Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine

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Abstract.—This study describes the stomach contents of 95 harbor porpoises (*Phocoena phocoena*) killed in groundfish gill nets in the Gulf of Maine between September and December, 1989–94. The importance of prey was assessed by frequency of occurrence, numerical proportion, and proportion of ingested mass. Atlantic herring (*Clupea harengus*) was the most important prey, occurring in 78% of noncalf porpoise stomachs and contributing 44% of ingested mass. Pearlsides (*Maurolicus weitzmani*), silver hake (*Merluccius bilinearis*), and red and white hake (*Urophycis* spp.) were common prey items. There were no significant differences among diets of sex and maturity groups, but the calf diet differed significantly from adults in number of Atlantic herring eaten and the total mass of food consumed. At four to seven months of age, calves were eating pearlsides, small silver hake, and euphausiids (*Meganyctiphanes norvegica*) while still nursing.

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Harbor porpoises (*Phocoena phocoena*) from the Bay of Fundy and Gulf of Maine are believed to comprise a single population, hereafter referred to as the Gulf of Maine population (Palka et al., 1996; Wang et al., 1996). To date, studies of the food habits of this population have been restricted to samples collected in the Bay of Fundy during summer, where porpoises feed primarily on Atlantic herring (*Clupea harengus*; Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992). Many porpoises leave the Bay of Fundy in fall, moving southward into the Gulf of Maine (Gaskin, 1977; Gaskin, 1984; Read and Westgate, 1997). During winter, a portion of the population disperses over the continental shelf from New England to North Carolina (Polacheck et al., 1995; Read et al., 1996).

Because of their small size and limited energy stores, harbor porpoises must remain close to food resources to avoid starvation (Koopman, 1994). Moreover, their unusual life history incurs high energetic costs; most females attain sexual maturity at three years of age and give birth to a calf each year (Read and Hohn, 1995). Lactation lasts for at least eight months; thus mature females spend most of their lives simultaneously pregnant and lactating. This intensive reproductive schedule requires calves to become nutritionally independent at a relatively early age, usually before the end of their first year (Smith and Read, 1992).

Large numbers of harbor porpoises are killed each year in gill nets in the Bay of Fundy, Gulf of Maine, and Mid-Atlantic Bight (Read and Gaskin, 1988; Read et al., 1993; Bravington and Bisack, 1996). For the Gulf of Maine, the estimated average annual harbor porpoise bycatch for 1990 to 1995 was 1800 (Bisack[1]). Little is known about the process by which porpoises become entangled in gill nets, and thus efforts are hampered in mitigating this conservation problem. Porpoises may become entangled because they feed on fish species targeted by the fish-

[1] Bisack, K. 1996. Harbor porpoise bycatch estimates in the U.S. Gulf of Maine sink gillnet fishery: 1994 and 1995. Paper presented to the International Whaling Commission Scientific Committee Meeting in Aberdeen, Scotland, June 1996 (in review).

ery or because they feed on the same prey as the target species.

In this paper, we examine the stomach contents of harbor porpoises in the Gulf of Maine during autumn and investigate dietary differences amongst various sex and maturity categories. Our main objectives were to elucidate seasonal changes in the harbor porpoise diet and expand our knowledge of the dynamics between porpoises and their prey that may be responsible for entanglement of porpoises in gill nets.

Methods

Sample collection

The sample consisted of 95 porpoises killed in gill nets during autumn (1 September– 31 December) of 1989 and 1991–94. All porpoises were captured in bottom tending gill nets set for groundfish, principally cod (*Gadus morhua*), pollock (*Pollachius virens*), goosefish (*Lophius americanus*), and several species of flatfish. Most porpoises were taken in the vicinity of Jeffreys Ledge in the west central Gulf of Maine, at water depths between 35 and 185 m (Fig. 1). All samples were obtained by fisheries observers working onboard gillnet vessels. Observers were instructed to retain whole porpoise carcasses whenever possible, but when sea conditions or other factors prevented retention of carcasses, observers excised stomachs in the field. Carcasses and excised stomachs were frozen after the vessels returned to shore (usually 12–48 hours post mortem) for later examination.

