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Diets of Steller sea lions off the coast of Hokkaido, Japan: An inter-decadal and geographic comparison

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Abstract

Inter-decadal and geographic variations in the diets of Steller sea lion, *Eumetopias jubatus*, were examined based on the contents of 408 stomachs collected from coastal areas around Hokkaido Island during the periods 1994–1998 and 2005–2012. The most important prey species in the 1990s were gadid fishes (walleye pollock [*Gadus chalcogrammus*], Pacific cod [*Gadus microcephalus*] and saffron cod [*Eleginus gracilis*]). The frequency of occurrence and gravimetric contribution of gadids decreased in the 2000s latter period at three study sites (Rausu, Shakotan and Rebun) and were replaced by Okhotsk Atka mackerel (*Pleurogrammus azonus*) and smooth lumpsucker (*Aptocyclus ventricosus*). However, analysis based on gravimetric composition indicated that the dietary diversity of prey showed only a slight inter-decadal difference, reflecting the wide diversity of prey ingested during both study periods. These results indicate that Steller sea lions along the Hokkaido coast are opportunistic feeders that utilize a wide variety of prey, and appear to feed mainly upon prey that is easily obtained.

KEYWORDS
diet, diet diversity, *Eumetopias jubatus*, Hokkaido, Steller sea lion

1 | INTRODUCTION

Steller sea lions (SSLs; *Eumetopias jubatus*) travel to the coast of Hokkaido Island, Japan, to overwinter (Nishiwaki, 1967). These SSLs belong to the Asian stock and their origins are in Russian rookeries (Isono, Burkanov, Ueda, & Hattori, 2010). After an acute decline in numbers during the 1960s, populations have rebounded slightly, but steadily, since the 1990s (Burkanov & Loughlin, 2007).

Steller sea lions are apex predators in subarctic marine ecosystems, and competition with fisheries for target species may occur at local scales in areas of dense populations (Smout & Lindstrom, 2007). In the Aleutian Islands, nutritional stress has affected the population dynamics of SSLs, and is one reason for the serious population decline (Loughlin, Perlov, & Vladimirov, 1992; Trites, Calkins, & Winship, 2007; Trites & Donnelly, 2003; Trites & Larkin, 1996; Trites, Miller, et al., 2007). Damage to fisheries by SSLs, such as damage to fishing nets and predation on caught fish, is a problem in Japan (Isono, Niimura, Hattori, & Yamamura, 2013). In addition, in areas of high-density populations, the high feeding pressure of marine mammals may affect fishery stocks at a local scale (Smout & Lindstrom, 2007). To develop mitigation measures against damage to fisheries, it is important to understand the relationship between the feeding habits of SSLs and their prey dynamics.

In Alaska, there is a correlation between the diversity of SSL diets and the rate of population change among the regions of the western distinct population segment (Lander et al., 2009; Merrick, Chumbley, & Byrd, 1997; Sinclair, Johnson, Zeppelin, & Gelatt, 2013). Although there appears to be no relationship between diet diversity and SSL population dynamics in Russian waters (Waite & Burkanov, 2006), it has been verified that nutritional stress can affect population dynamics (Calkins, Atkinson, Mellish, Waite, & Carperter, 2013; Rosen, 2009).

Since the 1950s, the feeding habits of SSLs have been investigated in every area they inhabit, from the Sea of Okhotsk to the California coast (Fiscus & Baines, 1966; Mathisen, Baade, & Lopp, 1962; Spalding, 1964). Results indicate that SSLs consume various prey species in each area they inhabit. SSLs primarily consume large demersal prey, such as gadids and cephalopods, or forage fishes, including herring (*Clupea pallasii*) and eulachon (*Thaleichthys pacificus*) (Calkins & Pitcher, 1982; Mathisen et al., 1962; Merrick et al., 1997; Pitcher, 1981; Sigler et al., 2009; Thomas & Thorne, 2001; Trites, Calkins, et al., 2007; Trites, Miller, et al., 2007). The diet of SSLs around the coast of Hokkaido was mainly studied intensively in the 1970s, during which time Okhotsk Atka mackerel (*Pleurogrammus azonus*) and smooth lumpsuckers (*Aptocyclus ventricosus*) were the most common prey in Funka Bay and near Rebun Island (Itoo, Kato, Wada, Shimazaki, & Arai, 1977a, 1977b). In the 1990s, Goto and Shimazaki (1998) reported that the prey of SSLs near the coast of Rausu, in the Nemuro Strait (part of the eastern region of Hokkaido) was composed almost entirely of walleye pollock (*Gadus chalcogrammus*; 5.8%–81.2% of the gravimetric composition) supplemented by Pacific cod (*Gadus microcephalus*). During recent years, populations of gadids have undergone marked declines around the Hokkaido coast. The walleye pollock population along the coast of the Sea of Okhotsk, including the Nemuro Strait, has experienced a steep decline, with a reduction in catch to one tenth within 25 years (111,000 tons in 1989 to 8,400 tons in 2015) (Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 2017b). Such changes in stock populations may have affected the feeding habits of SSLs, as they are opportunistic predators with a flexible foraging strategy, selecting abundant, accessible prey and switching among seasonally available species (Sigler et al., 2009). In the present study, we examined SSL prey species and prey diversity by analysing the stomach contents of SSLs captured or caught incidentally off the west coast of Hokkaido and in the Nemuro Strait (Figure 1). We combined these data with the SSL data collected from 1994 (Goto, 1999) to compare the prey composition between decades.

2 | MATERIAL AND METHODS

2.1 | Sample collection

A total of 408 stomachs were collected from November to June in 1994–1998 ($n = 161$) (1990s) and 2005–2012 ($n = 246$; Table 1) (2000s) from SSLs hunted at sea, stranded, or entangled in fishing nets off the coasts of Rausu, Shakotan Peninsula, Otaru, Point Ofuyu, Rishiri Island, and Rebun Island off Hokkaido (Figure 1). During the 1990s, samples were taken from Rausu, Shakotan Peninsula and

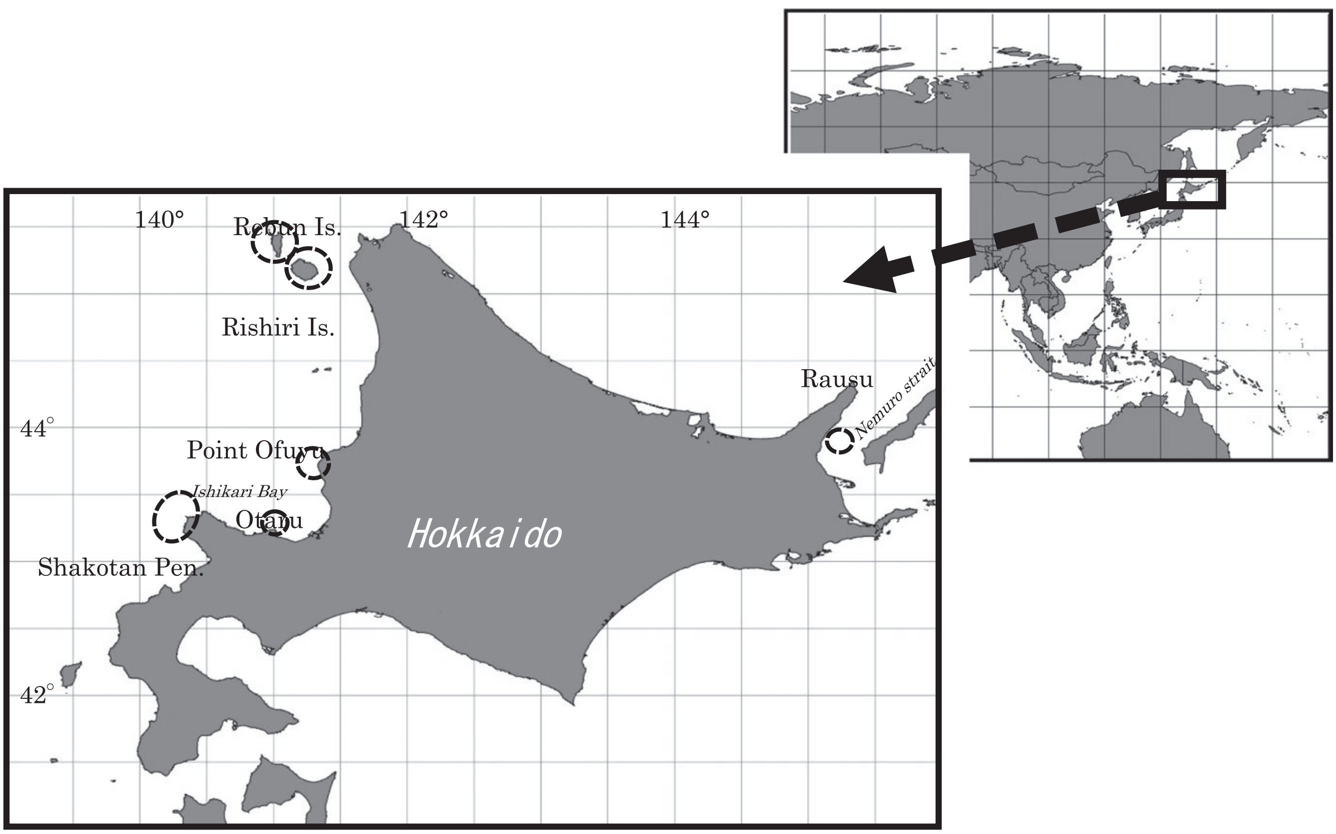

FIGURE 1 Location of the study area and Steller sea lion capture sites (Rausu, Shakotan Peninsula, Otaru, Point Ofuyu, Rishiri Island and Rebun Island) in Hokkaido, Japan

Rebun Island, with the greatest proportion (n = 119, 73.9%) being collected from Rausu. In the later sampling period (2000s), approximately 50 samples were collected from each sampling area, except for Otaru (n = 19) and Point Ofuyu (n = 14).

