

Feeding Habits and Trophic Levels of Pacific Salmon (*Oncorhynchus* spp.) in the North Pacific Ocean

Yuxue Qin¹ and Masahide Kaeriyama²

¹*School of Marine Science and Environmental Engineering
Dalian Ocean University, 52 Heishijiao St., Shahekou District, Dalian, China*

²*Arctic Research Center, Hokkaido University, N15 W8, Kita-ku, Sapporo 060-0815, Japan*

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Abstract: Feeding of Pacific salmon (*Oncorhynchus* spp.) was evaluated by diet composition and stable isotope analysis of carbon and nitrogen. Pacific salmon can be classified into 3 groups; Chinook salmon and steelhead trout as nekton feeders, chum and pink salmon as zooplankton feeders, and sockeye and coho salmon as alternative (zooplankton/nekton) feeders, depending on the conditions in their foraging habitats and intra- and inter-specific interactions. In some ecosystems of the North Pacific Ocean, food chains from phytoplankton to Pacific salmon have the same slope on the linear relationship between carbon and nitrogen stable isotopes based on the kinetic isotope effect. Based on the results of carbon and nitrogen stable isotope analysis, Chinook salmon occupied the highest trophic level (4.3 ± 0.3), followed by steelhead trout (4.1), sockeye (3.9 ± 0.1), coho (3.9 ± 0.4), chum (3.6 ± 0.3) and pink (3.5 ± 0.2) salmon. The framework and function of feeding patterns in Pacific salmon appears to be influenced by both the ecosystem structure in a given foraging habitat and their intra- and inter-specific interactions.

Keywords: Pacific salmon, feeding patterns, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, trophic level

INTRODUCTION

Research on the feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean has been conducted for more than 50 years (Kaeriyama et al. 2004). Their feeding patterns are influenced by climate events such as El Niño and La Niña. In the Gulf of Alaska, all Pacific salmon, except for chum salmon (*O. keta*), consume gonatid squids, mainly *Berryteuthis anonychus*, as a significant component of their diets. However, during the 1997 El Niño and 1999 La Niña event years, squids decreased sharply in the diets of all salmon except coho salmon (*O. kisutch*). Chum salmon changed diets from gelatinous zooplankton to a greater diversity of zooplankton species in both event years.

Prey selectivity in Pacific salmon is related to both intra- and inter-specific differences in functional morphology, physiology, and behavior. For instance, intra-specific variation in diets at different locations is often higher than inter-specific variation at a single location (Ito 1964; Auburn and Ignell 2000). Variation in Pacific salmon food habits is closely associated with spatial-temporal variation in prey abundance and availability (Aydin et al. 2000). At the same time however, chum salmon will shift their diet in response to competition with pink salmon (*O. gorbuscha*) (Tadokoro

et al. 1996). Chum salmon show greater diet plasticity than other Pacific salmon with increased population density in order to minimize intra-specific competition (Kaeriyama et al. 2012). Unfortunately, past research on the feeding habits of Pacific salmon have been carried on at relatively small scales in time and space. There are no long-term research projects or reviews of their feeding habits among ecosystems in the North Pacific Ocean, except for juvenile coho salmon in the Strait of Georgia from 1997 to 2007 (Sweeting and Beamish 2009).

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) provide trophic-level information for predator species in ocean food webs (Minagawa and Wada 1984). Isotopic examination of Pacific salmon shows that Chinook salmon occur at the highest trophic level, followed by steelhead (*O. mykiss*), coho, sockeye (*O. nerka*), chum and pink salmon in the Gulf of Alaska (Satterfield and Finney 2002; Kaeriyama et al. 2004; Johnson and Schindler 2009). Pink, sockeye, and chum salmon appear to have a high overlap in prey species and there was no consistent evidence for chum accessing alternative food webs dominated by gelatinous zooplankton. Chinook (*O. tshawytscha*) and coho salmon were distinctly enriched in $\delta^{13}\text{C}$, suggesting more extensive use of coastal habitats and food webs compared to the depleted signatures of pink, sockeye, and chum salmon (Johnson and Schindler 2009).

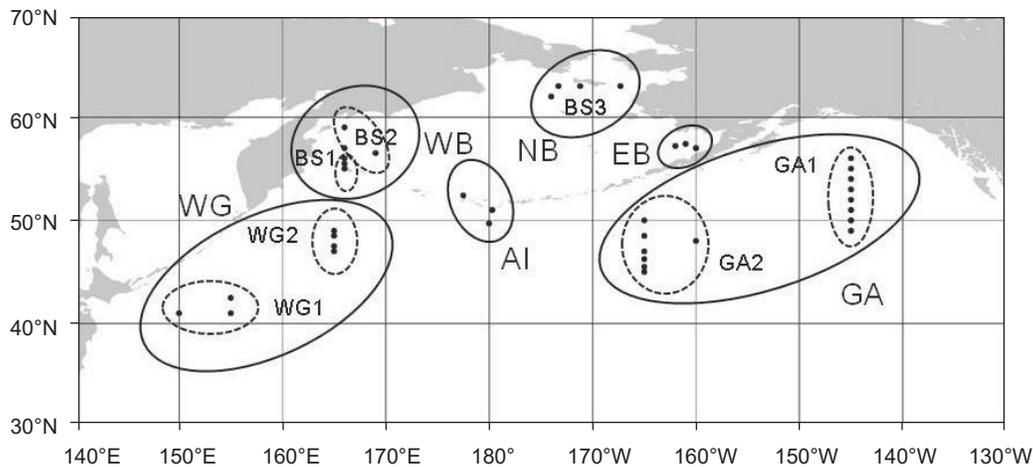


Fig. 1. Survey areas for comparing prey animals of Pacific salmon in the North Pacific Ocean: Gulf of Alaska (GA1–2), Western Subarctic Gyre (WG1–2), western Bering Sea (BS1–2), and northern Bering Sea (BS3). Also shown are areas for carbon and nitrogen stable isotope analysis: Gulf of Alaska (GA), Western Subarctic Gyre (WG), western Bering Sea (WB), northern Bering Sea (NB), eastern Bering Sea (EB), and the coastal sea along the Aleutian Islands (AI).

Vander Zanden et al. (2000) presented a dual isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) method for measuring the trophic level of aquatic consumers that corrects for variation in $\delta^{15}\text{N}$ signatures at the base of the food web among and between different feeding habits. In this method, trophic level was determined by

- (i) generating a primary consumer (baseline) $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ relationship specific to the 13 study lakes,
- (ii) using the $\delta^{13}\text{C}$ value of the aquatic consumer to define the appropriate $\delta^{15}\text{N}$ value from which to estimate trophic level, and
- (iii) estimating the consumer's trophic level using the consumer $\delta^{15}\text{N}$ value and the $\delta^{13}\text{C}$ -adjusted baseline $\delta^{15}\text{N}$ value using the formula

$$\text{Trophic level} = \left(\left(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}} \right) / 3.4 \right) + 2,$$

where 3.4 is the assumed per trophic level per mil increase in $\delta^{15}\text{N}$. The +2 term is added because trophic level is being estimated relative to primary consumers rather than to primary producers. However, stomach contents of consumers usually include a number of prey species. Allen and Aron (1958) Ito (1964), and Takeuchi (1972) observed that pink salmon foraged and stacked copepods, euphausiids, and amphipods in layers in their stomachs. Therefore, the trophic level of prey animals is necessarily not constant because of the variety of prey species.

