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Short Note

Diet of Harbour Porpoises (*Phocoena phocoena*) Around Hokkaido, Japan

Natsuki Matsui,[1] Ayaka Matsuda,[2] and Takashi Fritz Matsuishi[2,3]*

[1]*Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato, Hakodate, Hokkaido, Japan*
[2]*Faculty of Fisheries Sciences, Hokkaido University, 3-1-1 Minato, Hakodate, Hokkaido, Japan*
[3]*Global Institution for Collaborative Research and Education, Hokkaido University, 3-1-1 Minato, Hakodate, Hokkaido, Japan*
*E-mail: catm@fish.hokudai.ac.jp**

Little is known about the diet of the harbour porpoise (*Phocoena phocoena*) in Japanese waters because of the difficulty of obtaining stomach content samples from stranded animals. In the only previous study about the harbour porpoise diet in Japan, Gaskin (1993) collected 20 stomachs; however, 15 of those stomachs were empty, and the remaining five stranded porpoises sampled were limited to just two locations, Hakodate and Otaru. The cetacean research group Stranding Network Hokkaido (SNH) has been collecting dead bycaught and stranded cetaceans found along the coastline of Hokkaido since 2007; this effort afforded an opportunity to analyse the stomach contents of wild harbour porpoises. This study reports on the diet of harbour porpoises around Hokkaido based on an analysis of stomach contents obtained from bycaught and stranded individuals.

The stomachs of 32 individual harbour porpoises collected by SNH between 2010 and 2016 were examined. When reports were received from fishers or others who found dead cetacean bodies along the coast, we tried to collect as many stomachs as possible from those specimens. Bycaught porpoises were found dead in surface set nets without a ceiling net or in gillnets based on reports from fishers. Basic information recorded for each specimen included the date the carcass was found, the location, state of decomposition, whether bycaught or stranded, and sex. Latitude and longitude of the dead porpoises were recorded, and each carcass was classified as bycaught or stranded from along the coast of the Sea of Japan, the Sea of Okhotsk, or the Pacific Ocean (Figure 1). The decomposition state of all harbour porpoises found was classified following Perrin & Geraci (2009). It was not possible to determine the cause of death for any of the 32 specimens.

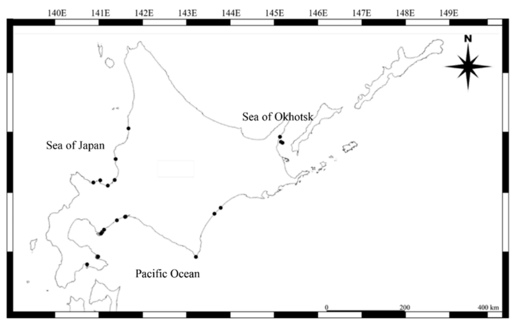

Figure 1. Black dots show the locations where stranded harbour porpoises (*Phocoena phocoena*) were collected between 2010 and 2016 (N = 32)

All harbour porpoises (N = 32) were necropsied, and each stomach was collected. All undigested prey items, such as fish otoliths and bones, cephalopod beaks, and crustacean parts, were separated and catalogued. The undigested prey items were identified to species level to the extent possible based on the shape of these hard parts. Fish otoliths were identified using Iizuka & Katayama (2008), cephalopod beaks were confirmed with Kubodera (2005) and the beak voucher collection in the National Museum of Nature and Science (Tsukuba, Japan), and crustacean parts were identified via Hayashi & Kim (1999). When left and right otoliths could be distinguished and counted separately, the total number of individuals of that fish prey species was derived from the larger number. If otoliths could not be determined as originating from the left or right side, the total number of individuals of that fish prey was estimated as equivalent to half the number of otoliths. To determine the cephalopod component of harbour porpoise diets, all cephalopod beaks were separated as upper and lower, and the prey taxon was identified and enumerated using the lower beak. If only the upper beak of a taxon was found, the total number of that prey taxon was defined as the number of upper beaks. The number of crustaceans was counted by number of abdominal parts or the tail that were digested but remained.

The occurrence and relative frequency of prey taxa found in harbour porpoise stomachs were estimated based on the counts described above. The percentage by number of occurrence (%*N*) and the percentage by frequency of occurrence (%*F*) were calculated using the following equations:

$$\%N_i = \frac{n_i}{\sum n_i} \times 100$$

$$\%F_i = \frac{m_i}{M} \times 100$$

where i denotes the prey species, and n_i is the number of prey i that were found in all stomachs sampled; m_i is the number of harbour porpoises that fed on prey species i, and M is the total number of harbour porpoises sampled.

