Similarity of Diurnal Rhythms of Pacific Salmon Feeding in the Western Bering Sea

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Volkov, A.F., and N.S. Kosenok. 2007. Similarity of diurnal rhythms of Pacific salmon feeding in the western Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 4: 327–333.

Abstract: Research on diurnal rhythms of salmon feeding is important for calculations of daily diets and evaluation of food sufficiency. The acquisition of such information requires datasets from trawling conducted during both day and night. The TINRO-Centre survey by RV *TINRO* in the western Bering Sea during the autumn of 2004 allowed for such data acquisition. Based on data averaged for several biostatistical areas, it was shown that small immature individuals (< 30 cm in fork length) of five Pacific salmon species had similar diurnal feeding patterns. They fed most intensively between 11:00 a.m. and dusk. Food was digested relatively quickly, and stomachs were essentially empty by 6:00 to 7:00 a.m. Older immature and maturing individuals had diurnal patterns that are less clear. This is probably related to food composition, and weak relationships between forage activity, time of day, and the time required to digest larger food items. If the degree of digestion is well defined, it is possible to define diurnal feeding patterns in some cases. When Hyperiidae are the primary food item, it is not possible to define the time of food intake precisely, because their chitinous shells hamper quick digestion.

Keywords: daily rhythms, salmon, feeding, diet, nekton, zooplankton

INTRODUCTION

One of the main challenges of marine nekton trophic ecology is defining the 24-hour food ration of organisms, especially fish. This is needed for practical calculations as well as for compiling total ecosystem balance equations. There are two ways of detecting the 24-hour food ration: experimental (in aquaria) or by measuring diets in the natural environment.

Natural observations are both preferable and possible using trawling surveys. In order to estimate the 24-hour food ration, however, it is necessary to estimate daily feeding rhythms, variability in food composition over 24 hours, and the speed of digestion. For these reasons, TINRO-Centre has developed a method (Chuchukalo and Volkov 1986) that has been used for several years in applied research. Depending on the particular objective, the daily feeding rhythms can be defined through measuring the daily dynamics of: a) stomach fullness, b) the presence of fresh or partially digested food, and c) the presence of empty or nearly empty stomachs (Volkov 1994; Volkov et al. 1997).

To study daily feeding patterns, the ideal approach would be to conduct frequent trawling surveys on several days at one location. However, in practice, during large-scale complex surveys this is not always possible. During one or several days a large number of fish stocks and dispersed individuals pass through a sampling area at a high rate of speed, which is typical for salmon. That is why, during the occupation of each station, the samples collected may not be representative of feeding at a particular site. This is why the observations from our trawls are combined, and a “synthetic” daily station is created with sufficient samples to arrange them into 1–2 hour intervals. This paper reports the results of a study of the 24-hour feeding patterns in pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon in the Russian Far Eastern seas.

MATERIALS AND METHODS

The basic method to detect 24-hour feeding rhythms is research on the dynamics of stomach fullness, i.e. the fullness indices that in Russian trophic ecology are traditionally expressed in parts per ten thousand ($^{o}/_{ooo}$). Studies on chum salmon feeding in the western Bering Sea which are based on the presence of fresh food, clearly show a single midday peak, using the 5-point system for identification of the level of food digestion (Fig. 1): 0 - fresh food, 1 - digestion hardly appreciable; loss of transparency, 2 - skin and muscles noticeably damaged, 3 - semi-digested fragments present, and 4 - digested matter present. However, in this example the dominant food item was *Clione limacine*. Its freshness in the stomach is reliably detected visually. One can also detect the freshness of recently eaten copepods and euphausiids,

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which are transparent in the plankton, but in stomachs they quickly turn opaque. However, if the food is hyperiid amphipods, a very common prey for salmon, it is difficult to determine their freshness visually, because their chitinous shells hamper quick digestion. That is why the presence of these species may result in a more complicated pattern than that shown in Fig. 1 (Volkov et al. 1997).