Wada et al. (2013) and Aita et al. (2011) examined trophic fractionation of carbon and nitrogen isotopes for food chains in various ecosystems, and determined that

- (i) the ratios of trophic fractionation of carbon and nitrogen isotopes ($\Delta\delta^{15}\text{N} / \Delta\delta^{13}\text{C}$) throughout the food chain were obtained as the slope of the linear regression line on the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ plot, and

- (ii) the slopes on the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ were not significantly different among various ecosystems.

They attributed the common slope to physiological aspects of feeding processes such as the kinetic isotope effect which changes the rate of a chemical reaction when one of the atoms in the reactants is substituted with one of its isotopes (Minagawa et al. 1992). In the trophic fractionation of carbon and nitrogen isotopes in a food web, the slope of the regression ($\Delta\delta^{15}\text{N} / \Delta\delta^{13}\text{C}$) can be assumed constant. We used this methodology to review the feeding habits and the trophic levels of Pacific salmon, and to define the framework and function of their feeding patterns.

MATERIALS AND METHODS

Data Sources

Our study on the feeding habits and trophic dynamics of Pacific salmon in the North Pacific Ocean is based on both our survey and an extensive literature review. In our survey, we collected stomach contents and muscle samples, 1–3 g/individual, of Pacific salmon and their prey on board the Hokkaido University vessel T/V *Oshoro maru* in the North Pacific Ocean. For the analyses of diets, we sampled more than 4,000 individuals, and for carbon/nitrogen stable isotope analysis, 600 individual Pacific salmon, 2 samples of phytoplankton, and 227 samples of zooplankton, respectively (Fig. 1, Table 1). Our literature review examined LeBasseur (1966), Percy et al. (1988), and Kaeriyama et al. (2004) for Pacific salmon stomach contents.

Table 1. Number of samples* for analyses of stomach contents and $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ of Pacific salmon in the North Pacific Ocean

Organism	Stomach content	Stable isotope
Pacific salmon		
Sockeye	1,768	82
Chum	1,038	202
Pink	907	183
Coho	481	81
Chinook	57	10
Steelhead	198	42
Total	4,449	600
Plankton		
Phytoplankton		2
Zooplankton		227
Total		229

*containing no literature information

Measurement of Stomach Contents

We weighed (wet mass, g) and counted prey animals and classified them into 12 taxonomic groups (Table 2). Stomach content weights were analyzed in terms of the stomach content index (SCI) as follows:

$$\text{SCI} = \text{PW} \times 100 / \text{BW},$$

where *BW* and *PW* are body weight of Pacific salmon and prey weight in their stomach. To assess the stomach contents of each fish, we estimated the index of relative impor-

tance (IRI) (Pinkas et al. 1971) as follows:

$$\text{IRI} = F(N + W),$$

where *F* is the frequency of occurrence of prey in the stomach, *N* is the percentage by number of prey, and *W* is the percentage by mass of prey. A catch per unit effort (CPUE) is expressed for each species in terms of the number of individuals per a tan (50-m panel) of gillnet.

Measurement of Carbon and Nitrogen Stable Isotopes

All samples for stable isotope analysis were washed using deionized water and dried at 60°C for at least 48 h. Following this, the samples were ground into fine powder with a mortar and pestle. We extracted lipids from all samples by rinsing with a 2:1 solution of chloroform-methanol. Approximately 0.5–1.5 mg of each sample was then packed into a tin cup and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by MAT252 mass spectrometry (Finnigan MAT, Bremen, Germany). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were expressed as follows:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{‰}) = \left(\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right) \times 1000,$$

where *R* is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, respectively. We used the Pee Dee Belemnite and atmospheric N_2 as standards for carbon and nitrogen stable isotope analysis, respectively.

Estimation of Trophic Level

We estimated the trophic level of Pacific salmon using the following formulas:

- for trophic level of prey in a stomach: Prey baseline TL = $\Sigma(\text{TL}_i \times P_i)$,

Table 2. Prey animals and food items of Pacific salmon

Food items	Species
Euphausiids (EU)	<i>Thysanoessa longipes</i> , <i>Thysanoessa</i> spp., <i>Euphausia pacifica</i> , <i>Euphausia</i> spp., Other euphausiids
Copepods (CO)	<i>Neocalanus cristatus</i> , <i>N. plumchrus</i> , <i>Eucalanus bungii</i> , Other copepods
Amphipods (AM)	<i>Themisto pacifica</i> , <i>Themisto japonica</i> , <i>Themisto</i> spp., <i>Hyperia medusarum</i> , <i>Hyperia</i> spp., Other amphipods
Decapods (DE)	Crab larvae (zoea, megalopa)
Squids (SQ)	<i>Berryteuthis anonychus</i> , <i>Gonatus middendorffi</i> , Other squids
Pteropods (PT)	<i>Limacina</i> spp., <i>Clione</i> spp.
Fishes (FI)	<i>Stenobranchius leucopsarus</i> , <i>Anoplopoma fimbria</i> , Myctophids, other fish eggs and larvae
Polychaetes (PO)	Polychaetes
Chaetognaths (CH)	<i>Sagitta elegans</i> , Chaetognaths
Gelatinous zooplankton (GE)	Coelenterates, Ctenophores, Salps
Other animals (OT)	Halocypridids, Cumacea, Octopoda, Ostracods, Barnacles, Debris
Unidentified material (UI)	Unidentified materials

