North Pacific Ocean Carrying Capacity—Is it Really too Low for Highly Abundant Salmon Stocks? Myths and Reality

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Carrying capacity is the ability of an environmental system to sustain reproduction and normal function of a given number of organisms. As for salmon-related issues concerning carrying capacity of the Subarctic Pacific and the Far Eastern seas, special attention is usually given to the amount of food available for salmon during their marine forage stage implying direct and indirect influence of prey-related factor. In this respect, much attention is given to competitive relationships between chum and pink salmon. This problem was first outlined by Japanese and American scientists (Ishida et al. 1993; Ogura and Ito 1994; Welch and Morris 1994; Bigler et al. 1996; Azumaya and Ishida 2000), and later was considered by Russian researchers (Volobuev 2000; Volobuev and Volobuev 2000; Gritzenko et al. 2001; Klovach 2003).

We believe that some of conclusions from these studies suggested too dramatic a course of events and hardly reflected the real pattern. The following statements seem groundless:

— the North Pacific carrying capacity has been surpassed for salmon stocks, and they are thought to experience degradation along with enhancement of hatchery chum stocks;
— extremely high abundance of chum has led to drastic rearrangements in the trophic structure of the North Pacific pelagic communities;
— pink salmon forces out and even suppresses chum salmon in most areas of their shared habitat. One of the exclusive statements is that these species exemplify the Gause principle of competitive elimination;
— chum salmon was forced to make an adaptive shift towards low-calorie prey (gelatinous species), which resulted in weakening of its skeletal musculature and in other pathologic body changes;
— salmon prey availability may be extremely low, especially in winter.

Large-scale comprehensive investigations conducted by TINRO-Centre made it possible to collect an expanded amount of data on these and related issues of salmon marine ecology, and in most cases these observations resulted in a different point of view on the above mentioned statements.

1. The greater part of the marine life of salmon is spent in deep-water regions, and this is shown by data on salmon species distribution in the Far Eastern seas and northwestern Pacific. Nektonic species density in deep-water regions is lower than in shelf areas, and is especially low in the upper epipelagic zone where most salmon stocks are distributed. The plankton to nekton biomass ratio exceeds several tens and even hundreds in the offshore epipelagic zone, while on the shelf it is usually significant lower. These observations imply that the density factor and intensiveness of competition for food should decrease oceanward. During the course of their ecological history, Pacific salmon species were successfully incorporated into the upper epipelagic zones of the vast pelagic biotopes distributed over deep-water regions of the seas and oceans. These areas contained plentiful food resources, and were weakly occupied by nekton.

2. However, during each season salmon occupy just a part of the potential distribution area. Thus, food competition may occur due to high abundance of salmon under condition of low plankton concentrations. This may affect their growth rate.

Inverse relationships between weight and total abundance of pink salmon were observed for both even- and odd-year generations during their summer migrations to the coast in the Okhotsk Sea (Table 1). On another hand, there is no definitive dependence of weight and abundance in odd and even generations of pink salmon from western Bering Sea stocks (Fig. 1). The average body sizes of more abundant odd-year generations pink salmon were larger than those of even-year generations for all Japanese stocks (Table 2). There is no definitive dependence of size and feeding rate upon macroplankton concentration for the Okhotsk Sea pink salmon stocks (Table 1) and the Bering Sea pink salmon stocks. These results may be indicative of much more complicated relationships between salmon sizes and the forage base.

The density dependence of stocks is a well-documented process, and it may impact salmon during their marine and oceanic forage period. However, variability in the size and growth rate of fish does not necessarily reflect the influence of a density factor, because these characters are not always dependent upon fish abundance and the abundance, quality, and availability of prey. Temperature and other hydrological factors, as well as heredity, may

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influence the metabolic processes of fish, including growth rate. The known genetic components of growth and their impacts are clearest in highly structured stocks. All the above mentioned observations suggest that not all of the factors responsible for the observed changes in the size structure of pink salmon stocks are known at present time.