After measuring body length, weight, and sex of the SSLs, the cardia and pylorus of stomachs were bound with string to prevent overflow. The stomachs were immediately frozen and brought back to the laboratory. After measuring the weight of the stomach plus contents, the contents were removed and the weight of the empty stomach was measured. The weight of stomach contents was determined by subtracting the weight of the empty stomach from the weight of the stomach plus contents. The stomach contents were fixed in a 10% neutral formalin solution or 70% ethanol (only samples collected in 1998) for storage and then analysed. In order to avoid dissolution of otoliths by formic acid, the length of time in fixative was kept as short as possible (overnight to several days). The digestive stage of the stomach contents was determined based on visual inspection.

2.2 | Identification and estimation of prey species

Following fixation, stomach contents were washed on 8-, 4- and 1 (or 2)-mm mesh sieves, and wet weights were measured. Intact prey specimens were measured for standard (or scale, mantle) length, total length and weight. For digested stomach contents, the matter was classified (i.e., bone, muscle, otoliths, subopercle of gadids, cephalopod beak, eyeball, residual substance), counted and the wet weight was measured.

Prey remains were identified to the lowest possible taxonomic level using a reference collection. Matsubara (1955) was used to identify completely digested fish, whereas cephalopod beaks, fish bones, and otoliths were classified using additional references (Arai, 1993; Clarke, 1986; Deguchi, 1996; Hotta, 1973; Kubodera & Furuhashi, 1987; Ohe, 1985; Sakamoto, 1984; Yabe, 1985).

The frequency of occurrence (FO) of a prey item was expressed as follows: (number of stomachs containing the prey/total number of stomachs containing food) × 100.

The gravimetric percentage of each prey was calculated using the weight of bones of identified fish species and muscles of cephalopods. In addition, the number of small bones of digested prey that could not be classified was divided proportionally by the total number of individuals of each identifiable prey (Goto & Shimazaki, 1998). The number of each prey item was estimated by counting the number of fish maxillaries (or heads in samples from the 2000s) and the number of cephalopod beaks with attached muscle that were found in the stomach contents. Because fish otoliths and subopercles are stored for longer periods in the stomach than other parts of fish (Kato, 1977), the number of otoliths may not equal the number of fish eaten in a single meal. Overall, there were only a few bones that could not be classified, and therefore this method did not affect the tendency of dominance of each prey. However, almost all stomachs contained digested contents for which we needed to reconstruct the weight of prey for gravimetrical analysis. According to the assessment of digestion stage, we judged the samples used to reconstruct weight (Figure 2). We estimated the body weight of each prey using the regression equation for the relationship between otolith length and body weight shown in Table 2. Because of the lack of sufficient data from the 1990s samples to reconstruct the weight of prey, only undigested samples (stages 1 and 2; Figure 2) were used in the following analysis. To calculate the reconstructed weight (RW) of prey consumed in the diet, we used deformed VBR (VBR means variable amount of reconstructed biomass) (Hammond & Rothery, 1996).

$$\mathrm{RW} = \sum_{k=1}^{s} n_{i,k} * \bar{w}_{i,k} \tag{1}$$

where s is the number of samples, $n_{i,k}$ is the number of prey of category i in sample k, and $w_{i,k}$ is the weight of the prey category i in sample k.

After RWs were calculated for each sample, the gravimetric percentage (RW%) of prey was calculated as: (total mass of prey item in all stomachs/total mass of all identifiable prey in all stomachs) × 100.

Because the weight of the contents of each stomach varied according to SSL body size in this study, in order to evaluate the importance of prey items in each sample, biomass was reconstructed by combining prey numbers and gravimetric composition [G_{jk} (%) = G%] using the following formula:

$$G_{jk} = \sum_{j=1}^{nj} \left(W_{i,j,k} / \sum_{k=1}^{s} W_{i,j,k} \right) / n_j * 10^2 \tag{2}$$

where i = individual within a collection, j = collection (each site and year combination), W = gravimetric percentage of each prey, n = number of samples and k = prey categories (species, genus [*Sebastes* spp., *Gymnocanthus* spp. and *Ammodytes* spp.], family [Pleuronectidae spp. and Octopodidae spp.], other [unidentified squids, crustaceans, and ribbon worms] and milk-like fluid). This formula is derived from the split-sample FO (SSFO) proposed by Olesiuk, Bigg, Ellis, Crockford, and Wigen (1990). Almost all the remains of *Sebastes* spp. and *Gymnocanthus* spp. prey were difficult to identify to the species level, because these species have similar otolith and bone shapes; therefore, they were classified as the same group. Species within the family Pleuronectidae, several of which were typically found in the stomachs of SSLs, were similarly difficult to identify, and were thus classified in the same group. The genus *Ammodytes* probably comprises three species, namely *Ammodytes hexapterus*, *Ammodytes japonicas* and *Ammodytes heian*, which are almost impossible to identify based on morphological features and can only be reliably identified by genetic analysis (Orr et al., 2015). Species of the family Octopodidae have similar beaks, and were accordingly difficult to identify from the beaks remaining in stomachs. Therefore these were not classified.

The diets of SSLs were compared among different areas using percentage similarity (PS):

$$\mathrm{PS} = 1 - 0.5 |pk - qk| \tag{3}$$

where pk and qk are the G % of prey category k in two areas (p and q; Schoenor, 1970).

Table 1 Total numbers of Steller sea lion stomachs collected off the coast of Hokkaido, Japan, during the periods 1994–1998 and 2005–2012

		Rausu								Shakotan Peninsula										OTARU			
		Hunted								Entangled					Hunted			Stranded		Hunted			
		M				F				M			F		M		F	M		M			
Year	Month	A	S	J	Y	A	S	J	Total	A	S	J	A	J	A	S	A	A	Total	A	S	J	Y
1994	February–March	1	4	3		18			26						1	1			2				
1995	February	1	4	3		18			26														
1996	January–March	1	3			10	1		15						3				3				
1997	January–April	2	3	5		10	1	1	22						7		1		8				
1998	January–May	2	1	3		21	1	2	30						3	2	1		6				
	Total	7	15	14		77	3	3	119						14	3	2		19				
2005	January–May		1			4		2	7	3	3		1	1				1	9				
2006	January–May		1	1	1	4		1	8	3	4	1	2						10				2
2006–2007	November–May		1			3		2	6	3	7	2	1	4					17				
2007–2008	December–March					4			4	6	4		1						11			1	
2008–2009	December–April			1		6		1	8	2	1			1					4			2	
2009–2010	December–May		2	1		5			8	2				1					3	2			
2010–2011	December–April		3			2		1	6		1		1	2					4	3			
2011–2012	December–June			1		7			8		1		2	1					4	3	2		
	Total		8	4	1	35		7	55	19	21	3	8	10				1	62	8	2	3	2
	Total	7	23	18	1	112	3	10	174	19	21	3	8	10	14	3	2	1	81	8	2	3	2

M, male; F, female; A, adult; S, subadult; J, juvenile; Y, yearling; UK, unknown.

All sexual stages classified by age (Isono, 1999) in 1990s samples and body length (BL) or weight (BW) in 2000s samples.

Male adult: >250 cm (BL) or >400 kg (BW); subadult: 200–250 cm (BL) or 200–400 kg (BW); juvenile: 150–200 cm (BL) or 100–200 kg (BW); yearling: <150 cm or <100 kg.

Female adult: >210 cm (BL) or >200 kg (BW); subadult: 150–210 cm (BL) or 100–200 kg (BW); juvenile: 100–150 cm (BL) or 80–100 kg (BW); yearling: <100 cm or <80 kg.

This criteria determined according to data in Isono and Wada (1999) and Ishinazaka (1999). In spite of female body size, if an individual was observed to be pregnant or had a trace of lactation, it was classified as adult automatically.

Next, the diet diversity index (DI), based on Simpson's index (Simpson, 1949), was calculated on a gravimetric basis by using sampling year and area.

$$\mathrm{DI}_j = 1 / \sum_{k=1}^{s} (G_{jk})^2 \quad (4)$$

In order to reduce the influence of differences in sample size, each value was multiplied by a correction factor as follows:

$$\text{correction DI} = n/(n-1) * \mathrm{DI} \quad (5)$$

				Point Ofuyu								Rishiri Island					Rebun Island								
		Stranded		Entangled		Hunted				Stranded		Hunted					Hunted								
F		M		M	F	M			F	M		M	F				M			F					
A	Y	J	Total	J	Y	A	S	Y	A	UK	Total	Y	A	J	S	Total	A	J	Y	A	S	J	Y	Total	Total
																									28
																									26
																	1	1	1	2		2		7	25
																	4	1	1	2				8	38
																			2	3		2	2	9	45
																	5	2	4	7		4	2	24	162
				1				1			2		5		1	6	1			1				2	26
		1	3				1		1	1	3		6			6									30
					1	3					4		5			5				6		1	1	8	40
			1		1	2					3	1	6			7			1	6				7	33
			2				1				1		4			4			1	4				5	25
1			3										5			5		1	6	6		1		14	33
	1		4						1		1		7	1		8				4		1		5	28
1			6										6	1		7	1			4	1			6	31
2	1	1	19	1	2	5	2	1	2	1	14	1	44	2	1	48	2	1	8	31	1	3	1	47	246
2	1	1	19	1	2	5	2	1	2	1	13	1	44	2	1	48	7	3	12	38	1	8	3	71	408

The 1990s survey was conducted from January to March, whereas the 2000s survey was conducted from November to June. Therefore, for the decadal comparison, we used only the data obtained from samples collected in January to March in the 2000s.

