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Prey switching of Dall's porpoise *Phocoenoides dalli* with population decline of Japanese pilchard *Sardinops melanostictus* around Hokkaido, Japan

Hiroshi Ohizumi[1,*], Toshiaki Kuramochi[2], Masao Amano[1], Nobuyuki Miyazaki[1]

[1]Otsuchi Marine Research Center, Ocean Research Institute, The University of Tokyo, Akahama, Otsuchi, Iwate 028-1102, Japan

[2]Department of Zoology, National Science Museum, Hyakunincho, Shinjuku, Tokyo 160-0073, Japan

ABSTRACT: The stomach contents of 150 Dall's porpoises collected during 6 surveys in the Sea of Japan and Sea of Okhotsk around Hokkaido in 1988 to 1996 were examined. A total of 49 prey types, including 29 species, were identified. Epipelagic prey items were found in samples collected during midday, and mesopelagic and some benthopelagic prey species were found in samples collected in the morning. Although the size range of prey was great, most prey were small. The dominant prey species switched in both seas from the late 1980s to the early 1990s as the *Sardinops melanostictus* (Japanese pilchard) populations in the both seas declined. In the Sea of Japan, the diet of Dall's porpoises switched to *Theragra chalcogramma* (walleye pollock), and in the Sea of Okhotsk, their diet switched to *Engraulis japonicus* (Japanese anchovy) and *Berryteuthis magister* (magistrate armhook squid). The utilization of new prey species did not always coincide with the fluctuation in catch statistics for the prey in local fisheries. Dall's porpoises fed on many benthopelagic prey species when epipelagic prey species were not available, suggesting that epipelagic prey species are the preferred prey. The vertical distribution of prey presumably affects prey selection.

KEY WORDS: *Phocoenoides dalli* · Sea of Japan · Sea of Okhotsk · Prey switching · population decline · *Sardinops melanostictus* · Prey distribution

INTRODUCTION

Dolphins and porpoises in coastal waters often feed on small shoaling fishes, such as sardines. Sometimes, the abundance of such prey varies drastically, and it is expected that population changes in prey species will affect the feeding habits of dolphins and porpoises. Population change in prey would provide a good opportunity to study the foraging strategy of predators.

A major population decline of *Sardinops melanostictus* (Japanese pilchard) occurred near Japan in the late 1980s (Watanabe et al. 1995). In the Sea of Japan and Sea of Okhotsk, the commercial catch of *S. melanostictus* declined from about 10000 t in 1990 to 1000 t in 1993. *S. melanostictus* was the main summer prey for Dall's porpoise *Phocoenoides dalli* in the southern Sea of Okhotsk in 1988 (Walker 1996); however, the effect of this population decline on the feeding habits of Dall's porpoises has not been examined.

Dall's porpoises are widely distributed in the northern North Pacific and adjacent waters, including the Bering Sea, Sea of Okhotsk and Sea of Japan (Houck & Jefferson 1999). A population of Dall's porpoises, which was investigated by Walker (1996), is distributed off the Tajima area in the Sea of Japan in winter, and migrates to the northeastern Sea of Japan and southern Sea of Okhotsk around Hokkaido in summer (Noguchi 1946, Amano & Kuramochi 1992).

The major prey of Dall's porpoises varies among populations and local habitats. Dall's porpoises in offshore regions feed on mesopelagic fishes and squids, but those in nearshore waters feed on various prey common

*Present address: National Research Institute of Far Seas Fisheries, Orido, Shimizu, Shizuoka 424-8633, Japan. E-mail: ohizumi@enyo.affrc.go.jp

to the continental shelves (Walker 1996). Dall's porpoises in the northwestern North Pacific feed primarily on myctophid fishes and gonatid squids (Wilke et al. 1953, Wilke & Nicholson 1958, Kuramochi et al. 1993).

The biogeography of the Sea of Japan and Sea of Okhotsk differs from that of the North Pacific, particularly in that myctophid fishes (Nishimura 1974) and squids of the genus *Gonatus* (Okiyama 1993) are not found in the Sea of Japan. As a result, the prey of Dall's porpoises in the Sea of Japan and Sea of Okhotsk are different from those in the North Pacific. Changes in the feeding habits of Dall's porpoises after the population decline in *Sardinops melanostictus* will also presumably occur.

In this paper, we compare the prey composition of Dall's porpoises before and after the *Sardinops melanostictus* population decline using data collected from 6 surveys in coastal areas of the northeastern Sea of Japan and southern Sea of Okhotsk. Fluctuations in the prey items are compared to the catch statistics of local fisheries. Foraging strategies are discussed in light of prey switching.

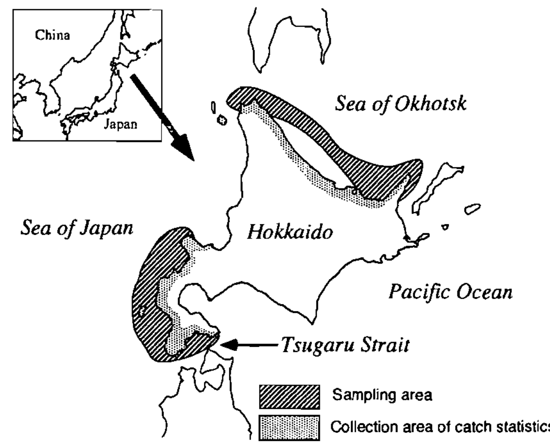

Fig. 1. Sampling areas for Dall's porpoises and catch statistics for prey species

MATERIALS AND METHODS

Field surveys. Dall's porpoises were collected in the Sea of Japan (JS) in May of 1989, 1995 and 1996, and in the Sea of Okhotsk (OK) in June 1988, October 1994, and August 1995 (Fig. 1). In these areas, porpoise are fished, and we used the catch. Dall's porpoises were captured by hand-harpoon. Stomachs were removed intact, the esophageal and duodenal ends were tied, and stomachs were then frozen for later analyses. Gonads were removed and fixed in 10% neutral formaldehyde solution. A total of 150 stomachs were examined. These included 69 (42 male, 27 female) from the JS and 81 (50 male, 31 female) from the OK.

