Food habits of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off the coast of New England

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Abstract—Although the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) is one of the most common dolphins off New England, little has been documented about its diet in the western North Atlantic Ocean. Current federal protection of marine mammals limits the supply of animals for investigation to those incidentally caught in the nets of commercial fishermen with observers aboard. Stomachs of 62 *L. acutus* were examined; of these 62 individuals, 28 of them were caught by net and 34 were animals stranded on Cape Cod. Most of the net-caught *L. acutus* were from the deeper waters of the Gulf of Maine. A single stomach was from the continental slope south of Georges Bank. At least twenty-six fish species and three cephalopod species were eaten. The predominant prey were silver hake (*Merluccius bilinearis*), spoonarm octopus (*Bathypolypus bairdii*), and haddock (*Melanogrammus aeglefinus*). The stomach from a net-caught *L. acutus* on the continental slope contained 7750 otoliths of the Madeira lanternfish (*Ceratoscopelus maderensis*). Sand lances (*Ammodytes* spp.) were the most abundant (541 otoliths) species in the stomachs of stranded *L. acutus*. Seasonal variation in diet was indicated; pelagic Atlantic herring (*Clupea harengus*) was the most important prey in summer, but was rare in winter. The average length of fish prey was approximately 200 mm, and the average mantle length of cephalopod prey was approximately 50 mm.

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The Atlantic white-sided dolphin (*Lagenorhynchus acutus*) is restricted to the temperate and subpolar North Atlantic Ocean, ranging from west Greenland (approximately 64°N) to North Carolina (about 35°N) in the western North Atlantic, and from Norway to the Bay of Biscay in the eastern North Atlantic (Leopold and Couperus, 1995). There are thought to be three populations in the western North Atlantic—the Gulf of Maine, Gulf of St. Lawrence, and Labrador Sea populations (Palka et al., 1997). Seasonal shifts in the Gulf of Maine population have been reported; highest numbers are found in summer and fall and lowest numbers in winter (Northridge et al., 1997; Palka et al., 1997). Most of our animals, however, were obtained during the winter.

This study is the first detailed analysis of the food habits of the Atlantic white-sided dolphin in the western North Atlantic Ocean, hereafter referred to as *L. acutus* rather than the more cumbersome Atlantic white-sided dolphin. Previously, only three live-caught specimens from off New England have been examined for stomach contents and reported in the literature. A single specimen collected in 1954 (Schevill, 1956) and a second collected in 1976, likely a discarded incidental take from a gillnet set near Jeffreys Ledge (Katona et al., 1978), were taken in summer and contained the same species of fish and squid. These records indicated that Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), and northern shortfin squid (*Illex illecebrosus*) could be significant components of the diet. A single animal driven ashore in Trinity Bay, Newfoundland, also contained Atlantic herring and northern shortfin squid (Sergeant and Fisher, 1957).

Other observations have reported a few more prey species for *L. acutus*. Stomachs of 14 of 40 stranded *L. acutus* examined from Cobscook Bay, Maine, contained one silver hake, nine shortfin squid, five rainbow smelt (*Osmerus mordax*), and fragments of unidentified decapod shrimp (St. Aubin and Geraci, 1979; Sergeant et al., 1980). Katona et al. (1978) reported probable feeding on sand lances (*Ammodytes* spp.) by *L. acutus* associated with feeding humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*). The only *L. acutus* feeding incident recorded was on December 20, 1997, on Stellwagen Bank, southwestern Gulf of Maine, when a

