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The relationship between pink salmon biomass and the body
condition of short-tailed shearwaters in the Bering Sea:
can fish compete with seabirds?

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Summary

Seabirds and large fishes are important top predators in marine ecosystems, but few studies have explored the potential for competition between these groups. This study investigated the relationship between an observed biennial change of pink salmon (*Oncorhynchus gorbuscha*) biomass in the central Bering Sea (23 times greater in odd-numbered than in even-numbered years) and the body condition and diet of the short-tailed shearwater (*Puffinus tenuirostris*) spending post-breeding season there. Samples were collected with research gill nets over seven summers. Both species feed on krill, small fishes and squids. Although the mean pink salmon catch per unit effort (in mass) over the study region was not related significantly with shearwater's stomach content mass or prey composition, the pink salmon biomass showed a negative and significant relationship with the shearwater's body mass and liver mass (proxies of energy reserve). We interpret these results as evidence that fishes can negatively affect mean prey intake of seabirds if they feed on a shared prey in the pelagic ecosystem.

Key words: top predator, marine ecosystem, competition, body condition, prey

Introduction

Large fishes, marine mammals and seabirds feed heavily on forage fishes, micronekton, and zooplankton (Bax 1991; Furness 2002) and impact prey populations (Birt *et al.* 1987; Baum & Worm 2009). They can also logically be assumed to compete with one another for food (Laws 1977; Springer 1992). Understanding such competitive interactions is becoming increasingly important since the recent overexploitation of large predatory and forage fishes can induce ecosystem change through trophic cascades (Pauly *et al.* 1998; Myers & Worm 2003; Furness 2003). To our knowledge, however, no quantitative evidence has been presented that supports competition among top-predators in the pelagic marine ecosystem, except the short-term behavioural responses of a penguin species to the presence of whales (Ainley *et al.* 2006).

Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant (200-270 million fish, Rogers 2001) salmonid in the western and central Bering Sea and northern North Pacific Ocean (Ruggerone *et al.* 2003), and feeds on krill, myctophid fishes, and small squids at 10 - 40 m depth (Davis *et al.* 2000; Kaeriyama *et al.* 2004). It has a two-year life cycle, and the population in the northern

North Pacific and basin areas of the Bering Sea shows wide annual fluctuations in abundance (Ruggerone *et al.* 2003), with biomass more than ten times higher in odd-numbered years than in even-numbered years. This provides a unique opportunity to investigate the ecological impact of this species, and it has been shown that in odd-numbered years, the body mass of other salmon species decrease, and they switch to other prey (Tadokoro *et al.* 1996; Ruggerone *et al.* 2003).

Short-tailed shearwaters (*Puffinus tenuirostris*) breed mainly in Tasmania from October to March and spend their non-breeding season (May to September) in the northern North Pacific Ocean (Brooke 2004). About 16 million shearwaters visit the Bering Sea every summer (Serventy 1967; Schneider & Shuntov 1993), where they feed on krill, fishes, and small squids in upper 70 m of the water column (Ogi *et al.* 1980; Weimerskirch & Cherel 1998; Hunt *et al.* 2002). Thus, they potentially compete for food with pink salmon.

In this study, we compared interannual changes in the biomass of pink salmon with the body condition and stomach contents of short-tailed shearwaters that had become accidentally entangled in experimental gill nets in the central Bering Sea (fig. 1) during a salmon survey. Our

aim was to determine if the body condition of the shearwaters worsened or if they changed their diet to mitigate competition with pink salmon in odd-numbered years when pink salmon are more abundant.

Study area and methods

Study area and sampling: Research gill-net sampling was conducted aboard the R/V *Wakatake-maru* (Hokkaido Prefectural Government) in the central Bering Sea between 2002 and 2008 as part of the Bering-Aleutian Salmon International Survey (North Pacific Anadromous Fish Commission 2001). Samples were collected annually at 5 to 14 stations in the study area (fig. 1). Each year the surveys began between 28 June and 10 July and ended between 12 and 15 July.