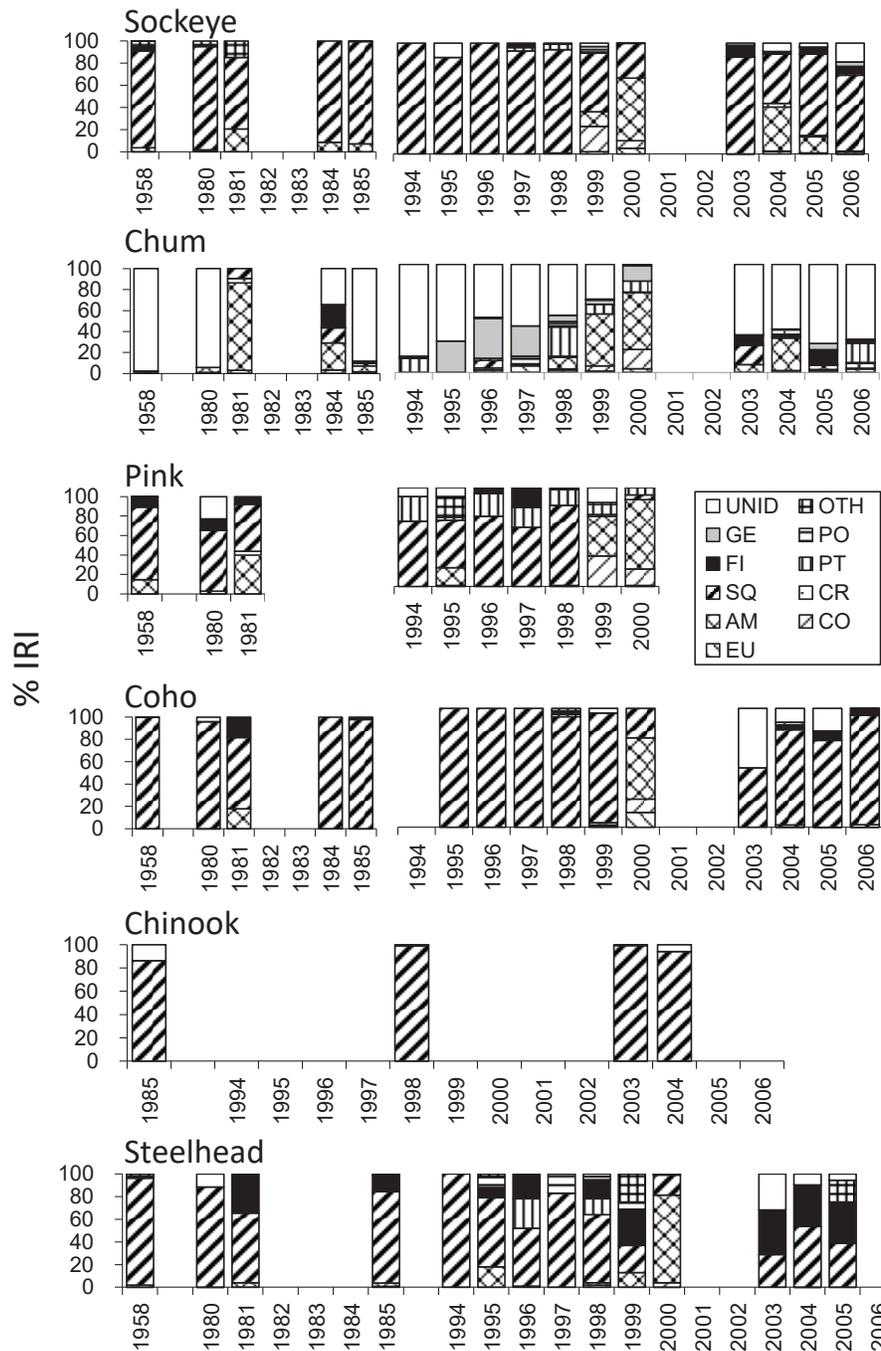


Fig. 2. Annual change in stomach contents of Pacific salmon in the Gulf of Alaska. EU: euphausiids, CO: copepods, AM: amphipods, DE: decapods, SQ: squids, PT: pteropods, FI: fishes, PO: polychaetes, CH: chaetognaths, GE: gelatinous zooplankton, OT: other animals, UI: unidentified material. (See Table 2 for identified prey animals and food items.)

- the $\delta^{15}\text{N}$ of prey in a stomach: Prey baseline $\delta^{15}\text{N} = \sum(\delta^{15}\text{N}_i \times P_i)$,
 - trophic level of Pacific salmon: Salmon TL = (Salmon $\delta^{15}\text{N}$ - Prey baseline $\delta^{15}\text{N}$) / 3.4 + Prey baseline TL
- where TL_p , $\delta^{15}\text{N}_p$, P_i and 3.4 are the trophic level, nitrogen stable isotope, ratio of prey animal i in the stomach, and the assumed increase in $\delta^{15}\text{N}$ per trophic level per ml, respectively.

Data Analysis

The Shannon-Wiener index - H' (Colwell and Futuyama 1971) was used to estimate prey diversity, and the simplified Morishita's index - C_H (Horn 1966) was used to estimate the food-niche overlap between species pairs. The average linkage clustering method of Krebs (1998) was used to estimate food-niche similarity among six spe-

cies of Pacific salmon based on the result of the food-niche overlap analysis in their prey composition. Average linkage clustering begins with the two most similar groups, and is a hierarchical agglomerative, polythetic method that avoids extremes of nearest neighbor and farthest neighbor techniques (Krebs 1998).

One-way analysis of variance (ANOVA) was used to compare carbon and nitrogen stable isotope levels. Carbon and nitrogen stable isotopes were analyzed using simple regression. Significance in all tests was measured at $P < 0.05$. Analysis of covariance (ANCOVA) and the general linear model (GLM) were used to test for differences among the slopes ($\delta^{15}\text{N} / \delta^{13}\text{C}$) of regression lines among different oceanic regions. Regression analysis was used to examine the overall trend in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of animals in food chains. The $\delta^{13}\text{C}$ was treated as a covariate, and sampling region was the independent variable. The interaction between $\delta^{13}\text{C}$ and sampling region had no significant effects on the $\delta^{15}\text{N}$ of the samples and was therefore discarded from the analyses. In cases where ANCOVA tests were significant, the overall significance of differences among the sampled seasons or regions was tested using Tukey's honestly significant difference (HSD) post hoc tests at $P < 0.05$. For each sample, linear regression analysis was also applied to examine the relationships of $\delta^{15}\text{N}$ with $\delta^{13}\text{C}$. Relationships among SCI, H' , CPUE, body sizes of sockeye, chum, and pink salmon in the Gulf of Alaska and the

Western Subarctic Gyre are evaluated by stepwise multiple regression analysis. All statistical analyses were conducted using SPSS ver. 21 (IBM ver. 21).

RESULTS AND DISCUSSION

Feeding Patterns

In the Gulf of Alaska, Pacific salmon, with the exception of chum salmon, did not change their stomach contents, and dominantly fed on gonatid squids, mainly *Berryteuthis anonychus* (Fig. 2). However, in the 1999–2000 La Niña event, squids decreased sharply in stomach contents of all Pacific salmon. This indicates that strong climate events such as the super El Niño and La Niña will affect feeding habits of Pacific salmon (Kaeriyama et al. 2004). Chum salmon showed the highest prey diversity as exhibited by a range of zooplankton, e.g., *Themisto* spp., pteropods, and gelatinous zooplankton.

In our analysis of spatial diet variation (Fig. 3), sockeye and pink salmon fed on squids in the Gulf of Alaska, and zooplankton in other areas. Coho salmon ate squids in the Gulf of Alaska, mainly euphausiids in the Western Subarctic Gyre, and fish larvae in the Bering Sea. Chinook salmon fed on squids in the Gulf of Alaska and fishes in the Western Subarctic Gyre. Steelhead trout foraged on squids and fish-

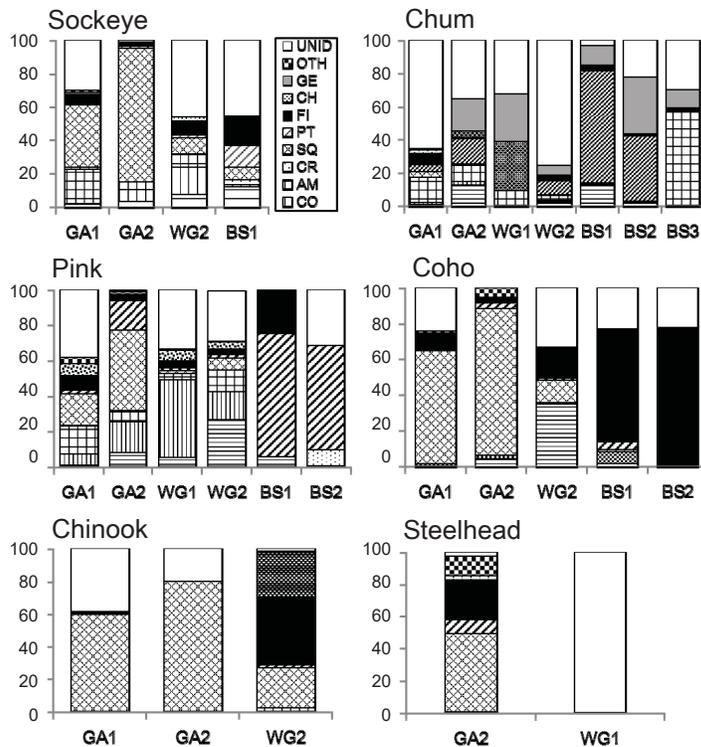


Fig. 3. Stomach contents of Pacific salmon in the North Pacific Ocean ecosystems. GA: Gulf of Alaska, WG: Western Subarctic Gyre, BS: Bering Sea. Letter/number codes represent sampling areas in Fig. 1. Abbreviations as in Fig. 2.

Table 3. Results of the stepwise multiple regression analysis of prey diversity (H') and stomach content index (SCI) for sockeye, chum, and pink salmon in the Gulf of Alaska and the Western Subarctic Gyre.

