DIETS OF COASTAL BOTTLENOSE DOLPHINS FROM THE U.S. MID-ATLANTIC COAST DIFFER BY HABITAT

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ABSTRACT

We recorded 31 species in the stomachs of 146 coastal bottlenose dolphins (*Tursiops truncatus*) from North Carolina, U.S.A. Sciaenid fishes were the most common prey (frequency of occurrence = 95%). By mass, Atlantic croaker (*Micropogonias undulatus*) dominated the diet of dolphins that stranded inside estuaries, whereas weakfish (*Cynosicon regalis*) was most important for dolphins in the ocean. Inshore squid (*Loligo* sp.) was eaten commonly by dolphins in the ocean, but not by those in the estuaries. There was no significant pattern in prey size associated with dolphin demography, but the proportion of the diet represented by croaker was higher for males than for females, and mature dolphins ate more croaker than did juveniles. Dietary differences between dolphins that stranded in the estuaries and those that stranded on ocean beaches support the hypothesis that some members of the population inhabit the ocean primarily while others reside principally in estuaries. The overwhelming majority of prey were soniferous species (75% of numerical abundance), which is consistent with the hypothesis that bottlenose dolphins use passive listening to locate noise-making fishes. However, spatiotemporal patterns in consumption of Sciaenid fishes did not coincide with their spawning, which is when peak sound production is thought to occur.

Key words: coastal bottlenose dolphin, *Tursiops truncatus*, food habits, feeding, foraging ecology, Sciaenidae, soniferous fishes, mid-Atlantic, estuary, coastal ocean.

In this paper we quantify the food habits of coastal bottlenose dolphins, *Tursiops truncatus*, in the waters off the mid-Atlantic coast of the U.S. using traditional stomach content analysis techniques. Previous analyses of bottlenose dolphin food habits in this region were based on small samples, and none investigated differences in feeding habits associated with season, habitat, sex, or age. True (1885) identified common gurnard (*Prionotus carolinus*) in the stomachs of two dolphins taken by the dolphin fishery in Cape May, New Jersey. Fishermen from Cape Hatteras, North Carolina, told Townsend (1914) that the bottlenose dolphins in that region

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primarily ate seatrout (*Cynoscion* spp.). Mead and Potter (1990) conducted the most thorough investigation of bottlenose dolphin food habits in the mid-Atlantic region, using a sample of 64 dolphins stranded on the coasts of North Carolina, Virginia, and Maryland. These authors calculated frequencies of prey occurrence and numerical abundance, both of which require large sample sizes, and neither accounts for prey mass (Hyslop 1980). The most important prey found by Mead and Potter (1990) included spot (*Leiostomus xanthurus*), croaker (*Micropogonias undulatus*), seatrouts, silver perch (*Bairdiella chrysoura*), hake (*Urophycis* sp.), and squid (*Loligo* sp.).

We investigated variation in food habits with respect to habitat (coastal ocean *vs.* estuary), season, and demography. In North Carolina bottlenose dolphins move between the ocean and the estuaries.[2] However, there is evidence from photographic identification and the presence of ectoparasites that some dolphins occupy estuaries primarily, while others stay mainly in the ocean. Some authors hypothesize that pseudostalked barnacles *Xenobalanus* sp., which attach to the appendages of dolphins, can be used as an indicator of ocean residence (Caldwell and Caldwell 1972, Barros 1993). If some coastal dolphins are primarily oceanic while others are primarily estuarine, one might expect to find differences between the two groups with regard to food habits. We tested the hypothesis that the dolphin diet changes seasonally because many of the species eaten by bottlenose dolphins undergo seasonal migrations. Faced with migrating prey, dolphins can either follow their prey or switch to a different set of prey.

Developing the skills to locate and capture prey probably requires an extended period of learning for young bottlenose dolphins. Mann and Smuts (1999) noted that young dolphins begin "play snacking" behavior as early as three weeks of age with objects such as seagrass. Play snacking with fish begins at about week seven. While developing hunting skills, young dolphins may eat prey that are less elusive than those species normally eaten by older dolphins. Smith and Read (1992) found that harbor porpoise (*Phocoena phocoena*) calves eat euphausiids (*Meganyctiphanes norvegica*), which are rare in the diets of adult porpoises. Young franciscana (*Pontoporia blainvillei*) feed on shrimp, whereas adults eat fishes and cephalopods (Rodríguez *et al.* 2002). Mead and Potter (1990) also concluded that weaning is gradual in bottlenose dolphins, which may reflect the need for young dolphins to augment energy intake from solid food with that of their mother's milk until they have become proficient at capturing prey.

Lactating female mammals typically have the highest energy demands of any demographic group within their species and often have nutrient requirements that differ from other members of their species (*e.g.*, Clutton-Brock *et al.* 1982, Close *et al.* 1985, Perez and Mooney 1986). In a comparison of the diets of pregnant and lactating spotted dolphins (*Stenella attenuata*), Bernard and Hohn (1989) found that lactating spotted dolphins ate more food and increased the proportion of fish relative to squid in their diet. Robertson and Chivers (1997) also found that female spotted dolphins increased their food consumption during lactation. However, Robertson and Chivers (1997) came to the opposite conclusion regarding the relative proportions of squid and fish in the diets of lactating females: lactating females increased the amount of squid in their diet. Cockcroft and Ross (1990) found dietary differences among life history stages of bottlenose dolphins in South Africa. Recently, Kastelein *et al.* (2002) documented that captive bottlenose dolphins increased their

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[2] Personal communication from Keith Rittmaster, North Carolina Maratime Museum, 315 Front Street., Beaufort, NC 28516, June 2003.

consumption of food little during gestation but that their consumption increased by 58%–97% during lactation.

METHODS

We examined the stomach contents of coastal bottlenose dolphins that died of natural causes or that were captured accidentally by commercial fisheries in the estuaries and ocean waters of North Carolina from 1993 to 2001. Two ecotypes of *T. truncatus* are recognized on the east coast of the U.S.: a nearshore form known as the "coastal" ecotype and a pelagic form known as the "offshore" ecotype (see Hersh and Duffield 1990; Mead and Potter 1990, 1995; Torres *et al.* 2003). We restricted our analyses to the coastal form. Offshore dolphins are not thought to come any closer to shore than 7.5 km and coastal dolphins are found from the estuaries out to a distance of 34 km from shore (Torres *et al.* 2003). We used a hierarchical approach to distinguish between members of the two ecotypes. Dolphin stomachs containing prey known to inhabit only waters greater than 25 m were excluded from analysis (Mead and Potter 1995). The remaining dolphins were categorized on the basis of parasite assemblages. Coastal dolphins were identified by the presence of the trematode *Braunina* in pyloric and main stomach chambers and offshore dolphins were recognized by the cestodes *Phyllobothrium* and *Monorhygma* and by the nematode *Crassicauda* (Mead and Potter 1990, 1995). Categorization of some dolphins was corroborated independently by sighting histories and capture locations. Photographic sighting data of individual dolphins ($n = 10$) were collected by the contributors to the Mid-Atlantic Bottlenose Dolphin Catalog.[3] These ten dolphins were only sighted within 7.5 km of shore and were, therefore, assumed to be of the coastal ecotype. The location of capture was known for seven dolphins; five were captured in pelagic fisheries (>34 km from shore: offshore ecotype) and two were taken in coastal fisheries (<7.5 km from shore: coastal ecotype).