3. Pink and chum salmon are key species for understanding salmon biology and dynamics of abundance. As mentioned above, some authors even suggested that these two species might exemplify a principle of competitive elimination (Volobuev and Volobuev 2000). From our point of view, these conclusions are groundless. The results of most Russian investigations conducted in Asian waters since the 1980s have suggested that chum and pink salmon are somewhat different in terms of trophic relationships (Volkov 1996; Naidenko 2002, 2003; Naidenko and Kuznetsova 2002; Kuznetsova 2004; Temnykh et al. 2004).

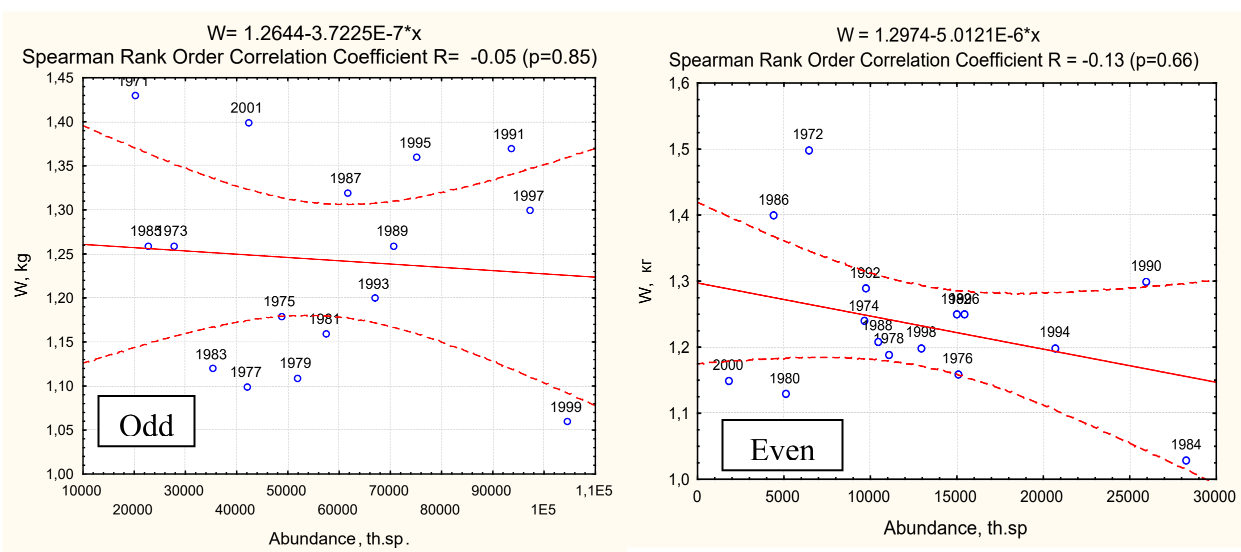
Table 1. Correlation matrix for relationships between parameters indicating the abundance and size of pink salmon from the Okhotsk Sea stocks, feeding intensity, and concentration of prey organisms in 1991–2003. 1 – pink salmon biomass, 10^3 t; 2 – average pink salmon weight in the Okhotsk Sea, kg; 3 – average pink salmon weight in Kuril oceanic waters, kg; 4 – feeding intensity of pink salmon in the Okhotsk Sea, 0/000; 5 – feeding intensity of pink salmon in Kuril waters, 0/000; 6 – macroplankton biomass in the southern Okhotsk Sea, t/km^2; 7 – biomass of euphausiids, hyperiids and pteropods, t/km^2; 8 – biomass of small nekton (fishes, squids), t/km^2. Statistically significant correlation coefficients are marked by bold font.

	1	2	3	4	5	6	7	8
1	1	**-0.66**	**-0.64**	0.19	-0.22	-0.35	-0.12	-0.01
2	**-0.66**	1	0.62	-0.17	0.23	-0.23	-0.44	0.45
3	**-0.64**	0.62	1	0.30	0.36	-0.19	-0.31	0.19
4	0.19	-0.17	0.30	1	-0.24	-0.05	-0.04	-0.13
5	-0.22	0.23	0.36	-0.24	1	-0.19	-0.28	0.23
6	-0.35	-0.23	-0.19	0.05	-0.19	1	**0.81**	-0.33
7	-0.12	0.44	-0.31	-0.04	-0.28	**0.81**	1	-0.37
8	-0.01	0.45	0.19	-0.13	0.23	-0.33	-0.37	1

Table 2. Average catches (10^3 t) and weight (kg) of pink salmon from Japan sea stocks in 1971-2002.

