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An unusual mortality event for bottlenose dolphins links to altered diets resulting from ecological changes

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Bottlenose dolphins (*Tursiops truncatus*) often have served as sentinel species for ecological changes in estuarine and marine systems. In 2013, the population of bottlenose dolphins in the Indian River Lagoon exemplified this role because an unusual mortality event involving malnourishment followed ecological changes. Potential causes of mortalities were investigated using surveys of key habitats and abundances of potential prey, stable isotope ratios from dolphins and potential prey, estimations of energy densities for key types of prey, and surveys of environmental conditions. The ecology of the lagoon changed substantially after 2011, with shading by intense, extensive, and long-lasting blooms of phytoplankton resulting in a > 50% decrease in the mean cover of seagrass and a > 75% decrease in mean biomass of drifting macroalgae. These reductions in key structural habitats preceded changes in ratios of stable carbon and nitrogen isotopes in samples of muscle from stranded dolphins. Changes in isotopic ratios indicated 9–25% increases in consumption of *Archosargus rhomboidalis* (sea bream) and 14–20% decreases in consumption of *Elops saurus* (ladyfish). The changes in diet reflected availability of prey, with a fisheries independent monitoring program yielding parallel changes in catches of sea bream and ladyfish. The dietary shift may have contributed to the 2013 unusual mortality event because sea bream yielded a lower mean energy density than ladyfish. Additionally, below average temperatures in 2010 and 2011 may have stressed some dolphins, particularly those that were garnering less energy from their diet. In contrast, osmotic stress was unlikely, given increasing salinities in the system. Overall, the results provided an example of links from blooms of phytoplankton to changes in habitat, availability of prey, and diets of dolphins followed by an unusual number of mortalities. Loads of nutrients that fueled the blooms are being reduced, with safe loads scheduled to be reached in 2035 and recognition that additional, adaptive efforts may be necessary to obviate harmful algal blooms.

KEYWORDS

Tursiops truncatus truncatus, Indian River Lagoon, unusual mortality event, phytoplankton bloom, habitat loss, stable isotope ratios, energy density

1 Introduction

Bottlenose dolphins (*Tursiops truncatus*) are large, long-lived, mammalian predators that can serve as sentinel species (Bossart, 2006). In part, their value as indicators of healthy estuarine and marine systems is due to life spans of 40–60 years and a reliance on intact trophic webs (Bossart, 2006). The structure of trophic webs matters because bottlenose dolphins require large quantities of prey to meet daily energetic needs and their diets often include prey from multiple trophic levels and multiple habitats (Shane et al., 1986; Berens McCabe et al., 2010; Rossman et al., 2013; 2014; 2015). Thus, ecological changes that alter trophic links can affect feeding by bottlenose dolphins in a way that is detrimental to their health (Wild et al., 2019).

Identifying changes in feeding by bottlenose dolphins requires repeated sampling. Obtaining the requisite samples without disrupting individuals or a population is challenging, and it can involve examining stomach contents and visual observations of feeding (Barros and Wells, 1998). However, stomachs of deceased individuals may be empty, and differences in the rates of digestion among prey may bias results (Rossman et al., 2013). Furthermore, visual observations entail considerable time and expense, and surveys made from above the water's surface may yield results that overestimate consumption of prey living higher in the water column (Rossman et al., 2013). Fortunately, analysis of stable isotopes in frozen and archived samples of various tissues can elucidate the feeding habits of bottlenose dolphins (Rossman et al., 2013; 2014; 2015; Browning et al., 2014b). Ratios of stable isotopes of carbon ($\delta^{13}\text{C}$) differ among primary producers, with signals transferred through trophic webs to consumers, such as dolphins (Peterson and Fry, 1987). Thus, $\delta^{13}\text{C}$ values can distinguish individuals that consistently feed in habitats with isotopically distinctive primary producers, such as seagrasses and their epiphytes that tend to be enriched in ^{13}C (Hemminga and Mateo, 1996; Fry, 2006; Rossman et al., 2013; Duarte et al., 2018). In addition, increasing ratios of stable isotopes of nitrogen ($\delta^{15}\text{N}$) have a strong, positive correlation with increasing trophic levels (Peterson and Fry, 1987; Harrigan et al., 1989; Gould et al., 1997; Newsome et al., 2010). Furthermore, these ratios can document changes in the source of nitrogen incorporated into the base of a trophic web, with higher ratios often indicating the presence of wastewater (McClelland and Valiela, 1997; Rossman et al., 2013; Duarte et al., 2018). In combination, isotopic ratios of carbon and nitrogen can differentiate changes in feeding for individuals and populations of bottlenose dolphins (Rossman et al., 2013; 2014; 2015; Browning et al., 2014b).

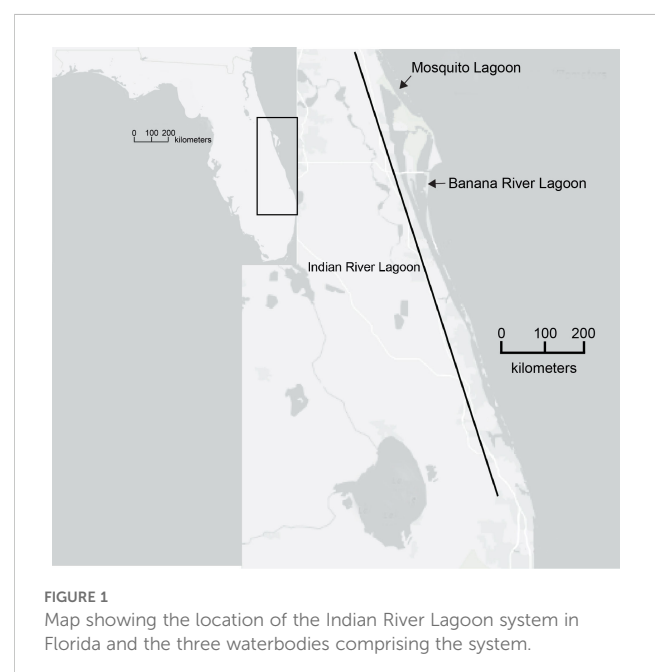
Analyzing stable isotopes to identify changes in the diets of bottlenose dolphins in the Indian River Lagoon (IRL) may help explain the most recent spate of mortalities. Three unusual mortality events (UMEs) in 2001 (34 mortalities), 2008 (47 mortalities), and 2013 (77 mortalities) represent the highest number of events recorded for any resident population of coastal bottlenose dolphins in the United States (Stolen et al., 2007; NOAA, 2015; Durden et al., 2023a; <https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events>).

In particular, altered diets may be a major factor in the 2013 UME, which is the only event attributed to a known cause that is listed as “ecological factors.” This event follows substantial changes in ecological conditions throughout the IRL that began in 2011 and include decreases in key structural habitats used by the prey of dolphins. Decreases in seagrass and drifting macroalgae result from shading by intense, extensive, and long-lasting blooms of phytoplankton (Morris et al., 2021; 2022; Phlips et al., 2021; Hall et al., 2022). An unresolved question is whether such ecological changes are linked to a shift in feeding by bottlenose dolphins that affects their health detrimentally.