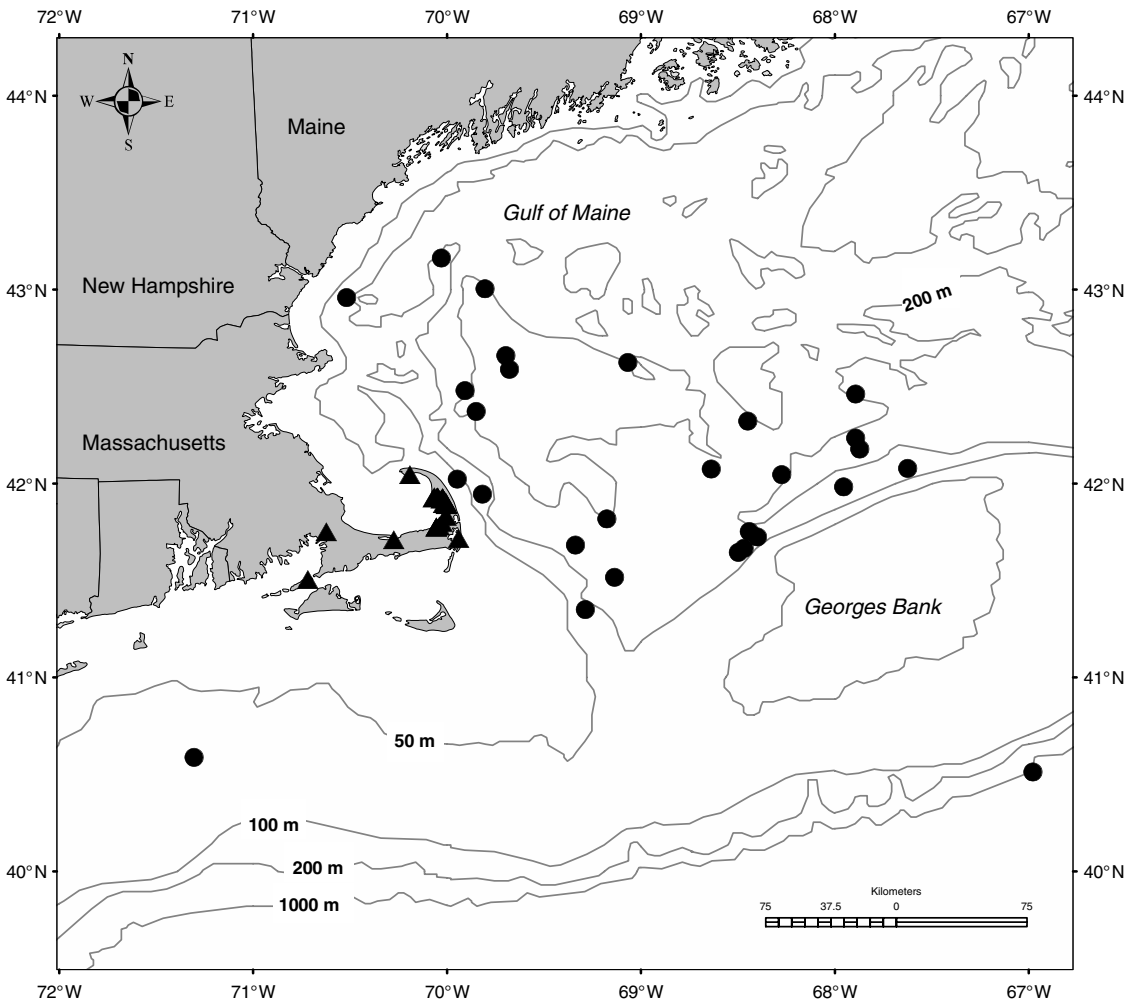

Figure 1

Occurrences from 1991 to 2006 of 62 Atlantic white-sided dolphins (*Lagenorhynchus acutus*) collected in the Gulf of Maine and south of Georges Bank and examined for stomach contents in this study. Circles are locations of net-caught dolphins; triangles are locations of stranded dolphins.

group was observed circling and feeding on a school of sand lance (Weinrich et al., 2001).

Materials and methods

This study records stomach contents from 28 incidentally caught and 34 stranded *L. acutus* from the Gulf of Maine population off the coast of New England (Fig. 1). The animals examined were collected between 1991 and 2006, most of them from 2004–5. The incidentally caught (hereafter referred to as net-caught) animals were taken either by otter trawl (22 stomachs) or by sink gillnet (six stomachs). Of these, 26 were from the Gulf of Maine, one was from deep water (500 m) on the continental slope south of Georges Bank near Munsen Canyon, and one was from the continental shelf south of Narragansett Bay. Thirty-four stomachs were from strandings: 33 from outer Cape Cod, Barnstable County, MA, and one from Naushon, Elizabeth Islands, Dukes County, MA (Table 1).

We have examined every available stomach of net-caught *L. acutus*. All were taken in the U.S. commercial fishery and sampled aboard ship by fisheries observers of the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC, Woods Hole, MA), Northeast Fisheries Observer Program (NEFOP). NEFOP is the permitting and monitoring agency of the commercial fishing fleet in compliance with the Marine Mammal Protection Act (MMPA) and the U.S. Endangered Species Act (ESA).

Stranded animals were obtained by volunteers of the Cape Cod Stranding Network, currently known as International Fund for Animal Welfare (IFAW), Yarmouth, MA. Most of the stomachs were initially frozen and curated by the NEFSC.

Contents from stomachs determined to be intact (reliable) were examined for frequency, relative abundance,

Table 1

Summary comparison of numbers, sex, and stomach contents of 34 stranded vs. 28 net-caught Atlantic white-sided dolphins (*Lagenorhynchus acutus*) collected in the western North Atlantic Ocean off the coast of New England, between 1991 and 2006; and seasonality of the net-caught individuals. Total net-caught includes two calves with empty stomachs; seasonal net-caught excludes the two calves; S. of Georges = South of Georges Bank. Nontrace = whole prey.

