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1 **Intraspecific differences in the diet of Kuril harbor seals (*Phoca vitulina stejnegeri*) in Erimo, Hokkaido, using**

2 **DNA barcoding diet analysis**

3

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17

18 **Abstract**

19 Competition between Kuril harbor seals (*Phoca vitulina stejnegeri*) and salmon set-net fishing industries has become a
20 serious problem with the recent increase in the number of seals in Erimo, Hokkaido, Japan. We aimed to understand the
21 detailed dietary structure of Kuril harbor seals focusing on intraspecific differences and verify whether “problem seals”
22 who habitually use salmon set-nets could be characterized by intrinsic factors such as sex and maturity. We estimated the
23 diet of Kuril harbor seals in two fishing seasons using DNA barcoding diet analysis on colon contents and verified
24 intraspecific differences in their diet. In spring, their diets showed different tendencies between maturity stage; each adult
25 seal fed on different prey items, suggesting that they avoid the intra-species competition over food during the breeding
26 season. Additionally, it was implied that some adult females habitually stole from salmon set-nets. Our dietary analysis
27 showed dietary changes of Kuril harbor seals with different tendencies depending on maturity or sex, suggesting that
28 problem individuals who habitually use set-nets can be characterized by intrinsic factors. This detailed dietary information
29 can offer an accurate assessment of seal predation effects on fishing targets and the selective management of Kuril harbor
30 seals, especially in mitigating seal–commercial fishery conflicts.

31

32 **Keywords:** mitochondrial COI, NGS, food habit, seal-fishery conflict

33

34 **Introduction**

35 Competition between pinnipeds and coastal fisheries occurs in various places worldwide (e.g. Yodzis 1998; Lance et al.
36 2012). Fishing grounds in shallow areas could be easy foraging sites for pinnipeds who can learn to steal fish from fishing
37 gear such as set-nets, gillnets, and longlines. In coastal areas where pinnipeds reside throughout the year, such conflicts
38 cause more serious problems, as is the case in Hokkaido, Japan.

39 Kuril harbor seals (*Phoca vitulina stejnegeri*) are the only year-round resident pinniped in Japan. They are distributed
40 on the eastern coastline of Hokkaido, Japan (Shaughnessy and Fay 2009; Kobayashi et al. 2014), and Cape Erimo is their
41 largest haul-out site (Fig. 1). They show a high level of philopatry and use the same rocky shore throughout the year. The
42 competition between the seals and coastal fisheries has recently become a serious problem due to the increase in seal
43 numbers in Erimo. The most part of damage to the fishery is damage to catches of salmon set net such as biting off the
44 head, abdomen and other parts of the salmon (Fig. 2), which results in economic loss as the damaged catch becomes
45 worthless as a commodity. Salmon set-net fishing operates twice a year in spring (May to early July) and fall (September
46 to early November) in Erimo. Although depredation by seals is observed in both seasons, the scale of the fishery and the
47 damage are greater in the fall. The economic impact of seal depredation on salmon in set-net fishing is especially prominent
48 (Hokkaido Government 2015). Previous study has suggested that most seals do not tamper with fishing gear; generally,
49 individual “problem seals” cause most of the damage to salmon set-net fishing (Masubuchi et al. 2017). However, it is
50 challenging to verify this hypothesis and characterize these individuals because the available information on their diets has
51 been limited.

52 Diet estimations on Kuril harbor seals in this area have mainly been conducted through stomach content analysis (the

53 Ministry of Environment, Japan 2017). However, this analytical method is likely to yield inaccurate results because prey
54 species identification from undigested hard parts (e.g., fish otoliths or bones and cephalopod beaks) is highly biased due
55 to rapid and differential prey digestion (Bowen 2000). Salmon otoliths are smaller and easier to digest than otoliths of other
56 fish; therefore, few of them remain in the stomach as undigested substances (Jobling and Breiby 1986; Boyle et al. 1990).
57 Additionally, Kuril harbor seals do not swallow salmon whole, but they bite parts of the salmon body (Fig. 2). Therefore,
58 in most cases, salmon otoliths are rarely ingested by seals even if seals eat salmon. Previous studies note that salmonids
59 were rarely detected as undigested substances even though the stomach samples were collected from seals caught by salmon
60 set-nets as bycatch (the Ministry of Environment, Japan 2017).

61 In order to deal with this problem, we used DNA barcoding analysis to accurately identify prey organisms. DNA
62 barcoding (Herbert and Gregory, 2005) is a powerful tool to analyze the community structure of a sample containing
63 various intermingled organisms (e.g. Deagle et al., 2009; Tollit et al., 2009). Organisms are identified on the basis of short
64 base sequences in particular gene regions, called the “DNA barcode,” reflecting differences between species. With this
65 technique, researchers can detect and identify prey organisms with high accuracy via amplicon sequencing on prey-derived
66 DNA in predator feces. Prior to this study, Hui et al. (2017) showed that DNA barcoding techniques are more accurate than
67 hard parts techniques in detecting salmonids in fecal samples. Therefore, we reassessed the diet of Kuril harbor seals using
68 DNA barcoding analysis.

69 We also verified intraspecific differences in the diet of the Kuril harbor seals. Some researchers indicated that harbor
70 seal food habits varied depending on age and sex (e.g. Lewis et al. 2006; Beck et al. 2007). Such variation in diet could be
71 due to foraging ability, prey preference, or both (Smith and Metcalfe 1997; Bundy et al. 2000). Differences in energy

72 demands based on sexual body size dimorphism or breeding costs might also influence prey preference (Beck et al. 2003;
73 Breed et al. 2006). If such intraspecific differences in food habits occur in Kuril harbor seals in Erimo, we might be able
74 to characterize the sex and maturity of the specific individuals damaging the salmon set-nets. Therefore, we compared their
75 diet with intrinsic factors (e.g., sex and maturity) in each fishing season.