This study assesses links between the diets of dolphins and ecological changes with a focus on Mosquito Lagoon, Banana River Lagoon, and the northern section of the Indian River Lagoon proper by examining ratios of stable isotopes of carbon and nitrogen in archived samples of teeth and muscle collected from carcasses of bottlenose dolphins found in the system. In addition, the study characterizes ecological factors influencing the health of dolphins by evaluating availability of prey, changes in key structural habitats, differences in energy density among prey, osmotic stress from low salinity (Carmichael et al., 2012; Ewing et al., 2017), and thermal stress from low temperatures (Williams et al., 2001; Yeates and Houser, 2008; Carmichael et al., 2012). The primary goal is to elucidate factors contributing to mortality of dolphins in 2013.

2 Materials and methods

The study took place in the IRL, a shallow, bar-built, estuarine system along the east coast of Florida comprising three, interconnected waterbodies: Mosquito Lagoon, Banana River Lagoon, and the Indian River Lagoon proper that spans ~250 km (Figure 1). Depths averaged 1.9 m, and semidiurnal lunar tides



ranged from 0.2 cm to 18.1 cm, with more substantial changes in water level driven by wind and the seasonal rise and fall of the coastal ocean (Smith, 1987; Pitts, 1989; Steward et al., 2005). Significant exchange with the coastal ocean was limited to five inlets located primarily in the southern portion of the Indian River Lagoon proper. This configuration contributed to residence times of over a year in the portions of the system that were far from inlets (Steward et al., 2005).

Substantial ecological changes appeared in the system after 2011. The mean biomass of phytoplankton in blooms increased from 2–5 $\mu\text{g carbon ml}^{-1}$ to 14–24 $\mu\text{g carbon ml}^{-1}$, and elevated levels of biomass persisted for 3–6 months (Phlips et al., 2021). The resultant shading led to a loss of approximately 20,000 ha of seagrass, a decrease in mean percent cover of seagrass from ~20% to ~4%, and a loss of 21%–93% of drifting macroalgal biomass (Morris et al., 2021; 2022; Hall et al., 2022). Such drastic changes in key structural habitats could have altered the trophic web and affected feeding by bottlenose dolphins.

A resident stock of a nominotypic subspecies of common bottlenose dolphins (*Tursiops truncatus truncatus*) had a mean population size of approximately 1,032 individuals (Durden et al., 2021). These dolphins remained in the IRL year-round, and they exhibited strong site fidelity, linear ranges that averaged ~28 km, feeding at similar trophic levels, and slight variations in the proportions of prey comprising their diets (Odell and Asper, 1990; Mazzoil et al., 2005; Browning et al., 2014b; Durden et al., 2019). Several ecological and health related studies of this population documented a variety of stressors, including compromised immune systems, morbillivirus infections, respiratory infections, high body burdens of mercury, increasing burdens of chemical contaminants, accumulation of algal toxins, and interactions with fishing gear (Odell and Asper, 1990; Bossart et al., 2003; Johnson-Restrepo et al., 2005; Goldstein et al., 2006; Reif et al., 2006; Durden et al., 2007; 2009; 2021; Stolen et al., 2013; Fire et al., 2020). Given such a baseline level of stress, additional stress from changes that detrimentally affected feeding or metabolism could have contributed to an unusual mortality event (UME).

To evaluate links among habitats, potential prey, and the diet of dolphins, this study relied on multiple sources of data. Hubbs-SeaWorld Research Institute provided samples of teeth and muscle from stranded dolphins for analysis of stable isotopes. A fisheries independent monitoring program, undertaken by the Florida Fish and Wildlife Conservation Commission, provided samples of fishes known to be eaten by dolphins in the IRL (Barros, 1993) for isotopic analyses and calculation of energy density, along with catch per unit effort for common prey and biomass of drifting macroalgae (FWC-FWRI, 2016). Additional data on the biomass of drifting macroalgae and data on percent cover of seagrass came from surveys of fixed transects by the St. Johns River Water Management District (Hall et al., 2022; Morris et al., 2022).

Teeth came from stranded, deceased dolphins found in the IRL between 1991 and 2015. Stable isotopes of carbon and nitrogen were analyzed in samples from 2–3 mm near the tip of the crown of each tooth. The collagen in this region was formed during gestation or before a newborn calf reached one year of age; therefore, the carbon

and nitrogen isotopic signatures were derived from the maternal diet with any relevant enrichment, and they were unaffected by subsequent feeding (Rossman et al., 2013; Evacitas et al., 2017). A DremelTM tool separated the crown from the rest of the tooth, and the resulting sample was demineralized in 1N hydrochloric acid for 72 h, which left the collagen. The collagen was dried, and a 1-mg aliquot was transferred to a tin cup for analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The birth year for dolphins was estimated from counts of dentinal growth layer groups, which was treated as the year the collagen was created (Hohn et al., 1989).

Muscle was obtained from stranded, deceased dolphins found between 1993 and 2013, which spanned the 2001, 2008, and 2013 UMEs. Stable isotopes in muscle reflected diets over multiple months (Vander Zanden et al., 2015; Browning et al., 2014a). Samples were freeze-dried, lipids were extracted, and the resulting sample was homogenized to a fine powder in a ball and capsule amalgamator (Crescent Industries). Aliquots of approximately 1 mg were transferred to tin capsules for analysis of stable isotopes of carbon and nitrogen.

Abundances of stable isotopes of carbon and nitrogen in teeth and muscle from dolphins were measured with a EurovectorTM elemental analyzer interfaced to an Elementar IsoprimeTM mass spectrometer. Standards that calibrated relative to Vienna Pee Dee Belemnite for carbon and air for nitrogen also were analyzed, with a precision of $\pm 0.2\text{‰}$. Isotopic ratios were calculated as:

$$\delta X = \left\{ (R_{\text{sample}} - R_{\text{standard}}) - 1 \right\} \times 1,000$$

where X was ^{13}C or ^{15}N and R was a ratio of the abundances of the heavier and lighter isotopes, i.e., $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Potential prey were collected from sites that spanned the IRL via hauls of a 183-m $\times$ 2.5-m center-bag seine with 38-mm stretched nylon mesh (FWC-FWRI, 2016). Every other month from 2000 to 2013, fish were culled from seines deployed from a vessel in a rectangle adjacent to the shoreline. Markings at 40 m from each end of the net helped guide consistent deployments. The net was hauled by hand, and it swept approximately 4,120 m^2 (40 m $\times$ 103 m) in ≤ 2.5 m of water, which overlapped the depth of water where dolphins commonly forage (Durden et al., 2019). Individuals of targeted species were frozen immediately and stored at -20°C until processed.