A variable-mesh research gill net (C-net; 30 panels of variable mesh size, each 50 m long) and a commercial-mesh gill net (19 panels of 115 mm mesh, each 50 m long) were set at about 0–7 m depth at 16:00 (local time) on calm days (Beaufort numbers 1–4) and retrieved at 04:00 the next morning, giving a fixed fishing effort at each station. Seabirds entangled in the nets were

stored in a freezer (-30°C) until analysis. Sea surface temperature (SST) and chlorophyll-a concentration (Chl-a) of bucket-sampled surface water at each station were measured with a calibrated thermometer and Turner 10-AU fluorometer, respectively. Chl-a was not measured in 2004 and at some stations during other years. Vertical temperature depth data at each station (collected with a Seabird SBE-19 CTD, Sea-Bird Electronics Inc, Washington, USA) showed that a thermocline occurred each year between 10 and 30 m depth.

Shearwater body condition and prey: Nine to 157 short-tailed shearwaters were collected each year (Appendix 1). In a laboratory, the samples were thawed, washed in freshwater and wiped dry with tissue paper repeatedly until the mass change was less than 5 g. Body mass was then measured to the nearest 1 g with an electronic balance. The bill length, bill depth, head length, tarsus length, wing length, and tail length of each bird were then measured. We performed a principal component analysis with these parameters and used the first component as the body size index. Birds with broken bills or tarsi were excluded from the body size analyses, but were included in the analyses of liver mass, fat score

and stomach content. The body mass and liver mass were both positively, linearly and significantly correlated with the body size index (body mass, $r = 0.205$, $P = 0.001$, $n = 278$ birds; liver mass, $r = 0.014$, $P = 0.014$, $n = 280$ birds), so the residual values of these on the linear regressions were used to standardize the body size.

Each bird was dissected, and the wet mass of the liver, which functions as a reservoir for lipids and carbohydrates in birds (Ziswiler & Farner 1972), was measured to the nearest 0.1 g. As an indicator of fat reserve (Ankney & MacInnes 1978), subcutaneous fat under the ventral skin of a subsample of birds was scored (*Rank 1*, the calamus was apparent under the skin and only a little adipose tissue was observed; *Rank 2*, the calamus was less apparent but visible, and some orange adipose tissue was observed; *Rank 3*, the calamus could not be seen, and a thick layer of white adipose tissue covered most of the skin).

The proventriculus (referred to as the stomach in this study) of subsamples of birds was removed and stored in 60% ethanol. Prey items in the stomachs were sorted into krill, amphipods, fish, and squid, and each prey type was weighed to the nearest 0.01 g. Twenty-seven of 186 stomachs contained no prey items and were excluded from

the prey-composition analysis (Appendix 1).

Fat score and stomach content data was available for subsamples of birds collected in 2003-2008. Using these subsamples, birds with heavier liver had higher fat score (Spearman's rank correlation, $r_s = 0.44$, $P < 0.01$, $n = 131$ birds, fig. 2); indicating that the liver mass well reflected the fat reserve. There was also strong correlation between the body mass and that without stomach contents ($r = 0.99$, $n = 182$ birds) with the slope very close to 1 ($0.964 \pm 0.01(\text{se})$). Thus, the size corrected body mass can be used as a body condition index.

Analyses: To examine the effect of pink salmon biomass on the body condition and stomach content of short-tailed shearwaters, we constructed four Linear Mixed Models and evaluated the relative plausibility of these with Akaike's information criterion adjusted for small sample size (AIC_c : Burnham & Anderson 2001). We calculated a $\bullet AIC_c$ value for each model, and then normalized these values to obtain an Akaike weight (w_i) for each model using R ver. 2.7.2 (R Development Core Team 2005).

