

Lipid content of chum salmon *Oncorhynchus keta* affected by pink salmon *O. gorbuscha* abundance in the central Bering Sea

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ABSTRACT: To assess effects of intra- and inter-specific interactions on chum salmon in the central Bering Sea, chum salmon lipid content was analyzed as a proxy for body condition. We measured the lipid contents of 466 immature individuals collected during summer from 2002 to 2007. Individual variation in log-transformed lipid content was tested using multiple regression analysis with biological and environmental variables. A regression model that included chum salmon fork length and pink salmon CPUE (number of fish caught per 1500 m of gillnet) was the most effective in describing variation in lipid content. Path analysis showed that the negative effect of pink salmon CPUE was stronger than the effect of chum salmon CPUE on chum salmon lipid content. Stomach content analysis of 283 chum salmon indicated non-crustacean zooplankton (appendicularian, chaetognath, cnidarian, ctenophore, polychaete, and pteropod) was higher under conditions of high pink salmon CPUE. Increased consumption of non-crustacean zooplankton containing a low lipid level could lower the lipid content of chum salmon. Thus, chum salmon lipid content could be affected directly by their shift in prey items and indirectly by interspecific competition with pink salmon.

KEY WORDS: Lipid content · Chum salmon · Pink salmon · Central Bering Sea · Competition · Prey selection

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INTRODUCTION

For the most part, chum salmon *Oncorhynchus keta* and pink salmon *O. gorbuscha* abundances have been increasing since the 1976 to 1977 regime shift (Ruggerone et al. 2010), and these 2 species constitute the dominant proportion of the total salmonid catch in the North Pacific Ocean (NPAFC 2002). Simultaneously, body size of chum and pink salmon

has decreased during the 1970 to 2000 time period (reviewed by Bigler et al. 1996, Ishida et al. 2002). Several studies have indicated density-dependent effects on growth within stocks and among species of Pacific salmon (Ogura et al. 1991, Ishida et al. 1993, Welch & Morris 1994, McKinnell 1995, Bugaev et al. 1996). Since individuals of the same species have very similar requirements for growth, density-dependent growth is likely to be caused by intraspecific

competition (Begon et al. 1996). Strength of interspecific competition is usually weaker than intraspecific competition in many terrestrial, marine, and freshwater systems (Connell 1983). However, in the epipelagic North Pacific Ocean and Bering Sea, pink salmon is one of the dominant plankton feeders and its abundance affects local biomass of crustacean zooplankton (Brodeur 1988, Tadokoro et al. 1996). Recent studies have indicated significant interspecific competition between pink salmon and other plankton feeders such as chum salmon, sockeye salmon *O. nerka*, and short-tailed shearwaters *Puffinus tenuirostris* in the North Pacific Ocean and Bering Sea (Tadokoro et al. 1996, Walker et al. 1998, Azumaya & Ishida 2000, Ruggerone et al. 2003, Toge et al. 2011).

Pink salmon are the most abundant salmon species (Ruggerone et al. 2003). Pink salmon have a 2-year life cycle and there is a strong biennial cycle in the Bering Sea with high pink salmon abundance in odd-numbered years and low abundance in even-numbered years (Ruggerone et al. 2003). Chum salmon are also abundant in this area and require similar natural resources (e.g. habitat, prey items) as pink salmon. Although chum salmon mature after 2, 3, or more winters at sea, its CPUE (number of fish caught per 1500 m of gillnet) was negatively correlated with pink salmon CPUE in a gillnet survey in the Bering Sea (Azumaya & Ishida 2000). Cyclic fluctuations in chum salmon CPUE in the Bering Sea might be caused by high pink salmon abundance affecting the distribution of chum salmon (Azumaya & Ishida 2000). To assess fluctuations in abundance of chum salmon in the North Pacific Ocean and Bering Sea, competition between these 2 species deserves further investigation.