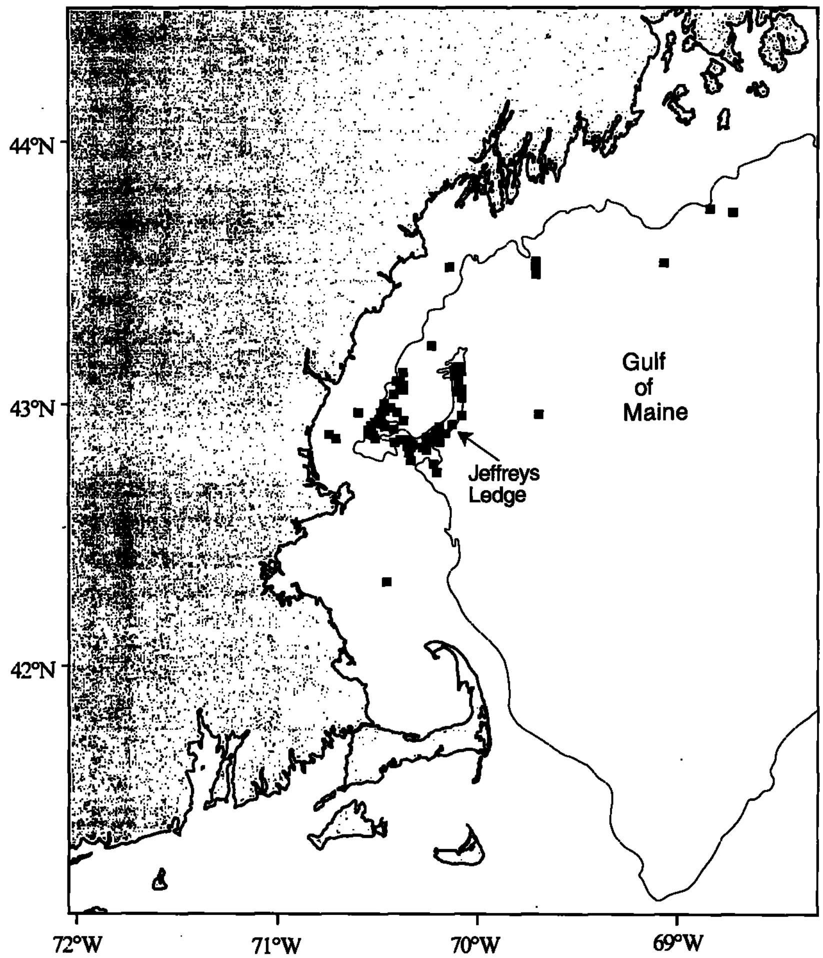

Figure 1

Capture locations of harbor porpoises taken during the autumn (1989–94) in the Gulf of Maine sink gillnet fishery and used in this analysis of food habits. The isobath shown is 91.4 m (50 fathoms).

On the basis of age (determined from dentinal growth layers and body length; see Read and Hohn, 1995) and reproductive condition (determined by examination of gonads and mammary glands; see Read and Hohn, 1995), porpoises were classified to the following sex, maturity, and reproductive categories: porpoises were considered calves (less than one year of age, not fully weaned), juveniles (older than one year but sexually immature), or sexually mature. The sex and maturity composition of the sample was as follows: (males and females combined) calves = 13; female juveniles = 12; male juveniles = 18; female mature adults = 10; male mature adults = 34; and unknown sex or maturity = 8. Because sample sizes were small, pregnant (n=4), simultaneously pregnant and lactating (n=5), and resting adult females (n=1) were pooled in the "mature female" group for statistical analyses. However, to facilitate comparisons with the findings of Recchia and Read (1989), data for lactating and nonlactating mature females are also presented separately.

Prey identification

The contents of all three stomach chambers were examined in the laboratory. Intact prey were removed first, then loose flesh was decanted. The remaining stomach contents were poured through a 1-mm metal sieve to separate hard parts from liquefied digesta. Solid prey remains used for identification were separated from other skeletal remains by hand. Structures used to identify partially digested food items included sagittal otoliths, dentary bones, and skulls of teleosts; lower mandibles ("beaks") from cephalopods; tooth cusp plates ("combs") from agnathans; and exoskeletons and eyes from crustaceans. Prey items were identified with the aid of a laboratory reference collection and published guides, including those of Bigelow and Schroeder (1953), Clarke (1986), Harkonen (1986), and Scott and Scott (1988).