In the laboratory, whole fish were processed to yield average isotopic ratios across all tissues, which has proven useful in characterizing diets (Cherel et al., 2005; Giménez et al., 2016). In the IRL, yellowfin menhaden (*Brevoortia smithi*) hybridized with Atlantic menhaden (*B. tyrannus*), so they were treated as menhaden (*Brevoortia* spp.; Dahlberg, 1970). Furthermore, fish identified as croaker were not a genetic match for either Atlantic croaker (*Micropogonias undulatus*) or whitemouth croaker (*M. furnieri*), so they were treated as croaker (*Micropogonias* spp.; Vincent et al., 2019). Lipids were extracted from all samples using petroleum ether. Subsamples were frozen at -80°C until analyzed. Frozen tissues were ground to a fine powder using a Wig-L-Bug Amalgamator (Crescent Dental Manufacturing), and aliquots (0.9–1.2 mg) were sealed in 5 mm $\times$ 9 mm tin capsules. Samples were shipped to the Stable Isotope and Ecology Lab, University of

Georgia, Athens, Georgia for analysis by mass spectrometry (Thermo Finnigan DELTAplus and DELTA C). Standard reference materials for ^{15}N and ^{13}C were used to calibrate isotopic values to atmospheric nitrogen and Vienna Pee Dee Belemnite, respectively. For both isotopes, analytical errors were ± 0.01 standard error based (SE) on analyses of bovine tissue. Quality assurance for stable isotope ratios was evaluated by running a known standard for every 12 samples of potential prey.

Isotopic ratios were analyzed to address two questions: 1) did ratios in collagen from teeth exhibit trends indicative of changes in loading of ^{13}C or ^{14}N that were transferred to dolphins and 2) did ratios in muscle indicate changes in diets among three groups of years selected to differentiate UMEs. Any variations in the diets of dolphins were examined in the context of changes in the availability of potential prey, cover of seagrass, and biomass of drift macroalgae.

Trends in isotopic ratios in collagen from the crown tips of teeth were evaluated by regressing those values against estimated years of birth. The regressions based on $\delta^{13}\text{C}$ values were meant to identify changes in the relative amount of ^{13}C in the atmosphere due to the burning of depleted fossil fuels or the Suess effect (Quay et al., 2003; Rossman et al., 2013). The regressions based on $\delta^{15}\text{N}$ values were meant to identify changes in the relative amount of ^{15}N introduced into the lagoon from sewage and septage, which are enriched in ^{15}N (McClelland and Valiela, 1997; Rossman et al., 2013; Duarte et al., 2018). If the estimated Suess effect or the change in ^{15}N over the full period of record was statistically significant, individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were adjusted to account for the appropriate effect before further analysis.

Variations in diets were examined with MixSIAR applied to stable isotope ratios in muscle from dolphins and means and standard errors for ratios from whole prey (Stock and Semmens, 2016). The analyses examined temporal variation in diets for two age classes because this approach yielded more than ten replicates in each cell of the models and because previous work had shown that stable isotope ratios did not differentiate diets of female and male dolphins in the IRL (Browning et al., 2014b). Thus, the models involved two fixed factors and their interaction: age class parsed as adult (≥ 220 cm from the tip of the rostrum to the median notch in the tail) or non-adult (< 220 cm in length) and period parsed as early, mid, or late. The early period spanned 1993–1999, which preceded the first UME in 2001. The mid period spanned 2000–2010, which was approximately a decade after ^{14}N enriched discharges from sewage treatment plants were removed from the lagoon (Indian River Lagoon National Estuary Program, 1996) and included UMEs with undetermined causes in 2001 and 2008 (www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events). The late period spanned 2011–2013, which included the first major bloom of phytoplankton, loss of vegetated habitats, and the UME in 2013 that was attributed to ecological factors (www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events). Before analysis, the isotopic ratios for muscle from dolphins were adjusted for any significant Suess effect and any significant trend in $\delta^{15}\text{N}$. In addition, $\delta^{15}\text{N}$ values were adjusted by 2‰ for trophic enrichment, with that factor calculated by previous comparisons of

isotopic ratios of muscle from stranded dolphins with isotopic ratios of prey commonly found in stomach contents or identified via analysis of deoxyribonucleic acid in feces (Rossman et al., 2013).

Changes in diets were placed in the context of additional stresses on dolphins and their prey. The likelihood of altered trophic webs was deduced from temporal coherence between dietary changes and changes in availability of potential prey and status of their habitats. Metabolic stress was explored by examining variation in energy density among prey that characterized changes in diets according to analysis of stable isotopes. Osmotic and thermal stress were assessed by evaluating data on salinities and water temperatures, respectively.

Trophic webs were evaluated using data on availability of potential prey and the habitats they utilize. Changes in availability were assessed using data from hauls of the 183-m seine that provided samples for isotopic analyses (FWC-FWRI, 2016). The same hauls also provided information on bycatch of drifting macroalgae, which represented an alternative habitat for prey of dolphins. Macroalgae were quantified to the nearest 0.1 gallon in the field, with reliable data containing a mixture of species due to the challenges associated with identifying species visually. These data were converted to dry weights using a conversion factor of $99.24 \text{ g DW gallon}^{-1}$ that was derived empirically. In May and June 2012, samples containing up to 5 gallons of mixed macroalgae were collected at several sites, transferred to mesh bags, and spun to remove excess water. The mesh bags were weighed to yield wet weights per gallon, the algae were dried at 80°C and reweighed to yield dry weights (DW) per gallon, and the conversion factor was derived from a regression forced through the origin. Multiplying gallons of drift macroalgae by the conversion factor and dividing the results by the area sampled by the seine yielded g DW m^{-2} for macroalgae. Additional data on the biomass of drifting macroalgae and data on the mean percent cover of seagrass, another structural habitat, came from surveys of fixed transects spanning the IRL (Hall et al., 2022; Morris et al., 2022). Fixed transects were surveyed primarily in summer and winter, which approximated times of annual maximum and minimum abundance of seagrass shoots (Virstein and Morris, 1996). The location of each transect was marked with poles, and the path to be surveyed was delineated by a graduated line extending perpendicularly from the shoreline to the deep end of the seagrass canopy, which meant transects extended for 15–1,900 m across depths to 1.8 m. At predesignated points along transects, a suite of standardized, non-destructive measurements was taken within a 1-m^2 quadrat divided by strings into 100 cells, each $10 \text{ cm} \times 10 \text{ cm}$. The relevant measurement for seagrass was percent cover, and the relevant measure for drifting macroalgae was a visual estimate of the biomass of all species expressed as an index (0–5). Indices were converted to biomass using coefficients derived from regressions based on the dry weights of replicate samples for each value of the index, i.e., $0 = 0 \text{ g DW m}^{-2}$, $1 = 0.35 \text{ g DW m}^{-2}$, $2 = 1.98 \text{ g DW m}^{-2}$, $3 = 21.37 \text{ g DW m}^{-2}$, $4 = 47.74 \text{ g DW m}^{-2}$, and $5 = 141.94 \text{ g DW m}^{-2}$ (Hall et al., 2022).