For the analysis of the diurnal feeding rhythms of salmon, samples were collected during surveys for the TINRO-Centre aboard the RV *TINRO*. Materials were collected from 11 September to 23 October 2004 in a deepwater zone of the western Bering Sea and western North Pacific Ocean (Table 1, Fig. 2).

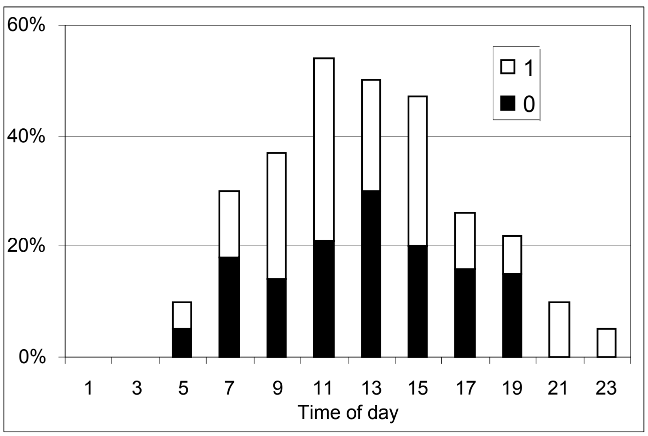

Fig. 1. Diurnal rhythms of chum salmon (50–70 cm in fork length) in the Bering Sea in summer. 0 = fresh food (solid); 1 = digestion hardly appreciable, loss of transparency (open); Y axis = % fullness (after Volkov 1994).

The charts with daily feeding patterns of salmon are based on data collected from trawls (Table 1). For tests on the feeding of nekton we sampled 25 stomachs of each size class, and for salmon 10 stomachs were sampled. Smaller samples of salmon were necessary as they often were in abundance.

RESULTS AND DISCUSSION

The daily rhythms of feeding intensity of immature salmon (30 cm or less in fork length) for all five species had much in common (Figs. 3–7). At daybreak most stomachs were empty or nearly empty. After sunrise, feeding activity rose rapidly, stomach fullness increased, and by mid-day it reached its first maximum. Then the digestion process exceeded food consumption, as evidenced by the decline in stomach fullness. By the end of the day feeding activity rose again, and during the period from twilight to early darkness stomach fullness reached its second maximum, which was usually greater than the first. Stomach fullness then declined as food was digested during the night, although some fish might continue feeding.

We note that salmon feed predominantly during daylight. As a result, their consumption of plankton should be calculated based on catches in the upper 50-meter layer (Volkov 1994) to estimate the daylight food base. The results of tagging programs using archival tags show that salmon are able to live and feed throughout a wide range of depths (down to 200 m) and temperatures, but the main feeding area is in the upper pelagic (i.e. water layer not deeper than 50 m). In order to make a quantitative estimation of the salmon food