Prey importance

Relative food importance in the autumn diet of the harbor porpoise was determined by 1) frequency of occurrence, 2) proportion of numerical abundance, and 3) proportion of total ingested mass. Frequency of occurrence is the percentage of porpoise stomachs containing a particular food type. Proportion of numerical abundance is the number of individuals of a prey species recovered from all stomachs, divided by the total number of all prey from all stomachs. The number of individuals from each fish species in each stomach was determined by summing the number of intact fish and half the number of free otoliths. The number of either upper or lower beaks (whichever were more abundant) from each species was used to determine the number of squid present.

Proportion of prey mass is the percentage of total prey mass in the stomach at the time of death that was represented by a particular species. Reconstituted mass, or the mass of prey prior to ingestion, rather than the existing mass of partially digested prey, was used in this calculation. Reconstituted prey masses were estimated from body lengths of intact prey and the lengths of otoliths or cephalopod beaks (Table 1). If a stomach contained more than 25 otoliths from the same species, all otoliths from that species were counted, and a subsample of 25 was randomly selected and measured. Otoliths were scored on a scale from 0 (undamaged otoliths re-

Table 1

Equations used to estimate length and mass of harbor porpoise prey. ML = mantle length; H = hood length; M = mass; FL = fork length; OL = otolith length; LRL = lower rostral length; and SL = standard length. Length is in millimeters and mass is in grams.

Prey species	Equations	Source
Bathypolypus arcticus (North Atlantic octopus)	$ML = 15.4 + 12.28\ H$ $\ln M = 1.06 + 2.55 \ln H$	Clarke, 1986 Clarke, 1986
Clupea harengus (Atlantic herring)	$FL = 69.23\ OL - 27.48$ $\log M = 3.12 \log FL - 5.41$	Recchia and Read, 1989 Recchia and Read, 1989
Gadus morhua (Atlantic cod)	$\ln(FL/10) = 3.3138 + 1.6235 \ln(OL/10)$ $M = 0.0124\ (FL/10)^{2.93}$	Hunt, 1992 Bowen and Harrison, 1994
Illex illecebrosus (Northern short-fin squid)	$\ln M = 1.773 + 2.4 \ln LRL$	Clarke, 1962
Loligo pealei (Long-fin inshore squid)	$\log ML = 1.767 + 1.4 \log LRL$ $M = 0.25662\ (ML/10)^{2.1582}$	Gannon et al., 1997b Lange and Johnson, 1981
Maurolicus weitzmani[1] (Weitzman's pearlsides)	$FL = 9.82 + 28.75\ OL$ $M = 0.3737\ OL^{2.503}$	Harkonen, 1986 Harkonen, 1986
Merluccius bilinearis (Silver hake)	$FL = 20.9\ L - 0.41$ $\log M = -2.26 + 3.08 \log(FL/10)$	Recchia and Read,1989 Kohler et al., 1970
Peprilus triacanthus[2] (Butterfish)	$SL = -9.15919 + 25.01871\ OL$ $\log M = -0.67576 + 3.222 \log OL$	Present study (r^2=0.983) Present study (r^2=0.924)
Pollachius virens (Pollock)	$\ln(FL/10) = 3.251 + 1.6251 \ln(OL/10)$ $M = 0.0134\ (FL/10)^{2.94}$	Harkonen, 1986 Bowen and Harrison, 1994
Scomber scombrus (Atlantic mackerel)	$FL/10 = 7.33\ OL + 0.37$ $M = 0.00756\ (FL/10)^{3.082}$	Recchia and Read, 1989 Kulka and Stobo, 1981
Sebastes spp.[3] (Rockfish)	$FL = 16.165\ L^{1.224}$ $M = 0.0741\ OL^{3.295}$	Harkonen, 1986 Harkonen, 1986
Urophycis spp.[4] (Red and white hake)	$FL/10 = 1.525\ OL^{1.1456}$ $M = 0.003998\ (FL/10)^{3.1718}$	Clay and Clay, 1991 Clay and Clay, 1991

[1] Taxonomy of the genus *Maurolicus* has been revised recently (Parin and Kobylansky, 1996). The equations used to estimate *M. weitzmani* size are those given by Harkonen (1986) for *M. muelleri*.
[2] Standard length range: 49–153 mm; weight range: 3–104 g; n = 44.
[3] Equations given by Harkonen (1986) for *S. marinus*.
[4] Equations given by Clay and Clay (1991) for *U. tenuis*.