The stomach of each dolphin was extracted in its entirety (including esophagus and duodenal ampulla) during necropsies conducted either in the field or in the laboratory. In the lab, the contents of all three stomach chambers were removed for analysis. Intact prey were removed first, then the remaining stomach contents were put in a shallow tray. We topped the tray off with water, gently agitated it, and then decanted floating tissue into a 1-mm sieve. We repeated this process until all floating tissue was separated from the dense bones. We retained the skeletal parts that had sunken to the bottom of the tray and then inspected the contents of the sieve to make sure no hard parts, such as small otoliths, had adhered to the loose flesh that had been poured off. Structures used to identify prey included: sagittal otoliths, dentary bones, and skulls of teleosts; lower mandibles from cephalopods; and exoskeletons from crustaceans. Prey items were identified with the aid of reference collections at the Duke University Marine Laboratory, the University of North Carolina's Institute for Marine Sciences, and Mote Marine Laboratory. Published guides used to identify prey included Bigelow and Schroeder (1953), Chao (1978), Brouder (1979), Clarke (1986), Härkönen (1986), Robins *et al.* (1986), and Murdy *et al.* (1997). The number

[3] URIAN, K. W., A. A. HOHN AND L. J. HANSEN. 1999. Status of the Photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors. NOAA Technical Memorandum NMFS-SEFSC-425. (Available from the National Oceanic and Atmospheric Administration–Beaufort Laboratory, 101 Pivers Island Road, Beaufort, North Carolina 28516.)

of either upper or lower mandibles (which ever was more abundant) from each species was used to determine the number of squid present. The abundance of each fish species in a stomach was determined by summing the number of intact fish and half the number of free otoliths. Atlantic menhaden (*Brevoortia tyrannus*) possess delicate otoliths, but they have high rates of parasitism, up to 46%, by the isopod *Olencira praegustator* (Kroger and Guthrie 1972, Lindsay and Moran 1976). During trawl surveys in North Carolina's Neuse River estuary, *O. praegustator* was found to parasitize only menhaden and no more than one isopod was found in each fish (Eby[4]; D. Gannon, unpublished data). The isopod's chitonous exoskeleton is resistant to digestion, making it a good indicator of menhaden in the diet. Therefore, the minimum number of menhaden in each dolphin stomach was determined by either half the number of menhaden otoliths or by the number of isopods, which ever was greater.

Relative importance of prey in the diet of bottlenose dolphins was determined by three methods: (1) frequency of occurrence, (2) proportion of numerical abundance, and (3) proportion of reconstructed mass. Frequency of occurrence is the proportion of dolphin stomachs containing a particular food type. Proportion of numerical abundance is the number of individuals of a prey species recovered from a particular stomach, divided by the total number of all prey from that stomach, averaged across all stomachs. Proportion of reconstructed mass is the sum of the masses of individuals of a prey species recovered from a particular stomach, divided by the total mass of all prey from that stomach, averaged across all stomachs. Wet weights of individual prey prior to ingestion were estimated from their lengths. We determined the sizes of prey by measuring intact organisms and by regressing the lengths of skeletal parts on body length for well-digested prey. Standard lengths were used for fish and mantle lengths were used for cephalopods. Standard lengths of partially digested fish were estimated from the lengths of sagittal otoliths. Squid mantle lengths were estimated from the lower rostral lengths of their mandibles (Clarke 1986). Otoliths were scored on a scale from 0 (undamaged otoliths retrieved from skulls) to 5 (severely degraded, free otoliths) following the methods of Recchia and Read (1989). Including severely eroded otoliths in analyses of prey size can bias results negatively (da Silva and Neilson 1985, Jobling and Breiby 1986, Recchia and Read 1989). However, the ratio of surface area to volume affects the time required to digest a food item (Windell 1967), meaning that for a particular prey species, large individuals take longer to digest than do small ones. Therefore, it may be possible to over-estimate mean prey size by only including otoliths retrieved from intact skulls. To minimize these biases, we used otoliths categorized as 0, 1, and 2 to estimate sizes of prey. All intact prey and up to 30 undamaged otoliths of each species were measured from each stomach. Potential biases in selecting otoliths for measurement were minimized by the following protocol: (1) one otolith from each severed head was measured; (2) if a prey species was represented by fewer than 60 otoliths categorized as 0–2, half of those undamaged otoliths were randomly selected and measured; and (3) if a stomach contained more than 60 undamaged otoliths from one prey species, 30 were randomly selected and measured. For calculating the proportion of reconstructed mass, the lengths of damaged otoliths were estimated from the average lengths of undamaged otoliths contained in the same stomach. If all the otoliths of a particular prey species in a stomach were eroded, the sizes of these fish were

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estimated by taking the average size of that species eaten by other dolphins. Equations used to calculate standard length and weight of fish were obtained from Barros (1993) and Barros and Wells (1998). Equations for estimating the dorsal mantle length and wet weight of the squid *Loligo* sp. were those given by Gannon *et al.* (1997) and Lange and Johnson (1981) for *L. pealei*. Length-weight regressions were not available for all prey species. Therefore, analyses of reconstructed mass included only the seven most numerous prey; the combined masses of these seven species summed to 100%.

Bottlenose Dolphin Diet: Variation Between Habitats

To investigate potential dietary differences between habitats, we matched each dolphin in our estuarine sample ($n = 24$) to one from the ocean sample according to location, season, sex, and length. Locations of strandings inside the estuaries were matched to those on ocean beaches according to latitude. The mean difference in latitude for each pair was $0.12°$. We defined the seasons as: winter = December–February; spring = March–May; summer = June–August; and fall = September–November. For each sex, dolphins were categorized as "juvenile" or "adult" (*i.e.*, sexually mature) by body length. Mead and Potter (1990) estimated mean length at sexual maturity to be 233.5 cm for females that stranded in an area that overlapped our study area. Working on Florida's Gulf of Mexico coast, Wells *et al.* (1987) found that sexual maturity is reached at 230 cm and 245 cm for females and males, respectively. Since Wells *et al.* (1987) had data on both females and males, and their data on female maturation were similar to that of Mead and Potter (1990), we considered females to reach sexual maturity at 230 cm and males to mature at 245 cm, standard length. But it should be noted that Mead and Potter (1990) compared the age/length curve for bottlenose dolphins of the central Atlantic coast of the U.S. to that of animals from the Gulf of Mexico and found that the dolphins from the central Atlantic attained a higher asymptotic length (approximately 250 *vs.* 230 cm, both sexes combined).

Bottlenose Dolphin Diet: Seasonal Variation

We explored seasonal variations in species composition and prey size among dolphins that died in the ocean. Due to the small sample size, this analysis could not be performed on the sample of dolphins obtained in the estuaries. Seasons were defined as above.

Bottlenose Dolphin Diet: Demographic Variation

Among the sample of dolphins obtained from the ocean, we investigated whether different demographic groups tended to eat different species or whether there were any differences among demographic groups regarding the sizes of prey that they ate. The life history stages examined included: juvenile female ($\leq$ 230 cm and having no visible signs of milk in the stomach), adult female ($>$230 cm), juvenile male ($\leq$ 245 cm and having no signs of milk), and adult male ($>$245 cm; Wells *et al.* 1987).