2.3 | Statistical analysis

Redundancy analysis (RDA) was applied to investigate the effects of year, sampling site, sex and ontogenetic stages on dietary variation. RDA is an ordination technique to incorporate two matrices

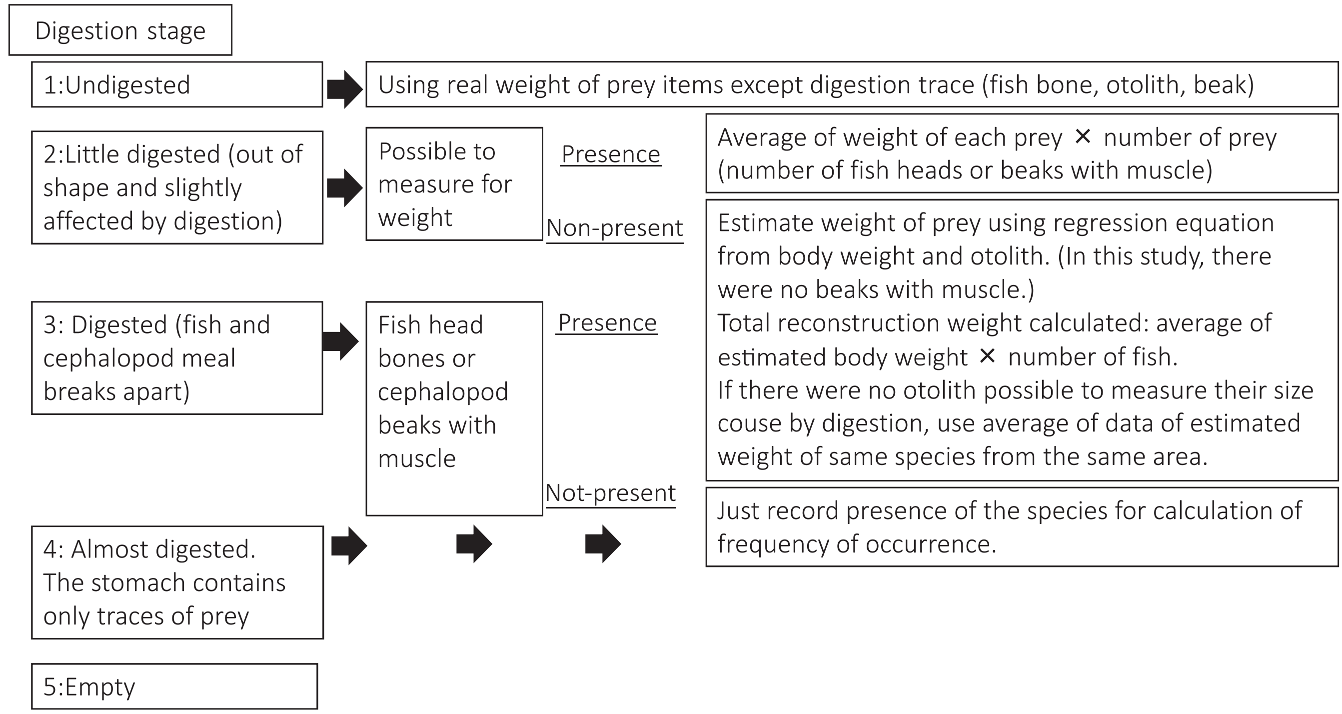

FIGURE 2 Flowchart of method used to reconstruct the weight of prey according to the digestion stage of stomach contents

representing ecological response (e.g., species composition or dietary composition) and constraining (or environmental) factors (ter Braak, 1995). The external parameters included in the RDA were sampling sites, year, sex, body length and ontogenetic stages. As mentioned above, some sites were sampled only in the 2000s. Therefore, two RDAs including the data from both periods (Shakotan, Rebun and Rausu) and from the 2000s (all sites) were performed separately to reduce the interaction between decades and sites. As RDA requires metric data for both ecological response and external parameters, sampling sites were coded to represent the geographic arrangement as Syakotan: 1, Rishiri: 2, Rausu: 3 (inter-decadal analysis) or Shakotan: 1, Otaru: 2, Ofuyu: 3, Rebun: 4, Rishiri: 5, Rausu: 6 (data from the 2000s). Similarly, sexes and ontogenetic stages were coded as male: 1, female: 2; yearling: 1; juvenile: 2, subadult: 3, adult: 4. Permutational multivariate analyses of variance (PERMANOVAs) were performed in order to determine the significance level of the external parameters. All statistical analyses were performed using the vegan package (Okasanen et al., 2017) in R v. 3.1.2 (R Core Team, 2014).

2.4 | Evaluation of prey availability

To evaluate prey availability, we collected data on commercial catches of walleye pollock and Pacific cod in Rausu, Shakotan and Rebun; Okhotsk Atka mackerel in Shakotan and Rebun; and giant Pacific octopus (*Enteroctopus dofleini*) in Shakotan from 'Hokkaido suisangensei' published by the Hokkaido Government (2017). Our assessment of the availability of walleye pollock as prey for SSLs was based on fisheries biomass estimates (Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 2017a).

3 | RESULTS

3.1 | Prey species and their proportions

Stomach contents were collected from 381 SSLs of all age classes. Stomach contents containing traces of digested and non-prey items (e.g., stones, parasites, and remnants of fishing nets) averaged 5.3 ± 5.9 kg (*SD*; range 0.0–36.49 kg). Among the non-prey items, parasites (nematodes) were found in most stomach samples. The FO of fishing net differed according to the survey area and survey periods (0%–49.5%), whereas stones occurred in approximately 50% of the overall stomachs (Table 3).

Prey items included at least 38 species of fishes from 20 families, 11 species of squid from six families, two species of octopuses, unidentified decapod crustaceans, ribbon worms, unidentified bones of mammals and birds, and milk-like fluid (Table A1).

Although differences among sample collection areas were observed, the major prey species of SSLs in all areas were octopuses ([*Octopodidae* spp.]; mainly giant Pacific octopus) and gadids (mainly Pacific cod and walleye pollock), which had the greatest FOs. Prey composition changed depending on the sampling period (Table 4).

In Rausu, walleye pollock was the most abundant prey, comprising 94.1% and 71.0% of FO, and 9.7% and 83.7% of RW% during the first and second survey periods, respectively. Pacific cod was most dominant gravimetric component (62.0% RW%) in the first period, but its contribution decreased to 3.9% in the second period. The second most dominant species in Rausu during the second period was flathead mullet (*Mugil cephalus*) (6.7%).

TABLE 2 Equations used in this study to determine the relationship between fish otolith length (OL) in millimeters and fish weight (body weight, BW) in grams. For each equation, the number of fish or otoliths measured (*n*), coefficient of determination (r^2) and range of fish weight are given

Species	Equation	r^2	*n*	Range: Minimum	Range: Maximum	Location	References
Pacific herring	BW = 13.328 $(OL)^{1.8779}$	.8616	8	21.0	279.0	Sea of Japan	
Japanese anchovy	BW = 0.0188 $(OL)^{5.3122}$	.7443	19	7.0	34.7	Pacific Ocean	
Pacific cod	FL = 4.51 (OL) − 22.97	.883	110	10.0	106.0	Bering Sea	Harvey, Loughlin, Perez, and Oxman (2000)
	BW = 3E-06 (estimated FL) 3.2331	.9161	59	743.0	9,270.0	Sea of Japan	
Walleye pollock	ln BW = 3.72 (OL) − 4.06	.84	302	195.0	3,280.0	Bering Sea	Deguchi, Goto, and Sakurai (2004)
Okhotsk atka mackerel	BW = 6.4238 $(OL)^{2.7844}$	.7754	296	129.0	1,910.0	Sea of Japan	
Blackedged sculpin	BW = 0.6403 $(OL)^{2.515}$	.4194	24	114.0	391.0	Sea of Japan	
Japanese sand lance	BW = 2.9665 $(OL)^{1.8704}$	.4997	100	19.2	46.3	Sea of Japan	
Flathead flounder	BW = 0.1471 $(OL)^{4.0606}$	.8489	53	8.0	297.0	Sea of Japan·Pacific Ocean	
Pointhead flounder	BW = 1.1176 $(OL)^{2.3764}$	.5535	47	22.0	188.0	Pacific Ocean	
Dusky sole	BW = 1.3492 $(OL)^{2.8228}$	.5507	20	74.0	4,202.0	Sea of Japan	
Sand flounder	BW = 27.769 $(OL)^{0.8543}$	.1594	12	64.0	150.0	Sea of Japan	
Yellow striped flounder (Rausu)	BW = 1.3461 $(OL)^{3.1702}$	.8282	15	137.0	763.0	Pacific Ocean	
Yellow striped flounder (Japan Sea)	BW = 2.8247 $(OL)^{2.1631}$	.6134	14	52.0	275.0	Sea of Japan	
Cresthead flounder	BW = 0.6236 $(OL)^{3.9857}$	.8269	12	66.6	830.0	Pacific Ocean	
Blackfin flounder (Rausu)	BW = 0.8256 $(OL)^{2.7406}$	.5287	50	5.0	97.0	Pacific Ocean	
Blackfin flounder (Japan Sea)	BW = 1.8323 $(OL)^{2.5762}$	.6761	29	45.0	190.0	Sea of Japan	

FL, folk length in millimeters.

TABLE 3 Frequency of occurrence (%) of non-prey items in Steller sea lion stomachs collected from the coast of Hokkaido, Japan, during the periods 1994–1998 (1990s) and 2005–2012 (2000s) according to survey period and location. Data were pooled across years and months. The sample number (*n*) is the total number, including empty stomachs

	Rausu		Shakotan		Otaru		Ofuyu		Rishiri		Rebun	
	1990s	2000s	1990s	2000s	1990s	2000s	1990s	2000s	1990s	2000s	1990s	2000s
n	119	55	19	62	N.D.	19	N.D.	14	N.D.	48	24	48
Nematoda	86.0	96.3	52.6	100		100		92.9		97.9	79.2	97.9
Fishing nets	32.8	30.9	36.8	11.3		42.1		0		6.3	20.8	12.5
Stones	25.2	40.0	36.8	51.6		52.6		57.1		25.0	54.2	43.8

N.D., no data.

Magister armhook squid (*Berryteuthis magister*) were ingested frequently in Rausu during both periods (42.3% in the 1990s and 80.4% in the 2000s; Table A1). Other species important in some years during the 2000s were flat fishes, sculpins (mainly black edged sculpin [*Gymnocanthus herzensteini*]), Japanese anchovy (*Engraulis japonicus*) and smooth lumpsucker.