trieved from skulls) to 5 (severely degraded, free otoliths) following the methods of Recchia and Read (1989). Otoliths categorized as 3 or higher were not used in size estimations, unless no undamaged otoliths were present. When only damaged otoliths from a particular prey species were present in a porpoise stomach, the available skeletal structures were measured; consequently the reconstituted prey mass for that stomach may have been underestimated (see Jobling and Breiby, 1986; Sekiguchi and Best, 1997)

These three measures of prey importance were applied to data from the 82 noncalf porpoises as a group and to each sex and maturity class. Food habit studies in which different methods are used can yield widely disparate results, making it difficult to draw comparisons between studies (Gannon et al., 1997a, 1997b). Because one of the primary objectives of this research was to obtain information on seasonal changes in the diet, it was important for these data to be treated in a manner similar to those of Recchia and Read (1989) and Smith and Read (1992).

Results

Overall sample

Table 2 lists the numbers and mean sizes of 15 prey taxa recovered from the 95 porpoise stomachs. Atlantic herring (78%), silver hake (*Merluccius bilinearis*, 68%), pearlsides (*Maurolicus weitzmani*, 38%), and red and white hake (*Urophycis* spp., 29%) occurred most frequently in the stomachs of the 74 noncalf porpoises (Table 3). Atlantic herring represented only 7% of the food by proportion of numerical abundance but accounted for 44% of ingested mass. Pearlsides accounted for 67% of food by proportion of numerical abundance but only 3% by ingested mass, owing to their small size. The unknown fish present in porpoise stomachs may have been alewives (*Alosa pseudoharengus*) but this could not be determined with certainty. Both red and white hake (*Urophycis chuss* and *U. tenuis*) were present; however it is difficult to differentiate between small, eroded otoliths from red and white hake, therefore all *Urophycis* otoliths were grouped together. Atlantic hagfish (*Myxine glutinosa*) and euphausiids (*Meganyctiphanes norvegica*) were included in analyses of frequency of occurrence only because the numerical abundance and mass of these two species were difficult to estimate. To allow comparisons to be drawn with the summer diet, data from Recchia and Read (1989) are also given in Table 3.

Figure 2 shows length-frequency distributions for the three most abundant prey: pearlsides, silver hake, and Atlantic herring. On average, Atlantic herring was the largest prey consumed by length (254 mm ±36 SD) with a range from 159 to 339 mm. The average fork length

Table 2

Number and mean sizes of food items present in the stomachs of harbor porpoises sampled in the Gulf of Maine during autumn. ML = mantle length, FL = fork length, and SL = standard length. Present = present in porpoise stomach contents but numerical abundance not determined.

Food item	n	Length measurement	Mean length ± SD (mm)	Mean mass ± SD (g)
Bathypolypus arcticus	1	ML	52	48
Clupea harengus	507	FL	254 ± 36	133 ± 56
Gadus morhua	5	FL	241 ± 133	137 ± 201
Illex illecebrosus	18	ML	—	55 ± 22
Loligo pealei	8	ML	129 ± 30	68 ± 29
Maurolicus weitzmani	5898	FL	50 ± 4	0.9 ± 0.2
Meganyctiphanes norvegica	present	—	—	—
Merluccius bilinearis	1605	FL	164 ± 96	65 ± 88
Myxine glutinosa	present	—	—	—
Peprilus triacanthus	38	SL	97 ± 12	24 ± 7
Pollachius virens	76	FL	195 ± 101	136 ± 130
Scomber scombrus	15	FL	224 ± 53	127 ± 91
Sebastes spp.	47	FL	37 ± 3	0.7 ± 0.2
Urophycis spp.	474	FL	159 ± 146	111 ± 172
Unknown fish	4	—	—	—
Milk	present	—	—	—

Table 3

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the diet of noncalf harbor porpoises during autumn in the Gulf of Maine (present study) and summer in the Bay of Fundy (Recchia and Read, 1989).