Short-tailed shearwaters tend to feed within a meso-scale area for an extended period (Baduini *et al.* 2006), so they can compete with pink salmon over food at

local (station) as well as regional (basin) scales. We used the biomass of pink salmon caught at each station (the number of salmon x mean body mass of subsamples of salmon) where shearwaters were caught (local pink salmon CPUE) and the annual mean pink salmon biomass CPUE across all gill-net stations each year (regional pink salmon CPUE) as fixed independent variables. Although local and regional pink salmon CPUEs were calculated using a part of the same data set, we assumed the inter-correlation between them could be ignored in the Linear Mixed Model analysis as variance inflation factor was relatively small (2.698). The same stations were sampled every year, so the identity of the sampling station was treated as a random effect. Dependent variables were 1) residual body mass, 2) residual liver mass, 3) the mass proportion of krill in the stomach contents, and 4) mass of stomach contents.

Results

Salmon density and shearwater body condition: The mean regional CPUE of pink salmon was 23 times higher in odd-numbered years (331.2 kg per 30 C-nets, $n = 3$ years) than in even-numbered years (14.5 kg per 30 C-nets, $n =$

4 years) ($U = 0.00$, $P < 0.05$, U -test, Appendix 1). A model, which included the station identity (random effect) only, was by far the most effective of all the models at describing the observed variations in the number of short-tailed shearwaters entangled in the C-nets (Table 1).

A model, which included the regional pink salmon CPUE as a fixed effect, was over 4.4 times more likely to describe the observed variations in the residual body mass of the shearwaters than the second best-fitting model (Table 1). Similarly, a model, which included the regional pink salmon CPUE as a fixed effect, was by far the most effective of all the models at describing the observed variations in the residual liver mass of the shearwaters (Table 1). Both the residual body mass and residual liver mass of the shearwater appeared to decrease with the regional pink salmon CPUE (fig. 3a, b).

Stomach content: The main prey of the shearwaters was krill (36-82% in annual mean wet mass), followed by fishes (8-40%) and squids (0-30%) (Appendix 1). A model, which included the station identity as random effect was by far the most effective of all the models at describing the observed variations in the proportion of krill in the

stomach contents (Table 1). No models were successful in describing the variation in the stomach content mass of the shearwaters (Table 1).

Environmental factors: As pink salmon biomass affected shearwaters' body condition at the regional scale, effects of the other potential factors on the shearwater's body condition were checked at this scale. The annual mean SST and mean Chl-a were not related to either the mean residual body mass, mean residual liver mass, nor the number of short-tailed shearwaters entangled in the nets (Spearman's rank correlation, $r_s = -0.511$ to $+0.663$, $P > 0.05$, $n = 6-7$ years, Appendix 1). Annual mean SST was not related to the regional pink salmon CPUE ($r_s = 0.175$, $P > 0.05$, $n = 7$ years), whereas the annual mean Chl-a was positively related to the regional pink salmon CPUE ($r_s = 0.816$, $P = 0.048$, $n = 6$ years).

Discussion

Large fishes and seabirds can logically be assumed to compete with one another for food, though quantitative evidence of negative effects on the nutritional status or population is scarce. We found, for the first time to our knowledge, that the abundant pink salmon in the

central Bering Sea can impact the body condition of the shearwaters and interpreted this as evidence that a fish can negatively affect overall prey intake of a seabird if both feed on a shared prey.

Pink salmon and shearwater's body condition: The body mass (524–655 g) and liver mass (20–29 g) of our birds (Appendix 1) sampled in late June and early July in the central Bering Sea (55–58°N) were similar to those (body mass, 583 g; liver mass, 23 g) observed in the northern North Pacific (48–55°N) in June to July when they recovered their body condition (Oka 2008). This suggests our birds had recovered the body fuel reserve that they had used during their migration from the breeding areas. Thus, the observed interannual variation in their body condition most likely reflected variations in food availability for shearwaters in the central Bering Sea.

