

## Variation in Summer Distribution of the Prey of Pacific Salmon (*Oncorhynchus* spp.) in the Offshore Gulf of Alaska in Relation to Oceanographic Conditions, 1994–98

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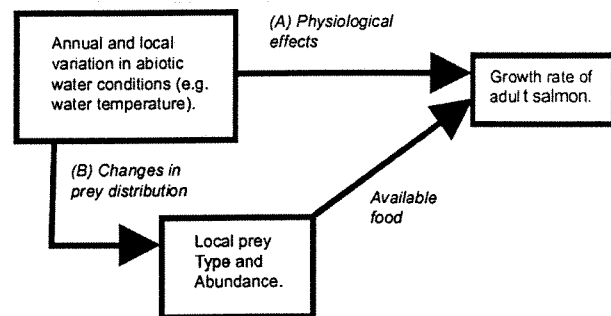
**Abstract:** We present the results of Pacific salmon (*Oncorhynchus* spp.) food habits studies from five years of high seas salmon research cruises along a July transect in the northeastern Pacific (50°–56°N, 145°W, 1994–98). The results suggest that there are two distinct latitudinal summer feeding zones for salmon associated with the July latitudinal sea surface temperature minimum. The southern zone is high in micronektonic squid between 6–12 mm mantle length, primarily the species *Berryteuthis anonychus*. The warmer, northern zone is higher in mesozooplankton in both net samples and salmon stomachs. The difference in the diet and body weights of pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) was substantial between the two regions. The latitude of the border between the two zones varied between 51°–54°N over the years of the study, a distance of over 300 km. This variation in the biogeography of salmon prey may explain part of the previously noted relationship between ocean sea surface temperature and the adult body weight of salmon.

### INTRODUCTION

The statistical relationships describing variation in adult Pacific salmon (*Oncorhynchus* spp.) body weights and environmental factors in the North Pacific Ocean have, to date, focused on large-scale correlations rather than on mechanisms. For example, several studies have reported a negative correlation between ocean temperature and the adult body weights of salmon that feed in the Gulf of Alaska (Hinch et al. 1995; Cox and Hinch 1997; Pypers and Peterman 1999). This correlation may be explained by a direct physiological mechanism linking temperature and growth, or by an indirect linkage through salmon prey (Fig. 1). Investigating the mechanisms behind such correlations requires measuring processes that act on smaller scales of time and space.

Correlation is only useful for prediction if the mechanism behind it remains constant. Therefore, it is important to determine which mechanisms play roles in determining salmon growth, and which mechanisms have the potential for “breaking down” in the face of large scale climatic change. Due to the difficulty of sampling on a fine scale across the North Pacific, relationships between ocean conditions and future salmon growth remain open to speculation (e.g., Welch et al. 1998).

Fig. 1. Two possible mechanisms underlying previously observed negative correlations between sea surface temperature and salmon body weight. Water temperature may either affect salmon (A) directly, through physiological interactions, or (B) indirectly, through prey.



Many salmon returning to North American waters put on up to 90% of their final adult body weight in the high seas of the Gulf of Alaska, mostly during the spring and summer prior to maturation (Ishida et al. 1998). Previous studies of salmon feeding suggest the existence of two distinct latitudinal “zones” of feeding for adult salmon in the portions of the Gulf offshore of the continental shelf. In the southern zone (south of 50–53°N), many of the larger salmon feed on the micronektonic squid *Berryteuthis anonychus*, while between 53°N and the northern continen-

tal shelf, squid are largely absent and lower trophic-level zooplankton dominate salmon diets (LeBrasseur 1966; Pearcy et al. 1988).

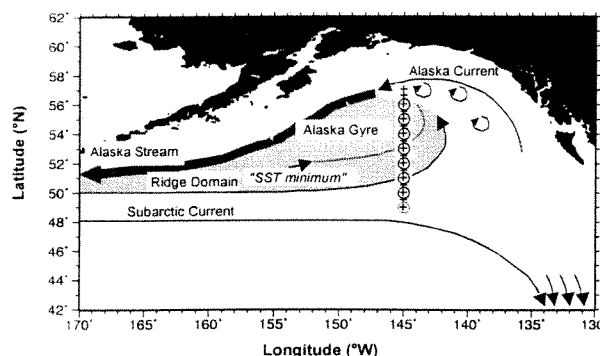
Within the Gulf of Alaska, there are several distinct oceanographic regions surrounding the central, cyclonic-circulating Alaska Gyre (Fig. 2). The structure of the water column in each of these regions possesses unique properties, reflecting differing sources of water (Musgrave et al. 1992). Thus, the Subarctic Current, entering the gyre along its southern border and carrying waters from the west, will be distinguishable from the upwelling center of the Alaska Gyre (Ridge Domain) in which water rises from intermediate depths to the surface (Van Scoy et al. 1991), and from the Alaska Current, where coastal and Subarctic Current waters meet and form the Alaska Stream, in a region rich with mesoscale eddies (Musgrave et al. 1992).

The borders between water masses may create important biological boundaries (Brandt 1993). In studying trends in the ocean, an important question to ask is "what is a fixed point?" If data are taken at a fixed latitude and longitude over a number of years, a biological trend at that location may result from changes occurring within a single water mass, or from a shifting spatial positioning of an adjacent water mass. The Alaska Gyre may shift from east to west on an interannual basis (Royer and Emery 1987; Musgrave et al. 1992), while the Subarctic Current may shift to the north and south (Hollowed and Wooster 1992). Pearcy et al. (1988) associated the north/south variation in salmon diet with the latitude of the Subarctic Current. However, at the time, not enough data existed to examine this hypothesis against a background of shifting oceanographic boundaries.

