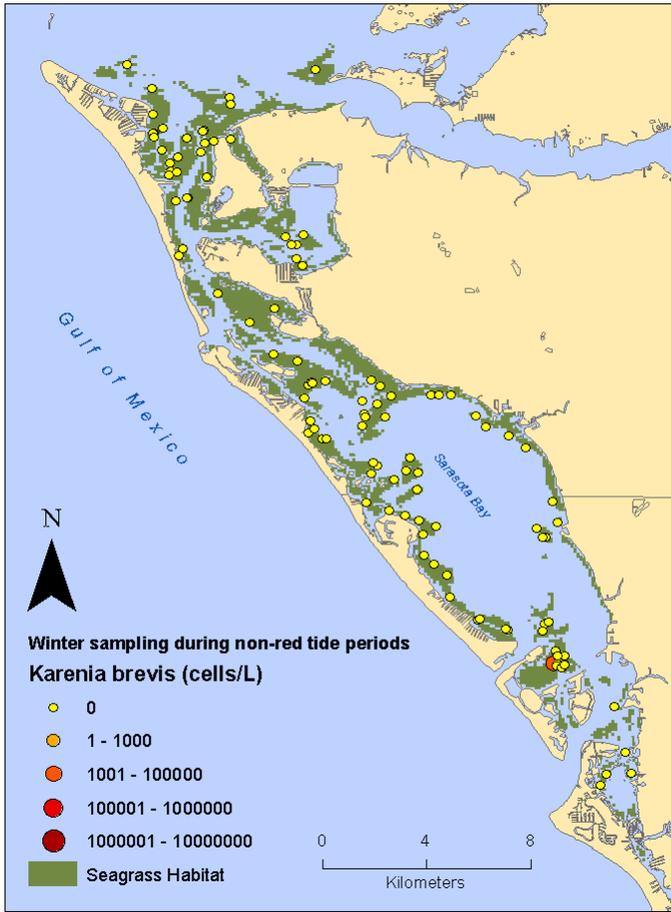
A. Summer: non-red tide



B. Summer: red tide



C. Winter: non-red tide



D. Winter: red tide

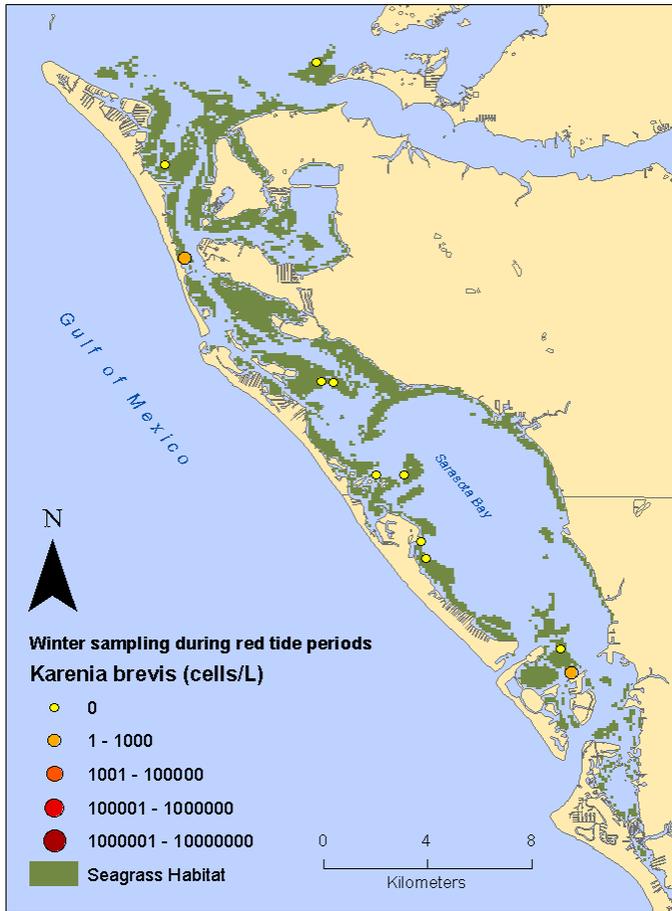
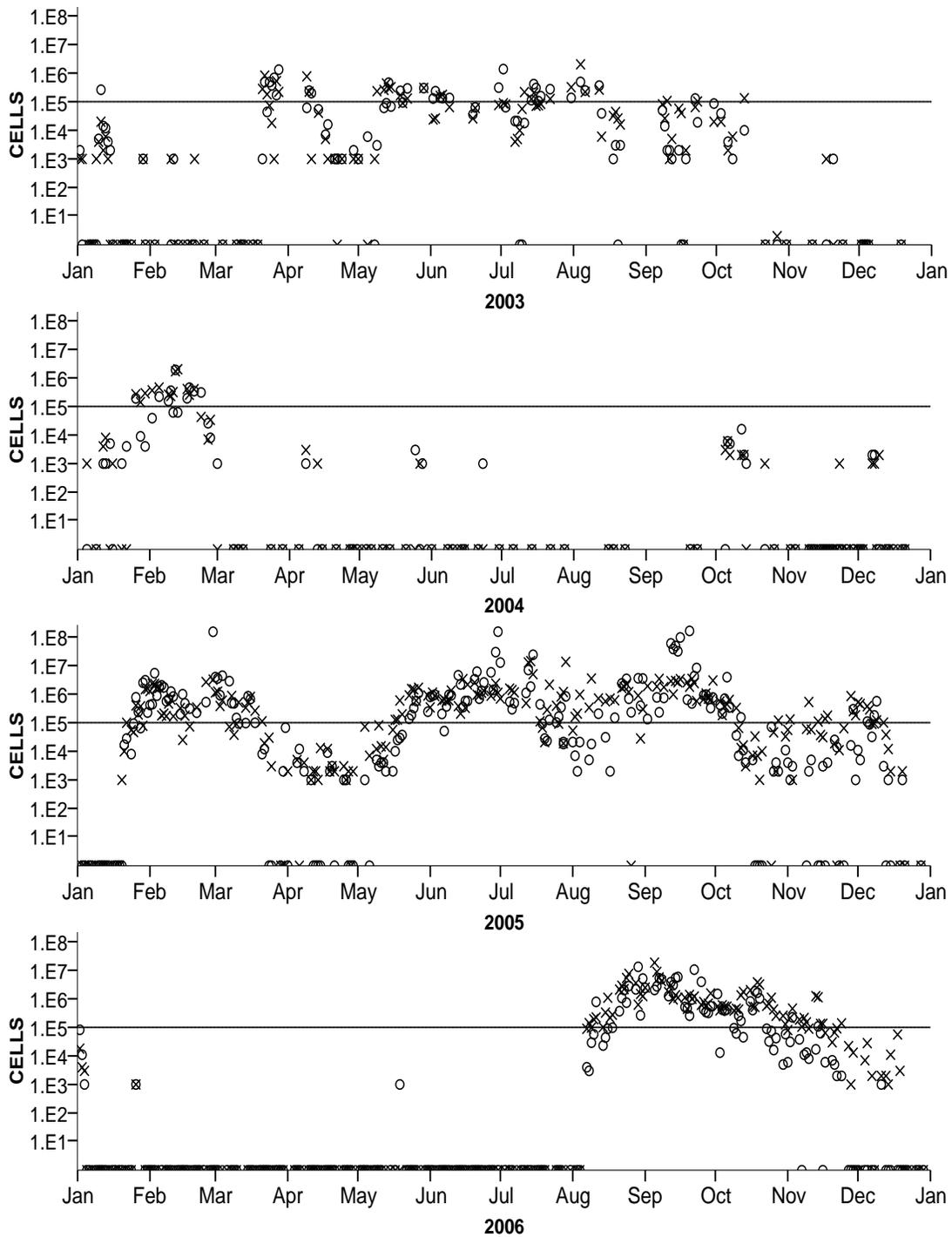


