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Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research

Abstract Increasing interest in the marine trophic dynamics of Pacific salmon has been motivated by the recognition of their sensitivity to changing climate and to the competitive effects of hatchery fish on wild stocks. It has become more common to use stable isotopes to supplement traditional diet studies of salmon in the ocean; however, there have been no integrated syntheses of these data to determine whether stable isotope analyses support the existing conventional wisdom of feeding strategies of the Pacific salmon. We performed a meta-analysis of stable isotope data to examine the extent of trophic partitioning among five species of Pacific salmon during their marine lives. Pink, sockeye, and chum salmon showed very high overlap in resource use and there was no consistent evidence for chum relying on alternative food webs dominated by gelatinous zooplankton. $\delta^{15}N$ showed that Chinook and coho salmon fed at trophic levels higher than the other three species. In addition, these two species were distinctly enriched in ^{13}C, suggesting more extensive use of coastal food webs compared to the more depleted (pelagic) signatures of pink, sockeye, and chum salmon. This paper presents the first synthesis of stable isotope work on Pacific salmon and provides $\delta^{15}N$ and $\delta^{13}C$ values applicable to research on the fate of the marine derived nutrients these organisms transport to freshwater and riparian ecosystems.

Keywords Trophic partitioning · Spatial partitioning · Carbon · Nitrogen · Meta-analysis · Stable isotope

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Introduction

There has been increasing interest in understanding the responses of Pacific salmon to marine climate variation (e.g., Pearcy 1992; Hare and Francis 1995; Mantua et al. 1997; Peterman et al. 1998; Hilborn et al. 2003) and to escalating hatchery stocking rates (e.g., Beamish et al. 1997; Cooney and Brodeur 1998; Ruggerone et al. 2003). Pacific salmon (*Oncorhynchus* spp.) spend from 1 to 5 years, depending on the species and population, feeding in the coastal and open oceans before migrating as adults to freshwater habitats to spawn (Groot and Margolis 1991). This marine stage comprises much of their lifetime mortality and most (>95%) of their growth (Groot and Margolis 1991; Quinn 2005). Traditional studies of the trophic ecology of salmon in the ocean have relied on direct diet habit studies (e.g., Pearcy et al. 1988; Brodeur and Pearcy 1992; Davis et al. 1996; Tadokoro et al. 1996; Davis 2003) and, arguably, have been relatively patchy in space and time relative to the scale of the North Pacific Ocean used by Pacific salmon for growth and maturation. In the last two decades there has been an increasing reliance on the stable isotope characteristics of salmon as a means to derive an integrated assessment of their marine foraging ecology (e.g., Welch and Parsons 1993; Kaeriyama et al. 2004). However, to date there has been no systematic synthesis of these data to determine whether the isotope derived patterns of trophic partitioning among the five North American species of Pacific salmon confirm the conventional wisdom regarding their trophic dynamics in the ocean.

The geographic range of North American Pacific salmon extends throughout the Subarctic North Pacific Ocean and Bering Sea. The migration patterns of sockeye, chum, and pink salmon have considerable overlap in the open ocean (Myers et al. 1996, reviewed in Quinn 2005). North American populations move north and west in coastal waters after entering the ocean, moving offshore into the pelagic North Pacific, Bering Sea, and Gulf of Alaska by the end of the first year at sea where

they remain for approximately 1–3 years prior to their spawning migration back to freshwaters (Myers et al. 1996). Many populations of Chinook and coho, on the other hand, tend to remain in coastal waters after migration to the sea with only some populations migrating to the open ocean (Myers et al. 1996; Quinn 2005). Because there is substantial spatial overlap among salmon species, they likely compete for prey resources (Margolis et al. 1966; Godfrey et al. 1975; Burgner et al. 1992).

Marine trophic dynamics have important implications for population dynamics of Pacific salmon. For example, climatically driven changes in ocean productivity have been suggested to drive shifts in the abundance of potential prey for salmon, substantially changing long-term salmon production patterns (Mantua et al. 1997). Moreover, salmon populations may be affected through competitive interactions with other salmon species by shifting their major prey items in response to increases in inter- and intra-specific abundance of competitors (Tadokoro et al. 1996; Walker and Myers 1998; Ruggerone et al. 2003). For instance, sockeye salmon growth and survival declined in response to competition in years with high pink salmon abundance where the two species overlap spatially in the North Pacific and the Bering Sea (Kaeriyama et al. 2000; Bugaev et al. 2001; Ruggerone et al. 2003), suggesting significant overlap in prey resources.

