Evidence of a dietary shift in Tamanend's bottlenose dolphins in South Carolina waters during a cold-water anomaly

Megan M. Krzewinski[1] **and Wayne E. McFee**[2]

Contact email: megkrzewinski@gmail.com

ABSTRACT

Diet analysis can reveal how predators respond when prey distributions are altered. Cold-water temperatures in the winter of December 2010 to March 2011 were concurrent with a Tamanend's bottlenose dolphin (*Tursiops erebennus*) Unusual Mortality Event (UME) in 2011 in South Carolina. During this time, prey die-offs occurred that were documented in fishery surveys, and bottlenose dolphins consumed unusual prey items based on gross observation. We analysed the stomach contents of bottlenose dolphins that stranded from 2009 to 2014 and summarised frequency of occurrence (%F) and numerical abundance (%N) of prey species overall, annually and seasonally. Prey species with numerical abundance ≥ 5% overall were tested for significant differences annually and seasonally. From the stomach contents of 114 dolphins, the most frequently occurring (%F) and numerically abundant (%N) species were Atlantic croaker (*Micropogonias undulatus*; %F = 54%; %N = 16%) and star drum (*Stellifer lanceolatus*; %F = 45%; %N = 16%). Star drum, hake (*Urophycis* sp.) and squid (family *Loliginidae*) numerical abundances differed annually, while spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura*), bay anchovy (*Anchoa mitchilli*), hake and squid numerical abundances differed seasonally. Bottlenose dolphins consumed significantly more hake during the 2011 UME compared with 2009, 2010, 2012 and 2013. This dietary shift to hake likely occurred due to increased hake availability relative to other prey items typically available during this period. Numerical abundances peaked in the following seasons: summer for spot, winter for silver perch and bay anchovy, spring for hake, and the fall for squid. Our findings demonstrate that bottlenose dolphins can shift their diet when prey distributions are altered to maintain their caloric needs.

KEYWORDS: TAMANEND'S BOTTLENOSE DOLPHINS; FEEDING; FISH; FOOD/PREY; SHORT-TERM CHANGE; NORTH AMERICA; ATLANTIC OCEAN

INTRODUCTION

Diet analysis is an integral component of an animal's ecology, providing insights into behaviour, reproduction, energetics, habitat use and trophic interactions (Barros & Wells, 1998; Byrd *et al*., 2020). Furthermore, analysis of diet can elucidate ecosystem dynamics and important feeding habitats (Barros & Wells, 1998; Dunshea *et al*., 2013). Diet analysis can also shed light on long-term dietary trends, competition and prey abundance to understand and predict the impact on predators, especially if the environment is perturbed (Santos *et al*., 2013). For sentinel species, such as marine mammals, diet can help us understand how environmental events impact the ecosystem as a whole (Bossart, 2011).

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[1] Lowcountry Marine Mammal Network, North Charleston, South Carolina, USA
[2] National Oceanic and Atmospheric Administration, National Centers for Coastal Ocean Science, Charleston, South Carolina, USA

Stomach content analysis, the oldest and most widely used method to study marine mammals' diet, identifies prey hard parts (e.g., fish otoliths and cephalopod beaks) that resist digestion in the gastrointestinal tract to the lowest taxonomic level possible (e.g., Scott, 1903; Barros, 1987; Barros, 1993; Barros & Wells, 1998; Gannon & Waples, 2004; Pate & McFee, 2012). Using this technique, the diet of Tamanend's bottlenose dolphins (*Tursiops erebennus*) has been widely studied across the southeastern United States, revealing a primarily piscivorous diet. Many fishes found in the diet are soniferous, such as those from the family *Sciaenidae*, which indicates that dolphins may passively listen to sounds produced by their prey to detect them (e.g., passive listening hypothesis; Barros, 1993). Common prey items for Tamanend's bottlenose dolphins in various areas include the following: silver perch (*Bairdiella chrysoura*), Atlantic croaker (*Micropogonias undulatus*) and striped anchovy (*Anchoa hepsetus*) in the Indian River Lagoon, Florida (Barros, 1993); star drum (*Stellifer lanceolatus*), brief squid (*Lolliguncula brevis*), bay anchovy (*Anchoa mitchilli*) and spot (*Leiostomus xanthurus*) in South Carolina (Pate & McFee, 2012); and weakfish (*Cynoscion regalis*), Atlantic croaker and spotted seatrout (*Cynoscion nebulosus*) in North Carolina (Gannon & Waples, 2004; Byrd *et al*., 2020).

A cold-water winter anomaly occurred from December 2010 to March 2011 in South Carolina where the coastal monthly minimum average temperatures were below 8°C for 28 (21 consecutive) days, which is twice the number of consecutive days compared with other years with normal winter water temperatures (McFee & Arnott, 2012). In 2010, prey abundances were also impacted (Arnott *et al*., 2013), but water temperatures were below 8°C for only nine consecutive days (United States Geological Survey, unpublished data). Fish and shrimp kills occurred, and cumulative catch per unit effort (CPUE) of fishes in estuarine trammel net surveys conducted by the South Carolina Department of Natural Resources (SCDNR) decreased (Arnott *et al.*, 2013; Fig. 1). Impacted fish species from SCDNR estuarine fishery surveys included silver perch and star drum, which are some of the dominant prey items for bottlenose dolphins in the winter and early spring (Pate & McFee, 2012). Annual catch rates of silver perch in 2011 were one standard deviation below the 20-year statewide average (Arnott *et al.*, 2013), while catch rates of star drum in the winter and spring of 2011 were at least six times lower than catches in years in which data were available (2011–2014) (SCDNR, unpublished data). Estuarine fishery surveys are conducted year-round and consist of trammel net surveys in lower estuarine waters, electrofishing surveys in upper estuarine waters, and crustacean trawl surveys where fish bycatch was first noted in 2011 (Arnott *et al.*, 2013). Coastal nearshore trawl surveys are conducted in waters with depths of 15–30 feet from April to November; however, declines in CPUE in 2011 were not observed in coastal nearshore waters (SEAMAP-SA, 2024; SEAMAP-SA, 2025).