Our data, which were collected over three cycles of pink salmon abundance, show that shearwater's body condition indices were negatively affected by regional pink salmon CPUE. The effects of the local pink salmon CPUE, however, were negligible; indicating that body condition possibly reflected the cumulative result of a negative energy budget over a longer period and over a

wider area. Pink salmon are highly mobile in the Bering Sea during summer (Hartt 1966). Thus large temporal variation in local abundance of pink salmon might make the local effects difficult to be detected. Lobkov (1991) observed a larger number of dead seabirds, including short-tailed shearwaters, in odd-numbered years than in even-numbered years along the Pacific coast of the Kamchatka Peninsula (fig. 1), also suggesting that an impact of pink salmon could occur at a larger geographical scale.

In the central Bering Sea, pink salmon CPUE has been reported to negatively correlate with krill biomass (Tadokoro *et al.* 1996), negatively correlate with macrozooplankton biomass, and as we found in this study, positively correlate with Chl-a (Shiomoto *et al.* 1997). These suggest that pink salmon deplete krill in odd-numbered years and that abundant pink salmon might induce a top-down trophic cascade and a competition with the shearwaters.

Other potential factors: In the southeast Bering Sea, extraordinarily high SST in 1997, that depressed krill swarming activity, and/or a large surface bloom of coccolithophore in this year, that reduced light

transmission, might have caused the mass mortality of shearwaters through the decrease of krill availability for surface feeding seabirds (Baduini *et al.* 2001, Lovvorn *et al.* 2001). We found no significant correlation between SST and the shearwaters' body condition in the central Bering Sea. No strong coccolithophore blooms in the central or southeast Bering Sea occurred during our study period (T. Iida *pers comm*).

Upon their arrival in the North Pacific, first-year short-tailed shearwaters have much less body lipids than adults (Oka 2008). All but one of our sampled birds had no apparent bursa of Fabricius, which is a characteristic of fledgling Procellariiformes (Broughton 1994), and thus was likely to be adults. In short-tailed shearwaters, the timing of egg-laying and of migration varies interannually by less than a week (Bradley *et al.* 2000; Brooke 2004). This rather small variation cannot explain the relatively large interannual differences in body mass (27%) and liver mass (43%) observed in this study (Appendix 1). Therefore, all of these factors other than pink salmon biomass could not be major factors explaining the observed biennial change, at least, in the shearwater's body condition indices. We could not, however, exclude the potential of other drivers of shearwater's condition given the amount of within and

between year variations especially in even-numbered years where sample size was rather small (fig. 3).

Prey and stomach contents: In odd-numbered years, when pink salmon are abundant, short-tailed shearwaters were expected to switch their prey to secondary prey species such as gelatinous zooplankton that have a lower energy value than krill, fishes, or squids (Davis & Myers 1998), presumably to mitigate the competition with pink salmon, as found in the other salmon species (Tadokoro *et al.* 1996). However, the short-tailed shearwaters did not change the proportion of krill, main prey, in the stomachs with the change of regional pink salmon CPUE. Bill, palate, and tongue morphologies of short-tailed shearwaters are adapted to filter feeding on krill (Morgan & Ritz 1982). Because of these morphological constraints, shearwaters might not switch their prey to gelatinous zooplankton. Or the energy value of gelatinous zooplankton might be too small to be included in the shearwaters' diet.

Abundant pink salmon was expected to decrease prey intake, hence stomach content mass, of the short-tailed shearwaters, but no significant relationships between pink salmon biomass and the shearwaters' stomach content mass were detected. Short-tailed shearwaters feed mainly

in daylight (Ogi *et al.* 1980). Birds were entangled in the gill nets during the night, so their empty stomachs might simply reflect decreased foraging activity during the night or come from a local and opportunistic short-term absence of prey. Thus rather small samples of stomach content of birds collected during the night in this study might not well represent the long-term mean prey intake. Therefore, we could not determine the underlying behavioural mechanisms of reduced feeding opportunities for shearwaters during pink salmon abundant years.

In conclusion, although the behavioural mechanism has to be explored and the sample size was relatively small, our result suggests the impact of pink salmon on the energy reserve of the short-tailed shearwaters. Our study indicates the importance of potential competition between these aquatic and aerial top predators for understanding pelagic marine ecosystem changes.