Criterion variable	Species	Explanatory variable	Slope	r	P_r	R^2	P_{R^2}
H'	Sockeye	CPUE _{chum}	-0.226	-0.372	0.256	0.481	0.020
		FL	-0.008	-0.616	0.027	-	-
		Constant	5.096	-	-	-	-
	Chum	Area	-0.449	-0.546	0.054	0.299	0.142
		FL	0.003	0.338	0.259	-	-
		Constant	0.409	-	-	-	-
	Pink	CPUE _{chum}	0.211	0.500	0.379	0.687	0.001
		CPUE _{pink}	0.124	0.643	0.209	-	-
		Constant	0.571	-	-	-	-
SCI	Sockeye	CPUE _{chum}	-0.750	-0.625	0.079	0.768	<0.001
		CPUE _{sockeye}	-0.300	-0.697	0.038	-	-
		Constant	2.231	-	-	-	-
	Chum	Area	0.202	0.332	0.268	0.123	0.486
		CPUE _{pink}	-0.056	-0.306	0.309	-	-
		Constant	0.409	-	-	-	-
	Pink	CPUE _{chum}	-0.123	-0.164	0.592	0.282	0.609
		CPUE _{pink}	-0.072	-0.233	0.441	-	-
		Constant	1.072	-	-	-	-

es in the Gulf of Alaska. Chum salmon fed on a diversity of zooplankton including gelatinous zooplankton. Specifically, the main diets of Pacific salmon consisted of squids in the Gulf of Alaska, zooplankton in the Western Subarctic Gyre, and zooplankton and fishes in the Bering Sea (Fig. 3). It has also been reported that dominant prey of Pacific salmon are zooplankton in the Western Subarctic Gyre (Allen and Aron 1958; Ito 1964; Takeuchi 1972) but squids in the Gulf of Alaska, except for chum salmon (Percy et al. 1998; Kaeriyama et al. 2004). Coho salmon fed on not only nekton but also zooplankton in the Western Subarctic Gyre, although they ate predominantly nekton in the Gulf of Alaska and the Bering Sea (Fig. 3). Coho salmon are considered to feed on both zooplankton and nekton, and to be opportunistic feeders showing plasticity (Godfrey 1963; LeBrasseur 1966; Godfrey et al. 1975; Groot and Margolis 1991). Primary production and zooplankton biomass in the Western Subarctic Gyre are higher than those in the Gulf of Alaska during spring and summer (Sugimoto and Tadokoro 1997; Nishioka et al. 2007; Yamaguchi 2008) because high concentrations of dissolved iron, supporting biological production, are provided from the Sea of Okhotsk through the Okhotsk Sea Intermediate Water (Nishioka et al. 2007) and atmospheric dust (Duce and Tindale 1991). Biomass of gonatid squids in the Gulf of Alaska exceeds that in the West-

ern Subarctic Gyre (Nesis 1997; Okutani 2005). However, distribution densities of Pacific salmon (sockeye, chum, and coho) and steelhead trout in the Gulf of Alaska are higher than those in the Western Subarctic Gyre during spring and summer (Godfrey et al. 1975; French et al. 1976; Neave et al. 1975; Azumaya et al. 1999). Therefore, the differences in ecosystem structure between the Gulf of Alaska and the Western Subarctic Gyre result in spatial diet variation in Pacific salmon.

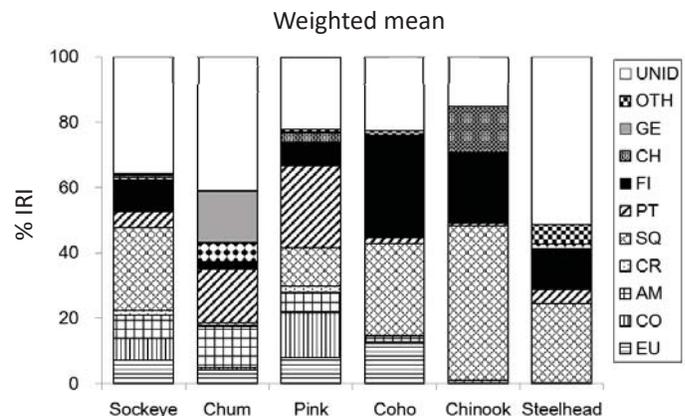


Fig. 4. Summarized prey composition of Pacific salmon in the North Pacific Ocean. Abbreviations as in Fig. 2.

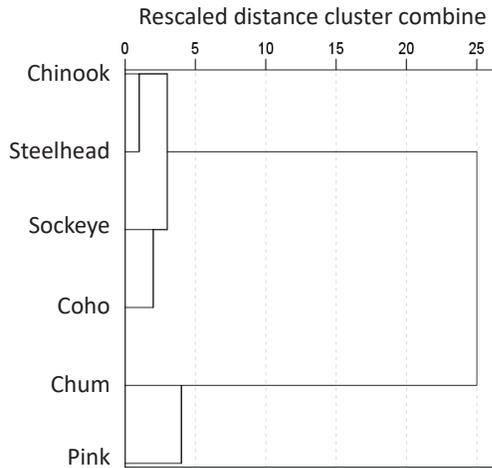


Fig. 5. Cluster analysis of the summarized prey composition of Pacific salmon in the North Pacific Ocean.

In Pacific salmon, only chum salmon fed significantly on gelatinous zooplankton (Figs. 2, 3), which have lower nutritional value than other prey (Davis et al. 1998). Chum salmon can feed on larger, lower-trophic prey animals because they have a relatively wide esophagus (Welch 1997), strong gastric acid (Azuma 1992), and more pyloric caeca (Kaeriyama and Urawa 1990) than other Pacific salmon. Gelatinous zooplankton are chiefly fed on by other animals such as ocean sunfish (*Mola mola*) and loggerhead turtle (*Caretta caretta*) (Gregory and Raven 1934; Nakamura and Sato 2014). In a captivity experiment, filefish (*Stephanolepis cirrhifer*) fed euphausiids and jellyfish showed significantly faster growth than those fed euphausiids alone. This indicates a metabolic role for jellyfish as prey despite its apparently low nutritional value (Miyajima et al. 2011). This evidence suggests that feeding habits of fish and the value of prey should not be judged solely by the energy and nutrition of prey. Chum salmon shifted from preying on copepods and euphausiids to gelatinous zooplankton during periods of high pink salmon abundance in the Bering Sea (Tadokoro et al. 1996). Also, pink salmon decrease the pro-

portion of squid in their prey (Ito 1964; Pearcy et al. 1988), and reduce body size (Ishida et al. 1998) during periods of high abundance. We found a positive correlation between an index of consumed food diversity and the CPUE of chum salmon in the Bering Sea (Kaeriyama et al. 2012). It has been suggested that chum salmon avoid feeding competition with other species (Welch 1997). Avoiding competition for prey may be linked to the chum salmon’s slow swimming speed relative to other Pacific salmon (Groot et al. 1995). Therefore, chum salmon show relatively high plasticity in their feeding, shifting their diets from dominant and preferred prey species when faced with intra- and inter-specific competition.

The results of stepwise multiple regression analysis on prey diversity and SCI of sockeye, chum, and pink salmon in the Gulf of Alaska and the Western Subarctic Gyre (Table 3) denoted that (i) sockeye salmon decreased food diversity with densities of sockeye and chum salmon, and increased food consumption with body size, and that (ii) pink salmon increased prey diversity with densities of chum and pink salmon. Pacific salmon change from small zooplankton (e.g., copepods and amphipods) to nekton with growth (LeBrasseur 1966; Pearcy et al. 1988). Tadokoro et al. (1996) also reported that chum salmon shifted diets from crustacean zooplankton to gelatinous zooplankton with increases in abundance of pink salmon. Therefore, these changes in the feeding patterns of sockeye and pink salmon will be based on intra- and inter-species competition and interaction.

