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

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ABSTRACT

Toxic Florida red tides of the dinoflagellate *Karenia brevis* have downstream consequences of 500–1000 km spatial extent. Fish stocks, shellfish beds, and harmful algal blooms of similar species occupy the same continental shelf waters of the southeastern United States, amounting to economic losses of more than 25 million dollars in some years. Under the aegis of the Center for Prediction of Red tides, we are now developing coupled biophysical models of the conditions that lead to red tides and impacted coastal fisheries, from the Florida Panhandle to Cape Hatteras. Here, a nitrogen isotope budget of the coastal food web of the West Florida shelf (WFS) and the downstream South Atlantic Bight (SAB) reaffirms that diazotrophs are the initial nutrient source for onset of red tides and now identifies clupeid fish as the major recycled nutrient source for their maintenance. The recent isotope budget of WFS and SAB coastal waters during 1998–2001 indicates that since prehistoric times of Timacua Indian settlements along the Georgia coast during 1075, ~50% of the nutrients required for large red tides of >1 µg chl l⁻¹ of *K. brevis* have been derived from nitrogen-fixers, with the other half from decomposing dead sardines and herrings. During 2001, >90% of the harvest of WFS clupeids was by large ichthyotoxic red tides of >10 µg chl l⁻¹ of *K. brevis*, rather than by fishermen. After onset of the usual red tides in summer of 2006 and 2007, the simulated subsequent fall exports of Florida red tides in September 2007 to North Carolina shelf waters replicate observations of just ~1 µg chl l⁻¹ on the WFS that year. In contrast, the earlier red tides of >10 µg chl l⁻¹ left behind off West Florida during 2006, with less physical export, are instead 10-fold larger than those of 2007. Earlier, 55 fish kills were associated with these coastal red tides during September 2006, between Tampa and Naples. Yet, only six fish kills were reported there in September 2007. With little export of red tides and their fish prey during the former year, the computed larger nutrient-sated, fish-fed growth rates of the model's dinoflagellates also replicate satellite-observed daily increments of *K. brevis* during fall maintenance in 2006, compared to simulated smaller fish-starved growth rates of decanted red tides during fall 2007. During the last few decades, *K. brevis* has remained a "prudent predator" of some clupeids, i.e. Spanish sardine, whereas humans have now overfished other Florida stocks of both thread herring and Atlantic shad. Thus, future operational forecasts of the land falls and durations of Florida red tides, from Louisiana to North Carolina, as well as prudent management of regional fisheries of the southeastern United States, require consideration of neglected fish losses, at intermediate trophic levels, to algal predators. Some clupeids are harvested by *K. brevis*, but these fish are separately supported by a longer parallel diatom-based food chain of calanoid copepods, feeding the zooplanktivores and thence other piscivore fish predators, while intersecting the shorter food chain of just diazotrophs and red tide dinoflagellates, poorly grazed in turn by harpacticoid copepods. The distinct phytoplankton functional groups, different herbivores, as well as zoophagous and piscivore fishes, must all be formulated as explicit state variables of the next set of complex ecological models, cued by satellite data and driven by nested circulation models, within an ecosystem-based management paradigm of commercial and sport harvests of biotic marine resources at higher trophic levels of the WFS and SAB.

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1. Introduction

Red tides of the fish killing dinoflagellate, now known as *Karenia brevis* and previously as *Ptychodiscus brevis = Gymnodinium breve*, are not new Florida phenomena. The ichthyotoxic dinoflagellate was identified more than a half century ago (Davis, 1948), when the number of dead fish then harvested by *K. brevis* during 1947 (Gunter et al., 1948) amounted to half of the recent commercial and recreational yields of fish from the West Florida shelf (WFS) during 2007, in the eastern Gulf of Mexico. Clupeid corpses of round scad, scaled sardine, and Gulf menhaden, as well as the dead piscivores, black and warsaw groupers, were among the estimated 50 million fish killed during the 1946–1947 red tides on the WFS (Gunter et al., 1947, 1948). Indeed, one can also infer that earlier red tides were found off the southeast Texas coast during 1529–1534 (Cabeza de Vaca, 1542), in the western Gulf of Mexico.

This survivor of the Narvaez expedition then wrote that despite their use of fish traps, the Capoque and Han Indians "do not have fish apart from this period … in November and December" (Adorno and Pautz, 1999). Their shellfish harvest in 1529 was also suspended seasonally (Cabeza de Vaca, 1542) around Galveston Bay, where he noticed that from Galveston Island "canoes crossed to the mainland to certain bays that had many oysters. And for three months of the year they eat nothing else … until the end of April, when we went to the seacoast where we ate blackberries the entire month". A few years later, along the South Texas coast, he also noted in 1534 that the Avavares Indians near the Nueces River estimated seasonal changes by "the times when the fruit comes to mature and when the fish die" (Adorno and Pautz, 1999).

Such red tides of *K. brevis* are not just restricted to the Gulf of Mexico. More recent red tides of *K. brevis* and its congeneric species *K. papilionacea* were discovered in the Mid Atlantic Bight (MAB), as Florida exports of both *Karenia* spp. (Brown et al., 2006) among the phytoplankton community on the Delaware shelf during September 2007. For example, by 6 September 2007, an equivalent chlorophyll biomass of ∼3.0 µg chl l^{-1} of an intermediate red tide of *K. papilionacea* was found by both ship, and satellite, at the mouth of Delaware Bay. There, the initial red tide of *K. brevis* was then instead only ∼0.2 µg chl l^{-1}, but it also represented another exogenous phytoplankton import of upstream origin, like North Carolina fish larvae found in the MAB (Warlen et al., 2002).

As part of this same 2007 export event, concentrations of *K. brevis* exceeding 10.0 µg chl l^{-1} of a large red tide, were later observed by aircraft (Fig. 1), satellite, and ship farther south, along Jacksonville Beach of Duval County, Florida on 27 September 2007, with associated local beach closures. Earlier, during 10–13 September 2007, other small populations of <1.0 µg chl l^{-1} of *K. brevis* and *K. papilionacea* were found by us along the WFS coast, between Tampa and Fort Myers, FL (Fig. 2), which is the major red tide epicenter (Walsh et al., 2006). To put these different sizes of small (∼1 µg chl l^{-1}) and large (∼10 µg chl l^{-1}) Florida red tides in perspective, background seed populations of *K. brevis* in the open Gulf of Mexico are ∼0.01 µg chl l^{-1}.

Such downstream exports of WFS red tides are also not new events. Eastward decantations of *K. brevis* blooms were inferred during 1972 (Murphy et al., 1975), 1976, 1983, 1987 (Tester et al., 1991), and 1990 (Tester et al., 1993). Moreover, it was observed even earlier during 1886 that "An oily scum"(Knowles, 1887) … 'probably consisting of great masses of plankton' (Brongersma-Sanders, 1957) … "extends for several miles out to sea, and affects the rivers for a long distance inland … Fish are … floating like chips on the surface of the water" … "the scum is found, and the coast is strewn with dead fish all the way"(Knowles, 1887), from the South Carolina border to within 10 miles of Cape Fear.


Fig. 1. FWRI photographs during 2007 of a precursor bloom of *T. erythraeum* within the offshore WFS red tide epicenter on (A) the 40 m isobath of clearer waters on the Florida Middle Ground (4/4/07) in relation to (B) a downstream bloom of *K. brevis* off Jacksonville Beach (9/28/07).

One hundred years later, a red tide of >1 µg chl l^{-1} of *K brevis* was found in these same North Carolina coastal waters in 1987 (Tester et al., 1991; Tester and Steidinger, 1997), within the South Atlantic Bight (SAB). When analyzed over the period of 1987–1992, these red tides of WFS origin accounted for roughly half of the annual average economic loss to the United States, estimated then to be a total of ∼49 million dollars (Anderson et al., 2000).

Other possible hints of earlier exports of WFS red tides were recorded by Jonathan Dickinson, a British sailor shipwrecked along the east coast of Florida during 1696. He observed dead fish on the seaward side of the barrier island to the north of Jupiter Inlet during 28 September 1696 as an "abundance of small fish … being much tainted … covered the shore for nigh a mile in length … 27° 45 min." (Andrews and Andrews, 1945). Within this same region, about 300 years later, respiratory irritations, red tides, and kills of baitfish were described on 8–20 November 1972 as an export of WFS red tide to the east coast of Florida (Murphy et al., 1975), when only a small red tide of ∼1 µg chl l^{-1} was left behind on the WFS (Fig. 2).

Compared to background levels of *K. brevis* in the open Gulf of Mexico of ∼0.01 µg chl l^{-1}, or small red tides of ∼1 µg chl l^{-1}, a large red tide of 10 µg chl l^{-1}, within just the upper 5 m of the euphotic zone of the WFS, requires an equivalent dissolved nitrogen inventory over the water column of 20 mmol N m^{-2} (Walsh and Steidinger, 2001). Yet, over the 50 m deep water column of the mid WFS, the mean nitrate depth integral was only 3.1 mmol NO$_3$ m^{-2} during four years of 1998–2001 (Vargo et al., 2008), compared to ∼20,300 mmol N$_2$ m^{-2} (Weiss, 1970).

An intermediate pool of dissolved organic nitrogen (DON), including urea as a favored source of red tide nutrition (Baden and Mende, 1979; Steidinger et al., 1998), then amounted to 477 mmol DON m^{-2} (Vargo et al., 2008). But, not all of the WFS DON is labile, readily available to the phytoplankton for growth as external estuarine supplies of DON (Jolliff et al., 2003). Moreover, at the mouths of the WFS estuaries, e.g. Tampa Bay, the ni-
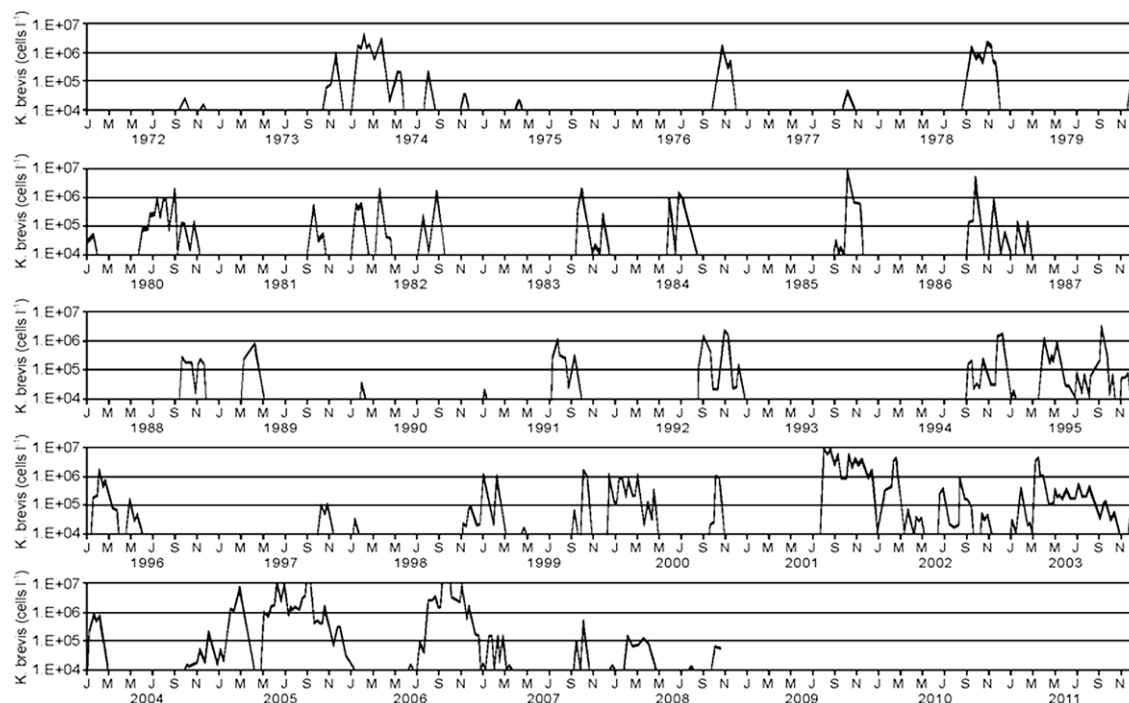
Fig. 2. A time series of the alongshore mean weekly abundance (cells l^{-1}) of *Karenia brevis* found at the surface during 1972–2008, within 9 km of the coast, between Tampa and Naples. It provides a 35-year record of interannual variation of intensity and duration of red tides within these coastal waters, with known eastward summer decantations during 1972, 1977, 1987, 1990, and 2007, thence leaving behind only small autumn amounts of these toxic dinoflagellates at the bottom of the WFS food web. Note the relative sizes, as well as durations of the 2006 and 2007 events. Here, 1×10^5 cells l^{-1} = 1 µg chl l^{-1}.

trate stocks during 2001 were 0.6 µmol NO_3 kg^{-1}, compared to 0.9 µmol PO_4 kg^{-1}, in a molar N/P ratio of 0.7 (Vargo et al., 2008), much smaller than the Redfield N/P ratio of ~16.0, required for balanced phytoplankton growth.

Thus, the major "new" nutrient supply for onset of Florida red tides had been hypothesized as iron-rich Saharan dust stimulation of nitrogen-fixation by *Trichodesmium erythraeum* of the ubiquitous dissolved dinitrogen gas at the shelf-break edge of the WFS (Walsh and Steidinger, 2001). There, the dissolved nitrate, phosphate, iron, and silicate ratios usually do not promote blooms of diatom competitors of the phytoplankton community.

This chemical milieu on the outer WFS instead favors the diazotrophs, fixing N_2, and subsequent transfer of recycled nutrients in the form of labile amino acids of DON and NH_4, from *T. erythaeum* to *K. brevis,* upon deposition of mineral aerosols at the sea surface (Walsh et al., 2003, 2006; Lenes et al., 2001, 2005, 2008). Increased global desertification, as in the Gobi and Sahara Deserts over the last century, may now be leading to larger red tides of greater spatial extent of those toxic dinoflagellates, which depend upon these precursor iron-starved diazotroph sources of recycled nutrients, beneath downstream regions of atmospheric dust plumes (Jickells et al., 2005).

Moreover, despite early suggestions of a dead fish source of nutrients (Wilson and Collier, 1955), after red tide initiation, the sources of additional recycled nutrients for continued maintenance of these harmful algal blooms remained unknown (Vargo et al., 2008). Yet, more recent studies confirmed that as much as 50% of some decomposing Florida fish are returned as dissolved nutrients of NH_4 and PO_4, at summer temperatures, during one day (Stevenson and Childers, 2004). We had also found ~5 µmol NH_4 kg^{-1} and ~0.2 µmol PO_4 kg^{-1} next to dead fish on the WFS during October 2001 (Vargo et al., 2008). Accordingly, we examine here the isotopic evidence for diazotroph and dead fish sources of recycled nitrogen, involving both the onset and maintenance of Florida red tides during 1998–2001 (Fig. 2), in relation to their simulated export and

growth rates during the subsequent years of 2006 and 2007 (Fig. 1).

The consistent mass fractionation of nitrogen isotopes during plankton and nekton metabolism leads to loss of the lighter isotope, ^{14}N, resulting in more positive, heavier $\delta^{15}N$ values of a relative ~+3.0‰ increment per higher trophic level of the marine food web (Minagawa and Wada, 1984; Peterson and Fry, 1987; Walsh et al., 1989). The metazoans excrete the lighter ^{14}N and accumulate heavier ^{15}N in their body tissues.

But, the actual value of the isotope ratio of $^{15}N/^{14}N$ at the base of the marine food web depends upon what mixture of dominant dissolved nitrogen sources initially fueled the phytoplankton at this lowest trophic level. Depending upon the number of trophic steps of a local marine food chain, from subtropical to polar regions (Walsh et al., 1989), the top predators exhibit monotonic increases of ~+3.0‰ $\delta^{15}N$ per food transfer through primary producers, herbivores and multiple levels of carnivores, including marine subsistence human hunters.

For example, within the aphotic source waters for the successive western boundary currents [Guiana, Antilles, Loop, Florida Currents, and the Gulf Stream] of the North Atlantic Ocean, the $\delta^{15}N$ value (Table 1): of nitrate is +5‰ (Altabet and McCarthy, 1985; Liu and Kaplan, 1989; Loepz Veneroni, 1998; Montoya et al., 2002); compared to dinitrogen gas of +0‰ (Macko et al., 1984); and ammonium of −3.0‰ (Checkley and Entzeroth, 1985; Cifuentes et al., 1988). As usual, $\delta^{15}N$ is defined here by [$^{15}N/^{14}N$ of sample/ $^{15}N/^{14}N$ of air standard − 1] 1000.