The thirty-two harbour porpoises sampled consisted of 16 males, 14 females, and two of unknown sex (Table 1). Nine porpoises were collected as bycatch in surface set nets without a ceiling net, and two porpoises were collected in gillnets (bycaught porpoises), while the remaining carcasses ($n = 21$) were found along the coastline (stranded porpoises). In the 32 specimens, 22 harbour porpoises were found along the Pacific coastline, seven from the Sea of Japan coastline, and three from the Okhotsk Sea coastline (Figure 1). The porpoises found on the Pacific coast occurred from April to September, and those along the Sea of Japan occurred from December to March. To compare diet among these three regions, niche overlaps were calculated by the following formula (Whittaker et al., 1973):

$$\text{PS} = 1 - 0.5\left|\frac{n_{iA}}{\Sigma n_A} - \frac{n_{iB}}{\Sigma n_B}\right|$$

Only one of the 32 stomachs from a sampled porpoise was found to be empty. In this study, the empty stomach was included. There were 27 prey species representing 15 taxonomic families identified in the 31 stomachs. Overall, sepiolid squids had the highest rate of frequency of occurrence (53.1%) across the pooled sampled stomachs. %*F* of fishes of the genus *Ammodytes* (sand lances) and the Alaska pollock (*Theragra chalcogramma*) had the second-highest frequency at 40.6 and 37.5%, respectively (Table 2). Even though 97.8% of the genus *Ammodytes* was found in only one stomach of a pregnant specimen, SNH14032, the %*F* and %*N* of the three prey species listed above in the 31 porpoise stomachs, excluding SNH14032, were still high (Table 3).

Squids of the family Sepiolidae and the genus *Ammodytes* and *Theragra chalcogramma* may be considered the most important food for these harbour porpoises because their frequency of occurrence was 38 to 50% across the 32 stomachs examined. Dunshea et al. (2013) suggested that stomach content analysis was representative of the diet of healthy, free-ranging individuals. Conversely, a diet based on fish seems to be more important for other harbour porpoise populations. Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), and Atlantic cod (*Gadus morhua*) were important prey species for harbour porpoises in the Bay of Fundy, Canada (Recchia & Read, 1989). Similarly, harbour porpoises in Scottish waters fed mainly on whiting (*Merlangius merlangus*) and the genus *Ammodytes* (Santos et al., 2004). Pelagic and mesopelagic fishes, such as herring (e.g., *C. harengus*), were consumed prey for porpoises in Norwegian waters, though in Danish and Swedish waters, benthic species were more often consumed (Aarefjord et al., 1995). Thus, globally, harbour porpoises seem primarily to feed on a major species in the local food web, though a wide range of species in their diet has been reported for populations in the northeastern Atlantic (Santos & Pierce, 2003).

Interestingly, this was also a variation in diet among the three regions of Japan. The percentage of prey overlap was relatively low, with 37.9% between the Pacific Ocean and the Sea of Okhotsk, 31.5% between the Sea of Japan and the Pacific Ocean, and 8.8% between the Sea of Japan and the Sea of Okhotsk. Harbour porpoises found along the Japanese Pacific coast fed mainly on Sepiolidae (%*F* = 52.4%, %*N* = 41.4%), *Ammodytes* spp. (%*F* = 42.9%, %*N* = 25.4%), and *T. chalcogramma* (%*F* = 42.9%, %*N* = 13.6%). However, Decapodiformes, such as Sepiolidae (%*F* = 57.1%, %*N* = 22.3%) and Loliginidae (%*F* = 28.6%, %*N* = 42.8%), were found mainly in the stomachs of harbour porpoises found along the Sea of Japan; while harbour porpoises in the Sea of Okhotsk mainly fed on Gagidae fish (*T. chalcogramma*; %*F* = 66.7%, %*N* = 26.9%), followed by Scorpenidae (%*F* = 66.7%) and Ammodytidae (%*F* = 66.7%). Family Crangonidae (Decapoda) was found only in harbour porpoises found along the Pacific Ocean (Table 4). Harbour porpoises around Japan fed upon a wide array of prey species, and it was suggested their diet is mediated by the distribution and abundance of local prey along a small scale.