	Gulf of Maine			Bay of Fundy		
Prey	%FO	%Num	%Mass	%FO	%Num	%Mass
Alosa pseudoharengus	0	0	0	3	<1	—
Bathypolypus arcticus	1	<1	<1	3	<1	<1
Clupea harengus	78	7	44	88	44	64
Gadus morhua	4	<1	<1	14	14	14
Illex illecebrosus	10	<1	<1	6	1	<1
Loligo pealei	4	<1	<1	1	<1	<1
Macrozoarces americanus	0	0	0	2	<1	—
Maurolicus weitzmani	38	67	3	0	0	0
Meganyctiphanes norvegica	12	—	—	—	—	—
Merluccius bilinearis	68	16	22	41	33	19
Myxine glutinosa	7	—	—	—	—	—
Peprilus triacanthus	12	1	1	0	0	0
Pollachius virens	7	1	2	0	0	0
Pleuronectes americanus	0	0	0	<1	<1	—
Scomber scombrus	9	<1	1	6	1	2
Sebastes spp.	11	<1	<1	0	0	0
Urophycis spp.	29	7	26	13	3	2
Unknown fish	1	<1	<1	26	4	—

for silver hake was 163 mm (±95 SD), with the length-frequency distribution showing a strong peak between 30 and 55 mm and another peak between 180 and 205 mm. The mean length of pearlsides was 50 mm (±4 SD), ranging from 40 to 62 mm.

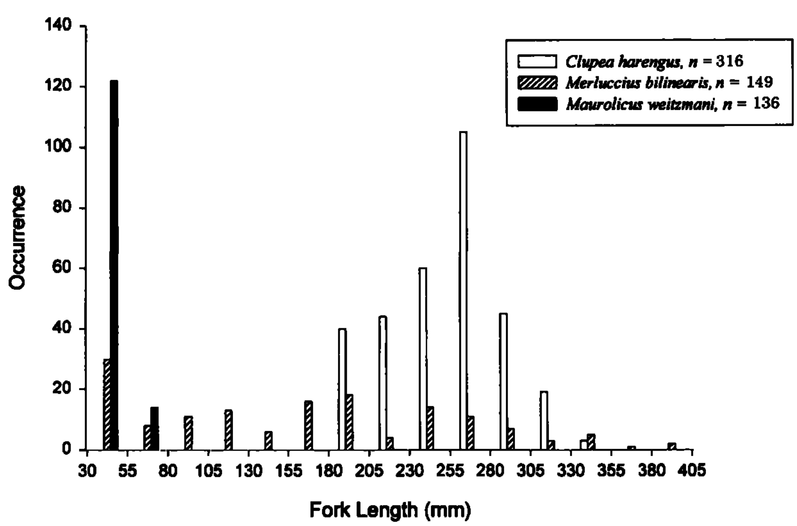

Figure 2

Length-frequency distributions of *Clupea harengus* (Atlantic herring), *Merluccius bilinearis* (silver hake), and *Maurolicus weitzmani* (pearlsides) eaten by harbor porpoises during autumn (1989–94) in the Gulf of Maine.

Diet of sex and maturity categories

The stomach contents of calves differed substantially from those of nutritionally independent porpoises. Pearlsides, silver hake, and euphausiids each occurred in more than half (7/13) of the calf stomachs (Table 4). Pearlsides (72%) and silver hake (26%) were the most numerous prey in calf stomachs and accounted for 53% and 27% of the calf diet by proportion of total mass, respectively. Only 11% of the ingested mass in calf stomachs comprised Atlantic herring (<1% of numerical abundance). Although euphausiids and milk were common in the calf diet, they were excluded from the analyses of

Table 4

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn harbor porpoise diet. Numbers in parentheses refer to frequency of occurrence values found by Smith and Read (1992) for the summer calf diet of the same population in the Bay of Fundy portion of their range.