All phytoplankton descriminate between the heavier ^{15}N and lighter ^{14}N isotopes of dissolved inorganic nitrogen (DIN), as well. The resulting microalgae thus have more ^{14}N, compared to ^{15}N, than the isotope ratio of the unutilized components of the DIN (NO_3, NH_4, and N_2), left behind in marine waters. Prior observations within the Gulf Stream yielded a fractionation factor, β, for nitrate assimilation by phytoplankton of 1.004 (Altabet and McCarthy, 1985), similar to more recent culture studies of diatoms (Waser

Table 1
A nitrogen isotope budget, $\delta^{15}N$ (‰), of the food web on the southeastern US shelf.

Dissolved source			
N_2 (+0.0)[1]	NO_3 (+5.0)[2,3,4]	NH_4 (−3.0)[1,5]	Urea (+3.0) = sum of equal amounts of diazotroph (−0.5) and Clupeid (+3.5) recycled sources
Phytoplankton			
Diazotroph (−1.0)[6,7]	Diatom (+1.0)[4]	Flagellate (+6.0)[8]	WFS 1998–2001 mean PON + 3.0 (*Karenia brevis* blooms)
Herbivore			
Harpacticoids (+2.0)[10]	Calanoids (+4.0)[11,12]	Zooplankton (+9.0)[5,6]	xxxxxxxxxxxx
Zooplanktivorous fish			
xxxxxxxxxxxx	Herring-sardine (+7.0)[13,14]	Menhaden (+12.0)[15]	xxxxxxxxxxxx
Piscivore fish			
xxxxxxxxxxxx	King mackerel, vermillion snapper (+10.0)[16,17]	xxxxxxxxxxxx	xxxxxxxxxxxx
Human harvester			
xxxxxxxxxxxx	St. Catherines (+12.8)[18]	xxxxxxxxxxxx	xxxxxxxxxxxx

Based on the literature, isotopic fractionation of dinitrogen gas[1], nitrate[2,3,4], ammonium[8], and urea[9] by the phytoplankton functional groups are assumed to be, respectively, 1, 4, 9, and 0‰ of $\delta^{15}N$. The realized trophic transfer of $\delta^{15}N$ of 3.0‰, by herbivores, zooplantivores, piscivores, and top human predators on St. Catherines Island, GA, before they ate maize (Schoeninger et al., 1983), of this budget is based also upon the observed body nitrogen isotopic contents of $^{15}N/^{14}N$, expressed as $\delta^{15}N$ within the WFS, SAB, or other ecosystems, next to western boundary currents.

[1] Miyake and Wada (1967).
[2] Liu and Kaplan (1989).
[3] Lopez Veneroni (1998).
[4] Altabet and McCarthy (1985).
[5] Checkley and Entzeroth (1985).
[6] Macko et al. (1984).
[7] Saino and Hattori (1987).
[8] Cifuentes et al. (1988).
[9] Waser et al. (1998).
[10] Wada and Hattori (1976).
[11] Checkley and Miller (1989).
[12] Montoya et al. (2002).
[13] Sullivan and Moncreiff (1990).
[14] Fry (1988).
[15] Deegan et al. (1990).
[16] Roelke and Cifuentes (1997).
[17] Thomas and Cahoon (1993).
[18] Schoeninger et al. (1983).

et al., 1998). In contrast, other phytoplankton fractionate ammonium, with β of 1.009 (Cifuentes et al. 1988), compared to β of 1.001 for diazotrophs assimilating N_2 (Wada and Hattori, 1976; Saino and Hattori, 1987).

Thus, marine phytoplankton grown solely on nitrate, dinitrogen gas, or recycled ammonium (Table 1), should have respective $\delta^{15}N$–PON values of +1‰, −1‰, or +6‰ within their particulate organic nitrogen (PON). Here, we report our measurements of the $\delta^{15}N$–PON of suspended particulate matter within surface waters of the inner WFS (<50 m depth) during September–December 1998–2001.

These WFS phytoplankton, in turn, are consumed by copepod, protozoan, and macrobenthic herbivores and by bacterial ammonifying saprovores. The two intermediate trophic levels recycle some of the nitrogen locally as ammonium and urea, with phosphorus in the forms of DOP (dissolved organic phosphorus) and phosphate, while passing energy to zooplanktivore chaetognath, jelly, and fish primary carnivores. However, the fish are not just predators of these coastal ecosystems, eating zooplankton and other fish, but are also a source of nutrients for the ichthyotoxic dinoflagellates.

Recall that in the vicinity of dead fish on the WFS during 2001, we found as much as 5 μmol NH_4 kg^{-1} (Vargo et al., 2008). If the recycled body nitrogen of decomposing zooplanktivore dead fish, killed by nearby *K. brevis*, is a significant source of nutrients for subsequent red tides, compared to zooplankton and macrobenthos herbivores at a lower trophic level, the $\delta^{15}N$–PON signature of the toxic dinoflagellates over time, should also increase, reflecting a shift of predominant recycled nutrient origin, from diazotrophs

to dead fish. If predation by *K. brevis* is a significant process, time series of commercial WFS fish stocks, as reflected (Gulland, 1983) in their relative Catch Per Unit Effort (C.P.U.E.)s, should also mirror changing harvests by the various piscivores: other fish; *K. brevis*; and adjacent humans.

Zooplanktivorous clupeid fish are the dominant intermediate members of the WFS marine food web, now harvested by: (1) humans, as baitfish; (2) other fish, i.e. groupers, mackerels snappers, and drums, as piscivores; and (3) red tides, as a supplemental source of recycled nutrients, on the WFS. The Spanish sardine, *Sardinella aurita*, is one of the most abundant clupeids on the WFS, based: on larval surveys (Houde et al., 1979; Ditty et al., 1988); commercial landings reported to FWRI; and fishery-independent, acoustic-assisted trawl catches (Pierce and Mahmoudi, 2001; Mahmoudi et al., 2002). It is mainly a summer spawner (Houde et al., 1979; Ditty et al., 1988, 1994), with the same adult populations extending from the Florida Panhandle downstream to at least off Charleston, South Carolina (Kinsey et al., 1994). Larval survival of *S. aurita* may thus be impacted by summer red tides, unlike that of the spring spawning clupeids, e.g. thread herring *Opisthonema oglinum* (Houde et al., 1979).

During 17 cruises to the WFS in 1971–1974 (Houde and Chitty, 1976; Houde, 1977a–c; Houde et al., 1979), monthly assessments were made of the abundances of fish eggs and larvae, as well as the adult forms of their zooplankton prey. Within the red tide epicenter, between coastal waters off Tampa and Naples, FL (Fig. 2), the zooplankton stocks were 10-fold less during November 1973, when a large red tide of >10 μg chl l^{-1} was observed there

(Fig. 2), than in 1972 during a small red tide of <1 μg chl l^{-1} (Fig. 2). A similar 10-fold variance of coastal zooplankton abundance was also found, between October 1998 (Sutton et al., 2001) and 1999 (Lester, 2005) on the WFS, during these respective small and large red tides (Fig. 2).

The near shore ichthyoplankton community exhibited the same interannual reduction of abundance during November 1972 and 1973 (Houde and Chitty, 1976), at a time of year, when summer spawners would be most susceptible to recruitment failure during red tides. During three days after hatching, post yolk-sac larvae of S. aurita must begin feeding on the younger stages of such coastal zooplankton (Ditty et al., 1994) at WFS surface temperatures of >30 °C (Walsh et al., 2003). A month earlier, during 22 October 1973, this red tide was first observed 5–15 km offshore of the coast, between Tampa and Fort Myers, FL. A subsequent massive fish kill was then found at the shoreline of Boca Grande, FL by 29 October 1973 (Habas and Gilbert, 1975).

Cardiac arrest of the pre-juvenile, transparent larval phases of bay anchovy, Anchoa mitchilli, was also observed during this large WFS red tide of 1973 (Quick and Henderson, 1975). Furthermore, A. mitchilli is one of the dominant clupeids within both the Tampa Bay environs (Peebles et al., 1996; Peebles, 2002) and downstream Biscayne Bay (Houde and Alpern Lovdal, 1985) on the Florida east coast. It also serves as an important intermediate member of the coastal food web, farther north within both the SAB and MAB (Scharf et al., 2002).

Note, moreover, that the small red tide, left behind on the WFS, during fall 1972 (Fig. 2) was instead associated with an export of K. brevis to the east coast of Florida that year (Murphy et al., 1975). No fish kills were related to red tides on the WFS during 1972. Whereas in 1973, red tide-related fish kills were found even within Tampa Bay – as during 1971 (Steidinger and Ingle, 1972). In 1971, another large red tide again prevailed along the West Florida coast (Walsh and Steidinger, 2001), like in 1973 (Fig. 2).

Farther downstream, within the SAB off Jacksonville, FL, spawning runs of another clupeid, the American shad Alosa sapidissima, persist from November to March. Total shad landings along the US Atlantic coast had declined 10-fold, between 1895 and 1960 (Walburg and Nichols, 1967). But, a maximum biomass persisted at the mouth of the St. Johns River during January of most years (Walburg, 1960), after 2–3 years spent as juveniles and adults within the adjacent SAB. During the subsequent January 1973, after fall export of red tide in 1972 (Murphy et al., 1975), the C.P.U.E. of A. sapidissima near Palatka, FL, within the tidal portion of the St. Johns River, was ~75% of that during January 1972 (Williams et al., 1975; McBride, 2000).

Before then, minimal export of the WFS red tide had instead occurred during fall of 1971, when a larger red tide was left behind that year off the West Florida coast (Fig. 2), like in 1973 (Walsh and Steidinger, 2001). A fishery for this largest clupeid, A. sapidissima, began near the mouth of the St. Johns River at Mayport, FL, in 1858 (Walburg, 1960), became stressed by 1970 (Williams and Bruger, 1972), and no longer provides commercial yields (McBride, 2000). As a sentinel for the consequences of both upstream exports of WFS red tides and local overfishing, interannual changes in relative spawning of American shad within the St. Johns River, after growth on the adjacent downstream SAB, reflect inferred ecological teleconnections between the WFS and the SAB (Tester and Steidinger, 1997). Thus far, however, no explicit simulation models have linked the plankton dynamics of these two regions.

Yields of the local dominant WFS clupeids, O. oglinum and S. aurita, to other human predators, for example, also declined, respectively, during the large 1995 red tide (Fig. 3) to 48% and 17% of those catches obtained from the WFS in 1994. Note that FWRI records also indicate the 1995 harvests of Atlantic shad, A.

sapidissima, another clupeid, declined by an even larger amount, to 10% of their 1994 yield.

Subsequently, commercial harvests of S. aurita from the WFS declined by 70%, from an average yield of 3.1 million pounds during 1986–1994 to a mean annual catch of 0.9 million pounds during 1995–2002 (Mahmoudi et al., 2002). The latest landings were 1.2 million pounds during 2007 (Fig. 3). Conventional wisdom suggested that the estimated potential yield of S. aurita to the purse seine fishery off west-central Florida should have been 1.5–2.2 million pounds during 1999 and 2000, i.e. 2–3 times the realized catches (Fig. 3).

Despite fishing bans and gear restrictions since 1992, moreover, fishery-independent trawl surveys on the WFS during each spring (March–April) of 1994–2002 found no increases of the estimated clupeid stocks of either S. aurita or O. oglinum, upon reduction of their fishing losses. Thus, other loss factors, in addition to human harvests, may effect population abundances of these dominant WFS baitfish (Pierce and Mahmoudi, 2001; Mahmoudi et al., 2002), i.e. predation by K. brevis.

After S. aurita, the next most abundant coastal clupeid on the WFS is O. oglinum. But, it is mainly a spring spawner (Houde, 1977b). Before closure of the fishery for S. aurita off Tampa Bay in 1992, O. oglinum was already a collateral target of the purse seiners, with 7.5 million pounds of thread herring caught during 1989 (Fig. 3). Presumably, just continued fishing pressure reduced the WFS yields of the spring spawning O. oglinum, from a mean of 2.2 million pounds during 1995–2001 (Mahmoudi et al., 2002) to 0.1 million pounds by 2007 (Fig. 3).

Yet, after a series of two successive years of red tides of >10^6 cells l^{-1}, or >10 μg chl l^{-1}, of K. brevis during 1984–1985, 1994–1995, and 2005–2006 (Fig. 2), the commercial yields of both the summer spawner S. aurita and spring spawner O. oglinum then fell by more than 50% during the subsequent years of 1985, 1995, and 2006 (Fig. 3). One could thus infer that it was mainly over fishing, rather than impaired larval survival of the summer versus spring spawning clupeids, which led to declines of the WFS stocks of both S. aurita and O. oglinum over the last decade. But, an independent estimate of red tide mortality of the clupeids, as well as their fishing mortality (Fig. 3) and consumption by fish predators (Okey and Mahmoudi, 2002), is required.

Here, we first use an isotope budget along coastal waters of the southeastern United States to estimate both the trophic status of the clupeid fish and the amount of their ^{15}N-labelled contribution, over time, to the seasonal nitrogen nutrition of WFS red tides. We thus place our own phytoplankton isotope data over 1998–2001 within the context of the upstream WFS and downstream SAB contiguous food webs of similar structure. If the recycled nitrogen of dead fish origin is a significant nutrient source for maintenance of red tides, then the inferred predation rate by the dinoflagellates must also be considered by future resource managers of these coastal regions. We then contrast fish-fed and fish-starved WFS red tides of maximal and minimal growth rates, during respective small and large physical exports of K. brevis to the downstream SAB, in 2006 and 2007.

Other piscivore fishes, for example, such as king mackerel Scomberomorus cavalla, vermillion snapper Rhomboplites aurorubens, and red drum Scianenops ocellatus, also eat the smaller clupeid fish as secondary carnivores, with characteristic elevated δ^{15}N–PON signatures of the higher trophic levels (Thomas and Cahoon, 1993; Roelke and Cifuentes, 1997). They are in competition with the local red tides and the fishermen. These other fish data of our budget (Table 1) thus provide an isotopic constraint on the clupeid versus diazotroph contributions to the seasonal nutrition of the resultant WFS red tides, labelled by the measured ^{15}N/^{14}N ratios of their own cellular PON (Particulate Organic Nitrogen).
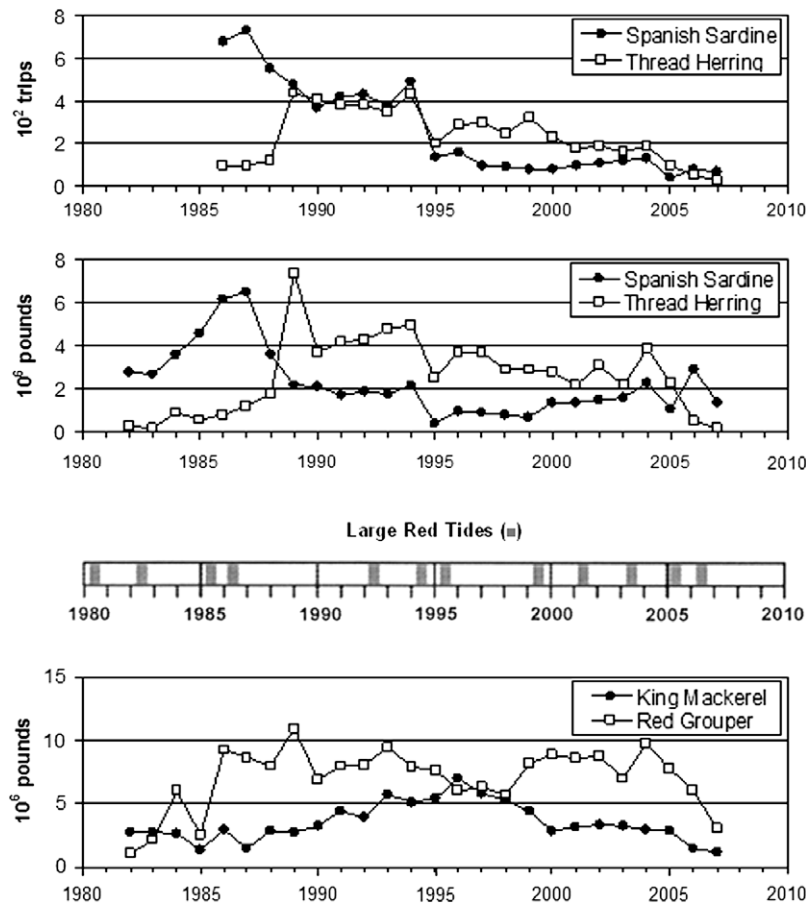
Fig. 3. A time series of yearly zooplanktivore and piscivore fish landings from the WFS during 1982–2007. It provides a 25-year record on the fishing effort (10^2 trips year^{-1}) and commercial landings (10^6 pounds yr^{-1}) of spanish sardine, *Sardinella aurita* (●), and of thread herring, *Opisthonema oglinum* (□), in relation to both large red tides of >10 μg chl l^{-1} of *K. brevis* (■) and the sum of concurrent commercial and recreational harvests (10^6 pounds year^{-1}) of red grouper, *Epinephelus morio* (□) and king mackerel, *Scomberomorus cavalla* (●) during 1982–2007 at the top of the WFS food web.