No difference was found between the sexes with respect to prey items identified, suggesting

Table 1. Basic data on the harbour porpoises (*Phocoena phocoena*) used in this study and collected by the Stranding Network Hokkaido (SNH), Japan, from 2010 to 2016. Stranded condition codes were (1) alive, (2) freshly dead, (3) moderate decomposition, (4) advanced decomposition, and (5) mummified/skeletal (Perrin & Geraci, 2009).

Specimen no.	Date (d/mo/y)	Sex	BL (cm)	Bycatch/ stranded	Location	Age class	Stranded condition
SNH10006	26/2/2010	--	140.0	Stranded	Pacific Ocean	Mature	3
SNH10010	31/3/2010	♀	121.5	Stranded	Sea of Japan	Immature	4
SNH10012	4/4/2010	♂	133.0	Stranded	Pacific Ocean	Mature	3
SNH10021	7/5/2010	♀	143.0	Stranded	Pacific Ocean	Mature	3
SNH11001	4/2/2011	♂	140.6	Stranded	Pacific Ocean	Mature	3
SNH11008	18/4/2011	♂	125.5	Bycatch	Pacific Ocean	Immature	2
SNH11018	18/6/2011	♀	174.0	Stranded	Pacific Ocean	Mature	3
SNH11039	10/8/2011	♂	119.0	Stranded	Pacific Ocean	Immature	4
SNH11041	3/9/2011	♀	128.5	Stranded	Pacific Ocean	Immature	3
SNH12001	12/1/2012	♀	123.9	Stranded	Sea of Japan	Immature	3
SNH12004	11/2/2012	♂	154.6	Strandedd	Sea of Japan	Mature	2
SNH12006	27/3/2012	♀	130.5	Stranded	Pacific Ocean	Immature	4
SNH12009-1	19/4/2012	♀	129.0	Bycatch	Pacific Ocean	Immature	2
SNH13002	4/2/2013	♀	160.0	Stranded	Sea of Japan	Mature	3
SNH13003	15/2/2013	♂	131.2	Bycatch	Sea of Japan	Immature	2
SNH13005-1	17/4/2013	♂	157.0	Bycatch	Pacific Ocean	Mature	2
SNH13005-2	17/4/2013	♀	140.5	Bycatch	Pacific Ocean	Mature	2
SNH13006	18/4/2013	♂	116.0	Bycatch	Pacific Ocean	Immature	2
SNH13009-1	23/4/2013	♂	131.0	Bycatch	Pacific Ocean	Immature	2
SNH13012	17/5/2013	♂	131.0	Stranded	Sea of Okhotsk	Immature	2
SNH13039	11/12/2013	--	120.0	Stranded	Sea of Japan	Immature	3
SNH14006	1/5/2014	--	110.0 (Head lost)	Stranded	Pacific Ocean	--	4
SNH14011	11/6/2014	♀	182.8	Bycatch	Sea of Okhotsk	Mature	2
SNH14032	2/7/2014	♀	124.0 (Tail lost)	Stranded	Pacific Ocean	Pregnant	3
SNH15005	26/2/2015	♀	125.0	Stranded	Sea of Japan	Immature	3
SNH15008	16/3/2015	♂	127.9	Stranded	Pacific Ocean	Immature	3
SNH15009	9/4/2015	♂	128.9	Stranded	Pacific Ocean	Immature	3
SNH15014	29/5/2015	♂	125.5	Stranded	Pacific Ocean	Immature	3
SNH15029	18/7/2015	♀	128.2	Bycatch	Sea of Okhotsk	Immature	2
SNH16011-2	26/4/2016	♂	127.2	Bycatch	Pacific Ocean	Immature	2
SNH16023	16/7/2016	♀	186.5	Stranded	Pacific Ocean	Mature	3
SNH16031	6/9/2016	♂	138.3	Bycatch	Pacific Ocean	Mature	2

there is no sexual segregation in the harbour porpoise diet.