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Legends for figures

Fig. 1. Study area. Samples collected at gill-net sampling stations (closed circles) in the central Bering Sea were used.

Fig. 2. Relationship between liver mass (g in wet) of individual birds and the score of subcutaneous fat ranked 1(lean) to 3 (fat).

Fig. 3. Relationship between annual mean pink salmon biomass across stations (regional pink salmon CPUE) and the body mass (a), and that between regional pink salmon CPUE and the liver mass (b) of short-tailed shearwaters. Body mass and liver mass were shown as residual values using the linear regressions with body size index to standardize the size effects. Plots, error bars, and the numbers indicate mean, SE, and year, respectively.

Table 1. Predictive factors considered to describe the observed variation in the number of short-tailed shearwaters entangled in the C-nets, the residual body mass, the residual liver mass, the mass proportion of krill and the content mass of the stomach of the shearwaters. The number of parameters (k), AICc, Δ AICc and Akaike weights (W_i) for the set of candidate models are shown. Independent variables are regional and local pink salmon CPUE as fixed and station (ST) as random factors. Samples were collected in 2002-2008 except stomach contents that were collected in 2003-2008. Models including variable(s) in bold were the best fit and effective ones. Sample sizes are in parenthesis.

Dependent variables	Independent variables	k	AICc	Δ AICc	W_i
No. of shearwaters (84 station-year) 2002-2008	ST	0	443.3	0.00	0.99
	Regional CPUE, ST	1	453.9	10.65	0.00
	Local CPUE, ST	1	455.3	12.05	0.00
	Regional CPUE, Local CPUE, ST	2	465.9	22.65	0.00
Residual body mass (277 birds) 2002-2008	Regional CPUE, ST	1	3086.0	0.00	0.80
	Local CPUE, ST	1	3089.0	3.01	0.18
	Regional CPUE, Local CPUE, ST	2	3093.0	7.04	0.02
	ST	0	3097.0	11.00	0.00
Residual liver mass (279 birds) 2002-2008	Regional CPUE, ST	1	1562.0	0.00	1.00
	Regional CPUE, Local CPUE, ST	2	1574.0	12.03	0.00
	Local CPUE, ST	1	1584.0	22.00	0.00
	ST	0	1599.0	36.99	0.00
%Mass krill in stomach (159 birds) 2003-2008	ST	0	192.8	0.00	0.93
	Local CPUE, ST	1	199.0	6.23	0.04
	Regional CPUE, ST	1	199.8	7.03	0.03
	Regional CPUE, Local CPUE, ST	2	214.4	21.58	0.00

Mass of stomach contents (186 birds)	Local CPUE, ST	1	1365.0	0.00	0.42
2003-2008	Regional CPUE, ST	1	1365.0	0.00	0.42
	ST	0	1367.0	1.98	0.16
	Regional CPUE, Local CPUE, ST	2	1374.1	9.04	0.00

0

Appendix 1. Interannual changes in the pink salmon catch per unit effort (CPUE; kg/30 C-net panels) and the short-tailed shearwater CPUE (no. of birds/30 C-net panels), sea surface temperature (SST) and chlorophyll-a concentration (Chl-a) of surface water, body and liver mass of the shearwater, no. of shearwater's stomachs sampled, no. of empty stomachs, total prey mass in the non-empty stomach, and prey composition in %mass. Mean±SD are shown. Numbers of birds are in parenthesis.