			Seasonal net-caught		
	Strandings	Total net-caught	Winter	Summer	S. of Georges
Number of dolphins	34	28	22	3	1
Depth where captured (m), mean (range)	0	189.8 (55–503)	186.9 (71–265)	107.0 (55–187)	503
Number of males	22	9	9	0	0
Length of males (cm), mean (range)	227 (156–280)	208 (173–260)	208 (173–260)	0	0
Adult males (>230cm)	10	2	2	0	0
Number of females	12	16	12	3	1
Length of females (cm), mean (range)	205 (168–219)	199 (161–253)	203 (171–253)	178 (161–203)	252
Adult females (>200cm)	10	6	4	1	1
Number unsexed	0	3	1		
Number of stomachs containing food	22 (65%)	25 (89%)	20 (91%)	3 (100%)	1 (100%)
Number of empty stomachs	12 (35%)	3 (11%)	2 (9%)	0	0
Number of otoliths	856	10287	2157	287	7843
unidentified	231	54	51	2	1
Number of fish species	8	21	17	6	7
Number of cephalopod beaks	34	535	519	11	5
Number of cephalopod species	3	3	3	2	1
Number of identified prey					
Nontrace fishes	0	50	35	15	0
Near nontrace fishes (skulls)	7	56	38	4	14
Total fishes	332	5179	1120	135	3924
Nontrace cephalopods	0	2	0	2	0
Near nontrace cephalopods	0	1	0	1	0
Total cephalopods	20	282	274	4	4

and size (length, weight) of prey. Two net-caught dolphins examined and subsequently eliminated from the analysis were one partly decomposed female with a mud-filled stomach and thoracic cavity and virtually no food in the stomach, and a partially decomposed male with an almost empty stomach taken on the continental shelf south of Narragansett Bay.

Stomachs were weighed whole, divided into their three components (forestomach, main, and pyloric), emptied of contents, and weighed again to determine both the size of the stomach and the mass of its contents. Whole prey (termed “nontrace” prey because they were found relatively intact [not in traces]) were separated, identified, weighed, and measured directly (standard length for fishes and mantle length for cephalopods); well-digested prey (termed "trace prey" because they were found in traces as hard parts, e.g. skull bones, otoliths, jaws, prootic bones of clupeids, teeth and opercula of bony fishes, toothplates of hagfish, and cephalopod beaks and pens) were separated, identified, weighed, and original length measurements were estimated indirectly (standard length for fishes and mantle length for cephalopods). Otoliths were removed from skulls of both nontrace and trace fishes and then cleaned, dried, and measured. The remaining contents were soaked overnight in hot water, if necessary, or elutriated directly through a series of sieves to remove soft tissue and retain hard parts. All items found were identified to the lowest taxonomic level possible (usually to species) by using our own reference collection and published guides (Campana, 2004; Clarke, 1962, 1986; Collette and Klein-MacPhee, 2002; Gregory, 1933; Harkönen, 1986; Smale et al., 1995; Vecchione, 2002). Forestomach contents were then counted and measured and used in all further analyses (Table 2). All fish hard parts, including bones and otoliths, and hagfish toothplates, were stored dried. Cephalopod beaks were removed from buccal masses, cleaned, and stored in 70% ethanol. Crustacean remains and all parasites were counted and also stored in 70% ethanol.

Prey lengths and weights were calculated from otolith lengths for fishes, from lower rostral lengths for squids, and from lower hood lengths for octopods (Tables 3 and 4). Calculations of prey size were used to construct the

Table 2

Summary comparison of abundance of identified prey found in the stomachs of both net-caught and stranded Atlantic white-sided dolphins (*Lagenorhynchus acutus*) collected between 1991 and 2006, in the western North Atlantic Ocean off the coast of New England. *n* = number of stomachs; S. of Georges = South of Georges Bank.

Prey species	Common name	Family	Net-caught winter *n*=20	Net-caught summer *n*=3	Net-caught calves *n*=2	Net-caught S. of Georges *n*=1	Stranded winter *n*=29
Alosa pseudoharengus	alewife	Clupeidae	2				
Ammodytes spp.	sand lance	Ammodytidae					271
Arctozenus risso	white barracudina	Paralepididae				5	
Benthosema glaciale	glacier lanternfish	Myctophidae	7			3	
Ceratoscopelus maderensis	Madeira lantern fish	Myctophidae	1			3875	
Clupea harengus	Atlantic herring	Clupeidae	5	29			
Diaphus dumerilii	Dumeril's lanternfish	Myctophidae	1				
Diaphus mollis	soft lanternfish	Myctophidae				2	
Enchelyopus cimbrius	fourbeard rockling	Phycidae	18				
Gadus morhua	Atlantic cod	Gadidae	1	4			
Hippoglossoides platessoides	American plaice	Pleuronectidae	4				
Limanda ferruginea	yellowtail flounder	Pleuronectidae					3
Maurolicus weitzmani	Atlantic pearlside	Sternoptychidae	2				
Melanogrammus aeglefinus	haddock	Gadidae	103				4
Merluccius bilinearis	silver hake	Merlucciidae	823	99		37	18
Myxine glutinosa	Atlantic hagfish	Myxinidae	87	2			16
Nezumia bairdii	marlin-spike	Macrouridae	4				
Osmerus mordax	rainbow smelt	Osmeridae					10
Scomber scombrus	Atlantic mackerel	Scombridae	2				
Sebastes fasciatus	Acadian redfish	Scorpaenidae		3			
Stomias boa	boa dragonfish	Stomiidae				1	
Tautogolabrus adspersus	cunner	Labridae					9
Ulvaria subbifurcata	radiated shanny	Stichaeidae					1
Urophycis chuss	red hake	Phycidae	90	13			
Urophycis tenuis	white hake	Phycidae	4			1	
Zoarces americanus	ocean pout	Zoarcidae	1				
Bathypolypus bairdii	spoonarm octopus	Octopodidae	210				2
Illex illecebrosus	northern shortfin squid	Ommastrephidae	1	5			2
Loligo pealeii	longfin inshore squid	Loliginidae	63	1		4	16
Total			1429	156	0	3928	352

