

$\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.)

DAVID W. WELCH¹ AND
TIMOTHY R. PARSONS²

¹Department of Fisheries and Oceans, Biological Sciences
Branch, Pacific Biological Station, Nanaimo, British Columbia,
Canada

²University of British Columbia, Department of Oceanography,
Vancouver, British Columbia, Canada

ABSTRACT

Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values for five species of Pacific salmon indicate that they form a trophic hierarchy on the high seas. On the basis of an analysis of these stable isotope ratios, chinook salmon feed at the upper end of the food chain and pink salmon at the lower end, in the sequence pink → sockeye → coho → chinook, with chinook and pink salmon separated by ca. 0.8 of a trophic level. Chum salmon occupy a peculiar position, with low $\delta^{13}\text{C}$ values and high $\delta^{15}\text{N}$ values, possibly reflecting an unusual diet that includes large amounts of gelatinous zooplankton (salps, ctenophores, and medusae). Chum appear to occupy a unique trophic position, at a trophic level nearly as high as that of chinook but at the end of a different branch of the food chain. If true, the potential for trophodynamic competition with other salmon species is small. Our results suggest that the greatest potential for trophodynamic competition occurs within the pink-sockeye-coho grouping. A similar analysis, restricted to five stocks of North American sockeye, shows that four widely separated stocks have similar heavy isotope compositions but that the separation between these stocks is still statistically significant. The Chilko stock is strikingly different, however, suggesting that it is located in the central Gulf of Alaska, a region of intense upwelling. Circumstantial evidence supporting the possibility that the Chilko and other sockeye stocks are geographically separated within the Gulf of Alaska is reviewed.

Key words: diet, food chains, gelatinous zooplankton, *Oncorhynchus*, stable isotope analysis, Pacific salmon, trophic dynamics

INTRODUCTION

Whether or not the production of Pacific salmon can be limited during the pelagic phase of their life histories is beginning to be seriously debated, as salmon population sizes return to abundances near those present at the start of the twentieth century. However, a satisfactory answer as to whether the carrying capacity of the North Pacific Ocean is limited for Pacific salmon will require an understanding of the relative trophic positioning of the different salmon species, as well as knowledge of the changing productivities of the ecosystem (Pearcy, 1992).

Despite the need to return to freshwater to spawn, the six North American species of Pacific salmon (genus *Oncorhynchus*) form the dominant fish fauna within the subarctic domain of the north Pacific Ocean (Ware and McFarlane, 1989). Within this vast region these species (sockeye, *O. nerka*; chum, *O. keta*; pink, *O. gorbuscha*; coho, *O. kisutch*; chinook, *O. tshawytscha*; and steelhead, *O. mykiss*) are differentially distributed, but to a large extent their oceanic distributions overlap (Burgner et al., 1992; Godfrey et al., 1975; Major et al., 1978; Margolis et al., 1966; Neave et al., 1976; Takagi et al., 1981).

Almost all somatic growth (>99%) occurs during life in the ocean for Pacific salmon, and many stocks and species of salmon complete most of their life history on the high seas. The food of salmon during the high seas phase of the life history has been studied most intensively during the summer (review by Brodeur, 1990). However, many stomach content analyses are based on salmon sampled in the coastal zone, an area characterized by substantially different physical processes and much higher densities of both salmon and their prey than is typical of the oceanic North Pacific.

Stomach content analyses reflect what an animal has most recently eaten and not necessarily the long-term accumulation of food. Pacific salmon prey on a wide range of organisms, including copepods, euphau-

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siids, squids, and myctophids or other small fishes. There are dietary differences between species, as well as differences for the same species when studied in offshore and coastal regions (Beacham, 1986; Brodeur, 1990; LeBrasseur, 1972). For example, both maturing coho and pink salmon feed on squids and fishes, but pink salmon tend to consume smaller prey items when offshore, including euphausiids and amphipods (Ito, 1964; Ogura et al., 1990). In contrast, the guts of chum salmon in offshore regions frequently tend to be packed with a well-digested white granular material, which appears to be at least partly composed of ctenophores and jellyfish (Black and Low, 1983; Percy et al., 1988). The contribution of this material to the diet is unclear and may in fact be underestimated because of its rapid rate of digestion (Arai, 1988).

Our current understanding of the relative trophic positioning of salmon is insufficient to allow firm conclusions as to the dependence of Pacific salmon on different parts of the food spectrum during the oceanic phase of their life history or the degree to which different species may compete for the same resources. However, given the relative abundance of salmon in the subarctic domain, it is possible that the trophic position of these animals may be separated in order to reduce competition.

Differential rates at which the naturally occurring heavy isotopes ^{13}C and ^{15}N are sequestered in tissues (Minagawa and Wada, 1984) allow an alternative approach to examining the trophodynamic position of Pacific salmon. The successive concentration of heavier isotopes as primary production moves up the food chain allows an indication of the trophic level of the food that salmon prey upon and is independent of some of the restrictions imposed by stomach content analysis. In general, $\delta^{15}\text{N}$ values increase by about 1.3–5.3‰ per trophic level in marine environments, independent of habitat (Minagawa and Wada, 1984; Wada et al., 1987), while $\delta^{13}\text{C}$ values increase by 1–2‰ per trophic level. This leads to approximately a 3:1 slope for the $\delta^{15}\text{N}:\delta^{13}\text{C}$ relationship in marine ecosystems (Wada et al., 1987).

The isotopic composition of muscle tissue integrate dietary changes over a period of a few weeks (Tieszen et al., 1983). Isotopic analysis of salmon flesh should therefore provide a broader picture of the trophic resources upon which salmon depend, one that may avoid some of the interpretive difficulties caused by differences in the rates at which organisms are digested. For example, Monteiro et al. (1991) demonstrated that the $\delta^{13}\text{C}$ isotope values for Southern Benguela anchovy is consistent with a predominantly

zooplanktivorous rather than herbivorous diet. This conclusion contradicts earlier assumptions that the high-standing biomass of pelagic fish stocks in upwelling areas is maintained by direct feeding on phytoplankton.

In addition to examining the relative trophic positioning of salmon species, our second objective is to examine how isotope values vary between different populations of the same species. Pacific salmon return to their birthplace with great fidelity. However, some stocks of salmon are believed to largely remain in coastal waters, while other stocks undertake extensive oceanic migrations. As the degree of isotopic enrichment of $\delta^{15}\text{N}$ tends to differ in different regions of the North Pacific (Saino and Hattori, 1987), stock-specific differences in migration routes or in dietary preferences could be reflected in identifiable differences in heavy isotope values.