In turn, some of the piscivore fish, as well as mullet detritivores, were consumed by humans, acting as subsistence tertiary carnivores along St. Catherines Island, Georgia during preColonial times in 1075. These last δ^{15}N–PON data of surviving relict bone collagen thus represent an Indian diet of mainly marine food, before their utilization of maize (Schoeninger et al., 1983). This prehistoric coastal habitat of the SAB was then presumably downwind of persistent summer Saharan dust loadings (Jickells et al., 2005), as first suggested by Darwin (1839).

In contrast, other contemporary bone residue δ^{15}N–PON data are also available for marine subsistence inhabitants of Santa Cruz Island during ~1150, within the California Current (Walker and DeNiro, 1986). The latter prehistoric habitat of these contemporary southern California Indians is instead now rarely visited by either Saharan, or Gobi, Desert dust storms (Jickells et al., 2005). These offshore Indians also did not eat maize, as did other Indian populations of the same prehistoric era on the California mainland (Walker and DeNiro, 1986).

Red tides have a very long recorded history off the west Florida coast, with the first red tide of *K. brevis* documented in 1844 (Feinstein, 1956). The first scientific report of respiratory irritation from a Florida red tide was not written until 1917 (Taylor, 1917), when the first death of *S. aurita* from red tide was also noted. But, other red tides were found during 1854, 1878–1879, and 1886, as inferred from descriptions of "dead fish in ... poisoned water ... of a reddish" and "red brick color" with "oysters ... in Tampa... spoiled" ... "and clams ... of Sarasota Bay ... of a repulsive green hue at their edges" (Porter, 1879; Glazier, 1880; Ingersoll, 1881).

Over 150 years later, extensive documentation of the spatio-temporal chronologies of Florida red tides (color + backscatter = phytoplankton biomass, as well as diazotroph and red tide components) and their causal factors (dust = atmospheric iron loading; temperature = coastal upwelling) is now provided by a suite of daily observations from orbiting NASA and NOAA satellites. Upon completion of the isotope budget, we thus use dust, thermal, and color data from these satellites to estimate onset and maintenance of the 2006 and 2007 red tides on the WFS, in relation to physical export within simulation models of both the particle trajectories and the growth of populations of *K. brevis*.

Red tides begin the same way each summer on the WFS. On-shore transports of entrained near-bottom seed populations occur within the bottom Ekman layer, of the co-occurring migratory diazotrophs and dinoflagellates, during wind-forced, coastal upwelling – as indicated by cold sea surface temperatures [http://fermi.jhuapl.edu/avhrr] along the coast (Fig. 4a). Seasonal nutrient transfers between the two groups of phytoplankton are triggered, after arrival of Saharan dust above outer shelf waters (Fig. 4b). Here, the slow growing diazotrophs (Fig. 4c), overlying the toxic dinoflagellates of similar slow growth rates (Fig. 4d), can successfully compete against the faster growing, silica-requiring diatoms of coastal waters (Walsh et al., 2003, 2006; Lenes et al., 2008). Along the 10 m isobath of the WFS during August 2006 and 2007, the observed near-surface populations of the sun-adapted diazotrophs, with 3- to 4-fold larger light saturation intensities than the red tides (Walsh et al., 2001), were underlain by co-occurring initial subsurface populations of dark-adapted *K. brevis*. With-
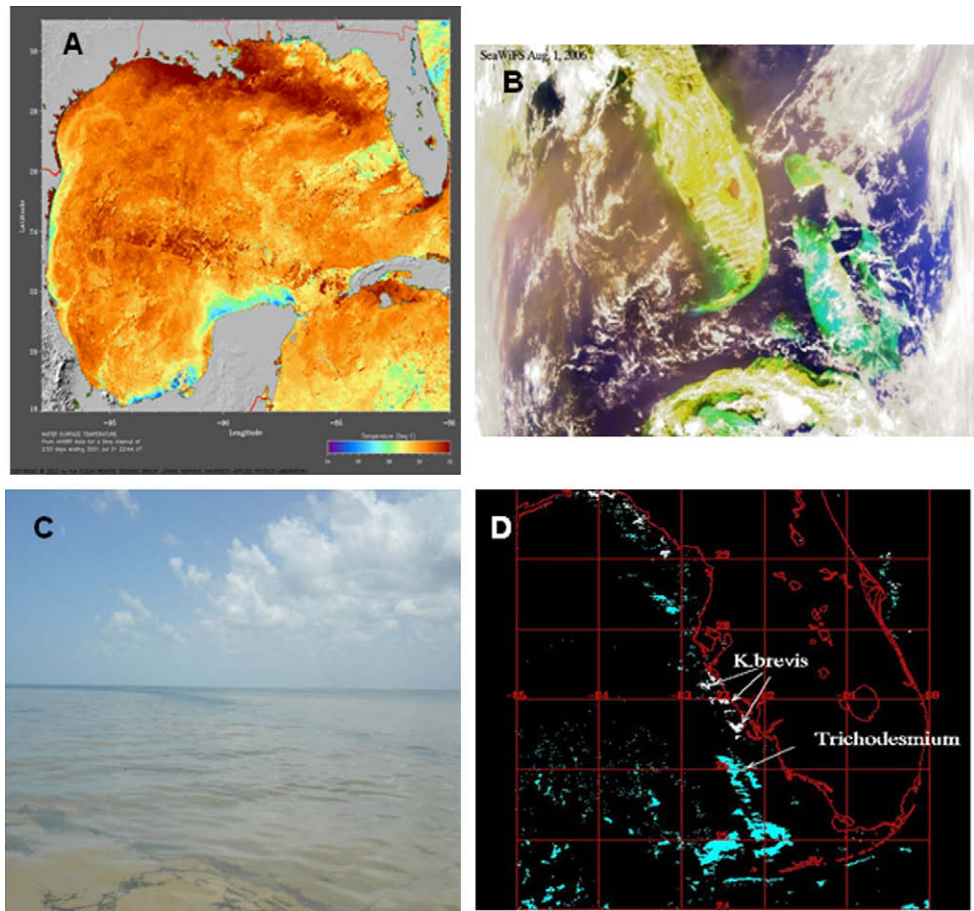
Fig. 4. Satellite estimates of (A) upwelled water off Charlotte Harbor, FL on 31 July 2006 [courtesy of Applied Physics Laboratory, Johns Hopkins University] and of (B) Saharan dust on 1 August 2006 in relation to (C) *in situ* and (D) satellite observations of *Trichodesmium* over the same region on 8–9 August 2006.

in these CDOM-rich coastal waters (Walsh et al., 2003), both *T. erythraeum* populations and CDOM serve as initial sun screens, until *K. brevis* photo-adapts (Shanley and Vargo, 1993) to higher light conditions of near-surface waters (Carder and Steward, 1985).

During 22–29 July 2006, for example, a sequence of imagery from the NASA OMI satellite sensor of atmospheric mineral aerosols detected transport of Saharan dust (Fig. 4b), from northwest Africa across the Atlantic Ocean and into the Gulf of Mexico (Carder et al., 2007). Similar westward propagating Saharan dust storms were also observed by NASA satellites during July 2008, 2007 (http://jwocky.gsfc.nasa.gov), 2005 (Hsu et al., 2007), 2001 (Walsh et al., 2006), and 1999 (Lenes et al., 2001, 2008). Within the surface Ekman layer, the usual near-surface biotic signals of the end results of such upwelling and dust stimulation are offshore transports of surface populations of *K. brevis* – seen by the satellite color signal during August 2001 (Fig. 5), as part of the large coastal red tide that year (Fig. 2).

During other years, stronger upwelling, as shown on 7 September 2005 by some of our daily satellite-tracked surface drifters (Fig. 6), led to eventual termination of those fall coastal WFS red tides. As monitored by FWRI, a 10-fold decline of the mean weekly alongshore cell counts of *K. brevis* populations then occurred within 9 km of the coast, representing an equivalent biomass reduction of ~100 to 10 µg chl l^{-1}, during early September 2005 (Fig. 2). A similar decline of *K. brevis* biomass occurred in September 2001, but the near shore populations were then replenished, until December of that year (Fig. 2).

Here, we test the hypothesis that small offshore summer/fall transports during 2006, allowed accumulation of large populations
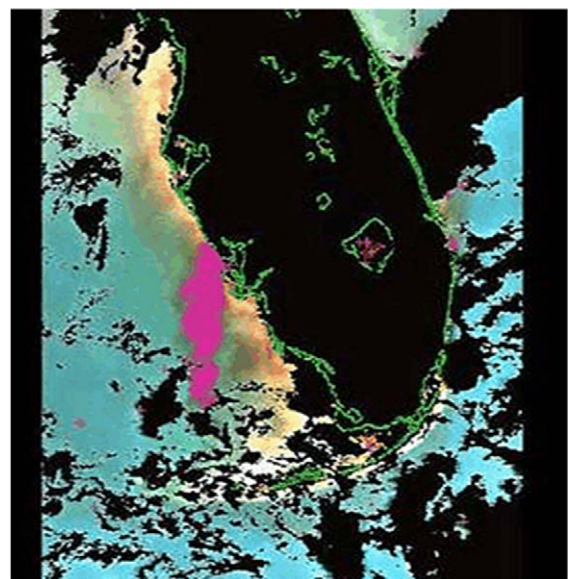
Fig. 5. A SeaWiFS satellite estimate of red tide export from the West Florida shelf on 30 August 2001, where the pink color denotes population levels of >0.1 µg chl l^{-1} of *K. brevis*.

of *T. erythraeum* (Fig. 7) and of *K. brevis* (Fig. 8), with associated fish kills (Fig. 9), promoting enhanced ichthyotoxic dinoflagellate growth rates during the fish-fed maintenance phase on the
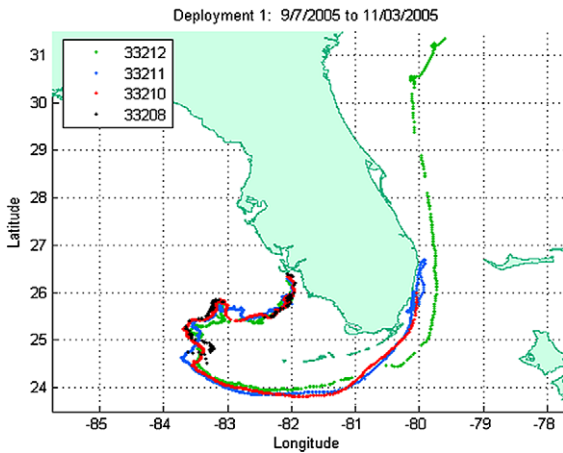
Fig. 6. Subsequent daily trajectories during 7 September–3 November 2005 of four satellite-tracked drifters (33208, 33210, 33211, and 33212), released on 7 September 2005 by USF/FWRI on the inner WFS, near Fort Myers, FL.

WFS – as a positive feedback mechanism. In contrast, during 2007 larger physical export of diazotrophs and dinoflagellates resulted

in minimal growth rates of smaller WFS red tides (Fig. 8) and less fish kills (Fig. 9) on the WFS, but larger ones downstream along the east coasts of Florida, Georgia, South and North Carolina. Any entrained near surface plankton populations would be transported seaward at speeds of ~10 cm s^{-1}, or ~10 km day^{-1}, within such a surface chlorophyll plume (Fig. 5), unless they change their vertical positions in the water column by sinking or swimming. Such vertical motions are usually observed in migrating phytoplankton, zooplankton, and post-settlement fish larvae. At the edge of the WFS, 10-fold faster currents prevail, of course, within the Loop Current, the contiguous Florida Current, and thence, after addition of the Antilles Current, within the subsequent Gulf Stream of the outer SAB.

But, within shelf waters of the inner SAB, adult clupeids, e.g. *O. oglinum*, migrate alongshore at ~10 km day^{-1} as well (Pristas and Creek, 1973). Thus we assume that red tides, not their living fish prey, are transported within this first coupled model of red tide maintenance, along the southeastern United States, during 2006 and 2007. Accordingly, local larval, juvenile, and adult fish populations instead are subject to vectors of dinoflagellate poisonings. These fish kills provide a fish nitrogen isotope tracer within the subsequent population increments of *K. brevis*, grown at nutrient-replete growth rates of fish-fed maintenance stages of Florida red tides throughout the WFS and SAB.
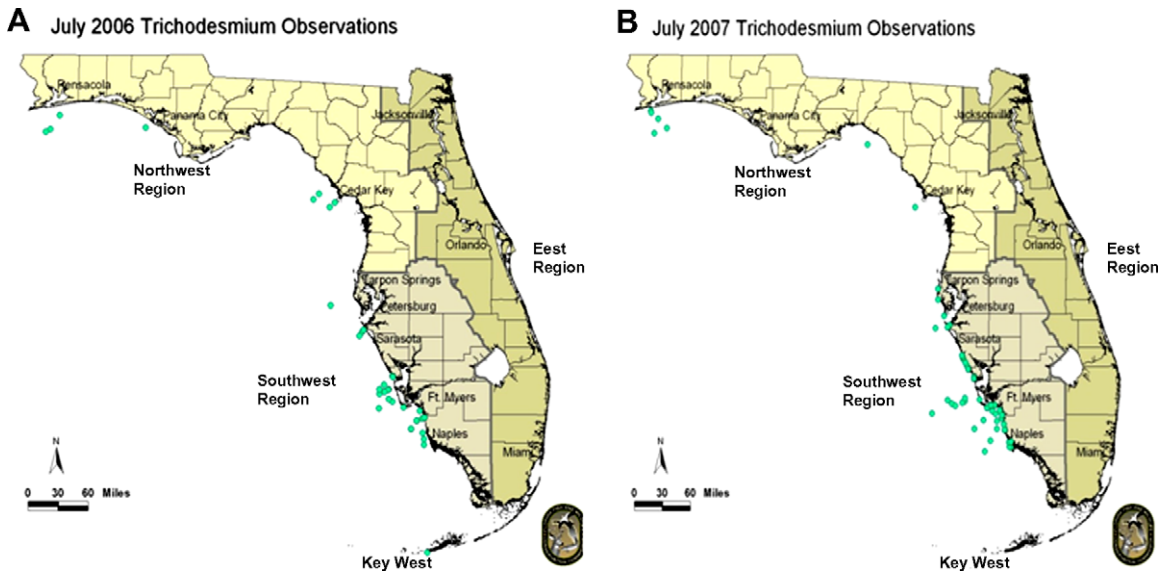
Fig. 7. The observed surface distributions of *T. erythraeum* over the West Florida shelf during July 2006 and 2007. In terms of abundance, similar amounts of diazotrophs were also found on the WFS as a pre-bloom index of red tides during these summers, after Saharan dust loadings.
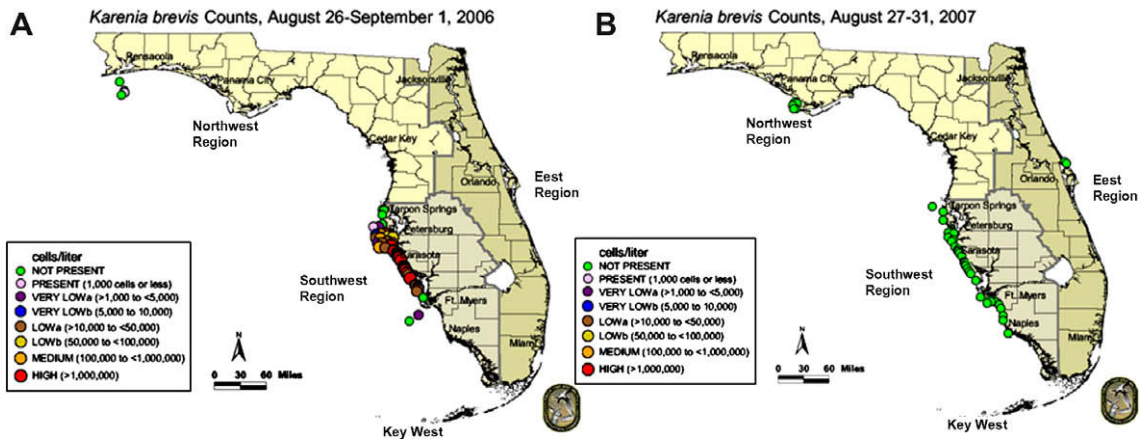
Fig. 8. *In situ* observations (cells l^{-1}) of *K. brevis* on the WFS during (A) 26 August–1 September 2006, and (B) 27–31 August 2007.
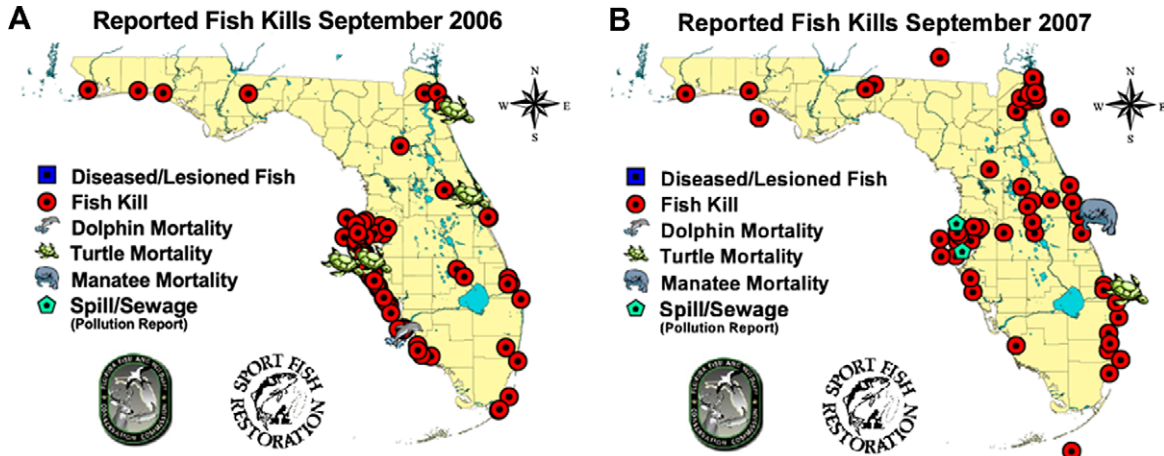
Fig. 9. Fish kills within Florida waters reported to FWRI during September (A) 2006 and (B) 2007 as a post bloom index of red tides.