Stomach-content analysis has been used extensively to evaluate the trophic partitioning of Pacific salmon during their marine phase. Common prey items of Pacific salmon include copepods, euphausiids, amphipods, myctophids, squid, and small fishes (Brodeur 1990; Brodeur and Pearcy 1992; Davis et al. 1996; Davis 2003). Although all salmon are considered trophic generalists, some trophic partitioning has been shown both among and within salmon species (LeBrasseur 1966; Pearcy et al. 1988; Brodeur 1990; Davis et al. 1996; Tadokoro et al. 1996). During their first year at sea, sockeye and pink salmon have similar diets that include zooplankton, small fishes, and squid (Brodeur 1990). However, during their second year at sea, pink salmon feed on larger prey than sockeye salmon (Brodeur 1990; Aydin 2000; Kaeriyama et al. 2000). Although chum salmon share many common prey items with other salmon species, they generally do not consume squid in the open ocean and they consume some unique prey items such as gelatinous zooplankton (Brodeur 1990). Coho salmon are known to be opportunistic foragers and mainly feed on prey fishes and invertebrates that are locally abundant in coastal habitats (Brodeur 1990; reviewed in Groot and Margolis 1991). Chinook salmon are mainly piscivorous and their diets reflect the regional prey abundance in coastal habitats as well (Brodeur 1990; Groot and Margolis 1991). Though the body of work is rich and informative, these stomach content analyses represent a snapshot in time, reflecting only the most recently consumed prey items (Gearing 1991) and may not necessarily reflect the diet of a single fish over time.

Stable isotopes of muscle tissues have been increasingly used to examine the trophic ecology of fishes. Muscle tissue integrates dietary composition over several months; therefore, isotope signatures may provide a different picture of dietary tendencies than diet samples (Tieszen et al. 1983; Hobson and Clark 1992). Stable isotope signatures of a consumer reflect two factors: the isotope composition of prey, and the systematic fractionation in isotope signatures that occurs during assimilation. $\delta^{15}N$ increases by 1.3–5.3‰ (average = 3.4) per trophic transfer, while ^{13}C trophic fractionation is subtle and $\delta^{13}C$ increases 0–1‰ per trophic transfer (Minagawa and Wada 1984; Wada et al. 1987; Vander Zanden and Rasmussen 2001). Therefore, the $\delta^{15}N$ signature of fish tissues is often used to infer the trophic position at which a particular fish fed during the last several months (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999). Because carbon fractionation is often negligible, $\delta^{13}C$ in tissues reveal less about the trophic position of a consumer but more about the source of production in a food web (Peterson and Fry 1987; France 1995). In general, carbon in open-ocean marine phytoplankton is depleted in ^{13}C compared to carbon fixed in coastal ecosystems (McConnaughey and McRoy 1979; Fry and Sherr 1984; Duggins et al. 1989). Differences in $\delta^{13}C$ values can be an indicator of offshore versus coastal resources in supporting growth of consumers (Hobson et al. 1994). For example, Schell et al. (1998) showed a pattern of increasingly depleted $\delta^{13}C$ values of zooplankton from on-shelf to pelagic regions in the Bering, Chukchi, and Beaufort seas. Thus, a combination of C and N stable isotope ratios in salmon tissue provides an integrated assessment of the degree of trophic overlap both in terms of trophic position and reliance on coastal versus open-ocean food webs.

Carbon and nitrogen stable isotopes have been used for characterizing differences in trophic ecology of Pacific salmon during their marine phase. For instance, Welch and Parsons (1993) suggested salmon form a trophic hierarchy where pink salmon feed low on the food chain followed in increasing order by sockeye, coho, and finally Chinook salmon, which feed at the highest trophic level. In addition, chum salmon used a different component of the marine food web altogether, likely one dominated by gelatinous zooplankton (Welch and Parsons 1993). Conversely, other studies have shown that chum salmon isotope signatures were similar to pink and sockeye salmon, suggesting that the trophic niches of these species overlap substantially (Satterfield and Finney 2002; Kaeriyama et al. 2004).

We performed a meta-analysis of new and previously published stable isotope data to characterize of the general trophic ecology of Chinook, coho, sockeye, chum, and pink salmon during their marine life-history phase. In particular, we evaluated the evidence for trophic partitioning among these five species of Pacific salmon and assessed the degree to which differences in isotope signature were associated with trophic position

or habitat partitioning associated with pelagic versus coastal food webs.

