



Effects of *Karenia brevis* red tide on the spatial distribution of spawning aggregations of sand seatrout *Cynoscion arenarius* in Tampa Bay, Florida

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ABSTRACT: A passive acoustic survey using a random stratified design detected spawning aggregations of sand seatrout *Cynoscion arenarius* over 2 sequential spawning seasons (2004 and 2005) in Tampa Bay, Florida. In 2005, an intense *Karenia brevis* red tide at ichthyotoxic concentrations entered Tampa Bay 3 mo after the spawning season began. The bloom persisted through the end of the spawning season and was temporally associated with significant changes in the spatial distribution of spawning aggregations. Red tide was most prevalent and concentrated within the lower portion of Tampa Bay and extended to a lesser degree into the middle bay, but remained absent from the upper bay. While the percentage of sand seatrout aggregations in the middle bay zone did not significantly change from 2004 to 2005, aggregations in the non-impacted area of the upper bay increased, and the red tide-exposed lower bay experienced a significant and pronounced decline. These significant bay-wide changes in the sand seatrout spawning population coincided with the red tide event, most notably the considerable decline in the lower bay, but the broad spatial distribution of the aggregations in concert with certain reproductive and life history characteristics may buffer the population from long-term effects. Typically, it is difficult to assess the effect of disturbances on marine fish populations due to complexities in measuring the extent of the perturbation and the magnitude of the loss to the population. Our spatially explicit sampling design further enabled us to demonstrate the widespread effects of red tide on fisheries and provides an important tool for assessing the extent of loss to a spawning fish population.

KEY WORDS: Spawning · Spatial distribution · Red tide · *Karenia brevis* · Sand seatrout · *Cynoscion arenarius* · Tampa Bay

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INTRODUCTION

To successfully define spawning populations of marine fish, a variety of factors acting over spatial, temporal, and demographic scales must be considered (Lowerre-Barbieri et al. 2009). Locating spawning areas over space and time is critical to population management (Rowe & Hutchings 2003), particularly when populations become stressed due to environmental perturbations (Rubec 1999). Overexploitation

of marine fishes has been identified as a prominent stressor to a variety of stocks (Hutchings & Reynolds 2004), but unpredictable events such as freezes, red tides, oxygen depletion, and oil spills can also dramatically affect fish populations (Rubec 1999). The geographic extent of these events on spawning populations can be measured by comparison with spatially explicit baseline reproductive data.

The distribution of estuarine spawning habitat for sand seatrout *Cynoscion arenarius* is unresolved.

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Sand seatrout is a common sciaenid found in near-shore and estuarine waters of the Gulf of Mexico, targeted by recreational and commercial fishers (Purtlebaugh & Rogers 2007, Knapp & Purtlebaugh 2008). Spawning typically occurs from March through September (Shlossman & Chittenden 1981), with juveniles appearing in Tampa Bay, Florida (USA) from April through October (Purtlebaugh & Rogers 2007). Reproductive data from offshore collections around Louisiana and the Mississippi Delta indicate that spawning occurs in deep coastal waters (Sheridan et al. 1984, Cowan & Shaw 1988), while in Texas spawning occurs in inshore Gulf waters and within the estuary (Shlossman & Chittenden 1981). Although these studies provide insight on spawning locations within a broad spatial context, the distribution of spawning habitat within estuarine systems is unknown. To address this issue, a passive acoustic survey was conducted over 2 years (2004 and 2005) in Tampa Bay to map the spatial distribution of spawning sites. Since male adult sand seatrout produce a species-specific call associated with reproduction (Locascio & Mann 2008), surveys using passive acoustic hydrophones can detect these calls and map spawning locations (Luczkovich et al. 2008, Walters et al. 2009).

Blooms of the toxic dinoflagellate *Karenia brevis* causing red tides have affected fish populations in marine and coastal southwest Florida for centuries, being reported annually since 1844 in the eastern Gulf of Mexico (Ingersoll 1882, Steidinger 2009). Fish kills usually originate with the lysis of *K. brevis* cells and the subsequent release of brevetoxins, potent neurotoxic ichthyotoxins that are absorbed directly across the gill membranes (Abbott et al. 1975, Baden 1989). Kills also result from ingestion of toxic cells, water, or vectored prey (Tester et al. 2000, Landsberg 2002, Naar et al. 2007, Landsberg et al. 2009). Neurotoxicity causes lack of muscle coordination, paralysis, convulsions, and, eventually, death by respiratory failure (Baden 1989, Landsberg 2002). Due to the complexities of reliably reporting fish kill data or impacts on fish communities, few substantive quantitative studies exist. Red tide blooms kill an estimated thousands to millions of fish per year, as well as higher vertebrates and invertebrates (Steidinger et al. 1973, Landsberg 2002, Flewelling et al. 2005, Landsberg et al. 2009). Fish kills caused by *K. brevis* red tides have not been reliably quantified because of their magnitude and the spatial and temporal scales over which they occur (Landsberg et al. 2009). Mortality is difficult to evaluate because fish die at different rates; carcasses are displaced by wind, tide,

and decomposition; and sink, escaping visual assessment (American Fisheries Society 1992) which leads to an underestimation of losses (Steffe et al. 2007). Although challenging, it is imperative that carcass reports be supplemented with baseline data to account for the condition of the resource before the event in order to contrast the magnitude of change (Underwood 1991). Quantifiable data are requisite to gain true perspective on the biological consequences of a die-off event and potentially construct management actions to account for the stressed resources.