Summarizing prey composition of Pacific salmon in all areas of the North Pacific Ocean, Chinook salmon and steelhead trout predominantly fed on squids and fishes; coho and sockeye salmon foraged on squids and zooplankton; and chum and pink salmon fed on a diversity of zooplankton (Fig. 4). In our analysis of food niche overlap (Fig. 5) Pacific salmon can be classified into three groups;

- nekton feeders: Chinook salmon and steelhead trout,
- zooplankton feeders: chum and pink salmon,
- alternative (zooplankton/nekton) feeders: sockeye and coho salmon,

depending on conditions in their foraging habitats (Fig. 6).

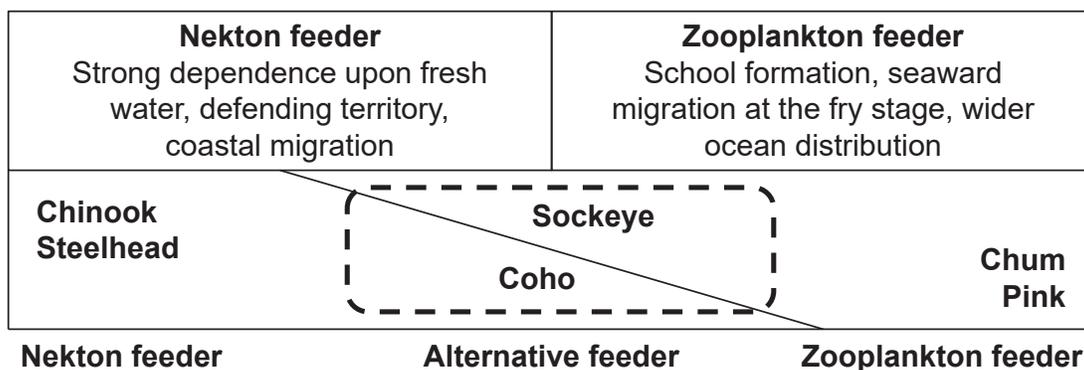


Fig. 6. Feeding patterns of Pacific salmon based on their life history.

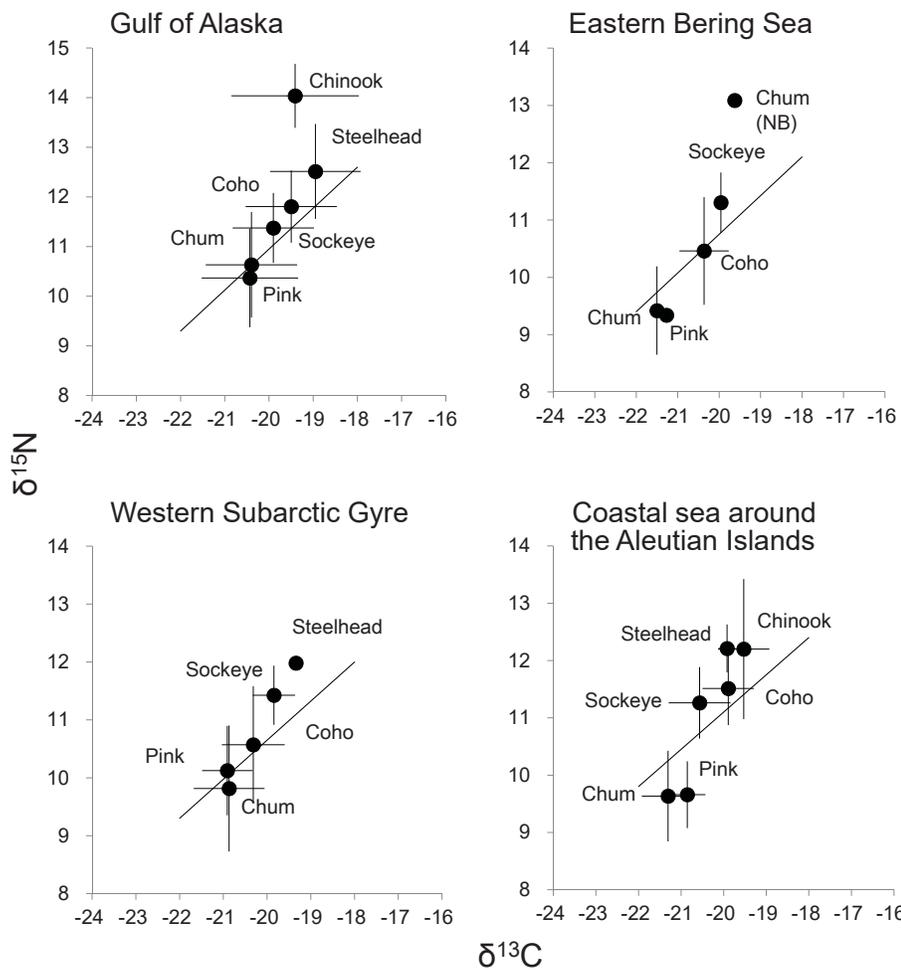


Fig. 7. Means and SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pacific salmon in the North Pacific Ocean and the Bering Sea. NB: northern Bering Sea.

Similarly, a review of the evolution and life-history variation in Pacific salmon suggests that their feeding patterns can be divided into three groups; nekton, zooplankton, and alternative feeders (Kaeriyama 1989, 1996; Stearley and Smith 1993; Murata et al. 1993; Quinn 2005). Chinook salmon and steelhead as nekton feeders are dependent on the freshwater portion of their life history and their coastal migration. Chum and pink salmon, as zooplankton feeders, show schooling, seaward migration immediately after emergence, and a wide distribution in the ocean. Sockeye and coho salmon can be either plankton or nekton feeders depending on the conditions in a given foraging habitat and in-

tra- and inter-specific interaction, although they mainly feed on squid, given the opportunity.

Trophic Level Evaluated by the Carbon and Nitrogen Stable Isotope Analysis

Figure 7 shows the relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pacific salmon in the Gulf of Alaska, the Western Subarctic Gyre, the eastern and northern Bering Sea, and the coastal sea around the Aleutian Islands. In most areas, Chinook salmon had the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, followed by steelhead trout, coho, sockeye, chum and pink salmon. An exception

Table 4. Results of analysis of covariance for the slopes and intercepts of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of Pacific salmon in the North Pacific Ocean.

Parameter	F	P	df	Slope	t'	P'	Intercept	SE ²
$\delta^{13}\text{C}$	29.365	<0.001	608, 4	0.436	15.733	<0.001	-25.197	0.283
Area	8.070	<0.001	-	-	-	-	-	-
$\delta^{13}\text{C}$ X Area	2.283	0.059	-	-	-	-	-	-