In Shakotan, octopus, Okhotsk Atka mackerel and Pacific cod were the most dominant prey for SSLs. These prey had high gravimetric contributions in almost every sampling year. However, gadids (i.e., Pacific cod and walleye pollock) were constantly important in the 1990s, making up >80% of the diet in terms of weight, but then decreasing dramatically in the 2000s to <20%. In the 2000s, Okhotsk Atka mackerel partially replaced gadids, with octopuses making the second most important contribution. Some prey items, namely spear squid (*Heterololigo bleekeri*), smooth lumpsucker and sand lances, occurred frequently, but their gravimetric contributions were comparatively small (7.4% in total). Octopuses were consistently ingested during both periods.

Gadids were also the most dominant prey species during the 1990s in Rebun, comprising 44.5% of total consumption (Table A1). An unidentified skate (*Rajadae* sp.) was also dominant, accounting for 35.5%, but was ingested by only a single SSL. In the 2000s, Pacific cod was the most dominant prey, followed by flat fishes (mainly flathead flounder [*Hippoglossoides dubius*]) and smooth lumpsucker.

In Rishiri, sand lances were the most dominant prey, accounting for 64.6% of the total diet in every year, except 2008–2009. Okhotsk Atka mackerel was second in importance, followed by octopuses. The only exception was in 2008–2009, when the most dominant prey was Okhotsk Atka mackerel, followed by sculpin.

In Otaru and Ofuyu, herring was the predominant prey, and its proportion increased after 2009 and 2010, respectively. Prior to 2009, the main prey differed according to year.

TABLE 4 Frequency of occurrence (FO%), percentage composition by weight (RW%) and gravimetric composition (G%) of prey species based on reconstructed weight in Steller sea lion stomachs collected from the coast of Hokkaido, Japan, during the periods 1994–1998 (1990s) and 2005–2012 (2000s) according to survey period. Data were pooled across years and months

Sampling year	1990s									2000s			
Area	Rausu			Shakotan			Rebun			Rausu			Shakotan
n	17			5			6			31			45
Prey item	FO%	RW%	G%	FO%	RW%	G%	FO%	RW%	G%	FO%	RW%	G%	FO%
Skates							16.7	35.5	12.5	3.2	0.2	2.4	2.2
Herring													
Japanese anchovy										6.5	0.14	0.4	
Japanese surf smelt	5.9	0.7	1.7							3.2	0.0	0.1	
Salmonidae spp.										3.2	0.0	0.0	2.2
Pacific cod	88.2	62.0	52.9	40.0	7.3	21.6	33.3	44.5	20.8	22.6	3.9	4.0	24.4
Walleye pollock	94.1	9.7	19.6	60.0	76.3	29.7				71.0	83.5	55.7	4.4
Saffron cod	70.6	9.8	6.8							3.2	0.1	0.0	
Yellow goosefish													11.1
Flathead mullet										16.1	6.7	13.1	4.4
Sebastes spp.													8.9
Hexagrammos spp.										3.2	0.1	1.8	4.4
Okhotsk atka mackerel				40.0	2.1	14.2	16.7	1.8	11.6	6.5	0.1	0.2	82.2
Sea raven													2.2
Elkhorn sculpin													
Gymnocanthus spp.				20.0	0.2	0.4				9.7	1.2	3.2	4.4
Unidentified sculpin				20.0	0.1	0.0	16.7	0.6	3.7				
Smooth lumpsucker	5.9	0.1	0.1				50.0	12.2	41.9	16.1	0.3	8.4	22.2
Unidentified eelpout										3.2	0.4	1.1	
Long shanny													2.2
Japanese sand lance										3.2	0.0	0.3	26.7
Bastard halibut													2.2
Flat fishes	23.5	1.6	5.0	40.0	0.4	0.1	16.7	0.1	0.6	19.2	1.6	3.2	22.2
Tetraodontidae sp.													2.2
Unidentified Pisces	29.4	2.2	0.0	40.0	1.3	15.7	16.7	0.1	0.6	3.2	0.0	0.1	2.2
Spear squid													11.1
Magister armhook squid										9.7	0.2	0.7	
Japanese flying squid													
Unidentified/unclassified squids	76.5	3.9	4.5	20.0	0.1	1.4							
Octopus	64.7	10.1	8.0	100	12.2	16.9	50.0	5.1	8.4	6.5	1.6	5.2	46.7

3.2 | Prey size

In this study, most of the stomach contents were well digested, and prey sizes were mainly unmeasurable. Some intact prey individuals occurred occasionally, and these were measured (summarized in Table A2).

Body lengths of major prey items varied among species (Table A2). Most of the prey ingested were <300 mm, but two Pacific cod ingested by a SSL from Shakotan measured 663 and 774 mm. The average body weight (±*SD*) of North Pacific giant octopus was 1,672 ± 1,493.57 g. As we did not statistically analyse prey size and body length due to the low number of samples, we were unable to identify any trend between these traits in SSLs..

3.3 | Diet diversity

The gravimetric DI ranged from 3.2 to 6.0 and 1.6 to 4.2 during the 1990s and 2000s, respectively (Table 5). The difference between the decades was less pronounced than that between different sites, of which Rishiri and Otaru showed lower values than the other sites.

		Otaru			**Ofuyu**			**Rishiri**			**Rebun**		
		6			**5**			**36**			**27**		
RW%	**G%**	**FO%**	**RW%**	**G%**	**FO%**	**RW%**	**G%**	**FO%**	**RW%**	**G%**	**FO%**	**RW%**	**G%**
0.3	0.2												
		71.4	78.3	71.0	40.0	33.9	40.0						
					40.0	51.7	28.2	5.6	0.2	0.4	7.4	1.4	3.3
0.3	0.3												
15.2	11.7							5.6	2.4	1.3	40.7	54.0	29.8
0.6	0.6							2.8	0.6	1.1	3.7	0.3	0.4
3.2	2.8												
0.2	0.1												
3.6	2.3							2.8	0.3	0.6			
0.6	0.7												
51.4	49.5	14.3	15.2	14.2	20.0	11.0	11.8	25.0	21.4	10.1	11.1	4.1	4.4
0.3	0.2										3.7	0.1	0.8
								2.8	0.3	0.2			
0.1	0.2							16.7	1.7	3.4	18.5	1.2	2.7
4.6	6.2										55.6	15.1	41.0
0.1	0.3				20.0	3.4	20.0	2.8	0.2	0.4			
2.6	4.2							88.9	64.6	75.3	7.4	3.0	3.9
0.9	0.6												
3.7	5.0							8.3	0.6	1.2	29.6	16.0	8.9
0.0	0.0												
0.0	0.1							2.8	0.0	0.1			
0.2	0.2	14.3	0.1	0.1									
											3.7	0.1	0.1
											11.1	4.1	3.9
12.0	14.9	28.6	6.4	14.7				19.4	7.6	6.0	14.8	0.7	0.8

TABLE 5 Diet diversity index (DI) based on reconstructed gravimetric composition of Steller sea lion prey collected from the coast of Hokkaido, Japan, during the periods 1994–1998 (1990s) and 2005–2012 (2000s)

	Rausu				Shakotan				Otaru		Ofuyu		Rishiri		Rebun			
	1990s January-March		2000s January–March		1990s January-May		2000s January–March		2000s January–March		2000s January–March		2000s January–March		1990s January-March		2000s January–March	
	n	DI	*n*	DI	*n*	DI	*n*	DI	*n*	DI	*n*	DI	*n*	DI	*n*	DI	*n*	DI
DI	17	3.2	17	4.0	5	6.0	44	4.2	6	1.7	4	3.6	27	1.6	6	4.7	14	3.8

PSI	Rausu	Shakotan	Otaru	Ofuyu	Rishiri	Rebun
Rausu		0.21	0.05	0.01	0.13	0.12
Shakotan			0.29	0.12	0.24	0.27
Otaru				0.52	0.16	0.05
Ofuyu					0.11	0.08
Rishiri						0.15
Rebun						

0.4–0.6 0.2–0.4

FIGURE 3 Matrix of percentage similarity (PSI) showing dietary similarity of Steller sea lions among the sampling areas

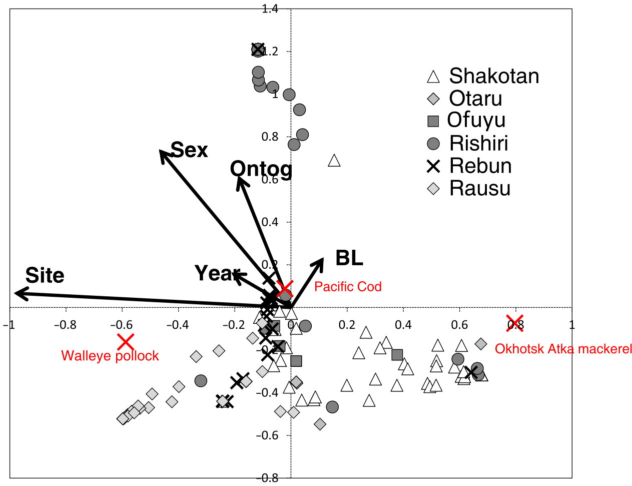

FIGURE 4 Plot showing the results of redundancy analysis of Steller sea lion diets from different sites sampled during the 2000s. Each point shows individual diet composition, whereas vectors and red crosses represent constraining factors and major prey items, respectively. BL, body length; Ontog, ontogeny stage

In Rausu, Shakotan and Rebun, there were no clear changes in DI between survey periods (Table 5). In these areas, gadids have been the predominant prey of SSLs since the 1990s, and the G% value was consistently high. However, the rates of consumption of other prey increased during the 2000s (Table 4). Therefore, compared with the 1990s, there was a greater number of prey families in the stomach contents of SSLs during the 2000s, despite no clear changes in DI.

In Otaru and Ofuyu, SSLs preyed heavily upon Japanese anchovy or herring during the migration season of these fishes (from January to March: this differs year by year). During other seasons, flounders, long shanny (*Stichaeus grigorjewi*), octopus and Okhotsk Atka mackerel, were dominant prey. However, there were fewer types of prey in these areas compared with other areas.