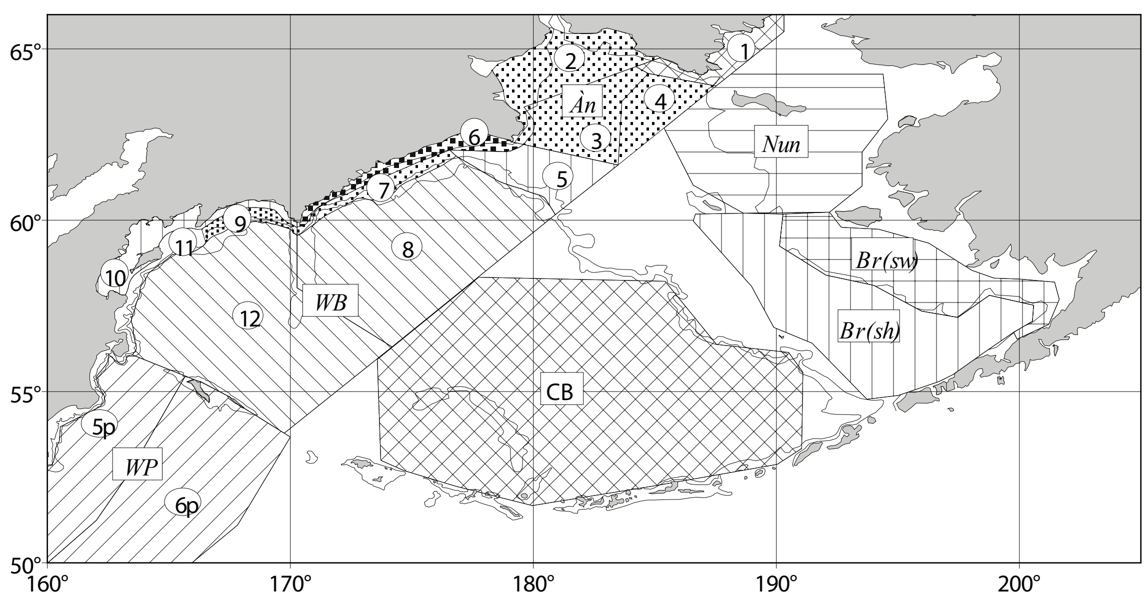

Fig. 2. Biostatistical areas of the Bering Sea and western North Pacific Ocean. WP = western North Pacific Ocean; WB = western Bering Sea; CB = central Bering Sea; An = Anadyr Bay; Nun = Nunivak; Br = Bristol Bay. Samples were collected in areas 8 (WB), 12 (WB), 5p (WP), and 6p (WP).

Table 1. Fork length categories of fish and number of trawls and stomach samples on which Figs. 3-7 are based.

	Pink		Chum		Sockeye			Coho		Chinook	
Fork length (cm)	15-20	20-30	15-20	30-40	15-25	30-40	40-50	20-30	30-40	20-30	40-50
Number of trawls	15	17	20	17	17	10	20	20	10	9	10
Number of samples	214	258	160	263	93	146	119	65	33	15	19