Table 3

Analysis of prey in 20 Atlantic white-sided dolphins (*Lagenorhynchus acutus*) incidentally net-caught during winter in the Gulf of Maine between 2001 and 2006. NA = not applicable; * = *Myxine glutinosa* double toothplates, 4 per individual; ** = may include a few *Urophycis tenuis*.

	Prey species			Otoliths or beaks			Prey length		Prey weight		
Fishes and cephalopods	Number of occurrences	Number of items	Number of individuals	Number measured	Average length (mm)	Length range (mm)	Average length (mm)	Length range weight (g)	Average (mm)	Weight range (g)	Total weight (kg)
Alosa pseudoharengus	2	4	2	4	3.7	2.5–4.9					0.27
Benthosema glaciale	3	13	7	7	0.9	0.7–1.4					<0.01
Ceratoscopelus maderensis	1	1	1	1	2.3	2.3					<0.01
Clupea harengus	4	8	5	5	3.3	1.8–4.4	202.4	97.1–277.1	88.2	7.4–177.8	0.44
Diaphus dumerilii	2	2	1	2	2.8	2.6–2.9					<0.01
Enchelyopus cimbrius	4	29	18	29	3.2	1.9–4.0	148.0	48.9–213.6	22.2	0.9–62.3	0.40
Gadus morhua	1	2	1	2	11.0	11.0					0.32
Hippoglossoides platessoides	2	7	4	7	3.1	2.5–3.7					0.35
Maurolicus weitzmani	2	2	2	2	1.6	1.5–1.8					<0.01
Melanogrammus aeglefinus	7	184	103	171	10.2	6.0–13.8	203.2	87.4–327.2	91.7	5.9–341.2	9.44
Merluccius bilinearis	18	1646	823	306	9.9	3.0–22.4	202.5	58.6–464.1	57.2	1.0–669.7	27.91
Myxine glutinosa	10	332*	87	NA			NA		NA		NA
Nezumia bairdii	1	6	4	6	5.6	4.0–6.2					NA
Scomber scombrus	1	2	2	2	3.8	2.5–5.0					0.58
*Urophycis chuss***	13	191	90	111	8.9	1.6–19.1	208.9	8.5–489.1	103.8	0.1–809.4	11.50
Urophycis tenuis	3	7	4	7	14.3	12.6–15.6					0.89
Zoarces americanus	1	2	1	2	3.0	3.0					<0.01
Total otoliths		2106		664							
Total fishes			1155								52.10
Bathypolypus bairdii	13	390	210	96	2.8	1.7–4.0	49.8	36.3–64.5	42.6	11.2–99.0	8.78
Illex illecebrosus	1	2	1	1	1.5	1.5					0.01
Loligo pealeii	12	127	63	63	0.9	0.4–1.7	51.6	16.8–118.9	10.9	0.8 – 52.8	0.69
Total cephalopod beaks		519									
Total cephalopods			274	160							9.48
Total all prey			1429	824							61.58

Table 4

Analysis of prey in 33 Atlantic white-sided dolphins (*Lagenorhynchus acutus*): 3 net-caught in the Gulf of Maine in summer between 1992 and 2003; 1 net-caught south of Georges Bank in summer 1993; and 29 stranded on Cape Cod in winter between 1994 and 2006. NA = not applicable; * = *Myxine glutinosa* double toothplates, 4 per individual.