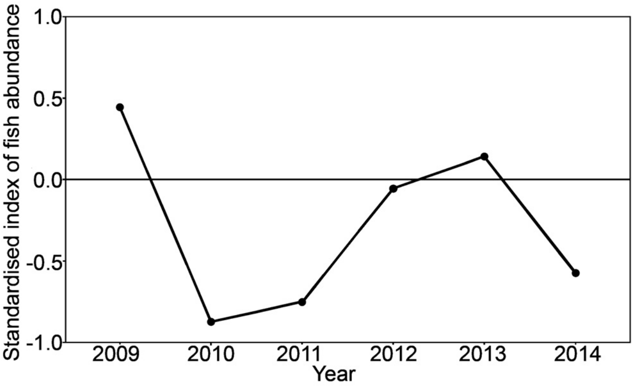

Figure 1. Standardised index of fish abundance, calculated as the Z-score of Catch Per Unit Effort (CPUE) at each sampling location and averaged across all sampling locations, for all fishes ≤ 300 mm total length in estuarine trammel net surveys in South Carolina per year from January to March of 2009 to 2014 (S. Arnott, South Carolina Department of Natural Resources, unpublished data). A value of 0 represents the mean CPUE across the time series, while positive and negative values represent above and below mean CPUE, respectively. Total length of 300 mm represents the maximum size fish typically consumed by Tamanend's bottlenose dolphins in South Carolina (Pate & McFee, 2012).

Concurrent with the cold-water winter anomaly, a bottlenose dolphin Unusual Mortality Event (UME) was declared by the National Oceanic Atmospheric Administration's (NOAA) National Marine Fisheries Services along the entire South Carolina coastline from February 2011 to May 2011 due to a 2.5 times increase in the 15-year mean (±2 standard deviations) number of strandings. The cause of this UME is undetermined (National Marine Fisheries Service, 2025). Emaciation was a contributing factor to the dolphins' demise based on gross and histopathological reports when nutritional status could be assessed in 56% of dolphins (n = 15); however, the frequency of empty stomachs during the UME was not higher than usual. Additionally, gross observation of intact prey items found unusual prey items for this area, such as one dolphin asphyxiating on a sheepshead (*Archosargus probatocephalus*; McFee & Arnott, 2012). Bottlenose dolphin mortality during the UME appeared to be strongly correlated to the cold-water temperatures that reduced prey availability in estuarine trammel net surveys (McFee & Arnott, 2012).

Reduced prey availability in the winter and spring of 2011 combined with unusual prey items in the stomachs of dolphins that stranded during the 2011 UME prompted closer analysis of bottlenose dolphin stomach contents to determine if their diet changed during the UME and cold-water anomaly compared to other years within this time period. We conducted a longitudinal analysis of Tamanend's bottlenose dolphin diet in South Carolina waters from 2009 to 2014 using stomach content analysis techniques. Numerical abundances of dominant prey items were tested for annual and seasonal differences.

METHODS

Data and sample collection

Tamanend's bottlenose dolphins that stranded dead across the state of South Carolina from 2009 to 2014 were responded to and necropsied opportunistically in the field or the laboratory. Level A data were collected for each stranding, including species, sex (if discernible), total length, date of stranding, location of stranding and condition code (alive – code 1; fresh dead – code 2; moderately decomposed – code 3; severely decomposed – code 4; skeletal/mummified – code 5; Wilkinson, 1991). Stomachs were collected whole during each necropsy by tying off the oesophagus and duodenal ampullae with string prior to resecting. The stomach was then placed in a labelled bag and stored in a –20°C freezer for future analysis. The oesophagus was analysed for additional prey items or contents during necropsy.

Strandings were grouped by year and season. Seasons were defined hydrographically based on local water temperature: winter (December–February); spring (March–May); summer (June–August); and fall (September–November).

Stomach and diet analysis

Stomachs were removed from the freezer and thawed for a minimum of 24 hours before analysis. Each stomach chamber was examined separately. The chamber was cut open, and any whole or partially intact prey items were removed and photographed. The remaining contents were rinsed into a 1 mm mesh sieve and systematically sorted by hand to collect any prey hard parts (e.g., fish otoliths and squid beaks). The hard parts were counted, and fish otoliths were stored dry until identification. This process was repeated for each stomach chamber, with contents from each chamber stored separately.