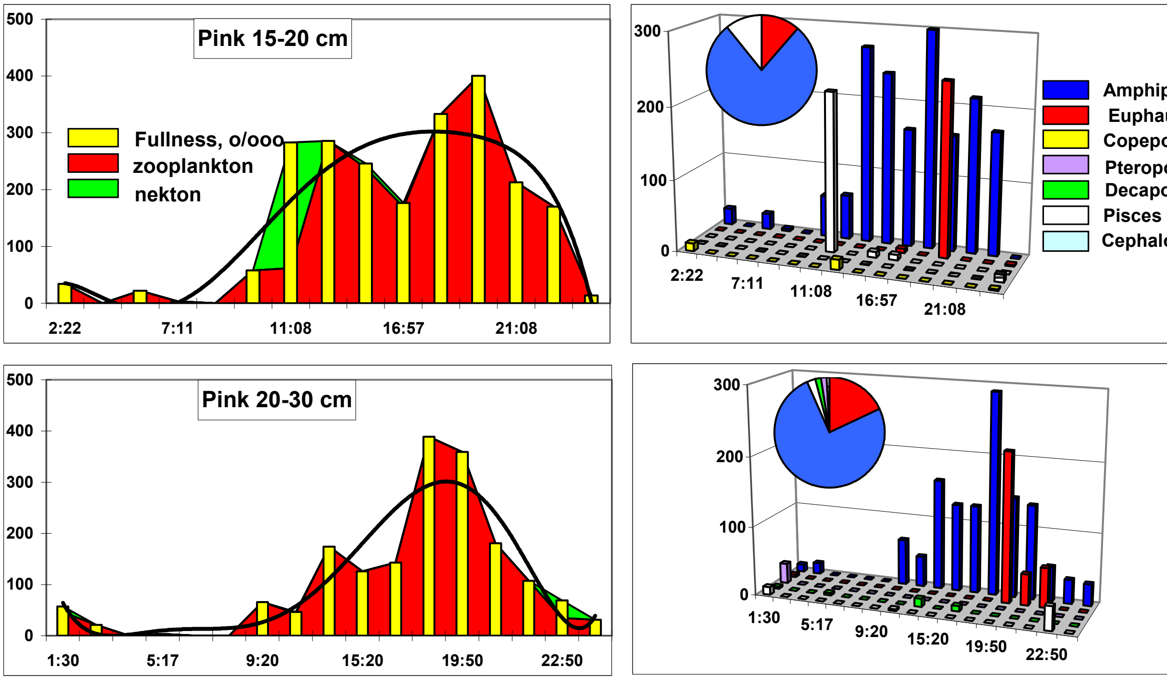

Fig. 3. Diurnal rhythms of pink salmon feeding in the Bering Sea during the autumn of 2004. Left-hand panels: stomach fullness ($^{0}/_{000}$), structure of plankton and nekton. Right-hand panels: taxonomic composition of foods. Circular diagram = daily average structure of foods. X axis = time of day; Y axis = $^{0}/_{000}$.

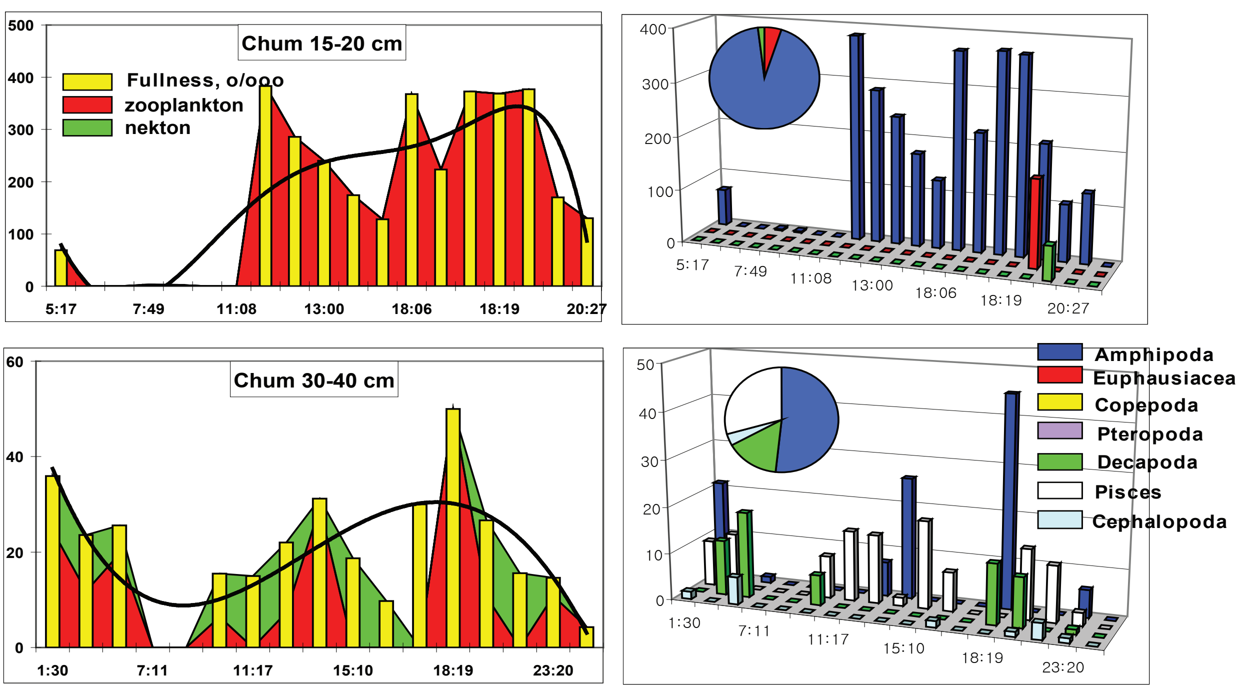

Fig. 4. Diurnal rhythms of chum salmon in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