Stocks	Odd- year generations		Even- year generations	
	Average catches	Average weight	Average catches	Average weight
Amur	1.2	1.32	1.96	1.17
Western Sakhalin	4.4	1.37	1.68	1.08
Primorye	2.1	1.66	1.88	1.27
Average total catches	7.7		5.52	

Fig. 1. Relationship between body weight and total abundance of pink salmon in the eastern Kamchatka region. th.sp. = thousands of fish



In the case of chum salmon, special attention should be paid to the gelatinous groups of prey. According to some researchers (Gritzenko et al. 2001; Klovach 2003), the feeding of chum salmon on gelatinous prey reflected an induced adaptation that resulted from food deficiency due to high abundance of chum and other salmon species, as well as competition with pink salmon. These groups of gelatinous prey may account for up to 30–50% or more of the total fish ration. However, a high occurrence of gelatinous animals was especially characteristic of mature fish distributed closer to the coast (Naidenko and Kuznetsova 2002; Starovoitov 2003; Temnykh et al. 2004). This indicates to us that these planktonic prey organisms may be important for fish physiology.

4. In order to test conclusions about salmon overpopulation in the North Pacific and rearrangement of energetic pathways in ecosystems related to high abundance of hatchery chum, it is necessary to analyze the trophic structure of nektonic communities in general and to estimate forage resources of the pelagic zone. In this respect, the point should be stressed that the scale of salmon aquaculture and the amount of food consumed by salmon species in general are much lower than the capacity of pelagic ecosystems and even separate trophic levels and their components. We have already noted (Shuntov et al. 1993; Shuntov 2001; Dulepova 2002) that the biomass and production of zooplankton and especially macroplankton are frequently underestimated by several times in modern-day publications. Salmon input into the trophic structure of pelagic communities is generally low, and an additional several hundred thousand tons of artificially reared salmon cannot significantly change this trophic structure.

Long-term dynamics in the amount of plankton consumed by nekton in the western Bering and Okhotsk seas may serve as examples. In the Bering Sea, the total absolute amount of food consumed by salmon increased only slightly from 1986 to 1990 (Fig. 2). However, the share of prey consumed by salmon in the total amount of prey consumed by all nektonic species increased from 2% in 1986 to 9% in 1990. This level has remained stable, accounting for 8% of prey consumed by all nektonic species in 2002, though the absolute amount of prey consumed by salmon was approximately three times higher than in 1990. In the Okhotsk Sea, the amount of food consumed by salmon increased during the 1990s, and was especially high by the late 1990s due to the rise in salmon abundance, primarily pink salmon and to a lesser extent chum salmon (Fig. 3). The share of food consumed by salmon persisted at a low level of approximately 1%, though the absolute numbers increased two times (from 0.7% to 1.5%; Temnykh et al. 2004). Though the amount of plankton consumed by nektonic animals is very high, it presumably does not exceed 10% of all the plankton production (Shuntov et al. 1993).

Fig. 2. Consumption (%) of zooplankton by abundant fish species in the epipelagic zone of the western Bering Sea during autumn (Temnykh et al. 2004).