Stomach contents were identified using a variety of methods and subsequently quantified. Whole fish were identified by a South Carolina Department of Natural Resources fisheries biologist or from photographs using published guides (Simpson *et al*., 2015; South Carolina Department of Natural Resources, n.d.). Fish otoliths were identified to the lowest taxonomic level by comparison to previously identified and sorted otoliths from Pate and McFee (2012) and published guides (Chao, 1978; Campana, 2004; Baremore & Bethea, 2010; McBride *et al*., 2010). Sagittal otoliths were classified as left or right depending on the orientation of the sulcus. If the otolith was too eroded or difficult (i.e., cusk eel) to distinguish as left or right, side was noted as unknown. For some species, such as star drum, which have large identifiable sagittal and lapilli otoliths, both otolith types were identified, and the greater count of either pair was used to estimate the minimum number of fish eaten. Otoliths that were too digested, eroded or cracked were not taxonomically identified. The minimum number of fish eaten was determined by the greater number of left or right otoliths, plus the number of intact fish. If otolith side could not be determined, the minimum number of fish eaten was determined by dividing the total number of otoliths by two, plus the number of intact fish. Squid beaks were not identified to the species-level for this study. Since 99% of squid beaks identified in Pate & McFee (2012) from the same study area were from brief squid, and all identified squid beaks in some stomachs after 2006 were brief squid, it is assumed in this study that the remaining squid beaks found in the stomachs analysed belong to the same species. Squid beaks were not identified by upper or lower beak, and instead, the number of squid beaks was totaled and divided by two, plus the number of intact squid, to determine the minimum number of squid eaten. Similarly, shrimp were grouped and summarised collectively as 'shrimp' due to their low occurrence in stomach samples and because all three morphologically similar species in South Carolina waters belong to the family *Penaeidae*. The minimum number of shrimp eaten was determined based on the greater count of rostra or telsons, or intact shrimp.

Statistical analyses

Frequency of occurrence (%F) and numerical abundance (%N) were calculated for each prey species overall, annually and seasonally. Frequency of occurrence (%F) is the percentage of stomachs containing a particular food item. Numerical abundance (%N) is the number of a particular prey species divided by the total number of prey items per stomach expressed as a percentage and averaged across all stomachs.

The most prominent prey items, considered to be those with numerical abundance ≥ 5%, were further analysed for statistical differences annually and seasonally using a Kruskal-Wallis test and a *post hoc* Dunn's test with the Holm-Bonferroni correction. Statistical analyses were conducted in R version 4.2.3 with a statistical significance level of a = 0.05 (R Core Team, 2023).

RESULTS

A total of 429 bottlenose dolphin strandings occurred along the South Carolina coastline from 2009 to 2014. Among these strandings, 237 dolphins either stranded alive, were not examined or did not have stomachs present and/or collected during necropsy. Furthermore, 78 dolphins, including 50 neonates, had either no contents or only milk present in their stomach and were excluded from further analysis. Empty stomachs ranged from 13% in 2012 and 2014 to 36% in 2009. During the 2011 UME, the percentage of empty stomachs (n = 13%) was comparable to other years. The stomach contents of the remaining 114 dolphins were analysed (Fig. 2). Estuarine and coastal dolphins were analysed together because stock identity could not be determined.

Hard parts in the stomach contents included 13,032 otoliths and 415 cephalopod beaks. In total, a minimum of 5,486 prey items were consumed, including teleost fish, shrimp, squid and crab. Only two of the 114 dolphins did not contain fish remains in their stomach contents: one contained shrimp alone, and the other contained shrimp and squid. The number of prey species identified per dolphin stomach ranged from 1 to 22 species, with a mean of 4.86 species. The number of prey items consumed per stomach ranged from 1 to 469, with a mean of 48.1 prey items and a median of 15.5 prey items. One hundred and three otoliths could not be identified and may represent additional species consumed by dolphins in this study.

A minimum of 38 different species representing 22 families were identified. The most frequently occurring species were Atlantic croaker (%F = 54%), star drum (%F = 45%), spot (%F = 39%) and silver perch (%F = 30%; Table 1). Atlantic croaker (%N = 16%), star drum (%N = 16%) and spot (%N = 9%) were the most numerically abundant species. Sciaenids were the dominant food item, comprising 56% of the prey items numerically and identified in 89% of the stomachs. All identified Sciaenids in this study are soniferous. The most numerically abundant prey items were analysed further, specifically Atlantic croaker (%N = 16), star drum (%N = 16), spot (%N = 9), silver perch (%N = 6), bay anchovy (%N = 6), squid (%N = 6), hake (*Urophycis* sp.; %N = 5) and shrimp (%N = 5).

Between 2009 and 2014, with the exception of 2011, the most numerically abundant prey species each year were either Atlantic croaker or star drum (family *Sciaenidae*). Numerical abundance (%N) ranged from 9–23% for Atlantic croaker and 2–28% for star drum. In 2011, hake were the most numerically abundant (%N = 18). The numerical abundances of Atlantic croaker (Kruskal-Wallis Test: H = 4.58, df = 5, p = 0.47), spot (H = 3.35, df = 5,