76

77 **Materials and methods**

78 *Field sampling*

79 We collected dietary samples from Kuril harbor seals that were caught by the salmon set-nets as bycatch during the
80 spring (late May to early July) and fall (late August to early November) fishing seasons in 2014–2017 in Erimo, Hokkaido,
81 Japan. We also collected samples from seals caught by seal trap nets in the spring of 2017 under the Erimo Area Kuril
82 Harbor Seal Specified Rare Wildlife Management Plan (Ministry of Environment, Japan 2018). In order to trap seals, we
83 used salmon set-net with grid nets at the entrance of a bag net. These grids are 20 cm on a side, allowing salmon to pass
84 through, but not seals. However, in one place, one square is 60 cm or 80 cm long, and a funnel-shaped net is attached so
85 that if a seal enters it, it cannot get out (Ministry of Environment, Japan 2017). Bodyweight was measured, and sex was
86 recorded. Age was determined based on a count of cementum growth layers (Mansfield and Fisher, 1960) of the seals'
87 upper right canine teeth after sectioning 10–16 μm and staining by Delafield's hematoxylin (Kobayashi et al. unpublished).
88 Kuril harbor seals undergo secondary growth at age 4–5 years, and almost all individuals start breeding at age 5 (Suzuki
89 and Yamashita 1986). Thus, we classified their maturity into three levels: pups (age 0), juveniles (age 1–4), and adults (age
90 ≥ 5).

91 Samples for dietary analysis were collected as the contents of approximately 15 cm of the colon, which was removed
92 from the anal side of each harbor seal (hereafter called “feces”). The colon samples were collected from dead seals within
93 12 hours of death and kept in a freezer (−20°C) until they were used for analysis. Feces were taken from the colon sample
94 and mixed well; then 0.15–0.43 g soft feces component (i.e., without the undigested hard parts) was used for DNA
95 barcoding diet analysis.

96

97 *DNA barcoding diet analysis*

98 DNA extraction from feces was conducted using the QIAamp DNA Stool Mini Kit (QIAGEN Inc.). All steps followed
99 the “Isolation of DNA from Stool for Human DNA Analysis” protocol recommended by the manufacturer (QIAamp DNA
100 Stool Handbook, June 2012) with slight modification (i.e., the amount of Buffer AE for DNA elution at the last step was
101 set to 100 µL). The concentration of each extracted DNA sample was measured and adjusted to 10 ng/µL (hereafter, these
102 samples are called “template DNA”).

103 Mitochondrial COI was chosen as the barcoding region for prey species identification (Hebert et al. 2003), because Kuril
104 harbor seals are thought to prey on various animals such as fish, cephalopods, and crustaceans. We prepared an amplicon
105 library for next-generation sequencing using the two-step tailed PCR method. In step 1, amplification of the target region
106 was performed with a combination of the forward primer *ml intF* (5'-ACA CTC TTT CCC TAC ACG ACG CTC TTC
107 CGA TCT GGW ACW GGW TGA ACW GTW TAY CCY CC-3') (Leray et al. 2013) and the reverse primer *HCOm* (5'-
108 GTG ACT GGA GTT CAG ACG TGT GCT CTT CCG ATC TTA HAC TTC NGG GTG KCC RAA RAA TCA-3') which
109 was modified from the universal primer HCO 2198 for the COI region (Folmer et al. 1994). Using these primer sets, 360 bp

110 in latter half of the region amplified by the universal primers for COI region was amplified. Blocking primer (5'-TAT CCT
111 CCC CTA GCT GGG AAC CTG GCT CAT GCA GGA-3') was also used to suppress the amplification of host-derived
112 DNA. The 20- μ L first PCR amplification reaction contained 1 ng of template DNA, 0.05 U of ExTaq polymerase (TaKaRa
113 Bio Inc.), 1 \times PCR buffer, 0.2 mM dNTP, 0.5 μ M of each COI primer, and 4.0 μ M of blocking primer. The thermal cycling
114 conditions were as follows: an initial denaturation of 94°C for 2 min followed by 35 cycles of 96°C for 30 s, 67°C for 15 s,
115 52°C for 30 s, and 72°C for 30 s, and a final cycle of 72°C for 5 min. The first PCR products were examined by 2% agarose
116 gel electrophoresis. After the amplification was confirmed, we measured the amount of the first PCR products and purified
117 it by adding the same amount of AMPure XP (Beckman Coulter, Inc.). The first PCR products were purified using the same
118 amount of AMPure XP (Beckman Coulter, Inc.). In step 2, the 20- μ L second PCR amplification reaction contained 1 ng of
119 the purified first PCR products, 0.05 U of ExTaq polymerase (TaKaRa Bio Inc.), 1 \times PCR buffer, 0.2 mM dNTP, and
120 1.0 μ M of each tailed primer (second forward primer: 5'-AAT GAT ACG GCG ACC ACC GAG ATC TAC AC- Index2 -
121 ACA CTC TTT CCC TAC ACG ACG-3' and second reverse primer: 5'-CAA GCA GAA GAC GGC ATA CGA GAT-
122 Index1 -GTG ACT GGA GTT CAG ACG TGT G-3'). The thermal cycling conditions were as follows: an initial
123 denaturation of 94°C for 2 min followed by 12 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 30 s, and a final cycle
124 of 72°C for 5 min. The second PCR products were examined by 2% agarose gel electrophoresis. After the amplification
125 was confirmed, we measured the amount of the second PCR products and purified it by adding the same amount of AMPure
126 XP (Beckman Coulter, Inc.). We measured the amplicon library concentration and checked the quality using the Fragment
127 Analyzer system (Advanced Analytical Technologies Inc.).