Neutral lipids are the primary energy source for salmonids (Navarro & Gutiérrez 1995) and the content of these lipids in chum salmon muscle decreases greatly in winter compared with summer (Nomura et al. 2000). Low neutral lipid content in winter suggests that chum salmon consume small amount of prey during winter (Nomura et al. 2000). In fall, large copepods descend to deep layers (Fulton 1973, Coyle et al. 1996) away from surface waters, which is the habitat of chum salmon, and epipelagic zooplankton biomass in winter (18.7 to 37.1 mg m⁻³) is lower than in summer (226.4 to 275.2 mg m⁻³) (Parsons & Lalli 1988, Brodeur et al. 1996, Nagasawa 2000). During a period of restricted food supply, salmonids consume lipids and proteins as their main energy sources (Parker & Vanstone 1966). Phospholipids and non-soluble proteins are structural components mobilized

for providing energy after neutral lipids have dropped below a critical level (Parker & Vanstone 1966, Love 1980, Bandarra et al. 1997, Shulman & Love 1999). Variation in total lipid content (neutral lipids + phospholipids) can be regarded as an indicator of the neutral lipid component (Shulman & Love 1999) because phospholipid content in chum salmon remains constant regardless of season (Nomura et al. 2000). In contrast, carbohydrates stored in the liver as glycogen do not serve for long-term energy storage (Navarro & Gutiérrez 1995); liver glycogen reserves of fish species, including salmon, rapidly decrease within 1 wk of starvation (Soengas et al. 1996, Larsen et al. 2001). Therefore, insufficient lipid storage during summer could increase starvation-based mortality in overwintering chum salmon.

No studies have examined the effects of inter- and intraspecific competition on the nutritional condition of salmonids. Our objective was to assess the interspecific effect of pink salmon and the intraspecific effect of chum salmon on the nutritional condition of chum salmon in the central Bering Sea during summer by examining the effects of environmental and biological factors on variation in chum salmon lipid content.

MATERIALS AND METHODS

Study area and field sampling

The study was conducted in the central Bering Sea ($55^{\circ}00'N$ to $58^{\circ}30'N$, $175^{\circ}00'E$ to $175^{\circ}00'W$, Fig. 1). Lipid content samples were obtained during ocean surveys conducted by the RV 'Kaiyo maru' (Fisheries

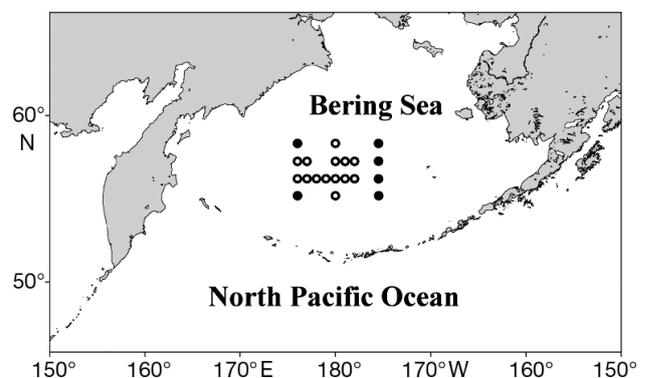


Fig. 1. Area where chum salmon *Oncorhynchus keta* lipid content samples were collected (○ and ●) and where other biological data and abundance of chum and pink salmon *O. gorbuscha* data were obtained (○) in the central Bering Sea during summer, 2002 to 2007

Agency of Japan) from 2002 to 2004 and by the RV 'Wakatake maru' (Education Bureau of Hokkaido Prefectural Government) from 2005 to 2007 (Table 1). At 5 to 14 stations per year, fish were sampled between 26 June and 14 July. On board the RV 'Kaiyo maru', a mid-water trawl (opening ca. 50 m in height and width, cod-end mesh size 12 mm) was towed at a speed of 5 knots from the surface to ca. 50 m for 1 h during the daytime. On board the RV 'Wakatake maru', a surface gillnet (10 different stretched meshes of 48, 55, 63, 72, 93, 106, 121, 138, and 157 mm; each panel of mesh was 150 m in length; Takagi 1975) was set at 16:00 h and retrieved at 04:00 h (local time) the following morning for a soak time of 12 h. In addition, a surface longline was set 30 min before sunset and retrieved 1 h later. Biological data including fork length (FL), gonad weight, sex, and ocean age (determined by counting annuli on a scale) were collected in association with each lipid sample from gillnet and trawl catches. Chum salmon maturity stage was classified by threshold gonad weight according to Takagi (1961). Whole fish for lipid analysis were packed in plastic bags and kept frozen at -40°C . A total of 467 immature chum salmon (ocean age 1 to 3) was collected for determination of lipid content ($n = 34, 86, 24, 131, 101,$ and 91 for 2002 to 2007, respectively). The CPUE of chum and pink salmon was calculated from the gillnet catch of the RV 'Wakatake maru' from 2002 to 2007.