¹t' and P' for slope, ²standard error of intercept

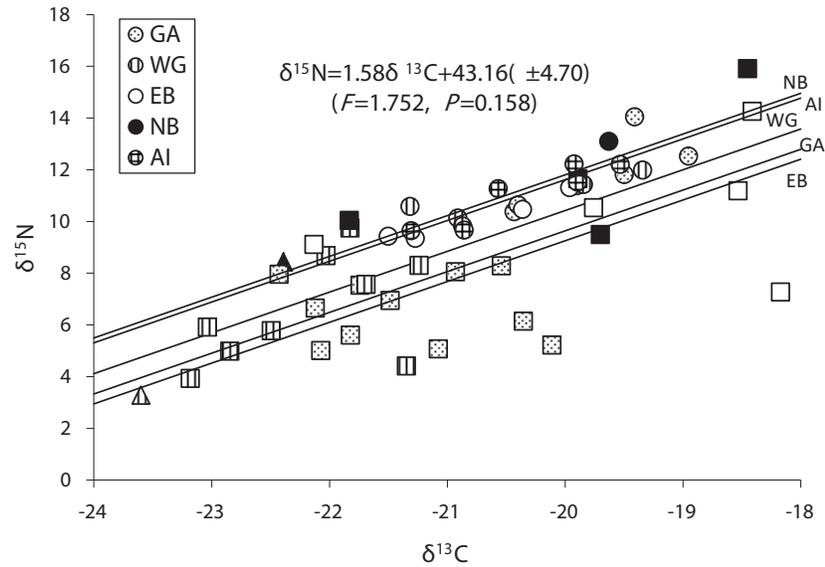


Fig. 8. Relationship between mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of phytoplankton (triangles), zooplankton (squares), and Pacific salmon (circles) in the North Pacific Ocean. GA: Gulf of Alaska, WG: Western Subarctic Gyre, EB: eastern Bering Sea, NB: northern Bering Sea, AI: coastal sea of Aleutian Islands in the Bering Sea.

was the northern Bering Sea in which chum salmon had the highest $\delta^{13}\text{C}$ (-19.63 ± 0.14 ‰) and $\delta^{15}\text{N}$ (13.09 ± 1.40 ‰). This exception may arise from upwelling and nutrients that enrich the marine environment in the southwestern Chukchi Sea and central Bering Sea shelf (Schell et al. 1998). Chum salmon in our study were collected near the strong upwelling area off St. Lawrence Island. Furthermore, these areas with maximum enrichment are presumed to result from the isotopic discrimination arising in the presence of high nutrient abundance and slow phytoplankton growth rates because of the cool climate (Schell et al. 1998).

The relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pacific salmon showed parallel regression lines for these four ecosystems ($\delta^{15}\text{N} = 0.436 \delta^{13}\text{C} - 25.197 \pm 0.283$). The ANCOVA resulted in a level of significance that failed to reject the null hypothesis of “no interaction” ($F = 2.283$, $P = 0.059$; Table 4, Fig. 7). Figure 8 shows mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of phyto- and zooplankton, and Pacific salmon in the Gulf of Alaska, the Western Subarctic Gyre, the eastern and northern Bering Sea, and the coastal sea around the Aleutian Islands. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of phytoplankton in the northern Bering Sea (-22.39 ‰, 8.43 ‰) were higher than those (-23.60 ± 0.67 ‰, 3.28 ± 0.23 ‰) in the Western Subarctic Gyre. The rela-

tionship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of those organisms showed parallel regression lines for these five ecosystems ($\delta^{15}\text{N} = 1.58\delta^{13}\text{C} + 43.16 \pm 4.70$). The ANCOVA results suggest “no interaction” between these parameters ($F = 1.752$, $P = 0.158$; Table 5, Fig. 8). These results suggest that there is a kinetic isotope effect (Wada et al. 2013) in North Pacific Ocean ecosystems. Each ecosystem should have a linear relationship on the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ map if all animal components in the system share the same ratio of trophic fractionation of carbon and nitrogen, $\Delta\delta^{15}\text{N} / \Delta\delta^{13}\text{C}$ reflecting the constraints of their metabolic processes provided that isotopic composition of primary producers is kept constant in time and space.

The kinetic isotope effect is a change in the rate of a chemical reaction when one of the atoms in the reactants is substituted with one of its isotopes (Minagawa et al. 1992). Following this idea, Wada et al. (2013) found a common slope among several ecosystems demonstrating the kinetic isotope effect during bulk amino acid synthesis. According to Aita et al. (2011), the Oyashio, which is a cold subarctic ocean current in the Western Subarctic Gyre, the warm core ring (off Sanriku, Japan), the Antarctic Ocean, and the Gulf of Alaska all show the following relationship: $\delta^{15}\text{N} = (1.53 \pm 0.25)\delta^{13}\text{C} + (40.9 \pm 5.6)$. There is no significant difference

Table 5. Results of analysis of covariance for the slopes and intercepts of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of phytoplankton, zooplankton, and Pacific salmon in the North Pacific Ocean and the Bering Sea.

Parameter	F	P	df	Slope	t ¹	P ¹	Intercept	SE ²
$\delta^{13}\text{C}$	23.257	<0.001	4, 49	1.580	6.918	<0.001	43.155	4.701
Area	2.473	0.050	-	-	-	-	-	-
$\delta^{13}\text{C} \times \text{Area}$	1.752	0.158	-	-	-	-	-	-

¹t and P for slope, ²standard error of intercept

between slopes derived in our results ($\delta^{15}\text{N} = 1.58\delta^{13}\text{C} + 43.16 \pm 4.70$) and the above formula. Specifically, the North Pacific Ocean can be classified into three ecosystems based on the isotopic composition of phytoplankton: (i) northern Bering Sea and coastal sea of the Aleutian Islands, (ii) Western Subarctic Gyre, and (iii) Gulf of Alaska and eastern Bering Sea. This supports the previous hypothesis that primary production and zooplankton biomass in the Western Subarctic Gyre is higher than that in the Gulf of Alaska because of the high concentrations of dissolved iron provided from the Okhotsk Sea (Sugimoto and Tadokoro 1997; Yamaguchi 2008). The mean and standard deviation of the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ and the trophic level of Pacific salmon (Salmon TL) form three groups in the North Pacific Ocean and the Bering Sea (Fig. 9). Chinook salmon occupied the highest trophic level (4.3 ± 0.3), followed by steelhead trout (4.1), sockeye (3.9 \pm 0.1), coho (3.9 \pm 0.4), chum (3.6 \pm 0.3) and pink (3.5 \pm 0.2) salmon.

CONCLUSION

Chum and pink salmon that migrate seaward at an earlier developmental stage are more abundant and have a wider area of ocean distribution than Chinook salmon and steelhead that rear extensively in fresh water (Kaeriyama 1985). Chum and pink salmon are relatively slim, have more gill rakers, form schools, and feed on zooplankton. In contrast, Chinook salmon and steelhead have a robust shape, larger mouth, fewer gill rakers, exhibit territoriality, and feed largely on nekton (Neave 1958; Hoar 1976; Kaeriyama 1996). It should be noted that chum and pink salmon are far more abundant and are found at higher biomasses than Chinook salmon and steelhead throughout the North Pacific and Bering Sea. The relative abundance of chum and pink salmon may reflect their ability to access more abundant prey species at lower trophic levels than Chinook salmon and steelhead. Each ecosystem in the North Pacific Ocean and the Bering Sea appears to conform to the kinetic isotope effect (Wada et al. 2013). The dominant prey of each Pacific salmon species changes in ocean ecosystems due to intra- and inter-specific competition, climate change, and shifts in oceanic productivity.

The structure and function of Pacific salmon feeding patterns are defined by both the ecosystem structure and intra- and inter-specific interactions (Fig. 10). In the North Pacific Ocean, the structure of each ecosystem is controlled by the kinetic isotope effect, in which the relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of phytoplankton, zooplankton, and Pacific salmon show parallel regression lines. These ecosystems can be classified into three groups: (i) northern Bering Sea and the coastal sea of the Aleutian Islands, (ii) the Western Subarctic Gyre, and (iii) the Gulf of Alaska and the eastern Bering Sea (Figs. 7, 8). The prey of Pacific salmon differed among ecosystems (Fig. 3). Further, the feeding patterns of Pacific salmon can be classified into three groups: nekton

feeders (Chinook salmon and steelhead trout), zooplankton feeders (chum and pink salmon), and alternative feeders (coho and sockeye salmon) (Fig. 6). The trophic levels of Pacific salmon show species specificity. Chinook salmon occupied the highest trophic level, followed by steelhead, sockeye, coho, chum and pink salmon (Fig. 9).