Laboratory analyses. In the laboratory, the stomachs were thawed, and the forestomachs were separated from the other chambers. Each forestomach was opened, and its contents were placed in a plastic pan. The inner walls of the forestomachs were rinsed carefully, and a pan was used to collect all prey remnants. Only the forestomach contents were examined, herefater referred to as 'stomach contents'.

Fish sagittal otoliths and squid lower beaks were removed from the stomach contents. Undigested and half-digested fishes, fish skull containing otoliths, and squid buccal masses with beaks were also removed. Identifiable prey remains were sorted secondarily into taxonomic groups by comparison with H.O.'s otolith collection and the cephalopod beak collection at the National Science Museum, Tokyo. The cephalopod beak and otolith references Clarke (1986), Kubodera & Furuhashi (1987) and Smale et al. (1995) were also consulted. Where possible, undigested and partially digested prey remains were identified to species based on external morphology.

Lower rostral lengths (LRL) of squid beaks were measured to the nearest 0.1 mm with vernier calipers or a profile projector (×10). Regressions listed in Table 1 were used to estimate dorsal mantle lengths (DML) and body weights from LRL. We did not measure all lower beaks. When large numbers of 1 prey species were present, a subsample composed of at least 10% of the total number was measured. All samples were selected from undamaged isolated beaks.

Standard body lengths of fishes were measured for undigested and, if possible, partially digested fishes to the nearest 1 mm. Many of the partially digested *Engraulis japonicus* (Japanese anchovy) had lost their cranial portions. Therefore, lengths from the first cervical vertebra to the end of the hypural were measured. These lengths were then multiplied by the coefficient 1.185 derived from the intact *E. japonicus* to estimate SL. All *Theragra chalcogramma* (walleye pollock) were at least half digested and broken into 2 or 3 pieces, and *Maurolicus muelleri* were digested completely, with only otoliths remaining. Therefore, sagittal otolith lengths were used to estimate the fork lengths of *T. chalcogramma* and SL of *M. muelleri* according to Frost & Lowry (1981) and Smale et al. (1995), respectively. Sagittal otolith lengths were measured to the nearest 0.1 mm with a profile projector. Body weights of fishes were estimated from the relationships shown in Table 1. The total contribution by weight of each prey species was calculated by multiplying the average estimated weight by the prey number of each species present.

Caloric values of prey were obtained from the literature (Table 2). Total caloric contributions were calcu-

Table 1. Relationships between measured variables and body length or body weight. DML: dorsal mantle length; LRL: lower rostral length; BW: body weight; FL: fork length; SL: standard body length; OL: otolith length

Species	Regression	y	x	r^2	n	Source
Squids						
Gonatopsis borealis	$y = 35.779x + 17.036$	DML (mm)	LRL (mm)	0.94	50	Kubodera (1986)
	$\ln y = 2.037\ln x + 2.145$	BW (g)	LRL (mm)	0.93	50	
Berryteuthis magister	$y = 46.214x - 14.021$	DML (mm)	LRL (mm)	0.91	31	Walker (1996)
	$\ln y = 2.66\ln x - 8.563$	BW (g)	DML (mm)	0.99	32	
Gonatus onyx	$y = 19.02x + 12.82$	DML (mm)	LRL (mm)	0.72	NA	Wolff (1984)
	$\ln y = 2.13\ln x + 0.086$	BW (g)	LRL (mm)	0.82	NA	
Other Gonatidae spp.	$y = 42.87x - 43.4$	DML (mm)	LRL (mm)	NA	17	Clarke (1986), obtained
	$\ln y = 3.33\ln x - 0.655$	BW (g)	LRL (mm)	NA	20	from *Gonatus* spp.
Taonius pavo	$y = 61.43x - 12.3$	DML (mm)	LRL (mm)	NA	72	Clarke (1986), obtained
	$\ln y = 2.19\ln x + 0.786$	BW (9)	LRL (mm)	NA	74	from Taoniinae spp.
Todarodes pacificus	$y = 37.44x + 18.53$	DML (mm)	LRL (mm)	0.97	NA	Wolff (1984)
	$\ln y = 2.64\ln x + 1.11$	BW (g)	LRL (mm)	0.98	NA	
Watasenia scintillans	$y = 40.55x - 2.66$	DML (mm)	LRL (mm)	0.93	NA	Wolff (1964), obtained
	$\ln y = 2.49\ln x + 0.847$	BW (g)	LRL (mm)	0.92	NA	from *Abraliopsis felis*
Fishes						
Theragra chalcogramma	$y = 2.246x - 0.510$	FL (cm)	OL (mm) < 10.0 mm	0.98	158	Frost & Lowry (1981)
	$y = 3.175x - 9.770$	FL (cm)	OL (mm) > 10.0 mm	0.97	98	
	$\ln y = 2.906\ln x - 4.867$	BW (g)	FL (cm)	0.998	109	
Maurolicus muelleri	$\ln y = 0.962\ln x + 3.156$	SL (mm)	OL (mm)	0.76	90	Smale et al. (1995)
	$\ln y = 3.097\ln x - 1.833$	BW (g)	OL (mm)	0.62	87	
Sardinops melanostictus	$\ln y = 3.15\ln x - 12.129$	BW (g)	SL (mm)	0.99	14381	Walker (1996)
Pleurogrammus azonus	$\ln y = 3.177\ln x - 12.068$	BW (g)	SL (mm)	NA	130	Sasaki (1987)
Ammodytes personatus	$\log y = 2.27\log x - 1.343$	BW (g)	SL (cm)	0.62	10	Present study
Engraulis japonicus	$\log y = 3.40\log x - 2.378$	BW (g)	SL (cm)	0.85	18	Present study

lated from these energy values and estimated prey weights.