To examine the annual change of prey composition of chum salmon, a total of 283 stomach samples ($n = 71, 50, 60, 49, 16,$ and 37 for 2002 to 2007, respectively) was sampled from ocean age 1 to age 3 immature chum salmon collected from gillnet and surface longline catches of the RV 'Wakatake maru' at survey stations in the central Bering Sea. Stomach content samples that were either empty or well-digested were omitted from the analysis. Stomach content weight was calculated by subtracting the empty stomach weight after removal of contents from total

stomach weight. A stomach content index was calculated as the ratio of stomach content weight to salmon body weight. Stomach contents were sorted into taxonomic categories, i.e. amphipod, chaetognath, copepod, decapod, euphausiid, fish, jellyfish (cnidarian and ctenophore), polychaete, pteropod, squid, and others (unidentified material). The major zooplankton and fish species identified within these taxonomic categories are listed in Davis et al. (2009). The percent by volume of each category was visually estimated following the method of Percy et al. (1984). Taxonomic categories were classified into 3 prey groups because feeding habits of Pacific salmon can be divided into consumption of micronekton (i.e. fish and squid), crustacean zooplankton (i.e. amphipod, copepod, decapod, and euphausiid), and non-crustacean zooplankton (i.e. chaetognath, jellyfish, polychaete, and pteropod) (Welch & Parsons 1993).

Sea surface temperature (SST, $^{\circ}\text{C}$) and chlorophyll *a* concentration (chl *a*, mg m^{-3}) were measured during the research cruise of the RV 'Wakatake maru' at each survey station in the central Bering Sea during June and July, 2002 to 2007. The SST was the temperature at 10 m depth since daily mixing and precipitation are evident in the upper 10 m of the water column. Water characteristics were measured using a conductivity, temperature, and depth profiler (SBE-19, Seabird Electronics). Chl *a* was estimated from the transparency depth (TD, m) measured by Secchi disk to the nearest 1 m. To obtain a conversion equation, actual chl *a* was determined with a Turner 10-AU fluorometer according to Welschmeyer (1994) from surface water (uppermost 1 m) collected by a bucket during the summer of 2002 to 2003 and 2005 to 2007. The TD was converted to chl *a* using an exponential relationship after Falkowski & Wilson (1992). The conversion equation was the following:

$$\text{CHL} = 55.1 \times \text{TF}^{-1.77} \quad (R^2 = 0.71, p < 0.0001)$$

Table 1. Sampling effort, mean lipid content (mean \pm SD; g) per 10 g of muscle homogenate by ocean age group of chum salmon *Oncorhynchus keta* collected by RV 'Kaiyo maru' and RV 'Wakatake maru' in the central Bering Sea, 2002 to 2007

Year	Date (dd/mo)	Latitude	Longitude	Sampling samples	Number of size	Lipid content		
						Age 1	Age 2	Age 3
2002	29/6–14/7	55.5–58.5°N	175°E–175°W	Trawl	34	0.24 \pm 0.08	0.65 \pm 0.32	0.68 \pm 0.31
2003	29/6–14/7	55.0–58.0°N	175°E–175°W	Trawl	86	0.21 \pm 0.11	0.40 \pm 0.26	0.82 \pm 0.37
2004	26/6–8/7	55.0–57.5°N	175°E–179°W	Trawl	25	0.32 \pm 0.08	0.51 \pm 0.21	0.59 \pm 0.17
2005	2/7–13/7	55.5–58.5°N	178°E–178°W	Gillnet	131	0.33 \pm 0.15	0.57 \pm 0.28	0.68 \pm 0.33
2006	10/7–14/7	55.5–58.5°N	179°E–180°W	Gillnet	81	0.38 \pm 0.13	0.41 \pm 0.20	0.87 \pm 0.40
2007	29/6–12/7	55.5–58.5°N	176°E–178°W	Gillnet	91	0.26 \pm 0.10	0.48 \pm 0.21	0.57 \pm 0.24

Annual averages of SST and chl *a* were calculated based on the measurements collected at all the survey stations.

Zooplankton was collected using an Ocean Research Institute net (ORI net, mouth diameter 1.6 m, overall length 7.5 m, mesh size 690 μm) at each station by researchers on board the RV 'Wakatake maru' from 2002 to 2007. Since zooplankton and micronekton migrate to the surface water at night, the ORI net was towed horizontally at 1.5 knot for 10 min from the surface to ca. 2 m depth around 23:00 h. Net samples were fixed with a 5% borax-buffered seawater formalin solution. Collected zooplankton was sorted into 4 prey groups (crustaceans, non-crustacean zooplankton, micronekton, and others). For each prey group, density (mg m^{-3}) was calculated from strained water volume measured by a flow meter (No. 5571-B, Rigosha). Annual average of prey density was calculated based on the measurements collected at survey stations.