Statistical Analysis

We used Spearman's rank correlation coefficient to assess differences in proportions of numerical abundance between samples of dolphins that died inside estuaries and those that died in the ocean, following the methods of Fritz (1974). Prey that were equally rare in both samples would exaggerate the dietary similarities between the groups. Therefore, only prey that accounted for $\geq 2\%$ of numerical abundance in at least one of the samples were included in the analysis. To investigate differences in the proportional contributions of individual prey species associated with season and with demography, we used Kruskal-Wallis tests. Differences in the sizes of prey eaten by dolphins in each sample were tested with either Mann-Whitney U tests or Kruskal-Wallis tests, depending on the number of samples being compared. For comparisons of prey length only food items represented by otoliths graded as 0, 1, or 2 were used; otoliths that were eroded more severely were excluded. The individual dolphin was the unit of analysis, meaning that the average lengths of each species consumed by each dolphin were used in these analyses. To facilitate interpretation of feeding data, we investigated whether there were any differences in the sizes of the dolphins between the estuarine and oceanic samples and among the samples from the four seasons using the Mann-Whitney and Kruskal Wallis tests, respectively. Standard deviation is given as a measure of variability about the mean and is presented using the convention $x \pm$ SD. All statistics were calculated using SigmaStat version 2.03.

RESULTS

We examined the stomach contents of 186 bottlenose dolphins that died in the estuarine and nearshore ocean waters of North Carolina (Fig. 1). Based on the presence of "offshore" prey (*e.g.*, Ommastrephid and Histioteuthid squids) and parasites, six dolphins were categorized as being the offshore ecotype and were excluded from further analyses. The 17 dolphins with stock identities known from sighting histories and location of death were classified correctly by the combination of prey and parasite assemblages. Of the 180 stomachs from coastal dolphins, 146 contained solid food, seven contained only milk, and 27 were empty (Appendix 1). The largest juvenile whose stomach contained only milk and had no evidence of solid food (prey remains or stomach parasites) was 164 cm in length. The smallest dolphin with solid food (and the stomach parasite *Braunina* sp.) was 146 cm. Of the dolphins that had remains of solid food, 71 (49%) bore evidence that interactions with humans caused death, such as entanglement in monofilament gill net and mutilation; 22 (15%) had no evidence of human interaction, and cause of death was not assessed in 53 (36%) cases.

At least 21 families and 31 species of prey were found in the diet of the dolphins (Table 1). Fishes from the family Sciaenidae dominated the diet, appearing in 95% of dolphin stomachs, and accounting for 73% of all food items eaten. Weakfish (*Cynoscion regalis*), croaker, and spot were the most important prey, followed distantly by inshore squid (*Loligo* sp.) and striped anchovy (*Anchoa hepsetus*). Length-frequency distributions of weakfish, spot, and croaker are shown in Figure 2. The weakfish eaten tended to be larger (mean $= 244\pm60$ mm) than the other prey (croaker: mean $= 157 \pm 35$; spot: mean $= 131 \pm 31$), which is reflected by this species' reconstructed mass values being substantially higher than its numerical abundance values.
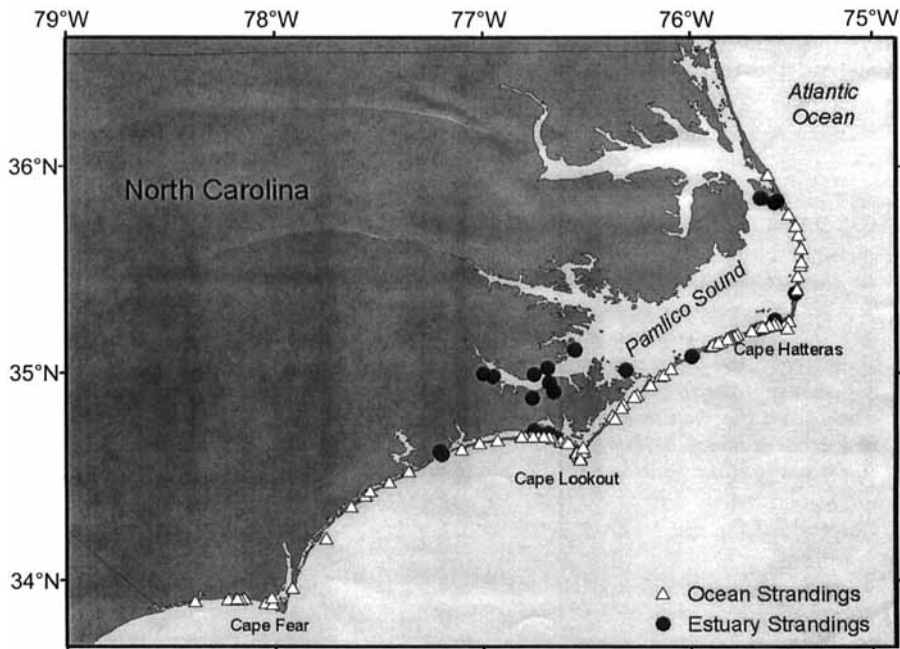
Figure 1. Stranding locations of bottlenose dolphins (*Tursiops truncatus*) that were included in analyses of food habits. Triangles indicate carcasses recovered from the ocean and circles indicate carcasses recovered from the estuary.

Bottlenose Dolphin Diet: Variation Between Habitats

There was no significant difference between the estuarine and oceanic samples regarding the sizes of the dolphins ($U = 352.5$, $P = 0.43$). Eight prey species accounted for $\geq 2\%$ of numerical abundance in either the "ocean" or "estuary" sample: croaker, weakfish, spot, inshore squid, striped anchovy, shrimp eel (*Ophichthus gomesi*), menhaden, and black drum (*Pogonias cromis*; Fig. 3). Croaker and spot dominated the stomach contents of dolphins stranded inside the estuaries (Fig. 3A). Croaker accounted for 51% of numerical abundance (92% by frequency of occurrence and 63% by proportion of mass) and spot contributed 26% (75% by frequency of occurrence and 19% by proportion of mass). Dolphins that stranded along ocean beaches had large amounts of weakfish, croaker, spot, inshore squid, and striped anchovy in their stomachs (Fig. 3B). The Spearman rank correlation coefficient (r_s) for numerical abundance values of estuary and ocean dolphins was 0.419 ($P = 0.213$), indicating that there was no statistical relationship between the rank orders of prey in the diets of these two groups.

The average sizes of weakfish, croaker, and spot eaten by dolphins in the ocean were larger than those eaten by dolphins in the estuaries. These differences were significant in the cases of weakfish and spot. The average standard length of weakfish eaten by dolphins in the ocean sample was 256 ± 56 mm, while that of weakfish eaten by dolphins in the estuary sample was 208 ± 57 mm (Mann-Whitney test:

Table 1. Relative importance of prey measured by (1) frequency of occurrence, (2) proportion of numerical abundance and (3) proportion of reconstructed mass, and proportion of otoliths recovered from skulls (Grade = 0) for prey of "oceanic" and "estuarine" coastal *Tursiops truncatus* from North Carolina ($n = 146$).