Blackbourn (1987) hypothesized that the interannual variation in the migration timing of Fraser River sockeye stocks may be caused by different stocks occupying different parts of the Gulf of Alaska. Differences in return times might therefore reflect the amount of time required to return from residence in different regions of the eastern North Pacific, as well as the influence of oceanic transport in different years (Thomson et al., 1992). Support for the theory that different sockeye stocks have different centers of distribution came from the correlation between sea surface temperatures in specific regions of the Gulf and the variation in sockeye return times. As the region of maximum correlation differed between stocks (Blackbourn, 1987), some indirect evidence exists for the theory.

To examine this hypothesis, we collected tissue samples from the spawning grounds of four sockeye stocks from Fraser River, British Columbia, and one stock from Bristol Bay, Alaska. The distribution of British Columbia sockeye is known from tagging studies to be largely confined to the Gulf of Alaska (Margolis et al., 1966). In contrast, Bristol Bay sockeye are chiefly distributed in the Bering Sea and the central North Pacific, although the distribution is known to extend eastward to overlap with that of British Columbia sockeye in the Gulf of Alaska (French and Bakkala, 1974). Differences in diet or geographic distribution might therefore be reflected in differences in heavy isotope composition, as the Bering Sea and coastal regions of the north Pacific are shallow, highly productive areas with relatively high rates of nitrogen recycling. In contrast, the central Gulf of Alaska and the open North Pacific are pelagic regions where the contribution of recycled nitrogen to the food chain is

lower because the amount of newly upwelled nitrate is larger (Anderson et al., 1969).

MATERIALS AND METHODS

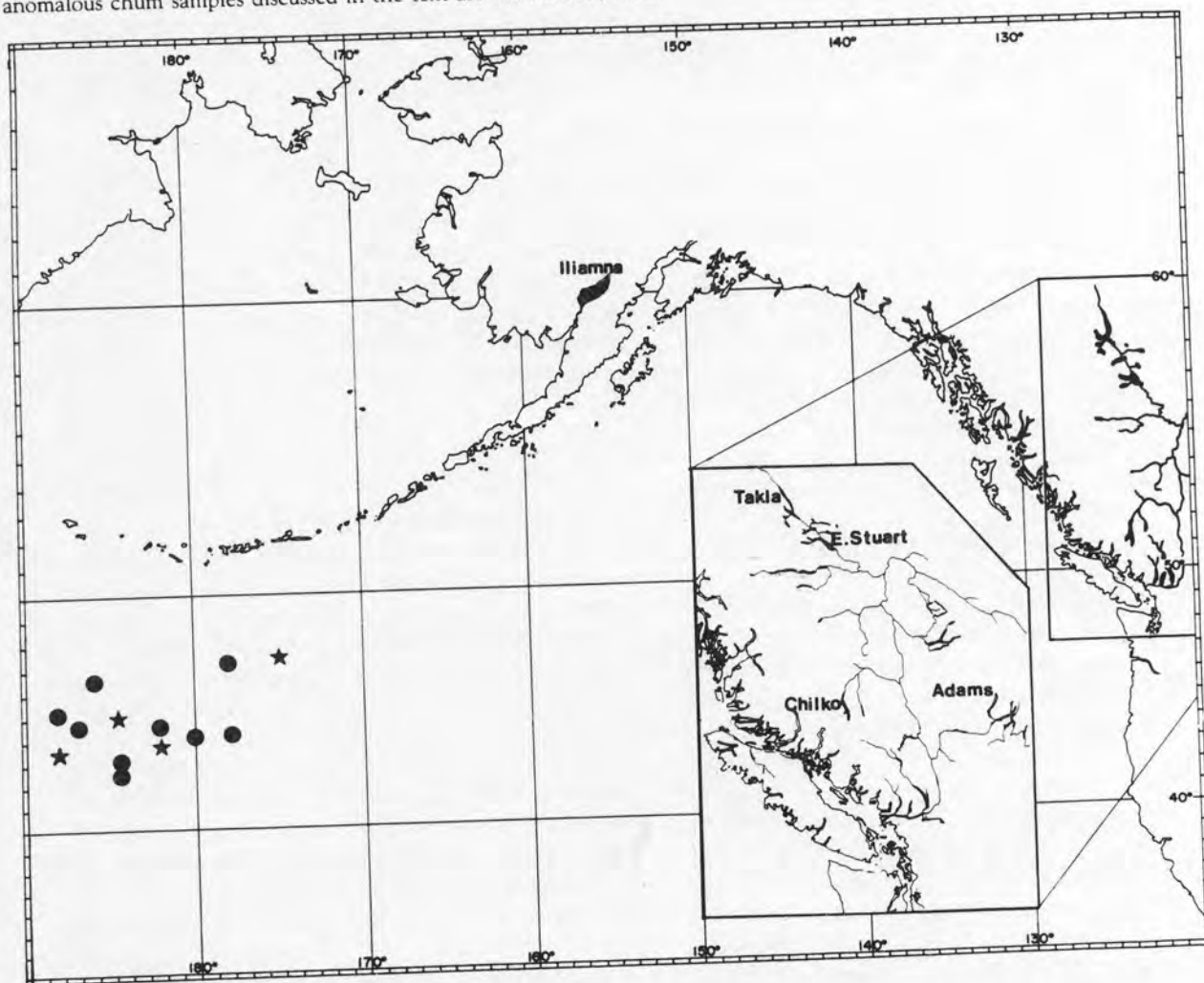
Samples

A Canadian observer aboard the Russian research vessel R/V TINRO collected tissue samples from salmon caught in the central North Pacific in late spring 1991 (Fig. 1). Wedges of muscle tissue weighing between 10 and 30 g were removed from the dorsal musculature just posterior to the head and frozen at -20°C until analysis. The species, fork length, sex, sampling locality (latitude and longitude), and stomach content were recorded for each salmon. The subsamples selected for isotopic analysis included roughly equal numbers of

both sexes and both the largest and smallest individuals sampled of each species, as well as samples from individuals of approximately average body size. The samples were thus chosen to maximize the likelihood of detecting trends in isotopic sequestering with the observed variables. Because the identification of immature Pacific salmon on the high seas can be quite difficult even for experienced samplers, the species identification of all high seas samples used in the analysis reported here were confirmed by enzyme electrophoresis. All initial identifications proved to be correct.

Samples of salmon tissue were also collected from sockeye spawning grounds in 1991, which allowed population-specific differences in isotope values to be examined. Field crews were requested to take muscle samples similar to those collected on the high seas from spawned-out sockeye that were either moribund or

Figure 1. Collection locations for the high seas and stock-specific salmon tissue samples. The locations of the statistically anomalous chum samples discussed in the text are indicated by a star.



freshly dead. Muscle samples were collected from adult sockeye taken from Chinkleyes Creek, a tributary to Iliamna Lake, the largest sockeye salmon-producing lake system within the Bristol Bay (Alaska, U.S.A.) complex, and from four Fraser River (British Columbia, Canada) sockeye stocks (Takla, Early Stuart, Adams, and Chilko; Fig. 1). Spawning ground samples were packed in salt. All stocks are important contributors to commercial fisheries.