Lipid content measurement

A fillet from the left dorsal muscle of chum salmon was skinned and homogenized. A 10 g sample of homogenate was collected and frozen at -40°C . After thawing the homogenate, lipids were extracted from the homogenate with a 2:1 mixture of chloroform and methanol according to the modified Bligh & Dyer (1959) technique. This technique extracts both neutral lipids and phospholipids. We added a 3% zinc acetate dihydrate aliquot to the extracted solution and obtained a bi-layer solvent. The chloroform-layer solvent was retrieved and evaporated to a stable dry weight (nearest 0.001 g) using a rotary evaporator. To prevent sample degradation, solvent removal in the rotary evaporator was stopped while a small amount of solvent remained in the flask because auto oxidation can be reduced by keeping the extract in solution. Final evaporation to dryness was carried out in a stream of nitrogen. The lipid content was expressed as lipid weight (g) in a 10 g wet weight (ww) of homogenate.

Statistical analyses

Analysis of covariance (ANCOVA) was used to determine whether the relationship between FL and lipid content differed among chum salmon ocean ages and sexes. Since lipid storage increases allometrically with increase in body size (Sogard &

Spencer 2004), both log-transformed lipid content ($\ln\text{LIPID}$) and log-transformed FL ($\ln\text{FL}$) were used. Relational predictors for variation of $\ln\text{LIPID}$ were tested using stepwise multiple regression analysis to assess the effects of biological and environmental variables on lipid content of chum salmon. Relational predictors included $\ln\text{FL}$, ocean age, year (as a categorical variable), SST, Pacific Decadal Oscillation index (PDO; averaged through September of the previous year to August of the survey year; obtained from the University of Washington, USA, <http://jisao.washington.edu/pdo>), North Pacific Index during winter (NPI; December to March; obtained from the Japan Meteorological Agency, <http://jma.go.jp/>), chl *a*, average density of crustaceans and non-crustacean zooplankton collected by the ORI net, and average log-transformed CPUEs of chum salmon ($\ln\text{CHUM}$) and pink salmon ($\ln\text{PINK}$). The effects of micronekton and other zooplankton were not tested because the weights of these components in samples collected by the ORI net were negligible. Lipid content was assumed to be independent of the level in the previous year. This assumption was made because chum salmon have low lipid content in winter ($<1.7\%$ of total wet weight (WW); Nomura et al. 2000); therefore, there cannot be much carryover of lipids from the winter into the following spring. Akaike's information criterion was used to compare and evaluate the validity among candidate models (Burnham & Anderson 2001).

We used path analysis to evaluate the strength of intra- and inter-specific effects of chum and pink salmon abundance on chum salmon lipid content and to interpret relationships among variables. The sem package (v. 3.0-0, Fox et al. 2012) for the statistical package of R (version 2.14.2, R Development Core Team 2012) was used for the path analysis. To construct the initial model, $\ln\text{CHUM}$ and paths among explanatory variables that were ignored in the multiple regression analysis were added to the best-fit model from the previous multiple regression analysis. Backward elimination of paths was performed based on the Bayesian information criterion to select the best model.

To test whether pink salmon abundance affected prey selection by chum salmon, we used nonparametric multivariate analysis of variance (MANOVA) (Anderson 2006, Anderson et al. 2006). We compared stomach content composition (proportional volume) between odd- and even-numbered years with $\ln\text{PINK}$ using analysis of multivariate homogeneity of group dispersions with the Horn-Morisita index

(Horn 1966, Anderson et al. 2006). To assess whether the dispersions of groups were different, we performed a nonparametric test of 1000 permutations (Anderson 2006) with the vegan package (v.2.0-4, Oksanen et al. 2012) using R statistical software (v. 2.14.2).

To examine annual changes in prey availability, we compared the log-transformed density of crustaceans and non-crustacean zooplankton between odd- and even-numbered years using the *t*-test, and the relationship between lnPINK and crustaceans was tested by correlation analysis.