Figure 2. *Karenia brevis*. Cell densities (cells l^{-1}) measured daily at the New Pass (×) and City Island Grass Flats (○) reference stations during 2003-2007. (Reproduced from Gannon et al. 2009.)



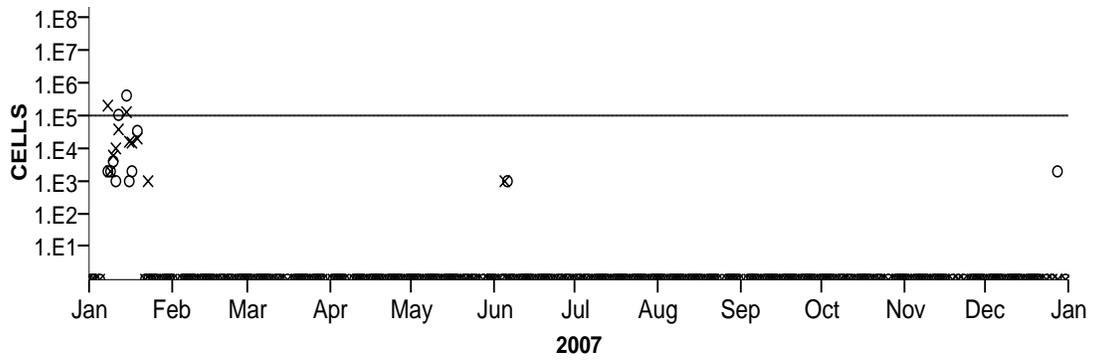


Figure 3. Overall catch per unit effort (all species combined) in seagrass habitat sampled in Sarasota Bay during winters and summers from 2004 through 2008.

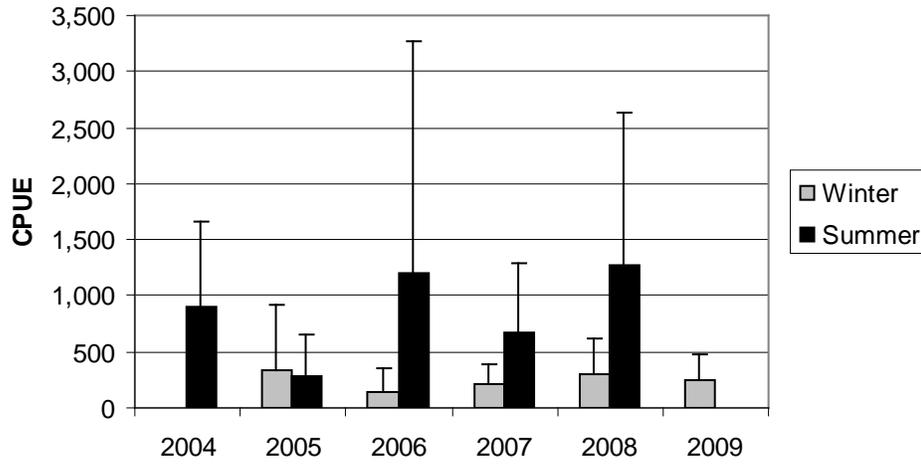


Figure 4. Densities of fishes in the seagrass habitat of Sarasota Bay as measured by purse seine catches (catch per unit effort, CPUE), broken down by season (summer and winter) and red tide designation (red tide vs. non-red tide).