Preparation

Before analysis, all samples were washed in distilled water and air dried at 65°C for 48 hours before being ground to a fine powder. Because we were primarily interested in the isotopic signature in the whole animal, lipids were not extracted prior to analysis. Samples were subsequently analyzed by using a PRISM mass spectrometer (VG Isotech) at the Department of Oceanography, University of British Columbia. Silver was added to salted tissue samples prior to analysis to remove halogens.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values are reported as

$$\delta X = 10^3 \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) (\text{‰}), \quad (1)$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$ and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Standards are relative to the carbon ratio in Peedee belemnite (PDB) limestone or the ammonium sulphate isotopic nitrogen ratio versus NBS 14. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were reproducible to precisions of $\pm 0.1\text{‰}$ and $\pm 0.2\text{‰}$, respectively, much smaller than the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between individuals that we describe below.

Statistical methods

Direct comparison of differences in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values can lead to incorrect conclusions about whether or not two groups of organisms are statistically different unless the covariance between isotopic values is also taken into account. To more precisely define the relative positioning of different species in terms of their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we calculated the areas defining the 95% joint confidence regions about the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each species and stock using Hotelling's T^2 distribution. Hotelling's T^2 test is a likelihood ratio test useful for testing hypotheses concerning the equality of means of vectors of normally distributed variables with unknown variance-covariance structure. Use of the test assumes that estimates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for individual species or stocks are approximately normally distributed about some mean value but with a possibly nonzero covariance; that is, fish with larger

$\delta^{13}\text{C}$ values may tend to have larger (or smaller) than average $\delta^{15}\text{N}$ values as well.

We examined the variability of the species and stock specific estimates using a series of exploratory data analysis techniques, including both box-and-whisker plots and quantile-quantile (QQ) plots (Chambers et al., 1983). Although some evidence of nonnormal sample distributions was indicated for a few of the species or stocks, taken together the data reveal no systematic departure from normality (Fig. 2), with the exception of several outliers discussed below. We therefore concluded that the assumption of Gaussian variability was reasonable and that occasional evidence of departures from normality was due to the limited sample sizes available when examining the data for individual species or stocks.

The joint confidence region about the mean isotopic values is calculated from

$$T^2 \leq \frac{p(n-1)}{(n-p)} F_{p, n-p, 1-\alpha}, \quad (2)$$

where

$$T^2 = n\Delta'S^{-1}\Delta. \quad (3)$$

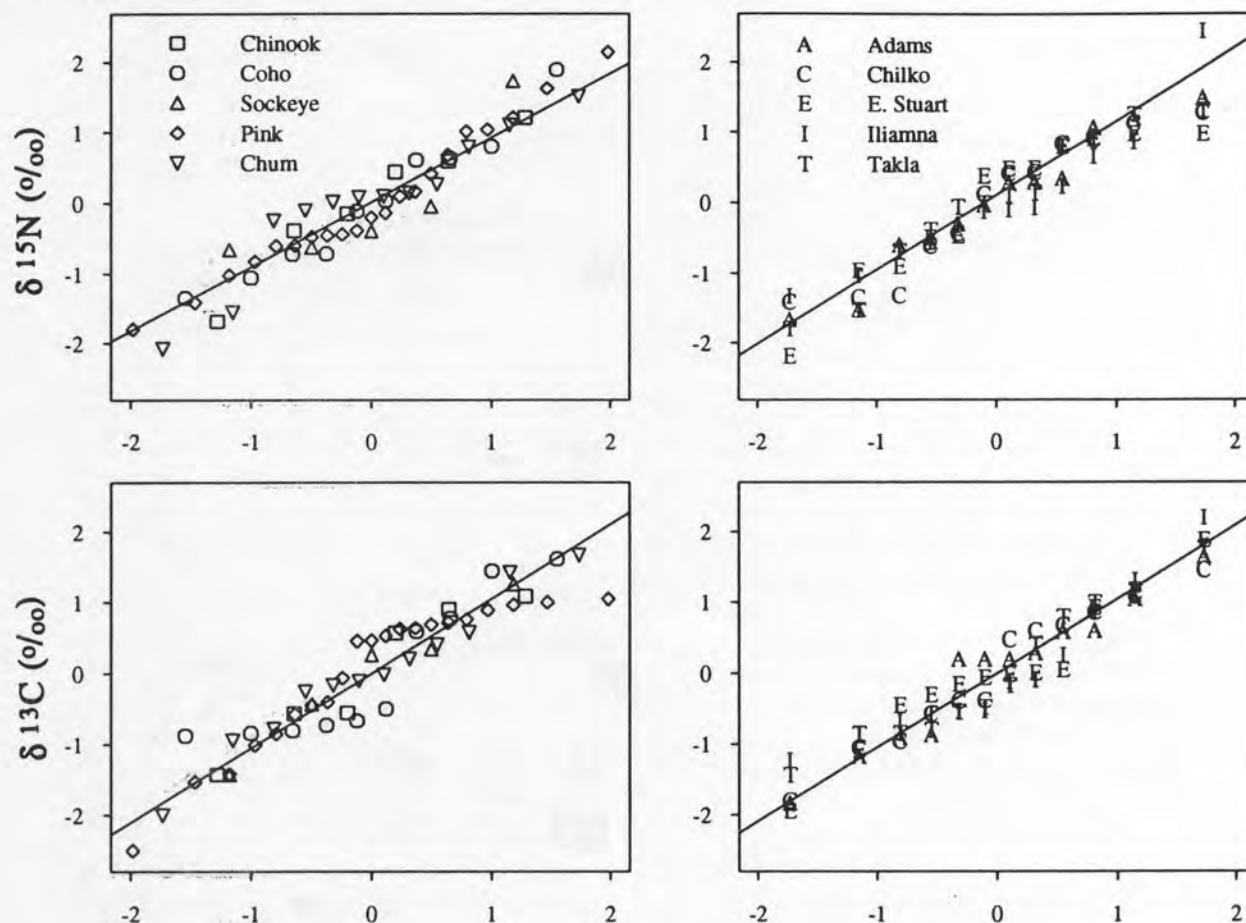
Here n is the number of animals examined, $p = 2$ is the number of means being simultaneously compared, Δ is the matrix of differences between the contour limits and the estimated means, that is, $\Delta' = (\delta^{13}\text{C}_{\text{Lim}} - \bar{\delta}^{13}\text{C}, \delta^{15}\text{N}_{\text{Lim}} - \bar{\delta}^{15}\text{N})'$, where $\bar{\delta}^{13}\text{C}$, $\bar{\delta}^{15}\text{N}$ are the estimated mean values and S is the estimated variance-covariance matrix for the n observations. Equation (2) may be explicitly solved for the equation of the ellipse that contains the true mean values with 95% certainty (Welch, 1987). The T^2 test may also be used to directly test whether the between-species differences in average isotopic values are in fact statistically significant (Press, 1972). The statistic