	Prey species			Otoliths or beaks (mm)			Prey length(mm)		Prey weight		
Fishes and cephalopods	Occurrences	Items	Individuals	Measured	Mean length	Length range	Mean length	Length range	Mean weight (g)	Weight range (g)	Total weight (kg)
Net-caught summer Gulf of Maine (3 stomachs)											
Clupea harengus	3	56	29	43	4.1	3.0–5.0	259.7	180.2–318.7	154.4	48.2–271.5	3.85
Gadus morhua	2	8	4	8	4.5	4.3–5.0	76.0	67.2–89.2	5.0	3.29–7.55	0.03
Merluccius bilinearis	2	193	99	79	6.9	2.6–12.0	139.8	50.2–246.7	18.0	0.6–91.5	1.78
Myxine glutinosa	1	7*	2	NA							
Sebastes fasciatus	1	4	3	4	1.7	1.1–2.1					
Urophycis chuss	1	24	13	23	2.2	1.5–4.7	25.0	5.7–93.6	0.4	0.05–4.1	<0.01
Illex illecebrosus	2	9	5	5	2.8	1.8–3.5	145.2	96.3–179.4	70.9	18.3–115.9	0.35
Loligo pealeii	1	2	1	1	1.5	1.5	117.2		40.5		0.04
Total		303	156								6.05
Net-caught summer south of Georges Bank (1 stomach)											
Arctozenus risso	1	9	5	6	3.4	3.3–3.6					
Benthosema glaciale	1	5	3	4	1.3	1.1–1.5					
Ceratoscopelus maderensis	1	7750	3875	100	2.9	2.2–3.7	59.9	45.8–75.1	1.5	0.9–2.0	5.60
Diaphus mollis	1	2	2	2	1.7	1.4–2.0					
Merluccius bilinearis	1	73	37	32	12.9	11.0–15.4	269.2	229.5–321.5	120.0	70.0–210.0	3.94
Stomias boa	1	2	1	0							
Urophycis tenuis	1	1	1	1	10.0	10.0					
Loligo spp.	1	5	4	1	1.8		144.9		67.4		0.07
Total		7847	3928								9.61
Strandings winter (29 stomachs)											
Ammodytes spp.	1	541	271	32	2.2	1.9–2.9	140.9	124.8–172.2	15.1	10.3–29.0	4.09
Limanda ferruginea	1	6	3	0							
Melanogrammus aeglefinus	1	8	4	8	11.6	10.5–12.5	249.7	212.2–279.7	152.1	90.0–210.6	1.22
Merluccius bilinearis	2	31	18	15	5.2	3.9–6.3	107.3	81.1–131.3	7.0	2.7–12.5	0.13
Myxine glutinosa	6	53	16	NA							
Osmerus mordax	2	20	10	0							
Tautogolabrus adspersus	1	16	9	16	1.0	0.9–1.2					
Ulvaria subbifurcata	1	2	1	2	2.5	2.5					
Bathypolypus bairdii	2	2	2	2	2.1	1.4–2.8					
Illex illecebrosus	1	4	2	2	3.7	3.7–3.8	191.7	189.2–194.1	135.1	130.3–139.8	0.27
Loligo pealeii	4	28	16	12	1.6	0.4–2.9	126.5	15.7–246.4	89.3	0.7–283.6	1.07
Total		711	352								6.78