128 The DNA samples were paired-end sequenced (2 \times 250 bp) on a MiSeq platform (Illumina, Inc.) at the the

129 Bioengineering Lab. Co., Ltd., Kanagawa, Japan. Quality filtering of the reads was performed using `fastq_barcode_splitter`
130 in the FASTX-Toolkit version 0.0.14 (http://hannonlab.cshl.edu/fastx_toolkit/). The reads in which the beginning of the
131 sequence exactly matched the used primer sequences were selected, and the used primer sequences were trimmed from the
132 reads. After that, the sequences with quality values less than 20 or with lengths of less than 40 bases were discarded using
133 `sickle` tools version 1.33 (Joshi and Fass, 2011; <http://gensoft.pasteur.fr/docs/sickle/1.33>). The paired-end merge script
134 `FLASH` version 1.2.11 (Magoč and Salzberg, 2011; <http://gensoft.pasteur.fr/docs/FLASH/1.2.11>) was used to merge the
135 sequences that passed the quality filtering. The merging conditions were: merged fragment length 320 bases, read fragment
136 length 230 bases, and minimum overlap length 10 bases. The sequences were assigned to operational taxonomic units
137 (OTUs) using the commands `fastx_uniques`, `sortbysize`, `cluster_otus`, and `usearch_global` in the USEARCH version
138 8.1.1861 (Edgar, 2010; <http://www.drive5.com/usearch/manual8.1/>) under the condition of 97 sequence homology, and a
139 BLAST search for each OTU sequence was performed against the full NCBI nucleotide (nt) database for prey species
140 identification.

141 The obtained OTU with BLASTN E-value $> 1e-20$ or Identity $< 90\%$ were treated as errors following Deagle et al. (2013),
142 OTUs with a read count < 10 were customarily treated as contamination, and these OTUs were excluded from subset
143 analysis. Fishes (Actinopterygii), cephalopods (Cephalopoda) and crustaceans (Decapoda) were considered to be seal prey
144 organisms based on previous knowledge (the Ministry of Environment, Japan 2017; Hui et al. 2017). Data about the prey
145 species were treated as occurrence data, and it was noted whether the prey organisms were detected (1) or not detected (0)
146 in the fecal sample.

147

148 **Statistical analysis**

149 Samples were grouped by season (spring and fall), sex, maturity (pup, juvenile, and adult), seal catch type (bycatch and
150 capture), and the combination of those categories (season × sex, season × maturity, sex × maturity, sex × catch type, and
151 maturity × catch type). The percent frequency of occurrence (hereafter referred to as “FO”) of certain prey items was
152 calculated in the respective diet groups:

153

154
$$FO_{Ai} = \frac{n_{Ai}}{n_A}$$

155

156 where n_A is the number of samples in which at least one prey species is detected and n_{Ai} is the number of samples in
157 which the prey item i is detected in group A.

158 The relative FO (hereafter referred to as “RFO”) and the Shannon–Wiener diversity index (hereafter referred to as “H’”) (Newton-Fisher, 1999) were calculated to assess prey composition in the respective diet groups:

160

161
$$RFO_{Ai} = \frac{n_{Ai}}{\sum_i^s n_{Ai}}$$

162
$$H'_A = \left(- \sum_i^s RFO_{Ai} \cdot \log RFO_{Ai} \right)$$

163

164 where s is the total number of prey items in group A. Higher values of H' indicate the increased number of prey species
165 and the prey’s homogeneity coefficient.

166 To verify which factors (“season,” “sex,” “maturity,” and “catch type”) affect the seals’ diet structure, the prey

167 composition of each group were compared using permutational multivariate ANOVA (PERMANOVA) based on Horn's
168 dissimilarity index ($1-C_H$) (Anderson 2001; Doi and Okamura 2011). The Horn index (hereafter referred to as " C_H "), which
169 indicates the similarities of prey composition between groups, was calculated following Krebs (1999):

170

$$C_H = \frac{2 \sum_i^s RFO_{Ai} \cdot RFO_{Bi}}{(\sum_i^s RFO_{Ai}^2) + (\sum_i^s RFO_{Bi}^2)}$$

171

172

173 This statistical analysis was conducted using the "adonis" function in the *vegan* package (Okasen et al. 2017) in R
174 ver.3.3.3 (R Core Team, 2017).

175 Additionally, the Jaccard similarity coefficient (hereafter referred to as " J ") (Jaccard 1908) was calculated as an indicator
176 of inter-individual overlap of preys:

177

$$J'(x, y) = \frac{S_{xy}}{S_x + S_y - S_{xy}}$$

178

179

180 where S_x and S_y are the total numbers of prey species detected from seal x and seal y , respectively. S_{xy} is the number of
181 prey commonly detected in both seals.