$$U = \frac{2n-p-1}{2p(n-1)} T^2 \quad (4)$$

is distributed as an F -statistic with p , $2n-p-1$ d.f., where Δ is now the matrix of differences between two species, for example, $\Delta' = (\delta^{13}\text{C}_{\text{chum}} - \delta^{13}\text{C}_{\text{coho}}, \delta^{15}\text{N}_{\text{chum}} - \delta^{15}\text{N}_{\text{coho}})$ and S is the variance-covariance matrix estimated from the pooled data. We report these values scaled by the critical F -statistic as $U/F_{p, 2n-p-1}$. This allows a direct examination of whether the joint species means are statistically significant, since such values are greater than 1. These values also provide a natural scale for comparing trophic overlap because they compare the between-species differences in mean isotopic values with the within-species variability caused by individual dietary differences.

The power of Hotelling's T^2 test is reduced if the

Figure 2. Normal quantile-quantile (QQ) plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values for the species- and stock-specific data. Nonnormality is indicated by deviance from a straight-line relationship. Species- or stock-specific samples were normalized to zero mean and unit variance for simplicity of comparison. Statistically anomalous data for one chinook and three chum salmon were excluded from the analysis (see text).



variance of the two data sets is unequal. There is some evidence (F test) that the variance in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values may not be equal between all species or stocks. Calculations reported below of whether the pairwise differences in species or stock specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are significantly different (from a statistical viewpoint) should therefore be considered approximate.

RESULTS

Species-specific differences

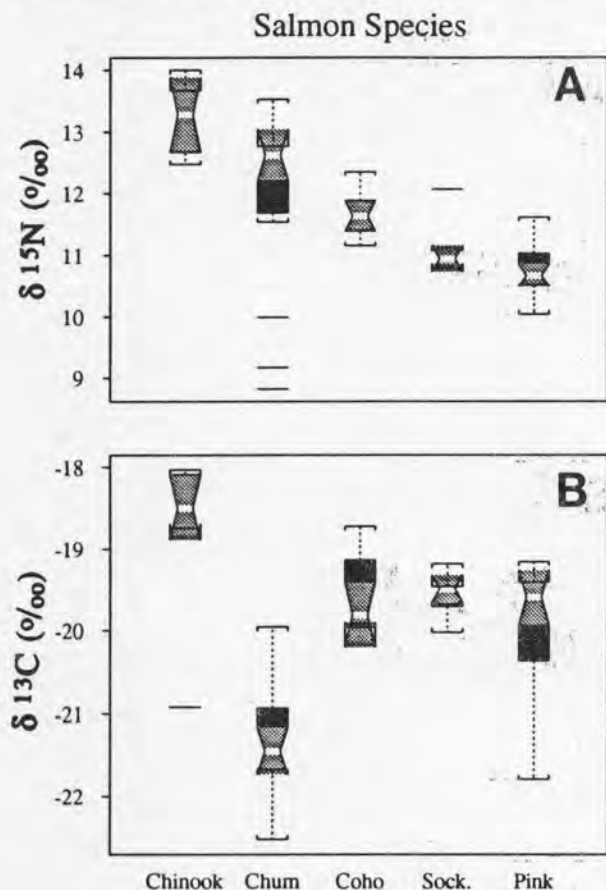
Initial examination of the variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic variations revealed little evidence for a significant effect of any variable other than species on the observed differences in isotope values. Sex, length

(with one exception discussed below), and high seas collecting location all showed no discernable pattern of influence.

Box-and-whisker plots of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values show clear differences between the five salmon species (Fig. 3). However, the plots also identify $\delta^{15}\text{N}$ isotope values for three chum (Fig. 3A) and the $\delta^{13}\text{C}$ value for one chinook salmon (Fig. 3B) as outliers. A single outlier was also identified for sockeye salmon (Fig. 3A). However, because the sample size for sockeye was small ($n = 5$) and inclusion of the outlier did not significantly influence the QQ plot (Fig. 2), we included this data point in all subsequent analyses. Treatment of the remaining outliers is discussed below.

A clear trend toward larger $\delta^{15}\text{N}$ values (implying higher trophic position) is evident for the high seas samples, with chinook salmon having the greatest

Figure 3. Box-and-whisker plots of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for high seas salmon data. The center line indicates the median of the data, while the limits of the box and whiskers contain 50% and 75% of the data, respectively. Differences in mean isotopic values are statistically significant at an approximate 95% significance level for those species pairs whose notches do not overlap. This analysis is approximate and does not consider the effect of covariance between isotopes. The location of outliers are individually shown.



mean value and pink salmon the least (Fig. 3A). Considering only the $\delta^{15}\text{N}$ values, chum salmon would therefore rank as the second highest species within the trophic hierarchy. However, although $\delta^{13}\text{C}$ ratios are generally consistent with this trend, $\delta^{13}\text{C}$ ratios for chum salmon are much lower than those for the other species (Fig. 3B).

Scatter plots in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ plane show that the differences in isotope values are generally consistent with stomach content analyses reported in the literature, as well as our own field observations, and clarifies the reason for the discrepancy for chum (Fig. 4). Isotope values for all but one chinook salmon, the most

piscivorous species, cluster in the upper-left quadrant, with the remaining species (other than chum salmon) tending to cluster along a line running down and to the right (Fig. 4). Most chum salmon occupy a discrepant position, with very low $\delta^{13}\text{C}$ values but $\delta^{15}\text{N}$ values near those of chinook.

We calculated a regression line using the data for all species except chum salmon and excluding one outlying point for chinook salmon, which we discuss below. The equation for this line (± 2 s.e.) is

$$\delta^{15}\text{N} = 27.61 (\pm 5.67) + 0.83 (\pm 0.29) \delta^{13}\text{C}. \quad (5)$$

The values therefore indicate a trophic chain with positioning running pink \rightarrow sockeye \rightarrow coho \rightarrow chinook. A more detailed examination, using Hotelling's T^2 test as an indicator of the closeness of the overlap, indicated that chinook and pink salmon tend to be the most different in their trophic positioning (Table 1). Coho and sockeye salmon show the closest overlap in trophic positioning but relatively high overlap of pink and sockeye salmon is evident as well. In contrast, chum salmon show extreme trophic separation from all other salmon species.