The difference in food types across the north/south boundary play an important role in determining salmon growth. Squid are a higher-energy food than zooplankton, and salmon growth models suggest that salmon feeding on squid may grow at a much faster rate (Davis et al. 1998; Aydin unpublished results). At the same time, squid may compete with smaller salmon for access to zooplankton. If shifting oceanographic boundaries change the biogeographic range over which salmon and squid overlap, and this boundary movement is associated with changes in sea surface temperature, a correlation between temperature and salmon size and growth may be the result—and this relationship may change substantially with long-term climate shifts.

In this study, we report the results of five years of studies on summer salmonid food habits studies, conducted between 1994–98. Specifically, we examine the link between physical ocean conditions and salmon prey variation during the sampling period. We examine prey distribution with respect to the temperature and salinity of the water column, and

**Fig. 2.** Transect line of the T/S *Oshoro maru* at 145°W in the Gulf of Alaska, early July 1994–98. Circles indicate gill-net stations, while crosses indicate oceanographic stations. Stations shown by dashed symbols were only sampled in a few years. Between years, annual variation may shift the boundaries of the oceanographic regions with respect to the transect line: boundaries shown are approximate.



with respect to the annual variability of the position of oceanographic features such as fronts, water masses, and eddies. The primary purpose of this study is to examine salmon prey in relation to these shifting water masses.

## MATERIALS AND METHODS

### Study Area

The data for this study were collected by the Japanese research vessel *Oshoro maru* along a transect line running from 50°N to 56°N along 145°W in 1994–98 (Fig. 2). Stations were sampled between 1 July and 11 July in each year. Gillnet sampling was conducted at every degree of latitude, while oceanographic and plankton sampling were conducted at every half degree. In 1994, oceanographic and plankton data collection alternated between 145°W and 146°W; this relatively slight longitudinal variation was ignored in the analysis. Due to weather conditions and time limitations in 1995, fishing stations at 50°, 51° and 52°N were cancelled and replaced with a single fishing station at 51.5°N. The sampling methods and resulting oceanographic data from each cruise are published annually by Hokkaido University (e.g., Faculty of Fisheries 1998).

### Oceanographic and Zooplankton Sampling

Vertical casts to 1500 or 3000 meters depth were made with a Neil Brown Mark IIIB CTD at each half degree of latitude. Temperature (°C) and salinity (psu, practical salinity units) were recorded continuously. Values of  $\sigma_t$ , the water density anomaly from 1000 g/m<sup>3</sup>, were calculated by shipboard computer.

Zooplankton samples were collected by a 150 m depth-to-surface tow of a twin plankton NORPAC net (0.45 m ring diameter; 0.35 mm mesh size (#200

filtering cloth; 1.8 m length) while the ship drifted (speed 0 knots). Samples were bottled with formalin and wet weight of each sample was determined. For most samples, gelatinous zooplankton was removed before bottling.

### Salmon Sampling

During July in the offshore Gulf of Alaska, maturing stocks of sockeye salmon (*O. nerka*) and pink salmon (*O. gorbuscha*) east of 155°W longitude are primarily fish from Central Alaska, Southeastern Alaska, British Columbia, and Washington (Myers et al. 1996). In addition, immature sockeye are found from other North American stocks including Bristol Bay, although their numbers increase to the west of 155°W, south of the Aleutian Islands. Coho salmon (*O. kisutch*) may be from any North American stock. Immature chum salmon (*O. keta*) in the region are a mix of North American and Asian fish (Myers et al. 1996, Urawa et al. this volume). Variation in prey availability in the study region may affect any or all of these stocks. Other salmonid species were not caught in large enough numbers to be analyzed in this study.

Salmon surface gillnet gear (0–6 m fishing depth) was set prior to sunset and retrieved at sunrise at each station. The gillnet consisted of 47 to 49 panels of 50 m-long tans (total length 2.45 km). The net was divided into panels of commercial gear and research gear, with 25–30 tans of research gear (multiple mesh sizes for non-size selective sampling) used at each station.

Biological data—scale samples, species, fork length (mm), body weight (g) sex, and gonad weight (g)—were taken from the first 60 fish of each species from each mesh size, which included almost all fish from the research mesh. Stomach contents were examined from up to 30 fish of each species in each gillnet set. Stomachs were sub-sampled from both commercial and research meshes as fish were being processed, with an attempt to apportion the collection among all size classes present. The methods used for stomach examination were similar to those of Percy et al. (1988), and are described in Kaeriyama et al. (this volume). Total prey weights were determined, and percent volume of each identifiable prey type was estimated visually.

The freshwater and ocean age class of each fish were determined by counting the number of freshwater and ocean annuli on acetate impressions of scales. Maturity of salmonids in the samples was determined from gonad weights. The criteria used for determining maturity is reported by Takagi (1961). Log-transformed catch-per-unit-effort (CPUE) of each gillnet operation was calculated from the total number of each species, age, and maturity class of salmon caught in the research (non-selective) gillnet. The

research gear from an overnight net set, or approximately 30 tans of mixed-mesh gear, was considered to be a single unit of effort.

### Data Analysis

#### *Oceanographic analysis*

Summary CTD data at standard depths were used to determine latitude/depth isopleths using the Generic Mapping Tools software package (Wessel and Smith 1995). The depths of the top and bottom of both the seasonal and permanent pycnoclines at each station were estimated by locating the standard depths closest to the inflection points of curves fitted to the  $\sigma_t$  plot. The strength of the density gradient across the pycnocline was calculated as the buoyancy frequency  $N$  (Mann and Lazier 1996, p. 62) across each pycnocline. Due to the smoothing procedure used across standard depths, the pycnocline depth was not resolvable to an accuracy greater than  $\pm 5$  m. Daily mixing and precipitation was evident in the upper 10 m of the water column, so stratification in the upper 10 m could not be determined reliably.

Many physical properties of the water column may be correlated during a single sampling period: for example, sea surface temperature may show a strong correlation with mixed-layer depth. If a biological variable is related to either variable, it would not be clear which of the physical variables has a direct effect on the biological process. This is important to consider if scenarios of climate change predict changes in the relationships between physical variables.