An unusually persistent *Karenia brevis* red tide event occurred in Tampa Bay during summer 2005. Initiated off the west-central Florida coast in early January 2005, the red tide bloom affected coastal waters through January 2006, causing extensive mortalities of fish, turtles, birds, marine mammals, and benthos (Landsberg et al. 2009, Dupont et al. 2010, Flaherty & Landsberg 2011, Florida Fish and Wildlife Conservation Commission (FWC) unpubl. data). Although an almost annual event on the west coast of Florida, red tide rarely encroaches on and persists in Tampa Bay (Steidinger & Ingle 1972, FWC unpubl. data) because salinity limitations are usually at the lowest tolerance level of ~24 (Steidinger & Ingle 1972, Landsberg & Steidinger 1998, Brown et al. 2006, Magaña & Villareal 2006, Steidinger 2009). This relatively high optimal salinity requirement of *K. brevis* along with the hydrology of Tampa Bay usually prevents its occurrence in lower salinity areas of the bay, typically those of the upper bay (Flaherty & Landsberg 2011). However, in summer 2005, fish kill reports attributed to *K. brevis* for the Tampa Bay area reached record high numbers (FWC unpubl. data). Community shifts in small- and large-bodied nekton, as well as declines in recruitment for 3 economically important fish species, including sand seatrout, were noted in Tampa Bay during and following the 2005 red tide (Flaherty & Landsberg 2011). The 2005 red tide was also responsible for radical shifts in the structure of the artificial reef epibenthic macroinvertebrate and fish communities located 19 to 25 km west of Tampa Bay, with fish species richness declining by >50% and significant reductions in the abundances of most species (Dupont et al. 2010). Inshore fish communities in a southern neighboring estuary (Sarasota Bay) also experienced decreased abundance and diversity with changes in community structure during red tide months (Gannon et al. 2009).

In this study, we located spawning sites of sand seatrout in the Tampa Bay estuary in 2004 and 2005 using a passive acoustic survey. Spawning areas of

sand seatrout in Tampa Bay were exposed to red tide partway through the 2005 spawning season, providing an opportunity to assess the bloom's influences on spawning activity compared to 2004, when there was no red tide during the spawning season. Since red tide did not affect the northernmost portion of the bay, this area ultimately served as a nonimpacted area, while the rest of the bay was potentially exposed. Here, we evaluate how the red tide bloom affected sand seatrout spawning locations by comparing spawning site distribution and occurrence between areas of the bay in 2004 and in 2005.

MATERIALS AND METHODS

Red tide data

Red tide data utilizing methods used to quantify *Karenia brevis* were obtained from the Harmful Algal Bloom (HAB) group of the FWC Fish and Wildlife Research Institute (FWRI). Water samples were collected approximately weekly from 4 fixed stations near the mouth of Tampa Bay (Fig. 1) for *K. brevis* cell concentrations. In addition to the fixed stations, event-driven sampling based on fish kill reports and observations occurred at a variety of locations throughout the bay and along the southwest Gulf coast. Sampling increased in frequency and geographic coverage once red tide was detected in the bay to better monitor its movement and intensity. Water samples were collected at a depth of 0.5 m using weighted bottles, Niskin bottles, or buckets. Samples were immediately put into 250 ml amber plastic bottles, 125 ml clear plastic bottles, or Whirl-Pak bags and stored in a cooler with site water. Additionally, 125 ml of each sample was immediately preserved with 2 ml of Lugol's unacidified iodine solution and stored in a separate cooler. All samples were returned to FWRI and processed within 24 h of collection.

Samples collected for analysis of *Karenia brevis* were analyzed by FWRI staff. Live samples were screened for the presence of *K. brevis* cells. Lugol's preserved samples were used to determine *K. brevis* cell concentrations. Samples were mixed by inverting 20 times, then 3 ml of the sample was placed in a Lab-Tek Coverglass Chamber (Nunc #155380). Cells were allowed to settle for at least 30 min before enumeration. Samples were examined and enumerated at 100 \times and 400 \times using an inverted microscope. Identification of *K. brevis* followed Steidinger et al. (2008).

Background levels (≤ 1000 cells l^{-1}) of *Karenia brevis* are found year-round in the Gulf of Mexico (Tester & Steidinger 1997). Ichthyotoxic concentrations are considered to be 100 000 cells l^{-1} (Quick & Henderson 1974, Landsberg & Steidinger 1998, Gannon et al. 2009), although toxicity may vary due to the concentration of brevetoxin in the water and is not necessarily a reflection of cell concentration. Cell concentrations can be much lower than 100 000 cells l^{-1} , yet the toxin concentration in the water can still be ichthyotoxic, so cell counts are an approximation of potential lethality (Landsberg et al. 2009). To approximate environmentally relevant red tide conditions, samples were ranked as being at background concentration (0 to 1000 cells l^{-1}), bloom concentration (1001 to 100 000 cells l^{-1}), or possible ichthyotoxic conditions ($> 100\,000$ cells l^{-1}). To discern the extent and severity of *K. brevis* within Tampa Bay for each year, individual plots were constructed using Arc GIS 9.2.

Sand seatrout hydrophone sampling

A simplified description of the sampling design is provided here (for details see Walters et al. 2009). Seasonal and diel sampling periodicities for this study were dictated by the spawning behavior of spotted seatrout *Cynoscion nebulosus*, a congener of sand seatrout and the original focus of the passive acoustic survey. However, because spawning seasonality and diel periodicity in sand seatrout are similar to those in spotted seatrout, the survey also encompassed sand seatrout spawning activity. Sampling was conducted from the first week of April through the last week of September in 2004 and 2005, from approximately 20:00 h EDT (sunset) to 01:00 h EDT.