RESULTS

Effects of biological and environmental variables on chum salmon lipid content

There was a significant linear and positive relationship between lnFL and lnLIPID ($p < 0.0001$) of chum salmon. The relationship was not different among ocean ages (ANCOVA: slope, $F_{2,460} = 0.85$, $p = 0.43$; intercept $F_{2,462} = 1.75$, $p = 0.18$) or between sexes (ANCOVA: slope, $F_{1,462} = 0.06$, $p = 0.80$; intercept $F_{1,463} = 0.08$, $p = 0.78$). Lipid content was within the range of 0.097 to 2.001 g in 10 g WW of homogenate (0.97 to 20.01% in WW of homogenate) in fish with FL ranging from 262 to 608 mm. Residuals from regression of lnLIPID on chum salmon lnFL fluctuated in a biennial cycle, with negative values in odd-numbered years and positive values in even-numbered years (Fig. 2). The lnPINK explained 20% of the lnLIPID residual variances and the effect was significant ($r = -0.84$, $p < 0.05$).

The best model describing the variation of lnLIPID included lnFL and lnPINK as independent variables (Table 2). Effects of other biological and environmental variables were statistically insignificant. Regression coefficients of lnFL and lnPINK were significantly different from zero (lnFL, $p < 0.0001$; lnPINK, $p < 0.05$). The best model explained 81% of the lnLIPID variability for chum salmon, although a simple model using only lnFL explained 77% of the lnLIPID variability for chum salmon.

The lnPINK affected chum salmon lnLIPID and lnCHUM (Fig. 3). Path coefficients from lnFL to lnLIPID, from

lnPINK to lnLIPID, and from lnPINK to lnCHUM were significant ($p < 0.0001$, $p < 0.05$, $p < 0.0001$, respectively). The signs of both path coefficients from lnPINK to lnLIPID and from lnPINK to lnCHUM were negative, indicating interspecific competition between pink and chum salmon. A path from lnCHUM to lnLIPID was removed from the best model based on the Bayesian information criterion. Removing the path from lnCHUM to lnLIPID indicated that interspecific competition was stronger than intraspecific competition on the variation of lnLIPID in chum salmon.

Table 2. Stepwise regression analysis of environmental and biological factors on variation in chum salmon *Oncorhynchus keta* lipid content from samples collected in the central Bering Sea during summer, 2002 to 2007. AIC: Akaike information criterion; R^2 : coefficient of determination; AGE: ocean age; chl *a*: surface chlorophyll *a* concentration; lnCHUM and lnPINK: log-transformed CPUEs of chum salmon and pink salmon *O. gorbuscha*; CRUS and NCZP: densities of crustaceans and non-crustacean zooplankton; lnFL: log-transformed chum salmon fork length; NPI: North Pacific Index; PDO: Pacific Decadal Oscillation; SST: sea surface temperature; YEAR: year as a categorical variable. * $p < 0.05$, *** $p < 0.001$

Independent variables	AIC	Δ AIC	R^2	p
lnFL***, lnPINK*	-11.9	0.0	0.81	<0.0001
lnFL***	-8.5	3.4	0.77	<0.0001
AGE, chl <i>a</i> , lnCHUM, CRUS, lnFL*, NCZP, NPI, lnPINK, PDO, SST, YEAR	-2.9	9.0	0.84	<0.0001

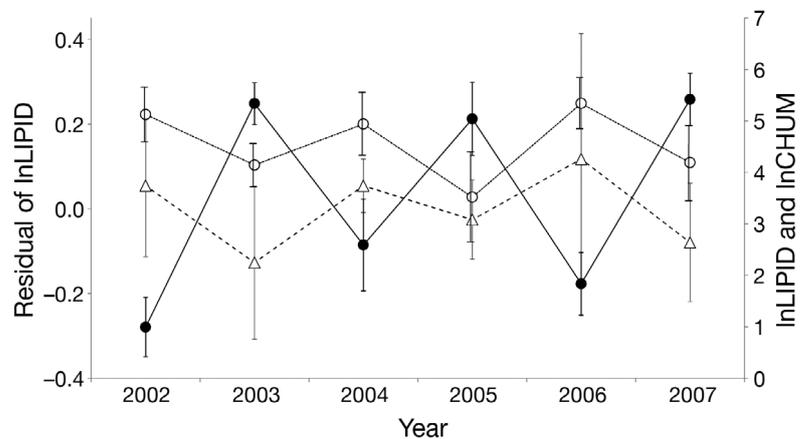


Fig. 2. Residuals from regression analysis of chum salmon *Oncorhynchus keta* log-transformed lipid content (lnLIPID) on log-transformed fork length (Δ) and log-transformed CPUE (number of fish caught per 1500 m of research gillnet) of chum salmon (\circ) and pink salmon *O. gorbuscha* (\bullet). Vertical bar: SD