Principal Components Analysis (PCA) was used to determine the common modes of variability for eight oceanographic variables: sea surface temperature (SST) and salinity, 100 m temperature and salinity, seasonal pycnocline depth and maximum buoyancy frequency, and permanent pycnocline depth and maximum buoyancy frequency (Mathsoft 1995). These principal components were used to determine relationships between physical and biological properties during the study period. Using transformed principal components rather than individual variables such as SST emphasizes that oceanographic properties tend to covary.

#### *Oceanographic domain determination*

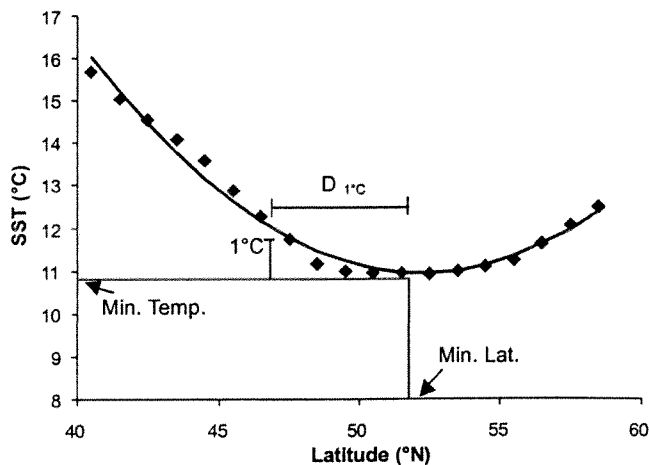
Two data sources were used to determine regional oceanographic boundaries. The first set of data was the CTD temperature, density, and salinity data collected along the transect. The second set was the July monthly averaged 1° x 1° resolution SSTs for the years 1981–present, calculated as described in Reynolds and Smith (1994) and published electronically in the Integrated Global Ocean Services System

Products Bulletin (IGOSS). All boundaries were considered to occur halfway between two sampling stations, so every station was placed on one side of an oceanographic boundary.

The boundary between the Subarctic Current and the Ridge Domain was placed between the two CTD stations showing the largest change in depth of the 4°C temperature isotherm, which rises from below 300 m in the Subarctic Current to near 100 m in the Ridge Domain. This differs slightly from the method of marking the boundary at the latitude where the 4°C isotherm rises above 100 m (Pearcy et al. 1988), because along 145°W the relatively weak Ridge Domain did not rise above 100 m during the course of this study.

In addition to this Ridge/Subarctic Boundary, it has been suggested by Aydin et al. (1998) that SST in the Alaska Gyre has a latitudinal minimum associated with a potential temperature discontinuity, which occurs at a boundary between central Gyre upwelling waters and water moving into the Alaska Gyre from the west. A plot of a single year of IGOSS data along the transect shows that the SSTs along 145°W between 40°N and 58°N in a given year may be fit with little error to a quadratic curve with three parameters: the latitude of minimum temperature, the minimum temperature, and the “curvature” or rate of change of the north/south warming trend (Fig. 3). These three parameters were fitted to the curve for each year using the Solver routine in Microsoft Excel®, and the calculated latitude of minimum temperature (hereafter SST minimum) was used as a boundary distinct from the Subarctic Current/Ridge Domain boundary.

**Fig. 3.** Points show actual 1x1° IGOSS sea surface temperatures for a single year. The solid line represents the smoothed 2nd degree curve fit using three parameters. The parameters may be manipulated to have specific physical meaning. In this case, the three parameters are minimum latitude (the latitude at which temperature is at a minimum), minimum temperature (the fit temperature at this minimum) and  $D(1^\circ)$ , or the distance in degrees latitude required for the temperature to rise 1°C from the minimum.



The boundary between the Ridge Domain and the Alaska Current was placed at the latitude of northern descent of the 4°C isotherm from 100 m to below 300 m (Pearcy et al. 1988). Salinity plots (not shown) were also used to determine the presence of the Alaska Current.

The Alaska Current may create eddies that move into the Ridge Domain, obscuring the Ridge Domain's presence while transporting coastal water, or water from the southern portions of the Subarctic Current, into the Ridge Domain (Thomson and Gower 1998). Locations where mesoscale features appeared during the study were reported in Onishi et al. (2000) and are examined here for correlation with biological variables.

#### *Zooplankton analysis*

Zooplankton density measurements ( $\text{mg}/\text{m}^3$ ) were log-transformed, and all stations at which  $\ln[\text{density}]$  was greater than 7 were excluded from the analysis as representing the combined weights of gelatinous and non-gelatinous zooplankton. The cut-off was determined after examining the statistical distribution of the raw data. Therefore, the samples should not be considered to represent concentrations of gelatinous zooplankton.

Due to this exclusion, and equipment difficulties, raw zooplankton measurements were not available at all stations. For each station, we averaged all undiscovered log-transformed zooplankton measurements taken within a 100 km radius during the same year. The distance of 100 km was chosen because (1) it would include multiple measurements at most gillnet stations, (2) it would leave mesoscale features, generally 200+ km in size, resolvable, (3) it would provide smoothing over the area in which a salmon travelling 30–50 km a day may have been feeding, and (4) a spatial study by Rand and Hinch (1998) showed that zooplankton concentrations in the Gulf were strongly autocorrelated to a range of 100 km, with correlation in some years falling off sharply outside that distance.

The difference between day and night sampling in integrated 0–150 m zooplankton tows is not significant in high latitude areas in the summer and is not taken into account in this analysis (Sugimoto and Tadokoro 1997). Phytoplankton data were also considered, as proxied by secchi depth (Sugimoto and Tadokoro 1997). However, due to the amount of error inherent in this method, limited analysis was performed on these data.

#### *Salmon stomach contents and squid density estimation*

The patchy nature of prey distribution requires the use of detailed bioenergetics simulation modeling

and Monte Carlo techniques to determine the effect of each prey type on salmon growth (Aydin, unpublished data). Details of the abundance and importance of individual prey types in the salmon diet are presented in Kaeriyama et al. (this volume).