Prey	Frequency (%)	Numerical (%)	Mass (%)	Grade-0 Otoliths (%)
CHORDATA	98	96	–[a]	–
Sciaenidae	95	73	–	–
Weakfish (*Cynoscion regalis*)	65	24	36	3.0
Croaker (*Micropogonias undulatus*)	47	22	24	2.5
Spot (*Leiostomus xanthurus*)	54	20	23	1.7
Silver perch (*Bairdiella chrysoura*)	29	3	2	0.0
Kingfish sp. (*Menticirrhus sp.*)	13	1	–	–
Black drum (*Pogonias cromis*)	12	1	–	–
Red drum (*Sciaenops ocellatus*)	6	1	–	–
Star drum (*Stellifer lanceolatus*)	3	<1	–	–
Unidentified fish	31	7	–	–
Unidentified fish spp.	31	7	–	–
Engraulidae	24	6	–	–
Striped anchovy (*Anchoa hepsetus*)	24	6	2	0.0
Clupeidae	19	2	–	–
Menhaden (*Brevoortia tyrannus*)	19	2	4	13.3
Sparidae	19	2	–	–
Pinfish (*Lagodon rhomboides*)	8	1	–	–
Sparidae spp.	12		–	–
Spottail pinfish (*Diplodus holbrooki*)	1	<1	–	–
Pigfish (*Orthopristis chrysoptera*)	17	1	–	–
Bothidae	15	1	–	–
Flounder (*Paralichthys sp.*)	8	<1	–	–
Whiff (*Citharichthys sp.*)	12	<1	–	–
Gadidae	8	1	–	–
Hake (*Urophycis sp.*)	8	1	–	–
Ophichthidae	4	1	–	–
Shrimp eel (*Ophichthus gomesi*)	4	1	–	–
Mugilidae	3	<1	–	–
Mullet (*Mugil cephalus*)	3	<1	–	–
Synodontidae	3	<1	–	–
Lizardfish (*Synodus foetens*)	3	<1	–	–
Percichthyidae	2	<1	–	–
Striped bass (*Morone saxatilis*)	2	<1	–	–
Carangidae	2	<1	–	–
Jack (*Caranx sp.*)	1	<1	–	–
Carangidae sp.	1	<1	–	–
Pomatomidae	1	<1	–	–
Bluefish (*Pomatomus saltatrix*)	1	<1	–	–
Batrachoididae	1	<1	–	–
Toadfish (*Opsanus tau*)	1	<1	–	–
Soleidae	1	<1	–	–
Hogchoker (*Trinectes maculatus*)	1	<1	–	–

Table 1. Continued.

Prey	Frequency (%)	Numerical (%)	Mass (%)	Grade-0 Otoliths (%)
Order Lamniformes	1	<1	–	–
Unidentified shark	1	<1	–	–
MOLLUSCA	30	7	–	–
Loliginidae	30	7	–	–
Inshore squid (*Loligo* sp.)	26	7	9	0
Brief squid (*Loliguncula brevis*)	4	<1	–	–
CRUSTACEA	8	<1	–	–
Order Stomatopoda	1	<1	–	–
Mantis shrimp (4 families)	1	<1	–	–
Penaeidae	6	<1	–	–
Shrimp (species?)	6	<1	–	–
Alpheidae	1	<1	–	–
Alpheus sp.	1	<1	–	–
Portunidae	1	<1	–	–
Blue crab (*Callinectes sapidus*)	1	<1	–	–

[a] – = no data.

$U = 186.5$, $P = 0.007$). The average spot eaten in the estuary was 118 ± 34 mm, while the average spot consumed in the ocean was 141 ± 25 mm ($U = 206.0$, $P = 0.001$). For croaker, the average size in the ocean sample was 165 ± 38 mm whereas that of the estuary sample was 144 ± 22 mm ($U = 194.0$, $P = 0.062$). Stomachs of dolphins in the estuary sample contained significantly more prey items (115 ± 143) than those from the ocean sample (48 ± 67; $U = 876.0$, $P = 0.002$).