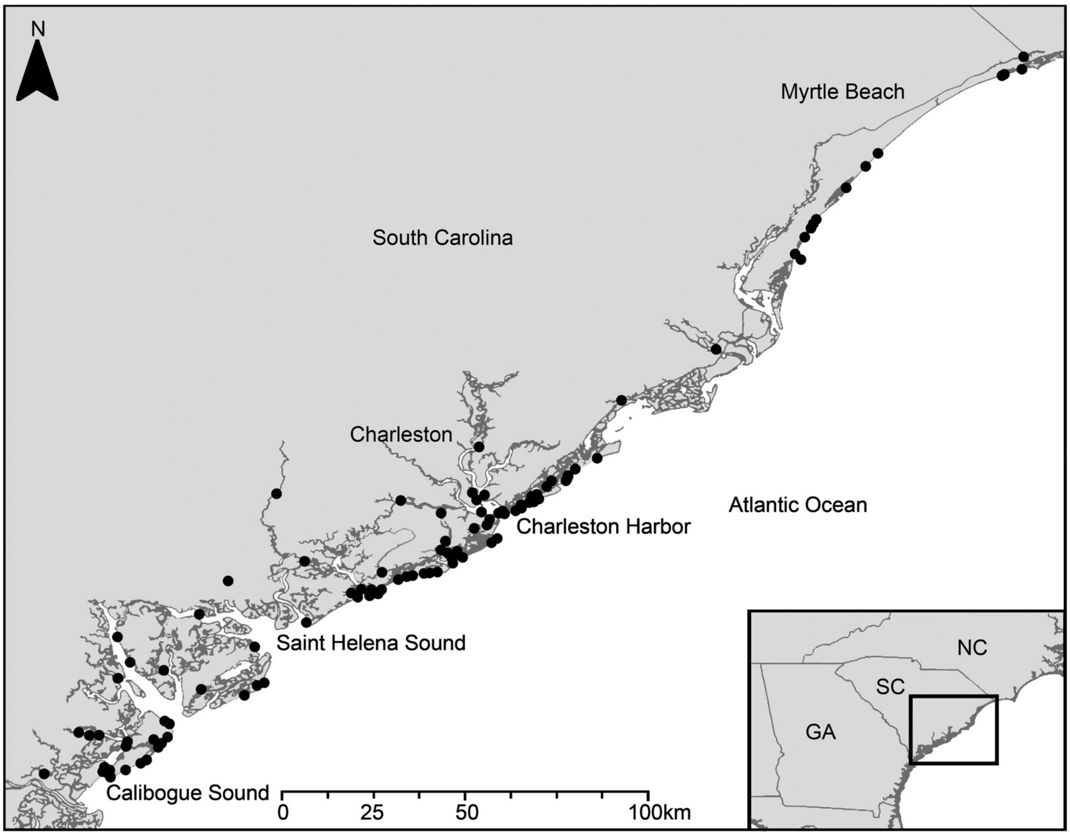

Figure 2. Map of the stranding locations of Tamanend's bottlenose dolphins (*Tursiops erebennus*) with stomach contents present and analysed along the South Carolina coast (n = 114) from 2009 to 2014.

p = 0.65), silver perch (H = 2.02, df = 5, p = 0.85), bay anchovy (H = 5.98, df = 5, p = 0.31) and shrimp (H = 10.14, df = 5, p = 0.071) did not differ significantly among years. Star drum (H = 11.50, df = 5, p < 0.05), hake (H = 17.99, df = 5, p < 0.01) and squid (H = 18.38, df = 5, p < 0.01) differed significantly in numerical abundance annually. Star drum numerical abundance was significantly different in 2010 (%N = 28) and 2012 (%N = 2; p < 0.05). Significant differences in hake numerical abundance were found between the following years: 2009 (%N = 0) and 2011 (%N = 18; p < 0.05), 2010 (%N < 1) and 2011 (p < 0.01), 2011 and 2012 (%N < 1; p < 0.05) and 2011 and 2013 (%N = 4; p < 0.05). For squid, significant differences in numerical abundance were found between 2011 (%N = 1) and 2013 (%N = 10; p < 0.05) and 2012 (%N = 0) and 2013 (p < 0.05).

Seasonally, there were 25 strandings in the winter, 36 in the spring, 24 in the summer and 29 in the fall. Atlantic croaker (H = 5.55, df = 3, p = 0.14), star drum (H = 6.04, df = 3, p = 0.11) and shrimp (H = 4.35, df = 3, p = 0.23) numerical abundances did not differ significantly across seasons (Fig. 3). Conversely, numerical abundances of spot (H = 13.70, df = 3, p < 0.01), silver perch (H = 9.53, df = 3, p < 0.05), bay anchovy (H = 9,38, df –3, p < 0.05), hake (H = 19.24, df = 3, p < 0.001) and squid (H = 15.39, df = 3, p < 0.01) differed significantly seasonally. Spot numerical abundance differed significantly between the fall (%N = 6) and summer (%N = 20; p < 0.05) and spring (%N = 4) and summer (p < 0.01). A significant difference in numerical abundance between the summer and winter was found for both silver perch (%N < 1 for summer; %N = 14 for winter; p < 0.05) and bay anchovy (%N = 1 for summer; %N = 14 for winter; p < 0.05). Hake were entirely absent in the diet in both the summer and fall, and significant differences in numerical abundance were found between the summer and spring (%N = 10; p < 0.01) and fall and spring (p < 0.01). For squid, significant differences in numerical abundance were found between the fall (%N = 16) and spring (%N = 3; p < 0.01) and fall and winter (%N = 2; p < 0.01).