On the other hand, the feeding patterns of Pacific salmon can also be influenced by both environmental changes in an ecosystem and their intra- and inter-specific interactions. Ecosystems can be changed by environmental factors such as the ENSO, and long-term climate change, including regime shifts. Extreme climate changes can cause a decrease in squid abundance in stomachs of Pacific salmon in the Gulf of Alaska (Fig. 2). Pacific salmon feeding habits are also affected by intra- and inter-specific competition. Chum salmon fed significantly on gelatinous zooplankton, and showed the highest prey diversity (Figs. 2, 3). Sockeye salmon decreased food diversity with densities of sockeye and chum salmon, and increased food consumption with body size. In contrast, pink salmon increased prey diversity with densities of chum and pink salmon (Table 3). For Pacific salmon, therefore, feeding patterns relate to species specificity and plasticity.

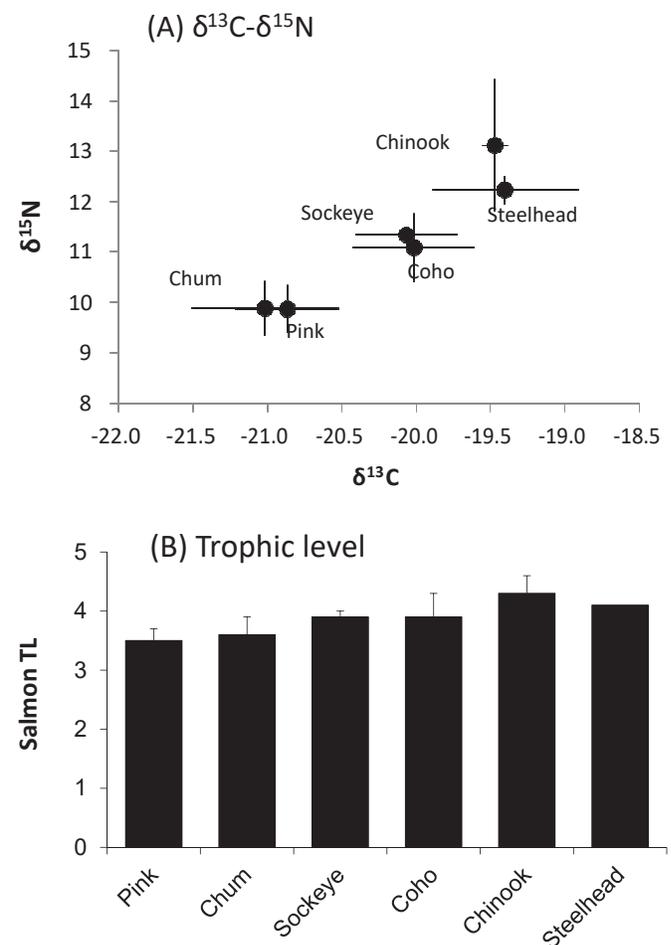


Fig. 9. Means and SD of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ (A) and trophic level (B) for Pacific salmon in the North Pacific Ocean.

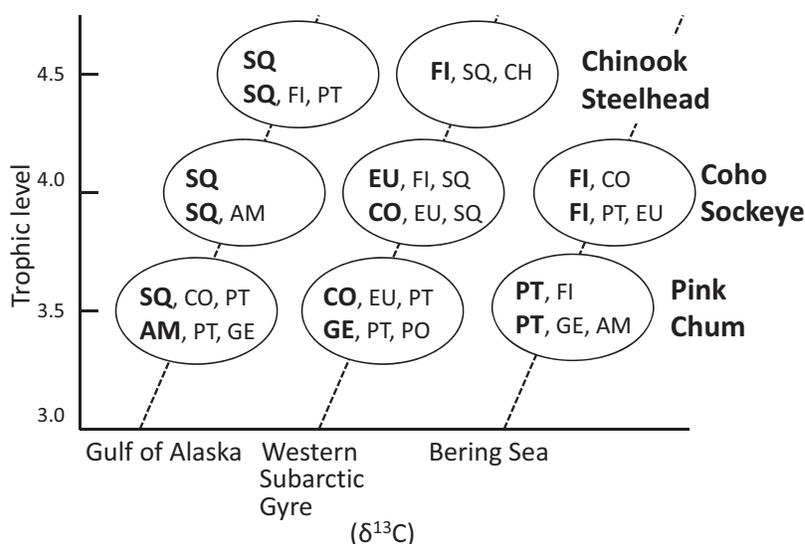


Fig. 10. Schematic view of the framework and function of feeding patterns for Pacific salmon in the North Pacific Ocean. Bold abbreviations are dominant prey animals in the stomach contents. Abbreviations as in Fig. 2.

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REFERENCES

- Aita, M.N., K. Tadokoro, N.O. Ogawa, F. Hyodo, R. Ishii, S.L. Smith, M.J. Kishi, Y. Saino, S. Saitoh, and E. Wada. 2011. Linear relationship between carbon and nitrogen isotope ratios along simple food chains in marine environment. *J. Plankton Res.* 33: 1929–1942.
- Allen, G.H., and W. Aron. 1958. Food of salmon fishes of the western North Pacific Ocean. U.S. Fish Wildl. Serv. Spec. Sci. Rep. 237: 1–11.
- Auburn, M.E., and S.E. Ignell. 2000. Food habits of juvenile salmon in the Gulf of Alaska July–August 1996. *N. Pac. Anadr. Fish Comm. Bull.* 2: 89–97. (Available at www.npafc.org).
- Aydin, K.Y., K.W. Myers, and R.V. Walker. 2000. Variation in summer distribution of the prey of Pacific salmon (*Oncorhynchus* spp.) in the offshore Gulf of Alaska in relation to oceanographic conditions, 1991–98. *N. Pac. Anadr. Fish Comm. Bull.* 2: 43–54. (Available at www.npafc.org).
- Azuma, T. 1992. Diel feeding habits of sockeye and chum salmon in the Bering Sea during summer. *Nippon Suisan Gakk.* 58: 2019–2025.
- Azumaya T., Y. Ishida, and Y. Ueno. 1999. The long-term mean spatial and temporal distribution of CPUE for pink salmon (*Oncorhynchus gorbusha*) and chum salmon (*O. keta*) in the North Pacific Ocean. *Salmon Rep. Ser.* 47: 130–136.
- Colwell, R.K., and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52: 567–576.
- Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. *N. Pac. Anadr. Fish Comm. Bull.* 1: 145–162. (Available at www.npafc.org).
- Duce, N.D., and N.W. Tindale. 1991. Atmospheric transport of iron and its deposition in the ocean. *Limnol. Oceanogr.* 36: 1715–1726.
- French, R., H. Bilton, M. Osako, and A. Hartt. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. *Int. North Pac. Fish. Comm. Bull.* 34: 1–113.
- Godfrey, H. 1963. Salmon of the North Pacific Ocean—Part IX. Coho, Chinook and masu salmon in offshore waters. 1. Coho salmon in offshore waters. *Int. North Pac. Fish. Comm. Bull.* 16: 1–39.
- Godfrey, H., K.A. Henry, and S. Machidori. 1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. *Int. North Pac. Fish. Comm. Bull.* 31: 1–80.
- Gregory, W.K., and H.C. Raven. 1934. Notes on the anatomy and relationships of the ocean sunfish (*Mola mola*). *Copeia* 5: 145–151.
- Groot, C., and L. Margolis (Editors). 1991. Pacific salmon life histories. Univ. British Columbia Press, Vancouver. 564 pp.
- Groot, C., L. Margolis, and W.C. Clarke. 1995. Physiological ecology of Pacific salmon. Univ. British Columbia Press, Vancouver. 510 pp.