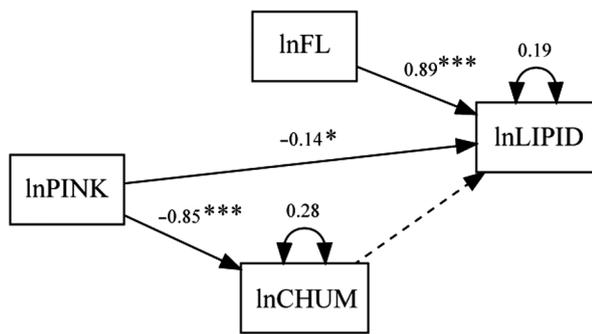


Fig. 3. Path diagram showing relationships among variables including chum salmon *Oncorhynchus keta* log-transformed lipid content (lnLIPID), log-transformed chum salmon fork length (lnFL), log-transformed pink salmon *O. gorbuscha* CPUE (lnPINK), and log-transformed chum salmon CPUE (lnCHUM). Solid arrow: significant path. Double arrow: residual variables. Dashed arrow: path that was eliminated because of low explanatory contribution. Number beside arrows: path coefficients. * $p < 0.05$, *** $p < 0.001$

Interannual variation in chum salmon prey composition

Stomach content composition of chum salmon differed between odd- and even-numbered years (nonparametric MANOVA, $R^2 = 0.098$, $p < 0.001$; Fig. 4). Inter-annual changes in stomach content composition were explained also by lnPINK (nonparametric MANOVA, $R^2 = 0.109$, $p < 0.001$). However, stomach content indices and percentages of fish with empty stomachs did not differ between odd- and even-numbered years. The prey of chum salmon was dominated by non-crustacean zooplankton in odd-

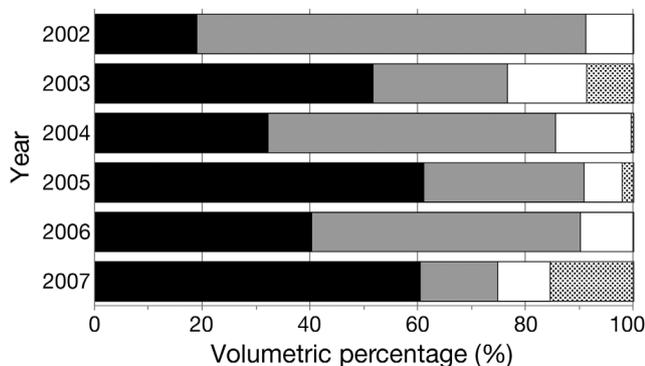


Fig. 4. Mean estimated volumetric percentage of prey composition of chum salmon *Oncorhynchus keta* stomach contents collected in the central Bering Sea during summer, 2002 to 2007. □: Micronekton (fish and squid); ■: crustaceans (amphipod, copepod, decapod, euphausiid, mysid, and ostracod); ■: non-crustacean zooplankton (appendicularian, chaetognath, cnidarian, ctenophora, polychaete, and pteropod); ▨: others

numbered years, which constituted $>52\%$ of the volume of stomach contents and crustaceans comprised 14 to 30% of stomach contents. Crustaceans increased to 50–72% of the composition of stomach contents in even-numbered years and non-crustacean zooplankton decreased to $<40\%$. A similar pattern was observed in crustacean density in net samples, which significantly decreased in odd-numbered years when lnPINK was at a high level as compared to even-numbered years (t -test, $p < 0.001$; with lnPINK $r = -0.473$, $p < 0.001$). On the other hand, non-crustacean zooplankton density was not different between odd- and even-numbered years after excluding the ORI net data in 2003, which showed anomalously high zooplankton density.

DISCUSSION

In the Bering Sea, chum salmon lipid content was significantly affected by chum salmon FL and pink salmon abundance. Chum salmon lipid content decreased in odd-numbered years when pink salmon abundance was high. Chum salmon lipid content was affected less by chum salmon abundance than by pink salmon abundance. Chum salmon shifted the composition of their prey from crustaceans to non-crustacean zooplankton in odd-numbered years when pink salmon was abundant, as has been shown by previous studies (Andrievskaya 1966, Tadokoro et al. 1996). Variability of chum salmon lipid content may be directly controlled by prey selection of chum salmon and indirectly by interspecific competition with pink salmon.