	Calves (*n*=13)			Juvenile males (*n*=18)			Juvenile females (*n*=12)			Mature males (*n*=34)			Mature females (*n*=10)		
Food items	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass
Bathypolypus arcticus	0 (0)	0	0	0	0	0	0	0	0	3	<1	<1	0	0	0
Clupea harengus	15 (4)	<1	11	89	8	44	75	38	66	79	6	66	70	20	35
Gadus morhua	0 (0)	0	0	0	0	0	0	0	0	6	<1	1	10	1	1
Illex illecebrosus	0 (0)	0	0	0	0	0	17	1	<1	3	<1	<1	20	1	<1
Loligo pealei	0 (0)	0	0	11	<1	1	0	0	0	3	<1	1	0	0	0
Maurolicus weitzmani	54 (0)	72	53	39	42	1	17	3	<1	41	87	7	30	7	<1
Meganyctiphanes norvegica	54 (63)	—	—	22	—	—	17	—	—	9	—	—	0	—	—
Merluccius bilinearis	54 (0)	26	27	78	38	31	67	50	32	62	4	19	70	65	37
Myxine glutinosa	8 (0)	—	—	0	0	0	8	—	—	3	—	—	40	—	—
Pandalus montagui	0(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peprilus triacanthus	15 (0)	<1	2	11	1	1	8	1	<1	21	1	1	0	0	0
Pollachius virens	0 (0)	0	0	6	<1	1	0	0	0	9	1	2	20	4	10
Scomber scombrus	0 (0)	0	0	6	<1	1	8	1	<1	15	<1	2	0	0	0
Sebastes spp.	23 (0)	1	<1	17	3	<1	25	1	<1	6	<1	<1	0	0	0
Urophycis spp.	15 (0)	1	7	39	7	21	33	6	1	24	1	1	20	2	18
Unknown fish	0(8)	0	0	0	0	0	0	0	0	0	0	0	10	2	—
Milk	23 (29)	—	—	0	0	0	0	0	0	0	0	0	0	0	0

numerical and mass proportions because it was not possible to quantify their contributions. To facilitate comparisons between seasons, Table 4 also contains data from Smith and Read (1992) on the summer diet of calves from the Bay of Fundy.

Significant differences in stomach contents existed among the five sex and maturity groups regarding the mass proportion of Atlantic herring (no. of cases=87, df=4, K [the Kruskal-Wallis test statistic] =16.077, P=0.003), the number of Atlantic herring present (Table 5; K=18.313, P=0.001), and the existing mass of all stomach contents (K=11.594, P=0.021). The stomach contents of calves were the most divergent of these three categories and when the Kruskal-Wallis tests were repeated with calves excluded, none of the results were significant (Atlantic herring mass proportion: no. of cases=74, df=3, K= 4.284, P=0.232; number of herring: K=1.739, P=0.628; existing mass of stomach contents: K=0.270, P=0.855). No other significant dietary differences were noted between any of the sex and maturity groups at the α = 0.05 level.

Qualitative comparisons between lactating and nonlactating mature females revealed that the former had higher frequencies of occurrence for most prey (Table 6). The proportion of total reconstituted mass represented by herring was much higher in nonlactating females. The mass proportions of silver hake and red and white hake were higher in lactating females. It is also interesting to note that three of five lactating females ate hagfish, a frequency far greater than that of any other sex and maturity group.

Discussion

Atlantic herring was the most important prey of harbor porpoises in the Gulf of Maine during autumn; silver hake, red and white hake, and pearlsides were of secondary importance. Although herring was the most significant prey for porpoises in autumn, it was not as dominant as in the summer diet in the Bay of Fundy (Recchia and Read, 1989). Recchia and Read (1989) found Atlantic herring in 88% of noncalf porpoise stomachs, contributing 64% of ingested prey mass; we found herring in 78% of stomachs from noncalves, contributing 44% of prey mass. The relative importance of silver hake, of red and white hake, and of pearlsides was greater in the autumn than in the summer. For example, pearlsides occurred in 38%

Table 5

Prey consumption by harbor porpoises of different maturity and reproductive conditions caught incidentally in Gulf of Maine sink gill nets during autumn 1989–94 (mean ± standard deviation). *Clup.* = *Clupea harengus*, *Maur.* = *Maurolicus weitzmani*, *Mer.* = *Merluccius bilinearis*, and *Uroph.* = *Urophycis* spp.