The reproductive condition of each Dall's porpoise sample was determined by examining its gonads. Females with ovarian corpora and males in which spermatogenesis was observed in more than half of the testicular tubules in histological sections were classified as mature (Amano & Kuramochi 1992).

Data processing of catch statistics. The catch statistics of *Sardinops melanostictus*, *Ammodytes personatus* (Japanese sandlance), *Pleurogrammus azonus* (greenling), and *Therogra chalcogramma* were analyzed. These data included monthly records of catch weight at 70 local fishery cooperative unions in 1988, 1989, 1994 and 1995. Data were recorded for all types of fishing gear, but only local set-net fisheries, local common right fisheries including small set-nets and gill nets, and free fisheries including mainly angling were selected to examine local catch fluctuations. The statistics were collected from the same area as the sampling area of Dall's porpoises (Fig. 1).

Table 2. Caloric values of prey species

Species	Caloric value (kJ g^{-1})	Source
Sardinops melanostictus	11.76	Walker (1996)
Engraulis japonicus	8.28	Resources Council (1982)[a]
Ammodytes personatus	4.44	Resources Council (1982)
Theragra chalcogramma	4.64	Perez (1994)
Pleurogrammus azonus	6.61	Perez & Bigg (1986)
Berryteuthis magister	5.52	Perez (1994)
Gonatopsis borealis	4.69	Perez (1994)
Other Gonatidae	3.78	Clarke et al. (1985)[b]
Taonius pavo	1.69	Clarke et al (1985)[c]
Todarodes pacificus	4.01	Clarke et al (1985)[d]
Watasenia scintillans	4.60	Resources Council (1982)

[a]Moisture content for *E. japonicus in* Resources Council (1982) was corrected
[b]*Gonatus* sp. in Clarke et al. (1985)
[c]*Teuthowenia* sp. in Clarke et al. (1985)
[d]*Todarodes sagittatus* in Clarke et al. (1985)

RESULTS

Porpoises examined

Average body lengths for Dall's porpoises in the JS ranged from 177.0 to 184.1 cm for females, and from

Table 3. Sample composition of Dall's porpoises caught from the Sea of Japan and Sea of Okhotsk. F: female; M: male

	Sea of Japan						Sea of Okhotsk						Total
	May 1989		May 1995		May 1996		Jun 1988		Oct 1994		Aug 1995		
	F	M	F	M	F	M	F	M	F	M	F	M	
Average body length (cm)	178.5	194.3	184.1	181.3	177.0	192.0	187.4	195.1	179.6	187.4	186.5	202.3	189.0
SD	12.0	8.2	13.6	18.0	11.7	13.7	7.0	12.7	7.1	10.8	7.9	13.9	14.4
No. of sexually immature porpoises	2	2	11	15	11	9	4	4	4	10	4	10	86
No. of sexually mature porpoises	0	5	1	3	2	8	16	9	0	3	2	14	63
No. of unidentified porpoises	0	0	0	0	0	0	0	0	1	0	0	0	1
Total number of porpoises	2	7	12	18	13	17	20	13	5	13	6	24	150

181.3 to 194.3 cm for males. Proportions of sexually mature porpoises varied, but most females were immature (Table 3).

Average body lengths in the OK ranged from 179.6 to 187.4 cm for females and from 187.4 to 202.3 cm for males. Sexually mature individuals were more numerous in the OK than in the JS; however, few were collected in October 1994 (Table 3).

Composition of prey species

A total of 29 types of prey, including 6 identified fish species and 12 identified cephalopod species, were found in specimens from the JS (Table 4). In 1989, *Sardinops melanostictus* was the dominant prey by number, total mass and caloric contribution; all porpoises fed on *S. melanostictus*. *Theragra chalcogramma* was the next major fish prey; it was consumed by 44% of the porpoises. In 1995 and 1996, however, very few *S. melanostictus* were found in the stomach contents. During these years, porpoises fed largely on *T. chalcogramma*. Other prey species, such as *Engraulis japonicus*, *Ammodytes personatus*, *Pleurogrammus azonus*, *Todarodes pacificus* (Japanese common squid), and *Berryteuthis magister* (magistrate armhook squid), were also relatively important as supplemental prey. In 1996 the consumption of *T. chalcogramma* was lower, and the prey composition was more diversified than in 1995. Percent occurrences of prey in 1996 were not prominently high, excluding 77% for Gonatidae juveniles (G-A-1) which were not so important in weight and calory contributions. This also indicates diversification of prey in 1996. Mesopelagic fishes other than *Maurolicus muelleri* were not found. *Gonatus* squids that have not been reported to occur in the JS were found in the stomach contents of porpoises from the JS. This may have been because the sampling area in the JS is near the Tsugaru Strait, which connects the JS to the Pacific Ocean.

In the OK, 37 prey types were found, including 14 fish species and 11 squid species (Table 5). In 1988, *Sardinops melanostictus* was the most important prey, and *Berryteuthis magister* was the next most important prey. In 1994, *S. melanostictus* was not observed, and *Engraulis japonicus* and *B. magister* were dominant. In 1995, *Berryteuthis magister* was the dominant prey, and neither *S. melanostictus* nor *E. japonicus* were found. Bathylagid fishes formed the largest proportion of fish prey, but were consumed by fewer than one-third of the porpoises. Unlike the JS data, mesopelagic fishes such as myctophids and bathylagids were found, but their numerical contributions were small. We could not estimate the amount of these species consumed, but assume it was small since these fishes are relatively small, and were numerically unimportant.