Dead fish in advanced stages of decay are, of course, neutrally buoyant, such that they can also be detected at the sea surface by aircraft (Gunter et al., 1947, 1948). Usually, they remain within coastal waters, as seen by aircraft during August 2001 by MOTE observers (G. Kirkpatrick, personal communication), concurrent with the satellite color observations (Fig. 5). Dead fish at coastal fronts along the 10 m isobath then demarcated the transition between coastal waters of >40 μg chl l^{-1} of *K. brevis* off Port Charlotte, FL and the offshore waters of <0.2 μg chl l^{-1} of this ichthyotoxic dinoflagellate at background levels. Some dead fish are also advected ∼80 km offshore of Naples, FL, after winds from the northeast as during November 1954, for example, but such metazoan exports are rare (Wilson, 1958).

During 25–26 June 2007, Saharan dust again blanketed the Gulf of Mexico [http://toms.gsfc.nasa.gov]. Since *K. brevis* is shade-adapted during initial phases of its red tides (Shanley and Vargo, 1993), before photo-adaptation, it was probably at depth, remaining undetected by either NASA/NOAA satellite, or *in situ* FWRI, surface sampling protocols, during early summer of 2007. However, the diazotrophs, *T. erythraeum*, and dead fish are tandem surface proxies for the presence of *K. brevis*: the former predicts where the red tide will be; and the latter confirms where it has been. The diazotrophs responded to the iron-rich dust loading by 2–3 July 2007, for example, with an accumulation of *T. erythraeum* biomass along the West Florida coast (Fig. 7b), from Cedar Key (29.0°N, 83.2°W) to Naples (26.1°N, 81.8°W).

Some diazotrophs were found off Pensacola (30.2°N, 87.1°W) on 21 July 2007 (Fig. 7b). Most remained on the southeast WFS, throughout July and August 2007, until 8 September 2007, when the diazotrophs were once again stranded off Panama City (30.0°N, 86.0°W). They now persisted along the Florida Panhandle: by 6 October 2007 off Pensacola: and by 6 November 2007 within St. Joseph Bay (29.7°N, 85.4°W). Dead fishes, associated with red tide and respiratory irritations, were also reported on 1–4 October 2007 along the Panhandle beaches, from Panama City to Pensacola. Fish kills continued here (Fig. 9b) until 28 December 2007. Earlier, 55 fish kills were associated with these coastal red tides, between Tampa and Naples, during September 2006. Yet, only six fish kills were reported there in September 2007. Instead, like the Panhandle region of Florida, dead fish (Fig. 9b) and red tides (Fig. 8b) were first noted on 21 September 2007 off Jacksonville, FL. Along a similar length of coastline, between Melbourne and Fernandina Beach, a mirror image prevailed: during September 2006, only seven fish kills were reported to FWRI, all associated with low oxygen concentrations; in contrast, 43 fish kills were observed here during September 2007, of which 39 were caused by *K. brevis*. After 13

October 2007, dead fish and red tides extended from St. Augustine to Ormond Beach, near Cape Canaveral. Fish kills persisted there until 27 December 2007.

Other red tides of *K. brevis* had been observed near Mobile Bay in 1990 (Tester et al., 1993), 1996 (Brown et al., 2006), and 2005. Earlier red tides of >10 μg chl l^{-1} were also found above the Florida Middle Ground (∼28.5°N, 84.5°W), associated with drifting dead fish at the sea surface during November 1979 (Walsh et al., 2002), where *Trichodesmium* precursors occurred during April 2007 (Fig. 1). Previously, to the north of this region, another red tide of ∼10 μg chl l^{-1} of *K. brevis* was again sampled during 29–31 July 1964, above the ∼25 m isobath within Apalachee Bay (Steidinger et al., 1966) of the Big Bend region of the WFS.

Then, in 1964 the usual coastal red tides to the south of Tampa Bay (Steidinger et al., 1967) were negligible. *Trichodesmium* was present in Apalachee Bay during 1964, moreover, as well as concurrent dead fish, and dying schools of scaled sardine, *Harengula jaguana* (Ingle and Williams, 1966). Thus, in two cases of the circulation model: we first release populations of *K. brevis* just along the coast, between Tampa Bay and Fort Myers, where prior surface drifters had exited the WFS (Fig. 6); and next from both this coastal red tide epicenter (Fig. 2) and the offshore Florida Middle Ground, where the precursor *Trichodesmium* was found during April 2007 (Fig. 1).

2. Methods

To explore the role of poisoned fish as a supplemental nutrient source for maintenance of WFS red tides, after initiation by other nutrient transfers from diazotrophs, we consider; (A) a nitrogen isotope budget for the WFS–SAB food web, based upon more than
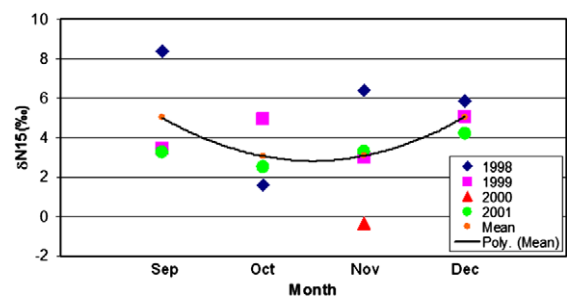

Fig. 10. The monthly mean isotopic ratio of ^{15}N/^{14}N, expressed as δN^{15} (‰), of suspended particulate nitrogen within surface waters of the inner West Florida shelf (<50 m depth) during September–December 1998–2001.

Table 2
The annual catch per unit effort (C.P.U.E.), pounds per fishing trip, of zooplanktivorous fish – Spanish sardine and thread herring – in relation to those of piscivores, red and gag grouper, king mackerel, red and vermillion snapper, before and after larger fall (September–November) red tides and fish kills during 1995, 2001, 2005, and 2006 on the West Florida shelf (WFS), between Tampa and Naples. Additional information is the same fall mean ratio of $^{15}N/^{14}N$ ($\delta^{15}N$) within suspended matter during a small (2000) and large (2001) WFS bloom of *Karenia brevis*.

Year	1994	1995	1996	2000	2001	2002	2004	2005	2006	2007
Spanish sardine	4334	2419	9508	15,749	16,550	16,104	17,089	22,347	36,902	36,266
Sardinella aurita										
Thread herring	11,841	11,692	12,457	10,619	11,929	15,550	20,679	17,918	8538	3662
Opisthonema oglinum										
Red grouper	505	553	574	772	778	752	764	883	913	738
Epinephelus morio										
Gag grouper	241	281	253	321	462	447	460	484	281	233
Mycteroperca microlepis										
King mackerel	185	258	305	346	363	300	464	457	396	475
Scomberomorus cavalla										
Red snapper	194	195	243	346	413	353	387	304	334	625
Lutjanus campechanus										
Vermillion snapper	433	512	431	364	400	419	399	445	571	764
Rhomboplites aurorubens of										
Karenia brevis										
Red tide (μg chl l^{-1})	~1	>10	<1	~1	>10	<1	<1	~10	>10	<1
Fish kills (number)	4	20	2	7	45	17	3	50	59	6
$\delta^{15}N$–PON (‰)	*	*	*	−0.34	+3.03	*	*	*	*	*

500 measurements of the $\delta^{15}N$ (Fig. 10) of suspended PON during the 1998–2001 red tides (Havens, 2004) and the above literature (Table 1); (B) simulation analyses of the export and growth of red tides of *K. brevis* left behind on the WFS during the contrasting large one of 2006 and the small one of 2007 (Figs. 1, 2, and 8); and (C) the seasonal harvests and C.P.U.E.s, of the dominant clupeids and their piscivores from the WFS (Fig. 3) during 1994–2007 (Table 2). Consequently, the required state variables of a coupled biophysical model for future operational forecasts of red tide landfall, duration, dispersal, and food web consequences are then discussed.

Most clupeids of the WFS experience red tide mortalities, based upon prior observations since at least 1916: i.e. *S. aurita*, originally known as *Clupanodon pseudohispanica* (Taylor, 1917); thread herring *O. oglinum* (Landsberg, 2002); scaled sardine, *H. jaguana* (Gunter et al., 1948; Ingle and Williams, 1966; Houde, 1977b); and bay anchovy, *A. mitchili* (Quick and Henderson, 1975). But how important is this intermediate trophic level as a source of nutrients for red tides?

To answer this question, we begin with an isotope budget (Table 1), based upon our analyses of >500 samples of the 1998–2001 red tides, between the 50 m isobath and the coast. The budget is constrained by prior observations of the $\delta^{15}N$ ratios of both other marine trophic levels and adjacent human harvesters. Next, we perform simulation analyses of the physical transport and growth of the contrasting large and small red tides during 2006 and 2007. Finally, we consider the seasonal harvests of *S. aurita* and *O. oglinum* during the preceding decade of 1994–2007, in relation to red tides, these clupeid C.P.U.E.s, and those of the major piscivores (Table 2).

2.1. Isotopic analyses

Upon sampling at sea during 1998–2001, >500 filtered samples of particulate matter were frozen. In the laboratory, the unfrozen samples were rinsed with 1 ml of 10% HCL to remove any carbonates. The lyophilized filters were introduced into a continuous flow dual analysis mass spectrometer, upon combustion with a Carlo-Erba Elemental Analyzer, for determination of both carbon and nitrogen isotopic composition of the particulate matter (Havens, 2004). The results are reported here as the monthly means of $\delta^{15}N$ of suspended PON for each year, at the surface of the inner (<50 m depth) WFS.

With respect to the isotope budget of WFS food web interactions at the trophic level of ecological complexity (Table 1), other $\delta^{15}N$ values of dinitrogen gas, ammonium, nitrate, urea, phytoplankton (diazotrophs, diatoms, microflagellates), zooplankton (calanoids, harpactacoids), nominal fish herbivores (menhaden, mullet), zooplanktivore clupeids (herring, sardine,), piscivores (king mackerel, vermillion snapper), and top predators (humans) are also taken from the literature of food webs within and adjacent to western boundary currents of the Gulf of Mexico, the SAB, the MAB, and other regions of the Southern California Bight.

2.2. Simulation analyses

To focus mainly on the balance between advective losses and nutrient-regulated growth of Florida red tides, we use a simplified version of our coupled biophysical model. Here, the water circulation effects transport of the early maintenance phase of a red tide, after initiation within both coastal and offshore (Fig. 1) red tide epicenters on the WFS during 2006 and 2007.

The circulation model (Weisberg et al., 2009) is a regional application of the ROMS (Song and Haidvogel, 1994), nested in the HYCOM (Chassignet et al., 2003). The biological model assumes various exponential growth rates of the phytoplankton community, reflecting variable nutrient limitation of diatoms and dinoflagellates, constrained by daily satellite estimates of surface biomass of light-adapted (Walsh et al., 2002) *K. brevis*.

The ROMS [Regional Oceanic Modeling System] and HYCOM [HYbrid Coordinate Ocean Model] formulations are both fully baroclinic, primitive equation models, driven by complete physical forcing fields of wind and buoyancy, over 5-km spatial resolution of the WFS and SAB. The boundary conditions of the models are thus both the entire North Atlantic Ocean and the local WFS estuaries (Weisberg et al., 2009), while wind forcing is an optimal interpolation of the NCEP (National Centers for Environmental Prediction) 3 h forecasts at $2.5° \times 2.5°$ spatial resolution (He et al., 2004). Initial conditions of the maintenance phase of local red tides each year are set by satellite specification of the onset of WFS diazotroph-fed, *K. brevis* populations of 1 μg chl l^{-1} on 20 August 2006 and 2 September 2007.

In addition to physical dispersal of coastal red tides from the epicenter, between Tampa Bay and Fort Myers, less frequent red tides of *K. brevis* and its congeneric species *K. papilionacea* (Brown et al., 2006) have been observed along the Florida Panhandle. Thus, each day, during fall of 2006 and 2007, 148 simulated surface drifters were launched along seven cross-shelf sections of the WFS. We

first consider the 75-day trajectories of the model's coastal surface drifters, representing water parcels of entrained WFS red tides of *K. brevis*, with respective start dates of 21 September and 6 October 2006, in relation to those set on 6 August and 6 September 2007. All of these Lagrangian populations of *K. brevis* were released along the 10–20 m isobaths, within 30 km of the West Florida coastline, where color changes depict days after release.

A second set of 75-day trajectories of the model's surface drifters thus instead represented water parcels of other entrained WFS red tides of *K. brevis*, with again a start date of 6 September 2007, but instead released along both the (A) 10–20 m and (B) 60–80 m isobaths, as well as above the 30–45 m isobaths of the Florida Middle Ground. Once more, the same color changes again depict days after release.

Furthermore, in this numerical study, we also allow *K. brevis* populations to grow at their nutrient-limited, realized exponential growth rate of only 0.08 day^{-1} during a maintenance phase of meager fish-fed nutrition of the 2007 simulation case. In contrast, during another case of the model, the toxic dinoflagellates grow at a maximal rate of 0.25 day^{-1} during their fish-fed, nutrient-sated maintenance phase of 2006.

A similar large *in situ* growth rate of 0.25 day^{-1} for *K. brevis* was observed at the June start of the 1980 red tide (Fig. 2), after Saharan dust loading and precursor growth of the diazotrophs (Walsh and Steidinger, 2001). Their recycled nutrients are sufficient for a small red tide of 1.0 µg chl l^{-1}, but large ones of 10.0 µg chl l^{-1} follow fish kills in the Gulf of Mexico (Walsh et al., 2006). Diatoms instead grow in the model at a nutrient-replete exponential rate of 1.00 day^{-1} (Walsh et al., 2001).

2.3. Validation data

Building upon the diagnostic color and back scatter designations of *K. brevis* populations on the WFS, from satellite algorithms (Carder et al., 2007; Cannizzaro et al., 2008), we compiled daily estimates of the spatial extent (1410–5826 km^2) of >1 µg chl l^{-1} of these toxic dinoflagellates during August–September 2006 and 2007, after arrival of Saharan dust above the WFS, e.g. Fig. 4b. We then averaged these spatial data to provide validation criteria for the mean size of ichthyotoxic algal populations of >1 µg chl l^{-1} (Landsberg, 2002), growing exponentially at respective rates of 1.00 [diatoms], 0.25 [nutrient-replete *K. brevis*], and 0.08 [nutrient-impaired *K. brevis*] day^{-1}.

2.4. C.P.U.E.s of WFS clupeids and their predators

Of the eight species of commercially harvested groupers, seven species of snappers, and two species of mackerels caught (http://research.myfwc.com) by both Florida sport anglers and commercial fishermen during 2007, most of the yields to humans were of red and gag groupers, king mackerels, and vermillion and red snappers from the WFS. Here, 87–96% of the total state landings of these serranids, scrombrids, and lutjanids were then reported along the Florida west coast. Moreover, the summed consumption on the WFS of herrings and sardine each year, by these first and last groups of fish predators, was estimated to be >90% of the annual moralities of the clupeids, compared to predation losses of <10% from previous fishing harvests, imposed on herrings and sardines by humans during 1997–1998 (Okey and Mahmoudi, 2002).

But, the earlier simulation analyses ignored red tide mortalities (Okey and Mahmoudi, 2002), such that food web transfers of *K. brevis* to fish (Tester et al., 2000), as well as direct impacts of their brevitoxins on the adults (Wilson and Collier, 1955), must be considered in this and future analyses of the impacts of fish predation by WFS red tides. Furthermore, unknown time lags of element and energy transfer prevail among such complex coastal ecosystems.