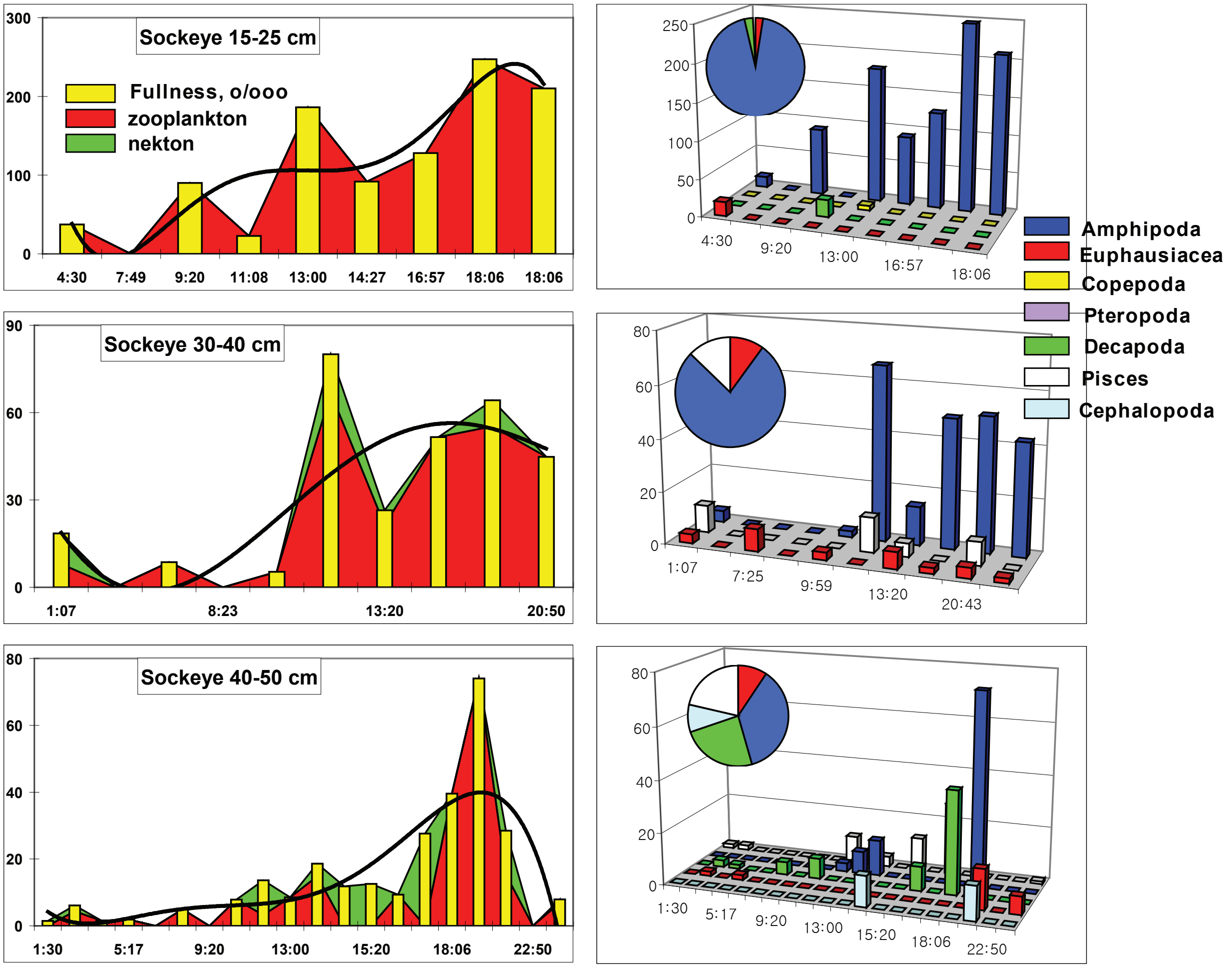

Fig. 5. Diurnal rhythms of sockeye salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

