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Variation in the biogeography of Gulf of Alaska micronekton as a driving mechanism for observed growth trends in Pacific salmon

By Kerim Y. Aydin
School of Aquatic and Fishery Sciences
University of Washington
Box 355020
Seattle, WA 98195 USA
e-mail: kerim@fish.washington.edu

Abstract

The adult body **lengths** and weights of many Pacific salmon stocks (*Oncorhynchus* spp.) are negatively correlated with sea surface temperature in the northeastern Pacific Ocean. The mechanisms behind the correlation may be due to (1) a physiological response of salmon to warming surface waters; or (2) shifts in the abundance or composition of prey species. Determining the relative importance of each mechanism is critical to predicting the effect of climate change on salmon populations. In this study, I summarize empirical studies of oceanographic conditions, salmon food habits, and salmon growth in the Gulf of Alaska during the **1950s**, **1980s**, and 1990s. I use bioenergetics models to determine the variation in the factors determining salmon growth.

In particular, I show a relationship between oceanographic boundaries, the southern limit of salmon distribution, and the northern limit of a micronektonic squid species (*Berryteuthis anonychus*), a dominant salmon prey item in the region. I use the area of species overlap to define a zone of "highest salmon growth," the size of which **varies** on interannual time scales. I calculate the area of squid/salmon overlap from oceanographic data for the years 1950-98, and show that variation in this overlap explains much of the negative correlation between sea surface temperature and adult salmon body weight. This suggests that biogeographic variation in food web structure, with micronektonic squid as a keystone species, is a mechanism that contributes to the interannual variation in salmon growth in the northeastern Pacific.

Introduction and methods

Between the late 1970s and late **1990s**, the mature body size (both length and weight) of adult Pacific salmon (*Oncorhynchus* spp) declined in 43 out of 45 North American stocks that spend part of their life history in the high seas of the Gulf of Alaska (**Bigler** et al. 1996). This cause of this decrease has been related to two factors: (1) the increase in the numbers of maturing salmon in the North Pacific, leading to limitations in salmon food supply across the Pacific (Pyper and

Peterman 1999), and (2) the increase in seawater temperature throughout the northeast Pacific Ocean between the 1970s and 1990s (Hinch et al. 1995; Welch et al. 1998). This increase in temperature may have decreased growth rates in adult salmon either by raising the metabolic cost of foraging or by limiting the distribution of prey.

In the months prior to maturation, several species of Pacific salmon depend on micronektonic squid, especially the pelagic species *Berryteuthis anonychus*, as an important food source in the Gulf of Alaska (Pearcy et al. 1988; Aydin et al. in press). Little is known about the distribution and interannual variation of this squid species.

In this study, an index of squid abundance was derived from salmon food habits data, using over 10,000 salmon collected between 1950-1998 to calculate a baseline level of squid feeding from which variations could be measured at any point in time and space at which salmon were collected (Aydin 2000). Values of this index, calculated from salmon collected in the 1990s, were compared with oceanographic data to determine the relationship between Gulf of Alaska oceanography and squid distribution. Bioenergetics models were used to associate values of this index with the growth rates of salmon in the area.

The relationship between squid/salmon overlap and oceanography was then extrapolated between 1950-1998 using existing sea surface temperature records for the time period. This historical extrapolation was compared with historical data of salmon body sizes to determine if the variation of squid in the Gulf of Alaska was an important factor controlling salmon growth.

Results and discussion

The squid index revealed a latitudinal boundary in the Gulf of Alaska: south of which, several species of salmon fed almost entirely on squid in the months immediately prior to maturation, north of which, salmon fed on less nutritious zooplankton (Figure 1). The results of bioenergetics models indicate that for several salmon species, growth rates were much higher in the southern, squid-rich region (Figure 2).

Furthermore, the latitude of this boundary varied from year to year and was strongly associated with the latitudinal sea surface temperature minimum, an oceanographic feature of the Gulf of Alaska that may mark a transition between eastward-flowing waters in the south and central gyre waters in the north (Aydin et al. 1998). This latitudinal boundary in salmon feeding had been noted in previous studies (e.g., Percy et al. 1988). However, these previous studies were not conducted over enough years to measure this association.