Bottlenose Dolphin Diet: Seasonal Variation

For the dolphins that stranded on ocean beaches, there was no difference in dolphin size with regard to the seasons in which stranding occurred (Kruskal-Wallis test: $H = 0.42$, df $= 3$, $P = 0.94$). However, there was considerable variation in the diet associated with season (Fig. 4). For example, the numerical proportion of croaker varied by an order of magnitude across seasons, reaching a high of 61% in summer and a low of 6% in winter ($H = 23.1$, df $= 3$, $P < 0.01$). The contributions of spot were consistent at about 15% from winter to summer, but increased to 35% in fall ($H = 14.25$, df $= 3$, $P < 0.01$). Weakfish were extremely important during winter (47%) and spring (34%), but dropped in importance in summer (8%) and fall (6%; $H = 21.19$, df $= 3$, $P < 0.01$). Inshore squid comprised 8%–10% of the diet for most of the year, but then dropped to just 1% in summer. However, differences in the numerical proportions of inshore squid across seasons were not significant ($H = 0.78$, df $= 3$, $P = 0.855$). Despite the large variations in diet composition throughout the year, there were no differences in sizes of prey associated with season (weakfish: $H = 5.94$, df $= 3$, $P = 0.114$; spot: $H = 4.19$, df $= 3$, $P = 0.242$; croaker: $H = 2.09$, df $= 3$, $P = 0.554$; Table 2).
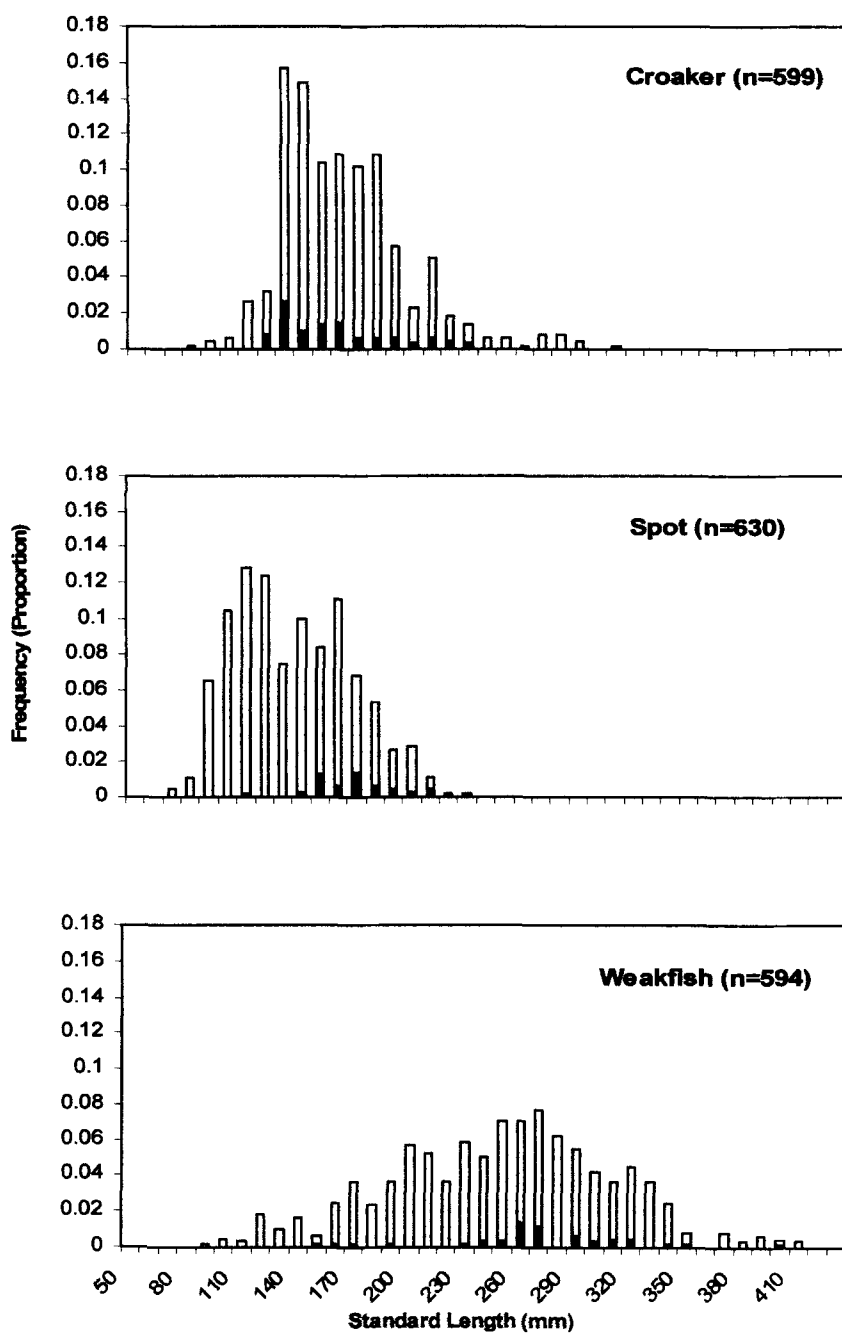
Figure 2. Length-frequency distributions of croaker, spot, and weakfish eaten by coastal bottlenose dolphins in North Carolina waters. Solid bars indicate length estimates made from otoliths graded as 0 (retrieved from skulls) and open bars are from otoliths graded as 1 (free in the stomach, undamaged) and 2 (free in the stomach, slightly damaged).
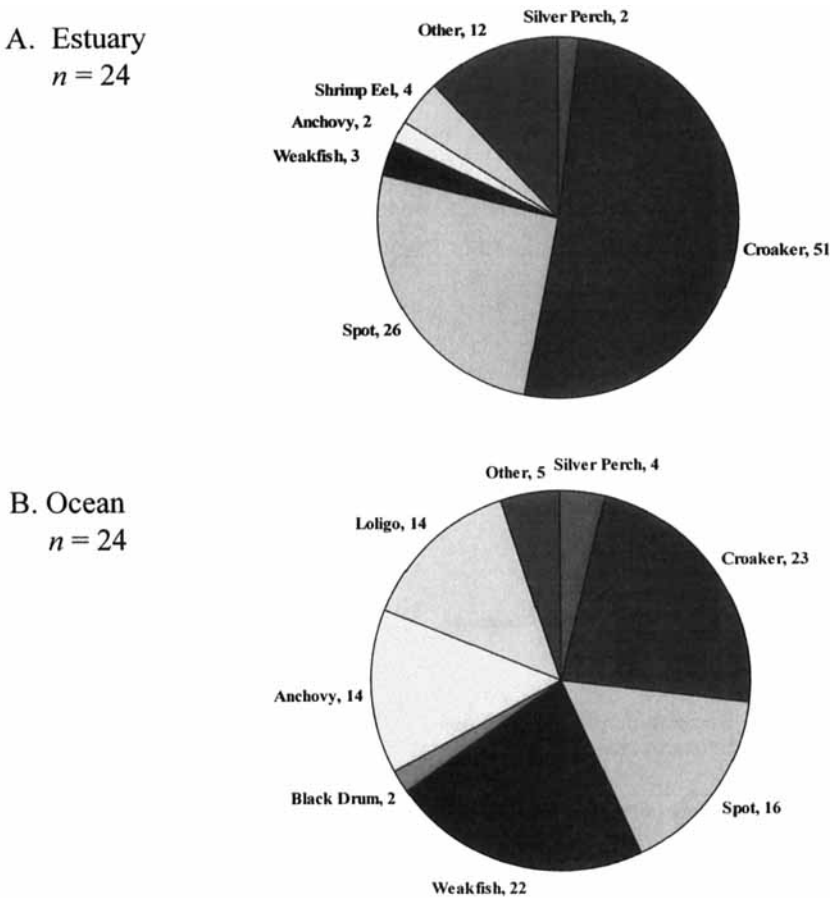
A. Estuary
n = 24

Other, 12   Silver Perch, 2

Shrimp Eel, 4
Anchovy, 2
Weakfish, 3

Croaker, 51

Spot, 26

B. Ocean
n = 24

Other, 5   Silver Perch, 4

Loligo, 14

Croaker, 23

Anchovy, 14

Black Drum, 2

Spot, 16

Weakfish, 22

Figure 3. Numerical abundance (%) of prey from stomach contents of coastal bottlenose dolphins that died in the (a) estuarine and (b) ocean waters of North Carolina. Each dolphin in the estuary sample is matched with one in the ocean sample by season, demographic group, and latitude.

Bottlenose Dolphin Diet: Demographic Variation

Croaker comprised a greater percentage of the diet for males than for females, and mature dolphins ate more croaker than did juveniles (Fig. 5). The differences in the numerical proportions of croaker eaten by each demographic group were significant ($H = 8.82$, $df = 3$, $P = 0.032$). Juvenile dolphins ate proportionately more spot than did adults, whereas adults ate more weakfish. However, among the four demographic groups investigated, there were no significant differences in the numerical proportions of spot, weakfish, or inshore squid eaten (spot: $H = 6.88$, $df = 3$, $P = 0.076$; weakfish: $H = 2.22$, $df = 3$, $P = 0.528$; inshore squid: $H = 1.99$, $df = 3$, $P = 0.575$). There were no significant differences among the four dolphin demographic groups regarding the sizes of prey (Table 3). As with the investigation of the effects
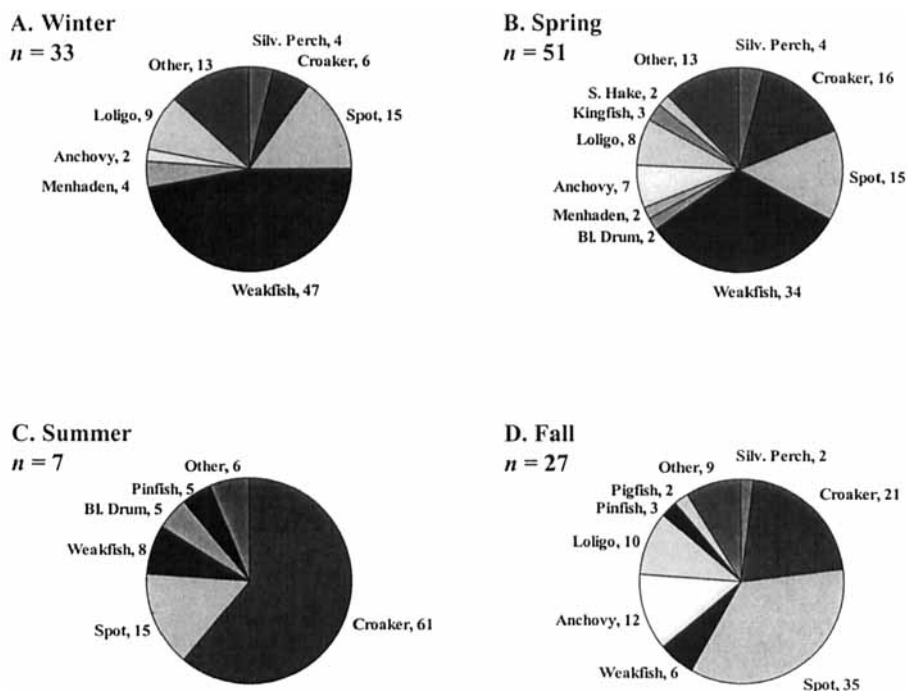
Figure 4. Numerical abundance (%) of prey from stomach contents of oceanic coastal bottlenose dolphins by season.

of season on prey size, sample sizes of some prey eaten by some demographic categories of dolphins were small.