Energy densities for individual samples of prey spanning all years were analyzed with a PERMANOVA that was based on

Euclidean distances and treated the groups of prey as a fixed factor (Anderson et al., 2008). Energy density was estimated from data on water content, lipid content, and ash weight. Water content was calculated as the difference between wet weight and freeze-dried weight. Lipid content was determined gravimetrically after extraction with petroleum ether. Ash weight was measured after combusting samples at 550°C. Protein content was calculated as the difference between wet weight and the sum of water content, lipid content, and ash weight. Energy density (ED) in kJ g^{-1} was estimated from the percent of wet weight represented by lipids (%L) and protein (%P) according to:

$$ED = (37.7 \times \%L) + (16.8 \times \%P)$$

Data from the long-term sampling of water quality by the St. Johns River Water Management District were used to assess osmotic and thermal stress (St. Johns Water Management District, unpublished data). Osmotic stress was evaluated by examining mean monthly salinities from multiple stations in each of the three waterbodies. Similarly, thermal stress was evaluated using mean monthly water temperatures for the waterbodies.

3 Results

Teeth came from 44 dolphins born between 1957 and 2015, and the samples included teeth from non-adult and adult males and females (Table 1). Values of $\delta^{13}\text{C}$ decreased significantly over the 58 years at the rate of 0.012‰ per year (Figure 2A) and values corrected for this decrease did not vary significantly ($R^2 = 0.0001$, $df = 1, 42$, $p = 0.94$), so $\delta^{13}\text{C}$ values for muscle from dolphins were adjusted for this Suess effect in subsequent analyses. The adjustments were calculated by multiplying the rate of change in $\delta^{13}\text{C}$ values by the difference between the year a sample was collected and 1993, the year the earliest samples were collected. Isotopic ratios of nitrogen were not adjusted beyond the 2‰ enrichment factor because $\delta^{15}\text{N}$ values from teeth did not show a strong relationship with the year of birth (Figure 2B).

Twelve groups of potential prey were delineated based on isotopic ratios, feeding habits, and taxonomy of 2,751 individuals from fifteen taxa that yielded at least ten individuals (Table 2; Figure 3A). The groups were 1) menhaden (*Brevoortia* spp.); 2) Atlantic threadfin herring (*Opisthonema oglinum*); 3) spotted seatrout (*Cynoscion nebulosus*); 4) croaker (*Micropogonius* spp.); 5) southern kingfish (*Menticirrhus americanus*); 6) oyster toadfish (*Opsanus tau*); 7) silver perch (*Bairdiella chrysoura*); 8) ladyfish (*Elops saurus*); 9) scaled sardine (*Harengula jaguana*); 10) sea bream (*Archosargus rhomboidalis*); 11) pigfish, pinfish, and spot (*Orthopristis chrysoptera*, *Lagodon rhomboides*, and *Leiostomus xanthurus*) that were combined because they are benthic predators inhabiting seagrass with similar isotopic ratios; and 12) striped and white mullet (*Mugil cephalus* and *M. curema*) that were combined because they are members of the same genus with similar isotopic ratios.

These groups of potential prey bracketed mean isotopic ratios for samples of muscle from 147 dolphins apart from samples taken from 17 non-adults and 14 adults between 1993 and 1999 (Table 1; Figure 3B). The mean isotopic ratios for non-adult and adult dolphins indicated progressive depletion of ^{13}C and ^{15}N in muscle from 1993–1999 through 2000–2009 (n for non-adults = 17 and n for adults = 43) to 2011–2013 (n for non-adults = 11 and n for adults = 45), with adults exhibiting the largest shift (Figure 3B).

The results from MixSIAR indicated that the model with two fixed factors, age and period, yielded the best predictions of diets (Table 3). The Gelman diagnostic (0 of 228 variables > 1.05) indicated convergence of the model using three chains with 300,000 iterations, burn-ins of 200,000, and thinning by 100, and the Geweke statistics also indicated reasonable convergence, with 3%–6% of the 228 values having z-scores outside the range of ± 1.96 . The epsilon values for $\delta^{13}\text{C}$ (mean $\pm$ SE = 4.2 ± 1.2) and $\delta^{15}\text{N}$ (9.8 ± 3.3) indicated that the data did not include all prey that contributed to isotopic ratios for dolphins, but the available data supported detection of potential changes in diets. In fact, the diets of both non-adult and adult dolphins changed over the three periods (Figure 4). For non-adult dolphins across the periods 1993–1999 to 2000–

TABLE 1 Samples from stranded dolphins available for analysis of stable isotopes.

Age class	Sex	Teeth	Muscle			
			Early 1993–1999	Mid 2000–2010	Late 2011–2013	Total
Non-adult	Unknown	13	0	0	0	0
	Female	3	6	6	7	19
	Male	7	11	11	4	26
	Subtotal	23	17	17	11	45
Adult	Unknown	3	1	2	6	9
	Female	9	9	26	23	58
	Male	9	4	15	16	35
	Subtotal	21	14	43	45	102
Total		44	31	60	56	147