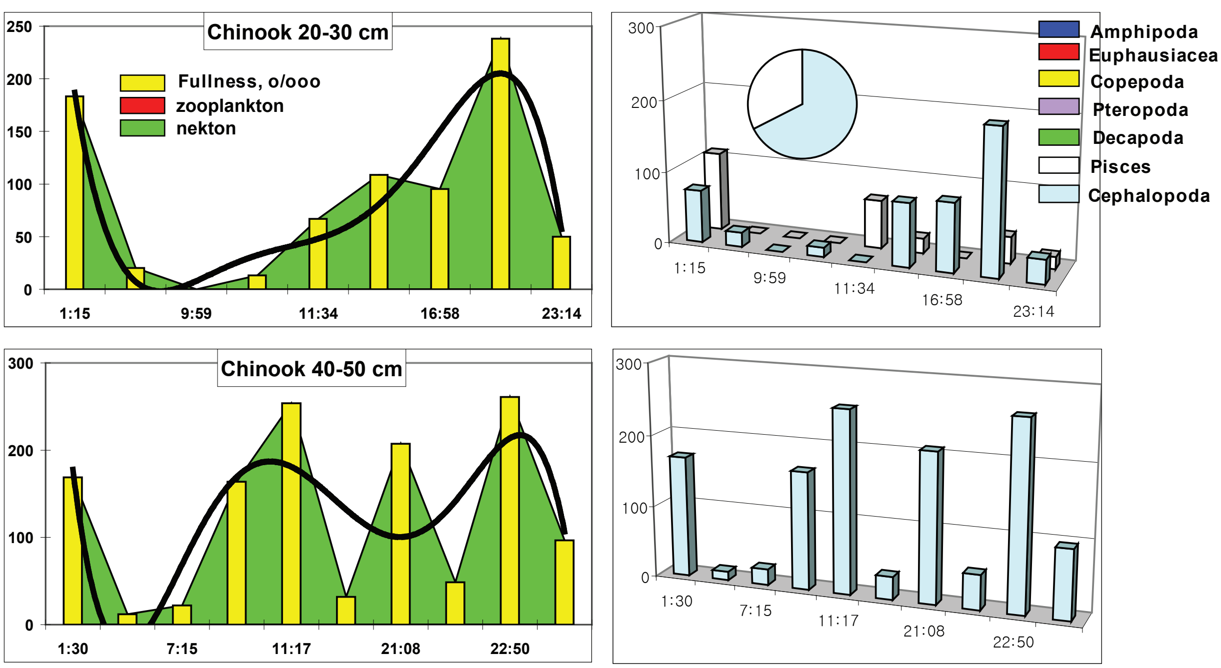

Fig. 6. Diurnal rhythms of coho salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