DISCUSSION

We analysed the stomach contents of Tamanend's bottlenose dolphins that stranded dead in South Carolina waters from 2009 to 2014 to determine if dolphin diet changed during the 2011 UME that was concurrent with

Table 1

Numerical abundance (%N) and frequency of occurrence (%F) summarised overall and by stranding year for identified prey items in the stomachs of Tamanend's bottlenose dolphins stranded in South Carolina coastal and estuarine waters from 2009 to 2014. The less than (<) sign denotes prey items with < 1% numerical abundance. An asterisk (*) indicates species or genus that are soniferous.

	All dolphins		2009		2010		2011		2012		2013		2014	
	n = 114		*n* = 9		*n* = 22		*n* = 22		*n* = 13		*n* = 28		*n* = 2 0	
Prey items	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F
Bony fishes														
Sciaenidae														
Atlantic croaker (*Micropogonias undulatus*)*	16	54	21	67	9	35	13	55	23	69	18	54	18	55
Star drum (*Stellifer lanceolatus*)*	16	45	10	56	28	61	15	45	2	15	10	32	22	55
Spot (*Leiostomus xanthurus*)*	9	39	15	67	11	35	12	27	5	54	7	36	5	35
Silver perch (*Bairdiella chrysoura*)*	6	30	15	22	4	39	5	27	8	15	7	32	4	30
Spotted seatrout (*Cynoscion nebulosus*)*	2	16	<	11	–	–	2	9	5	31	2	21	5	25
Southern kingfish (*Menticirrhus americanus*)*	1	19	2	44	1	17	2	18	–	–	2	25	1	15
Silver seatrout (*Cynoscion nothus*)*	1	15	4	44	1	13	1	14	<	8	1	11	<	15
Weakfish (*Cynoscion regalis*)*	1	11	<	11	1	13	2	18	–	–	1	14	<	5
Red drum (*Sciaenops ocellatus*)*	1	7	–	–	<	9	1	9	6	15	–	–	<	10
Banded drum (*Larimus fasciatus*)*	1	11	1	11	1	9	1	18	3	15	–	–	<	20
Cynoscion spp.	1	3	–	–	5	4	–	–	–	–	1	4	<	5
Sciaenid sp.	1	9	<	11	1	26	–	–	1	8	–	7	–	–
Black drum (*Pogonias cromis*)*	<	3	–	–	<	9	–	–	1	8	–	–	–	–
Engraulidae														
Bay anchovy (*Anchoa mitchilli*)	6	25	10	22	4	30	5	36	–	–	9	21	9	30
Striped anchovy (*Anchoa hepsetus)*	4	20	2	22	4	9	1	18	10	23	6	29	4	20
Mugilidae														
Striped mullet (*Mugil cephalus*)	4	17	5	22	1	13	1	18	11	23	5	11	6	20
Phycidae														
Urophycis sp.*[1]	5	15	–	–	<	4	18	41	<	8	4	11	<	15
Ophidiidae														
Cusk eel spp.*	2	18	2	33	<	9	5	18	1	15	<	11	3	35
Clupeidae														
Menhaden (*Brevoortia tyrannus)*	<	10	<	11	–	–	1	23	1	15	1	7	<	5
American shad (*Alosa sapidissima*)	1	1	–	–	–	–	–	–	5	8	–	–	–	–
Ophichthidae														
Snake eel sp.	1	2	4	11	4	4	–	–	–	–	–	–	–	–
Centropomidae														
Common snook (*Centropomus undecimalis*)*	1	3	–	–	5	9	–	–		–	<	4	–	–
Triglidae														
Prionotus sp.*	1	7	–	–	<	4	<	9	6	8	1	11	<	5
Batrachoididae														
Oyster toadfish (*Opsanus tau*)*	1	7	–	–	3	9	–	–	–	–	1	7	3	20
Midshipman (*Porichthys plectrodon*)*	1	3	–	–	–	–	–	–	–	–	2	7	1	5
Synodontidae														
Lizardfish (*Synodus foetens*)	1	2	–	–	–	–	–	–	4	8	<	4	–	–
Trichiuridae														
Cutlassfish (*Trichiurus lepturus*)*	1	7	1	11	–	–	–	–	6	23	1	11	<	5
Elopidae														
Ladyfish (*Elops saurus*)*	<	1	–	–	–	–	–	–	–	–	<	4	–	–
Paralichthyidae														
Paralichthys sp.	<	8	<	11	1	4	1	14	<	15	<	4	<	5
Haemulidae														
Pigfish (*Orthopristis chrysoptera*)*	<	1	–	–	–	–	–	–	–	–	<	4	–	–
Serranidae														
Black seabass (*Centropristis striata*)*	<	1	–	–	–	–	–	–	–	–	<	4	–	–
Sparidae														
Pinfish (*Lagodon rhomboides)*	<	2	–	–	–	–	–	–	–	–	<	4	<	5
Sheepshead (*Archosargus probatocephalus*)	<	2	–	–	<	4	<	5	–	–	–	–	–	–
Lobotidae														
Tripletail (*Lobotes surinamensis)*	<	1	–	–	<	4	–	–	–	–	–	–	–	–
Belonidae														
Needlefish sp.	<	1	–	–	–	–	<	5	–	–	–	–	–	–
Unidentified fish	3	18	<	11	1	17	9	18	1	8	3	25	2	15
Cephalopods														
Loliginidae														
Squid sp.	6	26	7	44	5	22	1	5	–	–	10	46	11	35
Crustaceans														
Penaeidae														
Penaeus sp.	5	28	2	11	13	39	3	23	–	–	5	29	2	45
Portunidae														
Unidentified crab	<	2	–	–	–	–	–	–	–	–	–	–	1	10

[1] Of the two hake species caught in SCDNR estuarine surveys, sound production has been confirmed in spotted hake (*Urophycis regia*) but not in southern hake (*Urophycis floridana*).