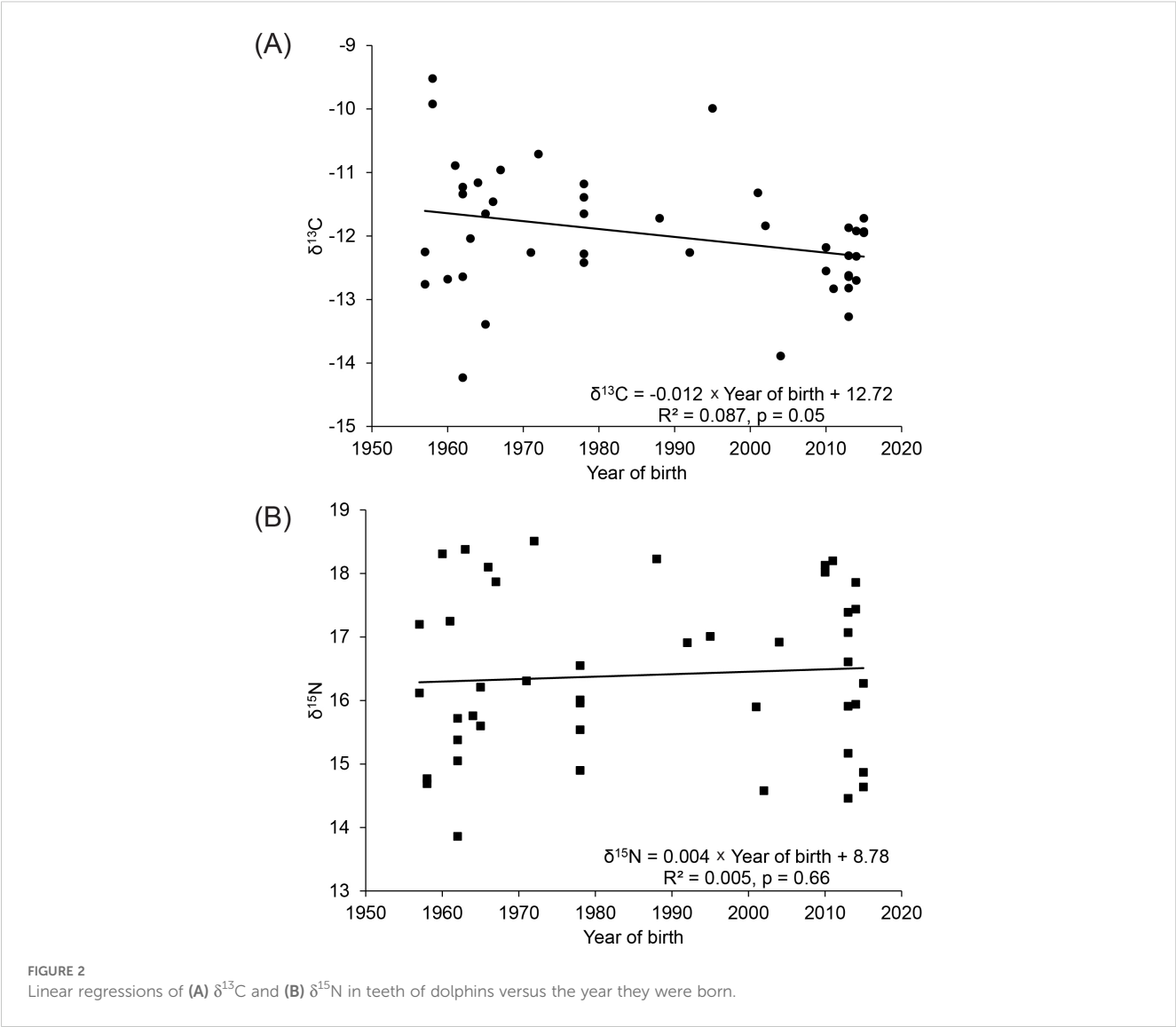


TABLE 2 Samples of potential prey available for analysis of stable isotopes and energy density.

Taxon	Name	Count
<i>Harengula jaguana</i>	scaled sardine	10
<i>Elops saurus</i>	ladyfish	11
<i>Archosargus rhomboidalis</i>	sea bream	15
<i>Opsanus tau</i>	oyster toadfish	32
<i>Opisthonema oglinum</i>	Atlantic threadfin herring	47
<i>Brevoortia</i> spp.	menhaden	65
<i>Micropogonius</i> spp.	croaker	88
<i>Menticirrhus americanus</i>	southern kingfish	106
<i>Cynoscion nebulosus</i>	spotted seatrout	145
<i>Leiostomus xanthurus</i>	spot	177

(Continued)

TABLE 2 Continued

Taxon	Name	Count
<i>Orthopristis chrysoptera</i>	pigfish	197
<i>Mugil cephalus</i>	striped mullet	264
<i>Bairdiella chrysoura</i>	silver perch	479
<i>Lagodon rhomboides</i>	pinfish	548
<i>Mugil curema</i>	white mullet	567
Total		2,751

2010, changes in diet greater than 1% involved increased feeding on ladyfish (median contribution to diets changed from 42% to 47%), mullet (median contribution to diets changed from 6% to 10%), and scaled sardines (median contribution to diets changed from 5% to 9%) and corresponding decreased feeding on silver perch (median

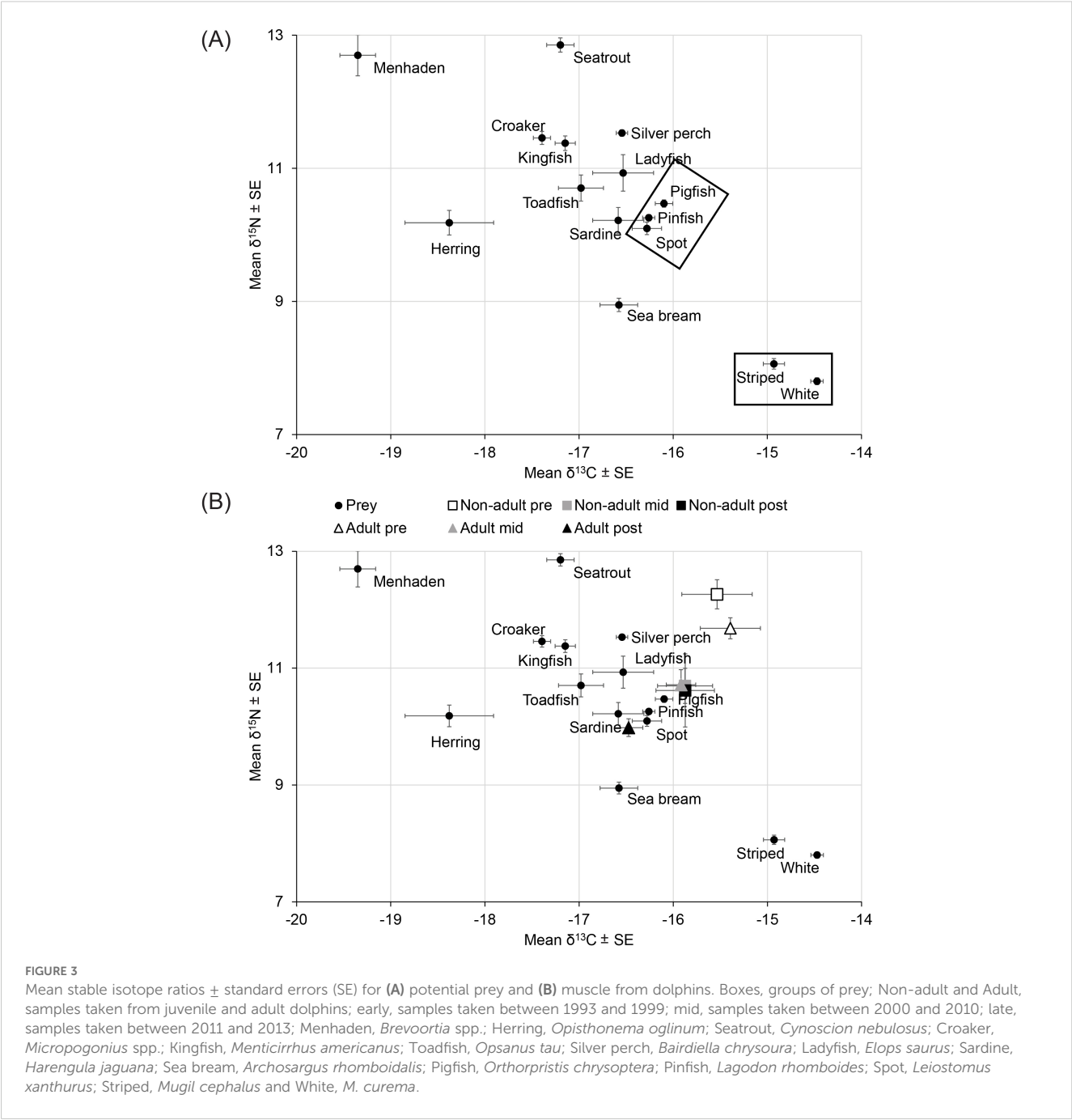


TABLE 3 Model diagnostics for four models predicting diets of dolphins.