DISCUSSION

Although coastal bottlenose dolphins from North Carolina ate a wide variety of prey, their diet was composed primarily of soniferous, demersal species from the family Sciaenidae. Three species—croaker, weakfish, and spot—accounted for 66% of the diet by proportion of numerical abundance. There were significant variations in the diet associated with habitat (ocean *vs.* estuary), season, and dolphin demography, which have not been investigated previously. These variations in the foods eaten may have resulted from spatial or temporal variations in prey availability, from ontogenetic changes in feeding preference, or from differences in habitat selection. It seems likely that demographic differences in diets among dolphins that died in the ocean resulted primarily from differences in feeding preferences, in feeding abilities, or in habitat selection. Dietary differences among seasons and between habitats may have also reflected differences in prey availability. For example, weakfish was more prominent in the diets of mature dolphins than in those of juveniles, perhaps reflecting the difficulty of capturing this swift prey. Inshore squid was far more important to mature females than it was to the other demographic groups, which may have resulted from mothers with calves having different habitat preferences from other demographic groups or it could have resulted from reproductive females

Table 2. Mean and standard deviations of standard lengths (mm) of weakfish, croaker, and spot eaten by oceanic coastal bottlenose dolphins off North Carolina during all four seasons. Sample size (*n*) refers to the number of dolphin stomachs with measurable prey.

	Weakfish	*n*	Croaker	*n*	Spot	*n*
Winter	274 ± 55	23	158 ± 0	2	130 ± 14	4
Spring	247 ± 55	29	171 ± 39	8	131 ± 24	18
Summer	214 ± 54	6	134 ± 15	6	138 ± 21	3
Fall	258 ± 54	8	166 ± 38	12	152 ± 30	17

broadening their diet to meet the increased energy demands of lactation. Similar patterns have been found in other delphinids. Robertson and Chivers (1997) noted in spotted dolphins (*Stenella attenuata*), that the diet of lactating females contained higher proportions of squids than did that of pregnant females (but see Bernard and Hohn 1989).

Dietary differences between dolphins that died in estuaries and those that died in the ocean were consistent with the habitat partitioning hypothesis, whereby some members of the population are principally estuarine and others are primarily oceanic. The diet of dolphins in the estuaries was dominated by Atlantic croaker and spot, while the diet of the dolphins that died in the ocean was dominated by weakfish. Additionally, the prey consumed by dolphins in the ocean tended to be larger than those eaten by dolphins in the estuaries. The differences between the two habitats regarding prey composition and prey size were not likely to have been caused by sampling bias, since we controlled for size, sex, season, and location. We could not determine whether any of these differences in diet resulted from differences in prey availability between the two habitats or from differences in prey selection by the dolphins in the two habitats. Fisheries data are collected using different techniques in the two habitats and, therefore, are inappropriate for statistical comparisons. However, catches in demersal trawl surveys of the Neuse River estuary were similar to the diets of dolphins that died in the estuaries; croaker and spot were the two most abundant species and young-of-the-year fish represented the greatest proportion of the catch (Eby and Crowder 2002, Gannon 2003). Juveniles of all three major prey—weakfish, croaker, and spot—use estuaries as nursery habitat (Chao and Musick 1977, Currin *et al.* 1984), and therefore the average sizes of individuals from these species may be smaller in the estuary than in the ocean. Coastal oceans tend to have higher species richness relative to estuaries

Table 3. Mean and standard deviations of standard lengths (mm) of weakfish, croaker, and spot eaten by four demographic groups of oceanic coastal bottlenose dolphins off North Carolina. Sample size (*n*) refers to the number of dolphin stomachs with measurable prey.

	Weakfish	*n*	Croaker	*n*	Spot	*n*
Female <230 cm	221 ± 73	9	151 ± 40	5	122 ± 23	7
Female ≥230 cm	269 ± 48	20	184 ± 19	4	158 ± 25	7
Male <245 cm	253 ± 57	22	150 ± 30	14	138 ± 24	20
Male ≥245 cm	262 ± 56	12	189 ± 39	5	154 ± 36	5

A. Juv. Female
$n = 24$

Silv. Perch, 4
Croaker, 7
Other, 16
S. Hake, 2
Kingfish, 3
Loligo, 8
Spot, 21
Anchovy, 5
Menhaden, 7
Bl. Drum, 2
Weakfish, 25

B. Mat. Female
$n = 29$

Other, 10   Silv. Perch, 4
Croaker, 13
Red Drum, 3
S. Hake, 2
Loligo, 14
Spot, 13
Menhaden, 2
Weakfish, 38

C. Juv. Male
$n = 42$

Other, 7   Silv. Perch, 3
Pinfish, 3
Loligo, 6
Croaker, 21
Anchovy, 9
Weakfish, 24
Spot, 27

D. Mat. Male
$n = 18$

Other, 7
Loligo, 8
Croaker, 31
Anchovy, 8
Bl. Drum, 2
Spot, 12
Weakfish, 32

Figure 5. Numerical abundance (%) of prey from stomach contents of oceanic coastal bottlenose dolphins by demographic group.

(Remane and Schlieper 1971), and this difference in diversity was reflected in the diets of our two dolphin samples.

Our findings that sciaenids dominate the diet of coastal bottlenose dolphins agree well with those of Mead and Potter (1990) and Barros (1993). With a sample of stranded bottlenose dolphins from North Carolina, Virginia, and Maryland, Mead and Potter (1990) found weakfish, spot, and croaker to be the most frequently occurring prey. The largest differences were in the occurrences of engraulids, sparids, haemulids, and gadids (24%, 19%, 17%, and 8% in our sample, respectively). Mead and Potter found engraulids (8%), haemulids (2%), and sparids (0%) to be much less common, and gadids (16%) to be more common. Barros's (1993) sample from dolphins stranded on ocean beaches in northeast Florida was very similar to our ocean sample. However, Barros's sample from the Indian River Lagoon in northeast Florida contained relatively few weakfish but did include large numbers of spotted seatrout (*Cynoscion nebulosus*), silver perch, oyster toadfish (*Opsanus tau*), and striped mullet (*Mugil cephalus*). Working with stranded specimens from the area of Sarasota Bay, Florida, Barros and Wells (1998) found relatively few sciaenids in the diet; the three most abundant prey were pinfish (*Lagodon rhomboides*), striped mullet, and pigfish (*Orthopristis chrysoptera*). The paucity of sciaenids in the diet of Sarasota Bay dolphins may reflect lower relative abundance of these fishes in the subtropical fish community of southwest Florida (Wessel and Winner 2003). None of these other studies were able to investigate differences in the diet associated with season or demography.