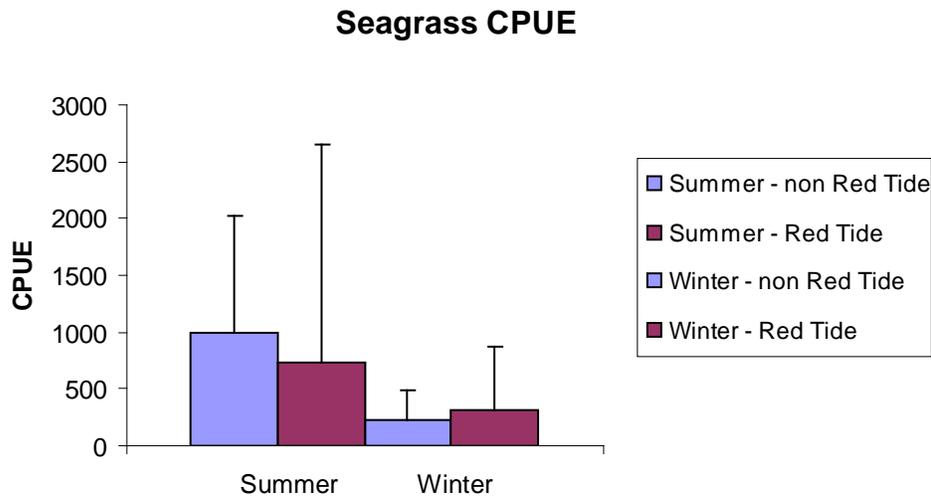


Figure 5. Densities of birds in the seagrass habitat of Sarasota Bay as measured by sightings per unit effort, SPUE) from R/V Lorry, broken down by season (summer and winter) and red tide designation (red tide vs. non-red tide).

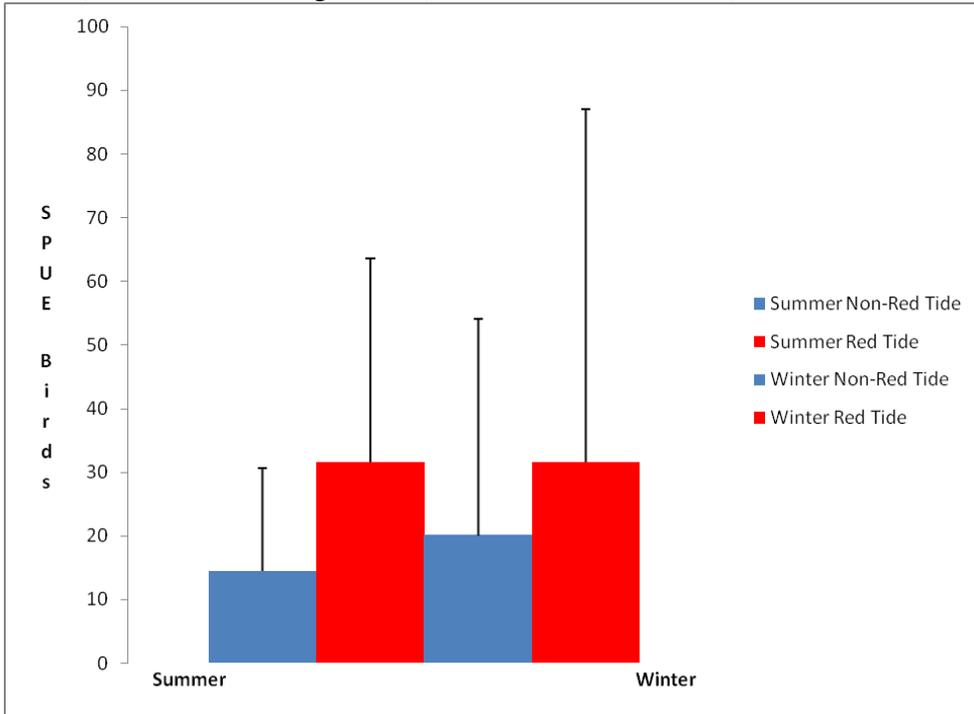
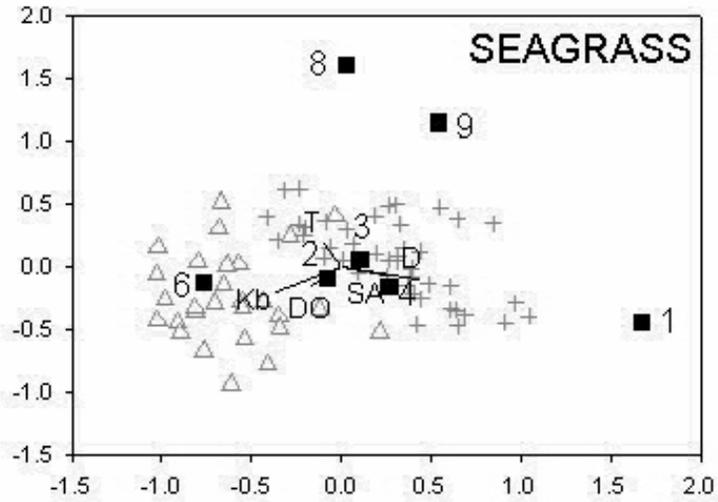


Figure 6. Canonical correspondence analysis (axes 1 and 2) of purse seine catches during summers (2004-2007) in the seagrass habitat of Sarasota Bay. Symbols: triangles = purse seines conducted during red tide periods, crosses = purse seines conducted during non-red tide periods; numbers: trophic guilds (see text for description); environmental vector codes: D=depth (m), DO=dissolved oxygen (mg/l), T=temperature (deg. C), Sa=salinity (ppt), Kb= *Karenia brevis* cell count (cells/liter). (Reproduced from Gannon et al. 2009.)



Eigenvalues: axis 1 = 0.077, axis 2 = 0.015, axis 3 = 0.006.
 Total inertia: 0.517

Figure 7. CART analysis with overall CPUE (all fish species combined, log+1 transformed) as the dependent variable and *K. brevis* cell count (cells/liter, log+1 transformed), depth (m), temperature (deg. C), dissolved oxygen (mg/l), and salinity (ppt) as predictor variables. Summer samples only.