Relationship between lipid content and fork length

Large fish may allocate more energy to lipid storage (mainly in the form of triacylglycerol) than to somatic growth (MacFarlane & Norton 2002, MacFarlane et al. 2005). Accumulated energy reserves (i.e. lipid content) increase more than proportionally with body size in fish (Shul'man 1974, Larson 1991, Schultz & Conover 1997, Huss et al. 2008). For small fish, somatic growth appears to take precedence over deposition of energy reserves in the form of lipids because small individuals are subjected to higher rates of predation mortality than large individuals (Sogard 1997, Sogard & Spencer 2004). The primary mortality source for fish in temperate and cold regions in winter might be starvation, while predation might be the dominant mortality risk in other

seasons (Hurst & Conover 2003). As shown in our results, chum salmon increased allocation to lipid storage as they increased in body size probably as a strategy to offset the risks of overwinter starvation.

Interannual change in chum salmon lipid content

Low lipid content of chum salmon in odd-numbered years might be caused by increased feeding on non-crustacean zooplankton. The composition of non-crustacean zooplankton (appendicularian, cnidarian, ctenophore, and pteropod) is mostly water and to a lesser extent, protein. Non-crustacean zooplankton contains considerably less lipids (0.02 to 5.8% of dry weight) than crustaceans (4.5 to 44.4%) and micronekton (4.3 to 37.2%; Bailey et al. 1995). Fish can efficiently digest and assimilate dietary lipids and often deposit large quantities of lipids in body tissues (Robinson & Mead 1973, Tocher 2003). Feeding experiments have shown increasing dietary lipids increase neutral lipids in fish (Oku & Ogata 2000, Azevedo et al. 2004a,b, Solberg 2004, Budge et al. 2011). On the other hand, dietary protein is used for growth and energy (Phillips 1969). Increasing dietary protein usually depresses hepatic fatty acid synthesis and lipid deposition (Yeh & Leveille 1969, Abdel-Tawwab et al. 2010). Chum salmon lipid storage could be depressed by increased feeding on protein-rich and lipid-poor prey, such as non-crustacean zooplankton when pink salmon are abundant.

In addition, non-crustacean zooplankton contains less energy than crustacean zooplankton (Davis et al. 1998, Davis 2003). Lipids can be synthesized from glucose derived from dietary carbohydrate or glucogenic amino acids in the liver in addition to the synthesis from dietary fatty acids absorbed by intestinal mucosae (Newsholme & Start 1973). Hepatic lipogenesis is enhanced by consumption of high surplus energy (Alvarez et al. 2000). If the amount of energy intake by chum salmon was lower in odd-numbered years when chum salmon fed mainly on non-crustacean zooplankton, the amount of lipid synthesis could also be lower.

Depleted lipid reserve is often assumed to be a major source of overwintering mortality in young fish (e.g. Bernard & Fox 1997, Hurst & Conover 1998, Pratt & Fox 2002, Simpkins & Hubert 2003, Biro et al. 2004). Young or small fish usually have lower energy reserves than old or large fish (Schultz & Conover 1997) and tend to use energy reserves more rapidly because the mass-specific metabolic rate is higher for small fish than for large ones (Shuter & Post 1990,

Post & Lee 1996). During the freshwater phase, overwintering mortality of young rainbow trout *Oncorhynchus mykiss* is high, size-dependent, and linked to the depletion of lipid reserve to a threshold minimum lipid level (<1% of total wet mass; Biro et al. 2004). In the ocean, lipids in immature chum salmon decrease considerably in winter (<1.7% of total WW; Nomura et al. 2000). In years with high pink salmon abundance, juvenile and immature chum salmon increase their feeding on non-crustacean zooplankton in summer, which leads to low lipid reserve in fall. Low lipid reserve of chum salmon, especially in young fish, could raise starvation-based mortality in winter when prey availability is low.