Tampa Bay was divided into 3 zones based on geographic and logistical criteria: Zone 1 (upper bay), Zone 2 (middle bay), and Zone 3 (lower bay). Each zone was composed of 1 nautical mile-square grids (Fig. 1). Only grids containing water > 1.5 m depth in $\geq 5\%$ of the grid area were included in the sampling design ($n = 285$). Sampling was conducted twice weekly in a given zone and scheduled within 2 d of the occurrence of quarter, full, last quarter, or new moon phases. One zone was sampled per week and zones were rotated monthly to ensure that each zone was sampled over all the lunar phases during the spawning season. Sampling grids were chosen by random selection with replacement to account for seasonal variability. The number of grids sampled

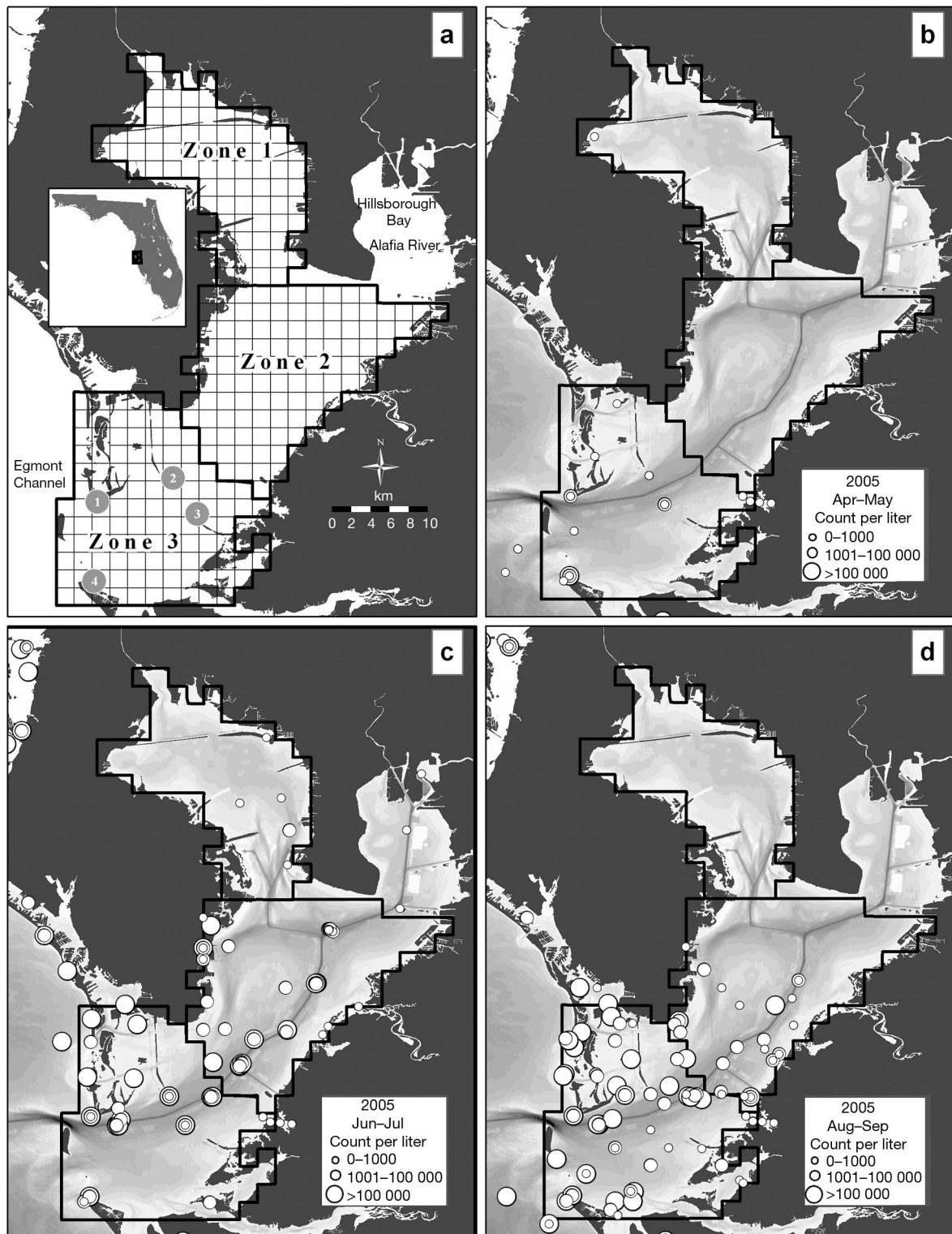


Fig. 1. Tampa Bay, Florida. (a) Grid cells and sampling zones: Zone 1 (upper bay), Zone 2 (middle bay), and Zone 3 (lower bay) used in the hydrophone survey. The 4 gray circles in Zone 3 indicate the fixed sampling stations for *Karenia brevis*. (b) 2005 *K. brevis* concentrations at fixed stations and event-responsive sampling sites during April and May, (c) June and July, and (d) August and September. Overlapping circles indicate locations where multiple samples were taken on different days over the given time period

per night was proportional to the size of the zone: 5 grids were sampled per trip in Zone 1 and 6 grids were sampled per trip in Zones 2 and 3.

To ensure representative sampling of the grids, 4 stations were sampled per grid and station locations were distributed as evenly as possible over 4 targeted bottom types: submerged aquatic vegetation, structure, channel, and nonchannel designations. If these 4 bottom types were not present within a grid, then the 4 sampling stations were selected based on differences in depth. If depth was constant throughout the grid, then the 4 sampling stations were distributed equidistant from one another throughout the grid.