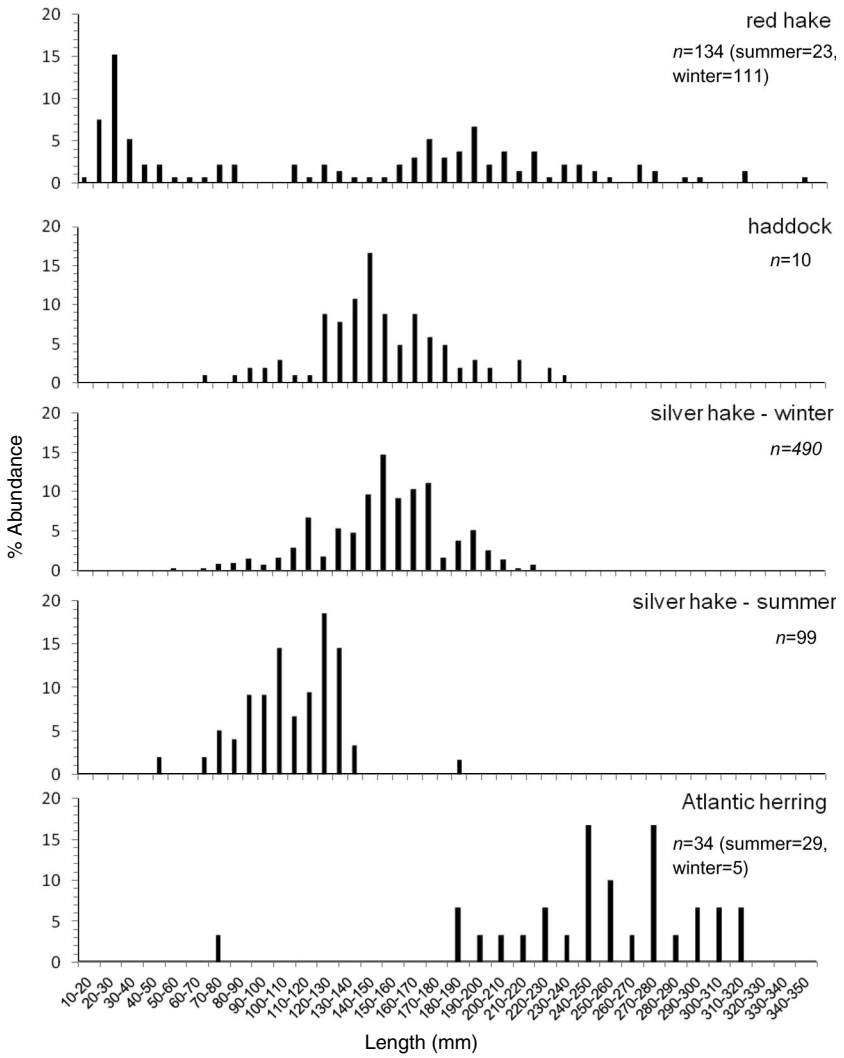

Figure 2

Length-frequency distributions for fishes eaten by Atlantic white-sided dolphins (*Lagenorhynchus acutus*) in the Gulf of Maine (1991–2006). (**A**) Red hake (*Urophycis chuss*) all seasons; (**B**) haddock (*Melanogrammus aeglefinus*) all seasons; (**C**) silver hake (*Merluccius bilinearis*) winter; (**D**) silver hake summer; (**E**) Atlantic herring (*Clupea harengus*) all seasons.

frequency diagrams shown in Figure 2 for the most abundant species.

Results and discussion

Stomachs of immature and adult dolphins of both sexes were examined. The two calves were 119 cm and 139 cm in length and had milk but no solid prey in their stomachs. The smallest juvenile was 161 cm and contained solid prey but no milk in its stomach. Females longer than 200 cm and males longer than 230 cm were considered mature (Sergeant et al., 1980) (Table 1).

Altogether, the 62 *L. acutus* stomachs contained 5561 fishes of at least 26 species, and 304 cephalopods of one octopus and two squid species (Table 2). Most of the stomach contents were trace remains. The most commonly found prey species, in order of abundance, were: 1) Madeira lanternfish (*Ceratoscopelus maderensis*), 3876 individuals, all but one from a single stomach; 2) silver hake (*Merluccius bilinearis*), 945 individuals from 22 stomachs; 3) sand lance (*Ammodytes* spp.), 271 individuals from a single stranded dolphin; 4) spoonarm octopus (*Bathypolypus bairdii*), 212 individuals from 14 stomachs; 5) haddock (*Melanogrammus aeglefinus*), 107 individuals from eight stomachs; 6) Atlantic hagfish (*Myxine glutinosa*), 105 individuals

from 17 stomachs; and 7) red hake (*Urophycis chuss*), 103 individuals from 14 stomachs.

Gulf of Maine, winter

The 20 stomachs containing prey from *L. acutus* net-caught in winter in the Gulf of Maine provide our most complete data set for analysis (Table 3). These stomachs contained 1155 fishes of 17 species and 274 cephalopods of three species. Five species, three fishes and two cephalopods, silver hake (45.3%), spoonarm octopus (14.3%), haddock (15.3%), red hake (18.7%), and longfin inshore squid (1.1%) accounted for almost 95% of the mass of prey. We were unable to calculate the mass of hagfish; their toothplates (the only hard parts remaining in the stomachs) are not proportional to an individual's size.

In order of frequency of occurrence and numerical abundance 1) the demersal silver hake was found in 90% of the stomachs and accounted for 71% of the fishes eaten; 2) the benthic spoonarm octopus were found in 65% of the stomachs and accounted for 77% of cephalopods; 3) the demersal haddock were found in 35% of the stomachs and made up 8.9% of the fishes; 4) the demersal red hake were found in 65% of the stomachs and accounted for 7.7% of the fishes; 5) the benthic scavenger hagfish were found in 50% of the stomachs and accounted for 7.5% of the fishes; and 6) the pelagic longfin squid were found in 60% of the stomachs and accounted for 23% of the cephalopods. The four fish species constituted 96% of the fish prey eaten, and the two cephalopods made up nearly all of the cephalopods consumed. Fishes made up 81% of all prey, and cephalopods, the remainder (19%). Notable were the scarcity or absence in winter of pelagic fish species (e.g., herring, alewives, smelt, mackerel, and sand lance).

Gulf of Maine, summer

Only three stomachs were available from animals net-caught in the Gulf of Maine in summer. These three contained 150 fishes of six species and six squids of two species (Table 4). The most abundant prey were silver hake, Atlantic herring, and red hake, which numerically accounted for 63%, 19%, and 8% of total prey, respectively. These three species made up 29%, 64%, and less than 1% of total mass, respectively. Silver hake was numerically the most abundant species in both winter and summer stomachs. The pelagic Atlantic herring, which was almost absent in winter, was the most important species present in summer. The benthic spoonarm octopus, which was very abundant in the winter stomachs, was absent in summer.