To investigate the difference between bycaught and stranded harbour porpoises, we compared the stomach contents between these two specimen categories (Figure 2). %*F* of the bycaught and stranded individuals were 81.8 and 35.0%, respectively. Porpoise stomachs collected as bycatch contained more Sepiolidae than the stranded porpoises ($\chi^2 = 585.8$, $df = 28$, $p < 0.001$); caution is warranted, however, because the sample size of stranded porpoises in April and of bycaught porpoises outside of April are small. The porpoise stomachs collected from both bycaught and stranded animals contained more Sepiolidae in April than in the other months (Table 5). The %*F* and %*N* of Sepiolidae from stomachs that were obtained as bycatch in April were 100 and

Table 2. Diet samples from the 31 harbour porpoise stomachs with food

Order	Family	Species	Prey		
			Total pieces	%F	%N
Sepiolida	Sepiolidae	Unidentified sp.	725	53.1	11.2
		Euprymna morsei	3	6.3	0.0
Teuthida	Enoploteuthidae	*Watasenia scintillans*	4	3.1	0.1
	Loliginidae	Unidentified sp.	73	28.1	1.1
		Loliolus japonica	4	9.4	0.1
	Ommastrephidae	Unidentified sp.	12	6.3	0.2
		Todarodes pacificus	5	3.0	0.1
	Gonatidae	Unidentified sp.	9	6.3	0.1
		Berryteuthis magister magister	3	3.1	0.0
		Unidentified Decapodiformes	23	6.3	0.3
Clupeiformes	Clupeidae	Unidentified sp.	8	6.3	0.1
		Clupea pallasii	2	6.3	0.0
		Sardinops melanostictus	1	3.1	0.0
	Engraulidae	*Engraulis japonicus*	11	9.4	0.2
Gadiformes	Gadidae	Unidentified sp.	57	3.1	0.9
		Theragra chalcogramma	264	37.5	4.1
Myctophiformes	Myctophidae	Unidentified sp.	11	12.5	0.2
		Symbolophorus sp.	6	3.1	0.1
Pleuronectiformes	Pleuronectidae	Unidentified sp.	51	18.8	0.8
Salmoniformes	Salmonidae	Unidentified sp.	1	3.1	0.0
		Oncorhynchus masou	4	3.1	0.1
Scorpaeniformes	Hexagrammidae	*Pleurogrammus azonus*	39	9.4	0.6
	Sebastidae	Unidentified sp.	1	3.1	0.0
	Scorpaenidae	Unidentified sp.	36	15.6	0.6
Trachiniformes	Ammodytidae	*Ammodytes* spp.	4,916	40.6	75.7
Unidentified fish			188	43.8	2.9
Decapoda	Crangonidae	Unidentified sp.	13	12.5	0.2
		Crangon dalli	14	6.3	0.2
		Crangon amurensis	17	6.3	0.3

74.9%, respectively, and the two stranded harbour porpoises collected in April also fed heavily on sepiolids (%*F* = 100%, %*N* = 42.2%), whereas %*F* and %*N* for bycaught individuals in the other months were 50 and 8.8%, respectively, and percentages in stranded porpoises were 27.8 and 19.8%, respectively. These results excluded the pregnant individual SNH14032.

The stomach of specimen SNH14032 (a pregnant female) contained the most fish prey specimens (4,560 total fish), and 97.8% of these were of the genus *Ammodytes*. Moreover, this female's stomach contained more myctophids (lanternfishes) than found in the other specimens. The number of prey species in SNH14032's stomach was the largest for all harbour porpoises (Table 3). This finding is consistent with those reported for lactating and pregnant females ingesting more fish with a higher caloric intake than nonpregnant females or mature males (Recchia & Read, 1989). Furthermore, captive harbour porpoises increased their food intake during pregnancy (Blanchet et al., 2008, 2009), but additional samples of pregnant female harbour porpoises are needed to confirm this phenomenon in this population.

Little is known about the biological parameters, such as diet, age classes, or maturation, in this harbour porpoise population. This is the first report to describe the diet of this species in detail in Japan. Even though little is known about the feeding ecology of the Japanese harbour porpoise population, our study provides the first suggestions that

Table 3. Stomach contents of specimen SNH14032 (pregnant female) as compared with the 30 other stranded harbour porpoises that were sampled with food in the stomach