3.4 | Spatial variation in sea lion diet

For the samples obtained in the 2000s, the percentage similarity (PS) between areas was calculated based on G% (Figure 3). Each PS was generally low, with 10 out of 15 pairs showing values <0.4. Otaru and Ofuyu was the only pair showing a PS value of >0.6, due to the heavy ingestion of herring (Table 4).

Analysis of the RW of SSL by RDA according to site, year, sex, ontogenetic stage, and body length, revealed the characteristic species at each site. The characteristic prey for each site were: walleye pollock in Rausu, Okhotsk Atka mackerel in Shakotan during both sampling periods. Additionally, Japanese sand lance was identified as a characteristic prey only in Rishiri by RDA (Figure 4). Differences of sexual and ontogeny stage among samples showed that females and young were more frequent in the northern part of the Sea of Japan and Rausu than at the other sites. A permutation test for site comparison indicated that site and ontogenetic stage contributed to the difference of SSL prey significantly (Table 6).

On the basis of the RDA results obtained following the addition of decadal data in the analysis of three sites (Rausu, Shakotan, Rebun), separation of sampling term and site were shown to make a larger contribution than individual characteristics (sex, body length, and ontogenetic stage; Figure 5). Pacific cod was found to be one of the characteristic prey items in the 1990s samples especially in Rausu. The results of the permutation test for decadal comparison indicated that site, year, ontogenetic stage, and the site×year interaction contributed to the significant difference between the decades of SSL prey significantly (Table 7).

3.5 | Annual changes in commercial catches of main prey species

There was a trend of decreasing commercial catches of gadids in Rausu, Shakotan and Rebun during the study period (Figure 6). The relationship between the estimated biomass of walleye pollock in the northern region of the Sea of Japan was used as the independent variable and the FO% values of the SSL stomach samples for all digestion stages in Shakotan and Rebun were used as the dependent

TABLE 6 Permutation test for site comparison. Initially, all patterns were tested, subsequently, significant variables were selected, and the same test was repeated. Data shown are the results of the final analysis. Each test was repeated 999 times

Factor	df	SS	MeanSqs	F.Model	R^2	p (>F)
Site	1	7.327	7.3267	20.429	.11858	.001***
Year	1	0.574	0.5745	1.6018	.0093	.123
Ontogeny	1	1.187	1.1869	3.3094	.01921	.006***
Site:year	1	0.583	0.5833	1.6264	.00944	.104
Site:ontogeny	1	0.346	0.3461	0.9652	.0056	.46
Year:ontogeny	1	0.184	0.1836	0.5119	.00297	.865
Site:year:ontogeny	1	0.299	0.2987	0.8328	.00483	.55
Residuals	143	51.29	0.3586		.836	
Total	150	61.79			1	

F.Model, pseudo-F value; MeanSqs, mean squre; SS, sum of squares.
**p < .01.
***p < .001.

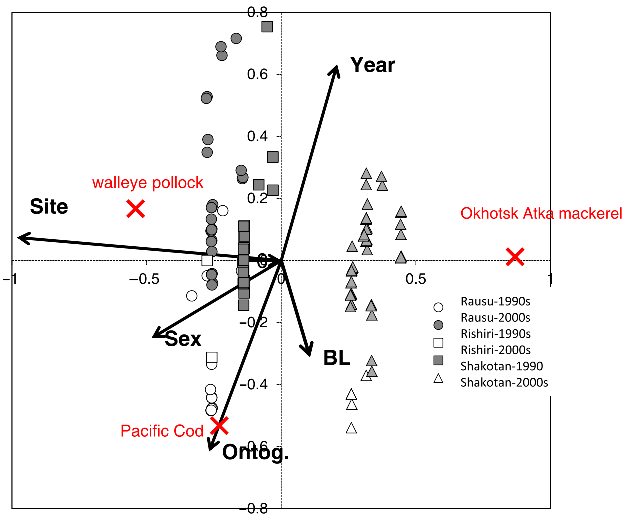

FIGURE 5 Plot showing the results of redundancy analysis of Steller sea lion diets from different sites during earlier ('90s: open symbols) and later ('00s: solid symbols) decades. Each point shows individual diet composition, whereas vectors and red crosses represent constraining factors and major prey items, respectively. BL, body length; Ontog, ontogeny stage

variables, which are shown plotted by year in Figure 7. Because there were many 0% RW samples for walleye pollock in the 2000s samples, we used the FO% value instead. There were significant relationships between estimated biomass of walleye pollock and FO% (regression analysis $p < .01$), with all of the FO% values for the 1990s samples being higher than those for the 2000s.

4 | DISCUSSION

4.1 | Important prey of SSLs in Hokkaido

In this study, we determined that the main prey species of SSLs were coastal demersal fishes and cephalopods, which is consistent with results obtained from the Bering Sea and the Gulf of Alaska (Merrick et al., 1997; Sinclair & Zeppelin, 2002; Spalding, 1964). The characteristic prey species in each sampling area were indicated by RDA.

4.1.1 | Walleye pollock

In Rausu, Shakotan and Rebun, gadids were important prey for SSLs, particularly in Rausu. However, the importance of these prey species diminished from the 1990s through the 2000s (from 79.3% to

TABLE 7 Permutation test for decadal comparison. Initially, all patterns were tested, subsequently, significant variables were selected and the same test was repeated. Data shown are the results of the final analysis. Each test was repeated 999 times

Factor	df	SS	MeanSqs	F.Model	R^2	p (>F)
Site	1	7.077	7.0765	22.898	.14073	.001***
Year	1	1.34	1.3398	4.3354	.02665	.003**
Ontogeny	1	1.577	1.577	5.1029	.03136	.001***
Site:year	1	1.725	1.7248	5.5809	.0343	.001***
Site:ontogeny	1	0.351	0.3506	1.1344	.00697	.326
Year:ontogeny	1	0.093	0.0928	0.3001	.00184	.953
Site:year:ontogeny	1	0.108	0.1085	0.3509	.00216	.917
Residuals	123	38.013	0.309		.75598	
Total	130	50.283			1	

F.Model, pseudo-F value; MeanSqs, mean squre; SS, sum of squares.
**p < .01.
***p < .001.

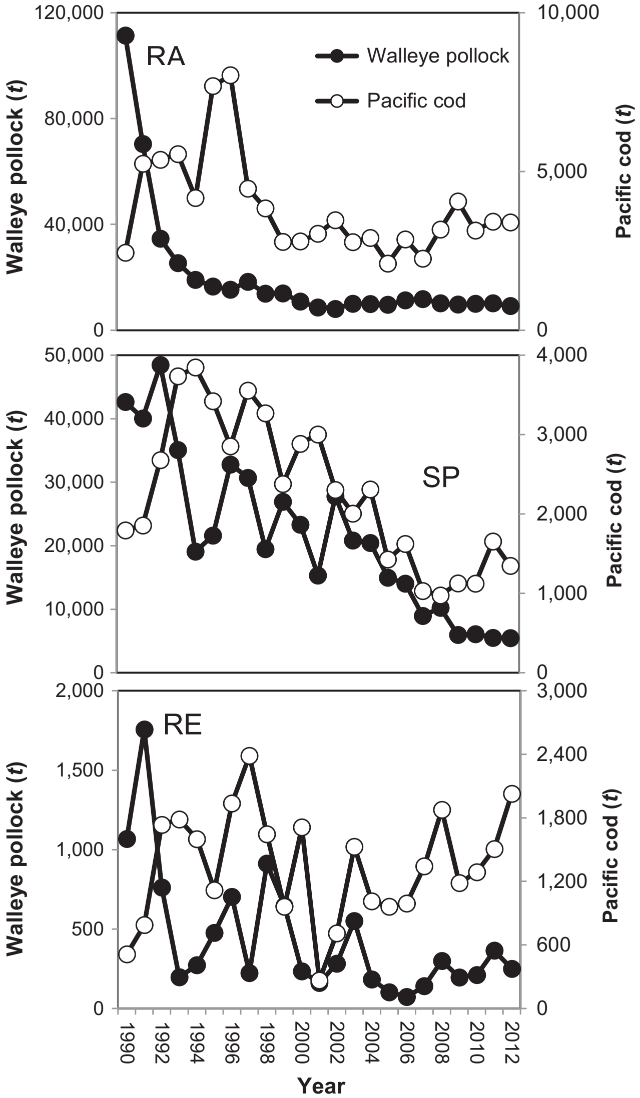

FIGURE 6 Annual change in gadid (walleye pollock and Pacific cod) catches off Rausu-cho (RA), jurisdiction of Siribeshi general subprefectural bureau (SP), and Rebun-cho (RE) during the period 1990–2012 (Statistics: Hokkaido suisangensei). The data were collected by the administrative district unit. Data for SP, and the catch of the offshore trawl fishery are also included

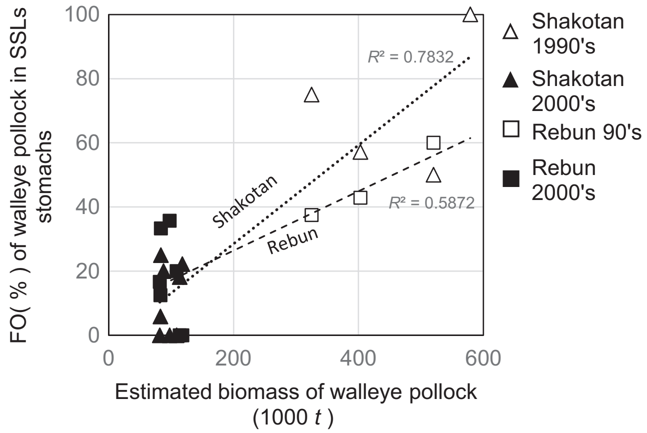

FIGURE 7 Relationship between estimated biomass of walleye pollock (Northern Sea of Japan stock) and frequency of occurrence (FO; %) of walleye pollock in stomach contents of Steller sea lion. FO calculated based on actual data including trace (i.e. using data of Table A1)

59.8% in G%), coinciding with the trend of decreasing commercial catches of walleye pollock and Pacific cod in the Nemuro Strait (Figure 6). Walleye pollock migrate to sites off the coast of Rausu from November to March for spawning. Most catches of walleye pollock occur from February to March in this area (Sasaki, 1984). Although we have little knowledge regarding the spawning areas of the walleye pollock off the coast of Rausu, according to Sasaki (1984) and Shida (2001), the main spawning layer lies at depths >200 m. Moreover, in a study of the depth distribution of walleye pollock in Rausu in November, this species was mainly observed at depths of 200 to 300 m (Ishida, 2012). When feeding, adult female SSLs typically dive to depths of between 50 and 200 m, whereas juveniles dive to approximately 50 m (Loughlin, Sterling, Merrick, Sease, & York, 2003; Merrick & Loughlin, 1997; Rehberg, Andrews, Swain, & Calkins, 2009). Although SSLs can dive to depths of over 250 m, the observed frequency of this is lower (Loughlin, Perlov, Baker, Blokhin, & Makhnyr, 1998). Therefore, it seems that walleye pollock are not a particularly accessible prey resource for SSLs in Rausu within their main distribution layer. It is more likely that predation on walleye pollock occurs mainly during the night when these fish move to the shallower depth along the Rausu coast. In addition, a large number of gill net remnants were found in the stomachs of SSLs sampled from this area (FO = 30.9% in 2000s), suggesting frequent predation by SSLs.