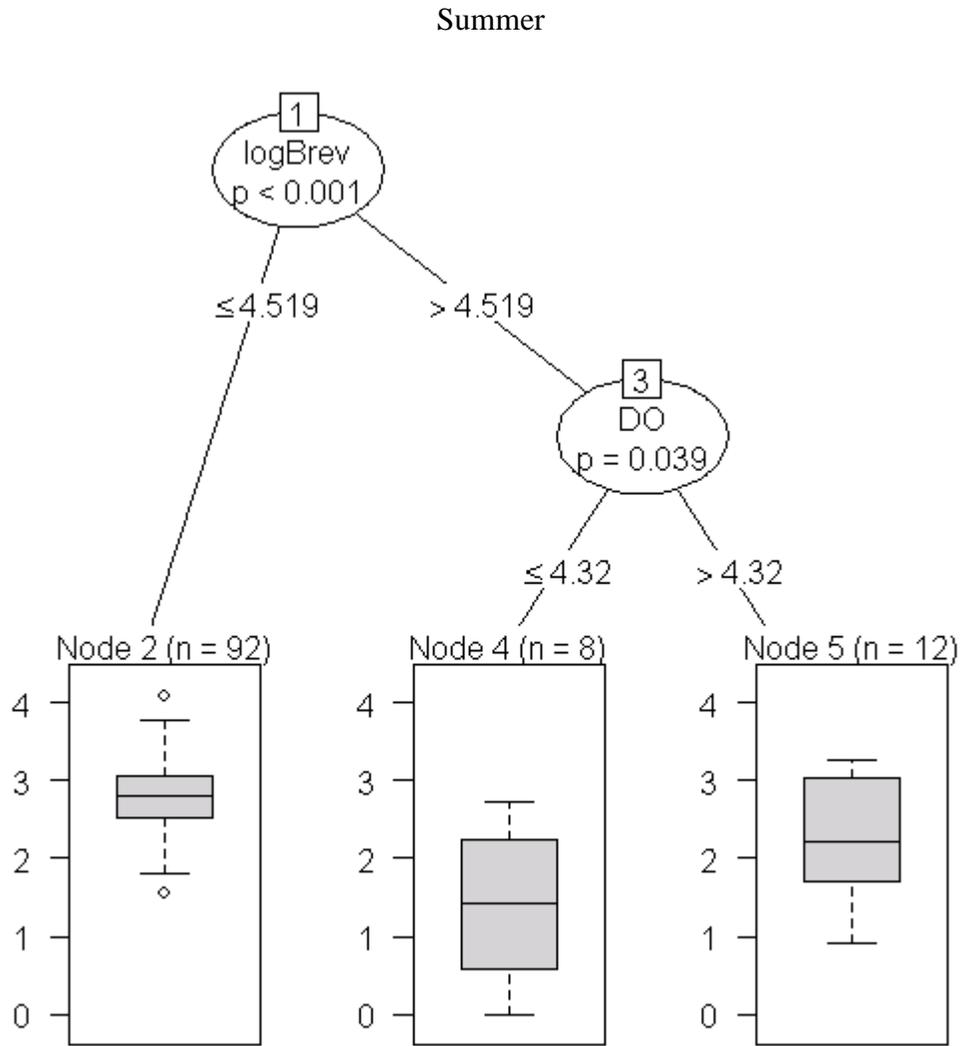


Figure 8. CART analysis with species richness (number of fish species caught per purse seine set) as the dependent variable and *K. brevis* cell count (cells/liter, log+1 transformed), depth (m), temperature (deg. C), dissolved oxygen (mg/l), and salinity (ppt) as predictor variables. Summer samples only.