If the sea surface temperature minimum is considered to be the northern limit of squid distribution, and this information is combined with the hypothesized summer 13°C southern sea surface temperature distribution limit of sockeye salmon (0. *nerka*; Welch et al. 1998), the total hypothesized ocean surface area of squid/salmon overlap fluctuated between 2 and 4 million square kilometers during the time period 1954-1998 (Figure 3). This fluctuating overlap area shows

a strong positive correlation with the body sizes (length and weight) of many adult Pacific salmon stocks. Since this overlap area is indexed by sea surface temperature, the relationship may explain the negative correlation between sea surface temperature and salmon body size in the northeast Pacific.

There is a complex interaction between the area of squid overlap and the density-dependent (competitive) growth in salmon. During years of high salmon abundance after the 1976 “climate shift” in the northeast Pacific, the relationship between the area of squid overlap and adult salmon body size was stronger for many stocks. Two hypotheses are possible: (1) during years of high salmon abundance after 1976, salmon may have competed more intensely for squid and thus have been more sensitive to changes in squid distribution, or (2) after 1976, squid abundance may have increased in the Gulf of Alaska, and the squid may serve as keystone species between salmon and lower **trophic** levels.

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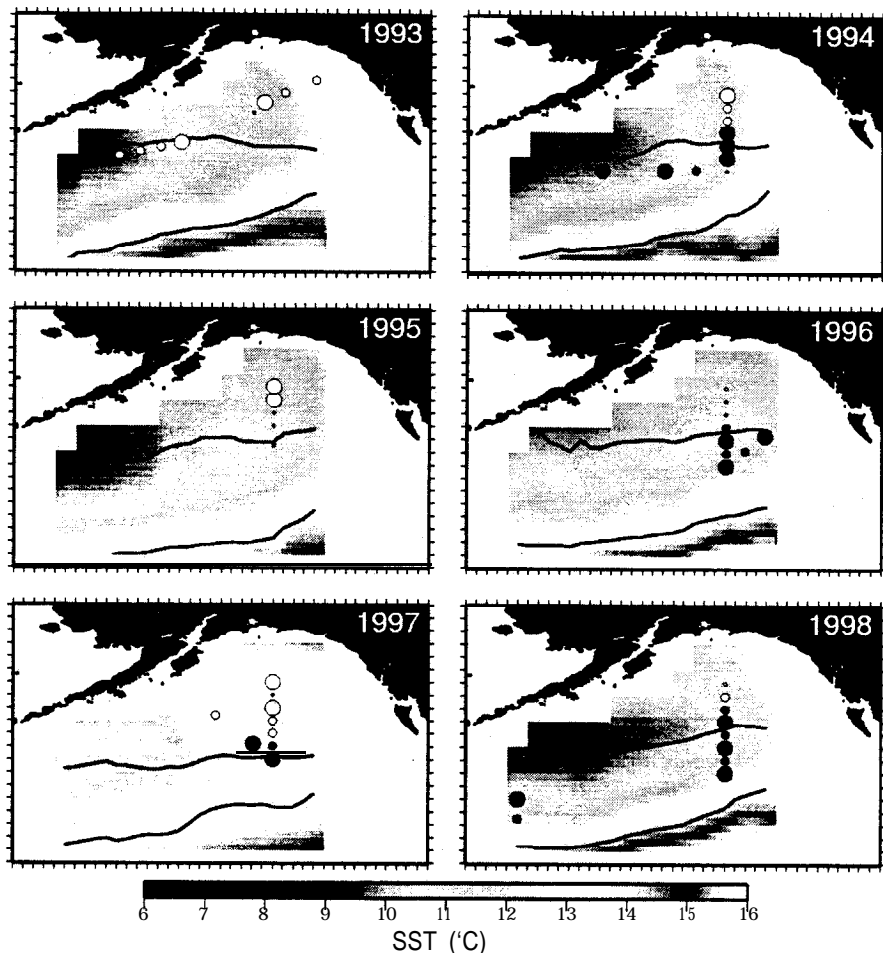


Figure 1. Sea surface temperature (shading), latitudinal sea surface temperature minimum (northern solid line), 13°C isotherm (southern solid line) and squid index values (circles), 1993-99. Black circles show positive index values (above average squid abundance) and white circles show negative index values (below average squid abundance). Hypothesized “squid/salmon overlap area” is area between the two lines, bounded by 140°W and 165°W.