Number of freshly consumed prey in reference to time of day

The number of prey with undigested flesh showed species-specific distributions in relation to the time of catch (Fig. 2). Numerous *Sardinops melanostictus*, *Engraulis japonicus* and *Todarodes pacificus* were found in stomachs collected throughout the day, and bathylagid fishes and gonatid squids other than *Berryteuthis magister* were found in those collected in the morning. Many *Pleurogrammus azonus* and *B. magister* were found in samples collected in the morning and before dusk. Partially digested *Theragra chalcogramma* were found in samples collected throughout the day, but in fewer numbers than those of other species of fresh prey.

Prey size

Fish prey for all surveys ranged in size from 1.9 (*Maurolicus muelleri*) to 52.5 cm (*Theragra chalcogramma*) (Fig. 3). Smaller fishes occurred in large numbers. Three peaks are apparent in the frequency distribution of fish size. *M. muelleri*, which had a 2.5 cm mean body length, formed the first peak. Bathylagid fishes and *Engraulis japonicus* formed the second peak at 13 cm. *Sardinops melanostictus*, *Ammodytes personatus* and *Pleurogram-*

Table 4. Prey contribution in the Sea of Japan. occ.: occurrence; NA: not available

Prey species	1989				1995				1996			
	% no.	% weight	% calory	% occ.	% no.	%weight	% calory	% occ.	% no.	% weight	% calory	% occ.
Fishes												
Clupeidae												
Sardinops melanostictus	37.9	45.9	68.8	100.0	–	–	–	–	0.4	0.4	0.9	13.3
Engraulididae												
Engraulis japonicus	0.3	0.2	0.2	11.1	4.0	3.5	6.2	16,7	7.7	5.2	8.5	53.3
Gadidae												
Theragra chalcogramma	9.2	37.8	22.4	44.4	8.9	63.9	62.9	83.3	4.4	44.1	40.6	66.7
Ammodytidae												
Ammodytes personatus	3.3	2.6	1.5	22.2	2.6	2.9	2.7	23.3	3.4	4.8	4.2	16.7
Hexagrammidae												
Pleurogrammus azonus	–	–	–	–	0.6	4.3	6.0	26.7	2.8	14.5	19,0	46.7
Sternoptychidae												
Maurolicus muelleri	–	–	–	–	0.5	<0.01	NA	16.7	14.6	0.1	NA	30.0
Pleuronectidae												
Pleuronectidae sp.	–	–	–	–	–	–	–	–	0.1	NA	NA	3.3
Zoarcidae												
Zoarcidae sp.	–	–	–	–	0.2	NA	NA	6.7	0.1	NA	NA	3.3
Unidentified												
Type 82	–	–	–	–	0.05	NA	NA	3.3	–	–	–	–
Type 85	–	–	–	–	0.05	NA	NA	10.0	0.1	NA	NA	10.0
Type 86	–	–	–	–	0.04	NA	NA	6.7	0.3	NA	NA	23.3
Type 87	–	–	–	–	0.01	NA	NA	3.3	–	–	–	–
Type 96	–	–	–	–	–	–	–	–	0.02	NA	NA	3.3
Squids												
Gonatidae												
Berryteuthis magister	6.3	2.7	1.9	33.3	3.3	2.9	3.4	56.7	4.2	10.2	11.2	46.7
Gonatopsis makko	9.5	7.3	3.5	33.3	2.7	2.3	1.8	40.0	3.0	3.6	2.7	53.3
Gonatopsis octopedatus	0.3	0.1	0.1	11.1	4.4	3.0	2.4	40.0	6.9	6.2	4.6	50.0
Gonatopsis borealis	–	–	–	–	0.02	NA	NA	3.3	0.02	0.1	0.1	3.3
Gonatus onyx	–	–	–	–	–	–	–	–	0.05	0.01	0.01	3.3
Gonatus berryi	–	–	–	–	–	–	–	–	0.05	NA	NA	6.7
Gonatidae spp. juvenile (G-A-1)	31.0	2.9	1.4	33.3	21.6	3.4	2.7	56.7	38.7	9.0	6.7	76.7
Other *Gonatus* spp.	–	–	–	–	0.1	NA	NA	10.0	0.02	NA	NA	3.3
Enoploteuthidae												
Enoploteuthis chuni					0.3	NA	NA	10.0	0.02	NA	NA	3.3
Watasenia scintillans	-	-	-	-	10.0	0.6	0.6	50.0	1.0	0.1	0.1	40.0
Ommastrephidae												
Todarodes pacificus	2.0	0.6	0.3	33.3	39.9	13.3	11.3	90.0	9.8	1.8	1.4	53.3
Loliginidae												
Loligo japonica	0.3	NA	NA	11.1	–	–	–	–	0.2	NA	NA	23.3
Loligo bleekeri	–	–	–	–	–	–		–	0.05	NA	NA	6.7
Sepiolidae												
Rossia pacifica	–	–	–	–	0.02	NA	NA	3.3	–	–	–	–
Euprymna morsei	–	–	–	–	0.5	NA	NA	20.0	2.1	NA	NA	13.3
Octopus												
Octopoda sp.	–	–	–	–	–	–	–	–	0.05	NA	NA	6.7
Absolute no. in total	348.5	21.0 kg	164.6 MJ		4185.5	140.0 kg	660.5 MJ		4385.5	126.6 kg	638.6 MJ	

Table 5. Prey contribution in the Sea of Okhostk. occ.: occurrence; NA: not available