For example, among the reduced landings of red grouper *Epinephelus morio* during 1996 (Fig. 3), the dominant year classes of these piscivores were 6–7-year-old groupers, spawned in 1989 and 1990 (Lombardi-Carlson et al., 2002), when red tides were instead minimal (Fig. 2).

Mackerels, sampled by Florida sport and commercial fisheries at younger ages of 1–3 years (Klima, 1959), instead exhibited an inverse increase of larger yields of *Scomberomorus cavalla* harvested during 1996 (Fig. 3), after the prior red tide (Fig. 2). Moreover, floating carcasses of groupers are frequently observed during large red tides, whereas adult mackerels seem to be unaffected (Gunter et al., 1947). In any event, the δ^{15}N designations of trophic status for some surviving fish in the WFS and SAB are available (Peterson and Howarth, 1987; Deegan et al., 1990; Sullivan and Moncreiff, 1990; Thomas and Cahoon, 1993; Roelke and Cifuentes, 1997), averaging over such temporal–spatial biotic complexities. They provide an ecological end member, near the top of the WFS/SAB food web, for interpretation (Table 1) of the observed temporal changes of the ^{14,15}N isotope signatures of phytoplankton at the bottom (Fig. 10).

3. Results

3.1. Isotope budget

The overall mean δ^{15}N–PON of the surface phytoplankton during red tides (Vargo et al., 2008) of October–November 1998–2001 (Fig. 10) on the inner WFS (<50 m depth) was +3.0‰ (Table 1), compared to −1.0‰ for diazotroph-dominated coastal waters of the southern WFS (Macko et al., 1984). Near the bottom of the central WFS water column on the 50 m isobath during November 2001, moreover, the δ^{15}N–PON was instead −1.1‰ (Havens, 2004). Here, during September 2002 a diel time series documented vertical migration of *Trichodesmium* between surface and near-bottom waters along the 50 m isobath of the WFS (Walsh et al., 2006). Furthermore, when a small diazotroph-fed red tide of only ~1 µg chl l^{-1} prevailed on the WFS, the mean δ^{15}N–PON was −0.3‰ in 2000, compared to +3.0‰ during the 2001 red tide of >10 µg chl l^{-1} (Table 2).

If we assume that *Trichodesmium* is half of the usual nitrogen source for large red tides of *K. brevis* on the WFS at −1‰ (Table 1), then a supplemental nitrogen source of δ^{15}N of +7.0‰ is required to explain the surface mean of +3.0‰, found for suspended matter during October–November 1998–2001 (Fig. 10). Recall that fractionation of nitrogen isotopes during heterotrophic plankton and nekton metabolism leads to excretory loss of the lighter isotope, ^{14}N, resulting in more positive δ^{15}N values of +3.0‰ per higher trophic level of the marine food web (Minagawa and Wada, 1984; Peterson and Fry, 1987; Walsh et al., 1989).

A required δ^{15}N of +7.0‰ for the other major organic nitrogen source of nutrients could thus be met by pelagic zooplanktivores, i.e. clupeid fish feeding on zooplankton herbivores of WFS oligotrophic waters. Their prey, i.e. copepods and salps, in turn have δ^{15}N of +4.0‰ (Checkley and Miller, 1989; Lopez Veneroni, 1998; Havens, 2004; Montoya et al., 2002), upon ingestion of diatoms, with δ^{15}N of +1.0‰ (Table 1).

For this distinct diatom-based food chain of the WFS food web, we further assume in the isotope budget (Table 1) that the slope waters are the main source of nitrate, with δ^{15}N–NO$_3$ of +5‰ within the Loop Current (Lopez Veneroni, 1998), upwelled on to the WFS (Walsh et al., 2003). Such an isotope constraint at the bottom of the diatom food chain is analogous to those δ^{15}N of nitrate stocks in other western boundary currents of the upstream Guiana Current on the Venezuelan slope (Liu and Kaplan, 1989), the contiguous Antilles Current (Montoya et al., 2002), and the subsequent Gulf Stream (Altabet and McCarthy, 1985), as well as the similar

Kuroshio Current off Japan (Liu et al., 1996). In contrast, the $\delta^{15}N$–NO_3 of +16.6‰ for nitrate within Florida estuarine waters, e.g. Perdido Bay (Coffin and Cifuentes, 1999), is more typical of a soil source (Chang et al., 2002).

Additionally, the observed seasonal increase of $\delta^{15}N$–PON, from +3‰ in October to +5‰ during December (Fig. 10) is the wrong pattern for seasonal freshwater supplies of nutrients to the WFS. The mean salinity, over the near shore 5 m water column of the WFS, in October 2001 of 33.7 psu instead increased to 34.7 psu by December 2001 (Lester, 2005), reflecting instead offshore waters of the Loop Current (Walsh et al., 2003). Moreover, the mean $\delta^{15}N$–PON of the Texas–Louisiana shelf was a time-invariant +6.5‰ at <28 psu, as a consequence of the much larger freshwater discharge of the Mississippi River (Lopez Veneroni, 1998).

Herbivores of the microbial loop, i.e. protozoans of +9.00‰, in our isotope budget (Table 1), graze on microflagellates of +6.00‰, after fractionation (Cifuentes et al., 1988) of a dissolved nitrogen source of ammonium of −3.0‰ (Miyake and Wada, 1967; Checkley and Entzeroth, 1985), mediated by the bacterioplankton. They are the dominant late summer plankton of the WFS (Kleppel et al., 1996; Walsh et al., 2003). Indeed, during September 1998, their combined isotopic signature prevailed as a $\delta^{15}N$–PON of +8.4‰, observed by us for some of the WFS suspended matter (Fig. 10).

The mean $\delta^{15}N$ signature of WFS red tides then seasonally decreased to +3.0‰ during October 1998–2001 (Fig. 10), as a consequence of their prior utilization of DIN of diazotroph origin (Walsh et al., 2003; Mulholland et al., 2006). Next, it increased to +5.0‰ during December of those years (Fig. 10), as a result of uptake by K. brevis of DIN of clupeid origin, harvested by toxic levels of >1 µg chl^{-1} of the dinoflagellates during November (Vargo et al., 2008). Other clupeids, on Georges Bank for example, exhibit a similar +6.1‰ isotopic enrichment of $\delta^{15}N$ of Clupea harengus from the base of the marine food web (Fry, 1988). Within Mississippi coastal waters, the same WFS clupeids, i.e. H. jaguana and A. mitchilli, also have a similar +5.9–6.0‰ isotopic enrichment of $\delta^{15}N$ over the primary producers of edaphic algae (Sullivan and Moncreiff, 1990).

Piscivores, feeding in turn on the local WFS clupeids, should thus have a $\delta^{15}N$ of +10.0‰. Note that king mackerels, S. cavalla, harvest clupeids on the WFS as a dominant member of the fish community (Grimes et al., 1990), constituting ~5% of the annual fish landings from the WFS during 2007. They indeed have a $\delta^{15}N$ of +10.8‰ within Florida coastal waters, between Panama City and Fort Pierce (Roelke and Cifuentes, 1997). Similarly, vermillion snapper Rhomboplites aurorubens are also dominant piscivores on the WFS, constituting another 4% of the 2007 landings from there. Downstream on the North Carolina shelf (Grimes and Huntsman, 1980), these fish exhibit a $\delta^{15}N$ of +10.1‰ (Thomas and Cahoon, 1993). Moreover, the zooplanktivore clupeids – Spanish and scaled sardines, thread and round herring – are the dominant fish biomass on the WFS. They are eaten there by mackerels, groupers, snappers, drums, humans, and red tides. An omnivorous clupeid – Gulf menhaden, Brevoortia patronus – instead eats both phytoplankton and zooplankton as an adult in the open Gulf of Mexico, but with a $\delta^{15}N$–PON signature of +13.8‰ (Deegan et al., 1990).

Fish larvae of this region have a $\delta^{15}N$–PON of as much as +10.5‰ (Lopez Veneroni, 1998), reflecting a longer food web as well. Since nitrogen-fixers also prevail in the open Gulf of Mexico (Walsh et al., 2006), these isotopic observations suggest that adult clupeids of these slope waters are feeding at two higher trophic levels than that of the shelf clupeids and one higher than that of the shelf piscivores, as a consequence of the tightly coupled microbial loop of bacterial and protozoan components, nourishing nutrient recycling among the longer oceanic food web, based on ammonium, rather than mainly on nitrate and dinitrogen gas (Table 1).

Finally, the early isotopic signature of prehistoric Indians of St. Catherines Island, Georgia was a $\delta^{15}N$ of +12.8‰ by 1075 (Schoeninger et al., 1983), similar to that of +13.8‰ for menhaden in the Gulf of Mexico (Deegan et al., 1990). Yet, these early residents of the SAB instead harvested the parallel diatom-based food chain as mainly consumers of piscivorous fish of +10.0‰ (Table 1). Most of these fish were then available to both them and the contemporary Calusa Indians, adjacent to the upstream WFS. They made hooks to catch snapper, grouper, and mackerel and spear points for impaling both mullet and flounder (Widmer, 1988; Hann, 2003). Furthermore, skeletal remains indicate that mullet, grouper, drum, and other fish were ~80% of the Indian diet at the Venice shell midden of Sarasota County (Fraser, 1980; Ruppe, 1980).

They may then have instead consumed only a small amount of shellfish, like the seasonal diet of Texas Indians, described by Cabeza De Vaca in the 1500s, when inferred red tides also killed fish. A prior model of oyster production and food quality within a larger Venice, FL lagoon, at even earlier and thus lower preColumbian sea levels of ~2 m, has been formulated. It suggested that shellfish of this region might have fed at most 50 ancestors of the Calusa Indians for ~20 years, assuming a nominal plankton supply for mollusks, composing ~25% of the Florida Indian diet, about 2000 years ago (Lightfoot and Ruppe, 1980; Widmer, 1988).

During these measurements of $\delta^{15}N$–PON on the inner WFS during 1998–2001 (Fig. 10), a seasonal doubling of the mean near shore DON stocks, from 5.6 µmol DON kg^{-1} in September 1998 to 12.1 µmol DON kg^{-1} in December 1998, was also observed on the WFS, within surface waters between the 25 m isobath and the coast (Vargo et al., 2002). Most of this DON increment occurred mainly after the start of the red tide that year in November 2008, when just 7.8 µmol DON kg^{-1} were found (Vargo et al., 2002). The urea component of DON is readily used by K. brevis (Baden and Mende, 1979; Steidinger et al., 1998).

Similar fall increments of dissolved organic phosphorus (DOP) are also observed on the WFS (Vargo et al., 2008), where K. brevis can use DOP (Vargo and Howard-Shamblott, 1990). We believe that decomposing diazotrophs and dead fish are together the major organic nutrient sources for both formation and maintenance of toxic red tides of K. brevis within Florida coastal waters, from off the Panhandle to the SAB at the Georgia border.

Since the red tides use both DON and DOP, the observed accumulations of organic nutrients left behind in the water column (Vargo et al., 2002, 2008) reflect a net balance between the metabolic plankton processes of nutrient remineralization and utilization. The $\delta^{15}N$ of suspended PON during this time period (Fig. 10), together with the food web isotope budget (Table 1), thus allowed us to test the simplest hypothesis that each source of recycled nutrients, from diazotrophs and dead fish, supplied about half of the nutrient requirements of the 1998–2001 red tides.

Accordingly, direct harvest of shelf clupeids by K. brevis within the shorter shelf food web of the WFS is a most efficient energy transfer process, explaining why an annual primary production of ~200 g C m^{-2} year^{-1} occurred there, over bloom regions of ~2.3 × 10^4 km^2 extent, from Cedar Key to Naples, out to the 40 m isobath during 1978–1982 (Vargo et al., 1987). These 1978–1982 red tides were then mainly of 1–10 µg chl l^{-1} size, not the biomass accumulation of 10–100 µg chl l^{-1} found during 2006 (Fig. 2), such that their former spatial extent included red tide boundaries of >0.1 µg chl l^{-1}. Yet, the in situ ^{14}C estimates of daily total photosynthesis during the 1980 phytoplankton blooms of the WFS ranged from 1.1 to 2.9 g C m^{-2} day^{-1} (Vargo et al., 1987), compared to an annual carbon fixation of only ~25 g C m^{-2} year^{-1} for Biscayne Bay (Roman et al., 1983) on the east coast of Florida, where red tides are rare imports.

Harpactacoid copepods serve as grazers of Trichodesmium within the upstream Guiana (Calef and Grice, 1966) and downstream

Florida (Roman, 1978) Currents, but are rare on the WFS (Lester, 2005). Other copepods do not eat these diazotrophs on the North Carolina shelf (Guo and Tester, 1994), such that we also assume that little of their production is directly harvested by higher trophic levels of the WFS/SAB in the isotope budget (Table 1). In contrast, WFS diatoms are the preferred food of calanoid copepods (Kleppel et al., 1996). Similarly, when given a prey choice between diatoms and K. brevis off North Carolina within the SAB, Acartia tonsa – a usual near shore zooplankton resident of the WFS (Lester et al., 2008) – also ate only the diatoms (Turner and Tester, 1997).

We thus further assume that half of the WFS annual production of 200 g C m^{-2} year^{-1} is due to diatoms, supporting the parallel food chain of: calanoid copepods (Kleppel et al., 1996); first-feeding fish larvae (Ditty et al., 1994); juvenile and adult zoophagous fish (Houde and Chitty, 1976); and fish piscivores (Roelke and Cifuentes, 1997), leading to annual cohorts of the dominant WFS clupeids (Houde, 1977a–c). The isotope budget (Table 1) also suggests a 50% harvest of diatom-grown dead fish, via calanoid copepods, by K. brevis within the third intersecting parallel food chain of diazotrophs and toxic dinoflagellates.

Accordingly, we estimate the loss of secondary production of the zooplanktivore clupeids to dinoflagellate predation within this other companion food chain of: diazotrophs; ineffective harpacticoid copepods; red tides; and poisoned fish. It was ~50 g C m^{-2} year^{-1} during 1998–2001, or half of the remaining diatom primary production of 100 g C m^{-2} year^{-1}, since both dinoflagellates and diazotrophs [each ~50 g C m^{-2} year^{-1} of partitioned photosynthesis] are the dominant, larger net plankton components of the non-siliceous WFS phytoplankton community (Vargo et al.,

1987; Walsh et al., 2003). The smaller microflagellates of the microbial web are instead heavily grazed by microzooplankton protozoans (Strom and Strom, 1996), occasionally providing meals, in turn, for the calanoid copepods (Kleppel et al., 1996) and menhaden.

In comparison, ~8.0 million pounds of baitfish, including Spanish sardine and thread herring (Fig. 3), were caught on the WFS during 2001, between the Florida Panhandle and south of Tampa Bay (Mahmoudi et al., 2002). Since both S. aurita and O. oglinum are mainly seasonal spawners between the coast and the 30 m isobath (Houde et al., 1979), and fisheries-independent surveys of their adult abundance during 1994–2002 were taken over the same subregion of the inner WFS (Pierce and Mahmoudi, 2001; Mahmoudi et al., 2002), we first assume that the fishing harvests were mainly derived from this near-shore region.

Accordingly, we use a cumulative yield area of ~0.9 × 10^5 km^2 for the bait fish catches, from the coast to the 37 m isobath (Okey and Mahmoudi, 2002), instead of a total WFS area of ~2.1 × 10^5 km^2 (Walsh, 1988). On this basis, human harvests of instead only 0.007 g C m^{-2} year^{-1} of baitfish, with a fish dry weight (dw) of 25% wet weight and a carbon content of ~57% dw (Walsh et al., 2006), during 2001 were thus insignificant losses of the zooplanktivore fish populations, compared to inferred red tide harvests of these fish of ~50 g C m^{-2} year^{-1} over the same region.