These differences are summarized in Fig. 5, which shows the mean isotopic position and associated 95% joint confidence region about the mean for each species. The species fall into three distinct groupings: chinook, chum, and a pink-sockeye-coho complex. The departure of the chum salmon isotope values from the trophic line could be explained as an anomaly in either or both the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. However, all chum salmon samples (including outliers) have similar $\delta^{13}\text{C}$ values, suggesting that the $\delta^{13}\text{C}$ values are correct and that the chum salmon departure from the trophic line is caused by an enrichment in $\delta^{15}\text{N}$ relative to the other salmon species.

Table 1. Relative trophic separation between species. The statistic U was scaled by dividing by the relevant F -statistic; values greater than 1 indicate a significant difference in mean $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values. The larger this value, the more statistically certain this conclusion is and the greater the between-species trophic separation relative to the within-species trophic variability.

	$U/F_{p,2n-p-1,0.05}$			
	Chum	Coho	Sockeye	Pink
Chinook	10.59	7.62	4.80	20.53
Chum		11.62	10.31	18.76
Coho			3.03	11.94
Sockeye				3.78

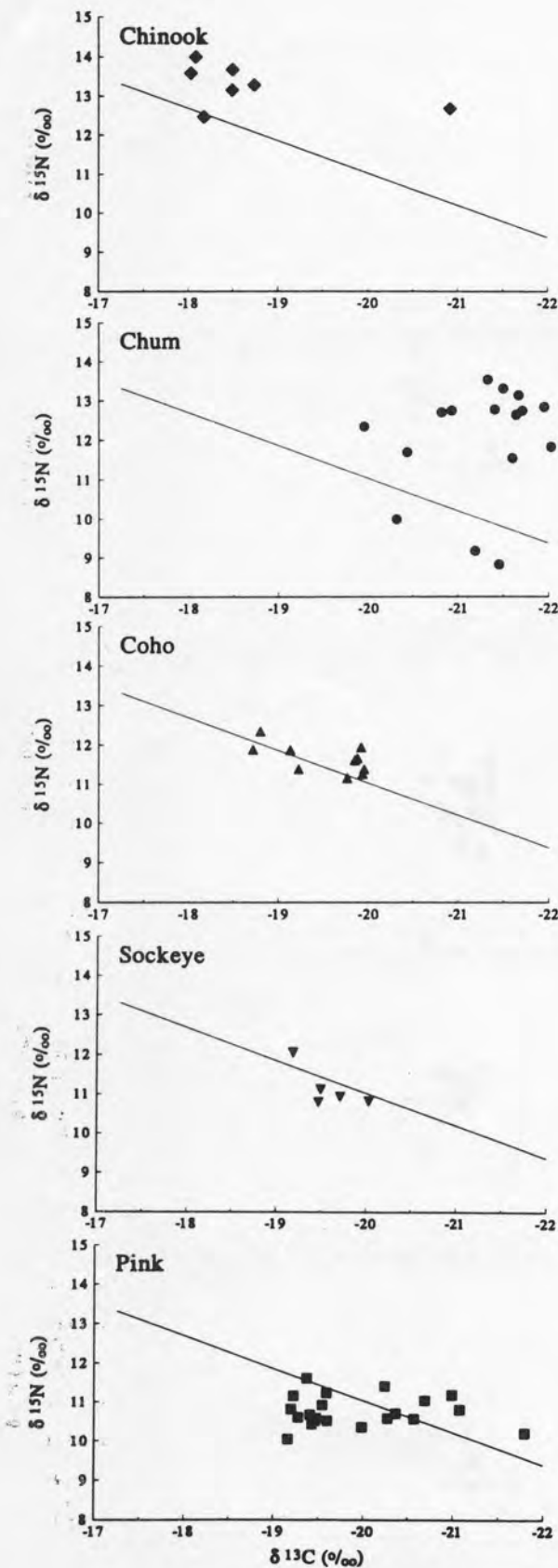


Figure 4. Scatter plots of individual $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values by species. The straight line is the least squares regression through the data for all species combined, excluding all chum and one chinook salmon.

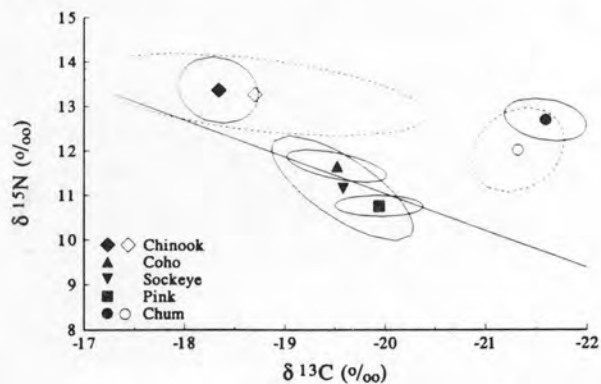
Source of outliers

The single outlying value for chinook salmon was for a 73-cm individual, much larger than any of the other chinook captured (range: 27–34 cm). This salmon would almost certainly have been maturing and nearly ready to begin the spawning migration inshore, at which time Pacific salmon develop large stores of fat as energy reserves in preparation for the freshwater spawning migration. Lipids are depleted in $\delta^{13}\text{C}$ relative to muscle tissue (Sholto-Douglas et al., 1991; Tieszen et al., 1983; Wada et al., 1987), so the displacement in $\delta^{13}\text{C}$ is consistent with a higher fat content in the muscle tissue at or near maturation. We therefore excluded the data for this fish from our analyses.

In contrast to the chinook outlier, the chum salmon identified as statistical outliers had relatively depleted $\delta^{15}\text{N}$ levels, which would be consistent if feeding took place primarily at a lower trophic level. However, we could not identify any unusual attributes of these salmon that differed from the remaining chum samples.

The size of the chum salmon with deviant isotopic values spanned the observed size range of the high seas

Figure 5. Mean isotopic position in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ plane for the high seas salmon species, and the associated 95% joint confidence regions calculated from Hotelling's T^2 distribution (see text). Broken ellipses and open symbols show the change in mean values and associated uncertainties for chum and chinook when outliers are included in the calculations.