An index of micronektonic squid abundance was calculated for each gillnet station using food habits data from pink, sockeye, and coho salmon. Chum salmon do not feed on squid often enough to be used for this index. The formula used was:

$$SquidIndex = \ln \left[ \frac{N_{squid,species} + \frac{1}{2}}{N_{total,species} - N_{squid,species} + \frac{1}{2}} \right] - \alpha_{species}$$

$$BW \geq BW_{cutoff_{species}}$$

$$species = \{pink, coho, sockeye\}$$

This formula gives three comparable estimates of the squid index at each station, provided all three species, pink, coho, and sockeye salmon, are sampled at the station.  $N_{total,species}$  is the number of fish stomachs sampled in a given species, where only fish with body weights above  $BW_{cutoff}$  are used.  $N_{squid,species}$  is the number of those fish with stomachs containing non-larval squid. The correction  $\alpha$  is used to calibrate the estimates with respect to each other. The body weight cutoff and correction  $\alpha$  for each species are given in Table 1.

The squid index is an empirical logistic variable (Cox and Snell 1989). If prey capture is considered to be a Poisson process, the squid index is approximately proportional to  $\ln[\text{density}]$  in the range  $-3 < \text{Index} < 3$ , where [density] is the numerical density of squid in the foraging area. Thus, this corrected squid index may be treated as a log-CPUE index, which uses the salmon as the sampling gear, and the differing  $\alpha$  for each of pink, sockeye and coho constituting empirical "gear corrections" for species-specific behavior. In this study, the three estimates of squid density were pooled into a single estimate for each gillnet station. The empirical corrections were determined by a site-by-site analysis of over 11,000 pink, sockeye and coho salmon stomachs collected between 1956 and 1998 (Aydin, unpublished data).

**Table 1.** Estimated empirical corrections for calculating a squid density index from sockeye, pink, and coho salmon. Corrections were calculated from over 11,000 fish sampled between 1956–98 (Aydin unpublished data).

Species	Body weight cutoff (g)	Alpha offset (intercept)
Sockeye	1000	-0.03
Pink	1000	-0.41
Coho	500	+0.60

### Determining relationships between variables

Each of the biological variables described above—zooplankton density, squid index values, CPUE and body weight of salmon (by species and age) and the prey weight—was analyzed with respect to physical variables. The physical variables considered were year, latitude, ocean domain/boundaries, and the principal components of the eight water column variables. The relationship between biological and physical variables was examined by constructing Generalized Linear Models (GLMs) for the potential biological/physical relationships (McCullagh and Nelder 1989).

The process used to select the best statistical models for each variable was a manual stepwise model selection procedure, where linear first-order interactions of each of the physical variables were examined in turn, and second- and higher-order interactions were examined where appropriate.

## RESULTS

CTD sampling occurred at 83 stations while NORPAC sampling included 131 zooplankton samples over these stations, five of which were discarded due to the presence of gelatinous material. A total of 876 pink, 1,124 sockeye, 412 coho and 1,320 chum salmon was measured at 33 gillnet stations. From these, a total of 2,471 stomach samples was taken. For sockeye and chum, ocean ages .1–.3 made up over 99% of the samples. For calculating the squid index, 1,738 pink, coho and sockeye stomachs came from fish with body weights above the species-specific cutoffs, with at least 22 and an average of 51 being sampled for squid at each station.

### Oceanographic Variables Along 145°W, 1994–98

In 1995, precipitation caused measurements of sea surface salinity to be anomalously low at a few stations (< 29 psu). These salinity values were replaced with salinity values at 1 m depth, which were all greater than 32 psu. No other corrections were made in the oceanographic data prior to analysis.

In all years, a seasonal thermocline was visible between 20–50 m depth. At most stations, the seasonal thermocline was the point of highest buoyancy frequency in the water column, although in 1995 and 1998 some strong surface stratification was visible in the top 5 m. In all years, mixed-layer water temperatures were highest in the south, decreased to a minimum between 51–53°N, and increased again in the north. The mixed layer was generally shallower and stronger in the north and weaker and deeper in the south. Temperatures were warmest in 1997 and cooler in 1996 and 1998. In 1997, the mixed layer

was shallow with strong stratification along the entire transect.

The maximum gradient in the permanent pycnocline occurs between 80–120 m at most stations. The exceptions are between 51–53°N in 1997, when the pycnocline was deeper, and between 55–57°N in 1995, when the pycnocline was not visible. This latter anomaly is due to the presence of a strong downwelling (clockwise) eddy between 55–57°N, which is also shown by the intrusion of 6°C water to depths of 200 m. Dynamic topography maps confirm the presence of this eddy in 1995 and numerous weaker eddies along the transect line (Onishi et al. 2000).

**Principal Components Analysis**

The first two principal components (PCs) together account for 58% of the variation in the oceanographic variables used in the PCA, while the first five PCs account for 91% of the variation (Table 2). By convention, only variables accounting for the first 90% of the variation are retained for further analysis (Mathsoft 1995). An examination of PC5 revealed that it was the result of a single anomalous data point in 1995 at 55.5°N, where the permanent pycnocline was not evident. Therefore, PCs 5–8 were not analyzed further.

PC1 is a measure of the properties of the seasonal thermocline. It represents the combined surface water characteristics of sea surface temperature, mixed-layer depth, and mixed-layer strength. Stations with maximum values of PC1 show very warm surface-layer temperatures with SSTs between 12–14°C, while stations with minimum values have surface-layer temperatures below 10°C. PC1 values show interannual variability, with 1997 having a warmer, shallower mixed layer, and 1996 and 1998 being cooler and more well-mixed on the surface.

PC1 values tend to increase from south to north (Fig. 4).