Conversely, using the smaller area of 1978–1982 red ides of >0.1 μg chl l^{-1}, i.e. ~2.3 × 10^4 km^2 extent (Vargo et al., 1987), the human fishing losses, if confined to just this red-tide infested area of the WFS, would have been 0.064 g C m^{-2} year^{-1} of baitfish. Instead, if we next normalize the fishing losses to only the WFS area
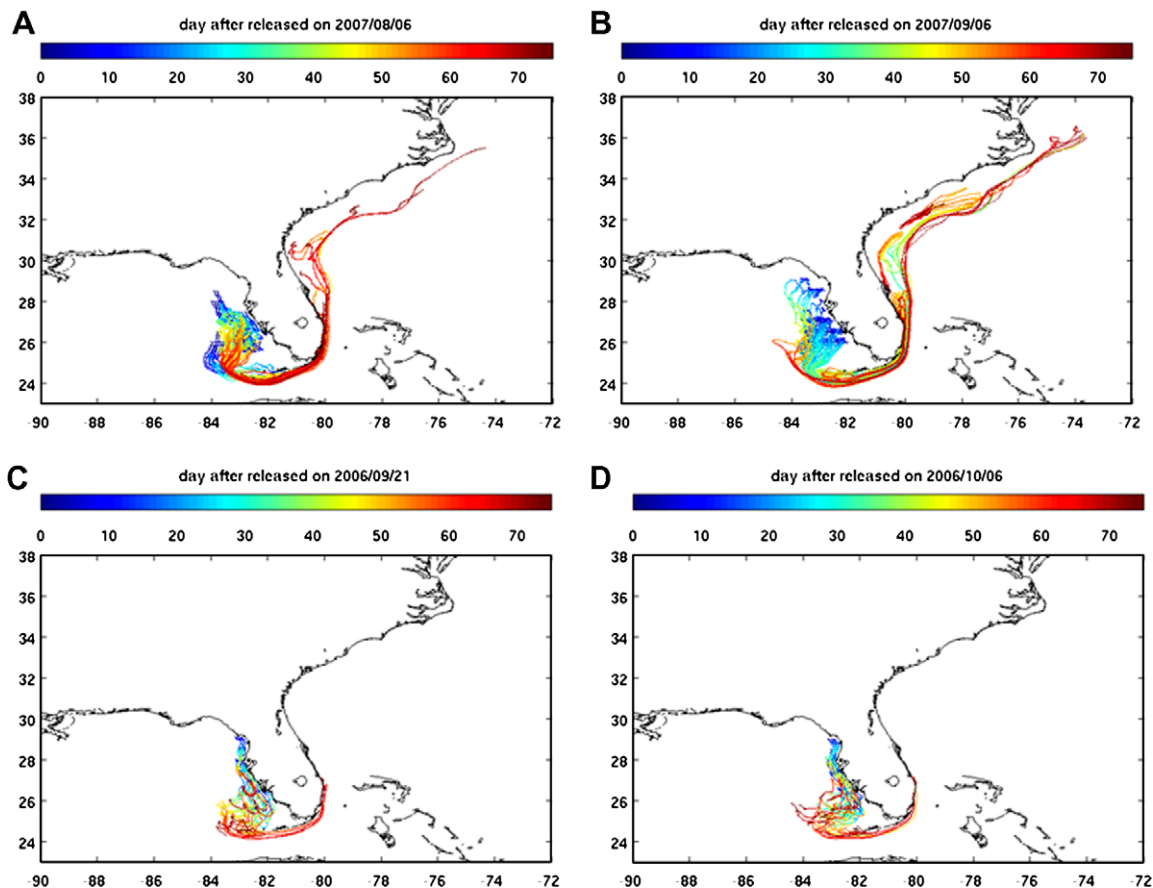
Fig. 11. The 75-day trajectories of the model's surface drifters, representing water parcels of entrained WFS red tides of K. brevis during 2006 and 2007. The respective start dates are (A) 6 August and (B) 6 September 2007 in relation those of (C) 21 September, and (D) 6 October 2006. All were released along the 10–20 m isobaths within 30 km of the West Florida coastline, where color changes depict days after release.

of the 2006–2007 red tides of >1 μg chl l^{-1}, i.e. ~3.8 × 10^3 km^2 extent (Figs. 12 and 13), we arrive at an estimated human fishing loss of 0.387 g C m^{-2} year^{-1} of baitfish. This last estimate of comparable fishing loss is still less than 1% of the above harvest of baitfish secondary production of ~50 g C m^{-2} year^{-1}, attributed to red tide predation during 1998–2001, based on this new nitrogen budget (Table 1).

Since red tides are only ichthyotoxic at populations levels of >1 μg chl l^{-1} (Landsberg, 2002), this last comparison suggests that "normal" predation losses of coastal clupeids to red tides were, at least, >90% during 2001, compared to a fisheries harvest of <10% that year – as a conservative estimate. Thus, the predatory impact of red tides can no longer be ignored in prudent management of either these fisheries at an intermediate trophic level, or those at higher trophic levels of the piscivore groupers, snappers, and mackerels.

3.2. CPR predicted export of the 2006 and 2007 red tides

Following the observed trajectory of satellite-tracked surface drifters (Fig. 6) at the demise of the 2005 red tides (Fig. 2), the simulated surface drifters, released during September–October 2007, were advected over the proper time span to the Loop Current, and thence to US east coast points farther north via the model's Gulf Stream (Figs. 11a and b). These model drifters represented trajectories of the entrained red tides during 2007. In contrast, the near shore 2006 drifting red tides remained mostly on the WFS (Figs. 11c and d), with only a few water parcels and thus minimal red tides (Fig. 8a) transported eastwards to the Miami environs.

Both winds, and Loop Current proximity to the shelf-break, were factors in occurrence of the 2007 decantation of red tides. Moreover, the same circulation that led to transport offshore, near the surface, led to onshore transport to the south, near the bottom. This accounts for the appearance of cells of K. brevis off Fort Myers (Fig. 2), coincident with red tides and fish kills along the east coast (Fig. 8b). With large enough decantation, the Fort Myers bloom of K. brevis was short lived during 2007 (Figs. 2, 8b).

The earlier occurrence of K. brevis populations at Jacksonville, and also their dispersal along the Florida Panhandle, during 2007 had to rely on previous water movements, for which in situ cell counts of K. brevis within both the offshore epicenter and the coastal one are not available. Nevertheless, a similar set of water parcel trajectory analyses, originating one month earlier, exhibited such decantations of surface drifters and entrained sun-adapted diazotrophs to the east Florida shelf (not shown).

Recall that surface precursors of red tides were observed as Trichodesmium populations within the coastal WFS red tide epicenter during July–August 2007 (Fig. 7b). We next do show the results of additional export from the Florida Middle Ground, which is effectively an offshore translation of earlier westward transport of coastal WFS red tides. Thus, a history of deduced shelf export of red tides from the WFS over the last ~120 years, since at least 1886 (Knowles, 1887; Brongersma-Sanders, 1957) to 2007 (Figs. 11a and b), provides testimony to the pervasive, ichthyotoxic nature of Karenia spp. red tides (Fig. 9b), and their downstream movement along the southeastern US seaboard.
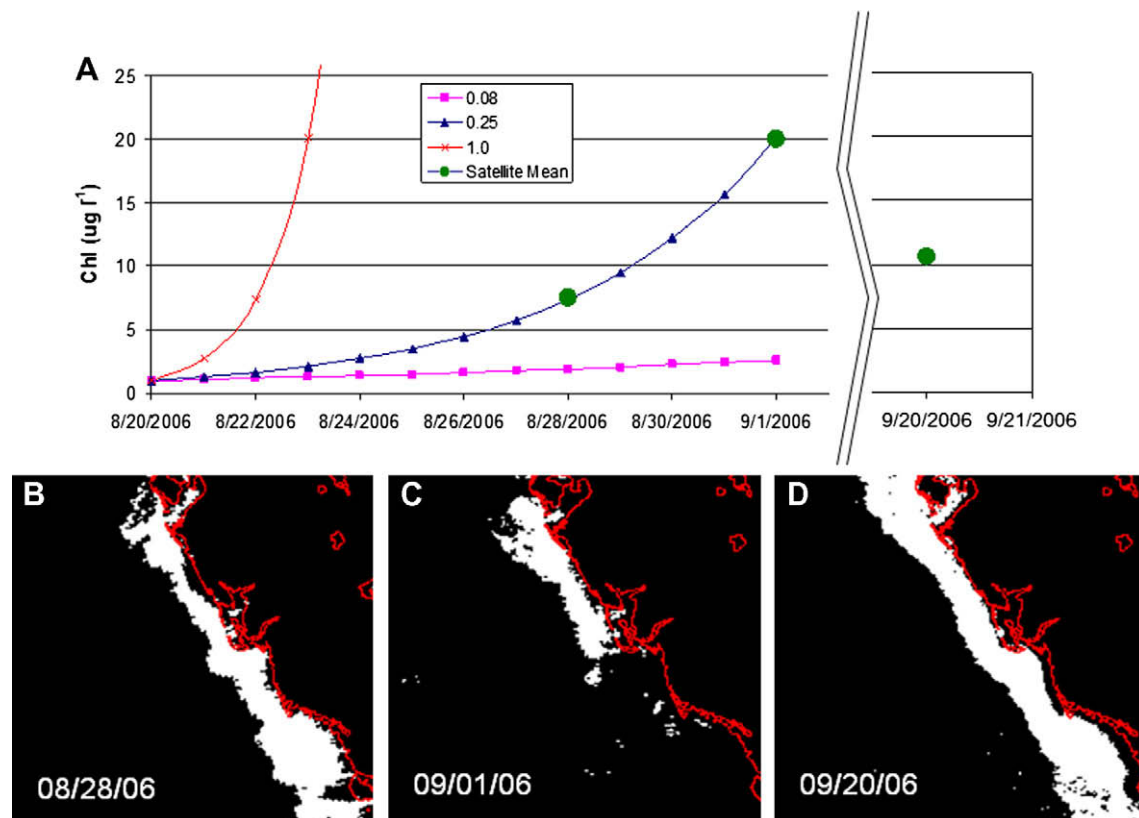
Fig. 12. The 2006 case of the CPR model has a respective fish-fed growth rate of red tide of 0.25 day^{-1}, as determined from model fits of the observed ichthyotoxic levels of K. brevis on 08/28/06 and 09/01/06. The satellite means of the first panel (closed circles of (A)) are from the areal white masks of >1 μg chl l^{-1} on those dates, as well as on 09/20/06, of (B–D). The different computed daily chlorophyll stocks of K. brevis in the model assume respective net specific exponential growth rates of 0.08, 0.25, and 1.00 day^{-1} in (A), with the onset of fish-fed maintenance begun on 20 August 2006.
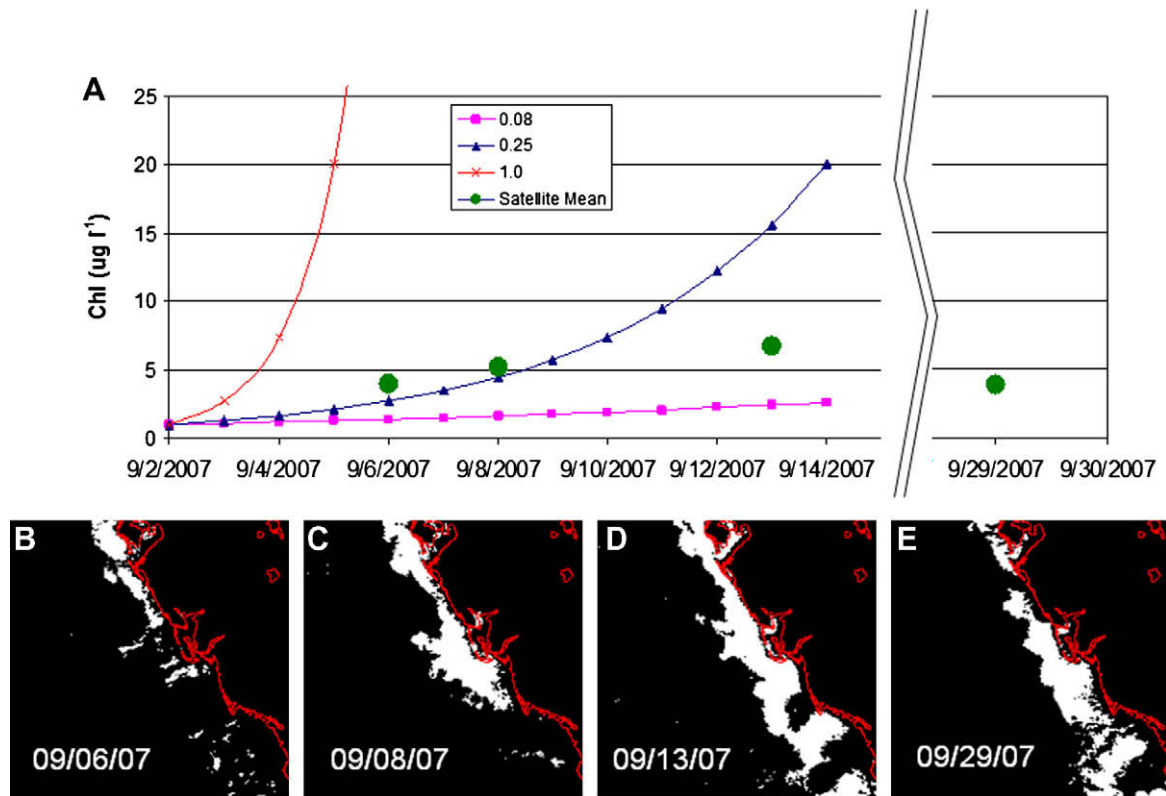
Fig. 13. The 2007 case of the CPR model has a respective fish-starved growth rate of red tide of 0.08 day^{-1}, as determined from model fits of the observed ichthyotoxic levels of *K. brevis* on 09/06/07, 09/08/07, and 09/13/07. Once more, the satellite means of the first panel (closed circles of (A)) are from the areal white masks of >1 μg chl l^{-1} on those dates, as well as on 09/29/07, of (B–E). Note that some fish kills were observed in 2007 on the WFS, but 10-fold less than in 2006, such that by mid-September 2007, a maximal growth of 0.25 day^{-1} was no longer realized in (A). Onset of the fish-starved scenario began at a diazotroph-fed stock of 1 μg chl l^{-1} of red tide on 2 September 2007.

3.3. Fish-fed and fish-starved red tides

Finally, to test our hypothesis of large and small nutrient supplies from decomposing fish for respective maximal and minimal growth rates of *K. brevis*, we used the USF satellite algorithms of the surface biomass of diazotrophs and dinoflagellates (Carder et al., 2007; Cannizzaro et al., 2008). We employed remote estimates of the daily changes of red tide abundance of >1 μg chl l^{-1} over the WFS during August–September 2006 and 2007 (Figs. 12 and 13), when 10-fold interannual variations of fall red tides (Fig. 8) and fish kills (Fig. 9) were noted, despite the same amounts of precursor diazotrophs (Fig. 7), in response to similar Saharan dust loadings (Fig. 4).

With little export of coastal red tides from the WFS during 2006 (Fig. 11), fish kills were 10-fold larger during September of that year, compared to 2007 (Fig. 9), providing presumably large amounts of ammonium, urea, and other DON for maximal growth of red tides. Using the daily satellite estimates of biomass increments within regions of >1 μg chl l^{-1} of *K. brevis* (the areal white masks of Figs. 12 and 13), a respective fish-fed growth rate of red tide of 0.25 day^{-1} correctly replicated the mean temporal change of WFS red tides, between 28 August and 1 September 2006 (Fig. 12). We assumed that the red tide began at a diazotroph-fed population level of 1 μg chl l^{-1} on 20 August 2006 (Fig. 12). The fish-starved growth rate for *K. brevis* of 0.08 day^{-1} was then too small during 2006, while a diatom growth rate of 1.00 day^{-1} (Walsh et al., 2001) was too large (Fig. 12).

In contrast, much larger physical export of coastal red tides during 2007 (Fig. 11), resulted in 10-fold less red tides (Fig. 8) and fish kills (Fig. 9) during August–September 2007 on the WFS. Accordingly, with presumably less recycled dead fish supplies of nitrogen

and phosphorus released to the water column, the maximal fish-fed growth rate of 0.25 day^{-1} in the CPR model only matched the observed ichthyotoxic levels of *K. brevis* between 6 and 8 September 2007 (Fig. 13).

Recall that the satellite means of the first panel (closed circles of panel A) of Fig. 13 are from the areal white masks of >1 μg chl l^{-1} on those dates, as well as on 29 September 2007, i.e. panels B–E of that Figure. After the dead fish nutrients were utilized, the satellite means of the first panel of Fig. 13 (closed circles of panel A) then reflected a reduced red tide growth rate of ~0.08 day^{-1} by 13 September 2007. Here, we assumed that the onset of fish-starved maintenance instead began on 2 September 2007 (Fig. 13). Again, a diatom growth rate of 1.00 day^{-1} was also much too large in the model to replicate observations of phytoplankton biomass in fall 2007 (Fig. 13), suggesting little estuarine supplies of nutrients at the correct, required N/P/Si ratios (Walsh et al., 2003, 2006; Darrow et al., 2003) to then fuel their coastal blooms (Fashnenstiel et al., 1995).

Note that although some of the observed red tides and fish kills were reflected in the 2007 trajectories from the coastal epicenters of the WFS (Fig. 11), other blooms and dead fish along the Florida Panhandle were not. A second set of 75-day trajectories of the model's surface drifters (Fig. 14) thus represented other water parcels of entrained WFS red tides of *K. brevis*, with again a start date of 6 September 2007. But, these initial red tides were instead released along both the (A) 10–20 m and B) 60–80 m isobaths, as well as above (C) the 30–45 m isobaths of the Florida Middle Ground in the Big Bend region off the West Florida coast. Once more, color changes again depict days after release (Fig. 14).