Year	2002	2003	2004	2005	2006	2007	2008
No. of station	13	14	14	10	5	14	14
Pink salmon CPUE(kg)	2.5±1.8	336.1±167.6	20.8±17.6	257.7±168.6	8.8±5.5	399.7±242.8	25.9±26.8
Short-tailed shearwater CPUE (n)	0.5±1.0	4.5±6.2	1.6±2.0	2.2±2.9	0.6±0.5	0.4±0.6	1.6±2.6
SST(°C)	7.2±0.3	8.0±0.4	8.3±0.5	7.9±0.5	7.2±0.3	7.3±0.7	7.4±0.6
Chl-a (mmg/m3)	0.87±0.34	1.06±0.71	-	0.92±0.51	0.56±0.29	1.13±0.44	0.36±0.15
Body mass (g)	609±8(22)	560±5(153)	608±8(52)	589±14(34)	655±33(9)	524±14(10)	555±13(30)
Liver mass (g)	28.5±0.6(21)	21.3±0.3(157)	26.0±0.6(52)	23.4±0.9(35)	24.9±1.2(9)	20.0±1.0(10)	24.6±0.9(30)
No. of stomachs sampled	-	89	37	15	7	10	28
No of empty stomachs	-	9	5	3	2	4	4
Total prey mass in the stomach (g)	-	2.7±3.8	5.6±9.2	14.7±14.3	16.8±10.1	5.3±9.9	13.4±14.8
Krill (%)	-	36±43	82±29	67±48	58±53	52±47	48±46
Fish (%)	-	20±37	8±26	8±29	40±54	22±39	29±43
Squids(%)	-	30±42	6±16	15±34	2±4	0±0	16±32