182

183 **Results**

184 *Prey items*

185 Sixty-eight fecal samples were collected in our study (Table 1). Seven samples of the total 68 samples were not carried
186 out for sequencing analysis because amplification of the target product was not confirmed. The sequencing of total 61 fecal
187 samples remained after quality filtering yielded 3,243,915 reads in total and 14,787-124,826 reads per sample. Prey
188 organisms were detected in 53 fecal samples. The average number of detected prey species per sample was 2.5 ± 0.2
189 (average \pm standard error, range: 0–8). We identified 19 fish species, 5 cephalopod species, and 1 crustaceans (Table 2).
190 The number of prey species with more than 5% FO was 9; these species included the North Pacific giant octopus
191 (*Enteroctopus dofleini*, FO = 90.6%), the Japanese common squid (*Todarodes pacificus*, FO = 47.2%), the Okhotsk atka
192 mackerel (*Pleurogrammus azonus*, FO = 37.7%), the chestnut octopus (*Octopus conispadiceus*, FO = 13.2%), the black
193 plaice (*Pseudopleuronectes obscurus*, FO = 13.2%), a small type of shrimp (*Crangon spp.*, FO = 11.3%), the masu salmon
194 (*Oncorhynchus masou*, FO = 9.4%), the rock greenling (*Hexagrammos lagocephalus*, FO = 7.5%), and the Japanese dace
195 (*Tribolodon hakonensis*, FO = 5.7%). Salmonids were only detected in six adult seals caught by seal trap nets in spring
196 2017: five females and one male.

197

198 *Seasonal and intraspecific differences in the diet structure*

199 Fourteen species from 10 families and 7 orders were detected in fall (the prey diversity; $H' = 2.16$), and 20 species from
200 10 families and 9 orders were detected in spring ($H' = 2.35$). The inter-individual prey overlap (J') was significantly higher
201 in spring ($J' = 0.72 \pm 0.23$ SD) than in fall ($J' = 0.62 \pm 0.18$ SD) (t -test: $t_{784} = -4.34$, $P < 0.01$) (Table 3).

202 The results of testing each factor's effects ("season," "maturity," "sex," and "catch type") on prey composition using
203 PERMANOVA were shown in Table 4. Prey compositions showed the differences between "season" in the adult group.

204 Additionally, it was indicated that the factors caused intraspecific differences in the diet to vary with each season.

205 In spring, prey composition differed depending on “maturity” and “catch type” but not “sex” (Fig. 3 and Table 4). Prey
206 diversity was highest in the adult group ($H' = 2.24$) and lowest in the pup group ($H' = 1.80$). The inter-individual prey
207 overlap of the adult group ($J' = 0.83 \pm 0.20$ SD) was significantly higher than that of the juvenile group
208 ($J' = 0.64 \pm 0.21$ SD) and the pup group ($J' = 0.57 \pm 0.23$ SD) (Tukey test: $P < 0.01$). The *RFO* of each prey item showed
209 similar composition between the pup group and the juvenile group; octopuses, squids, crustaceans, and greenlings
210 accounted for 80% of their diet. The adult group’s diet showed different tendencies; salmon occurred at a high frequency
211 ($RFO = 21.4\%$) in addition to the aforementioned prey items (Fig. 5).

212 In fall, the prey compositions did not differ significantly depending on “sex” and “maturity” (Fig. 4 and Table 4).

213 Octopuses, squids, greenlings, and flounders accounted for 80% of the fall diet.

214

215 **Discussion**

216 Despite the fact that all seals used in our dietary analysis were caught in salmon set-nets, the prey organism with the
217 highest *FO* was the North Pacific giant octopus, not Salmonids (Table 2). This result might correspond to the fact that
218 colon contents reflected the food record from 2.5 to 6 h ago (Markussen 1993). Considering that the average staying time
219 of the seals in the set-net is 24.1 ± 43.0 min (Masubuchi et al. 2017), the prey organisms detected in the colon contents
220 were eaten outside the salmon set-net, inside the salmon set-net during the last visit, or inside another salmon set-net. Since
221 bycatch of octopus in the salmon set-net is very rare, it is likely that most of seals preyed on the North Pacific giant octopus
222 outside the set-net and then entered the set-net.

223 Seasonal variation in the diet was not shown clearly in this study although it has been suggested in the previous studies
224 (e.g. Hui et al. 2017; Kobayashi unpublished). Our sample size was unbalanced between seasons, and may not be sufficient
225 to figure out the diets of harbor seals in the fall. As many researchers indicated, harbor seals are generally opportunistic
226 predators, and their food habits are influenced by the biomass and availability of prey, which changes spatially and
227 temporally in the ocean (Brown and Pierce 1998; Hall et al. 1998; Andersen et al. 2004). Since such an environmental
228 situation would be a major factor influencing the diet of Kuril harbor seals, conducting additional studies with larger sample
229 sizes to get a more accurate perspective of the fall diet is needed. On the other hand, no large population dynamics of
230 marine organisms affecting seal diets have been reported in the four years between 2014 and 2017, when the samples were
231 collected, therefore sampling bias between years is not expected to have a significant effect on the results.

232 Seasonal variation in the diet was significantly shown only in the adult group. The prey compositions of spring differed
233 depending on “maturity,” and the adult group’s diet was clearly different from that of the pup group and the juvenile group.
234 Spring, late May to early July, is the breeding season of Kuril harbor seals (Niizuma 1986). During the breeding season, it
235 is known that harbor seals, especially adults, stay near haul-out sites because they have a lek-type mating system (Boness
236 et al. 2006; Dietz et al. 2013). Despite their narrow home range, the prey diversity of the adult group was high, and inter-
237 individual prey overlap was low. This result might suggest that adults avoid competition over prey organisms during the
238 breeding season by consuming different prey items.