Prey species	1988 % no.	1988 % weight	1988 % calory	1988 % occ.	1994 % no.	1994 %weight	1994 %calory	1994 % occ.	1995 % no.	1995 % weight	1995 % calory	1995 %occ.
Fishes												
Clupeidae												
Sardinops melanostictus	38.6	36.5	56.0	72.7	–	–	–	–	–	–	–	–
Engraulididae												
Engraulis japonicus	1.3	0.7	0.7	12.1	23.6	26.2	39.7	61.1	–	–	–	–
Bathylagidae												
Leuroglossus schimidti	–	–	–	–	1.5	NA	NA	27.8	2.9	NA	NA	30.0
Bathylagus ochotensis	1.4	NA	NA	6.1	0.2	NA	NA	11.1	0.1	NA	NA	3.3
Other Bathylagidae sp.	–	–	–	–	2.9	NA	NA	27.8	2.3	NA	NA	33.3
Myctophidae												
Protomyctophum thompsoni	–	–	–	–	0.5	NA	NA	16.7	0.2	NA	NA	16.7
Diaphus theta	0.1	NA	NA	3.0	0.03	NA	NA	5.6	0.05	NA	NA	6.7
Stenobrachius nannochir	–	–	–	–	–	–	–	–	0.02	NA	NA	3.3
Lampanyctus regalis	–	–	–	–	–	–	–	–	0.1	NA	NA	6.7
Lampanyctus jordani	0.9	NA	NA	3.0	–	–	–	–	–	–	–	–
Ceratoscopelus warmingi	–	–	–	–	0.03	NA	NA	5.6	–	–	–	–
Gadidae												
Theragra chalcogramma	5.5	8.9	5.4	15.2	0.3	1.4	1.2	16.7	0.1	NA	NA	10.0
Gadus macrocephalus	–	–	–	–	0.1	NA	NA	5.6	–	–	–	–
Ammodytidae												
Ammodytes personatus	1.1	0.2	0.1	15.2	–	–	–	–	0.02	NA	NA	3.3
Hexagrammidae												
Pleurogrammus azonus	–	–	–	–	0.3	NA	NA	27.8	–	–	–	–
Zoarcidae												
Zoarcidae sp.	–	–	–	–	0.2	NA	NA	5.6	0.05	NA	NA	6.7
Unidentified												
Type 15	–	–	–	–	0.1	NA	NA	5.6	0.02	NA	NA	3.3
Type 47	–	–	–	–	0.1	NA	NA	5.6	–	–	–	–
Type 54	–	–	–	–	0.1	NA	NA	5.6	–	–	–	–
Type 56	–	–	–	–	0.03	NA	NA	5.6	–	–	–	–
Type 89	–	–	–	–	–	–	–	–	0.1	NA	NA	13.3
Type 90	–	–	–	–	–	–	–	–	0.02	NA	NA	3.3
Unknown total (in 1988)	2.0	NA	NA	12.1	–	–	–	–	–	–	–	–
Squids												
Gonatidae												
Berryteuthis magister	42.2	50.1	36.0	30.3	15.9	25.4	25.7	100.0	29.6	61.1	69.8	96.7
Gonatopsis makko	1.0	0.5	0.3	12.1	7.9	10.8	7.5	61.1	5.1	10.5	8.2	70.0
Gonatopsis octopedatus	2.1	1.1	0.6	3.0	1.6	2.2	1.5	27.8	0.7	0.7	0.6	26.7
Gonatopsis borealis	–	–	–	–	1.3	6.8	5.9	44.4	0.02	NA	NA	3.3
Gonatus onyx	0.7	0.1	0.1	9.1	1.8	1.3	0.9	55.6	3.7	2.5	1.9	73.3
Gonatus berryi	–	–	–	–	0.2	0.6	0.4	16.7	0.1	0.6	0.5	20.0
Gonatus madokai	1.0	1.5	0.7	3.0	8.9	10.0	6.9	88.9	6.8	8.9	6.9	80.0
Gonatidae spp. juvenile (G-A-1)	0.2	0.01	<0.01	3.0	23.3	4.4	3.0	77.8	30.6	3.0	2.3	96.7
Unidentified *Gonatus* sp. (G-C)	1.2	0.3	0.2	9.1	8.2	8.0	5.5	77.8	17.1	12.1	9.4	86.7
Cranchiidae												
Taonius pavo	–	–	–	–	0.4	0.6	0.2	27.8	0.1	0.2	0.1	10.0
Ommastrephidae												
Todarodes pacificus	–	–	–	–	0.7	2.2	1.6	44.4	0.1	0.5	0.4	13.3
Loliginidae												
Loligo japonica	0.2	NA	NA	3.0	–	–	–	–	–	–	–	–
Sepiolidae												
Rossia pacifica	0.3	NA	NA	6.1	–	–	–	–	–	–	–	–
Euprymna morsei	0.2	NA	NA	3.0	–	–	–	–	–	–	–	–
Absolute no. in total	575.0	44.7 kg	343.4 MJ		1968.5	51.4 kg	280.8 MJ		4083.0	126.0 kg	609.7 MJ	

mus azonus formed the third peak at 18 to 22 cm. With a mean body length of 34 cm, *T. chalcogramma* was represented in all body length categories over 29 cm.

Dall's porpoises tended to also feed on smaller squids; however, the size range was narrower than that of the fish prey (Fig. 3). The prey DML peaked at 3 cm. Juvenile Gonatidae spp. (G-A-1) were the most abundant squids in this size class. Most ranged in size from 2 to 12 cm. Many species were distributed in this size range and had mean DML sizes of about 10 cm. The mean sizes of *Gonatus berryi*, *Gonatopsis borealis* and *Taonius pavo* were larger.

The frequency distributions of estimated sizes for *Berryteuthis magister* were wide (Fig. 4); they typically ranged from 5 to 20 cm, except for samples in the JS in 1989. Distributions in the late 1980s showed a single size mode, but those in the 1990s showed several size modes.