Porpoise groups	Average mass of individual prey				Average no. of individual prey				Average mass of stomach contents		Average no. of prey taxa
	Clup.	*Maur.*	*Mer.*	*Uroph.*	*Clup.*	*Maur.*	*Mer.*	*Uroph.*	Existing	Reconstituted	
Calves	57 ±40	0.92 ±0.16	19 ±30	42 ±59	0.3 ±0.9	106.5 ±269.6	38.2 ±74.2	1.5 ±5.0	33 ±23	209 ±327	2.4 ±1.4
Juvenile males	131 ±35	0.95 ±0.20	51 ±56	108 ±105	4.2 ±5.0	21.3 ±46.8	19.1 ±38.7	3.6 ±10.8	284 ±288	1304 ±1036	3.2 ±1.3
Juvenile females	140 ±37	0.95 ±0.01	82 ±78	23 ±41	6.9 ±7.5	0.6 ±1.7	9.0 ±19.5	1.0 ±1.8	363 ±356	1389 ±1166	2.8 ±2.4
Mature males	125 ±30	0.95 ±0.05	73 ±103	50 ±46	8.1 ±10.6	117.0 ±372.3	5.6 ±9.5	0.6 ±1.6	274 ±285	1506 ±1526	2.9 ±1.5
Mature females	107 ±28	0.87 ±0.13	77 ±65	339 ±360	4.4 ±7.6	1.6 ±3.2	14.3 ±35.0	0.5 ±1.3	343 ±371	1378 ±1996	2.8 ±1.4

of porpoise stomachs in the autumn, representing 67% of numerical abundance and 3% of food mass but were absent from the summer diet. Recchia and Read (1989) found 11 prey taxa in the stomachs of 127 noncalf porpoises; we found 15 taxa in 82 noncalf stomachs. These results suggest that the diet of this population becomes more diverse as porpoises move out of the Bay of Fundy and into the Gulf of Maine. At the present time, we do not know whether these changes reflect seasonal differences in prey availability, interannual variability in prey populations, or choice on the part of foraging porpoises. Nevertheless, Atlantic herring remains the single most important prey of harbor porpoises in the Gulf of Maine during the autumn.

The size range of prey in the noncalf porpoise diet is larger in fall than in summer (Recchia and Read, 1989). Porpoises continue to eat large prey during autumn, such as adult herring and silver hake, but also eat a substantial number of smaller herring, silver hake, pearlsides, and red and white hake. The large standard deviations in Tables 2 and 5 reflect the wide range of prey sizes eaten.

With the exception of calves, the diet of porpoises did not vary significantly with age or sex. None of the comparisons of forestomach content mass, individual prey mass, or numbers of prey among the four noncalf categories yielded significant differences. Although previous studies of other marine mammal species have found measurable dietary differences between lactating and nonlactating adult females (Bernard and Hohn, 1989; Cockcroft and Ross, 1990; Cheal and Gales, 1991; Kastelein et al., 1993; Young and Cockcroft, 1994; Hobson et al., 1997; Robertson and Chivers, 1997), small sample sizes in this study prevented detailed investigation of potential dietary changes associated with changes in female reproductive condition. Therefore, the findings on diets of lactating and nonlactating mature females should be viewed with caution.

Table 6

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn diets of lactating and nonlactating mature female harbor porpoises.

Prey	Lactating (*n*=5)			Nonlactating (*n*=5)		
	% FO	% Num	% Mass	% FO	% Num	% Mass
Clupea harengus	80	7	14	60	52	71
Gadus morhua	20	1	1	0	0	0
Illex illecebrosus	40	1	<1	0	0	0
Maurolicus weitzmani	0	0	0	60	25	<1
Merluccius bilinearis	80	87	52	60	13	10
Myxine glutinosa	60	—	—	20	—	—
Pollachius virens	20	1	5	20	11	19
Urophycis spp.	40	3	28	0	0	0

At four to seven months of age (Read and Hohn, 1995), calves eat a variety of solid foods and continue to supplement their diet by nursing. The large standard deviations for calves in Table 5 may be an indication that some porpoise calves begin weaning sooner than others. The species composition found in the stomachs of calves in autumn begins to resemble that of older animals. However, the proportions of prey types and sizes of prey differ from those of adults. In autumn, calves eat a greater proportion of pearlsides and euphausiids than do older animals, and the sizes of Atlantic herring and silver hake are smaller than those eaten by older porpoises. Pearlsides, euphausiids, juvenile silver hake, juvenile herring, and juvenile red and white hake appear to be important in the "transitional diet" of calves, as they learn to forage independently. Calves eat a larger quantity and greater diversity of solid food in autumn than in the summer (Smith and Read, 1992). Our observations support and extend the findings of Smith and Read (1992), who suggested that porpoise calves eat euphausiids while their mothers are feeding on other euphausiid predators.