239 In fall, their diet did not differ depending on neither “maturity” nor “sex.” However, this result is likely due to the small
240 sample size used in this study, so it is premature to conclude that there is no variation in the fall diet. Higher specialization
241 in the fall diet of females has been reported in Salish Sea harbor seals (Voelker et al. 2020). Differences in diet were likely

242 because this species has different foraging strategies between males and females (Thompson et al. 1998; Wilson et al.
243 2014). Sexual and seasonal differences in harbor seal home range sizes are reported in Kattegat, Denmark (Dietz et al.,
244 2013), and Salish Sea (Peterson et al., 2012). In addition, females are more likely to perform deeper foraging dives because
245 of their high consumption of demersal fish (Wilson et al. 2014; Schwarz et al. 2018). Although the fall foraging behavior
246 of adult seals was not investigated in our study field, we propose further dietary analysis and to reveal whether their
247 foraging strategy differ depending on sex and maturity.

248 A clear difference in diet between seals caught as bycatch and seals captured intentionally in the seal trap nets was shown.
249 A noteworthy result is that salmonids were not detected in seals caught as bycatch; they were only detected in individuals
250 intentionally caught by seal trap nets in spring 2017. It might be difficult for seals to catch free-ranging salmon outside the
251 set-net because salmon are large and have high swimming capabilities. Therefore, the seals whose colon contents included
252 salmonids might eat salmon inside the salmon set-net and be captured by seal trap nets afterward. These suggest the
253 effectiveness of seal trap nets to selectively eliminate “problem seals” who repeatedly enter and leave salmon set-nets and
254 cause serious damage to the nets. On the other hand, individuals who enter the set-net for the first time or are unfamiliar
255 with stealing from the nets are caught as bycatch.

256 Selective wildlife management has been proposed as an effective way to mitigate human-wildlife conflicts (Swan et al.
257 2017). To reconcile conservation and the mitigation of fishery damage, it is important to aim for the selective removal of
258 “problem seals” rather than random culling for population adjustment. Some previous studies in other regions have shown
259 that male seals have higher rates of access to fishing nets or use of salmonids than female seals (e.g. Kauhala et al. 2015,
260 Schwarzs et al. 2018), however, our dietary analysis showed a different tendency. Although the number of samples of

261 salmon feeders is still insufficient to confirm the characteristics of problem seals, we indicated that some adult females
262 habitually eat salmon during spring. This result indicates that some adult females may be dependent on the catch of fishing
263 nets for the energy they need to give birth and breastfeeding, and they are more likely to be involved in the problem than
264 adult males, at least in spring. This may also suggest that the harbor seals in Cape Erimo are very accustomed to fishing
265 nets, considering that females are generally more cautious than males.

266 The identification of problem seals in fall, when fisheries damage is more serious than in spring, remains a future
267 issue. The samples used for the fall diet analysis might be not sufficiently comprehensive because no fall seal trap
268 nets were conducted during our study periods. Therefore, it is necessary to increase the sample size including seals
269 caught by seal trap nets in the fall and re-examine how intrinsic factors affect their feeding habits in the fall. Although
270 the DNA barcoding dietary analysis on colon contents showed high advantage in detecting the problem seals, this
271 dietary analytical method is not suitable for quantitative diet analysis. In order to assess the potential impact on prey
272 and fisheries, it is necessary to verify the extent to which the problem seals were actually dependent on salmonids.
273 For this purpose, a more detailed understanding of foraging ecology at the individual level is required through
274 behavioral analysis, fatty acid analysis, and stable isotope analysis.

275 Recommendations for future management are to minimize random culling based on bycatch as much as possible and to
276 base it on the characterization and selective removal of problem individuals. Researches should be conducted to determine
277 how effective it is to eliminate the problem individuals from the population. The high dietary diversity and low inter-
278 individual overlap of adult seals in the spring indicate that adults may avoid food competition in the spring. Therefore, it
279 should also be examined whether this is related to dependence on fishing nets, and studied whether the eliminate of problem

280 individuals results in their niches being quickly occupied by other individuals. Taking measures to mitigate the feeding
281 damage based on such scientific grounds will be important not only in Erimo, but also in all conflicts between pinnipeds
282 and coastal fisheries worldwide.

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290

291 **Author's contributions:** All authors contributed to the study conception and design. Material preparation, data collection
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299

300 **Data availability** The datasets generated during and/or analyzed during the current study are available from the
301 corresponding author on reasonable request.

302

303

304 **Compliance with ethical standards**

305 **Conflicts of interest:** The authors declare that the research was conducted in the absence of any commercial or financial
306 relationships that could be construed as a potential conflict of interest in the preparation of this article.

307 **Ethics approval** All harbor seal samples were collected as part of a project conducted by the Ministry of the Environment,
308 Japan, under the Erimo Area Kuril Harbor Seal Specified Rare Wildlife Management Plan.

309 **Consent for participate** All authors agreed to participate in this study and co-authorship.

310 **Consent for publication** All authors agreed with the content and that all gave explicit consent to submit.

311 **Code availability:** Not applicable

312

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435

Table 1 Sampling result. P = pup, J = juvenile, A = adult. The figures in parentheses indicate the number of samples in which the target region was not amplified or no prey was detected. *Total 25 samples from spring 2017 were collected from seals caught by seal trap nets, and all other samples from 2014 to 2016 were collected from seals caught as bycatch.