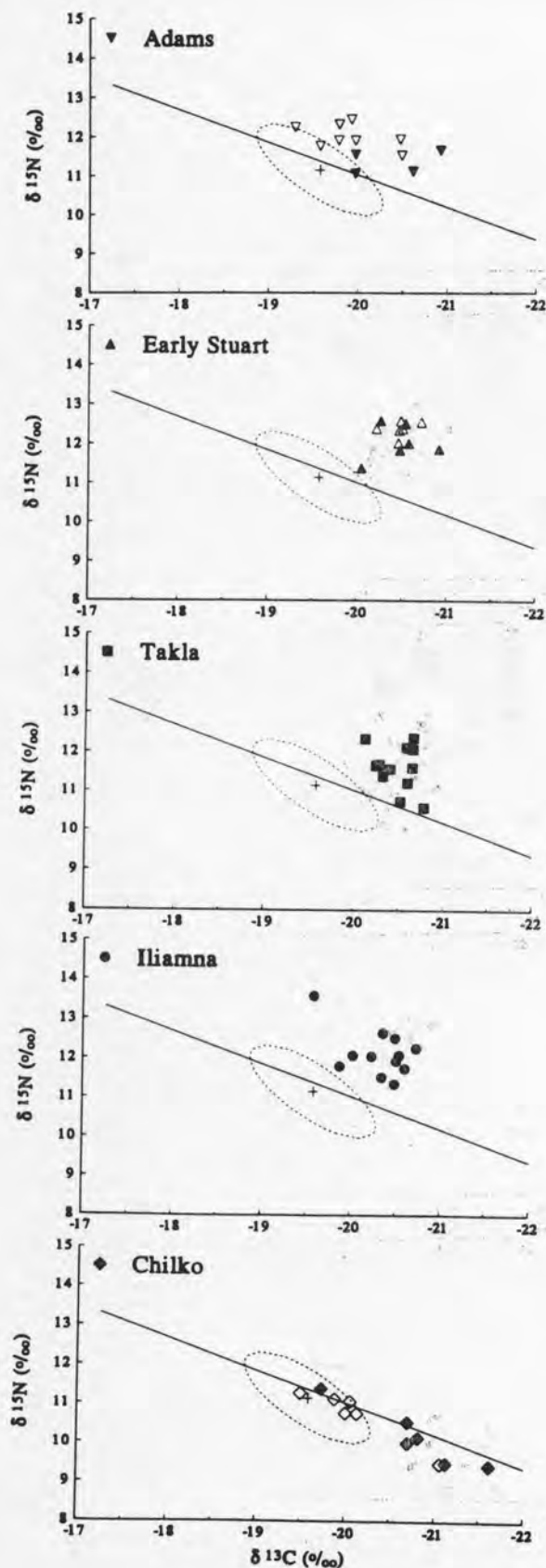


Figure 6. Scatter plots of individual $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values by sockeye stock. The straight line is the regression through the high seas species data shown in Fig. 5. The high seas estimate for sockeye is also shown. Open symbols indicate males, and closed symbols indicate females, except for the Takla and Iliamna stocks, for which sex was not recorded.

chum samples, and the five samples lying closest to the regression line (Fig. 4) came from widely separated sampling locations (Fig. 1). The diet of these fish, as indicated by stomach contents at time of capture, also showed no unusual contents: copepods (two fish), tunicates (two fish), and unidentifiable white granular matter (WGM) (one fish). The remaining cluster of 12 fish had varying but similar stomach contents: WGM (four), copepods (two), chaetognaths (one), euphausiids (1), and tunicates + WGM (one). Stomach contents were not examined for two fish, and one chum salmon stomach was empty. Thus the cause of the unusually low $\delta^{15}\text{N}$ values for some of the chum salmon cannot be readily explained but cannot be related to the types of prey present in their stomach at the time of capture.

Stock-specific differences

The variability in isotopic values between individuals of the same species evident in Fig. 4 is substantially larger than the error involved in estimating the stable isotope ratio. The level of within-species variability therefore requires additional consideration of secondary effects that can influence the overall trophic relationship. Such effects include the proximity of salmon to the coast when feeding (where nitrogen recycling is enhanced and $\delta^{15}\text{N}$ levels are therefore increased), stock-specific differences in prey preference or ocean migration routes, and possibly the effect of metabolic differences on rates of isotope sequestering that may develop as salmon sexually mature during their last year at sea and prepare for the spawning migration.

To assess the importance of stock-specific effects, we examined the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values for muscle tissue taken from 60 carcasses collected from the spawning grounds of four populations within the Fraser River watershed of British Columbia (Adams, Chilko, Stuart, and Takla) and the Iliamna stock of Bristol Bay sockeye salmon in Alaska (Fig. 6). Figure 7 shows a box-and-whisker plot of these values. In each case there is some displacement of mean $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratios from that for the five high seas sockeye samples available (i.e., $\delta^{15}\text{N}$ between 10.5 and 12.5‰ and $\delta^{13}\text{C}$ between –20 and –21‰; see Fig. 8).

Figure 7. Box-and-whisker plots of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for five stocks of sockeye salmon. See Fig. 3 for interpretation.

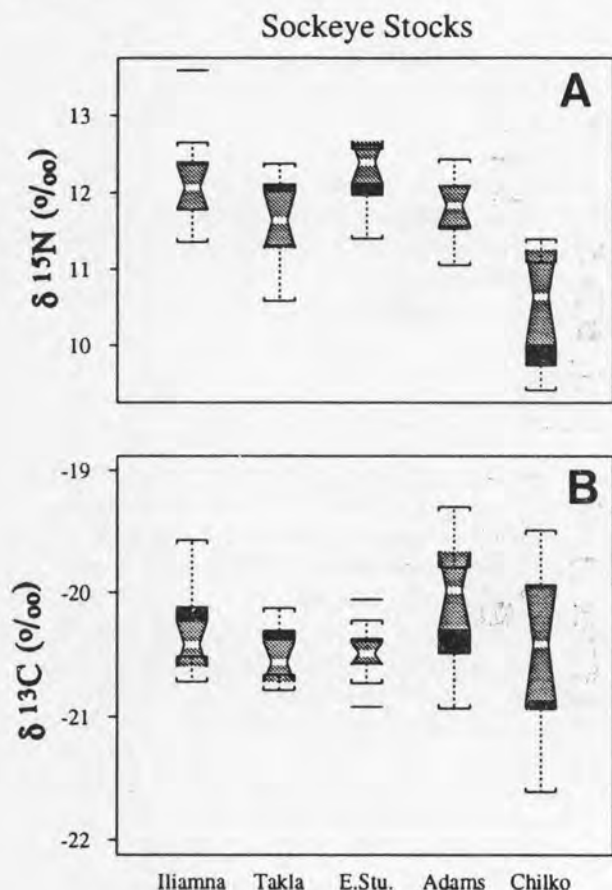


Figure 8. Mean isotopic position in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ plane of the five sockeye salmon stocks and the associated 95% joint confidence regions calculated from Hotelling's T^2 distribution (see Fig. 5). The dashed ellipse shows the position and uncertainty of the mean values for the high seas sockeye sample.