4.1.2 | Okhotsk Atka mackerel

The main prey species of SSLs collected from Shakotan were Pacific cod, Okhotsk Atka mackerel, and octopuses. Commercial catches of Pacific cod and walleye pollock around the Shakotan Peninsula coast decreased markedly during the 2000s (Figure 6), whereas in contrast, catches of Okhotsk Atka mackerel remained stable from the 1990s through 2009 (calculated from 'Hokkaido suisangensei'). Okhotsk Atka mackerel spawn over a wide area along the Hokkaido coast (Natsume, 2003). Since the late 1980s, catches and imports of walleye pollock have decreased on a global scale (Itoo, 2017; Natsume, 2003). The estimated biomass of the Northern Sea of Japan stock of walleye pollock has been declining since the 1990s, as a consequence of decreasing recruitment since around 1990 (Funamoto, 2011). Thus, Okhotsk Atka mackerel is used in surimi as an alternative, and fishing intensity for this species has accordingly increased, particularly in the Sea of Japan (Natsume, 2003). Okhotsk Atka mackerel with body lengths of approximately 20 cm are currently caught using offshore trawl-nets, and adult fish are caught in various other coastal fisheries (e.g., gill nets and set nets). On the basis of the average body length of Okhotsk Atka mackerel ingested by SSLs, it is assumed that these fish were adults, which is consistent with the size of fish caught by coastal fisheries and offshore trawl-nets (Hoshino et al., 2010). Because Okhotsk Atka mackerel was abundant, it was considered to be an important prey species for SSLs after the collapse of gadid populations. Hattori, Isono, Wada, and Yamamura (2009) discovered SSLs in the offshore region of Musashi-tai Bank (>20 km from the shoreline), an important trawl-fishing area for demersal fishes, particularly Okhotsk Atka mackerel, and concluded that SSLs appeared to be attracted to this area by the Okhotsk Atka mackerel. The congeneric Atka mackerel (*Pleurogrammus monopterygius*) is also a main prey species of SSLs in the Aleutian Island area (Sinclair & Zeppelin, 2002). Atka mackerel are demersal batch spawners (from July through October), with males often guarding nests for up to 6 months of the year, whereas females aggregate in large schools close to the spawning ground, presumably to feed (McDermott, Haist, & Rand, 2016). Historically, the Atka mackerel trawl fishery operated close to SSL rookeries, resulting in competition between the fishery and SSLs (McDermott et al., 2016). It is considered that a similar situation has arisen with respect to Okhotsk Atka mackerel off Hokkaido. In recent years, the abundance of Okhotsk Atka mackerel has decreased rapidly, and this species has not been detected in the stomach contents of SSLs captured in Rebun since 2010, although the previous FO of this prey in Rebun was relatively high (actual FO = 33.3%–50% between 2005 and 2009). Given the decreases in gadids and Okhotsk Atka mackerel, it will be of interest to monitor future changes that occur in the diet and nutritional status of SSLs.

4.1.3 | Octopuses and others

In the Sea of Japan, octopus (mainly giant Pacific octopus) were ingested constantly throughout the study period. In addition, octopus are important prey in Otaru and Ofuyu when the availability of schooling fish is low (e.g., herring; mentioned later). Giant Pacific octopus catches appear to have remained almost stable (calculated from "Hokkaido suisangensei"), as there have been no significant changes in the stocks of this species in recent years (Wakkanai Fisheries Research Institute 2014). A similar situation may exist for another of the SSL prey species, the smooth lumpsucker in Rebun; however, information on the abundance of this species is sparse, as this fish is not a target of fisheries along the Northwestern Hokkaido coast (Yoshida & Mihara, 2015). This species is also distributed offshore in the open ocean (Kyushin, 1975) and it can be eaten by SSLs during the spawning season from January to April.

Herring is an important prey for SSLs in Southeast Alaska (e.g., Womble & Sigler, 2006), and in recent years has also become an important prey item in the Sea of Japan. Herring became a major prey item during 2009 at Otaru and Ofuyu after catches exceeded 1,800 tons in this year for the first time in 20 years (Takayanagi, Yamaguchi, & Ishida, 2010). The herring that currently occur in Ishikari Bay are part of the Ishikari Bay population, which is different from the Hokkaido-Sakhalin population that supported large-scale fishing in the first half of the 20th century (Kobayashi, 1993). The catch of `Ishikari Bay herring' stock at Ishikari Bay (i.e., Shiribesi and Ishikari subprefectures), which had been consistently low since the early 1990s (Takayanagi et al., 2010). In Ofuyu and Otaru, catches of herring increased after 2009 (Takayanagi et al., 2010). Therefore, the increased ingestion of herring by SSLs reflects an increase in herring abundance. Although herring aggregate along the coast for spawning during late January to early May, they are rarely seen in coastal waters during the non-spawning season (Tanaka, 2003), and thus herring are probably of limited importance as prey items for SSLs.

4.2 | Changes in prey composition and diversity

Compared with the 1990s, prey diversity at Rausu had increased slightly in the 2000s, but decreased slightly at Shakotan and Rebun.

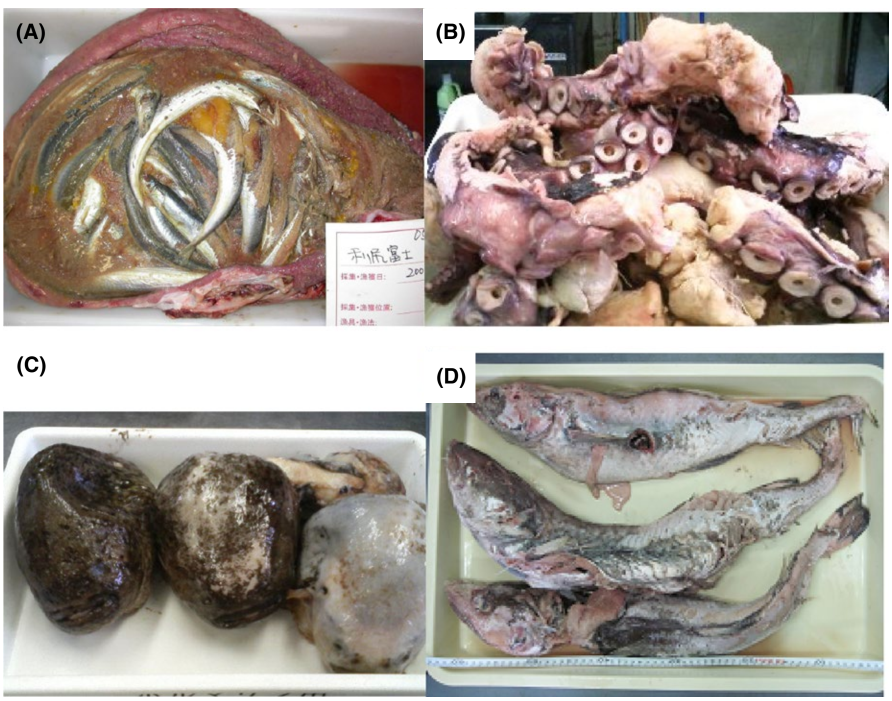

FIGURE 8 Examples of undigested stomach contents. (A) Sand lances in Risihi sample (2005), (B) giant Pacfic octopus in Shakotan sample (2005), (C) smooth lumpsuckers in Rebun sample (2008), (D) Pacific cods in Shakotan sample (2010)

Although the results of the RDA suggest significant decadal differences, stating that DI specifically reflects the diversity of SSL diet is speculative. Despite the changes in major prey species, the DI did not change significantly over the years. This reflects the fact that SSLs tend to prey intensively on gathered schools of fish, and thus only one prey species per stomach was detected in almost all of the stomach contents examined. For example, in the Rishiri samples, almost all stomach contents were made up of sand lance, and these fish numbered in their hundreds (Figure 8A). The greater diversity observed at Rausu was due to the number of prey species (e.g., Pacific cod and flatfishes) ingested, possibly to compensate for the decrease in gadid abundance. Prey switching presumably had no negative effects on SSL population dynamics in this area. As a consequence of the recent recovery of the Asian stock of SSLs, including those in the Kurile Archipelago (Burkanov & Loughlin, 2007), the numbers migrating to the Hokkaido coast have increased, with an estimated population size of 5,800 (14.4%: coefficient of variation [CV]) individuals in the period 2005–2009, and 6,237 (12.3% CV) individuals between 2010 and 2013 (Hattori & Isono, 2017). Moreover, a trend of earlier arrival and remaining longer has been observed compared with the 1980s (Hoshino et al., 2006).