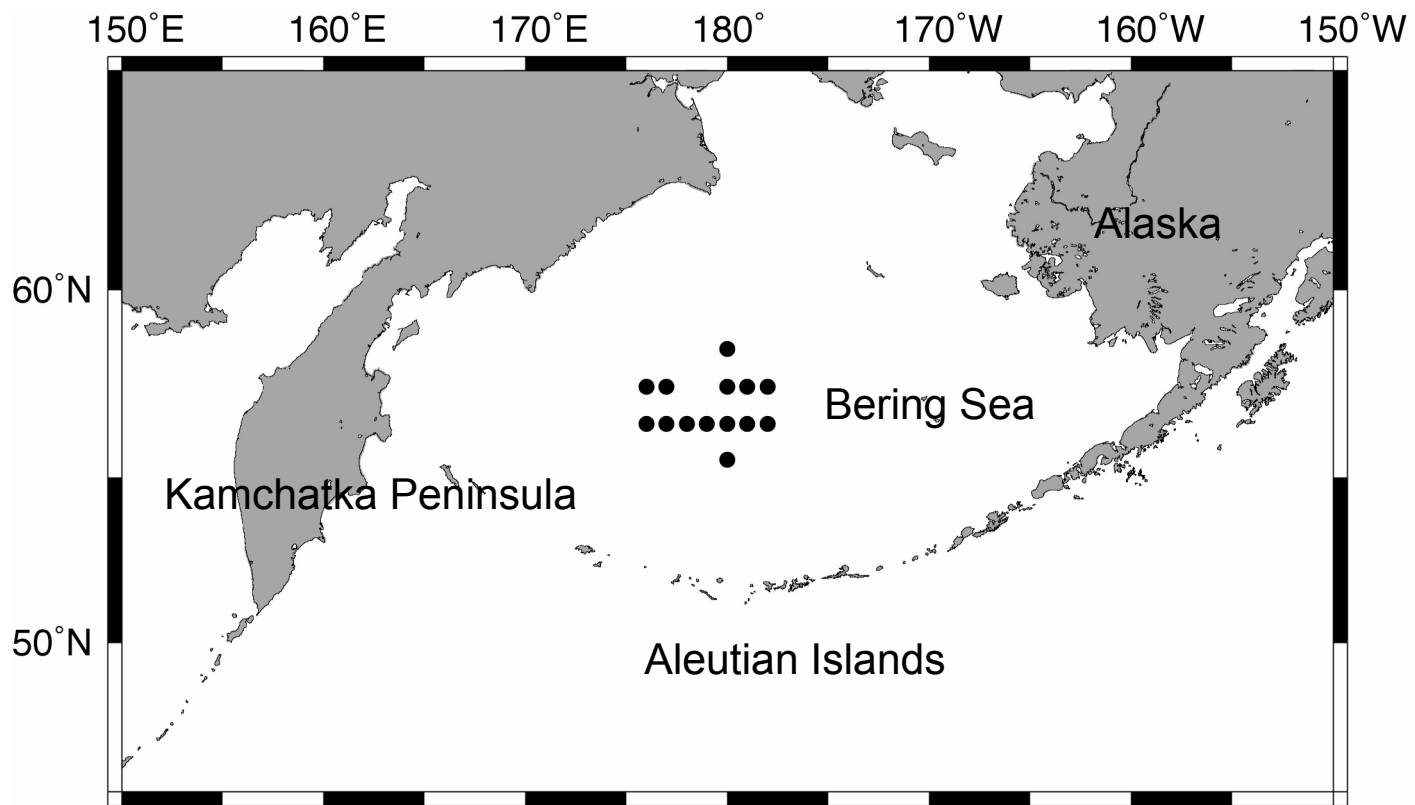
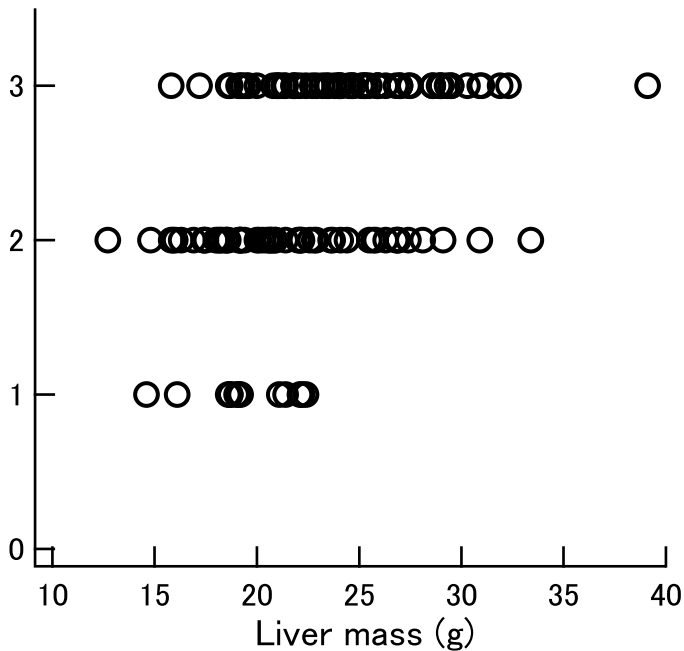
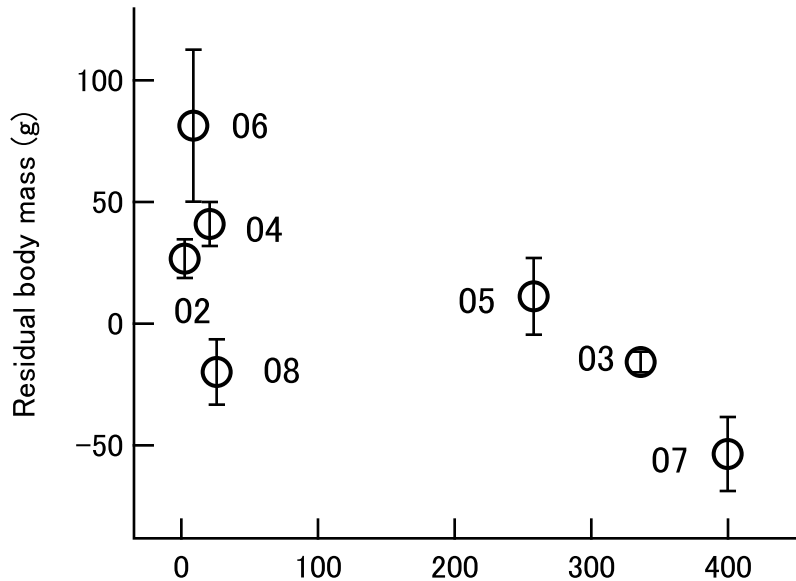