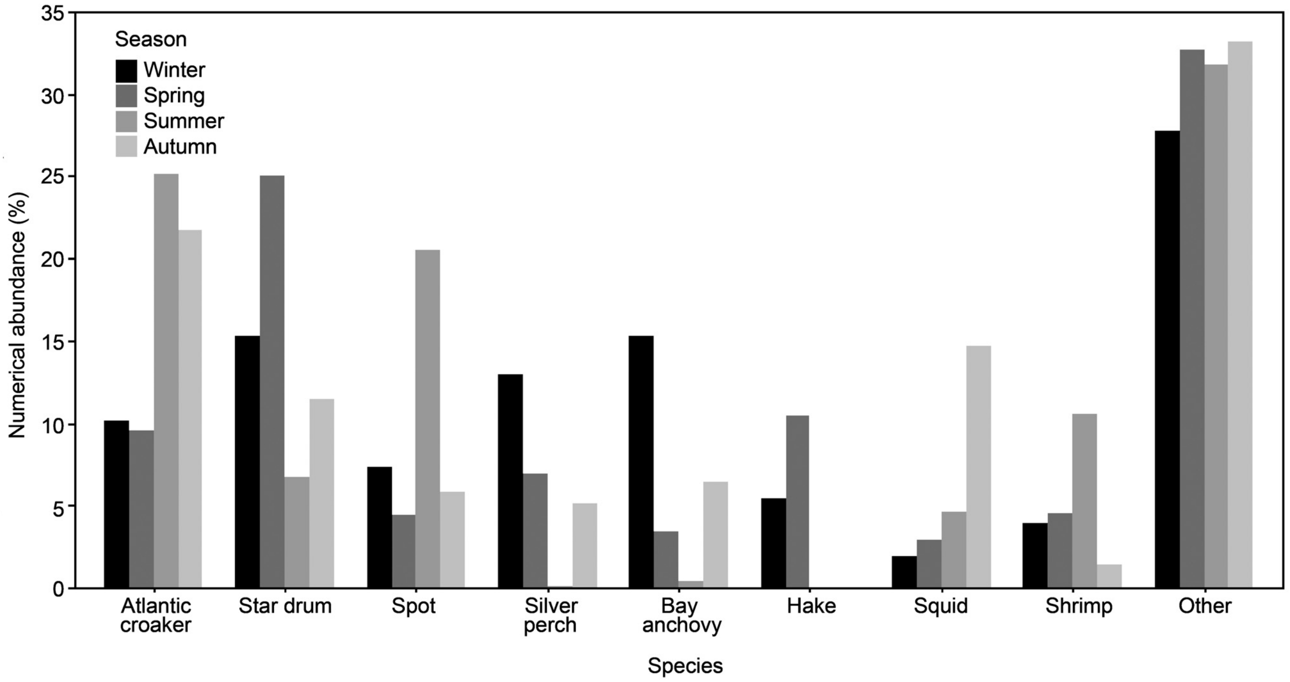

Figure 3**.** Numerical abundances of the most prominent prey items by season (winter = December–February; spring = March–May; summer = June–August; fall = September–November) in the stomachs of Tamanend's bottlenose dolphins stranded from 2009 to 2014 in South Carolina coastal and estuarine waters. All other prey items are summarised in the 'other' category.

a cold-water anomaly. Atlantic croaker and star drum were both the most frequently occurring and numerically abundant prey species overall. Of the eight prey species with numerical abundances ≥ 5%, the consumption of hake, squid and star drum differed annually, with hake consumption increasing significantly in 2011 when the UME and cold-water anomaly occurred. Seasonally, numerical abundances of spot, silver perch, bay anchovy, hake and squid differed. Spot numerical abundance was highest in the summer compared with the fall and spring. Silver perch and bay anchovy were consumed more in the winter compared to the summer. Hake consumption was highest in the spring, while no consumption occurred in the summer and fall. The highest numerical abundance of squid occurred in the fall compared with the spring and winter. Tamanend's bottlenose dolphins in South Carolina waters are from four estuarine stocks and two coastal stocks (Krzewinski *et al*., 2024). Each stock uses both estuarine and coastal waters (Laska *et al.*, 2011), and dolphins likely forage in both areas, thus the annual and seasonal differences observed could be due to changes in the estuarine and coastal nearshore composition of the fish community.