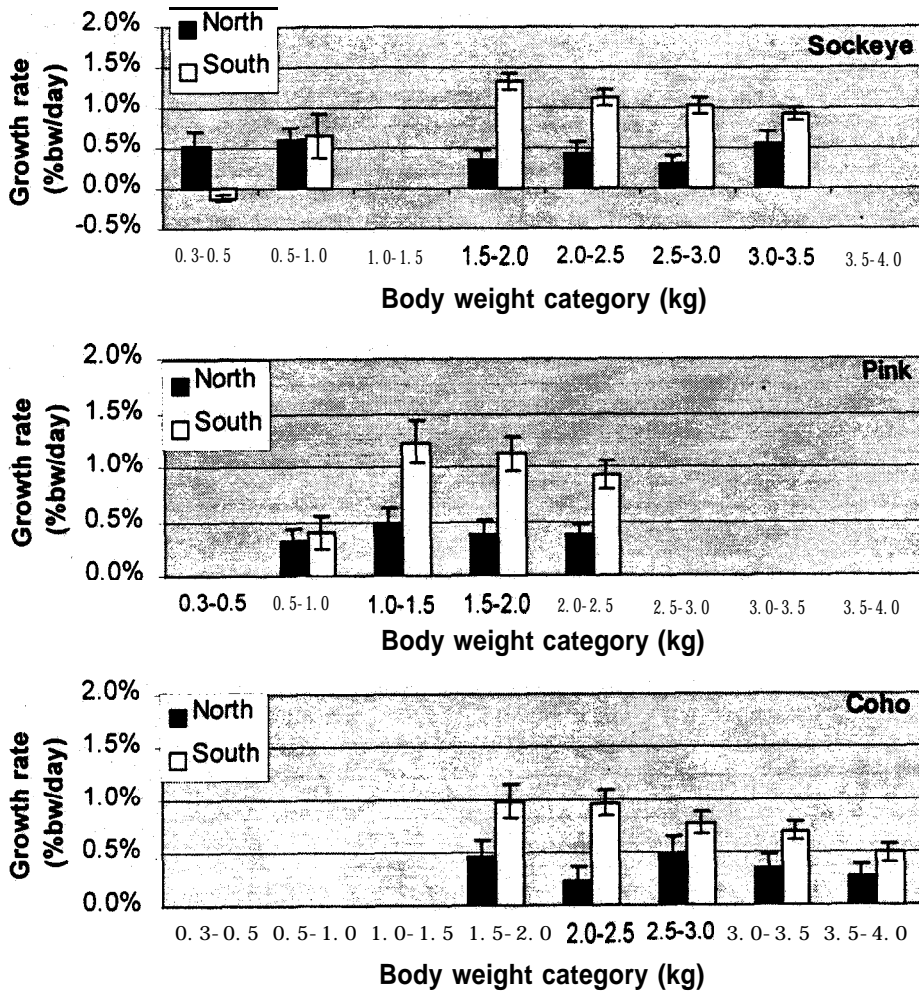


Figure 2. Modeled growth rates (percent body weight/day) of sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), and coho salmon (*O. kisutch*), north and south of the sea surface temperature boundary, 1994-98. Growth rates were calculated from stomach contents in each region and are grouped by salmon body weight.

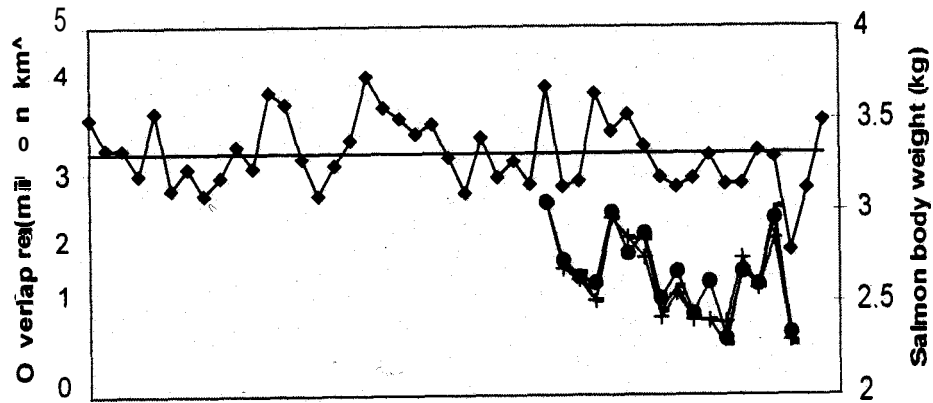


Figure 3. The hypothesized squid/salmon overlap area, 1954-98 (upper line, mean value shown) and body weights measured in three British Columbia area (Fraser River) sockeye salmon fisheries, 1982-97 (lower lines). Body weights are shown only for the period of highest correlation with overlap area (post-1976 climate shift).