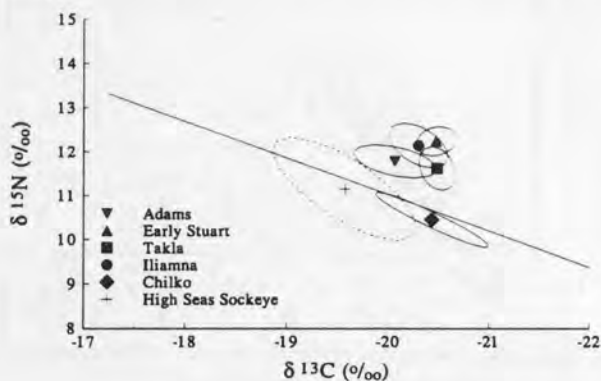


Table 2. Relative trophic separation between sockeye stocks, as indicated by mean $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values. Interpretations are as for Table 1. The relatively small statistical separation between Chilko and Adams sockeye is a consequence of the large variability in $\delta^{13}\text{C}$ values for these stocks.

	$U/F_{p,2n-p-1,0.05}$			
	Takla	Early Stuart	Adams	Chilko
Iliamna	9.29	8.09	4.01	7.11
Takla		9.57	2.30	6.63
Early Stuart			5.56	5.67
Adams				1.51

The Alaskan stock of sockeye and three Fraser River stocks show similar values, despite coming from widely separated locations, although the mean values are in all cases significantly different (Figs. 7 and 8, Table 2). In general, these displacements are consistent with a depletion in ^{13}C and an enrichment in ^{15}N relative to the high seas sockeye samples. The depletion in ^{13}C for adult sockeye is consistent with our finding for the large chinook salmon, since increasing lipid levels should reduce $\delta^{13}\text{C}$ values. The enrichment in ^{15}N for four stocks is also consistent with expectation, since mature sockeye are larger and should feed higher up the food chain than immature sockeye. However, the Chilko stock is unusual in having much lower $\delta^{15}\text{N}$ values than the other sockeye stocks (Fig. 7A).

DISCUSSION

Relatively little quantitative information is available on the trophic position and potential competitive overlap of Pacific salmon, and none has been reported using isotopic tracers. The role of marine nutrients supplied to freshwater lakes by returning adult salmon has been studied by using ^{13}C and ^{15}N isotopic tracers (Kline et al., 1990; Mathisen et al., 1988). The limited data reported in these studies are generally similar to our own analyses but show some interesting differences.

Measurements on pink salmon eggs collected from Sashin creek, Alaska (Kline et al., 1990) showed a large depletion in ^{13}C relative to our tissue samples ($\delta^{13}\text{C} = -23.4$ versus -21.3). This depletion is consistent with, but much greater than, the ^{13}C depletion observed for the nearly mature chinook salmon caught on the high seas and the spawning ground sockeye samples. In both cases, lipid levels for eggs or mature salmon should be considerably higher than for either immature or spawned-out salmon.

The slight depletion of ^{13}C in postspawning adult sockeye salmon relative to the high seas samples is probably the result of residual lipid remaining after freshwater migration. In general, sockeye catabolize >90% of lipids during freshwater migration (Idler and Clemens, 1959). Lipid levels declined the spawning migration by 91% and 96% in male and female Stuart Lake and Adams sockeye, whereas in Chilko, sockeye lipid levels declined by 78% for males and 91% for females (Idler and Clemens, 1959; Gilhousen, 1980). As Chilko (and possibly Adams) sockeye are the only stocks to show good evidence of sex-specific differences in $\delta^{13}\text{C}$ values (Fig. 6), the observations are consistent with the differences in mean lipid retention levels between the sexes. The length of adult freshwater residence is on the order of one month, during which time roughly half the carbon originally present in muscle tissue will have turned over (Tieszen et al., 1983). Presumably, the more negative tissue $\delta^{13}\text{C}$ values (lower ^{13}C levels) observed for Chilko females are the result of greater amounts of ^{13}C -depleted carbon released during fat catabolism being incorporated into muscle.

In general, typical enrichment levels of ca. $\delta^{15}\text{N} = 1.3\text{--}5.3$ per trophic level are encountered in marine environments, independent of habitat (Minagawa and Wada, 1984; Wada et al., 1987), while enrichment levels for $\delta^{13}\text{C}$ are on the order of 1–2‰ per trophic level. However, the slope of the $\delta^{15}\text{N} : \delta^{13}\text{C}$ regression

line for the high seas salmon data, 0.83 ± 0.29 , is significantly different from the 3:1 ratio found in some previous studies of marine trophic relationships (Wada et al., 1987). The interpretation of $\delta^{13}\text{C}$ values is more complicated than for $\delta^{15}\text{N}$, since $\delta^{13}\text{C}$ values are known to be affected by both the temperature at which primary production takes place (Monteiro et al., 1991; Stephenson et al., 1984) and the amount of lipid present (Rau et al., 1991, 1992; Wada et al., 1987).

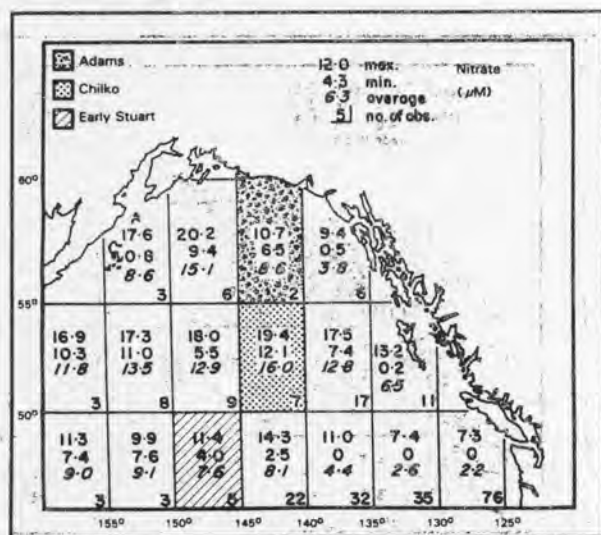
In contrast to the depletion of ^{13}C in mature sockeye, the ^{15}N enrichment of three Fraser River sockeye stocks and the Iliamna River stock is consistent with expectation for a food chain mechanism, since larger fish should feed higher up the food chain. However, this mechanism cannot explain the remarkable depletion in ^{15}N for the Chilko stock.

A depletion in ^{15}N results from an increase in the proportion of new versus recycled nitrogen present in the diet. Saino and Hattori (1985) demonstrated that as surface nitrate levels increase, the $\delta^{15}\text{N}$ of particulate organic nitrogen drops. This leads to geographic differences in the $\delta^{15}\text{N}$ level of organic material in surface waters (Saino and Hattori, 1987). In contrast, Altabet and McCarthy (1985) demonstrated that shelf waters are enriched in ^{15}N ($\delta^{15}\text{N}$ values > 10‰) as a result of the early stratification of coastal waters due to the presence of a strong halocline. Stratification results in a decrease in the input of new nitrate from deep water ($\delta^{15}\text{N}$ values < 5‰) to the food chain and the dominance of recycled nitrogen. As a result of euphotic zone recycling, $\delta^{15}\text{N}$ values can exceed 20‰ in estuaries during the late summer (Mariotti et al., 1984).

