Feeding Habits, Consumption Rates, and Growth of Juvenile Salmon in Relation to Fluctuations of the Forage Base and Salmon Abundance

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Total salmon abundance in the North Pacific has increased over the last thirty years. In the 1990s, there was some evidence of density-dependent effects in salmon populations that led researchers to conclude there were shortages of food resources and an overpopulation of the North Pacific by Pacific salmon (Ishida et al. 1993; Bigler et al. 1996; Kaeriyama 2003; Klovach 2003). Over the past decade, Pacific salmon abundance has continued increasing. This might cause intensification of competitive interactions between and among Pacific salmon species. This study aims to determine whether feeding habits, consumption rates, growth, and food supply (degree of satisfaction of the feeding requirements of the fish) of juvenile pink and chum salmon changed in 2001-2010, and how this was related to salmon abundance and their forage base.

This study is based on findings of 18 complex epipelagic surveys conducted in the Sea of Okhotsk and western Bering Sea by TINRO-Center in September-November from 2001 to 2010. The surveys included biomass estimation of salmon, ecologically-related plankton and nekton species, and fish diet analysis. Fish were sampled with pelagic trawls (vertical opening 25–45 m, horizontal opening 35-50 m) equipped with a small-size mesh (1 cm) lining the cod end. Zooplankton samples were obtained using a Jedy net (0.1 m^2 mouth opening and 0.168-mm mesh). Stomach contents were analyzed aboard the vessel using the method described by Volkov and Chuchukalo (1986). For more details see Glebov et al. (2005) and Zavolokin et al. (2007).

Due to the large number of trophic indices used, such as daily ration, stomach fullness, diel feeding rhythm, trophic niche breadth, number of prey, diet overlap, and share of minor food, their interpretation in terms of forage conditions and food supply is potentially biased. I suggest the food supply index (FSI) as a quantitative measure of food supply. The FSI is the average of values (k) for all indirect indices (i): $FSI = \Sigma\, k_i/n$. k assumes the values -1, 0 and 1, which means unfavorable, normal, or favorable conditions of the food supply, respectively. The FSI allows for the quantitative measure of food supply and makes statistical analysis possible.

In the Sea of Okhotsk, relatively low salmon food supply occurred in 2001, 2002, 2004 and 2006 (Table 1). In 2002 and 2004, this was indicated by low feeding intensity and a high share of minor food items in salmon stomach contents. In 2001, there was high diet overlap between pink and chum salmon associated with consumption of copepods and chaetognaths. Due to the increase in the share of pteropods in the pink salmon diet and chaetognaths in the chum salmon diet in 2006, a broad feeding spectrum and divergence in salmon feeding testified to a relative decrease in the salmon food supply. High FSI values observed in 2003 and 2007 resulted from high consumption rates and a low proportion of minor food items.

Table 1. Trophic characteristics and food supply index of juvenile pink and chum salmon in the Sea of Okhotsk in 2001-2010.

Trophic feature	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Daily ration	0	-1	1	-1	0	0	1	0	0	0
Stomach fullness	0	-1	1	-1	0	0	1	0	0	0
Diel feeding rhythm	0	0	0	0	0	0	0	0	0	0
Trophic niche breadth	0	0	0	0	0	-1	0	0	0	0
Number of prey	0	0	1	0	0	-1	0	0	0	0
Diet overlap	-1	0	0	0	0	-1	0	1	0	-1
Share of minor food	-1	-1	1	0	0	0	0	0	1	0
Food Supply Index	-0.3	-0.4	0.6	-0.3	0	-0.4	0.3	0.1	0.1	-0.1

In the Bering Sea, relatively low food supplies occurred in 2006, 2008 and 2010 (Table 2), when food consumption rates decreased. The role of copepods and chaetognaths in salmon diets was insignificant, diet overlap was low, and relatively high daily rations were observed in samples collected during those years.

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Table 2. Trophic characteristics and food supply index of juvenile pink and chum salmon in the western Bering Sea in 2002-2004 and 2006-2010.