Soniferous fishes account for 75% of the total number of prey in Table 1 (Sciaenids, Sparids, Haemulids, Carangids, and Batrachoidids; see Fish and Mowbray 1970). The Sciaenidae, in particular, is one of the most prolific sound-producing families of fish. The dominance of soniferous species in the diet is consistent with Barros's hypothesis that coastal bottlenose dolphins use passive listening to locate noise-producing prey (Barros and Odell 1990, Barros 1993, Barros and Wells 1998). Listening is an important mode of prey detection for a wide variety of taxa including owls (Bye *et al.* 1992) and bats (Marimuthu and Neuweiler 1987, Bailey and Haythornthwaite 1998). There is also evidence that odontocetes hunt by passive listening. Mammal-eating killer whales (*Orcinus orca*) appear to rely heavily on passive listening for prey detection. Whereas fish-eating killer whales use echolocation extensively, their mammal-eating conspecifics echolocate sparingly (Barrett-Lennard *et al.* 1996). Barrett-Lennard and his colleagues attributed the differences in hunting strategies of the two forms to differences in the ecological costs of echolocation incurred by each form. Pinnipeds and cetaceans can hear the killer whales' echolocation signals but salmonid fishes cannot. Therefore, when mammal-eating whales echolocate, they reveal their presence to their prey.

Other coastal delphinids may also use passive listening to locate chorusing sciaenids. Pilleri *et al.* (1982) noted a high degree of co-occurrence between the Indian humpback dolphin (*Sousa plumbea*) and chorusing aggregations of *Johnius belangerii*. De Olivera Santos *et al.* (2002) found that 92% of the teleosts eaten by marine tucuxi dolphins (*Sotalia fluviatilis*) in Brazilian waters were sciaenids, leading these authors to hypothesize that tucuxi locate prey via passive listening.

If piscivores use acoustic cues to locate prey, then sound production could be a very costly activity for fishes, and the risks of calling should be traded off with the benefits of this behavior. Sound production in sciaenids is often associated with spawning (Fish and Mowbray 1970, Connaughton and Taylor 1995, Luczkovich *et al.* 1999). Calling may be a way for males to attract mates or may play a role in synchronizing the release of gametes. Therefore, the potential costs of remaining silent may be reduced reproductive success. Given that both the risks and benefits of calling appear to be high for fish, one might expect them to be under intense selection pressure to be able to detect their predators and to modify their calling behavior when predators are present. Indeed, Luczkovich *et al.* (2000) documented a reduction in the received amplitude of silver perch spawning choruses in response to playbacks of recorded sounds from bottlenose dolphins.

Despite data indicating that many vertebrate taxa detect prey by passive acoustics and that the prey eaten by coastal bottlenose dolphins in North Carolina produce sound, it is still not clear how the dolphins in this study could have used passive listening to detect their prey. The spatiotemporal pattern in consumption of Sciaenid species did not correspond with the pattern of their spawning, which is when they are thought to produce sound most frequently (Fish and Mowbray 1970, Connaughton and Taylor 1995, Luczkovich *et al.* 1999). For example, Atlantic croaker spawn in the ocean during winter (Hildebrand and Cable 1930, Chao and Musick 1977, Warlen and Burke 1990), but they were eaten most often by dolphins inside the estuaries and by dolphins in the ocean during summer (Fig. 3, 4). Weakfish, on the other hand, spawn in the estuaries during May and June (Connaughton and Taylor 1995, Luczkovich *et al.* 1999), but they were eaten most commonly in the ocean during winter. These data suggest two possibilities: (1) that bottlenose dolphins do not rely on passive listening to any great extent for detecting prey, or (2) that these fishes have a larger repertoire of sounds than is

currently believed, including sounds that are not associated with spawning. To understand the nature of the interactions that take place between coastal bottlenose dolphins and their prey, and to gain better insights into the ecology of sound production by fishes, the passive listening hypothesis needs to be tested experimentally, and more rigorous behavioral studies of sound production by sciaenids need to be conducted.

ACKNOWLEDGMENTS

LITERATURE CITED

BAILEY, W. J., AND S. HAYTHORNTHWAITE. 1998. Risks of calling by the field cricket *Teleogryllus oceanicus*; potential predation by Australian long-eared bats. Journal of Zoology (London) 244:505–513.

BARRETT-LENNARD, L. G., J. K. B. FORD AND K. A. HEISE. 1996. The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behaviour 51:553–565.

BARROS, N. B. 1993. Feeding ecology and foraging strategies of bottlenose dolphins on the central east coast of Florida. Ph.D. dissertation, University of Miami, Coral Gables, FL. 328 pp.

BARROS, N. B., AND D. K. ODELL. 1990. Food habits of bottlenose dolphins in the Southeastern United States. Pages 309–328 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

BARROS, N. B., AND R. S. WELLS. 1998. Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Journal of Mammalogy 79: 1045–1059.

BERNARD, H. J., AND A. A. HOHN. 1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). Journal of Mammalogy 70: 211–215.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. Fishery Bulletin of the U.S. Fish and Willdlife Service, Volume 53, No. 74 (First Revision).

BROUDER, R. D. 1979. Guide to otoliths of some northwest Atlantic fishes. National Marine Fisheries Service/Northeast Fisheries Science Center Lab Reference Document 79-36. NOAA/Northeast Fisheries Science Center, Woods Hole, MA. 70 pp.

BYE, F. N., B. V. JACOBSEN AND G. A. SONERUD. 1992. Auditory prey location in a pause-travel predator: Search height, search time and attack range of Tengmalm's owls *Aegolius funereus*. Behavioral Ecology 3:266–276.

CALDWELL, D. K., AND M. C. CALDWELL. 1972. The world of the bottlenosed dolphin. Lippincott, New York, NY.

CHAO, L. N. 1978. A basis for classifying western Atlantic Sciaenidae (Teleostei, Perciformes). NOAA Technical Report, NMFS Circ., No. 415. 64 pp. (Available

from the National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia 22161.)

CHAO, L. N., AND J. A. MUSICK. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fishery Bulletin, U.S. 75:657–702.

CLARKE, M. R., ED. 1986. A handbook for the identification of cephalopod beaks. Oxford University Press, Oxford, UK.

CLOSE, W. H., J. NOBLET AND R. P. HEAVENS. 1985. Studies on energy metabolism of the pregnant sow. British Journal of Nutrition 53:267–279.

CLUTTON-BROCK, T. H., G. R. IASON, S. D. ALBON AND F. E. GUINNESS. 1982. Effects of lactation on feeding behavior and habitat use in wild red deer hinds. Journal of Zoology 198:227–236.

COCKCROFT, V. G., AND G. J. B. ROSS. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. Pages 295–308 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

CONNAUGHTON, M. A., AND M. H. TAYLOR. 1995. Seasonal cycles in the sonic muscles of the weakfish, *Cynoscion regalis*. Fishery Bulletin, U.S. 92:697–703.

CURRIN, B. M., J. P. REED AND J. M. MILLER. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: A comparison of tidal and nontidal nursery areas. Estuaries 7(4A):451–459.

DA SILVA, J., AND J. D. NEILSON. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Canadian Journal of Fisheries and Aquatic Sciences 42:1439–1442.

DE OLIVEIRA SANTOS, M. C., S. ROSSO, R. A. DOS SANTOS, S. H. BULIZANI LUCATO AND M. BASSOI. 2002. Insights on small cetacean feeding habits in southeastern Brazil. Aquatic Mammals 28:38–45.