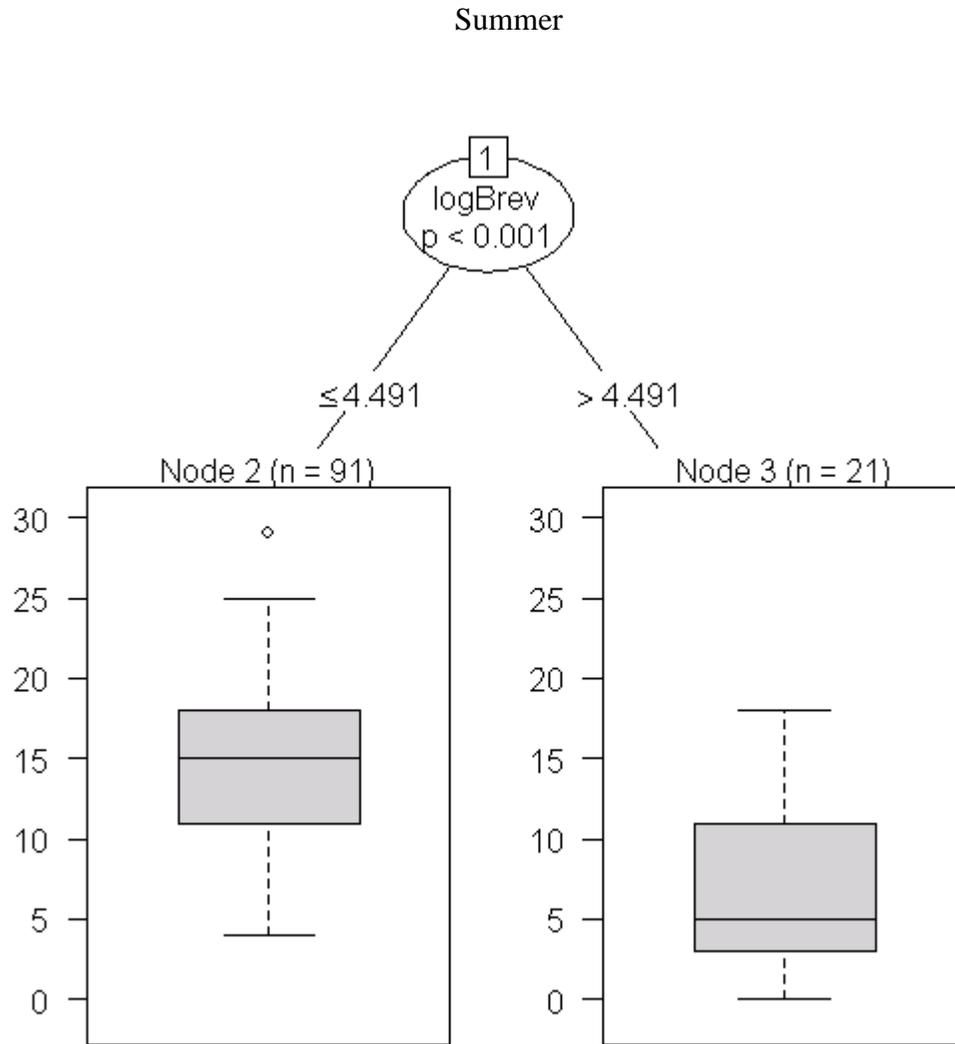


Figure 9. CART analysis with overall CPUE (all fish species combined, log+1 transformed) as the dependent variable and *K. brevis* cell count (cells/liter, log+1 transformed), depth (m), temperature (deg. C), dissolved oxygen (mg/l), and salinity (ppt) as predictor variables. Winter samples only.

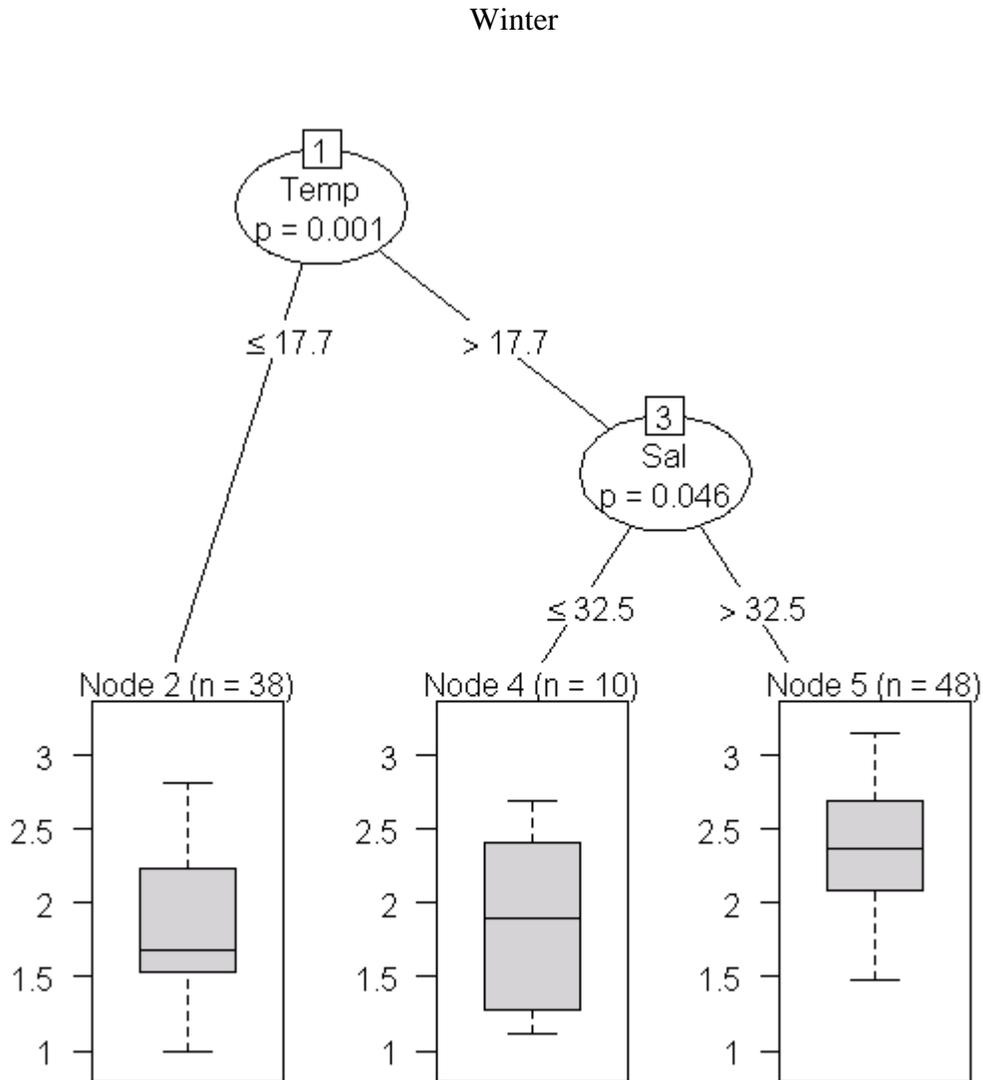
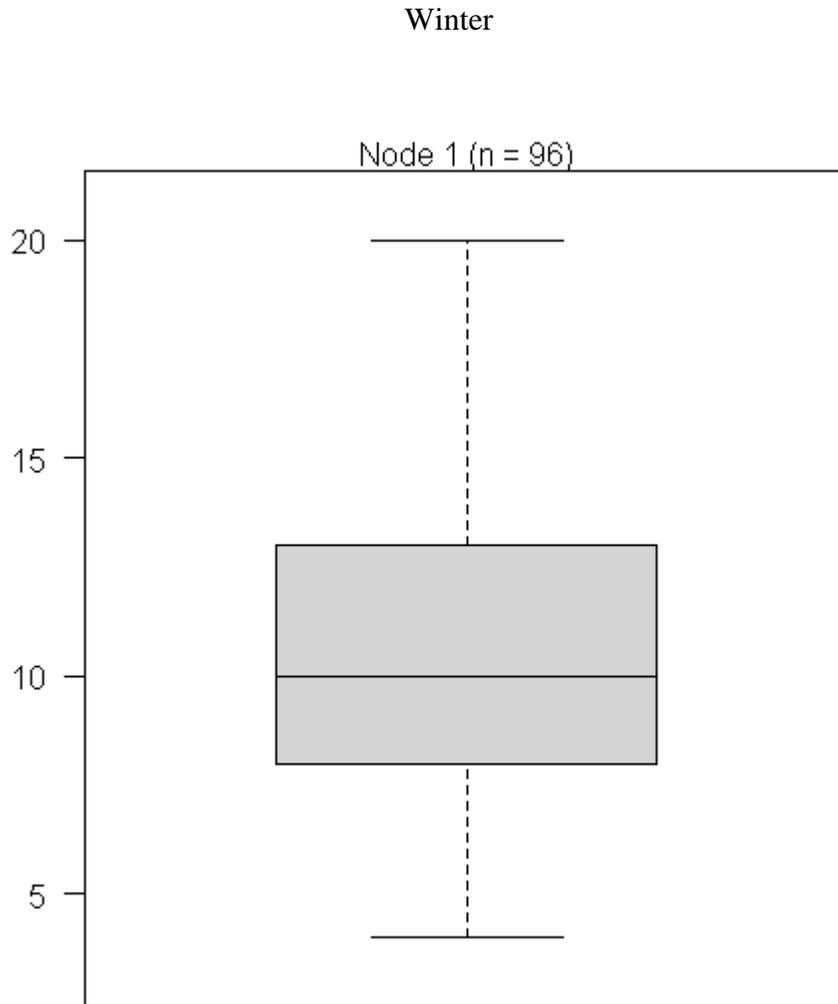