At each sampling station in a grid, GPS location and depth were recorded, and a mobile hydrophone (HTI, model 96-min, sensitivity–164 dBV μPa^{-1}) was lowered 1 m into the water. After a 2 minute waiting period, all sciaenid courtship calls were identified and recorded. The estimated number of sand seatrout producing sound was categorized as (1) 1 to 2 individuals, (2) 3 to 5 individuals, or (3) an aggregation, the category used as the proxy for spawning. In the laboratory, field recordings were cross-referenced and verified against a standard sound reference library for other fish species of interest. Locations of sand seatrout aggregations were mapped with Arc GIS 9.2, and the fixed effects of zone, year, and their interactions on aggregation percentage were tested by means of a generalized linear model

(GLM) using a binomial distribution and maximum likelihood estimation (MLE) in PROC GLIMMIX of SAS 9.1 (SAS Institute). All tests were performed at $\alpha = 0.05$.

RESULTS

Red tide data

Red tide was not detected in Tampa Bay during the 2004 sand seatrout spawning period (April to September). Although *Karenia brevis* at ichthyotoxic concentrations was detected in 20 % of samples ($n = 80$) from lower Tampa Bay in January and February, no other Tampa Bay samples ($n = 52$) collected from March through the end of 2004 contained *K. brevis* cells (FWC unpubl. data).

In 2005, red tide was initiated offshore and transported via the bottom Ekman layer into Tampa Bay through the Egmont channel (Fig. 1) (Weisberg et al. 2009), eventually intruding into Zone 3 and then Zone 2. Background concentrations of *Karenia brevis* were first detected the second week of January at Stns 2 and 4 (Fig. 2). By mid-January, all 4 stations had *K. brevis* concentrations at bloom levels. Bloom conditions persisted through February and increased to ichthyotoxic concentrations at Stn 3 on February 10 and at Stn 4 on February 28, continuing until mid-March. Through the end of May, *K. brevis* remained

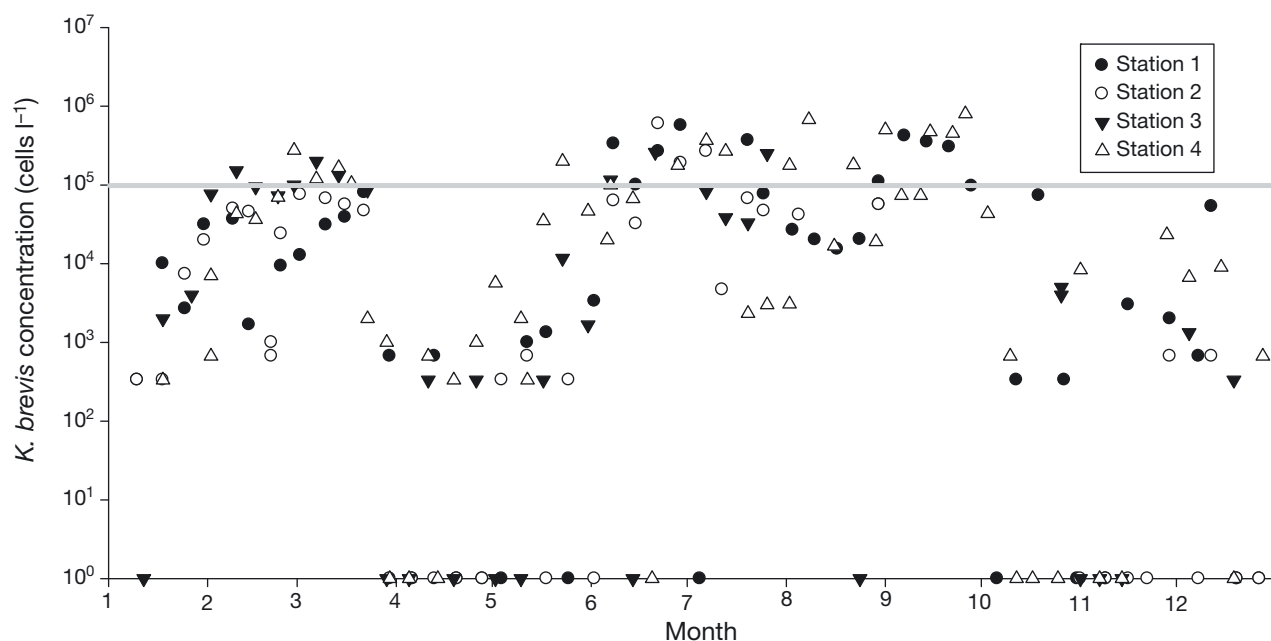


Fig. 2. *Karenia brevis*. Concentrations at the 4 fixed sampling stations during 2005. Gray line at 100 000 cells l^{-1} shows the concentration typically associated with ichthyotoxicity

near background concentrations, periodically reaching bloom levels (Fig. 2) until Stn 4 reached ichthyotoxic concentrations (Fig. 1). By June, 56% of samples from all 4 stations were at ichthyotoxic levels persisting throughout June and July (Table 1), as well as at multiple supplemental sampling stations in

Table 1. For each of the 4 fixed sampling stations in 2005 (see Fig. 1a), the number of samples with *Karenia brevis* counts at ichthyotoxic levels ($>100\,000$ cells l^{-1}) over the total number of samples for each month. Dashes indicate months samples were not taken

Month	Samples at ichthyotoxic level/total				Stations at ichthyotoxic level (%)
	S1	S2	S3	S4	
1	0/4	0/4	0/2	0/1	0
2	0/3	0/5	2/5	1/6	15.8
3	0/5	0/5	2/4	3/6	25
4	0/4	0/4	0/4	0/5	0
5	0/4	0/4	0/5	1/6	5.3
6	4/5	2/5	2/3	2/5	55.6
7	1/3	1/4	1/4	2/4	33.4
8	1/5	0/3	0/2	3/6	25
9	3/4	–	–	4/6	70
10	0/5	–	0/4	0/5	0
11	0/3	0/5	0/3	0/4	0
12	0/4	0/4	0/2	0/4	0