Trophic feature	2002	2003	2004	2006	2007	2008	2009	2010
Daily ration	1	0	1	0	-1	-1	0	0
Stomach fullness	1	1	-1	-1	0	0	0	0
Diel feeding rhythm	0	0	0	0	0	0	0	0
Trophic niche breadth	0	1	1	0	0	0	0	0
Number of prey	-1	0	0	0	0	-1	0	-1
Diet overlap	0	1	1	-1	0	0	0	0
Share of minor food	-1	1	1	0	0	0	0	-1
Food Supply Index	0	0.6	0.4	-0.3	-0.1	-0.3	0	-0.3

The FSI correlated negatively with juvenile salmon biomass both in the Sea of Okhotsk (r = -0.78, p = 0.008, N = 10; Fig. 1) and the western Bering Sea (r = -0.56, p = 0.150, N = 8; Fig. 2). This means that increases in juvenile salmon biomass were accompanied by changes in feeding habits that resulted in the switch to minor food items (copepods, chaetognaths), widening of trophic niche breadth, change in diet overlap, and/or decrease in feeding intensity, i.e., a density-dependent effect. The question is what does this mean for salmon populations?

Feeding habits of juvenile pink and chum salmon changed in years when there was a high salmon biomass. However, these changes were not pronounced (Tables 1 and 2).

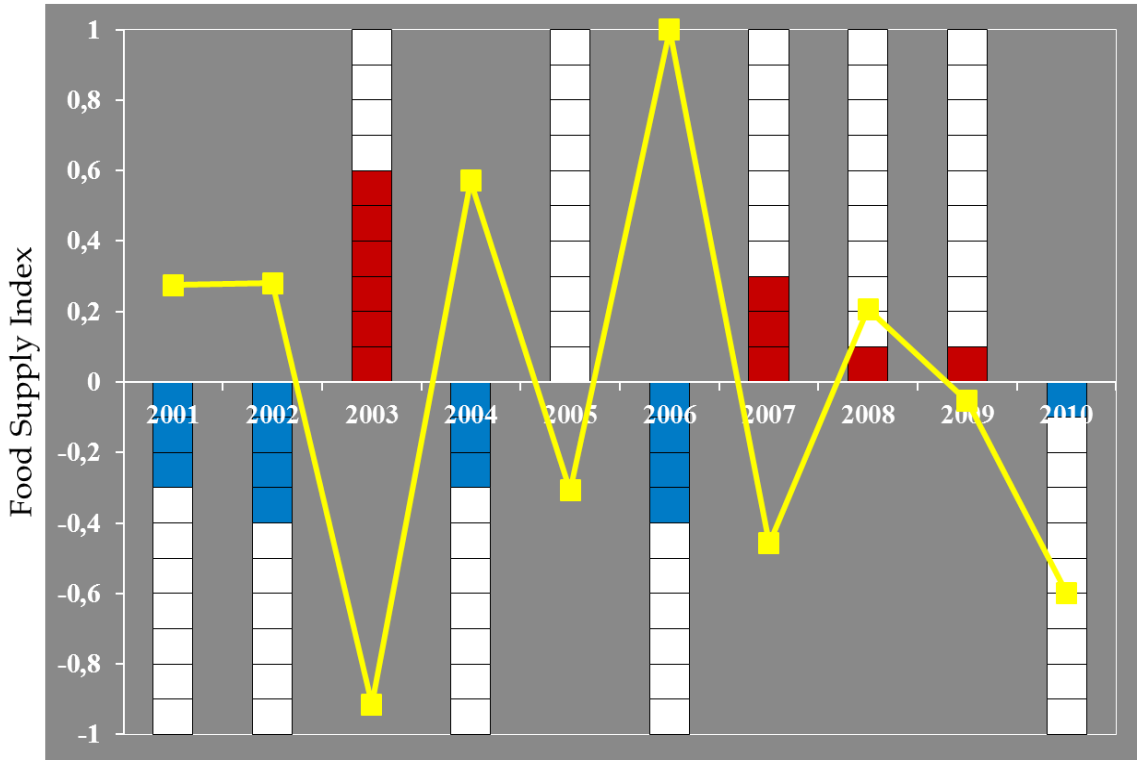

Fig. 1. Changes in the food supply index in relation to normalized juvenile salmon biomass in samples collected in the Sea of Okhotsk, 2001-2010.