Model	Leave one out information criterion				Weight
	Value	Standard error	Difference	Standard error for difference	
Age $\times$ Period	605.5	32.3	0.0	—	0.995
Period	616.0	33.0	10.5	6.2	0.005
Age	624.6	33.7	19.1	6.6	0.000
Null	629.0	30.3	23.5	7.8	0.000

SE, standard error; Age, non-adult or adult; Period, early from 1993 to 1999, mid from 2000 to 2010, and late from 2011 to 2013.

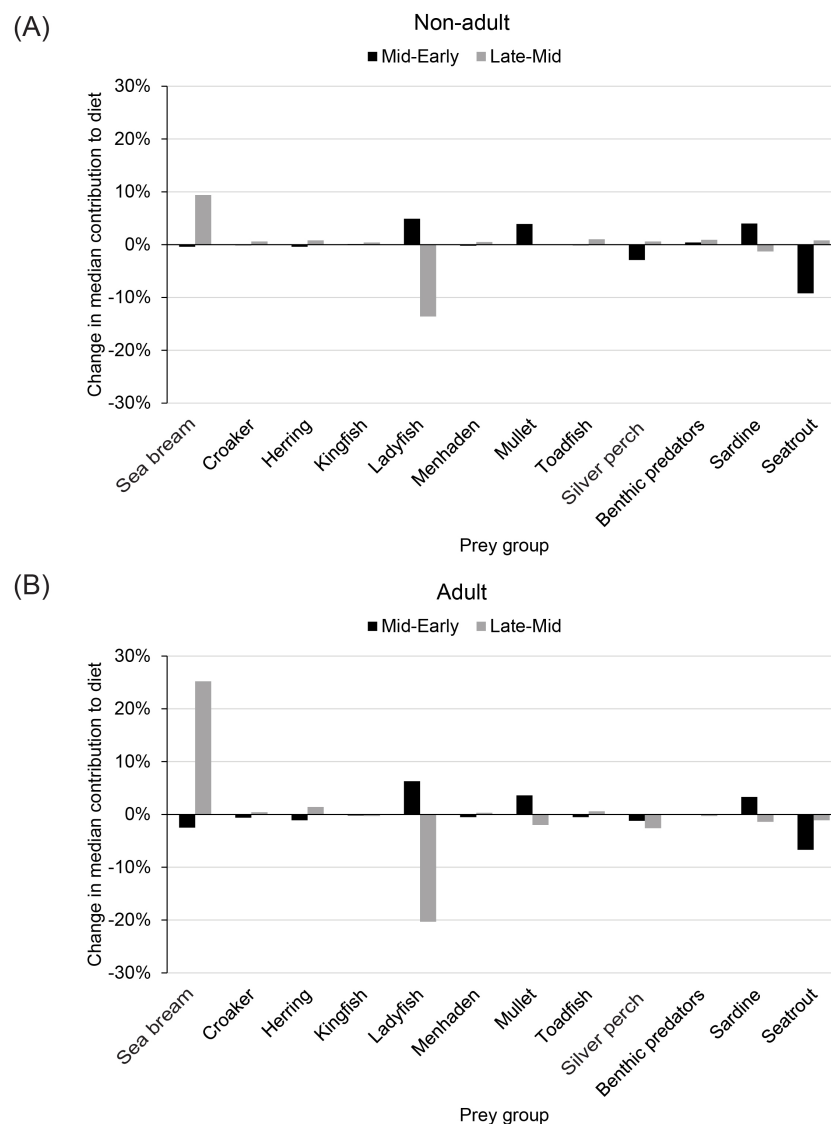


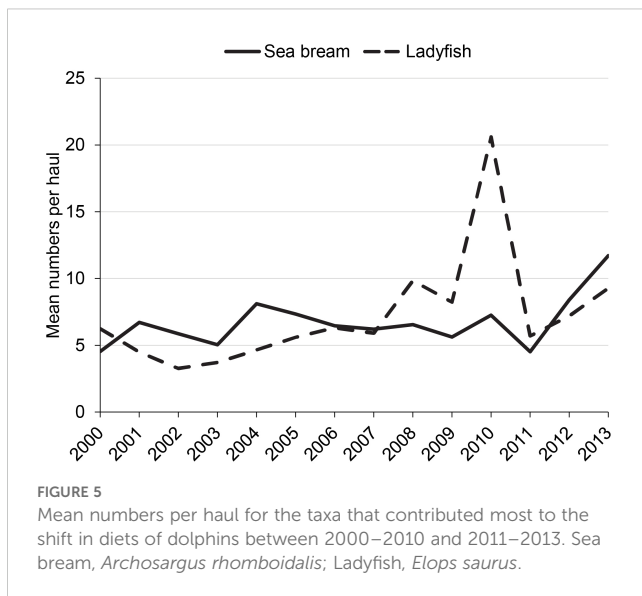
FIGURE 4

Changes in the proportion of diets for (A) non-adult and (B) adult dolphins. Mid-Early, change in proportion from 1993–1999 to 2000–2010; Late-Mid, change in proportion from 2000–2010 to 2011–2013; Sea bream, *Archosargus rhomboidalis*; Croaker, *Micropogonius* spp.; Herring, *Opisthonema oglinum*; Kingfish, *Menticirrhus americanus*; Ladyfish, *Elops saurus*; Menhaden, *Brevoortia* spp.; Mullet, *Mugil cephalus* and *M. curema*; Toadfish, *Opsanus tau*; Silver perch, *Bairdiella chrysoura*; Benthic predators, *Orthopristis chrysoptera*, *Lagodon rhomboides*, and *Leiostomus xanthurus*; Sardine, *Harengula jaguana*; Seatrout, *Cynoscion nebulosus*.

contribution to diets changed from 13% to 10%) and spotted seatrout (median contribution to diets changed from 17% to 8%). For non-adult dolphins across the periods 2000–2010 to 2011–2013, changes greater than 1% involved increased feeding on sea bream (median contribution to diets changed from 2% to 11%) and a corresponding decrease in feeding on ladyfish (median contribution to diets changed from 47% to 34%). For adult dolphins across the early and mid-periods, the key changes were increases in feeding on ladyfish (median contribution to diets changed from 32% to 38%), mullet (median contribution to diets changed from 8% to 12%), and scaled sardines (median contribution to diets changed from 7% to 10%) and corresponding decreases in feeding on sea bream (median contribution to diets changed from 7% to 5%) and spotted

seatrout (median contribution to diets changed from 13% to 6%). For adult dolphins across the mid and late periods, the major changes were an increase in feeding on sea bream (median contribution to diets changed from 5% to 30%) and corresponding decreases in feeding on ladyfish (median contribution to diets changed from 38% to 18%), mullet (median contribution to diets changed from 12% to 10%), and silver perch (median contribution to diets changed from 9% to 6%). Overall, the largest shifts in diets were similar for dolphins in both age groups: increased feeding on sea bream and decreased feeding on ladyfish during the late period.