We suggest that the model's circulation, driven by a combination of local wind, buoyancy, and Loop Current forcings, is a correct
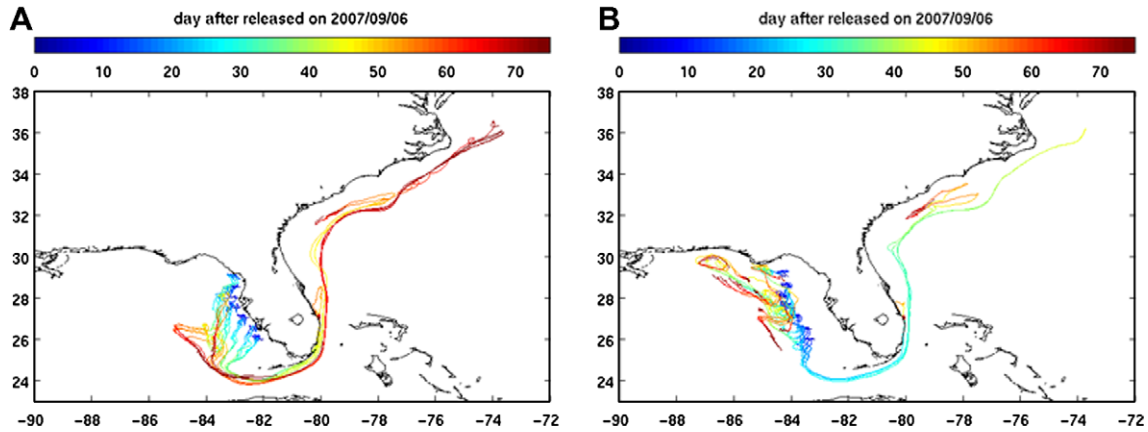
Fig. 14. A second set of 75-day trajectories of the model's surface drifters, representing water parcels of entrained WFS red tides of *K. brevis* with a start date of 6 September 2007, were instead released along both the (A) 10–20 m and (B) 60–80 m isobaths, as well as above the 30–45 m isobaths of the Florida Middle Ground in the Big Bend region off the West Florida coast, where color changes again depict days after release. Now the coupled CPR model suggests red tide landfalls off both the North Carolina and Alabama coasts.

depiction of plankton transport (Fig. 14). It now accounts for the 2007 decantation of Florida red tides from both the coastal and offshore epicenter regions of the WFS, respectively, to the Florida east coast of the SAB and off the Florida Panhandle to Alabama (Fig. 15). But, the model required an additional set of initial conditions, i.e. red tides fed initially by diazotrophs on the Florida Middle Ground (Fig. 1).

Previously, after first detection along western counties of the Florida Panhandle on 17 October 1996, a red tide of *K. brevis* and congeneric species, including *K. papilionacea*, led to a westward propagation of oyster accumulations of brevetoxins. By 9 November 1996, shellfish bed closures were enforced here and within

Louisiana coastal waters, east of the Mississippi River delta, at the state regulatory standards of >0.5 µg chl l^{-1} of *K. brevis* (Brown et al., 2006). Yet, these are relatively rare events on the northwestern WFS. Coastal blooms of *Karenia* spp. and dead fish have been observed off Pensacola, FL for just 16% of a 51-year interval [1957–2007] during 1960, 1964, 1969, 1990, 1996, 2000, 2005, and 2007.

Now the coupled CPR model replicated the 2007 red tide landfalls off both the North Carolina and Alabama coasts (Fig. 15). Satellite imagery provided validation data on 23 October 2007 of: (A) optical signatures of *T. erythraeum* (pale blue color) and *K. brevis* (reddish-black color); (B) total chlorophyll of the phytoplankton
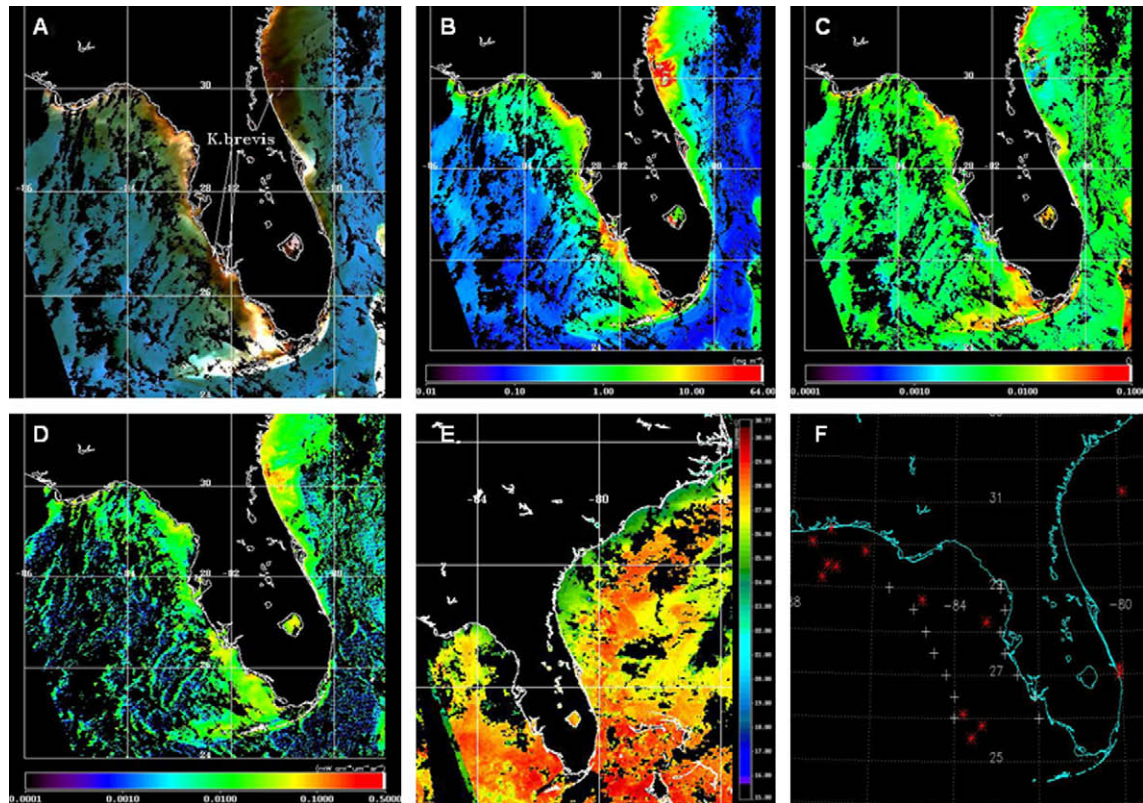
Fig. 15. Satellite imagery on 23 October 2007 of (A) optical signatures of *T. erythraeum* (pale blue color) and *K. brevis* (reddish-black color), (B) total chlorophyll of the phytoplankton community, (C) backscatter per unit chlorophyll, and (D) fluorescence line height to minimize CDOM contamination of the color signal of phytoplankton, and (E) sea surface temperatures, in relation to (F) the computed surface red tides on that day, when the red symbols now denote stocks of stocks of >34 µg chl l^{-1} of fish-starved *K. brevis* at a smaller growth rate of 0.08 day^{-1}. The white crosses indicate launch sites of surface drifters and entrained initial red tides on 6 September 2007.

community; (C) backscatter per unit chlorophyll; (D) fluorescence line height to minimize CDOM contamination of the color signal of phytoplankton; and (E) sea surface temperatures, in addition to *in situ* observations of *K. brevis* cell counts by FWRI.

The model's computed surface red tides on 23 October 2007 are the red symbols of Fig. 15f, denoting *K. brevis* of stocks of >34 µg chl l^{-1}. They were grown in the model at a fish-starved growth rate of *K. brevis* of only 0.08 day^{-1}, during transit of the water parcels. The white crosses of Fig. 15f indicate launch sites of surface drifters and entrained initial red tides on 6 September 2007. These simulation results suggest that spatial dislocations of the initial summer red tide growth along the coastline of the WFS are normal events during the fall maintenance season.

During 2001, after a summer export event to just mid shelf (Fig. 5), the coastal populations of *K. brevis* attained September biomass levels of ∼100 µg chl l^{-1}, like those of 2005 and 2006, but not of 2007 (Fig. 2). The population decreases of these local stocks during 1972, 1977, 1987, 1990, and 2007 (Fig. 2) were instead associated with even longer transits of *K. brevis* populations to as far away as Alabama and North Carolina coastal waters. The September biomasses of these physically diluted WFS red tides (Kierstead and Slobodkin, 1953), after export, were instead ∼1 µg chl l^{-1} (Fig. 2).

If red tides are indeed routinely exported, by physical decantation of entrained initial populations of *K. brevis* within ocean currents, away from at least the mobile adult fish populations, the reduction of this source of natural mortality from red tides may partially offset those from commercial and sport fishing. During the 1997–1998 small red tides (Fig. 2), for example, the fishing harvests of both *S. aurita* and *O. oglinum* increased during those years (Fig. 3), following increments of their C.P.U.E.s, and presumably stocks, in 1996 (Table 2). Recall that predation losses to serranid and lutjanid piscivores were then estimated to instead comprise >90% of the clupeid mortalities in 1997–1998 (Okey and Mahmoudi, 2002).

On the Florida Middle Ground and within Apalachee Bay, the zooplankton exhibit spring maxima of biomass accumulation (Grice, 1957; Austin and Jones, 1974), before the rare summer red tides. These zooplankton are, in turn, consumed by local clupeid populations, which are occasionally poisoned by the red tides (Ingle and Williams, 1966; Walsh et al., 2002). Over the last 50 years, only eight red tides and associated fish kills occurred along the Florida Panhandle coastline.

Yet, 69% of the landings of 2.2 million pounds of baitfish during 2001 were *O. oglinum* off Tampa Bay, compared to only 27% of the similar amount of 2.6 million pounds of baitfish caught off the Florida Panhandle (Mahmoudi et al., 2002), where red tide mortalities to all fish should be less. Since a large red tide was retained on the WFS during September 2001 (Fig. 2), we assume that physical exports to either Alabama, or North Carolina, coastal waters were then minimal. Over fishing by humans, rather than predation by "prudent" red tides and fish piscivores, is a more likely explanation for long term changes of the implied WFS clupeid stocks (Fig. 3).

Indeed, the annual C.P.U.E. for *O. oglinum* over the whole WFS increased by 30% during 2002, after the 2001 large red tide (Table 2). In the face of continued fishing pressure, the evolutionary strategy of thread herring as a spring spawner on the WFS (Houde, 1977b), with less larval susceptibility to predation by fall red tides, may no longer have conveyed a competitive advantage against the summer spawning *S. aurita* by 2007. After the 2005 and 2006 red tides, the annual C.P.U.E. of thread herring in 2007 was only ∼25% of that in 2002 (Table 2).

3.4. Prudent predation by red tides versus overfishing by humans

At higher trophic levels, yields of both king mackerel, *S. cavalla*, and red grouper, *E. morio*, (Fig. 3), as well as gag grouper, *Mycterop-*

erca microlepis, declined during the 1985 red tide (Fig. 2). These groupers, like red snapper, e.g. *Lutjanus campechanus*, and vermillion snapper, *R. aurorubens*, are desirable fish food at the top of the WFS food web, with a long history of exploitation by US commercial fishermen, since 1880 (Stearns, 1887) and earlier (Wood, 1883; Camber, 1955; Porch et al., 2007). All of these piscivores eat clupeids, which humans also fish, providing both competition and an assessment of the fluctuations of abundance of these fish predator and prey stocks.

In terms of annual catch per unit effort, the relative C.P.U.E.s of the dominant summer clupeid spawner, *S. aurita*, were the same during 2006 and 2007 (Table 2). Assuming that relative C.P.U.E. is an index of their adult abundance (Gulland, 1983), we infer that there was little interannual change of Spanish sardine stocks, as a consequence of 'prudent predation' by concurrent summer red tides. Over a longer decadal time interval, between the 1995 and 2005–2006 red tides, the annual C.P.U.E. of *S. aurita* actually increased ∼10-fold (Table 2).

In contrast, the relative annual C.P.U.E. of the dominant spring clupeid spawner, *O. oglinum*, during 2007 was 47% of that realized in 2006 (Table 2), implying that continued fishing over a few decades (Fig. 3) may now be impacting some of the WFS's food web components, and not others. After the 1995 red tide, the C.P.U.E. of thread herring in 1996 increased slightly. But by 2007, after the 2005–2006 red tides, it had decreased by ∼4-fold, compared to its C.P.U.E. during 1996 (Table 2).

As reflected in the seasonal C.P.U.E.s from the WFS (Fig. 16), *S. aurita* mainly spawns during summer. In 2007, it yielded a 33-fold larger annual commercial catch than that of *H. jaguana*, the other summer clupeid spawner (Houde, 1977b; Houde et al., 1979). Moreover, the monthly C.P.U.E.s of *S. aurita* during June–July 2006 of the 10-fold larger red tide (Fig. 2) were 2- to 3-fold larger than those of the same months in 2007 (Fig. 16d). These data suggest that red tide-induced mortalities had little impact on the survival of the Spanish sardines. We conclude that *K. brevis* is a prudent predator, compared to humans, within both evolutionary and resource management contexts.

The monthly C.P.U.E.s of thread herring, *O. oglinum*, reflect their spring spawning strategy as well (Fig. 16c). Unlike the Spanish sardine, however, the subsequent June 2006 C.P.U.E. was much smaller during the large red tide, than in the same month of June 2007 during the following small red tide. We thus infer that fishing mortality is of greater consequence for thread herring population dynamics than predation of red tides, outside their spring spawning window of larval survival on the WFS.

Serranid piscivores are also spring spawners on the outer WFS, with *M. microlepis* more abundant during March–April (Coleman et al., 1996; Fitzhugh et al., 2005) and *E. morio* instead dominant during April–May (Moe, 1969). Over the same decade of 1996–2007, when thread herring C.P.U.E.s and presumably their stocks declined 4-fold, those C.P.U.E.s of their serranid predators doubled for *E. morio* and remained the same for *M. microlepis* (Table 2). The selective decline of clupeid prey may have reflected increased consumption of *O.oglinum* juveniles and spawning adults by those fish predators, which may be more abundant during later spring, i.e. *E. morio*. The earlier spawning gag grouper may instead consume other baitfish, not as closely linked to fishing mortalities imposed by humans, i.e. Atlantic bumper and some shads.

In contrast, red, gray, and vermillion snapper, *L. campechanus, L. griseus,* and *R. aurorubens*, are mainly summer spawners within the same regions of the WFS (Houde et al., 1979; Allman and Grimes, 2002; Lyczkowski-Schultz and Hanisko, 2007). Over the same decade of 1996–2007, when Spanish sardine C.P.U.E.s and presumably their stocks increased 4-fold, the C.P.U.E.s of both lutjanid piscivores also increased as well, but only by 125–177%, not by 400% (Table 2). We thus infer that summer red tides also "prudently"
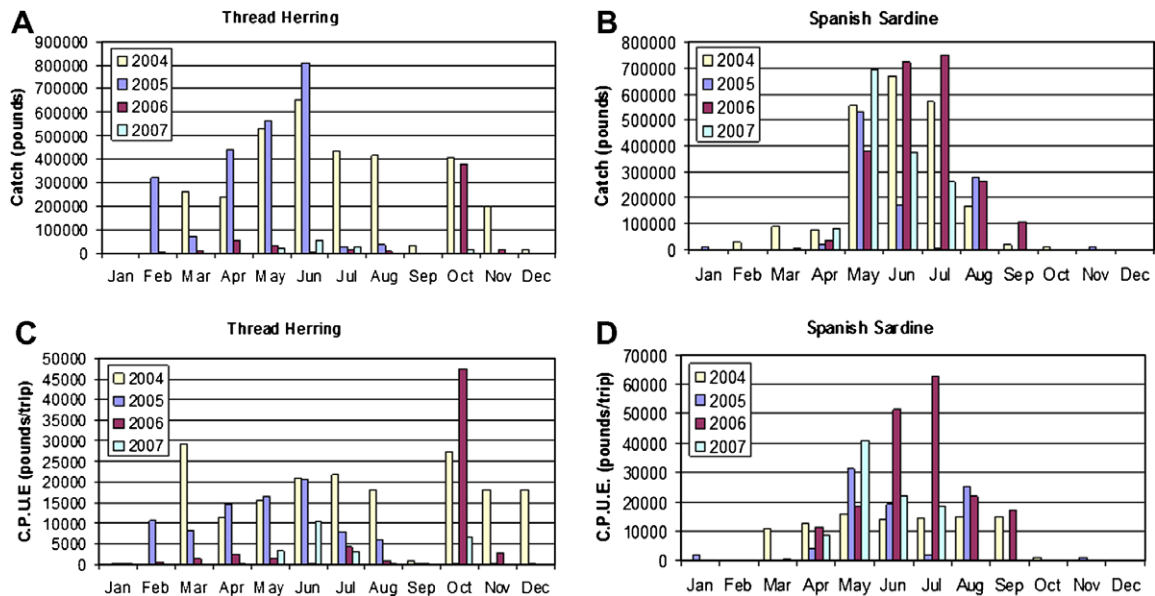
Fig. 16. The seasonal landings and C.P.U.E. of (A and C) thread herring and (B and D) spanish sardine during 2004–2007 from the West Florida shelf.

harvested these sardines, in addition to their losses imposed by adjacent fishermen and other marine piscivores (Fig. 16). Since fish predation by shelf-shaded, larger populations (Carder and Steward, 1985) of K. brevis is a positive feedback mechanism, involving upward migrations to harvest at the sea surface: light; sun-adapted diazotroph nutrients; and bloated, decomposing fish nutrients, fewer fish mean smaller red tides.