		All other specimens			Specimen SNH14032	
Family	Species	Total pieces	*%F*	*%N*	Total pieces	*%N*
Sepiolidae	Unidentified sp.	713	51.6	37.1	12	0.26
	Euprymna morsei	3	6.5	0.2		0.00
Enoploteuthidae	*Watasenia scintillans*	4	3.2	0.2		0.00
Loliginidae	Unidentified sp.	72	25.8	3.7	1	0.02
	Loliolus japonica	3	6.5	0.2	1	0.02
Ommastrephidae	Unidentified sp.	12	6.5	0.6		0.00
	Todarodes pacificus	5	3.2	0.3		0.00
Gonatidae	Unidentified sp.	9	6.5	0.4		0.00
	Berryteuthis magister magister	3	3.2	0.2		0.00
	Unidentified Decapodiformes	23	6.5	1.2		0.00
Clupeidae	Unidentified sp.	8	6.5	0.4		0.00
	Clupea pallasii	2	6.5	0.1		0.00
	Sardinops melanostictus	1	3.2	0.1		0.00
Engraulidae	*Engraulis japonicus*	11	9.7	0.6		0.00
Gadidae	Unidentified sp.	57	3.2	3.0		0.00
	Theragra chalcogramma	264	38.7	13.7		0.00
Myctophidae	Unidentified sp.	3	9.7	0.2	8	0.16
	Symbolophorus sp.	0	0.0	0.0	6	0.12
Pleuronectidae	Unidentified sp.	44	16.1	2.3	7	0.15
Salmonidae	Unidentified sp.	1	3.2	0.1		0.00
	Oncorhynchus masou	4	3.2	0.2		0.00
Hexagrammidae	*Pleurogrammus azonus*	39	9.7	2.0		0.00
Sebastidae	Unidentified sp.	1	3.2	0.1		0.00
Scorpaenidae	Unidentified sp.	36	16.1	1.9		0.00
Ammodytidae	*Ammodytes* spp.	447	38.7	23.2	4,470	97.75
	Unidentified fish	119	41.9	6.2	69	1.51
Crangonidae	Unidentified sp.	13	12.9	0.7		0.00
	Crangon dalli	14	6.5	0.7		0.00
	Crangon amurensis	17	6.5	0.9		0.00
	Total	1,928			4,574	

the diet will mainly include some squids and fish species and that it might possibly be associated with the abundance of the local prey (as seems to be shown through lower overlap between regions), indicating that the Japanese harbour porpoise will be a generalist predator. More observations are needed on this species and of their food choices in different parts of their range and throughout the year. Finally, our sample size is small and cannot represent the large variability of the range of the species, but our study adds to the slowly growing knowledge base for the harbour porpoise in Japanese waters.

Table 4. The *%N* and *%F* of prey taxa in the stomach contents of harbour porpoises (*n* = 31), according to location of the stranding

			Sea of Japan			Sea of Okhotsk			Pacific Ocean		
Order	Family	Species	Total	*%F*	*%N*	Total	*%F*	*%N*	Total	*%F*	*%N*
Sepiolida	Sepiolidae	Unidentified sp.	30	57.1	22.3	2	33.3	1.4	680.5	52.4	41.4
		Euprymna morsei	1	14.3	0.7	0	0.0	0.0	2	4.8	0.1
Teuthida	Enoploteuthidae	*Watasenia scintillans*	0	0.0	0.0	0	0.0	0.0	4	4.8	0.2
	Loliginidae	Unidentified sp.	58	28.6	42.8	0	0.0	0.0	14	28.6	0.9
		Loliolus japonica	0	0.0	0.0	0	0.0	0.0	3	9.5	0.2
	Ommastrephidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	11.5	9.5	0.7
		Todarodes pacificus	5	14.3	3.7	0	0.0	0.0	0	0.0	0.0
	Gonatidae	Unidentified sp.	2	14.3	1.1	0	0.0	0.0	7	4.8	0.4
		Berryteuthis magister magister	3	14.3	2.2	0	0.0	0.0	0	0.0	0.0
		Unidentified Decapodiformes	23	28.6	16.7	0	0.0	0.0	0	0.0	0.0
Clupeiformes	Clupeidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	8	9.5	0.5
		Clupea pallasii	1	14.3	0.7	0	0.0	0.0	1	4.8	0.1
		Sardinops melanostictus	1	14.3	0.7	0	0.0	0.0	0	0.0	0.0
	Engraulidae	*Engraulis japonicus*	2	14.3	1.5	0	0.0	0.0	9	9.5	0.5
Gadiformes	Gadidae	Unidentified sp.	0	0.0	0.0	57	33.3	39.3	0	0.0	0.0
		Theragra chalcogramma	1	14.3	0.7	39	66.7	26.9	223.5	42.9	13.6
Myctophiformes	Myctophidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	3	14.3	0.2
		Symbolophorus sp.	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Pleuronectiformes	Pleuronectidae	Unidentified sp.	0	0.0	0.0	1	33.3	0.7	42.5	19.0	2.6
Salmoniformes	Salmonidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	1	4.8	0.1
		Oncorhynchus masou	0	0.0	0.0	0	0.0	0.0	3.5	4.8	0.2
Scorpaeniformes	Hexagrammidae	*Pleurogrammus azonus*	0	0.0	0.0	0	0.0	0.0	38.5	14.3	2.3
	Sebastidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	1	4.8	0.1
	Scorpaenidae	Unidentified sp.	0	0.0	0.0	16	66.7	11.0	20	14.3	1.2
Trachiniformes	Ammodytidae	*Ammodytes* sp.	5	14.3	3.7	24	66.7	16.6	417.5	42.9	25.4
Unidentified fish			4	14.3	3.0	6	33.3	4.1	108.5	52.4	6.6
Decapoda	Crangonidae	Unidentified sp.	0	0.0	0.0	0	0.0	0.0	13	19.0	0.8
		Crangon dalli	0	0.0	0.0	0	0.0	0.0	14	9.5	0.9
		Crangon amurensis	0	0.0	0.0	0	0.0	0.0	17	9.5	1.0