Although harbor porpoises prey on some of the groundfish species targeted by the sink gillnet fishery in the Gulf of Maine, these species contribute just a small fraction of the overall diet. Furthermore, the size range of groundfish consumed by porpoises is much smaller than that targeted by the gillnet fishery because porpoises feed on only the juvenile age classes of those commercial species. The prey that represent the bulk of the porpoise diet (i.e. Atlantic herring, silver hake, and pearlsides) are important forage items for groundfish targeted by the sink gillnet fishery (Langton, 1982). These dietary similarities may lead to overlap between the distributions of groundfish and porpoises, leading both to be caught in the same nets. Silver hake found in porpoise stomachs were highly digested (only 0.1% of silver hake were intact), indicating that they had been consumed some time prior to entanglement. In contrast, herring were often found in a relatively undigested state (15.8% were intact), indicating that many porpoises had been feeding on herring at, or just before, the time of entanglement.

Several potential biases should be kept in mind when interpreting these results. First, all the porpoises we examined had been killed in gill nets anchored to the ocean floor. This capture method may have led to a bias towards demersal prey and against pelagic prey. Without comparable samples collected near the surface, it is not possible to fully address this potential bias. The samples of Recchia and Read (1989) and Smith and Read (1992) may be similarly biased because both studies also obtained samples from porpoises killed in sink gill nets. Second, differential digestion and retention of hard parts are unavoidable in studies of marine mammal stomach contents. Consequently, the importance of species that are resistant to digestion, or that accumulate in porpoise stomachs, will be overestimated. Without empirical data on digestion times for each prey species, it is not possible to evaluate this potential bias fully.

A third potential source of bias arises from the difficulty in discriminating between primary prey (consumed by porpoises) and secondary prey (consumed by porpoise prey). For example, it is possible that small organisms, such as pearlsides, euphausiids, and juvenile silver hake, were secondarily introduced into the porpoise stomach contents. Careful examination of species co-occurrences in porpoise stomachs can provide insights into whether these small organisms were actually eaten by the porpoises. Because many porpoise prey are euphausiid predators (Bigelow and Schroeder, 1953; Langton, 1982; Scott and Scott, 1988), it is difficult to evaluate the likelihood of secondary consumption of euphausiids. However, two calves had euphausiid remains but no other solid food in their stomachs, indicating that they had consumed the euphausiids directly. One calf had pearlsides remains and a herring in its stomach; herring are not considered predators of pearlsides (Bigelow and Schroeder, 1953; Scott and Scott, 1988). Five calves had remains of pearlsides together with juvenile red, white, and silver hake less than 57 mm in length, too small to be predators of pearlsides. We interpret the co-occurrence of pearlsides and juvenile gadiforms in stomachs of calves as an indication of their preference for small prey, rather than as the presence of predators and secondary prey in their stomachs. Among older porpoises, one individual had pearlsides with no other food remains; four had pearlsides and herring; one had 13 pearlsides (totaling 16 grams), a 14-gram butterfish, and a herring; and one had 1100 pearlsides (1052 g) and one butterfish (6 g). Therefore, it is apparent that porpoises do indeed prey directly on euphausiids, pearlsides, and juvenile gadiforms.

In conclusion, the seasonal movements of harbor porpoises are accompanied by changes in diet. Seasonal movements of porpoises may, in fact, be driven by their need to maintain proximity to sufficient concentrations of prey. Assuming that there have not been any major shifts in prey availability between the previous study in the Bay of Fundy (Recchia and Read, 1989) and the present study, the diet of harbor porpoises in the Gulf of Maine during autumn appears to be more diverse than that of harbor porpoises in the Bay of Fundy during summer. The winter ecology of this population probably differs also because many porpoises are believed to leave the Gulf of Maine and Bay of Fundy region during this season. Further information on the diet of this population in the winter and spring is required before we can fully assess the ecological relations between harbor porpoises and their prey in this system. We also suggest that further investigation of the ecological relations among Atlantic herring, groundfish, and harbor porpoises may provide information that will allow improved understanding of the causes of porpoise entanglement in gill nets and that will perhaps offer some insight into measures that may mitigate this problem.

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