Materials and methods

Our synthesis of stable isotopes in salmon consisted of two elements: collection and analysis of new samples from southwest Alaska salmon populations, and a meta-analysis including these data and previously published data to seek generalities in the stable isotope ecology of Pacific salmon in the ocean.

Tissue samples were collected from mature Pacific salmon as they entered spawning streams in the Wood River system of Bristol Bay, Alaska, and the Chignik River on the Alaska Peninsula. Salmon in these systems were sampled upon arrival to freshwater during their spawning season (June through September, 2002–2004). Sampling methods included angling, beach seining, and dip-netting. Locations were chosen because all five anadromous Pacific salmon species can be found in these systems.

Muscle tissue was collected from the dorsal musculature posterior to the dorsal fin and was eventually freeze dried and ground to a fine powder. Stable isotope analyses (of N and C) were performed at the University of California Davis stable isotope facility using a PDZ Europa Hydra 20–20 continuous-flow isotope ratio mass spectrometer. All $\delta^{13}C$ and $\delta^{15}N$ isotope values are reported versus the standard for carbon (VPDB) and nitrogen (atmospheric) as:

$$\delta\ (\text{‰}) = 10^3 [R_{\text{sample}}/R_{\text{standard}} - 1]$$
$$R = {}^{13}C/{}^{12}C \quad \text{or} \quad {}^{15}N/{}^{14}N.$$

The measurement precision was estimated at 0.13‰ for $\delta^{15}N$ and 0.05‰ for $\delta^{13}C$. Lipid content can alter $\delta^{13}C$ values if the C:N ratio is greater than ~ 3.5 (Post et al. 2007). The C:N ratio for samples in this study was less than 3.5 therefore lipid correction may not be necessary for salmon muscle tissue. However, to be consistent with other studies compiled for the meta-analysis, we normalized for lipid content (δ') according to McConnaughey (1978) and McConnaughey and McRoy (1979). Welch and Parsons (1993) data were not lipid corrected and C:N ratios were not given in the paper. Therefore, we applied a correction factor calculated for each species of our data to the same species data for Welch and Parsons (1993).

Synthesis of previous results for the meta-analysis was accomplished through a literature review of existing published Pacific salmon stable isotope ($\delta^{15}N$ and $\delta^{13}C$) data. Data for Welch and Parsons (1993) were not listed in tabular format and were, therefore, digitized from Fig. 4 of their manuscript using Engauge Digitizer software. Data were included in the meta-analysis from studies where: species was given, salmon were not juveniles, sample size, and both $\delta^{13}C$ and $\delta^{15}N$ values were reported (Table 1).

A random-effects meta-analysis was conducted for the stable isotope data in this study (Cooper and Hedges 1994). Data were compiled using the mean and SD (standard deviation) by species in each study. The meta-analysis estimates the mean ($\bar{\beta}$) isotopic values for each species and the variance around that mean ($\sigma_{\bar{\beta}}^2$). We assumed individual study means were normally distributed.

The random-effects variance of $\bar{\beta}$ for all studies (v_i^*) is due to the variance related to measurement uncertainty (estimation variance = v_i) and the variance of each study mean (β_i) around the species mean $\bar{\beta}(\sigma_{\beta}^2)$:

$$v_i^* = v_i + \sigma_{\beta}^2.$$

The variance of $\bar{\beta}$ among studies (σ_{β}^2) is calculated from the independent measurements (k) that comprise the study mean β_i and their estimation variances (v_i):

$$Q = \sum_{i=1}^{k} \frac{\beta_i^2}{v_i} - \frac{\left(\sum_{i=1}^{k} \frac{\beta_i}{v_i}\right)^2}{\sum_{i=1}^{k} \frac{1}{v_i}}$$
$$\sigma_{\beta}^2 = \frac{Q - (k-1)}{\sum_{i=1}^{k} 1/v_i - \frac{\sum_{i=1}^{k} (1/v_i)^2}{\sum_{i=1}^{k} 1/v_i}}.$$

The species mean ($\bar{\beta}$) is calculated as a weighted average of the study means β_i:

$$\bar{\beta} = \frac{\sum_{i=1}^{k} \frac{\beta_i}{v_i^*}}{\sum_{i=1}^{k} \frac{1}{v_i^*}}.$$

The variance of the species mean ($\bar{\beta}$) is:

$$\sum_{i=1}^{k} \frac{1}{v_i^*}.$$

We used reduced major axis regression analysis (RMA) to estimate the relationship between the $\delta^{15}N$ and $\delta^{13}C$ among the five salmon species both within each study considered in our meta-analysis, and across the species-specific means obtained from the meta-analysis. RMA is more appropriate than ordinary least squares (OLS) regression when the independent variable is measured with error, which produces a biased estimate of the slope (Sokal and Rohlf 1981). In this case, we assumed that both $\delta^{15}N$ and $\delta^{13}C$ were measured with error.