Zones 2 and 3 (Fig. 1). A similar spatial pattern was observed in August and September, along with a substantial increase in the number of detections of ichthyotoxic levels in Zone 3 (Fig. 1). In Zone 2, greater concentrations of cells were generally found in the central area, with levels less than ichthyotoxic concentrations along the shorelines to the west and east (Fig. 1). Although ichthyotoxic levels of *K. brevis* were continuously detected in Zones 2 and 3 throughout the summer, these levels never extended into Zone 1. Similarly, *K. brevis* data collected by the Environmental Protection Commission of Hillsborough Bay (EPC) during 2005 in Zone 1 and Hillsborough Bay did not contain bloom level concentrations of *K. brevis* (Flaherty & Landsberg 2011).

Sand seatrout hydrophone data

During 2004 sampling, sand seatrout aggregations were detected throughout the 3 zones and spawning season. Aggregations ($n = 351$) were detected at 41% of all sampled stations ($n = 851$) in Tampa Bay (Fig. 3), with slightly fewer aggregations detected during the first 3 mo of the season (39%) than the second half (44%). In all 3 zones throughout all 6 mo

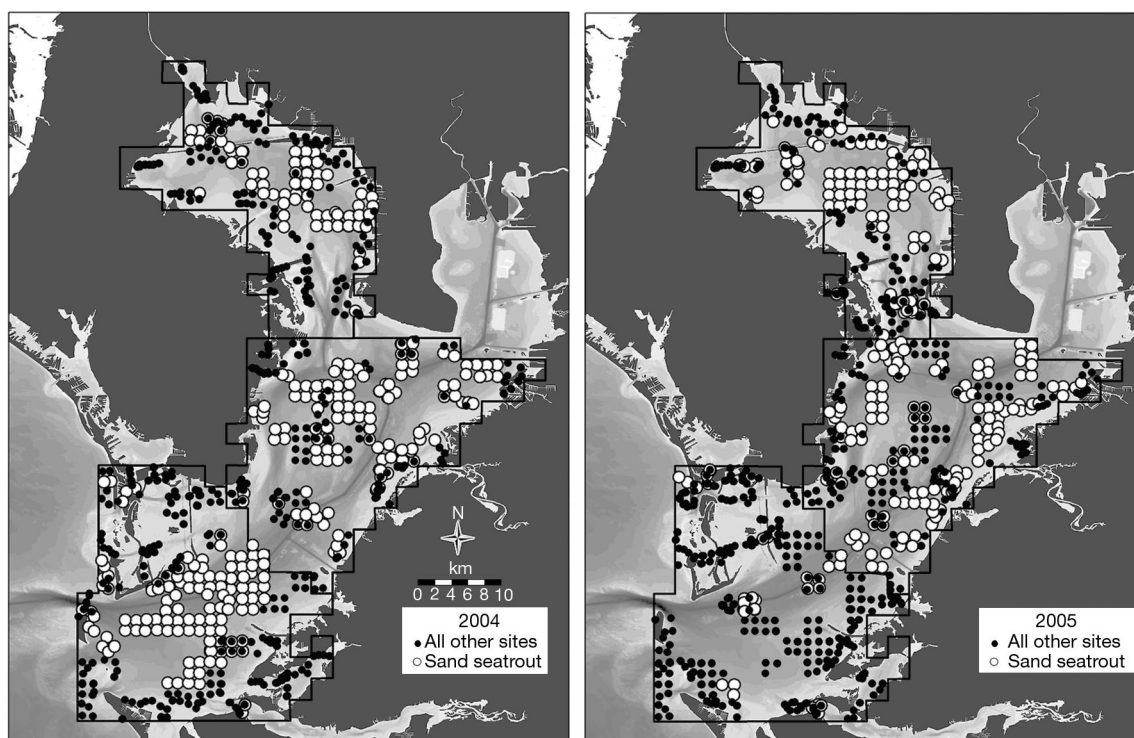


Fig. 3. *Cynoscion arenarius*. Tampa Bay hydrophone survey detections of sand seatrout aggregations (white circles) in 2004 and 2005 and all other sampled stations (black circles)

of sampling, aggregations were detected at 25% or more of the sampled stations each month (Table 2). When both years were tested together, there was a significant interaction between zone and year ($F_{2,1709} = 30.45$, $p < 0.01$) as seen in Fig. 4. For the 2004 spawning season, Zone 2 had a significantly higher occurrence of sand seatrout aggregations (51%) than did Zone 1 (35%) and Zone 3 (38%) (Fig. 4).

In 2005, the spatial distribution of sand seatrout aggregations differed from that observed in 2004. Aggregations ($n = 286$) were detected at 33% of sampled stations ($n = 864$) in Tampa Bay (Fig. 3). Significantly more aggregations occurred in Zone 1 (46%) and Zone 2 (49%) than in Zone 3 (10%) (Fig. 4). Compared to 2004, the location (Fig. 5) and frequency (Fig. 4) of aggregations shifted significantly in Zones 1 and 3, but remained static in Zone 2. Overall, more aggregations were detected in 2005 during the first 3 mo of the season (46%) than in the second

Table 2. Percentage of stations with aggregations of sand seatrout within each zone by month and year. Since zones were rotated monthly to ensure that each zone was sampled over all the lunar phases during the spawning season, certain zones were not sampled within each month (indicated by dashes)