Interspecific effect on chum salmon prey selection

Our results showed an interspecific effect of pink salmon abundance on chum salmon prey selection. Density-dependent growth of Pacific salmon has been reported not only within species but also between species (Ogura et al. 1991, Ishida et al. 1993, Welch & Morris 1994, McKinnell 1995, Bugaev et al. 1996), and pink salmon can influence growth of other salmon species by reducing availability of prey (e.g. Ogura et al. 1991, Salo 1991, Ruggerone et al. 2003). Chum salmon stomach content in even-numbered years was similar to that of pink salmon because chum salmon basically consume the same prey as pink salmon (Tadokoro et al. 1996). Pink salmon are more selective feeders than chum salmon (Takagi et al. 1981), and primarily consume crustaceans in the central Bering Sea (Tadokoro et al. 1996, Davis 2003). Pink salmon are considered more efficient foragers compared with chum salmon or sockeye salmon (Ruggerone & Nielsen 2004). Biomass of crustaceans decreased with the increase of pink salmon CPUE in the central Bering Sea (Tadokoro et al. 1996, present study). Low availability of crustaceans in the Bering Sea when pink salmon are abundant may create unfavorable feeding conditions for chum salmon, which then have to switch to lower energy prey.

Although availability of crustaceans could affect chum salmon lipid content, we failed to detect a significant relationship between crustacean zooplankton density collected using the ORI net and chum salmon lipid content. The ORI net was towed at night in surface waters. Chum salmon swim near the surface water at night and dive through the thermocline during the day (Walker et al. 2000, Ishida et al. 2001, Azumaya & Ishida 2005). Chum salmon consume prey at all times of the day and there is a peak in the

stomach content in the mid-afternoon (Davis et al. 2000). Since the ORI sampling did not cover the distribution layer of chum salmon during daytime, our zooplankton data might have given less accurate estimates of prey availability throughout the daily feeding period of chum salmon, making it insufficient to statistically detect the effect of zooplankton on chum salmon lipid content.

The effect of intraspecific competition on chum salmon lipid content was less than that of interspecific competition of pink salmon abundance. Immature chum salmon experience conditions of low crustacean biomass in odd-numbered years in the central Bering Sea (Tadokoro et al. 1996, present study). Strong intraspecific competition would occur in conditions of low availability of crustaceans for consumption by chum salmon. However, chum salmon are the most omnivorous feeders among Pacific salmon and occupy an unusual trophic position because they consume a large proportion of gelatinous zooplankton (Takagi et al. 1981, Welch & Parsons 1993, Davis 2003). Chum salmon shifted their primary prey from crustaceans to non-crustacean zooplankton with increased pink salmon abundance. Prey switching was observed in age-0 pollock and juvenile salmon (chum, pink, and sockeye salmon) by shifting their prey from large crustacean zooplankton to other prey in the southeastern Bering Sea in years of scarce crustacean zooplankton biomass (Moss et al. 2009, Coyle et al. 2011, Hunt et al. 2011). Pacific salmon and walleye pollock are the dominant species in the epipelagic system of central Bering Sea (Brodeur et al. 1999) and only chum salmon among the dominant species often consume non-crustacean zooplankton (Welch & Parsons 1993). Due to the fact that the biomass of gelatinous zooplankton in the Bering Sea has increased since the early 1990s and has remained at moderate levels in the middle of 2000s (Shuntov et al. 1996, Brodeur et al. 1999, 2002, Mills 2001, Parsons & Lalli 2002, Purcell 2005, Brodeur et al. 2008), intraspecific competition for food in chum salmon might be weak under the present level of gelatinous zooplankton. Omnivorous feeding characteristics of chum salmon could act as a buffer to reduce intraspecific competition.

We may have failed to detect intraspecific competition for a statistical reason. Long-term studies have shown intraspecific competition in chum salmon. Kaeriyama (1998) and Helle et al. (2007) showed negative relationships between population size and body size for Hokkaido and North American chum salmon. Ruggerone et al. (2012) suggested competition with Asian hatchery chum salmon may lead to

low productivity and abundance of wild chum salmon of Norton Sound. Those studies examined data collected for ≥ 36 yr. During the 6 yr of our study period, the fluctuation of CPUE of chum salmon was smaller than that of pink salmon in the central Bering Sea (Fig. 2). The variation of chum salmon CPUE might have been too small to explain the fluctuation of lipid content. With a longer time series, researchers might be able to detect the effect of intraspecific competition.

In summary, we conclude that lipid content of chum salmon decreased due to a shift in their prey selection from crustaceans to lower-lipid and higher-protein non-crustacean zooplankton due to interspecific competition with abundant pink salmon. Low lipid storage in chum salmon during summer, especially in young fish, could positively affect starvation-based mortality during the following winter.

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