These major changes in diet after 2010–2011 paralleled broad changes in the availability of the two key groups of prey as evidenced by data from hauls of the 183-m seine (Figure 5).



Catches of sea bream that averaged ~6 individuals per haul from 2000 to 2010 increased to up to 12 individuals per haul by 2013, and catches of ladyfish that had increased from ~6 individuals per haul in 2007 to a peak of ~20 individuals per haul in 2010 decreased to 6–9 individuals per haul from 2011 through 2013.

Changes in both catches of prey and diets of dolphins paralleled changes in structural habitats throughout the IRL (Figure 6). Mean percent cover of seagrass along 95 fixed transects decreased by ~57% between 2010 and 2012 (Figure 6A). Similarly, mean biomass of drifting macroalgae decreased by 79%–85% along the same fixed transects and in 3,654 hauls of the 183-m seine (Figure 6B). Both percent cover of seagrass and macroalgal biomass increased after 2012 (Figure 6).

A shift in diet may have stressed dolphins. Decreased consumption of ladyfish and increased consumption of sea bream reduced energetic benefits for dolphins because mean energy densities for those prey differed significantly (pseudo- $F = 11.81$, $df = 1, 24$, $p \leq 0.001$). Mean energy density $\pm$ SE was 4.5 ± 0.19 kJ g⁻¹ for ladyfish and 3.9 ± 0.06 kJ g⁻¹ for sea bream. Thus, dolphins would need to consume ~15% more sea bream than ladyfish to receive an equivalent amount of energy.

Changes in salinity and water temperature in the 2010–2011 period indicated osmotic stress was unlikely, but thermal stress on dolphins was possible (Figure 7). Compared to 2000–2009, mean salinities were higher and closer to 35 in 2010–2011 (Figure 7A; Mosquito Lagoon = 36 versus 34; Banana River Lagoon = 30 versus 22; Indian River Lagoon = 31 versus 25). Water temperatures fell to 9°C–10°C in early 2010 and 12°C–14°C in late 2011, which was lower than all other temperatures except those in early 2001 (Figure 7B).

4 Discussion

Analyses provided insights into links between environmental conditions and feeding by dolphins in the northern portion of the

IRL. Isotopic ratios for collagen in teeth from dolphins born between 1957 and 2015 indicated that burning of fossil fuel depleted in ¹³C created a signal that transferred through the trophic web to dolphins, but reducing loads of wastewater enriched in ¹⁵N did not create a parallel signal. Isotopic ratios in muscle sampled from 1993 to 2013 indicated that dolphins changed their diets between 2000–2010 and 2011–2013, with those changes following a bloom of phytoplankton in 2011 that led to losses of seagrass and drifting macroalgae and associated short-term changes in availability of prey. After 2011, the diets of dolphins included a higher proportion of prey with a lower energy density, which may have caused energetic stress. During the same period, thermal stress may have exacerbated energetic stress, but osmotic stress was unlikely.

The significant decline in $\delta^{13}\text{C}$ in the collagen of teeth indicated a Suess effect for the IRL, which also was recorded in Sarasota Bay (Rossman et al., 2013; 2014; 2015). In samples from dolphins residing in Sarasota Bay, $\delta^{13}\text{C}$ values that were corrected for the Suess effect still declined between 1944 and 2007. These changes in $\delta^{13}\text{C}$ were attributed to a 25% decrease in the presence of seagrass from 1950 to 1989 (Tomasko et al., 2005; Rossman et al., 2013). For the IRL, corrected $\delta^{13}\text{C}$ values for collagen of teeth did not decrease significantly. This difference from Sarasota Bay may have been related to the stable or increasing areal extent of seagrass in the IRL until the final four years of this study, which meant loss of seagrass affected isotopic signatures in only the 13 dolphins born after 2010 (Morris et al., 2022).

The lack of a significant temporal trend in $\delta^{15}\text{N}$ values from the collagen of teeth also suggested that the three waterbodies comprising the IRL differed from Sarasota Bay (Rossman et al., 2013; 2014; 2015). The increase in $\delta^{15}\text{N}$ values in Sarasota Bay tracked the increase in population from < 50,000 people in 1940 to > 700,000 people in 2010 (Rossman et al., 2013), and the IRL region experienced a similar increase in population (~97,000 in 1940 to ~1,600,000 in 2010). Sarasota Bay was receiving ~27 mgd of wastewater in the early 1990s (CDM, 1992), and the IRL was receiving ~43 mgd (Steward and Van Arman, 1987). In both systems, wastewater discharges were decreased dramatically by the mid-1990s, but septage remained another source of enrichment in ¹⁵N (Tetra Tech, Inc. and Closewaters LLC, 2021; Janicki Environmental, Inc. and Jones Edmunds, Inc., 1992). In Sarasota Bay, $\delta^{15}\text{N}$ values in dolphins did not increase substantially after 1989 (Rossman et al., 2013), but three situations may have resulted in persistently higher $\delta^{15}\text{N}$ values in dolphins from the northern portion of the IRL. First, the volume of the IRL was about 10× greater than Sarasota Bay, so the initial influence of wastewater loads would have been less. Second, decomposition of organic matter in significant deposits of fine particulate matter labeled “muck” were estimated to supply 20%–50% of the total loads of nitrogen to the IRL (Tetra Tech, Inc. and Closewaters LLC, 2021). Because the same processes drove decomposition of organic matter in wastewater, septage, and muck, the isotopic signatures of nitrogen were similar (Fox and Trefry, 2023). A third major difference between Sarasota Bay and the IRL was residence time. Little Sarasota Bay had the longest residence time of the regions in



FIGURE 6

Changes in habitats for potential prey of dolphins represented as changes in (A) percent cover of seagrass and (B) biomass of drifting macroalgae.

Sarasota Bay, which was estimated at 129 days for 99% replacement (<https://sarasotabay.org/directors-note-recent-findings-on-water-quality/>). In contrast, all regions in the IRL, except the one closest to the inlets, took 500–1,000 days to achieve 99% replacement (Steward and Lowe, 2010). Thus, changes in the abundance of ¹⁵N due to reductions in loads of wastewater were expected to be delayed in the IRL.