Month	2004			2005		
	Z1	Z2	Z3	Z1	Z2	Z3
4	38	61	27	50	75	23
5	26	46	–	45	63	24
6	35	49	33	38	67	–
7	–	33	33	53	21	0
8	43	–	40	–	31	0
9	–	69	49	40	–	0

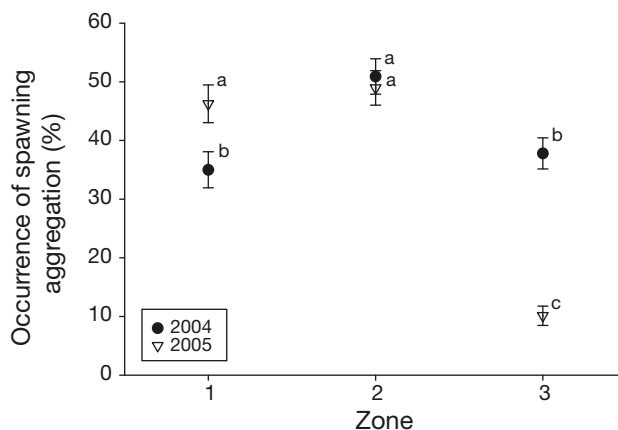


Fig. 4. *Cynoscion arenarius*. The interaction between zone and year on aggregations. Means sharing letters do not differ significantly ($p > 0.05$)

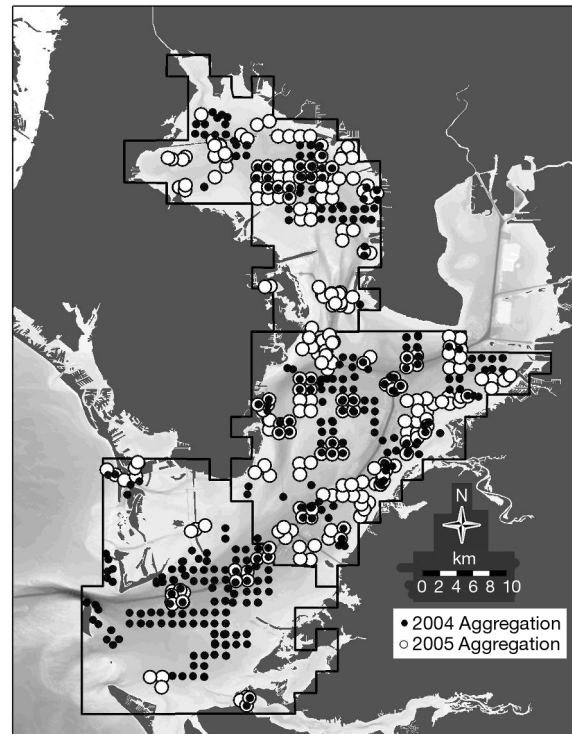


Fig. 5. *Cynoscion arenarius*. Sand seatrout aggregations detected during the Tampa Bay hydrophone survey in 2004 (black circles) and 2005 (white circles)

half (21%), a marked reduction driven by the drop in the number of aggregations in the lower 2 zones coinciding with the arrival of red tide (Table 2). While a considerable decrease in aggregations was observed in Zone 2 after the bloom's onset, it was not of the same magnitude as in Zone 3. Following the bloom, no aggregations were detected at any sampled stations ($n = 192$) in Zone 3 (Fig. 6), a substantial contrast to 2004, when the aggregations were detected at 42% of sampled stations ($n = 216$) during same months (Table 2).

DISCUSSION

Ichthyotoxic levels of *Karenia brevis* paralleled a cessation of sand seatrout aggregation sounds in Zone 3 and a reduction in the number of aggregation sounds in Zone 2 during the second half of the 2005 spawning season, but it is difficult to determine with this methodology alone whether this decline was due to fish movement, cessation of spawning activity, or mortality. Coastal waters out to a depth of 50 m were affected by red tide from January 2005 through January 2006 (Hu et al. 2006), resulting in massive fish

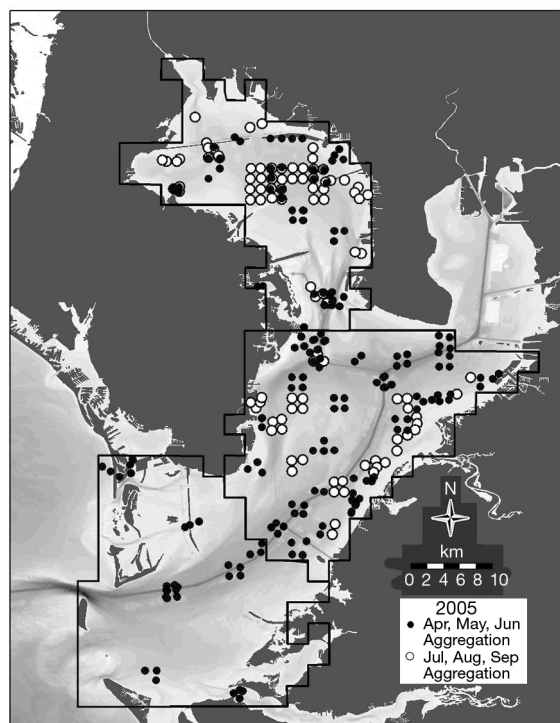


Fig. 6. *Cynoscion arenarius*. 2005 Tampa Bay hydrophone survey detections of sand seatrout aggregations before (black circles) and after (white circles) the arrival of red tide in sampled areas