Continental Slope south of Georges Bank

A single *L.acutus* was obtained south of Georges Bank near Munsen Canyon, in 500 m of water. This dolphin was a 252-cm lactating female. Its stomach contained over 3900 fishes of seven species (Table 4). Except for 37 silver hake and one white hake, this individual had been feeding on open-ocean pelagic fishes, of which 99% (3875) were Madeira lanternfish. Two other lanternfishes (the glacier lanternfish [*Benthosema glaciale*] and the soft lanternfish [*Diaphus mollis*]), the white barracudina (*Arctozenus risso*), and the boa dragonfish (*Stomias boa*) were also present. This stomach contained 9.6 kg of prey, the largest amount of any *L. acutus* in this study; Madeira lanternfish made up 58% of the prey mass, and silver hake 41%.

Strandings

Stomachs of the stranded dolphins contained little identifiable material (Table 1). No nontrace fish or cephalopods were present in any of these stomachs. About one-quarter of the otoliths (27%) were too digested to be identified or measured and therefore could not be used for further analysis. Of the identifiable otoliths, 87% were those of sand lance, all from one stomach (Table 2). The presence of these fish in that stomach was the only evidence indicating recent feeding.

Twenty-nine of the 34 strandings occurred in the winter. Stomachs of these dolphins contained eight fish species and three cephalopod species. Sand lance constituted 79% of all prey (both fishes and cephalopods) and made up 60% of the total mass. Silver hake and longfin squid made up 18% and 16% of the total mass, respectively. Five fish species present in the stomachs of stranded animals—cunner (*Tautogolabrus adspersus*), radiated shanny (*Ulvaria subbifurcata*), rainbow smelt, sand lance, and yellowtail flounder (*Limanda ferruginea*)—were not found in the stomachs of our net-caught dolphins. Of the five stomachs from nonwinter strandings, four were empty and the fifth (in September) contained only one identifiable fish, a silver hake.

Prey species

In the Gulf of Maine, silver hake was by far the most important prey species in the stomachs that we examined. A schooling, demersal fish, silver hake is found only along the Atlantic coast of North America, from Florida to Newfoundland, at a wide range of depths, from shallow waters to 900 m (Collette and Klein-MacPhee 2002; Iwamoto 2002). Previously, reports indicated the presence of silver hake in *L. acutus* diets but not as an important prey. Among the few otoliths found in stranded *L. acutus* stomachs, silver hake was the second most abundant prey species (Table 4).

Silver hake is also an important prey for other marine mammals in the Gulf of Maine. It was a primary prey for harbor porpoise (*Phocoena phocoena*) during summer in the Bay of Fundy (Recchia and Read, 1989) and in autumn near Jeffreys Ledge in the western Gulf of Maine (Gannon et al., 1998). It was also the predominant prey for net-caught young of the year harbor seals (*Phoca vitulina*) taken in shallow waters in the western Gulf of Maine (Williams, 1999).

Atlantic herring was present in stomachs of both winter and summer net-caught dolphins. It was of minor importance in the winter (only five individuals identified in 20 stomachs analyzed), but was of primary importance (the largest biomass of all prey) in the summer; 29 individuals were present in the three stomachs analyzed. *Lagenorhynchus acutus* feeds on Atlantic herring in the summer months when the lipid content of herring is highest (Yasui and Gaskin, 1986). Even though only three stomachs from the summer were analyzed, our findings are similar to those reported in the literature.

Lagenorhynchus acutus is rarely observed in the deeper waters of the continental slope south and east of New England (Selzer and Payne, 1988; Waring et al., 2008). The stomach contents of our single *L. acutus* taken incidentally in water 500 m deep, south of Georges Bank, were unlike those from the Gulf of Maine. The primary prey of this dolphin was the Madeira lanternfish, a myctophid living between 330 and 600 m during the day in slope water and on the continental slope (Backus et al., 1968). This indicates that *L. acutus* is not limited to feeding on shallow-water and epipelagic species.

We have found that other species of cetaceans, when on the continental slope off the east coast of the United States and southeastern Canada, feed primarily on Madeira lanternfish. We found large numbers, often more than 1000 individuals, in common dolphin (*Delphinus delphis*), Atlantic spotted dolphin (*Stenella frontalis*), and pantropical spotted dolphin (*Stenella attenuata*), which had maximum numbers of 3646, 568, and 870 Madeira lanternfish, respectively. A single harbor porpoise (*Phocoena phocoena*) taken incidentally off Cape Hatteras in winter had nearly 500 Madeira lanternfish in its stomach (Read et al., 1996).

In the eastern North Atlantic Ocean, *L. acutus* feeds for the most part on oceanic fishes, primarily silvery pout (*Gadiculus argenteus*), lanternfishes, and pearlsides (*Maurolicus muelleri*) (Couperus, 1997). Couperus found that, in certain years, southwest of Ireland, *L. acutus* follow the spawning migration of mackerel (*Scomber scombrus*) inshore in the late winter and spring and are caught by net in the mackerel fishery. A comparison of trace and nontrace prey in their stomachs indicated that although mackerel represented 88% of the fresh prey, the dolphins' prior meals had comprised 88% mid-water fishes. *Lagenorhynchus acutus* feeds on herring when in shallow water off Norway (Jonsgård and Nordlii, 1952).