The remaining three principal components reflect processes in the permanent pycnocline that are associated with the oceanic domains. For example, PC2 indicates dilute surface waters and a deeper, less stratified permanent pycnocline, typical of the Alaska Current. Because PC2–PC4 are indicators of oceanographic domain characteristics, they are redundant with the domain definitions (Subarctic Current, Ridge Domain, Alaska Current) determined by examination of the TS plots.

**Oceanographic Boundaries**

In all years, the Ridge Domain of ~4°C water was evident along the transect, rising from below 300 m to depths of 100–200 m (Fig. 5). In 1994, the rise was between 50° and 51°N, and in 1995–97 the rise was between 51° and 53°N. In 1998, a weak rise occurred at 51°N and a sharper rise occurred between 53° and 54°N, with an intrusion of warmer water to 150 m between the two rises, perhaps due to an eddy reported by Onishi (2000). The sharper northern rise was chosen for the Ridge Domain boundary. In all years, north of 55°–56°N the Ridge Domain was not evident, either due to eddy activity in the north or the presence of the Alaska Current.

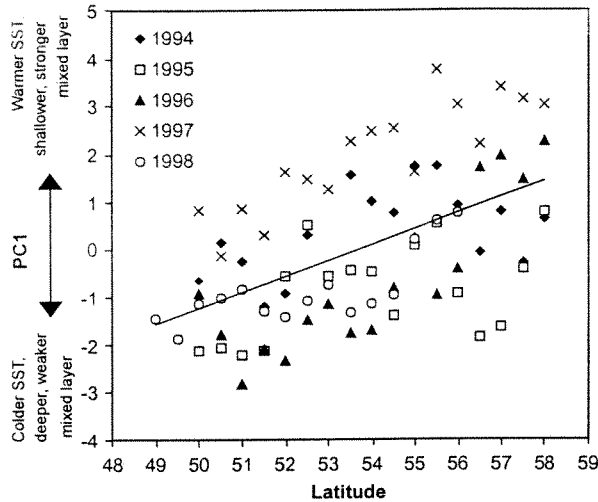
The SST minimum from IGOSS data ranged between 50°30'N and 53°30'N. The minimum was furthest to the south in 1997 and furthest to the north in 1996 (Fig. 5). The minima generally corresponded with locations of SST minima seen in the *Oshoro maru* data, except in 1995 when turbulent conditions may have affected shipboard measurements.

All three of the first-order models for PC1 (pooled by domain, pooled north or south of the SST minimum, and fit linearly to latitude) were significantly better than the null model at explaining the

**Table 2.** Principal components of oceanographic data. The eigenvectors (loading coefficients) are shown for all eight principal components. The individual and cumulative percent of variance explained by each component are also shown. For the first four PCs, coefficients with absolute values > 0.35 are shown in bold (cutoff is arbitrary).

Variable	Principal Component							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
T0	<b>0.55</b>	0.22		-0.11		-0.40	-0.68	
S0	0.14	<b>-0.39</b>	<b>0.40</b>	<b>-0.45</b>	-0.57	0.34	-0.11	
T100	-0.17	0.25	<b>-0.46</b>	<b>-0.82</b>				
S100	0.20	<b>-0.49</b>	<b>-0.49</b>	0.10	-0.13			0.67
Sdepth	<b>-0.46</b>	-0.24	0.12		-0.35	-0.77		
Sstrn	<b>0.59</b>		0.17			-0.31	0.72	
Pdepth	-0.21	<b>0.53</b>	<b>0.38</b>		-0.20	0.13		0.67
Pstrn	-0.11	<b>-0.40</b>	<b>0.44</b>	-0.29	0.70			0.25
Percent of variance explained								
Individual	30	28	15	10	8	6	2	1
Cumulative	30	58	73	83	91	97	99	100

**Fig. 4.** The first principal component of the eight oceanographic variables sea surface temperature and salinity, 100 m temperature and salinity, mixed-layer depth and maximum buoyancy frequency, and permanent pycnocline depth and maximum buoyancy frequency, regressed vs. latitude ( $R^2 = 0.28$ ,  $p < 0.001$ ). The first PC's primary components are SST, mixed-layer depth, and mixed layer buoyancy frequency.



latitudinal variation in PC1. However, the SST minimum explained a greater proportion of the variance (32% of the total variance) compared with 21% and 18% for latitude and domain, respectively (Table 3). Using latitude as an additive term in the two-pool SST minimum model did not increase the amount of variance explained.

This result indicates that in any given year, variation in the common mode of sea surface temperature and seasonal mixed-layer variation is best explained by distinguishing two zones, with a discontinuity located at the yearly SST minimum. PC1 varied significantly among the five years in both the north and the south, with high values in 1994 and 1997 (1-way ANOVA,  $p < 0.005$ ).

**Table 3.** Percent of variance explained by single- and two-term linear models for PC1, Ln[Zooplankton], and Squid Index values. "N/S" indicates the term defined as north or south of the IGOSS SST minimum. Single-term models are listed as "n.s." if they were not significantly different from the null model (F-Test,  $p > 0.05$ ). Two-term models are listed as "n.s." if they were not significantly different from a single-term model that contained one of the two terms (F-Test,  $p > 0.05$ ).