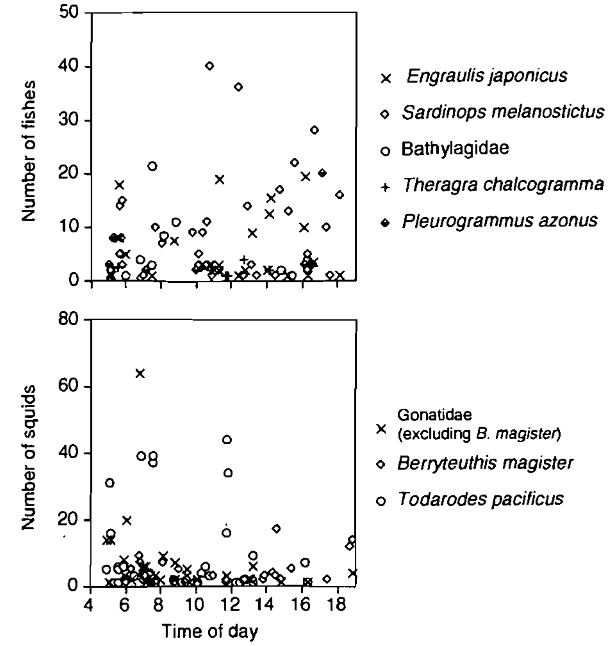

Fig. 2. Distributions of fresh prey in the daytime. Data from the Sea of Japan and Sea of Okhotsk are pooled

Variations in catch statistics versus variation in stomach contents

The commercial fisheries catch statistic patterns sometimes differed from feeding patterns of Dall's por-

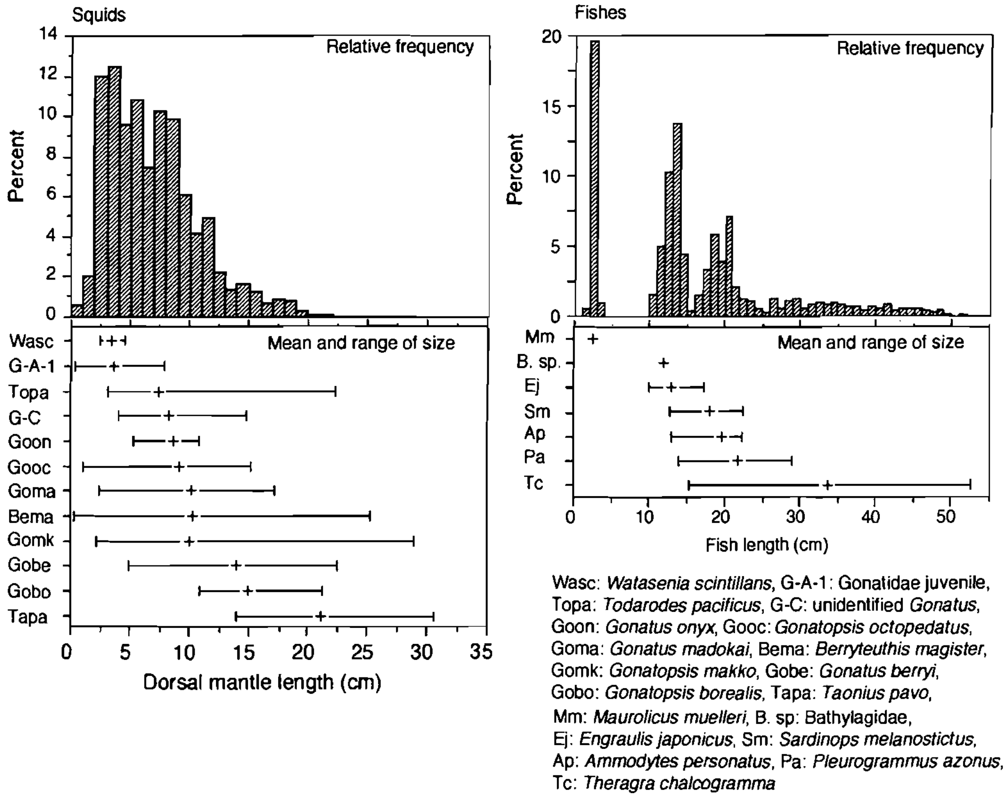

Fig. 3. Estimated size of prey species. Data from the Sea of Japan and Sea of Okhotsk are pooled. The number of measured subsamples varied among species. Therefore, relative frequency distribution of body lengths of fishes and squids at intervals of 1 mm for each species were weighted by the number of each prey species found in the forestomach, and rounded up to the nearest integer. These weighted frequencies were used to describe the total frequency distributions for squids or fishes