We compared the RMA slope between $\delta^{15}N$ and $\delta^{13}C$ among the five species of salmon to that which would be expected if this relationship was based on trophic fractionation of N and C isotopes alone, rather than by habitat partitioning among species. We used data from Vander Zanden and Rasmussen (1999), who compiled the trophic fractionation factors for N and C isotopes for several fishes in both field and laboratory situations. Assuming trophic fractionation factors are normally distributed and using first-order error propagation, we

Table 1 Studies included in the synthesis of C and N data for the five species of Pacific salmon

Study	Location	Species	$\delta^{13}C$ (‰)	SD	$\delta^{15}N$ (‰)	SD	n	RMA slope
This study	Southwest Alaska	Sockeye	−21.33	0.48	11.09	0.48	19	2.41
		Chum	−21.90	0.68	10.66	0.95	23	
		Pink	−21.60	0.82	10.48	1.55	27	
		Coho	−20.69	0.58	12.64	0.55	23	
		Chinook	−20.48	0.48	13.83	0.87	12	
Satterfield and Finney (2002)	Southeast, southwest, and south central Alaska	Sockeye	−21.35	0.49	11.24	0.56	47	1.23
		Chum	−21.28	0.72	11.01	1.21	25	
		Pink	−21.89	0.43	10.79	0.41	22	
		Coho	−20.02	0.37	13.81	0.49	12	
		Chinook	−17.85	0.65	15.23	0.34	15	
Kaeriyama et al. (2004)	North Pacific	Sockeye	−19.90	0.92	11.38	0.7	40	1.61
		Chum	−20.40	1.03	10.63	1.06	39	
		Pink	−20.43	1.09	10.37	0.99	37	
		Coho	−19.50	1.03	11.81	0.73	39	
		Chinook	−18.23	0.69	14.04	0.64	6	
Welch and Parsons (1993)	Central North Pacific	Sockeye	−20.66	0.31	11.22	0.53	5	0.93
		Chum	−22.47	0.61	12	1.45	16	
		Pink	−21.21	0.76	10.79	0.41	20	
		Coho	−20.63	0.49	11.62	0.37	10	
		Chinook	−19.72	1.01	13.25	0.54	7	
Chaloner et al. (2002)	Southeast Alaska	Pink	−20.60	0.5	12.7	0.4	5	
Piorkowski (1995)	Southcentral Alaska	Chum	−20.30	0.18	11.51	0.48	4	
		Pink	−21.86	0.44	11.85	0.58	5	
		Coho	−21.83	0.36	11.68	1.1	3	
		Chinook	−19.02	0.79	14.6	0.48	11	
Bilby et al. (1996)	Washington	Coho	−19.45	2.19	13.6	0.85	4	
Ben-David (1996)	Southeast Alaska	Chum	−20.29	0.32	11.57	0.74	3	
		Pink	−21.13	1.33	11.25	0.54	19	
		Coho	−18.62	0.82	12.99	0.59	20	
Meta-analysis		Sockeye	−20.74	0.61	11.29	0.13	123	1.55
		Chum	−21.27	0.96	11.1	0.43	113	
		Pink	−21.16	0.63	11.03	0.7	130	
		Coho	−20.18	0.48	12.67	0.92	107	
		Chinook	−19.06	1.34	14.21	0.84	51	

Isotope data are the average C and N values found for each species in each study, standard deviation (SD) and sample size (N). RMA slope is the reduced major axis regression slope through the species means for that study

calculated the mean and variance of the expected slope of $\delta^{15}N$ versus $\delta^{13}C$ due entirely to trophic fractionation. We calculated the value of these slopes using either only field-derived data from Vander Zanden and Rasmussen (1999) or all the data they compiled. We then compared the observed value determined from the RMA regression to these distributions to assess the possibility that the observed relationship was determined by trophic fractionation of C and N isotopes alone.

Results

Stable isotope values from the samples collected from southwest Alaska salmon were within the ranges of those determined in previous studies (Table 1). Pink salmon were the least enriched and Chinook salmon were the most enriched in ^{15}N from this region. There was much less inter-specific variation in $\delta^{13}C$ (range ~1.4‰) than in $\delta^{15}N$ (range ~3.4‰) and of the five species, chum salmon were the most depleted in ^{13}C while Chinook salmon were the most enriched (Table 1).