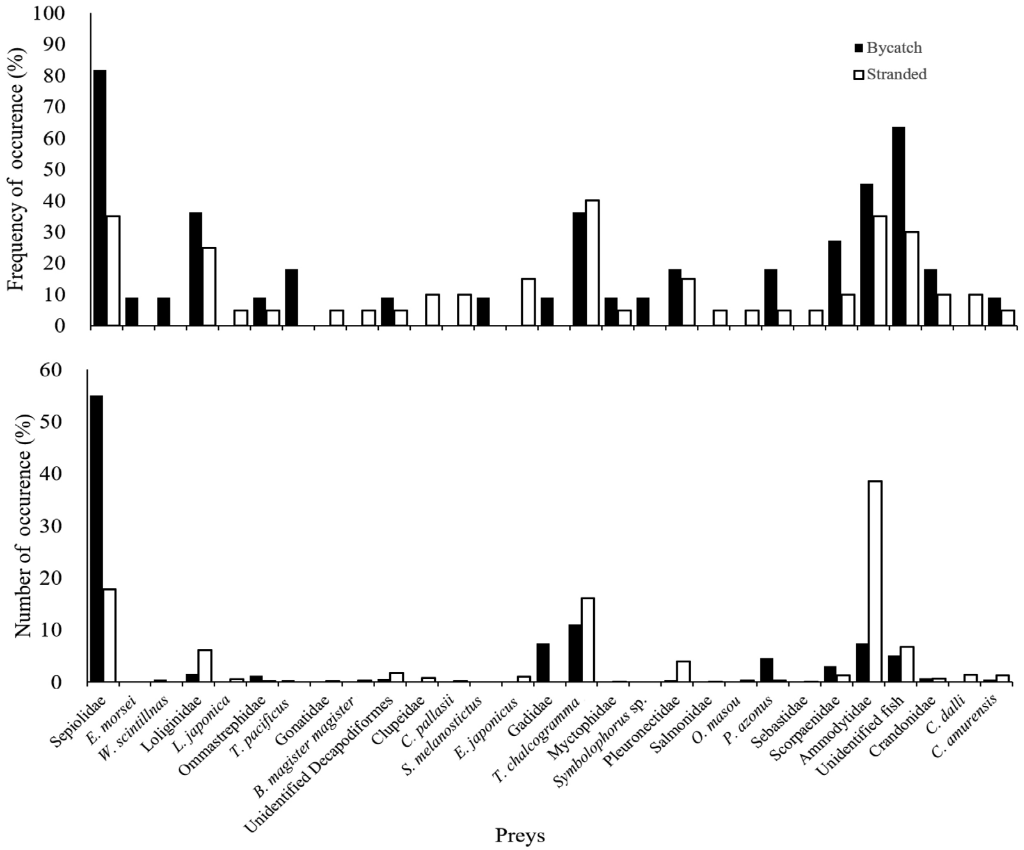

Figure 2. The difference of *%F* and *%N* between bycatch (black bars) and stranded harbour porpoises (white bars)

Table 5. Comparison of *%N* and *%F* for Sepiolidae in the stomachs of harbour porpoises (*n* = 31) collected as either bycatch or stranded in April and in all other months

		Bycatch	Stranded
April		7	2
	%N	74.9	42.2
	%F	100.0	100.0
All other months		4	18
	%N	8.8	19.8
	%F	50.0	27.8

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