kills and epibenthic community mortalities (Dupont et al. 2010). Although sand seatrout could potentially move out of the estuary and into these nearshore gulf waters, if they encountered the red tide conditions as described by Hu et al. (2006), they would likely have perished as the animals described in Dupont et al. (2010). The only potential refugia for spawning adults would have been the low-salinity areas of upper Tampa Bay, comprising Zone 1 and Hillsborough Bay, a small bay to the east (Fig. 1). Although the significant increase in aggregations in Zone 1 from 2004 to 2005 possibly indicates movement of fish from Zones 2 and 3, this increase was not adequate to compensate for the magnitude of loss measured in the areas affected by red tide. As sampling in 2005 did not include Hillsborough Bay, it is unknown if the spawning population changed considerably in this area. However, based on the significant decline in relative abundance of juvenile sand seatrout from the rivers leading into the estuary during 2005 and 2006 (Flaherty & Landsberg 2011), it is unlikely spawning adults used either Hillsborough Bay or Zone 1 as refuge. Hillsborough Bay is fed by 3 rivers that have some of the highest catch densities of juvenile sand seatrout in Tampa Bay (Purtlebaugh &

Rogers 2007). Historically, 1 of these 3 rivers, the Alafia (Fig. 1), has the greatest abundance of juvenile sand seatrout (Flaherty & Landsberg 2011). Since these rivers serve as prime recruitment areas, it would be expected to find comparable or perhaps even elevated densities of juveniles in 2005 if large numbers of adults had spawned in Hillsborough Bay or Zone 1, assuming that their larvae had been locally retained. Granted, the decline reported by Flaherty & Landsberg (2011) in juveniles in 2005 may have been due to the direct mortality of juveniles or larvae (Riley et al. 1989) if they encountered red tide as they transitioned from the more saline bay waters where they hatched to their riverine juvenile habitat. If the decline in juvenile abundance was primarily due to direct mortality while the adults survived, juvenile abundance should return to normal abundances within the following 2 yr. However, annual relative abundance for sand seatrout juveniles remained at record low numbers until 2009 (Fig. 7), indicating a disruption in the reproductive process. If sand seatrout adults had spawned without sound, migrated to another area, or skip-spawned during 2005 due to physiological stress from the red tide or because of movements to freshwater areas, this persistent annual reduction in juvenile abundance would not exist. Ultimately, the 4 yr depression in juvenile abundance along with the migration limitations previously discussed suggests that the decrease in spawning sounds in 2005 was likely attributable to adult mortality.

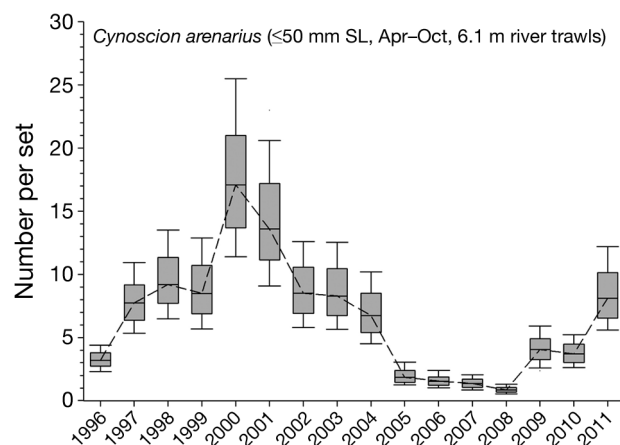


Fig. 7. *Cynoscion arenarius*. Relative abundance of juvenile sand seatrout collected from stratified-random sampling in Tampa Bay by the FIM group of FWC/FWRI. Boxes represent the 25th to 75th percentiles, error bars represent the 10th to 90th percentiles, and the line is the estimated median. SL is standard length. Fig. credit: Dr. Cameron Guenther, FWC/FWRI

Traditionally, without field observations of direct mortality, it has been difficult to prove that the absence of animals from an area during a HAB is due to direct lethal toxic exposure as opposed to behavioral avoidance. The production of bioactive or toxic products by algae during HABs, including *Karenia brevis*, is considered primarily a defense strategy, with allelopathy a common interspecific strategy, particularly in harmful phytoplankton species, for avoiding predation (Kubanek et al. 2005, Prince et al. 2008). It has also been postulated that the production of an ichthyotoxin by *K. brevis* is an opportunistic strategy used to maintain the bloom because of increased nutrient availability from recycling of decomposing fish (Walsh et al. 2009). Some HABs, e.g. nontoxic *Noctiluca* blooms, have caused significant reductions in fish populations; these were attributed to fish avoidance and direct mortality due to diminished water quality (Bhimachar & George 1950, Devassy 1989), and ichthyotoxicity was limited. Experimental data has clearly demonstrated that *K. brevis* is ichthyotoxic (Ray & Wilson 1957), but also that brevetoxin can be transferred up the food chain (Naar et al. 2007), representing another potential source of toxin exposure for sand seatrout, since toxin reservoirs are present in the system long after bloom dissipation (Landsberg et al. 2009). However, unequivocal data that would distinguish between significant and sustained fishery losses attributable to mortality from HAB toxicity and losses attributable to avoidance of an area have been difficult to obtain (Landsberg et al. 2009). In the present study, because of the spatial and temporal extents, the severity of the red tide bloom, the geographic restrictions on available refugia for adult sand seatrout, and the additional data indicating a 4 yr repression of juveniles, *K. brevis* toxicity is likely the principal cause of the reduction in spawning.