Individual studies indicated limited spatial and temporal difference in stable isotope signatures (Fig. 1) and different species exhibited relatively consistent isotope signatures across studies (Table 1). For instance, pink salmon generally had the most depleted and Chinook salmon had the most enriched $\delta^{15}N$ signatures. Inter-study mean $\delta^{15}N$ values ranged from 11.1 to 11.5‰ for sockeye, 10.6 to 12.0‰ for chum, 10.4 to 12.7‰ for pink, 11.6 to 13.8‰ for coho, and 13.3 to 15.2‰ for Chinook salmon. Inter-study means for $\delta^{13}C$ ranged from −19.9 to −21.4‰ for sockeye, −20.3 to −22.5‰ for chum, −20.4 to −21.9‰ for pink, −18.6 to −21.8‰ for coho, and −17.9 to −20.5‰ for Chinook salmon. Thus, the meta-analysis revealed that Chinook exhibited the most enriched isotope signatures for both $\delta^{15}N$ and $\delta^{13}C$ followed by coho salmon. Sockeye, chum, and pink clustered closely together, with pink salmon tending to be the least enriched in both isotopes (Table 1, Fig. 2). Sockeye salmon showed the least variation in $\delta^{15}N$ compared with other species (Fig. 2).

The slope of the RMA regression between $\delta^{13}C$ and $\delta^{15}N$ among all species means (Fig. 2) was 1.55 with a

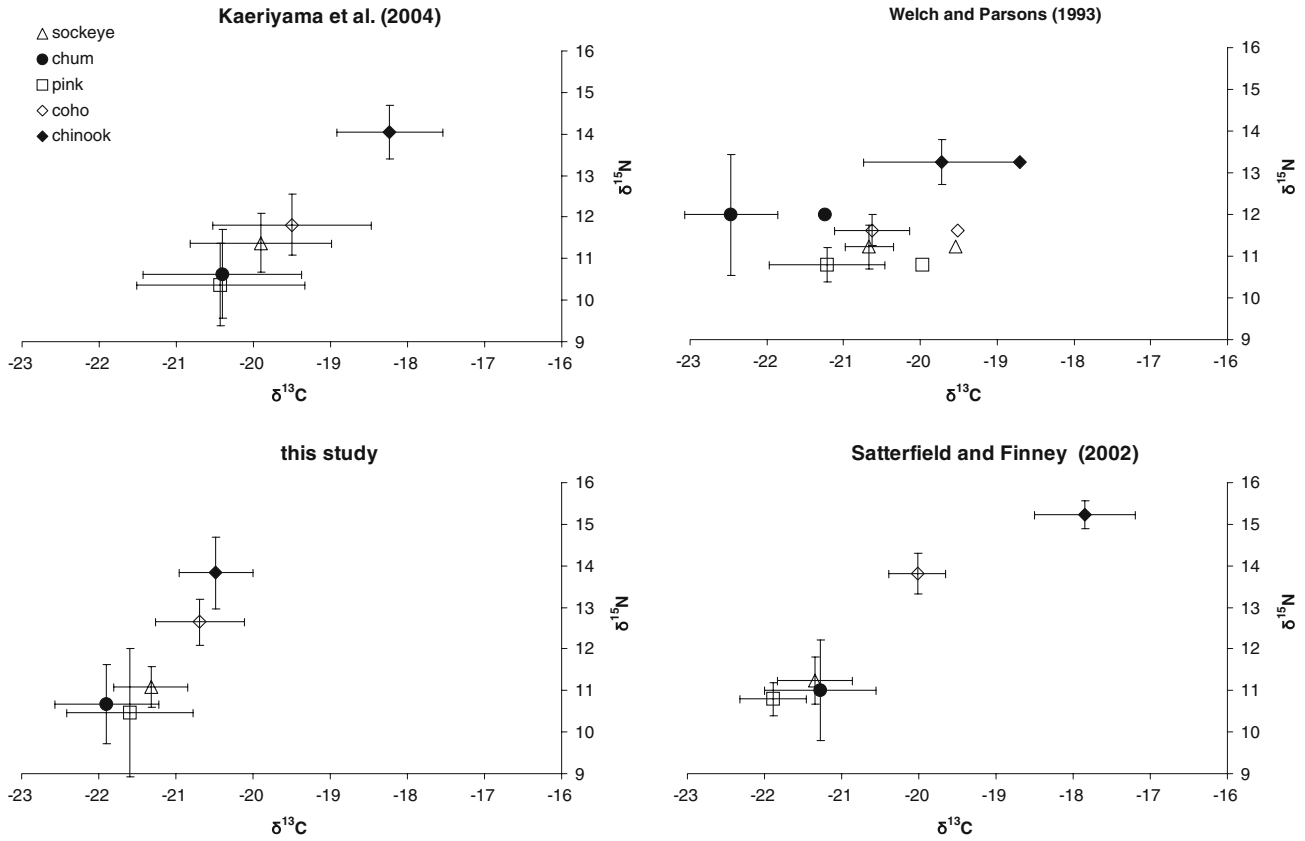**Fig. 1** $\delta^{13}C$ and $\delta^{15}N$ values for studies where values for five Pacific salmon species are listed in Table 1. Each *point* represents the mean isotopic value for the species. *Error bars* are ± 1 SD. *Points without error bars* in the Welch and Parsons (1993) are original data from paper. *Points with error bars* are lipid adjusted values
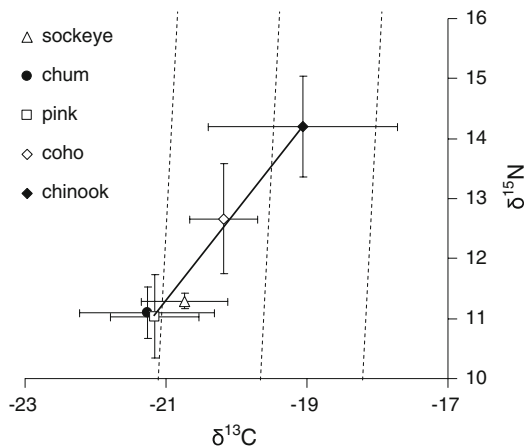