Independent Terms	DEPENDENT VARIABLE		
	PC1	Ln [Zooplankton] <sup>1</sup>	Squid Index
<b>Single-term models</b>			
Latitude	21%	n.s.	33%
Domain	18%	11%	n.s.
N/S	32%	21%	41%
<b>Two-term models</b>			
N/S + Latitude	n.s.	n.s.	43%
N/S + PC1	-	n.s.	51%
Latitude + PC1	-	n.s.	55%

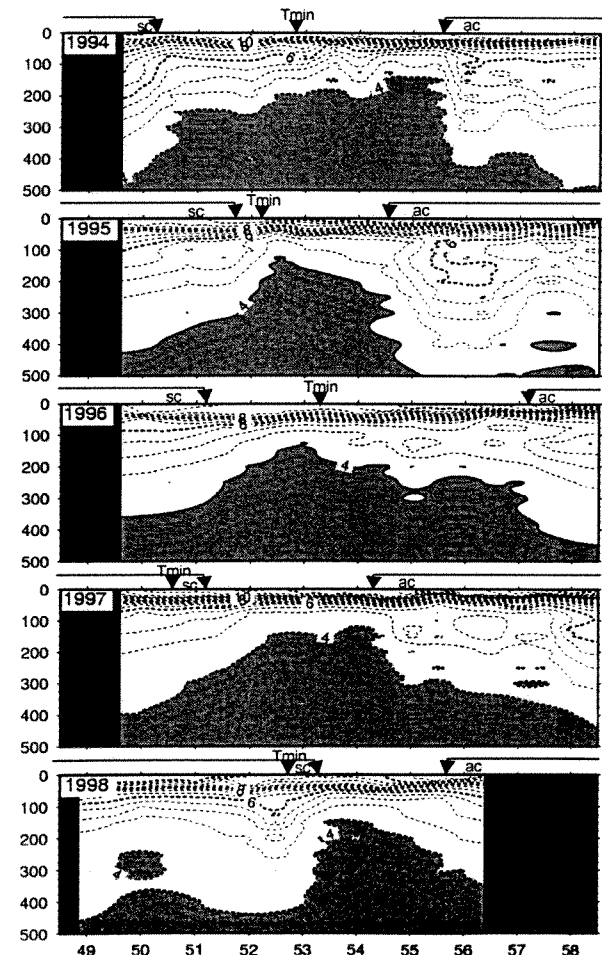
<sup>1</sup>after removal of stations in the Alaska Current.

### Zooplankton

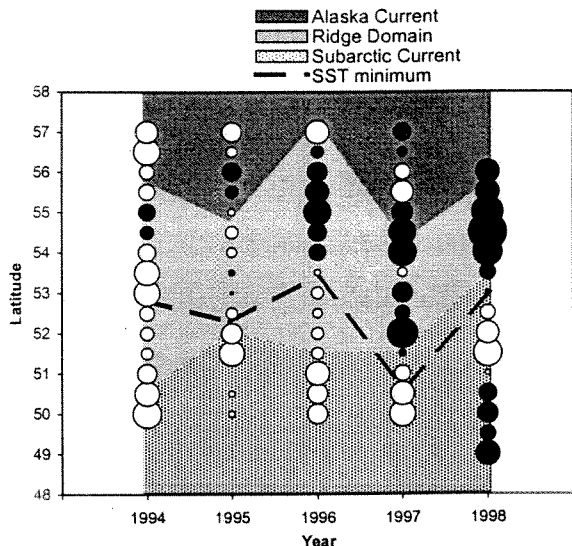
Stepwise linear model selection of the explanatory variables showed that log-transformed zooplankton measurements were significantly different between domains (1-way ANOVA,  $p < 0.04$ ). The average zooplankton density was lowest in the Subarctic Current (average: 180 g/1000 m<sup>3</sup>), and highest in the Ridge Domain (average: 253 g/1000 m<sup>3</sup>), with a middle value in the Alaska Current (average: 221 g/1000 m<sup>3</sup>; Fig. 6).

The north to south change from high to low zooplankton density along the transect was correlated with domain boundaries, and the change was steep and evident in the zooplankton data, especially between 1996–1998. However, within the Ridge Domain further patchiness was evident. An area of low

**Fig. 5.** Vertical transect of water temperature (°C; numbers and contours of 0.5°C) along 145°W to a depth of 500 m, 1994–1998. Shading indicates water below 4°C. The location and boundaries of the Subarctic Current (sc), Alaska Current (ac) and the IGOSS sea surface temperature minimum (Tmin) are shown. The area between the Subarctic and Alaska Currents is considered to be the Ridge Domain. Oceanographic regions were determined from temperature and salinity profiles as discussed in the text.



**Fig. 6.** Oceanographic regions and boundaries from Fig. 5 (shaded areas) and 0–150 m integrated zooplankton densities (wet weight, mg/m<sup>3</sup>; circles), by year and latitude. The area of each circle is proportional to the difference between the log-transformed, 100 km-smoothed zooplankton density at each station and the log-transformed mean value of all stations. Black circles are greater than the mean value, and white circles are less than the mean value. The largest circles are approximately +/- 3 s.d. from the mean.



zooplankton density between 51–53°N in 1998 corresponds with the mesoscale eddy mentioned above. In 1995, there seems to be a discontinuity in zooplankton values at the SST minimum, as well (Fig. 6).

When the stations in the Alaska Current were removed, the southern boundary between areas of high and low zooplankton densities was more strongly associated with the SST minimum than the Ridge/Subarctic Boundary. A 1-way ANOVA between the two models showed a significant difference in the amount of variance explained ( $p < 0.05$ ), with the SST minimum break explaining 21% of the zooplankton variance south of the Alaska Current, while the Ridge/Subarctic Current partitioning explained only 11% (Table 3). Relationships between zooplankton and either PC1 or latitude were not significant.

Zooplankton showed a weak positive correlation with phytoplankton as proxied by secchi depth ( $r = 0.11$ ). This is probably due to the effect of mesoscale vertical concentration and dilution features, such as the 1998 eddy, acting on both phytoplankton and zooplankton. Zooplankton showed a significant increase in the northern zone between 1994 and 1998 (1-way ANOVA,  $p < 0.005$ ), but did not vary significantly between years in the south.