		Male			Female			Total
		P	J	A	P	J	A	
2014	Spring						1	1
2015	Spring	7	6		7	5	1	26
	Fall	1	3	5		2		11
2016	Fall		2	2	1			5
2017	Spring*		3 (3)	5 (4)	1 (1)	2 (2)	14 (5)	25 (15)
	Spring total	7	9 (3)	5 (4)	8 (1)	7 (2)	16 (5)	52 (15)
	Fall total	1	5	7	1	2		16
Total		8	11 (3)	12 (4)	9 (1)	9 (2)	16 (5)	68 (15)

Table 2. List of fishes, cephalopods, and crustaceans detected from feces using DNA metabarcoding analysis and classification of each taxonomic group. Species in bold-faced type had FO > 5% and were considered the dominant prey of the harbor seal population in Erimo.

Class	Order	Family	Group name	Species	Spring	Fall	FO		
Cephalopoda	Octopoda	Octopodidae	Octopuses	<i>Enteroctopus dofleini</i>	+	+	90.6		
				<i>Octopus conispadiceus</i>	+	+	13.2		
	Teuthida	Enoploteuthidae	Squids	<i>Watasenia scintillans</i>	-	+	3.8		
		Loliginidae		<i>Heterololigo bleekeri</i>	-	+	1.9		
		Ommastrephidae		<i>Todarodes pacificus</i>	+	+	47.2		
Malacostraca	Decapoda	-	Crustaceans	-	+	+	9.4		
		Crangonidae		<i>Crangon sp.</i>	+	+	11.3		
Actinopteri	Perciformes	Hexagrammidae	Greenlings	<i>Hexagrammos lagocephalus</i>	-	+	7.5		
				<i>Pleurogrammus azonus</i>	+	+	37.7		
		Cottidae	Sculpins	<i>Enophrys lucasi</i>	+	-	1.9		
				<i>Gymnocanthus galeatus</i>	+	-	1.9		
				<i>Hemilepidotus papilio</i>	+	-	1.9		
				<i>Myoxocephalus polyacanthocephalus</i>	+	-	1.9		
						<i>Triglops nybelini</i>	+	-	3.8
				Liparididae	Snailfishes	<i>Liparis bathyarticus</i>	-	+	3.8
				Trichodontidae	Sandfishes	<i>Arctoscopus japonicus</i>	+	-	1.9
		Pleuronectiformes	Pleuronectidae	Flounders	<i>Cleisthenes pinetorum</i>	+	-	3.8	
	<i>Pseudopleuronectes herzensteini</i>				-	+	1.9		
	<i>Pseudopleuronectes obscurus</i>				+	+	13.2		
	Salmoniformes	Salmonidae	Salmons	<i>Oncorhynchus keta</i>	+	-	1.9		
				<i>Oncorhynchus masou</i>	+	-	9.4		
<i>Oncorhynchus tshawytscha</i>				+	-	1.9			
Cypriniformes	Cyprinidae	Corps	<i>Tribolodon hakonensis</i>	+	-	5.7			
Gadiformes	Gadidae	Cods	<i>Eleginus gracilis</i>	-	+	1.9			
Uranoscopiformes	Ammodytidae	Sand lances	<i>Ammodytes hexapterus</i>	+	-	3.8			
Clupeiformes	Clupeidae	Herrings	<i>Sardinops melanostictus</i>	-	+	1.9			

Table 3 Number of samples (N), the number of samples in which at least one prey species was detected (n), the total number of detected prey species (s), the Shannon–Wiener index (H'), and the average Jaccard similarity index (J') \pm SD in each group.

Group	Spring							Fall							Total						
	N	n	s	H'	J'	\pm	SD	N	n	s	H'	J'	\pm	SD	N	n	s	H'	J'	\pm	SD
Pup	15	14	10	1.80	0.57	\pm	0.23	2	2	11	2.35	n/a			17	16	16	2.18	0.61	\pm	0.23
Juvenile	16	11	11	1.99	0.64	\pm	0.21	7	7	8	1.83	0.63	\pm	0.17	23	18	14	2.11	0.63	\pm	0.20
Adult	21	12	12	2.24	0.83	\pm	0.20	7	7	7	1.68	0.55	\pm	0.21	28	19	15	2.26	0.76	\pm	0.23
Male	21	14	10	1.79	0.57	\pm	0.22	13	13	12	2.05	0.62	\pm	0.17	34	27	15	2.04	0.60	\pm	0.20
Female	31	23	18	2.41	0.77	\pm	0.22	3	3	9	2.09	0.77	\pm	0.11	34	26	23	2.55	0.77	\pm	0.21
Bycatch	27	27	13	1.93	0.58	\pm	0.24	16	16	14	2.16	0.62	\pm	0.18	43	43	20	2.18	0.60	\pm	0.21
Capture	25	10	12	2.56	0.84	\pm	0.22	n/a	n/a	n/a	n/a	n/a			25	10	12	2.56	0.84	\pm	0.22
Total	52	37	19	2.28	0.70	\pm	0.24	16	16	14	2.16	0.62	\pm	0.18	68	53	26	2.39	0.68	\pm	0.23