Fig. 2 Average $\delta^{13}C$ and $\delta^{15}N$ values for Pacific salmon from a random-effects meta-analysis. *Error bars* are ± 1 SD. *Solid line* is the RMA regression through the species means (slope = 1.55, $p = 0.007$, 95% CI = 0.75–2.11). *Dashed lines* represent contours of the expected relationship (slope = 17.5 per trophic level) based entirely on trophic fractionation of C and N among species

95% confidence interval of 0.4–2.5. The compilation of trophic fractionation factors for C and N isotopes suggested that this observed slope for the five species of Pacific salmon was unlikely to be derived from trophic fractionation alone. For field studies, average trophic fractionation for $\delta^{15}N$ was 3.4‰ (SD 0.2‰) per trophic level, and for $\delta^{13}C$ was 0.2‰ (SD 0.5‰) per trophic level, yielding an average slope of 17.5. The uncertainty in this estimate was high (SD 10.5), yielding a distribution of likely slope values that was very broad. Based on this distribution, the slope of the observed relationship between the $\delta^{13}C$ and $\delta^{15}N$ among the five species of salmon (Fig. 2) fell in the lower 7% of the distribution of expected slopes based only on trophic fractionation alone (Fig. 3). Similarly, we calculated the most likely slope between $\delta^{15}N$ and $\delta^{13}C$ that would result only from trophic fractionation using all data from Vander Zanden and Rasmussen (2001) (i.e., field and laboratory estimates). This calculation yielded a lower slope (3.9) but with substantially less uncertainty (SD 2.3), thereby producing a much more constrained range of likely slope values (Fig. 3). The value of 1.55 obtained from our meta-analysis fell within the bottom 16% of this distribution (Fig. 3). Thus, while the relationship we observed between the average $\delta^{15}N$ and $\delta^{13}C$ among the five species of Pacific salmon may have been produced simply due to trophic fractionation differences in the metabolism of salmon, it is more likely that this relationship indicates differential habitat use by these species; namely that coho and Chinook salmon feed in food webs with more enriched $\delta^{13}C$ signatures at the base of the food web.

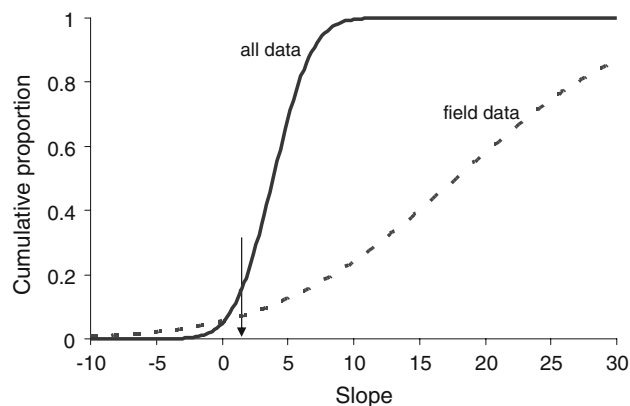Fig. 3 Cumulative distributions of expected slopes describing the relationship between $\delta^{13}C$ and $\delta^{15}N$ based entirely on trophic fractionation. The distributions were calculated based on the data compiled by Vander Zanden and Rasmussen (1999). The *solid line* used data from both laboratory and field studies of isotope fractionation in fishes, while the *dashed line* was derived from field studies only. The *arrow* indicates the observed value of the slope describing the relationship between $\delta^{13}C$ and $\delta^{15}N$ among the five species of Pacific salmon (i.e., 1.55)