In addition to the above mentioned species, stomachs of *L. acutus* stranded on the coast of northern Europe have contained otoliths of blue whiting (*Micromesistius poutassou*), tacauds (*Trisopterus* spp.), horse mackerel (*Trachurus trachurus*), pilchard (*Sardina pilchardus*), sand lances, pollock (*Pollachius virens*), whiting (*Merlangius merlangus*), haddock, gobies (Gobiidae), dragonet (Callionymidae), and argentine (*Argentina sphyraena*), (Desportes, 1985; Rogan et al., 1997; Santos et al., 1995[1], 1996[2]). Santos et al. (1995) also identified four species of cephalopods in the stomachs of *L. acutus* stranded in Scotland.

Despite previous observations of *L. acutus* feeding on sand lance (Weinrich et al., 2001), in this study we found sand lance in only one stomach, that of a stranded dolphin. Although approximately 50% of the stranded animals in our study had virtually empty stomachs, this one stomach contained 549 sand lance otoliths. The relatively empty stomachs indicate a lack of feeding before stranding. Little information exists on the digestion and egestion rates for cephalopod and teleost prey in cetaceans; therefore, it is impossible to accurately estimate how long a period elapsed between the last feeding and the stranding event (Mintzer et al., 2008). It is also possible that *L. acutus* regurgitates food because of the stress of a stranding event, leaving its stomach virtually empty. The trace sand lance otoliths found in the one stomach could have been trapped in the stomach rugae, giving a false impression of a recent meal. Regardless of when the sand lances were eaten, their presence in the stomach corroborates historic observations of *L. acutus* feeding on sand lance (Katona et al., 1978; Weinrich et al., 2001).

Lagenorhyncus acutus appears to exhibit size-selective predation; the average fish prey length is approximately 200 mm and cephalopod prey mantle length is about 50 mm during the winter (Fig. 2). The total lengths of the cephalopods (tentacle length plus the mantle length) are little more than half the length of the fishes. One large 464-mm silver hake, whose size was determined from a 22.4-mm otolith and two 100 mm dentaries, was found in the stomach of a winter net-caught dolphin. We assume that the dolphin ate only the head of this fish, which would itself have been approximately 200 mm. It is possible that the head had been cut off and discarded by fishermen.

Some very small red hake (less than 90 mm) were found in the stomachs of two *L. acutus* (Fig. 2A). These were smaller than the smallest silver hake, haddock, and herring eaten, and are therefore evidence of secondary consumption. There were no large red hake or haddock in either of the two stomachs. Large silver hake, the only predatory fish in each of the two *L. acutus* stomachs, was therefore the likely primary consumer of the small red hake.

Two cephalopods, spoonarm octopus and longfin inshore squid, were both important prey in our *L. acutus*. In winter stomachs, the benthic octopus was the second most abundant prey species, and the pelagic squid was the sixth most abundant (Table 3). Historical publications document northern shortfin squid in *L.*

[1] Santos, M. B., G. J. Pierce, G. Wijnsma, H. M. Ross, and R. J. Reid. 1995. Diets of small cetaceans stranded in Scotland 1993–1995. ICES Council Meeting (C.M.). 1995/N:6, 9 p.

[2] Santos, M. B., G. J. Pierce, A. Lopez, A. Barreiro, and A. Guerra. 1996. Diets of small cetaceans stranded in NW Spain 1994–95. ICES Council Meeting (C.M.). 1996/N:11, 6 p.

acutus diets, but give no record of spoonarm octopus or longfin inshore squid. Spoonarm octopus was rare (one individual in 95 stomachs) in harbor porpoise from the Gulf of Maine (Gannon et al., 1998).

Both Atlantic hagfish and spoonarm octopus are bottom-dwelling species associated with sandy to muddy substrates on the continental shelf and upper slope. Spoonarm octopus is restricted to the western North Atlantic, and is found from Greenland to Florida (Muus, 2002). Atlantic hagfish is found on both sides of the North Atlantic and is bipolar, inhabiting comparable latitudes in the southern hemisphere (Collette and Klein-MacPhee, 2002). *Lagenorhyncus acutus* probably does not dive to the bottom to forage. It probably consumes benthic octopus and hagfish in several ways, namely 1) it may feed on catch unwanted and discarded by fishermen and 2) it may feed on animals that have been forced off the bottom by otter trawls or that have come off the bottom on their own, as with hagfish, to feed on fishes disturbed by otter trawls. Most of our net-caught dolphins (79%) were taken in bottom otter trawls. Spoonarm octopus and Atlantic hagfish were only found in dolphins caught in bottom otter trawls, not from those in sink or drift gillnets. *Lagenorhyncus acutus* feed in the vicinity of nets (Leopold and Couperus, 1995), as do bottlenose dolphin (*Tursiops truncatus*) (Corkeron et al., 1990) and other cetaceans (Fertl and Leatherwood, 1997). This would explain both the capture of *L. acutus* by otter trawls and the occurrence of benthic animals in their diet.

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