Figure 10. CART analysis with species richness (number of fish species caught per purse seine set) as the dependent variable and *K. brevis* cell count (cells/liter, log+1 transformed), depth (m), temperature (deg. C), dissolved oxygen (mg/l), and salinity (ppt) as predictor variables. Winter samples only.



Appendix 1. Publications and presentations in which data from this grant were used.
Peer-reviewed papers and Newsletter article published:

Naar, J.P., L.J. Flewelling, A. Lenzi, J.P. Abbott, A. Granholm, H.M. Jacocks, D. Gannon, M. Henry, R. Pierce, D.G. Baden, J. Wolny, and J.H. Landsberg. 2007. Brevetoxins, like ciguatoxins, are potent ichthyotoxic neurotoxins that accumulate in fish. *Toxicon* 50:707-723.

Berens, E., D. Gannon, and S. Camilleri. 2008. Effects of Red Tide on Fish Abundance and Community Structure in a Florida Estuary. *Shellcracker* (newsletter of the Florida Chapter of the American Fisheries Society) January 2008 (<http://www.sdafs.org/flafs/PDF/Jan-08.PDF>).

Fire, S.E., L.J. Flewelling, J. Naar, M.S. Henry, R.H. Pierce, D. P. Gannon, Z. Wang, and R.S. Wells. 2008. Prevalence of brevetoxins in prey fish of bottlenose dolphins in Sarasota Bay, Florida. Initial review completed, revised manuscript submitted to *Mar. Ecol. Prog. Ser.* 368:283-294.

Gannon, D., E. Berens, J. Gannon, S. Camilleri, V. Palubok, R. Wells, G. Kirkpatrick, M.K. Brueggen, and A. Barleycorn. 2009. Ecological Effects of *Karenia brevis* Harmful Algal Blooms on Nearshore Fish Communities in Southwest Florida. *Mar. Ecol. Prog. Ser.* 378:171-186.

Manuscripts in review:

Gannon, J., R. Wells, J. Allen, D. Gannon, S. Hoffman, G. Kirkpatrick, and V. Palubok. In review. Sub-lethal effects of a harmful algal bloom on bottlenose dolphins. Submitted to *Mar. Ecol. Prog. Ser.*

Berens McCabe, E., D.P. Gannon, N.B. Barros, and R.S. Wells. Prey selection by resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Submitted to *Marine Biology*.

Manuscripts in preparation:

Camilleri, S., D. Gannon, E. Berens, K. Brueggen, J. Gannon, R. Wells. Effects of red tide on the detection rates of fish calls. To be submitted to *Copeia*.

Gannon, D., E. Berens, J. Gannon, S. Camilleri, G. Kirkpatrick, V. Palubok, R. Wells. Effects of red tide on abundance, habitat selection, and body conditions of clupeid fishes in Sarasota Bay, FL. To be submitted to *Transactions of the American Fisheries Society*.

Berens, E., D. Gannon, S. Camilleri, J. Gannon, G. Kirkpatrick, V. Palubok, R. Wells. Effects of red tide on abundance, habitat selection, and body conditions of

common snook and spotted seatrout. To be submitted to *Transactions of the American Fisheries Society*.

Presentations:

Gannon, D.P. 2006. Red Tide and the Ecology of Sarasota Bay. Public lecture, Sarasota Sailing Squadron, Sarasota, FL. Oct. 2006.

Gannon, D.P. Silent Dolphins, Noisy Fishes, and the Toxic Tide that Plagues Them. Invited Lecture, California State University, Northridge. Oct. 2006.

Gannon, D.P., J. Allen, E. Berens, D. Fauquier, J. Gannon, and R. Wells. Role of ecological disturbance in the foraging ecology of coastal bottlenose dolphins. Carnivores 2006 Conference, St. Petersburg, FL. Nov. 2006.

Gannon, D.P. 2007. Noisy fishes, silent dolphins, and the toxic tide that plagues them. Invited lecture, Florida State University, Tallahassee, FL. Apr. 2007.

Gannon, D.P. 2007. Noisy fishes, silent dolphins, and the toxic tide that plagues them. Fall seminar series, Mote Marine Laboratory, Sarasota, FL. Nov. 2007.

Gannon, D.P. 2007. Effects of *Karenia brevis* Harmful Algal Blooms on an Estuarine Fish Community. Invited lecture, Eckerd College, St. Petersburg, FL. Nov. 2007.

Gannon, D.P. 2007. Effects of *Karenia brevis* Harmful Algal Blooms on an Estuarine Fish Community. Invited lecture, Bowdoin College, Brunswick, ME. Dec. 2007.