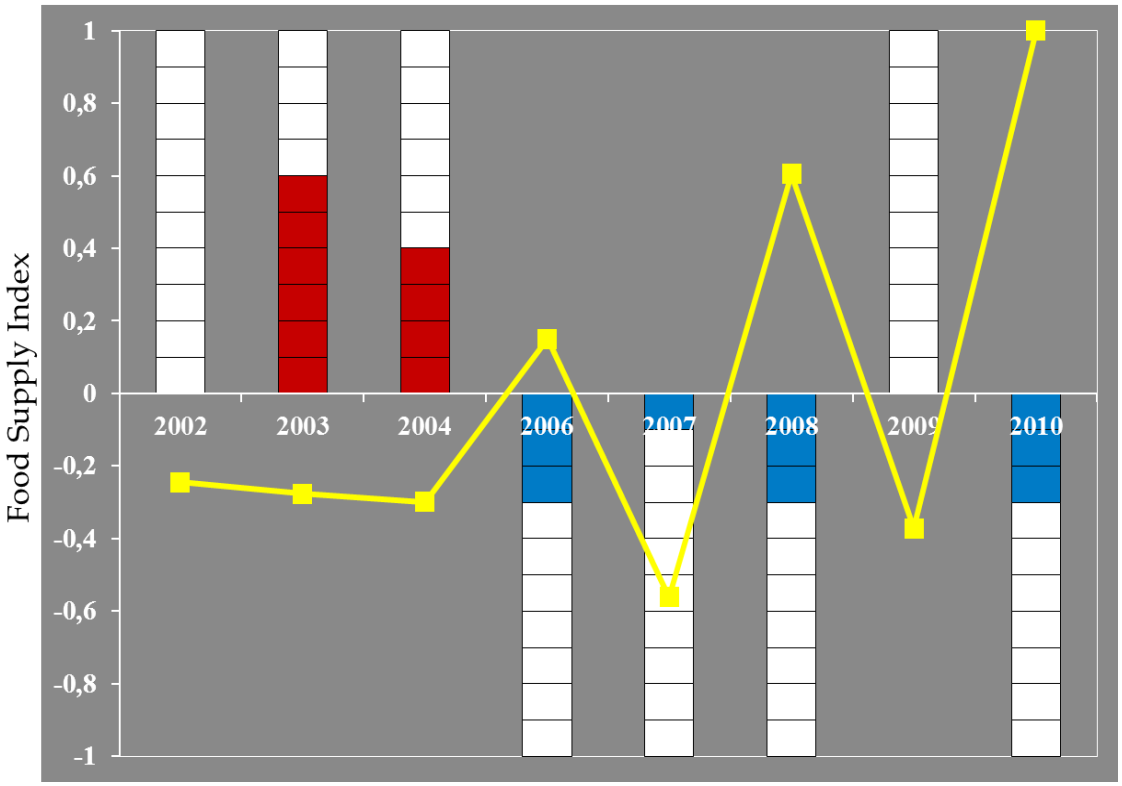

Fig. 2. Changes in the food supply index in relation to normalized juvenile salmon biomass in samples collected in the western Bering Sea, 2002-2004 and 2006-2010.

Daily ration of juvenile salmon was lower in years with a relatively low food supply as compared with other years. The daily ration decreased by 14% in the Sea of Okhotsk and by 9% in the Bering Sea, though these differences in daily ration between years of low and "normal" FSI were insignificant ($p = 0.05$).

Changes in feeding habits and consumption rates did not seem to negatively affect juvenile salmon growth. Body size of juvenile salmon did not significantly correlate either to their abundance or to the relative biomass of the forage base (Shuntov and Temnykh 2008, 2011). On the contrary, growth of juvenile chum salmon, as estimated by scale analysis, tended to be enhanced in the last decades of high salmon abundance (Kaeriyama et al. 2007; Seo et al. 2009; Agler et al. 2012; Zavolokin et al. 2012).

Thus, despite increased salmon abundance there were no strong negative consequences for juvenile salmon in the Sea of Okhotsk and western Bering Sea in 2001-2010. Possible strengthening of competition among salmon populations was compensated by adaptive changes in their feeding habits.

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