In Shakotan and Rebun, catches of Pacific cod and walleye pollock have decreased since the 1990s (Figure 6). A reduction in walleye pollock abundance has been particularly noticeable, decreasing by 90% in the 20 years after 1990. It is believed that this decline has been caused by a warming trend in the Sea of Japan (Funamoto et al., 2014). The amount of recruitment to the population of walleye Pollock in the northern Sea of Japan has been shown to be related to sea surface temperature and strength of the Tsushima Warm Current (Funamoto, 2011; Miyake, 2012). Since a 'regime shift' of marine environment in 1988/89 (Yasukawa & Hanawa, 2002), coastal water temperatures have continued to increase, and this is considered to have affected spawning ground formation and the survival of walleye pollock at the egg stage (Miyake, 2012).

In Rausu, the abundance of walleye pollock (Nemuro Strait stock) also declined significantly between the 1990s and the 2000s, with catches declining to a quarter of previous levels. However, it has remained an important prey species of SSLs, comprising 18%–97% of their diets. Similarly, in Shakotan and Rebun, it is considered that the same effects resulted in changes in the prey composition of SSL diets. In the 2000s, Pacific cod and walleye pollock were virtually absent from the stomach contents of SSLs in both areas: Okhotsk Atka mackerel and other prey species appeared instead. As such, it is considered that as gadid availability declined off the Hokkaido coast, SSLs began to prey on other fish species, resulting in higher prey diversity.

Research conducted in Alaska has indicated that that SSLs forage in environments where prey species are highly abundant and available (Merrick et al., 1997; Sinclair & Zeppelin, 2002). However, in such environments, SSL diets are presumably influenced by changes in prey availability (Merrick et al., 1997). Therefore, prey environments that sustain a greater number and abundance of prey species that can be substituted can easily maintain a population of SSLs (Merrick et al., 1997). In the present study, conducted off the Hokkaido coast, we observed that after walleye pollock had declined, the frequency of other species ingested increased as the abundance of other prey types increased. As it is estimated that the quantities of available species, such as sand lance and Okhotsk Atka mackerel, or fish not targeted by fisheries, such as smooth lumpsucker and sculpin, were also large, SSLs in this area would have been less affected by the decline in walleye pollock.

4.3 | Geographic variation

The differences in diversity of SSL prey among the sampling areas, indicated by the percent similarity and geographic diversity, were high. For instance, the main prey item differed in Rishiri and Rebun (sand lance and smooth lumpsucker, respectively), despite the fact that these two sites are only 19 km apart. Although SSLs can easily move between these two islands in a short period of time, different characteristic prey items occurred in the stomach contents of SSLs at these two sites, frequently undigested (Figure 8A,C). Therefore, it would appear that in these areas SSLs were captured immediately after feeding, which probably indicates that these prey were specifically available at respective sites. The prey species may differ at these islands because of differences in the fish fauna; however, details in this regard are still not known. There is currently little knowledge of the distribution of sand lance around Rishiri and Rebun, although samples from Rishiri in February and March indicate that they occur in large numbers during the spawning season. In addition, there are areas referred to 'ikanago-ba' by local people, meaning 'sand lance colonial areas', around Rishiri. Therefore, it would appear that the sea surrounding Rishiri contains a large sand lance spawning ground and a large number of sand lance aggregate here during the spawning season. Sand lances have enlarged eggs and testes during this period, and therefore have a high nutritional value for SSLs. In contrast, there appears to be no similar spawning ground around Rebun, or if one is present, it is probably of a smaller scale.

As a pair, Otaru and Ofuyu showed the highest similarity index (0.52) among the 15 pairs of sampling areas. During the sampling season, herring migrate in large numbers to the coast of Ishikari Bay to spawn, thereby resulting in a higher degree of similarity. However, herring migration began to increase in 2009, before which SSLs ate different prey species (e.g., long shanny and octopuses). One the basis of these results, it appears that SSLs predate on different prey species within their migration area at the mesoscale (from 10 to 200 km), and therefore, the SSLs distributed along the Hokkaido coasts have a generally high dietary diversity.

Steller sea lions are believed to alter their foraging strategy and distribution in response to changes in the availability of prey (Sigler et al., 2009). In Alaska, studies of the feeding habits of SSLs and distribution of eulachon, or herring, have shown a positive relationship between SSL abundance and the availability of these forage fishes (Womble & Sigler, 2006; Womble, Willson, Sigler, Kelly, & Van Blaricom, 2005). Although there are insufficient data regarding the movement of SSLs between areas around the Hokkaido coast during winter, they may move to Ishikari Bay off Hokkaido with a change in the centralized distribution of herring. Furthermore, it is believed that SSLs move to areas where other fish are abundant to meet their high energy requirements, and this warrants further study. However, we believe that the Hokkaido coast has high prey species diversity and that this has had a positive effect in terms of population increases of SSLs at Russian rookeries in recent years.

4.4 | Interactions with fisheries

In the Hokkaido coastal area, some of the prey species of SSLs are also fish targeted by the fishing industry, creating a potentially competitive relationship. For example, attacks and predation on fishing nets by SSLs have been reported (Isono et al., 2013). The FO of fishing net remnants in stomach contents in this study indicates that SSLs forage directly from fishing nets. In recent years, a reduction in the numbers of major prey species has led to an increase in predation on alternative species such as black-edged sculpin by SSLs. Furthermore, foraging from fishing nets by SSLs can also be considered as a tactic to efficiently utilize scarce prey. Competition between fisheries and SSLs over resources may be intensified with a continued overall downward trend in fish availability.

5 | CONCLUSIONS

Overall, the prey of SSLs in waters off Hokkaido were diverse and the dominant prey species differed among different areas. Furthermore, SSLs switched between main prey species depending upon availability. In addition to the decline of gadid stocks, the variability of stocks of Okhotsk Atka mackerel and herring in recent years (Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 2017c; Hoshino et al., 2010) has also probably affected availability of prey for SSLs. Therefore, it is necessary to continue to observe the population dynamics of the current main prey species, such as Okhotsk Atka mackerel and herring.

From the results of the RDA and PERMANOVAs indicated significant differences in the sampling areas, differences in the ontogenetic stage of SSLs were detected. In this latter regard, it is believed that the group composition on age and sex of SSLs in Hokkaido is not uniform (Hoshino et al., 2006; Itoo et al., 1977b). Further, the results of the RDA show that SSLs collected in the northern region of the Sea of Japan were younger than those collected in the central region, which may explain the observed regional differences in the diets of SSLs. Further monitoring of the diet of SSLs in the future will enable us to shed more light on these issues.

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APPENDIX

TABLE A1 Frequency of occurrence (FO%) and percentage composition by weight (W%) of prey species based on actual weight in Steller sea lion stomachs collected from the coast of Hokkaido, Japan, during the 1994–1998 and 2005–2012 survey periods. Data were pooled across years and months

	Sampling year	1990s					
	Area	Rausu		Shakotan		Rebun	
	n	119		19		24	
	Empty stomach	12		3		2	
Prey item		FO%	W%	FO%	W%	FO%	W%
Mottled skate	*Raja pulchra*						
Unidentified skate	Rajidae					4.5	23.1
Unidentified cartilaginous fishes	Chondrichthyes						
Herring	*Clupea pallasii*						
Japanese anchovy	*Engraulis japonicus*						
Japanese surf smelt*	*Hypomesus japonicus*	6.3	0.5				
Unidentified smelt	*Osmeridae* spp.						
Salmon	*Salmonidae* spp.	4.5	0.2				
Pacific cod	*Gadus macrocephalus*	73.0	20.9	60.0	10.9	36.4	36.1
Walleye pollock	*Gadus chalcogramma*	84.7	61.9	66.7	71.6	36.4	17.3
Saffron cod	*Eleginus gracilis*	25.2	2.4				
Unidentified cod	*Gaddidae* spp.						
Yellow goosefish	*Lophius litulon*						
Flathead mullet	*Mugil chephalus*						
Yellow body rockfish*	*Sebastes steindachneri*						
White-edged rockfish*	*Sebastes taczanowskii*						
Fox jacopever	*Sebastes vulpes*						
Korean rockfish	*Sebastes schlegeli*						
Three-stripe rockfish*	*Sebastes trivittatus*						
Unidentified rockfish	*Sabastes* spp.						
Okhotsk atka mackerel	*Pleurogrammus azonus*	4.5	0.6	53.3	3.7	9.1	1.4
Fat greenling	*Hexagrammos otakii*						
Unidentified greenlings	*Hexagrammos* spp.						
Sea raven	*Hemitripterus villosus*						
Antlered sculpin	*Enophrys diceraus*						
Unidentified scorpionfishes	*Myoxocephalus* spp.						
Plain sculpin	*Myoxocephalus jaok*						
Elkhorn sculpin*	*Alcichthys elongatus*						
Black edged sculpin*	*Gymnocanthus herzensteini*	1.8	0.1	13.3	0.2	4.5	0.4
Unidentified sculpin	*Cottidae* spp.	0.9	0.0	26.7	0.3	13.6	3.6
Smoothcheek sculpin	*Eurymen gyrinus*						
Spinyhead sculpin	*Dasycottus setiger*						
Unidentified fathead sculpins	*Psychrilutidae* spp.						
Smooth lumpsucker	*Aptocyclus ventricosus*	0.9	0.0			13.6	7.9
Unidentified lumpfish	*Cyclopteridae* sp.						
Unidentified eelpout	*Zoarcidae* sp.						
Long shanny*	*Stichaeus grigorjewi*						