Finally, note that the C.P.U.E.s of the scrombrid piscivore, S. cavalla, also remained the same over the decade of 1996–2007, exhibiting no long-term trend. With no commercial fishery for their presumed prey of mainly round herring, information is thus not available on stock fluctuations of Etrumeus teres. It is a winter spawner on the outer WFS (Houde et al., 1989), when stronger seasonal winds (Yang and Weisberg, 1999), then effect greater offshore transports of fish eggs and larvae within the surface Ekman layer. However, numerous information is present on various life stages of the predator S. cavalla on the WFS (Grimes et al., 1990; DeVries and Grimes, 1997; Gledhill and Lyczkowski-Schultz, 2000), with broad definition of its trophic status here and within the SAB (Roelke and Cifuentes, 1997).

Moreover, E. teres is also a winter spawner on the downstream North Carolina shelf (Hare and Govoni, 2005), playing presumably the same role as prey for local populations of king mackerel there (Clardy et al., 2008). Yet, if winter round herring are not harvested by red tides of the WFS, nor seen there during spring surveys of shallow waters of <30 m depth (Pierce and Mahmoudi, 2001; Mahmoudi et al., 2002), any population variances of E. teres and S. cavalla may be in steady state, as an unexploited clupeid fishery (Houde, 1977a). Future modeling studies of physical transports of entrained plankton populations: either red tides in search of fish food; or larval fish during recruitment to older stages of sustainable fisheries (Cushing, 1990), must thus resolve these past opaque sets of observations, linking both the inner and outer WFS to downstream parts of the SAB.

4. Discussion

In terms of maintenance of these red tides, dead fish on the WFS are not just inconvenient olfactory indices of concurrent toxic shellfish and airborne pulmonary events for the adjacent humans. At summer temperatures, as much as 50% of some Florida fish de-

cay to inorganic forms of phosphorus and nitrogen within one day (Stevenson and Childers, 2004). Moreover, some clupeids also provide about 50% of the nitrogen supply for red tides (Table 1). Thus, both these fish and the diatom-based food web supporting them (Table 1) must be included as explicit state variables of future operational models of Florida red tides (Fig. 17).

Pressing societal issues of K. brevis plague the WFS, involving: red tide initiation, transport, land fall; associated ecological impacts on coastal food webs, i.e. death of fish, manatees (Landsberg and Steidinger, 1998; Flewelling et al., 2005), and sea birds at higher trophic levels; as well as the socioeconomic and health consequences of neurotoxic shellfish poisoning, asthmatic events, interrupted commercial/recreational harvests of molluscs, baitfish, groupers, snappers, mackerels, and lost tourism receipts. To deal with these and other coastal ocean related societal problems of storm surges, navigational hazards, and trajectories of disabled vessels, we formed a joint Center for Prediction of Red tides (CPR) at the University of South Florida and the Fish and Wildlife Research Institute of the Florida Fish and Wildlife Conservation Commission.

The CPR builds upon our combined physical and biological expertise of in situ sampling via an emergent coastal observing system, remote sensing, and both the ocean circulation and biological aspects of red tide modeling in relation to stock assessments of fish within upstream Florida coastal waters – to wit, the present analysis. However, the present and future major ecological aspects of continuing public concern, here and along the downstream southeastern United States seaboard, remain a larger set of societal problems as: abatement of any significant eutrophication; exacerbation of present overfishing; and future red tide strandings, involved in their decantation to tourist-prone coastal regions.

Red tides and fish kills of K. brevis are not just local Florida events, but common to the Gulf of Mexico, the SAB, and occasionally the MAB over the last three centuries, since at least 1696–1886 (Knowles, 1887; Andrews and Andrews, 1945; Brongersma-Sanders, 1957). Beginning in 1792 (Lerdo de Tejada, 1850), moreover, fish kills were recorded off the state of Veracruz, Mexico like those found on the Tabasco shelf in 1648 (Lopez Collogudo, 1688) and on the Texas shelf during 1529–1534 (Cabeza de Vaca, 1542). Time series of fish kills, and most importantly as a diagnostic tool for the likely causal agent of K. brevis, of dry coughs and throat irrita-
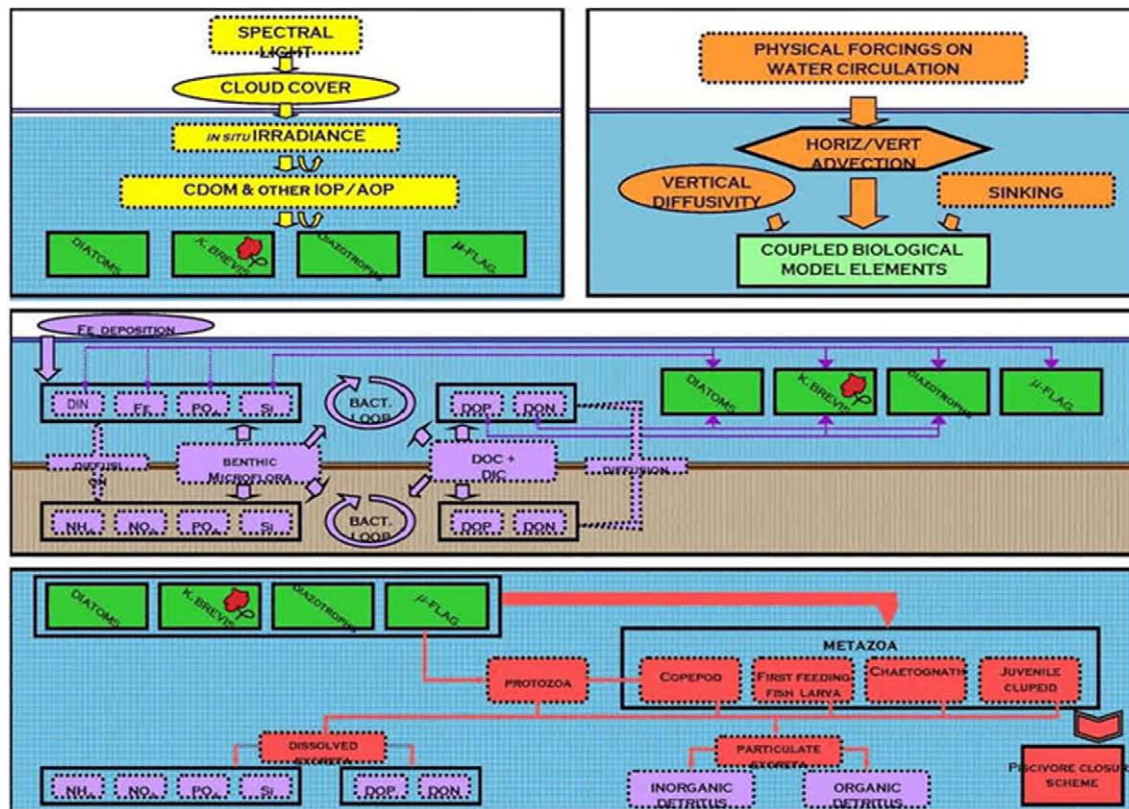
Fig. 17. Future ecological model, HABSIM, coupled to various nested circulation models, for eventual forecasts of an operational model of red tides along coastal regions of the southeastern United States, from the West Florida shelf to the South Atlantic Bight.

tions were then compiled for the Veracruz region during 1853, 1861, 1865, 1871, and 1875 (Nunez Ortega, 1879). He wrote "in the last days of October 1875, the inhabitants of Veracruz were repeatedly bothered by a dry cough caused by irritation of the throat... The north wind blew with major intensity ... and an enormous quantity of dead fish had washed ashore along the beach" (Magana et al., 2003).

Moreover, over an even longer millenium, we note that, unlike prehistoric Indians on Santa Cruz Island, harvesting sea food from the California Current with a resultant bone collagen of a δ^{15}N of 16.6‰, after 1150 (Walker and DeNiro, 1986), eastern Indians at the similar latitude of St. Catherines Island, Georgia had a smaller δ^{15}N of 12.8‰ (Table 1) by 1075 (Schoeninger et al., 1983). The Georgia Indians then also did not eat maize, but instead were predominantly marine resource harvesters of the adjacent SAB (Schoeninger et al., 1983).

At these latitudes, eastward propagation of Gobi dust storms to California are much rarer events, than westward transport of Saharan dust falls to Florida and Georgia (Duce and Tindale, 1991; Jickells et al., 2005). Within the SAB, the diazotrophs are, at times, dominant members of the plankton, amounting to >50% of the biomass (Dunstan and Hosford, 1977), downstream of aerosol influxes of Saharan dust. They have been associated with westward dust storms and toxic red tide events, since at least colonial times, as recorded by Darwin, Dickinson, Cabeza de Vaca, Nunez Ortega, Lerdo de Tejada, Lopez Collogudo, and others.

Within intermediate levels of the marine food web (Table 1), the zooplankton also reflect these isotope differences of both the primary producers and human consumers at higher trophic levels, with and without dust loading of the consequent nitrogen-fixers of lighter δ^{15}N. The zooplankton at the shelf-break, for example, have δ^{15}N of +5.4‰ within the upstream Antilles Current of the SAB

(Montoya et al., 2002), compared to +9.7‰ in the Southern California Bight (Mullin et al., 1984). Within costal regions, the δ^{15}N of estuarine zooplankton still reflect regional differences of nitrogen-fixation at the base of the food web, with values of +7.1‰ for zooplankton within Graveline Bay Marsh, Mississippi (Sullivan and Moncreiff, 1990), compared to +11.9‰ for pelagic invertebrates of the Tijuana River estuary, near San Diego (Kwak and Zedler, 1997).

To provide perspective on the food web yields of marine fish available to preColonial inhabitants of St. Catherines Island, Georgia during 1075 (Table 1), before they were forced to grow maize, with a δ^{15}N of +2.2‰ (Schoeninger et al., 1983), for subsequent Spanish slavers, historical observations of shipwrecked voyagers are available. For example, Jonathan Dickinson observed local Ais Indians fishing during 1696 along the east coast of Florida (Andrews and Andrews, 1945), as "In two hours time he got as many fish [striped mullet, *Mugil cephalus* – a detritivore, and red drum, *Scianenops ocellatus* – a piscivore] as would serve 20 men: there were others also fishing at the same time, so that fish was plenty ... boiled with scales, heads, and gills" served on "small palmetto leaves". Note that the same species of fish were also eaten much earlier at the Venice shell midden, along the Florida west coast, during ~1981 BP (Lightfoot and Ruppe, 1980; Fraser, 1980).

Another earlier shipwrecked Spaniard, Hernando d'Escalante Fontaneda, who lived at Calos with the Calusa Indians, near Fort Myers, from 1545 to 1566, wrote in 1575 about food sources for local Indians, north along the east Florida coast (True, 1945). He said that within the downstream SAB, off "Santa Elena" [Tybee Island, Georgia – Milanich (1995)], "the natives are poor ... some seed pearls are found there in certain conchs. The cat fish, oysters (roasted or raw) ... While they kill them, the women bring wood to cook or broil on grates" True (1945). Thus, not surprisingly,

the bone collagen of disinterred Indians of St. Catherines Island, GA had a δ^{15}N of +12.8‰ during 1075 (Schoeninger et al., 1983). This isotope marker places them at the apex of basically a subsistence marine food web (Table 1), supported at the bottom by nitrogen sources from ~50% nitrogen-fixers and 50% decomposing clupeids.

Red drum feed on fish, which eat zooplankton, like king mackerel and vermillion snapper (Table 1). Whereas, mullet consume bacterial degraded phytodetritus at a lower trophic level of the coastal food web. The plant diet of M. cephalus along Sapelo Island, GA is of equal phytoplankton origin, not just marsh grasses, Spartina spp., with a resultant δ^{15}N of + 7.6‰ (Peterson and Howarth, 1987), similar to the local WFS zooplanktivore clupeids (Table 1). The same light δ^{15}N of + 7.6‰ for M. cephalus is also found within the upstream northern Gulf of Mexico, in Mississippi coastal waters (Sullivan and Moncreiff, 1990). But, again without the WFS/SAB label of nitrogen-fixation, the same species of mullet in southern California coastal waters has instead a heavier δ^{15}N of + 16.0‰ (Kwak and Zedler, 1997).

Accordingly, for continued description of these complex interactions of the biotic response to physical forcing, any future operational model for automated predictions of the onset, maintenance, and dispersal of red tides within the WFS, the adjacent Gulf of Mexcio, and the downstream SAB and MAB must contain a minimal set of state variables (Fig. 17). Based upon these and prior simulation analyses, the physical variables are the hourly three-dimensional flow fields and mixing coefficients, as well as piston velocities across the air–sea interface, from a set of nested circulation models, providing appropriate far-field boundary conditions.

The embedded ecological model, HABSIM (Fig. 17), must also include spectral light; water-leaving irradiance; absorbence; backscatter; nitrate; ammonium; phosphate; silicate; dissolved iron; DIC; dissolved organic forms of carbon/nitrogen/phosphorus; CDOM; and bacterioplankton; that mediate competition among the functional groups of phytoplankton. These end results of the coupled circulation and ecological models, expressed as the respective chlorophyll contents of diatoms, K. brevis, microflagellates, and T. erythraeum, must be updated continuously with satellite data, e.g. Figs. 5, 12, 13, and 15, in a data assimilation mode.

Such phytoplankton functional groups must also be harvested by simulated zooplankton herbivores, i.e. protozoans and copepods (Milroy et al., 2008); as well as by bioturbating benthos (Darrow et al., 2003), in a future operational model of both red tide initiation and maintenance (Fig. 17). Finally, to provide a dead fish source of maintenance nutrients, these modeled zooplankton, in turn must be harvested by the dominant clupeids of the WFS: threadfin and round herring; scaled and Spanish sardines. As in the case of our prior use of extant physical circulation models (Weisberg et al., 2009), we have now begun to also adapt the existing FWRI (Okey and Mahmoudi, 2002) ECOPATH model of higher trophic levels on the WFS.

Fishing mortality, compounded by K. brevis culling, on the WFS of sardines and herrings is no longer thought to be small, based on our isotope budget (Table 1), compared previously to just natural harvests by grouper and other piscivores during 1997–1998 (Okey and Mahmoudi, 2002). A decade later, increased awareness and thus sampling has led to the realization that small and large red tides of Karenia brevis are annual events along the West coast of Florida, with establishment of a multi-decadal time series of their initiation, intensity, and duration each year (Fig. 2). The small red tides left behind on the WFS are a consequence of downstream export of phytoplankton, reminiscent of the "Tragedy of the Commons" (Hardin, 1968).

The historical record of Florida red tides and their related effects of downstream fish kills over the last ~125 years, since 1886, and perhaps over the last ~925 years, since 1075, is confirmed by the numerical results of the simulation analyses of recent 2006–2007 events (Figs. 11–15). These calculations encourage us to believe that future versions of CPR's HABSIM (Fig. 17) will allow us to progress past the present admittedly simple formulation of this first CPR coupled model.

It assumed: no other competitors of red tides; no grazing stress on K. brevis populations; and no diel vertical migration. Insufficient nutrients did curtail their growth, during an implicit fish-fed maintenance phase without sufficient fish prey, at a constant daily rate. Such a simple simulation case is an admittedly naive scenario, with also no data assimilation, beyond specification of the different initial conditions during fall of 2006 and 2007. Nevertheless, we were able to replicate the in situ and satellite observations of red tides within the eastern Gulf of Mexico and the downstream SAB on 23 October 2007 (Fig. 15a–d), with nutrient-starved computed stocks of ~43 µg chl l^{-1} of K. brevis off: Orange Beach, AL; Key West, FL; Fort Pierce, FL; and Wilmington, NC (Fig. 15f).

Other local WFS model results for both fall 2006 and 2007, validated by additional satellite data (Figs. 12 and 13), suggest that future CPR simulation analyses of eutrophication, overfishing, and red tide strandings may next be improved upon inclusion of (1) data assimilation and (2) explicit description (Fig. 17) of the recycled nutrient sources during the maintenance phases of red tide outbreaks. Without the dedication, persistence, and continuing insight of one of our colleagues, Karen Steidinger, this and prior (Walsh and Kirkpatrick, 2008) synthesis efforts would have been impossible. We look forward to implementation of an operational version of the coupled ROMS, HYCOM, HABSIM, and ECOPATH models (Fig. 17) over the next few years.

Acknowledgments

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