EBY, L. A., AND L. B. CROWDER. 2002. Hypoxia-based habitat compression in the Neuse River estuary: Context-dependent shifts in behavioral avoidance thresholds. Canadian Journal of Fisheries and Aquatic Sciences 59:952–965.

FISH, M. P., AND W. H. MOWBRAY. 1970. Sounds of western North Atlantic fishes: A reference file of biological underwater sounds. Johns Hopkins Press, Baltimore, MD.

FRITZ, E. S. 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 1:210–214.

GANNON, D. P., A. J. READ, J. E. CRADDOCK AND J. G. MEAD. 1997. Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the U.S. mid-Atlantic coast. Marine Mammal Science 13:405–418.

GANNON, D. P. 2003. Behavioral ecology of an acoustically mediated predator-prey system: Bottlenose dolphins and sciaenid fishes. Ph.D. dissertation, Duke University, Durham, NC. 244 pp.

HÄRKÖNEN, T. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu ApS. Biological Consultants, Hellerup, Denmark.

HERSH, S. L., AND D. A. DUFFIELD. 1990. Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. Pages 129–139 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

HILDEBRAND, H. H., AND L. E. CABLE. 1930. Development and life history of fourteen teleostean fishes at Beaufort, North Carolina. Bulletin of the U.S. Bureau of Fisheries 46:383–488.

HYSLOP, E. J. 1980. Stomach contents: a review of methods and their application. Journal of Fish Biology 17:411–429.

JOBLING, M., AND A. BREIBY. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265–274.

KASTELEIN, R. A., N. VAUGHAN, S. WALTON AND P. R. WIEPKEMA. 2002. Food intake and

body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Marine Environmental Research 53:199–218.

KROGER, R. L., AND J. F. GUTHRIE. 1972. Incidence of the parasitic isopod, *Olencira praegustator*, in juvenile menhaden. Copeia 2:370–374.

LANGE, A. M., AND K. L. JOHNSON. 1981. Dorsal mantle length-total weight relationships of squids *Loligo pealei* and *Illex illecebrosus* from the Atlantic coast of the United States. NOAA Technical Report, NMFS SSRF-745. 18 pp. (Available from the National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161.)

LINDSAY, J. A., AND R. L. MORAN. 1976. Relationships of parasitic isopods *Lironeca ovalis* and *Olencira praegustator* to marine fish host in Delaware Bay. Transactions of the American Fisheries Society 105:327–332.

LUCZKOVICH, J. J., M. W. SPRAGUE, S. E. JOHNSON AND R. C. PULLINGER. 1999. Delimiting spawning areas of weakfish *Cynoscion regalis* (family sciaenidae) in Pamlico Sound, North Carolina using passive hydroacoustic surveys. Bioacoustics 10:143–160.

LUCZKOVICH, J. J., H. J. DANIEL, M. HUTCHINSON, T. JENKINS, S. E. JOHNSON, R. C. PULLINGER AND M. W. SPRAGUE. 2000. Sounds of sex and death in the sea: Bottlenose dolphin whistles suppress mating choruses of silver perch. Bioacoustics 10(4): 323–334.

MANN, J., AND B. SMUTS. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136:529–566.

MARIMUTHU, G., AND G. NEUWEILER. 1987. The use of acoustical cues for prey detection by the Indian false vampire bat, *Megaderma lyra*. Journal of Comparative Physiology, A 160:509–515.

MEAD, J. G., AND C. W. POTTER. 1990. Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pages 165–198 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

MEAD, J. G., AND C. W. POTTER. 1995. Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: Morphologic and ecologic considerations. IBI Reports (Marine Biology Research Institute, Kamogawa, Japan) 5:31–44.

MURDY, E. O., R. S. BIRDSONG AND J. A. MUSICK. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, DC.

PEREZ, M. A. AND E. E. MOONEY. 1986. Increased food energy consumption of lactating northern fur seals, *Callorhinus ursinus*. Fishery Bulletin, U.S. 84:371–381.

PILLERI, G., C. KRAUS AND M. GIHR. 1982. The ambient noise in the environment of *Sousa plumbea* and *Neophocoena phocaenoides* (Cetacea) with special reference to the sounds of *Johnius belangerii* (Pisces, Sciaenidae). Investigations on Cetacea 14:95–126.

RECCHIA, C. R., AND A. J. READ. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. Canadian Journal of Fisheries and Aquatic Sciences 47:561–565.

REMANE, A., AND C. SCHLIEPER. 1971. Biology of brackish water. Wiley, New York, NY.

ROBERTSON, K. M., AND S. J. CHIVERS. 1997. Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. Fishery Bulletin, U.S. 95:334–348.

ROBINS, C. R., G. C. RAY AND J. DOUGLAS. 1986. Peterson field guides: Atlantic coast fishes. Houghton Mifflin Co., Boston, MA.

RODRÍGUEZ, D., L. RIVERO AND R. BASTIDA. 2002. Feeding ecology of the franciscana (*Pontoporia blainvillei*) in marine and estuarine waters of Argentina. Latin American Journal of Aquatic Mammals 1:77–94.

SMITH, R. J., AND A. J. READ. 1992. Consumption of euphausiids by harbour porpoise (*Phocoena phocoena*) calves in the Bay of Fundy. Canadian Journal of Zoology 70:1629–1632.

TORRES, L. G., P. E. ROSEL, C. D'AGROSA AND A. J. READ. 2003. Improving management of

overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. Marine Mammal Science 19:502–514.

TOWNSEND, C. H. 1914. The porpoise in captivity. Zoologica 1(16):289–299, 9 plates.

TRUE, F. W. 1885. The bottle-nose dolphin, *Tursiops tursio*, as seen at Cape May, New Jersey. Science 5(116):338–339.

WARLEN, S. M., AND J. S. BURKE. 1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461.

WELLS, R. S., M. D. SCOTT AND A. B. IRVINE. 1987. The social structure of free-ranging bottlenose dolphins. Current Mammalogy 2:247–305.

WESSEL, M. R., AND B. L. WINNER. 2003. Using a modified purse seine to collect and monitor estuarine fishes. Gulf and Caribbean Research 15:61–71.

WINDELL, J. T. 1967. Rates of digestion in fishes. Pages 151–173 *in* S. D. Gerking, ed. The biological basis of freshwater fish production. John Wiley & Sons, Inc., New York, NY.

Appendix 1. Numbers of *Tursiops truncatus* stomachs examined for analyses of food habits.

Total number of dolphin stomachs examined	186
Stomachs from dolphins recovered in the ocean	154
Empty "ocean" stomachs	19
Ocean stomachs containing only milk	7
Ocean stomachs containing solid food	128
Stomachs from offshore dolphins containing food	6
Stomachs from "coastal ocean" dolphins containing food	122
Females <230 cm with food	24
Females ≥230 cm with food	29
Males <245 cm with food	42
Males ≥245 cm with food	18
Sex unknown	9
Winter	33
Spring	51
Summer	7
Fall	27
Date unknown	4
Stomachs from dolphins recovered in estuaries	32
Empty "estuarine" stomachs	8
Estuarine stomachs containing only milk	0
Estuarine stomachs containing solid food	24
Females <230 cm with food	4
Females ≥230 cm with food	3
Males <245 cm with food	9
Males ≥245 cm with food	5
Sex unknown	3
Winter	4
Spring	10
Summer	6
Fall	4