Spawning sites were located in the more central areas of Tampa Bay, increasing the adult population's vulnerability to exposure to red tide and, ultimately, most likely their mortality from it. Red tide was transported into the bay via estuary exchange flow (Weisberg et al. 2009) and concentrated within and above the dredged shipping channel (as illustrated as dark gray lines in Figs. 1, 3, 5, 6) (Havens et al. 2010). Due to this centralized transport of *Karenia brevis* into the bay, sand seatrout aggregations located in Zones 2 and 3 near the shipping channel had the greatest probability of being affected by lethal brevetoxins produced by the persistent bloom. Spawning aggregations closer to the shorelines were less strongly affected, and, because the majority of

aggregations were in the deeper areas of the bay (as observed in 2004 and the first half of the 2005 spawning season), spawning in the lower bay during the second half of the 2005 spawning season was significantly reduced due to the spatial extent of the brevetoxin. The distribution of sand seatrout spawning aggregations along these central, high-current areas would tend to facilitate transport of larvae to juvenile riverine habitats through selective tidal stream transport (E. Peebles pers. comm.). A disadvantage of this strategy, however, is the inherent risk of exposure to other passively transported particles, such as red tide cells.

The abundance of sand seatrout spawning aggregations declined considerably in Zone 3 and was reduced in Zone 2 during the red tide-affected months of 2005, but certain reproductive and life history characteristics as well as the spatial distribution of aggregations may buffer the population from long-term effects. Sand seatrout are multiple batch spawners, with individuals continuously producing eggs over the 6 mo spawning period. Studies of other species have demonstrated that a result of this reproductive strategy, fecundity is not restricted by body cavity size (Garrod & Horwood 1984), and the number of individuals in the population has a greater effect on egg production than does spawning biomass (Lowerre-Barbieri et al. 1998). No aggregations were detected in Zone 3 following the red tide; however, if sand seatrout produce larger and more viable eggs earlier during a spawning period, such as occurs in cod (Kjesbu 1989, Chambers & Waiwood 1996, Marteinsdottir & Steinarsson 1998), then individuals would have contributed their most robust eggs during the 3 mo period before spawning ceased. In addition to producing multiple batches of eggs, early maturation could increase stock resilience. Sand seatrout mature at a small size and age (Shlossman & Chittenden 1981); a sand seatrout hatched early in the spawning season could become a mature adult and spawn within that same season. Since red tide affected the population halfway through the spawning season, those larvae produced before its appearance could have safely moved into the low-salinity areas and freshwater river systems and matured. Those recruits could have developed into first-time spawners by the end of 2005 and (1) spawned in either Zone 1 or Hillsborough Bay at the end of the 2005 season or (2) spawned in any area of the bay early in the 2006 spawning season. These early-spawned fish could contribute viable eggs at a young age, rebuilding the population along with the surviving adults. Finally, despite the significant loss

in the lower bay, mortality and recruitment failure were likely reduced because spawning occurred across broad spatial and temporal scales. The advantages of dispersing the risk of larval mortality in time and space by spawning at multiple sites over an extended period has been described for Icelandic cod (Begg & Marteinsdottir 2000, Marteinsdottir et al. 2000). Spawning locations were located throughout Tampa Bay and were not restricted to the saline waters of Zones 2 and 3 where red tide was prevalent. Adults inhabiting Zone 1 or Hillsborough Bay in 2005 were presumably less affected by the red tide, providing a group of repeat spawners for the following year. Despite these strategies, it is apparent from the prolonged depression in the juvenile abundance data that it takes a relatively substantial amount of time for the population to rebound.

At lethal concentrations, *Karenia brevis* has been documented to kill a range of species and life history stages in marine waters, including sand seatrout (Steidinger et al. 1973, Riley et al. 1989, Warlen et al. 1998, Landsberg 2002). The susceptibility of different species to brevetoxin may be in part a reflection of their ecology and the distribution of their life history stages in relation to the distribution of red tide cells, extracellular toxins, or toxins vectored in the food web. Euryhaline species that spend much of their life history in lower-salinity areas out of the range of red tides are less likely to be exposed, unless environmental conditions change, as, for example, during drought years when salinities in an estuary may be higher than normal (Landsberg & Steidinger 1998, Brown et al. 2006). Alternatively, brevetoxins may be vectored or persist in the food chain during a red tide bloom (Tester et al. 2000, Naar et al. 2007) or after one has dissipated (Flewelling et al. 2005, Landsberg et al. 2009); therefore, there is the potential for long-term low-level, chronic exposure that is not necessarily lethal. The extent to which chronic exposure to brevetoxins can contribute to reduced fecundity or growth in fish populations is unclear, but the potential has been demonstrated experimentally (Colman & Ramsdell 2003). The reduction in sand seatrout spawning aggregations in certain areas of Tampa Bay in 2005 demonstrates another probable consequence of red tide's impacts on aquatic organisms, by reducing reproductive success.

This spatially explicit research provides a means to assess changes to spawning aggregations following a red tide and additional work would help substantiate the relationship further. Incorporation of circulation models to approximate the spatial and temporal interactions between spawning sites, larval trans-

port, and red tide could elucidate the relative contribution of larvae by zone and potentially lend insight on the 4 yr depression in juvenile abundance. Testing if differences exist in spawning or larval success by zone would help weigh the long-term severity of the bloom's impacts. Since this study only involves 2 yr of data, there are limitations to inferring spawning trends without having data from the post-perturbation year (i.e. 2006). The addition of long term monitoring data from another study greatly assisted in determining the dynamics between red tide, reproduction, and juveniles. Establishing baseline data, such as the annual juvenile abundance measures, can facilitate determinations of how an animal, community, or ecosystem is affected and if the effects are causal or coincidental (Rubec 1999, Steffe et al. 2007, Flaherty & Landsberg 2011). To further our understanding of the influence of environmental alterations on marine populations, we need to commit to studies with comprehensive spatial and temporal components in order to quantify losses to ecosystems. Incorporating spatially explicit environmental data into stock assessments will allow managers to account for perturbations, which conventional assessment methods were not designed to address (Rubec 1999).

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