Discussion

This study is the first to synthesize the published stable isotope data for the five species of Pacific salmon. While there were small differences in isotopic characteristics of Pacific salmon among studies, there was also a distinct pattern among species across all studies.

Our analyses suggest there is a distinct pattern of trophic partitioning among species of Pacific salmon during their marine life stages. As expected, Chinook salmon occupied the highest trophic position, as indicated by enriched $\delta^{15}N$ values, followed by coho salmon at about half a trophic level lower in the food web. Pink, sockeye, and chum salmon had remarkably high overlap in their isotopic composition, suggesting high overlap in their feeding strategies. Because comprehensive food-web data were not included in all the studies incorporated in our meta-analysis, we assumed the $\delta^{15}N$ at the base of food webs to be roughly similar for all studies. Although this is not ideal for comparison, the pattern of trophic enrichment that we present here is consistent with that found in diet studies where coho and Chinook salmon feed at higher trophic positions than sockeye, pink, and chum salmon (Brodeur 1990; Quinn 2005).

Sockeye, pink, and chum salmon showed almost total overlap in isotopic values, which indicates that they may compete for food resources or at the very least feed on prey resources that occupy the same trophic level. Although Welch and Parsons (1993) hypothesized that chum salmon feed on a different branch of the food web dominated by jellyfish and gelatinous zooplankton, our synthesis of isotopic data from various sources reveals that chum do not consistently show distinctly different isotope values from sockeye or pink salmon. Diet studies have shown that in addition to feeding on jellyfish and

gelatinous zooplankton, chum salmon share prey items common to other salmon species such as amphipods, euphausiids, pteropods, and fishes (Brodeur 1990; Tadokoro et al. 1996). However, stable isotopes may not always be able to partition gelatinous zooplankton from other food web components. Specifically, Brodeur et al. (2002) showed that hydromedusae have a $\delta^{15}N$ signature indistinguishable from euphausiids, a common prey item of salmon and that jellyfish and gelatinous zooplankton showed a $\delta^{13}C$ signature similar to or more enriched than salmon. Our result does not support Welch and Parsons (1993) hypothesis that the depleted $\delta^{13}C$ carbon signature of chum salmon was due to their unique reliance on jellyfish as an energy source and highlights the need for a comprehensive study of trophic dynamics in addition to individual studies exploring spatial and temporal differences in feeding among and within species.

In general, coastal ecosystems (benthic based food webs) are enriched in $\delta^{13}C$ compared to offshore (pelagic based food webs) (e.g., Fry 1981; Duggins et al. 1989; Jennings et al. 1997; Schell et al. 1998; Hobson 1999; Kline 1999; Kline et al. 2008). Studies of various marine organisms have shown differences in $\delta^{13}C$ values obtained from coastal versus offshore environments (reviewed in Hobson 1999; Davenport and Bax 2000). Hobson et al. (1994) used $\delta^{13}C$ values to identify seabirds that foraged nearshore (enriched) from those that fed offshore (depleted). Marine mammals using a nearshore environment had enriched $\delta^{13}C$ values than those that foraged in a pelagic environment (Lusseau and Wing 2006; Sinisalo et al. 2006; Marcoux et al. 2007; Tucker et al. 2007). Studies in fishes have shown similar trends (Thomas and Cahoon 1993; Davenport and Bax 2000; Sherwood and Rose 2007).

Tissue $\delta^{13}C$ in Pacific salmon suggested that interspecific spatial partitioning occurs among these species. Chinook and coho salmon are widely known to use coastal regions and their more enriched $\delta^{13}C$ values suggest they rely more heavily on organic energy sources produced in coastal habitats (Hobson et al. 1994; Schell et al. 1998) compared to the more open-ocean oriented pink, sockeye, and chum salmon that have distinctly depleted $\delta^{13}C$ signatures. The coastal isotope signature of Chinook and coho salmon is in agreement with previous work showing that these species tend to remain in coastal waters after migration to sea, although many populations move offshore for some period of time (Groot and Margolis 1991; Quinn 2005). Additionally, maturing Chinook and coho are known to have a less direct route of migration to natal streams compared to sockeye, pink, and chum salmon; feeding more extensively in coastal waters during their migration (Quinn 2005).