**Squid Indices**

In most years, salmon were not collected far enough to the north to examine squid or salmon in

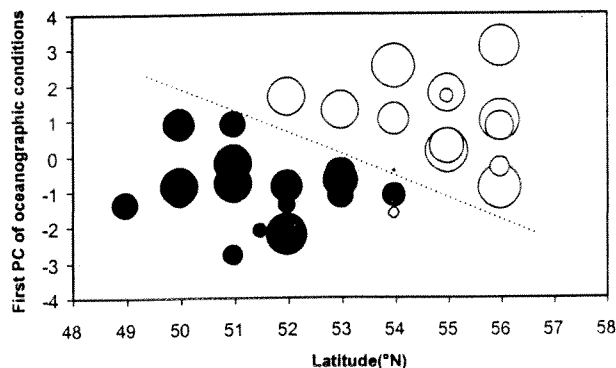
the Alaska Current. Therefore, all Alaska Current stations were removed from analysis of squid density and salmon biological characteristics. Examination of squid specimens from stomachs indicated that over 90% of the squid found in salmon stomachs were *Beryteuthis anomychus*, with the remainder being *Gonatus onyx* or unidentified species.

Examined station-by-station, the squid index values calculated separately for pink, sockeye, and coho salmon were highly correlated ( $r = 0.75$  to  $0.85$ ,  $p < 0.001$ ), confirming that most of the variation in index values was due to factors common to all three species varying between stations, such as the environmental density of squid. Values of the pooled index ranged from -2.5 and 2.5 across all stations. This corresponds to a range of from 5% to 95% squid in stomachs.

The pooled squid index showed significant first-order interactions with latitude, PC1, and the SST minimum. However, it was not immediately possible to choose a “best” model from among the multiple interactions of the three variables on squid densities, as the three explanatory variables were not independent, and several of the two-term models had significant explanatory power (Table 3).

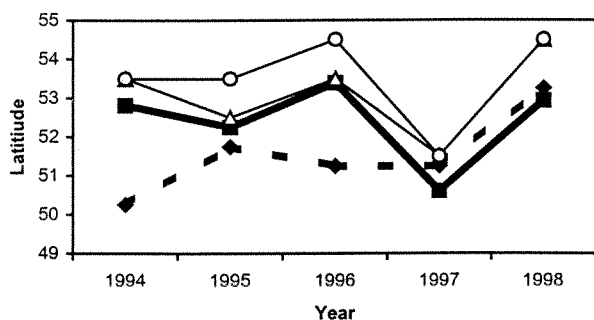
To clarify the situation, squid index values were plotted versus both latitude and PC1 (Fig. 7). While PC1 and latitude are not orthogonal, this graph shows the relationship of squid abundance to the three variables. Squid index values were higher in the south, and at colder surface temperatures with deeper seasonal mixed layers. More importantly, there was a sharp linear boundary between high and low squid index values (dotted line in Fig. 7). In any given year, all positive squid index values were on the southern end of the transect, and all negative values were on the northern end of the transect.

**Fig. 7.** Squid index values plotted by latitude and the first principal component of oceanographic conditions for all stations, 1994–1998. Size of circles indicates the distance of the squid index value from the mean over all stations. Black circles are larger than the mean, while negative circles are smaller than the mean. The largest circles are approximately +/- 2.5 squid index units from the mean. The dotted line shows the division between high and low squid densities fitted by eye.



The latitude of the cutoff varied from year to year (Fig. 8). The latitudes at which squid abundance drops and the SST minimum occurs each year are significantly correlated (Table 4). The correlation between the Ridge/Subarctic Boundary and the squid boundary is not significant. Within each zone, squid index values were not significantly different between years. When squid, zooplankton, and PC1 were examined on a station-by-station level within each year and region, there were no significant correlations.

**Fig. 8.** Latitudes of north/south borders between possible oceanographic or biological regions, using four criteria. Diamonds and dotted line, Ridge/Subarctic Boundary; solid squares and bold line, IGOSS temperature minimum; open circles, cutoff determined by the dotted line in Fig. 7; triangles, latitude south of which all squid index values are positive, north of which all values are negative.



**Table 4.** Correlation between the latitude of the yearly boundary between high and low squid index values and the yearly boundary between the IGOSS SST minimum and the Ridge/Subarctic Boundary. Two methods of determining the squid cutoff latitude: one uses the switch between positive and negative values, and one uses the dotted line in Fig. 6.

	Ridge/ Subarctic Border	IGOSS SST minimum	Squid positive/ negative cutoff
IGOSS SST minimum	0.12		
Squid positive/negative cutoff	0.42	0.86(*)	
Squid latitude/PC1 cutoff	0.37	0.97(**)	0.90(*)

(\*)  $p < 0.05$       (\*\*)  $p < 0.01$

**Salmon CPUE and Body weight**

Log-transformed CPUE for salmon showed few significant differences between ocean domains or across the SST minimum. The CPUE of most of the species and ocean age classes showed catches increasing linearly from the south to the north, most likely representing return migration patterns rather than feeding distribution. Ocean age .1-.2 sockeye had highest catches in the Ridge Domain, possibly due to the abundance of southern British Columbia stocks. Pink salmon, ocean age .2 and .3 chum salmon, and ocean age .3 sockeye salmon showed significant differences in CPUE by year (1-Way ANOVA,  $p < 0.05$ ), which are probably related to the

interannual variation in the population size of each stock (Myers et al. 1999).

Of the 14 age and maturity classes caught in large enough numbers for analysis, three groups of chum salmon showed significantly larger body weights north of the SST minimum, while coho, pink, and maturing .2-.3 sockeye salmon showed significantly larger body weights to the south (Table 5). These latter species feed exclusively on squid in the southern zones, while the chum feed on zooplankton in both zones. Ocean age .1 sockeye were not significantly different in size between the two zones.

Within the southern and the northern zones, several of the species/age-class combinations showed significant interannual variation in body weight (1-way ANOVA,  $p < 0.05$ ). Specifically, the fish with the largest average body weights—coho, ocean-age .3 chum and maturing ocean-age .2 sockeye salmon—were larger in 1996 and 1998 than in any other year. These coincide with the years that temperatures were coolest overall, and the SST minimum boundary and the squid were the farthest to the north (Fig. 8). Conversely, ocean age .1 sockeye salmon, both in the south and the north, were significantly larger in 1997 than in any other year (1-way ANOVA). This coincides with the year that waters were warmest and the SST minimum and squid were farthest to the south.