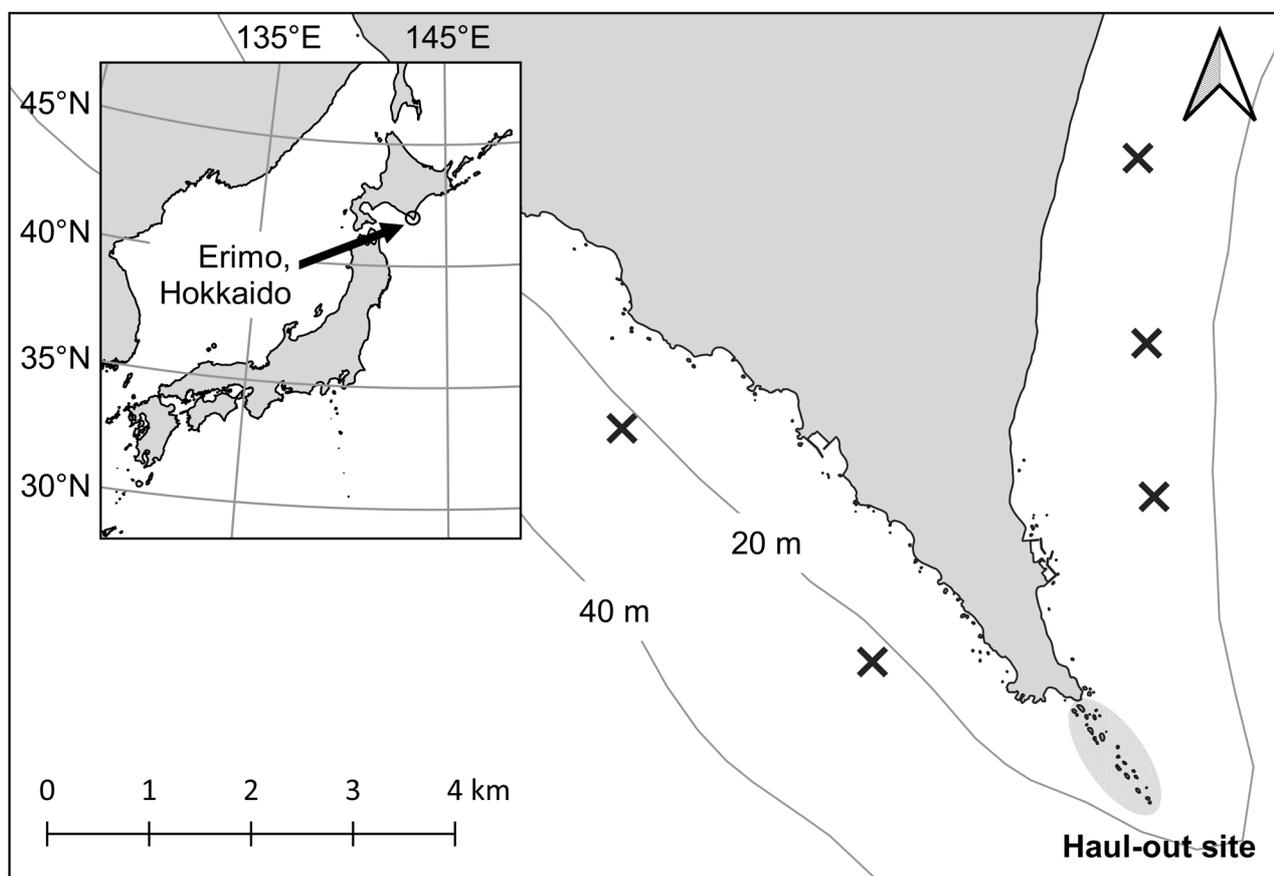
Table 4 Results of PERMANOVA. The prey compositions were compared between “season”, “sex”, “maturity”, and “catch type,” based on Horn’s dissimilarity index. Bold numbers indicate a significant difference ($P < 0.05$).

df = degree of freedom, *SS* = sum of squares, *MS* = mean of squares, *F* = F statistics, *P* = P-value.

Source	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>R</i> ²	<i>P</i>
Season	1	0.453	0.453	1.778	0.034	0.063
Sex	1	0.395	0.395	1.544	0.029	0.129
Maturity	2	0.794	0.397	1.571	0.059	0.059
Spring						
Sex	1	0.337	0.337	1.240	0.034	0.290
Maturity	2	1.143	0.572	2.232	0.116	0.008
Catch type	1	1.440	1.440	5.994	0.146	0.001
Fall						
Sex	1	0.079	0.079	0.362	0.025	0.931
Maturity	2	0.505	0.252	1.249	0.161	0.256
Male						
Season	1	0.242	0.242	1.235	0.047	0.287
Maturity	2	0.281	0.140	0.692	0.054	0.760
Catch type	1	0.315	0.315	1.631	0.061	0.061
Female						
Season	1	0.231	0.231	0.725	0.029	0.714
Maturity	2	1.011	0.506	1.691	0.128	0.026
Catch type	1	1.170	1.170	4.180	0.148	0.001
Pup						
Season	1	0.402	0.402	2.000	0.125	0.015
Sex	1	0.114	0.114	0.514	0.035	0.815
Juvenile						
Season	1	0.220	0.220	1.010	0.059	0.446
Sex	1	0.216	0.216	0.987	0.058	0.457
Adult						
Season	1	0.684	0.684	2.313	0.120	0.020
Sex	1	0.563	0.563	1.860	0.099	0.062
Catch type	1	1.178	1.178	4.417	0.206	0.001