Gannon, J.G., R.S. Wells, J.B. Allen, D.P. Gannon, E.J. Berens, and S. Hofmann. 2007. Effects of harmful algal blooms on bottlenose dolphins (*Tursiops truncatus*): changes in distribution and behavior. Oral presentation, 17th Biennial Conference on the Biology of Marine Mammals, Society for Marine Mammalogy, Cape Town, South Africa. December 2007.

Wells, R.S., S. Hofmann, J.B. Allen, K.W. Urian, K. Bassos-Hull, S.M. Nowacek, J.G. Gannon, N.B. Barros, D.A. Fauquier, M.D. Scott, and R.C. Lacy. 2007. Impacts of human activities and natural events on the abundance and vital rates of bottlenose dolphins in Sarasota, Florida. Oral presentation, 17th Biennial Conference on the Biology of Marine Mammals, Society for Marine Mammalogy, Cape Town, South Africa. December 2007.

Camilleri, S., D. Gannon, E. Berens, J. Gannon, and M.K. Brueggen. 2008. Effects of Red Tide on the Occurrence of Fish Calling. Poster presentation, annual meeting of the Florida Chapter of the American Fisheries Society. February 2008.

Gannon, D., E. Berens, J. Gannon, S. Camilleri, J. Allen, and R. Wells. 2008. Effects of *Karenia brevis* Harmful Algal Blooms on Bottlenose Dolphins and Their Prey. Oral presentation, Florida Marine Mammal Health Conference, St. Augustine, FL. April 2008.

Gannon, D.P., E.J. Berens McCabe, S.A. Camilleri, J.G. Gannon, M.K. Brueggen, A.A. Barleycorn, V.I. Palubok, G.J. Kirkpatrick, and R.S. Wells. 2009. Effects of *Karenia brevis* Harmful Algal Blooms on Nearshore Fish Communities of Southwest Florida. Society for Integrative and Comparative Biology (SICB) annual conference, Boston, MA. Jan. 2009.

Press coverage:

Zollo, C. 2006. Red Tide Dumps Fish on Beaches: The Toxic Bloom Moves Up The Coast From Venice To Siesta Key. Sarasota Herald Tribune, August 26, 2006.

Voiland, A. 2008. A Bay Rebounds. *Mote Magazine*, Winter 2008/2009.

Appendix 2. Membership of each trophic guild used in the analyses of community structure. Information on food habits and habitat selection, which was used to assign each species to a guild, was obtained from FishBase (<http://www.fishbase.org/search.php>, accessed on 15 April 2007), Hoese & Moore 1998, Robins et al. 1998, and references cited therein.

Species	Guild	Guild Name
Balistidae sp. (Filefish)	1	Demersal herbivore
Dotterel Filefish, <i>Aluterus heudeloti</i>	1	Demersal herbivore
Fringed filefish, <i>Monocanthus ciliatus</i>	1	Demersal herbivore
Orange filefish, <i>Aluterus schoepfi</i>	1	Demersal herbivore
Scaridae sp. (Parrotfish)	1	Demersal herbivore
Scrawled filefish, <i>Aluterus scriptus</i>	1	Demersal herbivore
Atlantic spadefish, <i>Chaetodipterus faber</i>	2	Demersal invert
Atlantic stingray, <i>Dasyatis Sabina</i>	2	Demersal invert
Bandtail puffer, <i>Sphoeroides spengleri</i>	2	Demersal invert
Barbfish, <i>Scorpaena brasiliensis</i>	2	Demersal invert
Bighead searobin, <i>Prionotus tribulus</i>	2	Demersal invert
Black drum, <i>Pogonias cromis</i>	2	Demersal invert
Blackcheek tonguefish, <i>Symphurus plagiusa</i>	2	Demersal invert
Bluntnose stingray, <i>Dasyatis say</i>	2	Demersal invert
Bonnethead shark, <i>Sphyrna tiburo</i>	2	Demersal invert
Brief squid, <i>Lolliguncula brevis</i>	2	Demersal invert
Clearnose skate, <i>Raja eglanteria</i>	2	Demersal invert
Cownose ray, <i>Rhinoptera bonasus</i>	2	Demersal invert
Crested blenny, <i>Hypoleurochilus geminatus</i>	2	Demersal invert
Goldspotted killifish, <i>Floridichthys carpio</i>	2	Demersal invert
Grass porgy, <i>Calamus arctifrons</i>	2	Demersal invert
Gulf killifish, <i>Fundulus grandis</i>	2	Demersal invert
Haemulid sp. (Grunts)	2	Demersal invert
Hogchoker, <i>Trinectes maculatus</i>	2	Demersal invert
Hogfish, <i>Lachnolaimus maximus</i>	2	Demersal invert
Lined sole, <i>Achirus lineatus</i>	2	Demersal invert
Lookdown, <i>Selene vomer</i>	2	Demersal invert
Mojarra sp.	2	Demersal invert
Pigfish, <i>Orthopristis chrysoptera</i>	2	Demersal invert
Planehead filefish, <i>Monocanthus hispidus</i>	2	Demersal invert
Rainwater killifish, <i>Lucania parva</i>	2	Demersal invert
Scrawled cowfish, <i>Lactophrys quadricornis</i>	2	Demersal invert
Sheepshead, <i>Archosargus probatocephalus</i>	2	Demersal invert
Silver perch, <i>Bairdiella chrysoura</i>	2	Demersal invert
Southern hake, <i>Urophycis floridana</i>	2	Demersal invert
Southern puffer, <i>Sphoeroides nephelus</i>	2	Demersal invert
Southern stingray, <i>Dasyatis Americana</i>	2	Demersal invert