Overall, bottlenose dolphins in South Carolina waters were found to be primarily piscivorous and consumed mostly demersal and soniferous fishes from the family *Sciaenidae*. These findings are consistent with past analysis of 86 bottlenose dolphins along the South Carolina coastline from 2000 to 2006 (Pate & McFee, 2012). The consumption of soniferous fishes in this area further supports the passive listening hypothesis that dolphins use sounds produced by their prey to passively detect prey (Barros, 1993). Specifically, Atlantic croaker and star drum were important prey items for bottlenose dolphins from 2009 to 2014. When compared with numerical abundances from 2000 to 2006 (Pate & McFee, 2012), Atlantic croaker numerical abundance increased fivefold, while star drum numerical abundance decreased twofold, and squid were found in fewer dolphin stomachs and decreased twofold in frequency of occurrence. Fisheries monitoring surveys reflect this increase in consumption, as Atlantic croaker abundance in estuarine and nearshore coastal surveys in South Carolina waters has increased over time (Arnott *et al*., 2013; SEAMAP-SA, 2025). This increase in consumption may therefore reflect increased availability of Atlantic croaker for bottlenose dolphins in the area, as seen in common dolphins (*Delphinus delphis*) in Spain targeting the most readily available prey items (Begona Santos *et al*., 2013). Star drum annual abundance remained stable in estuarine surveys for the years in which data were available (2011 to 2014) (SCDNR, unpublished data) and in nearshore coastal surveys over the study period (SEAMAP-SA, 2025). While a significant difference in star drum numerical abundance between 2010 and 2012 was found, it is unknown if this is due to changes in availability in estuarine waters or dolphins targeting other more readily available prey items, such as Atlantic croaker. Little is known about brief squid abundance in estuarine waters (Whitaker & Kingsley-Smith, 2015), but their annual abundance remained stable throughout the study period in nearshore coastal surveys (SEAMAP-SA, 2025). Squid numerical abundance was significantly lower in 2011 and 2012 compared with 2013; however, more information is needed to determine if brief squid abundance in estuarine waters has changed or if bottlenose dolphins are intentionally consuming less squid. It is important to note that fish length data are not available for all species or sampling locations in the estuarine and nearshore coastal surveys. Dolphins in this area primarily consume fish ≤ 300 mm total length (Pate & McFee, 2012), but it is unknown if this size range is represented in the catch data.

Hake (*Urophycis* spp.) consumption significantly increased in 2011 compared with 2009, 2010, 2012 and 2013 and was the only year a non-Sciaenid was the most numerically abundant prey species. While hake consumption by Tamanend's bottlenose dolphins has been noted in North Carolina (Gannon & Waples, 2004) and Virginia (Volker, 2020), and by common bottlenose dolphins (*Tursiops truncatus*) in Louisiana (Bowen-Stevens *et al*., 2021), Florida (Dunshea *et al*., 2013), Brazil (Milmann *et al*., 2016) and Italy (Neri *et al*., 2022), it has not been a dominant prey item in these areas (%N ≤ 4). Similarly, hake consumption was noted in South Carolina in low numbers according to previous analysis from 2000 to 2006 (%N < 1; Pate & McFee, 2012). Hake are cold-water species only encountered in South Carolina waters from January to May, with a peak in abundance of spotted hake (*Urophycis regia*) in estuarine surveys in March and to a lesser extent in April (SCDNR, unpublished data). Spotted hake, the primary hake species encountered in SCDNR estuarine surveys, spawn in offshore waters from late summer to winter, while juvenile fish use estuarine and nearshore coastal waters in the winter and spring before water temperatures increase (Burr & Schwartz, 1986). While spotted hake are soniferous, they are believed to make sounds primarily during spawning in offshore waters (Fish & Mowbray, 1970; Rountree *et al.*, 2002) where these dolphins are likely not foraging. While hake is typically consumed by bottlenose dolphins in low numbers in South Carolina waters in the spring (March–May), greater than usual numbers appeared in the diet from March to mid–April in 2011. The change in diet during this time was likely related to hake availability. SCDNR estuarine surveys indicate hake catches greatly increased in 2011 and were at least 20 times greater than catches from 2012 to 2014 (SCDNR, unpublished data). The increased catches could be due to the cooler water temperatures driving more hake to the area, which has also been observed in other cooler winters in North Carolina (Burr & Schwartz, 1986) and South Carolina (J. Ballenger & B. Renkas, pers. comm., 23 June 2025).

During 2011, decreased catches in other prey species typically consumed in the winter and early spring were also observed (Arnott *et al.*, 2013; SCDNR, unpublished data). Silver perch and star drum are a primary component of bottlenose dolphin diet in the winter and early spring (Pate & McFee, 2012) since all age classes of these species remain in the estuaries year-round (Shealy *et al*., 1974; Webster *et al.*, 2014). While newly settled juveniles are present in the estuaries year-round, other prey species (e.g., Atlantic croaker) migrate offshore in the fall to spawn and return to the estuaries in large numbers in the late spring and summer (Arnott *et al*., 2013). Silver perch annual estuarine catch rates in 2011 were one standard deviation below the 20-year statewide average (Arnott *et al*., 2013). Their catches fluctuate based on winter water temperatures and steeply decline after severe winters, as seen in 2011 (Arnott *et al.*, 2013; Webster *et al.*, 2014). Although annual estuarine catch rates of star drum from 2011 to 2014 were comparable, there was a sixfold decrease in catches specifically in the winter and spring of 2011 (SCDNR, unpublished data). The thermal tolerance of star drum is unknown, but this decrease may indicate that star drum is not a cold-tolerant species and consequently experienced die-offs during this severe winter. Based on data from SCDNR fish monitoring surveys and the results of this study, it appears that dolphins shifted their diet to include more hake during this period, likely in response to higher hake availability and reduced abundance of other prey items, namely silver perch and star drum.