Isotopic ratios in muscle revealed a shift in the diets of dolphins following a bloom of phytoplankton in 2011 and the resultant shading and loss of seagrass and drifting macroalgae (Morris et al., 2021; 2022; Philips et al., 2021; Hall et al., 2022). In combination, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated that dolphins shifted from consuming ladyfish to consuming sea bream. This shift in diet correlated with decreased catches of ladyfish and other potential prey (this study; Adams et al., 2023), increased catches of sea bream (this study; Adams et al., 2023), decreased catches of

Gulf pipefish (*Syngnathus scovelli*; Adams et al., 2022), and changes in the causes of morbidity and mortality for stranded dolphins throughout the IRL from 2002 to 2020 (Durden et al., 2023a). Across all years and the two initial unusual mortality events (UMEs), probable causes of stranding were pneumonia and other inflammatory disease (41%) and entanglement, ingestion of fishing gear or debris, propellor strikes, and other traumas (36%; Durden et al., 2023a). Across all years, starvation and exhaustion due to malnutrition accounted for 17% of the mortalities on average, but during the UME in 2013, the effects of malnutrition accounted for 61% of the mortalities (Durden et al., 2023a). Furthermore, dietary shifts may have affected the energy budgets of dolphins. The energy density of sea bream was lower than ladyfish, so more prey would be needed to meet an equivalent energetic demand. Given this information, the loss of seagrass and macroalgae, the reduced numbers of certain prey, and a

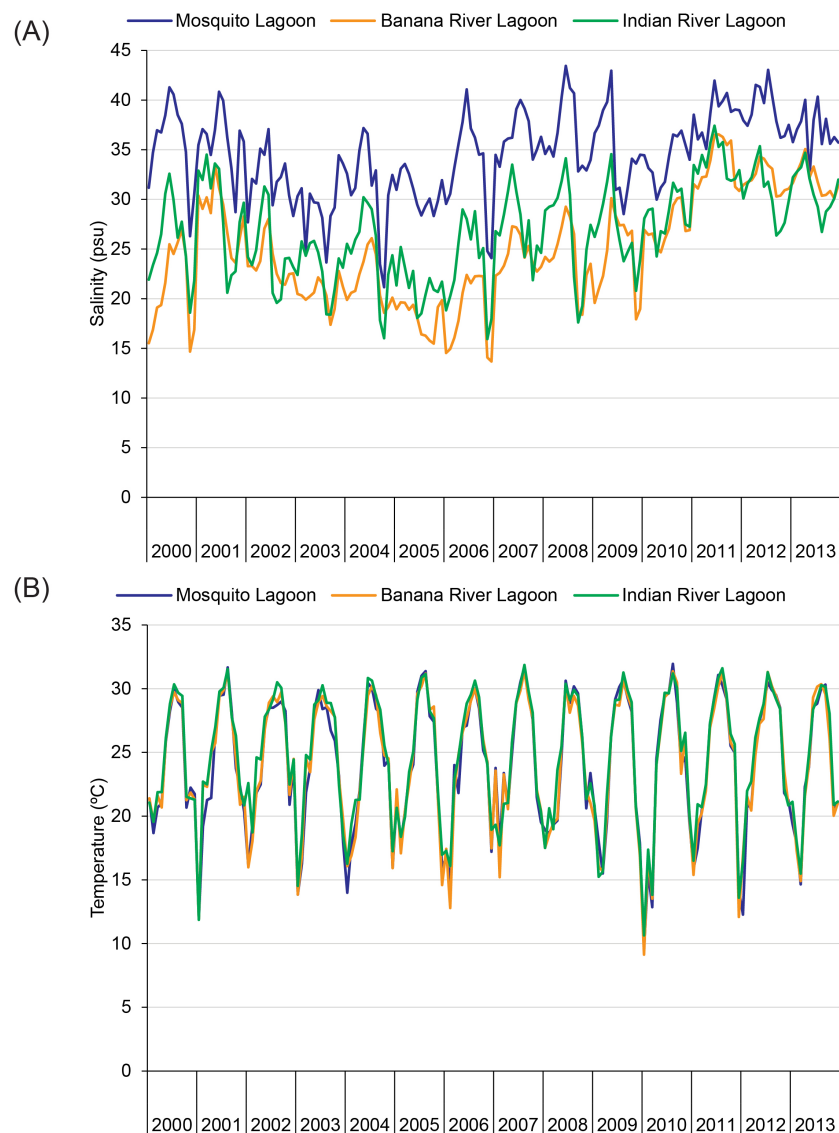


FIGURE 7
Mean values for (A) salinity and (B) water temperature from 2000 to 2013.

subsequent dietary shift appeared to be key stressors contributing to the UME in 2013. Beyond the data indicating a dietary shift that came from 56 dolphins that were stranded from 2011 to 2013 and the 77 dolphins (~8% of the population) that were involved in the 2013 UME, there was evidence of widespread malnutrition in free-swimming dolphins during 2013 (Durden et al., 2023b). Assessments of 337 free-swimming dolphins in the northern Indian River Lagoon and Banana River Lagoon indicated that 64% were underweight and 5% were emaciated (Durden et al., 2023b). Overall, an understanding of the net effect on the health of dolphins due to ecological changes would have benefited from expanded sampling of potential prey, targeted sampling that identified enrichment factors, and analysis of stable isotopes in samples of muscle from free-swimming dolphins to determine if their diets changed.

In addition to ecological changes and subsequent trophic stress, physicochemical conditions may have contributed to the 2013 UME as was postulated for the Gulf of Mexico (Litz et al., 2014). In the IRL, low water temperatures in 2010 and 2011 adversely affected fish, turtles, and manatees (Barlas et al., 2011), and these events may have added stress to dolphins consuming inadequate quantities and qualities of prey because temperatures approached the level where metabolic rates increased due to loss of heat (6–10°C; Williams et al., 2001; Yeates and Houser, 2008). Given increasing salinities in the system, osmotic stress was unlikely to have a substantial effect because salinities were above 10 ppt, which was the threshold for effects documented elsewhere (Litz et al., 2014; Ewing et al., 2017).

Overall, the results of this study pointed to multiple important effects from the intense, extensive, and long-lasting blooms that reduced the areal extent and biomass of seagrass and drifting

macroalgae throughout the IRL. The goal of managing the nutrient loads that fueled those blooms prompted development of total maximum daily loads and implementation of basin management action plans (Gao, 2009; FDEP, 2013a, 2013b, 2013c) or a reasonable assurance plan (Volusia County and Mosquito Lagoon RAP Stakeholder Group, 2019). Implementation was scheduled for completion in 2035, and additional adaptation was planned if success was not apparent.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

MS: Conceptualization, Investigation, Supervision, Writing – original draft, Writing – review & editing. WD: Investigation, Writing – original draft, Writing – review & editing. TJ: Investigation, Writing – review & editing. GW: Investigation, Writing – review & editing. RP: Investigation, Writing – review & editing. CJ: Formal analysis, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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