2000s											
Rausu		Shakotan		Otaru		Ofuyu		Rishiri		Rebun	
55		62		19		14		48		48	
4		0		0		1		1		4	
FO%	W%	FO%	W%	FO%	W%	FO%	W%	FO%	W%	FO%	W%
		1.6	0.5								
2.0	0.4										
								2.1	0.0	2.3	0.0
				57.9	89.5	30.8	48.6	2.1	0.0		
11.8	1.2	4.8	0.1	5.3	0.0	23.1	30.0	2.1	0.0	4.5	1.9
2.0	0.0										
		1.6	0.0								
5.9	0.5	3.2	0.5	5.3	0.6	7.7	1.3				
52.9	7.4	32.3	18.2					10.4	2.6	45.5	47.5
78.4	52.6	12.9	0.7					8.3	0.0	20.5	0.2
25.5	2.2										
		1.6	0.0							2.3	0.0
		12.9	4.2								
13.7	12.1	3.2	0.2								
								2.1	0.0		
		3.2	0.1	5.3	0.4						
		1.6	3.3	5.3	0.1			2.1	0.0		
				5.3	0.0						
		1.6	0.3								
3.9	0.0	12.9	0.5	10.5	0.0			6.3	0.5	9.1	0.0
17.6	0.6	80.6	34.4	15.8	6.0	15.4	6.8	31.3	23.3	27.3	3.3
		1.6	0.4								
3.9	0.3	8.1	0.5	5.3	0.0	7.7	0.1	2.1	0.0	4.5	0.2
		3.2	0.4					2.1	0.0	2.3	0.1
3.9	0.0										
										4.5	0.0
								2.1	0.1		
								2.1	0.2		
17.6	4.3	9.7	0.4					31.3	1.5	27.3	5.6
5.9	0.0	6.5	0.0	5.3	0.0	7.7	0.0	12.5	0.1	11.4	0.0
								2.1	0.0		
		1.6	0.0								
		1.6	0.0							4.5	0.2
25.5	1.3	40.3	7.2					2.1	0.0	40.9	16.1
										2.3	0.0
2.0	1.4										
		3.2	0.0	15.8	0.0	23.1	7.7	6.3	0.2		

APPENDIX 1 (Continued)

	Sampling year	1990s					
	Area	Rausu		Shakotan		Rebun	
	n	119		19		24	
	Empty stomach	12		3		2	
Prey item		FO%	W%	FO%	W%	FO%	W%
Dybowsky's gunnel*	*Pholidapus dybowskii*						
Unidentified prickleback*	*Stichaeidae* spp.						
Japanese sand lance	Ammodytidae spp.						
Bastard halibut	*Paralichthys olivaceus*					4.5	1.1
Scale-eye plaice	*Acanthopsetta nadeshnyi*						
Flathead flounder	*Hippoglossoides dubius*						
Pointhead flounder	*Cleisthenes pinetorum*	9.0	1.5				
Dusky sole	*Lepidpsetta mochigarei*	4.5	0.1				
Sand flounder	*Limanda punctatissimus*						
Yellow striped flounder	*Pseudopleuronectes herzensteini*						
Cresthead flounder	*Pseudopleuronectes schrenki*						
Black plaice*	*Pseudopleuronectes obscurus*						
Starry flounder	*Platichthys stellatus*						
Stone flounder	*Kareius bicoloratus*						
Blackfin flounder	*Glyptocephalus stelleri*						
Unidentified flatfishes	Pleuronectidae spp.	19.8	1.5	53.3	0.9	18.2	3.2
Unidentified pufferfish	*Tetraodontidae* sp.						
Unidentified fishes		24.3	1.2	33.3	1.2	22.7	0.4
Bobtail squid	*Sepiolinae* sp.						
Spear squid	*Heterololigo bleekeri*						
Japanese dwarf squid*	*Loliolus japonica*						
Sparkling enope squid	*Watasenia scintillans*	5.4	0.4				
Firefly squid	*Onychoteuthis borealijaponica*	8.1	0.3	6.7	0.0	9.1	0.1
Magister armhook squid	*Berryteuthis magister*	42.3	5.6				
Boreopacific gonate squid*	*Gonatopsis borealis*	17.1	2.4				
Clawed armhook squid	*Gonatus onyx*	0.9	0.0				
Shortarm gonate squid*	*Gonatus middendorffi*	0.9	0.1				
Armhook squid*	*Gonatus berryi*	1.8	0.1				
Unidentified armhook squid	*Gonatidae* spp.			6.7	0.0		
Japanese flying squid	*Todarodes pacificus*						
Neon flying squid	*Ommastrephes bartramii*						
Unidentified squids		7.2	0.1	13.3	0.1		
Giant Pacific octopus	*Enteroctopus dofleini*						
Chestnut octopus*	*Octopus conispadiceus*						
Octopus	*Octopodidae* spp.	12.6	0.1	73.3	11.1	40.9	5.3
Unidentified cephalopods							
Unidentified crustaceans		0.9	0.0	6.7	0.0		
Unidentified ribbon worm							
Unidentified mammals and birds							
Milk-like fluid							

*Species that has only a local name in Japan. There are no description in the FishBase (http://fishbase.org/search.php).

2000s											
Rausu		Shakotan		Otaru		Ofuyu		Rishiri		Rebun	
55		62		19		14		48		48	
4		0		0		1		1		4	
FO%	W%	FO%	W%	FO%	W%	FO%	W%	FO%	W%	FO%	W%
								2.1	0.0	6.8	0.2
9.8	0.0	50.0	2.6	10.5	0.0	7.7	0.0	91.7	57.5	25.0	5.5
		1.6	1.4								
		1.6	0.1								
9.8	0.0	4.8	0.1	5.3	0.0	7.7	0.0	8.3	0.1	22.7	12.1
17.6	4.1	6.5	0.2					2.1	0.1	2.3	0.2
9.8	0.6	1.6	0.0	5.3	0.0					2.3	0.2
5.9	0.0	1.6	0.0								
11.8	0.4	17.7	0.5	5.3	0.0	7.7	0.1	20.8	1.0	9.1	0.4
2.0	0.0	6.5	3.3	10.5	0.2			2.1	0.0		
2.0	0.0										
								4.2	0.0		
2.0	0.0	3.2	0.0								
7.8	0.3	6.5	0.7	5.3	0.0			4.2	0.0	2.3	0.0
15.7	0.9	14.5	0.2	10.5	0.0	30.8	2.0	10.4	0.1	11.4	0.0
		1.6	0.0								
31.4	1.1	24.2	0.3	15.8	0.0	53.8	1.0	16.7	0.2	20.5	0.0
						7.7	0.2			2.3	0.0
		25.8	0.9	15.8	0.6	15.4	0.1				
						7.7	0.2				
2.0	0.0										
80.4	1.4									4.5	0.0
2.0	0.0										
2.0	0.0	1.6	0.0							11.4	0.0
										9.1	4.3
2.0	0.2									11.4	0.0
3.9	0.0	3.2	0.0			7.7	0.0	2.1	0.0	6.8	0.0
5.9	0.1	8.1	2.1	15.8	0.1			14.6	0.0	11.4	0.2
		1.6	0.9							2.3	0.0
17.6	6.7	67.7	14.9	36.8	2.5	61.5	1.7	43.8	12.4	50.0	1.4
		1.6	0.0								
3.9	0.0			5.3	0.0					6.8	0.0
2.0	0.0										
								4.2	0.0	2.3	0.0
										4.5	0.1

TABLE A2

Prey species	Sampling year	Area	Measurement	N. of inds. ingested	Mean	SD	Body length (cm) of SSL	Sex
Japanese sand lance	'04/05	Rishiri	SL	68	230 mm	17.8	213	F
	'05/'06	Rishiri	SL	15	246 mm	15.2	205	F
	'05/'06	Rishiri	SL	11	216 mm	33.0	225	F
	'07/'08	Rishiri	SL	95	212 mm	28.1	245	F
	'08/'09	Rishiri	SL	36	230 mm	16.4	280	F
	'09/'10	Rishiri	SL	15	236 mm	12.8	263	F
	'10/'11	Rishiri	SL	3	237 mm	21.1	270	F
	'10/11	Rishiri	SL	60	228 mm	21.1	230	F
	'10/11	Rishiri	SL	8	208 mm	24.8	270	F
Okhotsk Atka Mackerel	'05/'06	Shakotan	SL	6	267 mm	20.7	273	M
	'06/'07	Rishiri	SL	14	271 mm	20.7	215	F
	'07/'08	Shakotan	SL	1	264 mm		240	M
	'07/'08	Shakotan	SL	8	269 mm	15.3	215	M
Smooth lumpsucker	'09/'10	Rebun	SL	3	183 mm	12.1	208	F
	'10/11	Rebun	SL	8	173 mm	12.6	240	F
Japanese anchovy	'11/12	Rebun	SCL	92	135 mm	4.0	220	F
Pacific cod	'09/'10	Shakotan	FL	2	692 mm	58.7	240	M
Fox jacopever	'10/'11	Shakotan	SL	3	227 mm	8.1	198	F
Black edged sculpin	'06/'07	Rishiri	SL	1	173 mm		215	F
Elkhorn sculpin	'07/'08	Rishiri	SL	1	190 mm		245	F
Yellow striped flounder	'05/'06	Rishiri	SL	1	212 mm		230	F
Cresthead flounder	'09/'10	Shakotan	SL	13	230 mm	27.0	240	M
Japanese flying squid	'11/'12	Rebun	ML	19	209 mm	22.1	220	F
Chestnut octopus	'04/'05	Shakotan	BW	1	1,804 g		209	M
North Pacific giant octopus	'04/'05	Shakotan	BW	3	569 g	157.9	n.d.	M
	'05/'06	Shakotan	BW	1	634 g		288	M
	'05/'06	Shakotan	BW	1	1,828 g		300	M
	'05/'06	Shakotan	BW	4	1,430 g	1,082.9	253	M
	'05/'06	Shakotan	BW	1	651 g		218	F
	'05/'06	Shakotan	BW	1	869 g		232	M
	'05/'06	Shakotan	BW	1	4,370 g		205	F
	'06/'07	Shakotan	BW	1	1,162 g		225	F
	'06/'07	Shakotan	BW	1	2,729 g		220	M
	'07/'08	Shakotan	BW	1	395 g		258	M
	'07/'08	Shakotan	BW	1	5,334 g		240	M
	'07/'08	Shakotan	BW	4	1,150 g	1,032.2	245	F
	'09/'10	Shakotan	BW	1	694 g		190	F
	'11/'12	Shakotan	BW	1	1,598 g		230	F

SL, standard length; SCL, scale length; ML, mantle length; BW, body weight; N. of inds. Ingested, number of individuals ingested by SSL; n.d., no data.