Bottlenose dolphins have been observed changing their diet in other areas in response to altered prey abundance. In Sarasota Bay, Florida, both common prey items and prey items preferentially selected by bottlenose dolphins declined during red tide blooms caused by *Karenia brevis* (Berens McCabe *et al*., 2021). During red tide blooms in 2005 and 2006, juvenile bottlenose dolphins exhibited behavioural changes during these blooms characterised by increased socialisation and an expanded range, suggesting a potential dietary shift to pelagic *Clupeid* species which did not decline during bloom conditions (Gannon *et al*., 2009; McHugh *et al*., 2011). In the Indian River Lagoon, Florida, bottlenose dolphins consumed more sea bream (*Archosargus rhomboidalis*) and fewer ladyfish (*Elops saurus*) during a UME in 2013, directly reflecting prey availability in fishery surveys. The decrease in prey species, such as ladyfish, were caused by phytoplankton blooms that impacted the habitat of key prey species. This UME also involved malnourishment, which could be linked to sea bream being less energetically dense than ladyfish (Stolen *et al*., 2025). The results of these studies show that bottlenose dolphins may alter their diet to maintain their caloric needs when prey availability is impacted, including consuming non-preferred or less energetically dense prey items.

Numerical abundances of spot, silver perch, bay anchovy, hake and squid differed seasonally. Bay anchovy consumption was highest in the winter compared with the summer, hake consumption was highest in the spring compared with the summer and fall, and squid consumption was highest in the fall compared with the spring and summer. For these three species, these peaks in consumption reflect their peaks in abundance in estuarine surveys (Good *et al*., 2025; SCDNR, unpublished data). Bay anchovy spawn in the warmer months in estuarine and coastal waters but distribution patterns suggest they use upper estuarine waters into near freshwater in the warmer months, and larger individuals move out of these upper estuarine waters into lower estuarine waters in the winter (Wenner *et al.*, 1981; Wang & Houde, 1995). More information is needed on brief squid movements in estuarine and nearshore coastal waters in South Carolina; however, findings suggest asynchronous spawning in the Charleston Harbor (Good *et al.*, 2025). Spot consumption peaked in the summer compared with the spring and fall. Spot catches peak in the spring in nearshore coastal waters (SEAMAP-SA, 2025) and in the fall in estuarine waters (Arnott *et al.*, 2013), likely reflecting when larger individuals are moving inshore from offshore spawning areas in the late fall and winter (Simpson *et al.*, 2015). High consumption of spot during the summer has also been documented through stomach content analysis (Pate & McFee, 2012) and fatty acid analysis of bottlenose dolphins in Charleston, South Carolina (Recks, 2004), indicating that spot is an important component of their summer diet, and dolphins may specifically target spot during this time. Silver perch consumption was greatest in the winter compared with the summer. Silver perch are one of the few year-round estuarine residents that spawn in estuarine waters in the spring (Webster *et al*., 2015) and are more prevalent in estuarine waters compared with nearshore coastal waters in South Carolina (Webster *et al.*, 2015; SEAMAP-SA, 2025). Both estuarine and nearshore coastal surveys document the same pattern of highest abundances in the spring and lowest abundances in the summer (Arnott *et al.*, 2013; SEAMAP-SA, 2025), although there are no catch data in the winter for nearshore coastal surveys. Dolphins have fewer prey choices in the winter when many other species migrate out of the estuaries to spawn in deeper waters, which is likely why this species is an important component of diet in the winter months both in this study and previous analysis (Pate & McFee, 2012).

While stomach content analysis is an accessible and valuable tool for diet analysis, there are limitations to this method. One limitation is that squid beaks accumulate more in the stomach compared with fish otoliths and other hard parts that are digested quicker (Bigg & Fawcett, 1985), thus squid may be overestimated in the diet. This technique represents more recent feeding events because the average passage time of food through the digestive tract of bottlenose dolphins is four hours (Kastelein *et al.*, 2003). False negatives can also occur due to the different digestion rates of otoliths (Bowen & Iverson, 2013). There were otoliths in this study that could not be identified, most of which appeared to be from the same species. Despite attempts to identify these otoliths with local fishery biologists, genetic analysis may be required for definitive identification. Despite these limitations, stomach content analysis is still considered to be representative of free-ranging dolphins' diet (Dunshea *et al*., 2013).

We found that Tamanend's bottlenose dolphins in South Carolina waters are opportunistic feeders that consume readily available prey based on overall, seasonal and annual results. During the cold-water anomaly and 2011 UME, dolphins unexpectedly consumed more hake likely in response to increased abundances of hake during this time. These results highlight the importance of long-term diet monitoring to detect both short-term and long-term diet changes. Future analysis should include an all-structures approach of identifying all diagnostic prey hard parts (e.g., operculum and dentary bones) to be more comprehensive (Bowen & Iverson, 2013), and the identification of unidentified teleost fish otoliths and squid to the species-level. These findings can also be compared with other years characterised by cold winters to determine whether hake consumption increases under similar environmental conditions. Bottlenose dolphin diet in South Carolina changed over time and in response to altered prey distribution during a cold-water event, highlighting the importance of diet analysis of this sentinel species that can shed light on ecosystem-level changes.

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