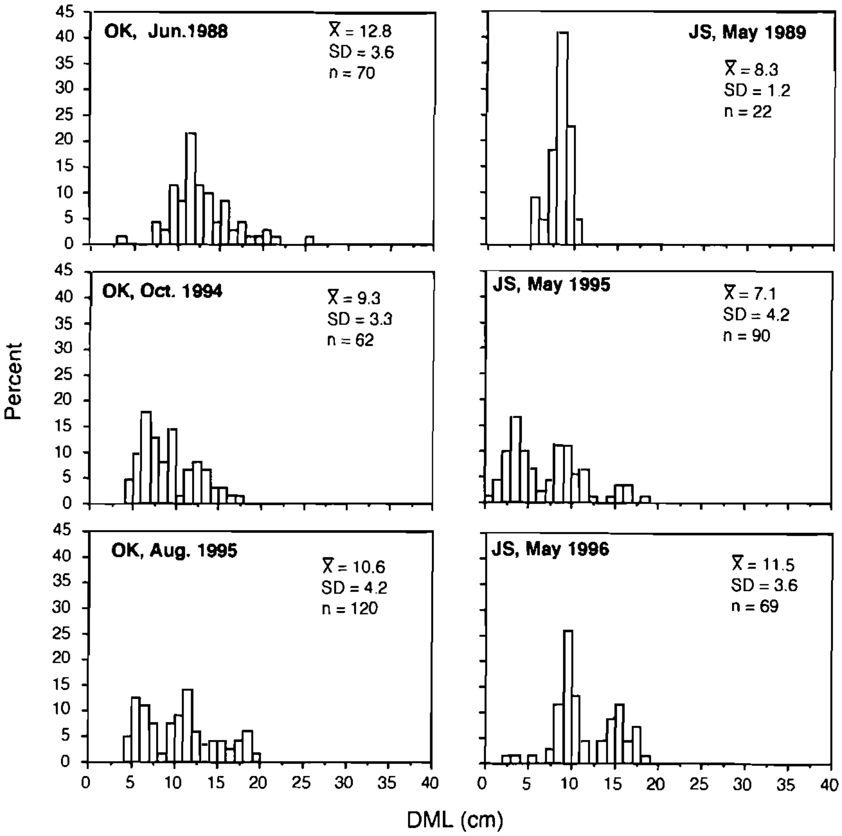

Fig. 4. Frequency distribution of estimated dorsal mantle length (DML) of *Berryteuthis magister*. JS: Sea of Japan; OK: Sea of Okhotsk

poises (Fig. 5). For example, *Theragra chalcogramma* in the OK was less important as prey than in the JS, although catch statistics in both seas were similar. *Pleurogrammus azonus* was caught in large numbers in both seas, but was not an important prey, especially in the OK. In the OK in June 1988, porpoises fed on relatively few *Ammodytes personatus*, which had a total catch in the fishery of about 2900 t. However, Dall's porpoises in early summer in the JS fed more commonly on *A. personatus*, while few *A. personatus* were caught by fisheries. In contrast to these inconsistencies between catch statistics and stomach contents, *Sardinops melanostictus* was the most common prey when they were abundant in the late 1980s.

DISCUSSION

Possible biases

The caloric value of a prey species may vary seasonally and with body size due to variation in fat content. This variation will affect the energy intake calculation (Gaskin 1982, Mårtensson et al. 1996, Walker 1996). The caloric value of *Sardinops melanostictus* used in this study was cited from Walker (1996), who used the fat content value in Kizevetter (1971). Walker (1996) compared the differences in the literature to the fat content of *S. melanostictus* and concluded that Kizevetter's value is more representative for *S. melanostictus*, because the fat content was based on a large sample size analyzed over a 5 yr period. The caloric values of *Theragra chalcogramma* and *Berryteuthis magister* (Perez 1994) and *Engraulis japonicus* (Oya et al. 1937) do not appear to exhibit variance due to body length.

Because of differences in the digestibility among prey species, comparison of weight and caloric contribution obtained from stomach contents containing mixed species may underestimate the more easily digested prey species. Crawford (1981) suggested that fishes are digested more rapidly than squids since fish muscle tissue tends to flake apart. However, Bigg & Fawcett (1985) noted that the squid *Loligo opalescens* was digested much faster than herring *Clupea pallasi* both in an *in vitro* experiment of digestion using an artificial digestive solution and in a seal stomach. A similar artificial digestion experiment showed that the digestion time of squids *L. opalescens* and *Todaropsis eblanae* is within the range of the digestion time of various other fishes (Sekiguchi 1994). Although digestion time differs among species, the time range of digestion for fishes and squids overlaps.

Differences among fish species in otolith digestion must also be considered. Härkönen (1986) noted that otoliths of gadid fishes are among the most resistant to digestion. Thus otoliths of *Theragra chalcogramma* may accumulate in stomachs; so the contributions of *T. chalcogramma* may have been overestimated.

Fresh prey and time of feeding

By comparing of the presence of freshly ingested intact or nearly intact prey with the time of collection, inferences can be made about time of feeding on different prey species (Walker 1996). Walker (1996) reported daytime foraging of Dall's porpoises on

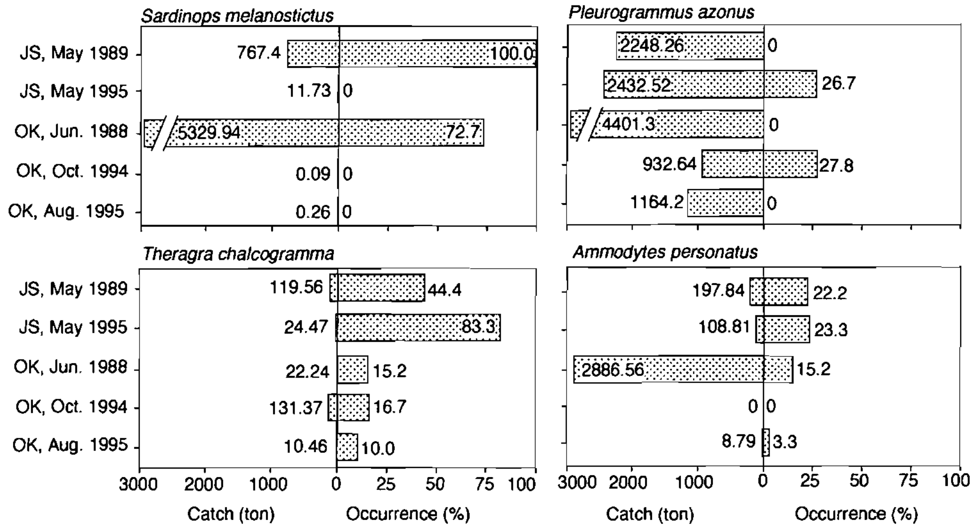

Fig. 5. Comparison of catch statistics from local fisheries and prey occurrences in the stomach contents. JS: Sea of Japan; OK: Sea of Okhotsk

Sardinops melanostictus in the OK in 1988, and our results support this. Findings of fresh *S. melanostictus*, *Engraulis japonicus* and *Todarodes pacificus* throughout the daytime suggest Dall's porpoises fed on these prey items in daylight hours. The absence of *T. pacificus* in the afternoon is due to the lack of sampling due to rough sea conditions in the JS in 1995. In contrast, the findings of fresh *Pleurogrammus azonus* and *Berryteuthis magister* in the morning and at dusk suggest that they were eaten around twilight or during the night. Similar conclusions could be made for gonatid squids and bathylagid fishes that were found in morning samples.