441 **Figure**

442



443

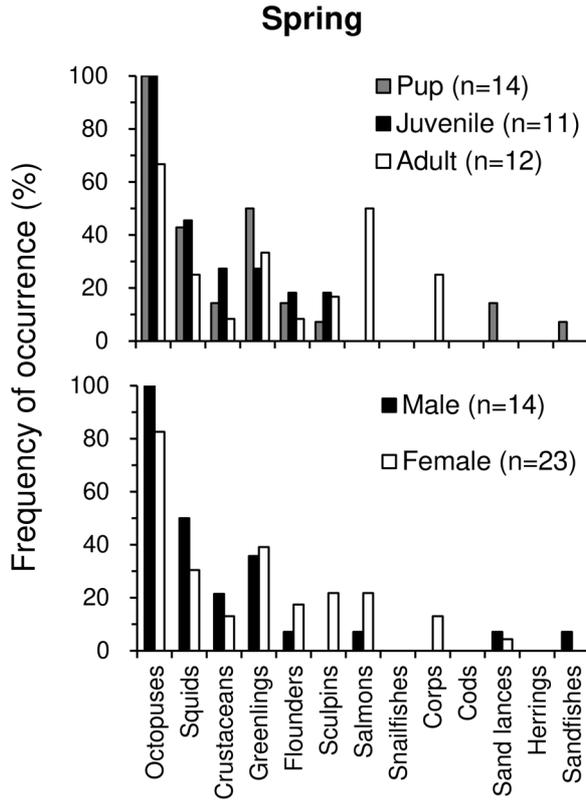
444 **Fig. 1** Map of Cape Erimo, Hokkaido, Japan. The rocky shore area (shaded in grey) is a Kuril harbor seal haul-out site;

445 cross marks indicate salmon set-net locations



446

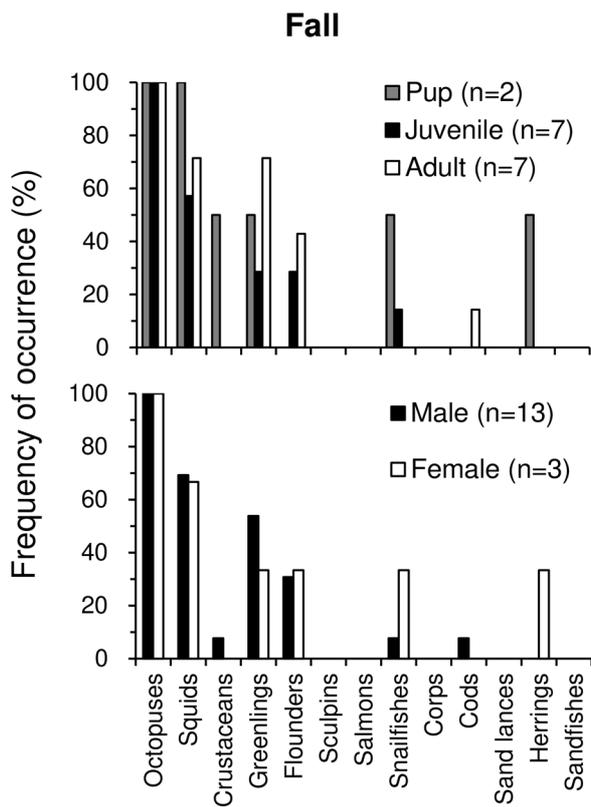
447 **Fig. 2** Photo of a chum salmon (*Oncorhynchus keta*) that was caught by the set-net and bitten by Kuril harbor seals



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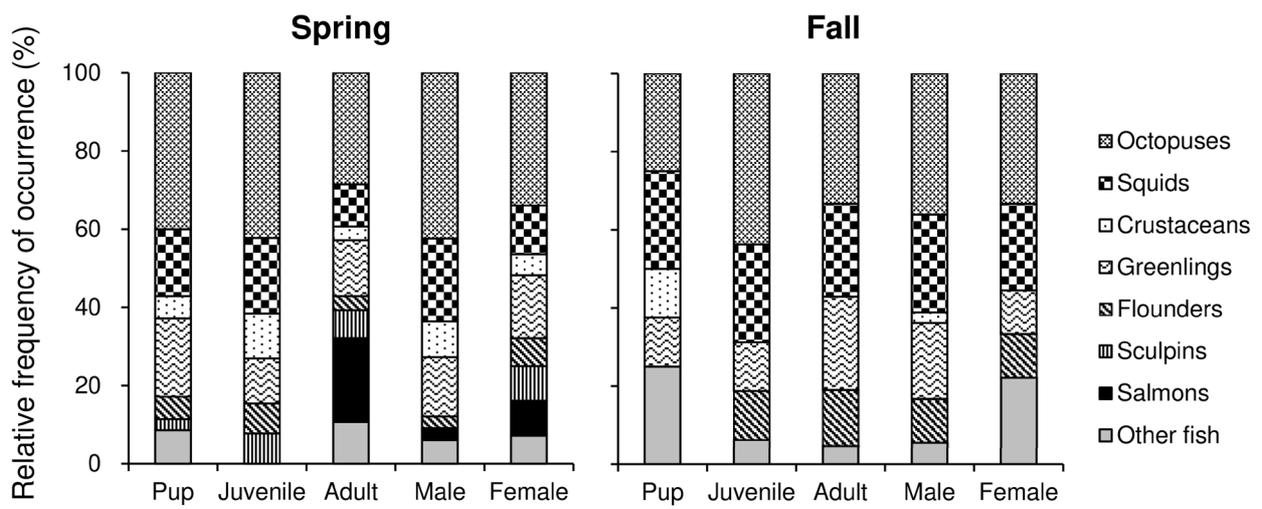
Fig. 3 The percent frequency of occurrence (*FO*) of fish, cephalopods, and crustaceans in spring



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Fig. 4 The percent frequency of occurrence (*FO*) of fish, cephalopods, and crustaceans in fall



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Fig. 5 The relative frequency of occurrence (*RFO*) of each prey item