Spot, <i>Leiostomus xanthurus</i>	2	Demersal invert
Spottail pinfish, <i>Diplodus holbrooki</i>	2	Demersal invert
Spotted eagle ray, <i>Aeobatus narinari</i>	2	Demersal invert
Spotted whiff, <i>Citharichthys macrops</i>	2	Demersal invert
Striped burrfish, <i>Chilomycterus schoepfi</i>	2	Demersal invert
Striped mojarra, <i>Diapterus plumieri</i>	2	Demersal invert
<i>Symphurus</i> sp. (Tonguefish)	2	Demersal invert
Tripletail, <i>Lobotes surinamensis</i>	2	Demersal invert
White grunt, <i>Haemulidae plumieri</i>	2	Demersal invert
Florida blenny, <i>Chasmodes saburrae</i>	3	Demersal omnivore
Pinfish, <i>Lagodon rhomboides</i>	3	Demersal omnivore
Sheephead minnow, <i>Cyprinodon variegatus</i>	3	
spp.		Demersal omnivore
Shrimp sp.	3	Demersal omnivore
Silver porgy, <i>Diplodus argenteus</i>	3	Demersal omnivore
Sparidae sp. (Porgies)	3	Demersal omnivore
Violet goby, <i>Gobioides broussonnetii</i>	3	Demersal omnivore
Black Grouper, <i>Mycteroperca bonaci</i>	4	Demersal piscivore
Black sea bass, <i>Centropristis striata</i>	4	Demersal piscivore
Catfish sp.	4	Demersal piscivore
Common snook, <i>Centropomus undecimalis</i>	4	Demersal piscivore
Gafftopsail catfish, <i>Bagre marinus</i>	4	Demersal piscivore
Gag grouper, <i>Mycteroperca microlepis</i>	4	Demersal piscivore
Goliath grouper, <i>Epinephelus itajara</i>	4	Demersal piscivore
Gulf flounder, <i>Paralichthys albigutta</i>	4	Demersal piscivore
Gulf toadfish, <i>Opsanus beta</i>	4	Demersal piscivore
Hardhead catfish, <i>Arius felis</i>	4	Demersal piscivore
Inshore lizardfish, <i>Synodus foetens</i>	4	Demersal piscivore
Kingfish sp. (<i>Menticirrhus</i> sp.)	4	Demersal piscivore
Lane snapper, <i>Lutjanus synagris</i>	4	Demersal piscivore
Leopard searobin, <i>Prionotus scitulus</i>	4	Demersal piscivore
Loligo sp.	4	Demersal piscivore
Longnose gar, <i>Lepisosteus osseus</i>	4	Demersal piscivore
Mangrove (gray) snapper, <i>Lutjanus griseus</i>	4	Demersal piscivore
Mutton Snapper, <i>Lutjanus analis</i>	4	Demersal piscivore
Ocellated flounder, <i>Ancylopsetta quadrocellata</i>	4	Demersal piscivore
Red drum, <i>Sciaenops ocellatus</i>	4	Demersal piscivore
Sand perch, <i>Diplectrum formosum</i>	4	Demersal piscivore
Sand seatrout, <i>Cynoscion arenarius</i>	4	Demersal piscivore
Serranidae sp.	4	Demersal piscivore
Slender inshore squid, <i>Loligo plei</i>	4	Demersal piscivore
Smooth butterfly ray, <i>Gymnura micrura</i>	4	Demersal piscivore
Southern stargazer, <i>Astroscopus y-graecum</i>	4	Demersal piscivore
Spotted seatrout, <i>Cynoscion nebulosus</i>	4	Demersal piscivore

Squid, Lolliguncula spp.	4	Demersal piscivore
Yellowedge grouper, Epinephelus flavolimbatus	4	Demersal piscivore
Blackchin tilapia, Tilapia melanotheron	5	Detritovore
Harvestfish, Peprilus alepidotus	5	Detritovore
Atlantic thread herring, Opisthonema oglinum	6	Pelagic filter
Half beak, Hyporhamphus unifasciatus	6	Pelagic filter
Menhaden, Brevoortia spp.	6	Pelagic filter
Rough silverside, Membras martinica	6	Pelagic filter
Scaled sardine, Harengula jaguana	6	Pelagic filter
Shad sp.	6	Pelagic filter
Spanish sardine, Sardinella aurita	6	Pelagic filter
Striped anchovy, Anchoa hepsetus	6	Pelagic filter
Yellowfin menhaden, Brevoortia smithi	6	Pelagic filter
Clupeidae sp. (Herrings)	6	Pelagic filter
Fundulidae sp. (Killifish)	7	Pelagic invert
Gulf butterfish, Peprilus burti	7	Pelagic invert
Inland/tidewater silverside, Menidia spp	7	Pelagic invert
Round scad, Decapterus punctatus	7	Pelagic invert
Cyprinodontidae sp. (Killifish)	8	Pelagic omnivore
Fantail mullet, Mugil gyrans	8	Pelagic omnivore
Striped (black) mullet, Mugil cephalus	8	Pelagic omnivore
Atlantic bumper, Chloroscombrus chrysurus	9	Pelagic piscivore
Atlantic needlefish, Strongylura marina	9	Pelagic piscivore
Blacktip shark, Carcharhinus limbatus	9	Pelagic piscivore
Blue runner, Caranx crysos	9	Pelagic piscivore
Bluefish, Pomatomus saltatrix	9	Pelagic piscivore
Carangidae sp. (Jack)	9	Pelagic piscivore
Cobia, Rachycentron canadum	9	Pelagic piscivore
Crevalle jack, Caranx hippos	9	Pelagic piscivore
Florida pompano, Trachinotus carolinus	9	Pelagic piscivore
Ladyfish, Elops saurus	9	Pelagic piscivore
Leatherjack, Oligoplites saurus	9	Pelagic piscivore
Permit, Trachinotus falcatus	9	Pelagic piscivore
Sharksucker, Echeneis naucrates	9	Pelagic piscivore
Spanish mackerel, Scomberomorus maculatus	9	Pelagic piscivore
Sphyraenidae sp. (Sennet)	9	Pelagic piscivore
Yellow jack, Caranx bartholomali	9	Pelagic piscivore
Yellowtail Snapper, Ocyurus chrysurus	9	Pelagic piscivore