**DISCUSSION**

The analysis of zooplankton and micronektonic squid along the transect line supports the existence of a biological boundary affecting salmon feeding ontogeny between 50-54°N, associated with the July sea surface temperature minimum (Tables 3-4 and Figs. 6-8). This boundary was noted by LeBrasseur (1966), who described the predominance of squid in salmon diets in the Subarctic Current. Pearcy et al. (1988) similarly noted a biological boundary along 155°W in 1984 and 1985, but associated the boundary with the border between the Subarctic Current and the Ridge Domain. However, our analysis shows that the SST minimum is more strongly correlated with the biological boundary than the Ridge/Subarctic border.

The importance of the latitudinal position of the SST minimum boundary in determining salmon growth is suggested by the body weights of the largest salmon, which have the highest predation rates on squid (Kaeriyama et al. this volume). All of these species are larger in 1996 and 1998, when the boundary was farther to the north, and smaller in 1997 when the boundary was farther to the south (Fig. 8).

It is possible that sea surface temperature, which is warm in 1997 and cold in 1996 and 1998, is a contributing physiological factor, causing poor growth in warm years. However, such a physiological effect of

**Table 5.** Average body weights by species, ocean age, and maturity status, of salmon caught south and north of the SST minimum. North/South *p*-value shows significance of difference between north and south for all years pooled using a 2-tailed *t*-test.

Species	Ocean age	Maturity <sup>1</sup>	N	Body weight north (kg)	Body weight south (kg)	North/South <i>p</i> -value	Significantly higher in:
Chum	.1	IM	332	0.75	0.67	<0.0001	North
		MT	28	0.77	0.84	0.55	
	.2	IM	763	1.29	1.18	<0.0001	North
		MT	100	1.52	1.41	0.21	
	.3	IM	54	1.68	1.59	0.62	
		MT	43	2.60	1.93	0.01	North
Coho	.1	MT	412	2.82	3.06	0.01	South
Pink	.1	MT	876	1.30	1.53	<0.0001	South
Sockeye	.1	IM	68	0.50	0.54	0.10	
		MT	39	0.79	0.95	0.57	
	.2	IM	82	1.75	2.01	0.07	
		MT	641	2.27	2.65	<0.0001	South
	.3	IM	2	2.78	-		
		MT	292	2.96	3.15	0.03	South

<sup>1</sup>IM, immature; M, mature.

sea surface temperature should act similarly for all salmon groups, but ocean age .1 sockeye salmon are larger in 1997 than in the colder years. These smaller fish, feeding mainly on zooplankton, grow larger in years in which their overlap with squid is minimized. Chum salmon, also zooplankton feeders, are larger in the north in all years (Table 5), supporting the idea that the difference in prey distribution on either side of the boundary is a determining factor in growth. This pattern suggests that the squid are a competitor with the chum and smaller sockeye for food.

There is no evidence of a small-scale, station-by-station negative correlation between squid and zooplankton within each region, perhaps due to mesoscale zooplankton structure associated with eddies (Fig.6). Zooplankton density is lower to the south and higher to the north, while the density of the micronektonic squid *Beryteuthis anomychus*, as indexed from salmon stomach sampling, is higher in the south than in the north. It is possible, but not confirmable, that lower densities of zooplankton are evidence of top-down control of zooplankton by squid and salmon.

The latitude of the SST minimum varies from year to year between 51°N in 1997 and 54°N in 1998, a distance of over 300 km. In the north, zooplankton density increased from 1994 to 1998 but it did not differ significantly in the south. Within each region, squid density did not vary significantly from year to year. Therefore, the processes determining the latitude of the SST minimum may be more important to salmon prey distribution than the variation in the amount of food within each region.

The mechanistic link between the SST minimum and the northern boundary of squid distribution is not clear. The SST minimum may represent a density or

temperature gradient unsuitable for squid. More likely, Aydin et al. (1998) suggest that the SST minimum may be a proxy for a frontal structure between internal Alaska Gyre waters and waters from the west. It is also possible that the SST minimum is a better proxy for the Subarctic Current than the 4°C vertical isotherm, or that squid respond to multiple conditions, entering the Gyre in the Subarctic Current and spreading north to the SST minimum. Surveys conducted in the 1950s–1970s show that Oyashio waters are associated with a cold front within the Ridge Domain which varies substantially in its eastern extent from year to year (Favorite and Hebard 1961; USBCFBL 1969). This component of westward transport, associated with the SST minimum, may be linked to squid distribution.

Fronts may propagate across the North Pacific and vary substantially from year to year (Yuan and Talley 1996). Percy et al. (1996) found a similar biological border further to the south that was important for larger species such as Pacific pomfret (*Brama japonica*) and Neon Flying Squid (*Ommastrephes bartrami*). The role of fronts in salmonid feeding has been cause for speculation (e.g., Brandt 1993), and the behavior of these fronts under climate-change scenarios may be critical to determining changes in salmon biogeography.

Because the squid are sampled from salmon themselves, it is possible that the change is not representative of squid abundance but of the changing ability of salmon to capture squid on one side of the border, or that at warmer temperatures catching squid ceases to be profitable causing salmon to switch to zooplankton. However, the fact that the switch occurs in pink, sockeye, and coho salmon simultaneously, three species with differing energy budgets,

suggests that the change is due to the presence or absence of squid.

The determination of the SST minimum as a proxy for the border between two distinct feeding modes of salmon has implications for both salmon growth and future populations. Because SST records exist in the region back to the 1950s, it would be worthwhile to examine the variation in this border back through time with large-scale salmonid growth trends, to determine the importance of this mechanism in salmon growth overall. Such retrospective studies in combination with continuing modeling on salmon growth would improve our ability to understand the consequences of global climate change.

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