Thus one possible explanation for the low $\delta^{15}\text{N}$ values for Chilko sockeye is that this stock feeds in regions with elevated nitrate levels. Alternatively, the Chilko stock must feed at a lower trophic level within the marine food chain, for which we have no direct evidence. Some support for the former hypothesis can be obtained from a review of relative nitrate levels in different regions of the Gulf of Alaska (Fig. 9). Both minimum and mean nitrate levels in 5° Marsden squares show striking variations within the Gulf, the highest values occurring in the central Gulf and values falling off sharply both in coastal regions and farther offshore. This variation in nitrate values mirrors differences in the intensity of upwelling (Tully and Barber, 1960).

Thus the depressed $\delta^{15}\text{N}$ values observed for the Chilko stock could be explained if this stock occupied the central Gulf of Alaska and remained geographically separated from the remaining stocks. Variations

Figure 9. Nitrate distribution in the Gulf of Alaska and regions of maximum correlation between sea surface temperature and Fraser sockeye migration timings. (Redrawn from Anderson et al., 1969.)



in the migration timing of Chilkó sockeye also have maximum correlation with sea surface temperature (SST) changes for the same 5° Marsden square (Blackbourn, 1987) that show elevated nitrate levels, while the migration timing of the Adams and Early Stuart stocks correlated most strongly with SST changes in Marsden squares north and southwest of the central Gulf (Fig. 9). The anomalously low $\delta^{15}\text{N}$ values observed for Chilkó sockeye therefore are consistent with the spatial distinctness of Fraser River sockeye stocks within the Gulf of Alaska, as Blackbourn originally hypothesized.

The other stocks shown in Fig. 7 do not appear as distinctly different in their heavy isotope composition as the Chilkó stock, although these differences are also statistically significant (Table 2). Because nitrate levels in other regions of the Gulf also vary, it is possible that the $\delta^{15}\text{N}$ variations between the remaining sockeye stocks may also reflect real differences in spatial distribution as well.

CONCLUSIONS

The distribution of heavy isotope values we have found support the separation of Pacific salmon species into a trophic hierarchy (Fig. 10). Sockeye salmon appear to be positioned between coho and pink salmon, with the potential for significant trophic competition to occur. If an average trophic separation is taken to be ca. $\delta^{15}\text{N} = 3\text{‰}$, chinook salmon occupy a trophic level ca. 0.8 of a trophic level above pink salmon. By using

the same criteria, pink, sockeye, and coho salmon are successively separated by only 0.13 of a trophic level.

In contrast, there would appear to be much less potential for chum salmon to compete with pink or sockeye salmon. Most chum salmon appear to be top predators on a different branch of the food chain, occupying a trophic level just below that of chinook salmon (Figs. 3A and 5). Although the diet of chum salmon does include copepods and various carnivorous zooplankton, the high $\delta^{15}\text{N}$ value suggests that much of the energy budget is derived from feeding on carnivorous coelenterates.

As we have noted, the guts of chum salmon caught on the high seas are frequently packed with an amorphous substance (Arai, 1988; Black and Low, 1983; Brodeur, 1990). Field examination of fresh material occasionally reveals fragments of ctenophore combrows, but the nature and relative species composition of most of this material remain uncertain. Although the contribution of gelatinous zooplankton to the energy budget of chum salmon is unclear, the rapid rate of digestion of this material, the frequency with which it is ignored during diet analyses (cf. Arai, 1988), and the need to examine stomach contents immediately, before hydrolysis takes place, all suggest that the importance of coelenterates, ctenophores, and tunicates to the diet of chum salmon may be underestimated.

These conclusions are consistent with empirical evidence for trophic competition on the high seas; coho salmon growth rates were lower in years of large pink salmon populations in the western North Pacific (Ogura et al., 1990, 1991), while sockeye growth rates were lower in years of large pink salmon populations in the western North Pacific (Krogius, 1960). In contrast, we have found no reports of chum salmon abundance influencing the growth rates of other salmon species, and empirical evidence indicates that the mean weight of stomach contents changes much less for chum salmon than for sockeye in years when pink salmon populations are high in the western North Pacific (Sano, 1963). This suggests that the unusual diet of chum salmon may help to buffer their populations by reducing direct trophic competition with other salmon. There is, however, good evidence for intraspecific trophic competition occurring for the abundant salmon species, with growth rates inversely related to stock size for pink (IPSFC, 1984; Peterman, 1987), sockeye (Peterman, 1984), and chum salmon (Kaeriyama, in press).

The potential for significant interspecific competition on the high seas has significant management implications. As a result of improved management of wild

Figure 10. The Pacific salmon food chain. Chum salmon occupy a trophic level nearly as high as that of chinook but on a different branch of the food chain. Solid lines indicate direct feeding at the indicated trophic level; dashed lines show indirect flow up through gelatinous plankton (Jellies) to chum. The relative importance of energy flow to chum salmon from the two branches needs to be quantified.



stocks, artificial enhancement initiative (hatcheries), and favorable environmental conditions, the abundance of Pacific salmon has increased to levels near those occurring before commercial exploitation. The drive to further increase salmon population sizes by countries surrounding the North Pacific raises the twin questions of whether or not the common property resource of the North Pacific Ocean can effectively limit the production of Pacific salmon and, if so, how salmon enhancement by one country could affect the productivity of other countries' salmon resources.

On the basis of our preliminary results, the greatest potential for interactions would appear to be between stocks of pink, sockeye, and coho salmon. However, this competitive interaction is unlikely to be symmetrical. Large populations of pink salmon are more likely to reduce the growth rates of sockeye or coho salmon than would the reverse situation because pink salmon feed at a lower trophic level. Empirical evidence appears to support this conclusion.

The evidence presented here on the potential geographic separation of sockeye salmon stocks based on differences in $\delta^{15}\text{N}$ levels is strongest for the Chilko stock, which we conjecture to be distributed in the region of most intense upwelling. The spatial distinctness of this stock, if true, is probably not a unique property of only this stock. Rather, it is possible that all Fraser sockeye stocks may occupy quasi-discrete areas of the Gulf of Alaska during their oceanic life. Because the onset of the spring bloom in the Gulf of Alaska is not uniform (Parsons and LeBrasseur, 1968), one management consideration is that changes in the ocean environment between areas and years (e.g., Brodeur and Ware, 1992) may result in different growth rates for different stocks.

These conclusions clearly deserve further study. In particular, the influence of different periods within the marine period of the life history on the production biology of Pacific salmon, as well as the effect of variability between years or areas of the North Pacific, needs to be examined further.

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