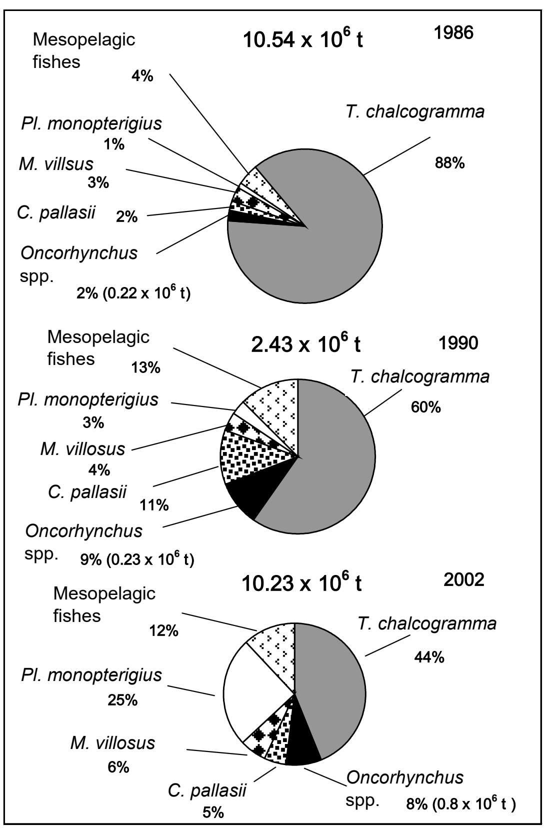
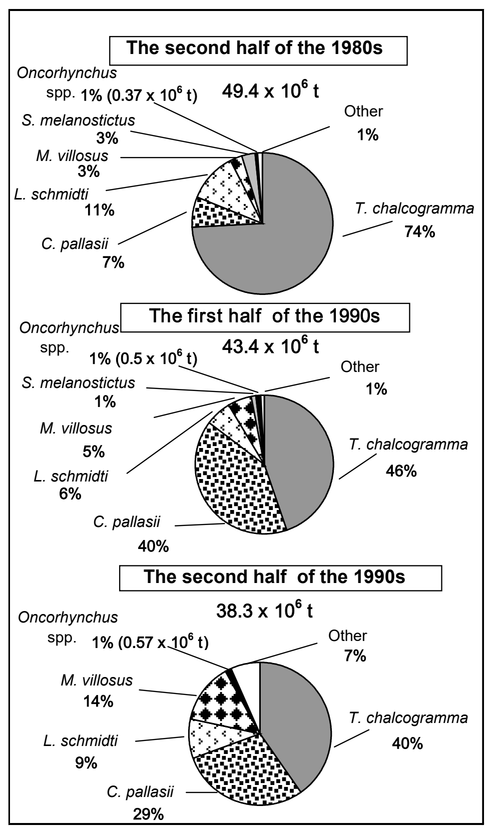


Fig. 3. Consumption (%) of zooplankton by abundant fish species in the epipelagic zone of the Okhotsk Sea during summer (Temnykh et al. 2004).



All these data suggest that though salmon species consume a large amount of food, especially during periods of high abundance, their role in trophic chains is far from being highly important. Even two- or three-fold variations in Pacific salmon abundance will hardly lead to significant changes in the trophic structure of nektonic communities. It is worth mentioning here that many highly important nektonic fluctuating species (pollock, sardine, herring, anchovy, mackerel, squids, etc.) regularly experience sharp variations in abundance, sometimes of one or two orders of magnitude, and their distributional ranges are smaller than those of salmon. At the same time, in spite of high variability of the species abundance and community structure (including trophic structure) there is no real base for considering these as critical or crisis events.

5. A number of observations also support the idea that salmon stocks are below the North Pacific carrying capacity, and that salmon do not overpopulate epipelagic ecosystems. These are as follows:

(a) A record number of salmon was estimated for the Russian sector of the Bering Sea in 2002–2003 (465–936 x 10^3 t). However, daily rations of salmon were maintained at the level observed in previous years (Efimkin in press).

(b) The most abundant salmon species (pink, chum, and sockeye) are known for highly expressed prey selectivity, especially during periods when their numbers are high. In particular, they prefer hyperiids and pteropods, which are subdominant groups in plankton communities.

(c) All salmon species can feed during any time of the day, though they prefer feeding in daytime and evening hours. If necessary, they may replenish their ration at night when concentrations of macroplankton and small nekton become notably higher in the upper water layers.

(d) Small-sized nektonic species (fishes, squids) are important prey items for salmon. Feeding upon these animals, salmon leave valuable quantities of small- and medium-sized plankton from being consumed, adding to the total zooplankton biomass.

(e) An increase in the abundance of any marine species is accompanied by expansion of their distributional ranges. Such a trend has been particularly observed in the late 20th century when an increase in abundance of chum from Japanese hatcheries resulted in extension of its marine range (Ogura and Ito 1994). The idea that salmon species do not overpopulate the North Pacific is also supported by their low occurrence in some areas.

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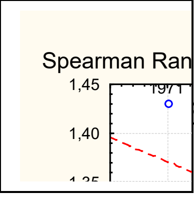

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