Fig. 1

Fat score





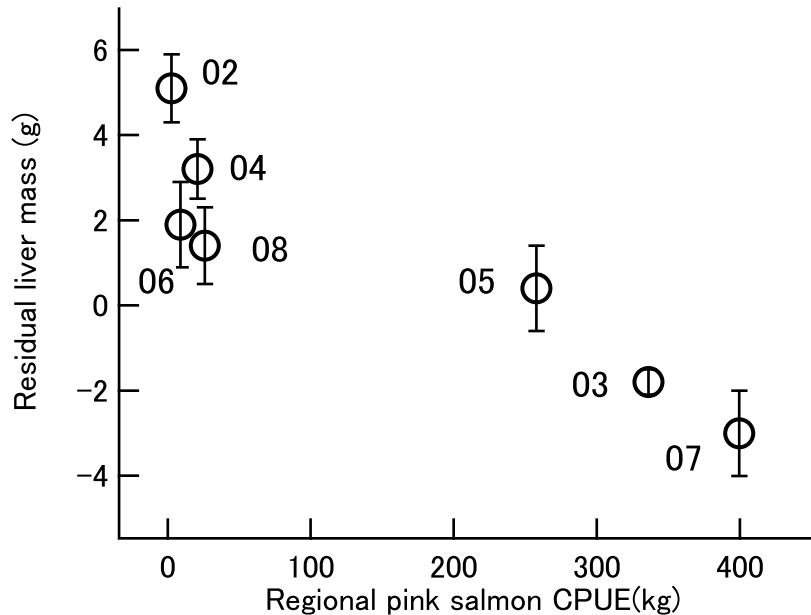


Table 1. Predictive factors considered to describe the observed variation in the number of short-tailed shearwaters entangled in the C-nets, the residual body mass, the residual liver mass, the mass proportion of krill and the content mass of the stomach of the shearwaters. The number of parameters (K), AICc, Δ AICc, and Akaike weights (W_i), for the set of candidate models are shown. Independent variables are regional and local pink salmon CPUE as fixed and station (ST) as random factors. Samples were collected in 2002-2008 except stomach contents that were collected in 2003-2008. Models including variable(s) in bold were the best fit and effective ones. Sample sizes are in parenthesis.

Dependent variables	Independent variables	k	AICc	Δ AICc	W_i
No. of shearwaters (84 station-year) 2002-2008	ST	0	443.3	0.00	0.99
	RegionalCPUE, ST	1	453.9	10.65	0.00
	LocalCPUE, ST	1	455.3	12.05	0.00
	RegionalCPUE, LocalCPUE, ST	2	465.9	22.65	0.00
Residual body mass (277 birds) 2002-2008	RegionalCPUE, ST	1	3086.0	0.00	0.80
	LocalCPUE, ST	1	3089.0	3.01	0.18
	RegionalCPUE, LocalCPUE, ST	2	3093.0	7.04	0.02
	ST	0	3097.0	11.00	0.00
Residual liver mass (279 birds) 2002-2008	RegionalCPUE, ST	1	1562.0	0.00	1.00
	RegionalCPUE, LocalCPUE, ST	2	1574.0	12.03	0.00
	LocalCPUE, ST	1	1584.0	22.00	0.00
	ST	0	1599.0	36.99	0.00
%Mass krill in stomach (159 birds) 2003-2008	ST	0	192.8	0.00	0.93
	LocalCPUE, ST	1	199.0	6.23	0.04
	RegionalCPUE, ST	1	199.8	7.03	0.03
	RegionalCPUE, LocalCPUE, ST	2	214.4	21.58	0.00
Mass of stomach contents (186 birds) 2003-2008	LocalCPUE, ST	1	1365.0	0.00	0.42
	RegionalCPUE, ST	1	1365.0	0.00	0.42
	ST	0	1367.0	1.98	0.16
	RegionalCPUE, LocalCPUE, ST	2	1374.1	9.04	0.00