In general, our results show salmon with enriched carbon signatures also had enriched nitrogen signals (Fig. 2). A positive relationship is expected based purely on trophic fractionation because both N and C become enriched in their heavier isotopes as organic matter is

passed up through food webs (Peterson and Fry 1987). The expected slope of this relationship, based entirely on trophic fractionation is broadly defined based on existing data derived from field situations (Fig. 3). However, the slope of the regression through the species means was distinctly lower than the bulk of the distribution of expected values based on trophic fractionation alone (Figs. 2, 3). Although the relationship observed among the five species of salmon was more comparable to the slope calculated from data derived from both laboratory and field studies, it still falls in the lowest 16% of the expected distribution. This comparison indicates that that the species are not simply feeding at different trophic levels in the same ecosystem (Fig. 2). Rather, this indicates that species are obtaining their carbon from different sources, specifically, that Chinook and coho appear to rely more heavily on prey resources that are enriched in $\delta^{13}C$ as is characteristic of nearshore or coastal food webs. This result suggests confirmation of conventional wisdom regarding the heavier use of coastal resources by coho and Chinook salmon (Quinn 2005).

The degree of trophic overlap among salmon species has important implications for understanding impacts of large hatchery programs on other species. There is increasing evidence that large hatchery releases of pink and chum salmon, through resource competition, may negatively impact ocean survival of wild populations of sockeye, pink, and chum salmon (e.g., Beamish et al. 1997; Ruggerone et al. 2003; Ruggerone and Nielsen 2004; Zaporozhets and Zaporozhets 2004). Specifically, the release of high densities of hatchery salmon competing for food resources could reduce the availability of prey resources for wild fish in times of diminished forage production and have negative consequences for wild stocks (Beamish et al. 1997). In fact, Cooney and Brodeur (1998) modeled the forage demand in coastal and oceanic feeding habitats by hatchery and wild pink salmon originating from Prince William Sound, Alaska, and found that annual food consumption tripled after hatchery production dominated the returns for these stocks. Our results help provide mechanistic insight into these findings—we observed a high degree of trophic overlap among species, suggesting that large releases of hatchery pink and chum salmon in the North Pacific may have negative effects on wild populations of pinks, chum and sockeye through resource competition.

A comprehensive understanding of the spatial and temporal context of trophic relationships among species is needed to model the carrying capacity of the North Pacific for salmon (Brodeur and Pearcy 1992; Pearcy 1992; Cooney and Brodeur 1998). This understanding becomes especially important when considering enhancement of stocks with hatchery fish, which may have consequences for both intra- and inter-specific competition. Generally, models assume that Chinook and coho salmon feed at higher trophic positions than pink, sockeye, and chum (Pearcy et al. 1988; Brodeur 1990; Groot and Margolis 1991) as is reflected in recent ecosystem models of the North Pacific Ocean (e.g., Aydin et al. 2005). We suggest extensive trophic overlap for chum, sockeye, and pink salmon feeding in the open ocean. Additionally, Chinook and coho salmon show trophic overlap in the coastal ocean. However, our meta-analysis, along with diet and tagging studies, show that it is unlikely that all five species spatially overlap with each other for extended periods of time during the marine phase of their life cycles. Ecosystem models should include separation between coastal and pelagic processes if these models are meant to capture the dynamics of all Pacific salmon species in the North Pacific.

In conclusion, our results suggest that there is high overlap in the trophic ecology of pink, sockeye, and chum salmon, which is relatively distinct from coho and Chinook salmon. Trophic differentiation of coho and Chinook may be a function of habitat preference (i.e., more benthic/coastal food webs compared to the pelagic food webs of pink, sockeye, and chum) corroborating previous diet studies (Brodeur 1990; Groot and Margolis 1991; Quinn 2005). Our analyses illuminate the inter-specific variation in stable isotope signatures of marine salmon and contribute to our understanding of the trophic and spatial partitioning of different salmon species feeding in the North Pacific. Although intra-specific spatial and temporal differences exist, this study highlights the overall pattern of isotope signatures in the five species of Pacific salmon and will be of use to studies examining the marine contribution of salmon to freshwater and terrestrial food webs (Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003).

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