These species-specific times of foraging are probably related to habitat-use patterns of the prey. Dall's porpoises fed on epipelagic species such as *Sardinops melanostictus*, *Engraulis japonicus* and *Todarodes pacificus* throughout the daylight hours. However, Dall's porpoises probably feed on mesopelagic species such as gonatid squids and bathylagid fishes when they ascend into the surface waters at night. Based on behavioral observations, Amano et al. (1998) concluded that the feeding time of Dall's porpoises changes according to habitat use of prey species. The present stomach content analysis results support this conclusion.

Size range of prey

Dall's porpoises fed on a wide size range of prey, but they preferred smaller prey species. Walker (1996) and Crawford (1981) reported maximum prey sizes of 60 and 48 cm for fishes respectively; the largest prey in the present study was 52 cm. About 50 to 60 cm is probably the upper limit of the prey size for Dall's porpoises.

In general, adult and juvenile *Berryteuthis magister* with a DML of over 10 cm are distributed on the slopes of continental shelves at depths of 200 to 1000 m (Naito et al. 1977). *B. magister* smaller than 15 cm DML are distributed near the bottom at depths shallower than 500 m in the southern OK (Kubodera 1982). The vertical distribution range for *B. magister* in the eastern Etorohu (Iturup) Islands is 300 to 600 m (Naito et al. 1977). On the other hand, juvenile *B. magister* whose DML is 14 to 15 cm in the JS off western Hokkaido occur at 500 to 800 m (Naito et al. 1977). The continental shelf in western Hokkaido is narrow and the slope drops down steeply to depths greater than 1000 m at a few kilometers off the coast. Dall's porpoises fed on juvenile and adult *B. magister*, which suggests they foraged near the bottom layer. However, due to the steep slope in the JS, *B. magister* may inhabit an even deeper depth, which may account for the fewer numbers of *B. magister* eaten by Dall's porpoises in this region.

Adult *Pleurogrammus azonus* typically inhabit rocky reef environments. The mean size of *P. azonus* (22.3 cm, SD = 3.7, n = 30) eaten by porpoises has been reported as the size of the 1 yr age class (Nagasawa & Torisawa 1991). In spring, yearling *P. azonus* often concentrate at the surface to feed on zooplankton (Nagasawa & Torisawa 1991). The limited size range of *P. azonus* found in the stomach contents suggests that Dall's porpoises probably fed on *P. azonus* in the surface of waters in the JS in spring.

Prey switching and a possible foraging strategy

Walker (1996) reported that *Sardinops melanostictus* was the main prey from the OK in August 1988, while we found *Berryteuthis magister* to be the main prey in August 1995. This suggests that *B. magister* inhabit the OK in August, but Dall's porpoises fed on few of them in 1988. Because the commercial fisheries catch statistics for *Engraulis japonicus* were incomplete, seasonal variation of the availability in *E. japonicus* is unknown. There are no catch statistics for *B. magister*. Still we could not evaluate the seasonality in prey change from *E. japonicus* to *B. magister* that was observed between October 1994 and August 1995.

The estimated abundance by cohort analysis of *Theragra chalcogramma* in the JS off western Hokkaido was 4.2 billion individuals in 1989, and 1.7 billion individuals in 1994 (Mizuno & Miyake 1996). Recent population declines have occurred in the JS for both *Sardinops melanostictus* and *T. chalcogramma*. In the JS, unlike the Pacific, Dall's porpoises have only limited opportunities to feed on mesopelagic prey, because mesopelagic fishes and squids have limited distribution in the JS (Nishimura 1974). As a result of the population declines of *S. melanostictus* and *T. chalcogramma*, and of the deeper distribution of *Berryteuthis magister*, recent available food resources in the JS may have became limited. This probably explains why Dall's porpoises fed more on supplemental prey species such as *Engraulis japonicus*, *Ammodytes personatus*, *Pleurogramus azonus* and *Todarodes pacificus* in the JS. Dall's porpoises in the JS might have had to diversify their prey especially in 1996.

Although there are some physical factors involved, such as appropriate prey size for basic prey selection, assuming that Dall's porpoises are not selective feeders seeking specific prey and feed on whatever appropriate prey they encounter, the composition and proportion of prey items should reflect the abundance of prey species in the environment. However, the proportional variation of actual prey items was not always consistent with catch statistics.

The prey switching that occurred between the 1980s and 1990s could be summarized as a switching from epipelagic to benthopelagic prey. This switching in the JS was not affected by the abundance of benthopelagic *Thergra chalcogramma*. This suggests that Dall's porpoises have an epipelagic preference for foraging. Dall's porpoises fed on mesopelagic prey that perform diel vertical migrations. This also suggests a preference for epipelagic foraging. An epipelagic preference for foraging has also been observed in harbor seals *Phoca vitulina* in Scotland. Tollit et al. (1997) reported that the harbor seal's tendency to feed on benthopelagic fishes was correlated with a decrease in abundance of epipelagic fishes and not on the abundance of benthopelagic fishes. Epipelagic foraging has the obvious advantages of saving time and energy, and facilitates efficient energy intake and utilization.

When *Sardinops melanostictus* are not available, Dall's porpoises seeking food presumably must dive to deeper waters, where they will encounter *T. chalcogramma* and *Berryteuthis magister* in the JS and OK. In the JS, the deeper habitat of *B. magister* may prevent Dall's porpoises from feeding on them. *T. chalcogramma* migrates vertically between the mesopelagic layer and the bottom (Maeda 1974). In the JS in May, it is distributed at the bottom at depths of about 250 m (Maeda 1974). Dall's porpoises in the JS might encounter *T. chalcogramma* more often than *B. magister* at mid-depths and near the relatively shallow bottom.

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