- Hoar, W.S. 1976. Smolt transformation: evolution, behavior, and physiology. *J. Fish. Res. Board Can.* 33: 1233–1252.
- Horn, H.S. 1966. Measurement of “overlap” in comparative ecological studies. *Am. Nat.* 100: 419–424.
- Ishida, Y., S. Ito, Y. Ueno, and J. Sakai. 1998. Seasonal growth pattern of Pacific salmon (*Oncorhynchus* spp.) in offshore waters of the North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 1: 66–80. (Available at www.npafc.org).
- Ito, J. 1964. Food and feeding habit of Pacific salmon (genus *Oncorhynchus*) in their oceanic life. *Hokkaido Reg. Fish. Res. Lab. Bull.* 29: 85–97. (In Japanese).
- Johnson, S.P., and D.E. Schindler. 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecol. Res.* 24: 855–863.
- Kaeriyama, M. 1985. Adaptation and differentiation of *Oncorhynchus*. *Aquabiology* 7: 426–432. (In Japanese with English abstract).
- Kaeriyama, M. 1989. Comparative morphology and scale formation in four species of *Oncorhynchus* during early life. *Jpn. J. Ichthyol.* 35: 445–452.
- Kaeriyama, M. 1996. Effects of population density and habitat environment on life history strategy and migration of juvenile sockeye (*Oncorhynchus nerka*) and chum salmon (*O. keta*). *Sci. Rep. Hokkaido Salmon Hatchery* 50: 101–111.
- Kaeriyama, M., and S. Urawa. 1990. Number of pyloric caeca of salmonids in the northern Japan. *Sci. Rep. Hokkaido Salmon Hatchery* 44: 1–9.
- Kaeriyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker, and K.W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* 13: 197–207.
- Kaeriyama, M., H. Seo, H. Kudo, and M. Nagata. 2012. Perspectives on wild and hatchery salmon interactions at sea, potential climate effects on Japanese chum salmon, and the need for sustainable salmon fishery management reform in Japan. *Environ. Biol. Fish.* 94: 165–177.
- Krebs, C.J. 1998. *Ecological methodology*. Addison Wesley Longman, Menlo Park, California. 620 pp.
- LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. *J. Fish. Res. Board Can.* 23: 85–100.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of $\delta^{15}\text{N}$ along food chains: further evidence and the relationship between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta.* 48: 1135–1140.
- Minagawa, M., S. Egawa, and Y. Kabaya. 1992. Carbon and nitrogen isotope analysis for amino acids from biological samples. *Mass Spectrosc.* 40: 47–56.
- Miyajima, Y., R. Mauda, A. Kurihara, R. Kamata, Y. Yamashita, and T. Takeuchi. 2011. Juveniles of threadsail filefish, *Stephanolepis cirrhifer*, can survive and grow by feeding on moon jellyfish *Aurelia aurita*. *Fish. Sci.* 77: 41–48.
- Murata, S., N. Takasaki, M. Saitoh, and N. Okada. 1993. Determination of the phylogenetic relationships among Pacific salmonids by using short interspersed elements (SINEs) as temporal landmarks of evolution. *Proc. Natl. Acad. Sci.* 90: 6995–6999.
- Nakamura, I., and K. Sato. 2014. Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. *Mar. Biol.* 161: 1263–1273.
- Neave, F. 1958. The origin and speciation of *Oncorhynchus*. *Trans. Roy. Soc. Can.* 551: 25–39.
- Neave, F., T. Yonemori, and R.G. Bakkala. 1975. Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. *Int. North Pac. Fish. Comm. Bull.* No. 35: 1–72.
- Nesis, K.N. 1997. Gonatid squids in the subarctic North Pacific: ecology, biogeography, niche diversity and role in the ecosystem. *Adv. Mar. Biol.* 32: 243–324.
- Nishioka, J., T. Ono, H. Saito, T. Nakatsuka, S. Takeda, T. Yoshimura, K. Suki, K. Kimura, S. Nakabayashi, D. Tsumune, H. Mitsudera, W.K. Johnson, and A. Tsuda. 2007. Iron supply to the western subarctic Pacific: Importance of iron export from the Sea of Okhotsk. *J. Geophys. Res.* 112: 1–15.
- Okutani, T. 2005. *Cuttlefishes and squids of the world*. Seizendo, Tokyo. 253 pp. (In Japanese).
- Pearcy, W.G., R.D. Brodeur, J. Shenker, W. Smoker, and Y. Endo. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches, and oceanographic conditions in the Gulf of Alaska, 1980–1985. *Bull. Ocean Res. Inst.* 26: 29–78.
- Pinkas, L., M. S. Oliphant, and L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *Calif. Fish Game Fish. Bull.* 152. 105 pp.
- Quinn, T.P. 2005. *The behavior and ecology of Pacific salmon and trout*. Univ. Washington Press, Seattle. 378 pp.
- Satterfield, F.R., and B.P. Finney. 2002. Stable-isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 30 years. *Prog. Oceanogr.* 53: 231–246.
- Schell, D. M., B.A. Barnett, and K.A. Vinette. 1998. Carbon and nitrogen isotope ratios in zooplankton in the Bering, Chukchi and Beaufort seas. *Mar. Ecol. Prog. Ser.* 162: 11–23.
- Stearley, R.F., and G.R. Smith. 1993. Phylogeny of the Pacific trout and salmon, *Oncorhynchus*, and genera of the family Salmonidae. *Trans. Am. Fish. Soc.* 122: 1–33.
- Sugimoto, T., and K. Tadokoro. 1997. Interannual interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* 6: 74–93.
- Sweeting, R.M., and R.J. Beamish. 2009. A comparison of the diets of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia from 1997–2007. *N. Pac. Anadr. Fish Comm. Bull.* 5: 255–264. (Available at www.npafc.org).

- Tadokoro, K., Y. Ishida, N.D. Davis, S. Ueyanagi, and T. Sugimoto. 1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuations of pink salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. *Fish. Oceanogr.* 5: 89–99.
- Takeuchi, I. 1972. Food animals collected from the stomachs of three salmonid fishes (*Oncorhynchus*) and their distribution in the natural environments in the northern North Pacific. *Bull. Hokkaido Reg. Fish. Res. Lab.* 38: 1–119. (In Japanese with English abstract).
- Vander Zanden, M.J., B.J. Shuter, N.P. Lester, and J.B. Rasmussen. 2000. Within- and among-population variation in the trophic position of pelagic predator, lake trout (*Salvelinus namaycush*). *Can. J. Fish. Aquat. Sci.* 57: 725–731.
- Wada, E., R. Ishii, M.N. Aita, N.O. Ogawa, A. Kohzu, F. Hyodo, and Y. Yamada. 2013. Possible ideas on carbon and nitrogen trophic fractionation of food chains: a new aspect of food-chain stable isotope analysis in Lake Biwa, Lake Baikal, and the Mongolian grasslands. *Ecol. Res.* 28: 173–181.
- Welch, D.W. 1997. Anatomical specialization in the gut of Pacific salmon (*Oncorhynchus*): evidence for oceanic limits to salmon production? *Can. J. Zool.* 75: 936–942.
- Yamaguchi, A. 2008. Comparison of mesozooplankton biomass down to the greater depths (0–3000 m) between 165E and 165W in the North Pacific Ocean: the contribution of large copepod *Neocalanus cristatus*. *In Pacific and Arctic Oceans: New Oceanographic Research. Edited by K.B. Towles.* Nova Science Publishers, New York. pp. 1–17.