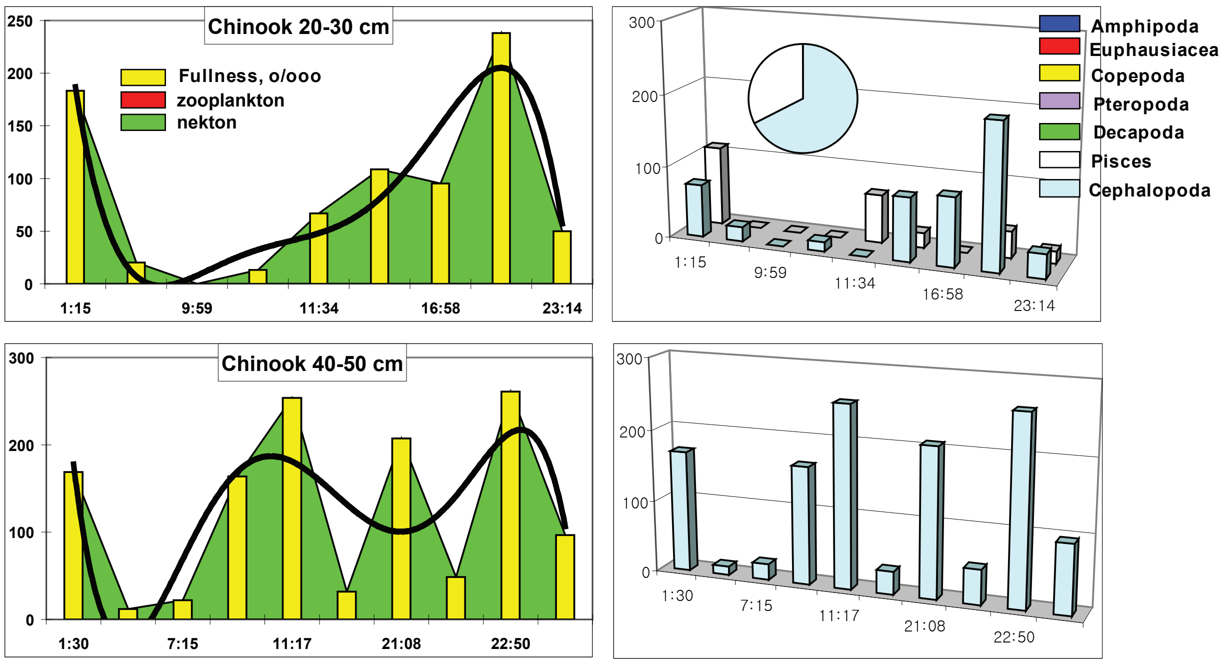

Fig. 7. Diurnal rhythms of chinook salmon feeding in the Bering Sea during the autumn of 2004. Legend as in Fig. 3.

base, it is necessary to take into consideration the type and time of feeding, and the selectivity for certain plankton types that constitute the food base.

We observed that the stomach fullness of salmon is lowest at daybreak. This is also typical for salmon in the eastern Bering Sea (Ueno et al. 1969; Godin 1981; Davis et al. 2000; Schabetsberger et al. 2003), as well as for underyearling and young salmon in the Okhotsk Sea (Shimazaki and Mishima 1969; Gorbatenko and Chuchukalo 1989; Volkov 1996a, b; Volkov et al. 1997; Lazhentsev and Bokhan 2001). Considering that salmon feed predominantly during the day, they should be regarded as optical or visual predators, although in some regions feeding also takes place at night. Birman (2004) has written that in certain cases visual receptors are not the only means by which salmon find food at night. However, many prey species consumed by salmon at night have luminous organs (euphausiids, squids, myctophids, e.g.). Because the type of luminescence (the number of photophores) is specific for each prey, this suggests that at night, salmon may be able to distinguish among different types of prey.

Plankton vertical catches indicated that the proportion of hyperiids in the plankton was relatively small compared to that of copepods, chaetognaths and euphausiids (Tables 2 and 3). The most common food for pink, sockeye, and chum salmon was hyperiids (e.g. see circular diagrams on the right-hand side of Figs. 3–5), and specifically *Themisto pacifica*. One explanation may be that because *T. pacifica* form very tight agglomerations on the water surface (Chebanov 1965), it becomes an easy prey for daytime predators. Salmon also preferred pteropods (Volkov 1994; Volkov et al. 1996b; Volkov et al. 1997). However, the biomass and quantity of pteropods throughout the season and years are subject to sharp changes. Further, their share in the salmon forage base also varies a great deal. For example, in 2004 the proportion of pteropods in the plankton samples and in the chum salmon diet was insignificant, but in 1992 they clearly dominated, reaching more than 50% (Volkov 1994).

The proportion of euphausiids in the salmon diet can also be great (Volkov 1994; Volkov et al. 1997), however it depends on their abundance in the plankton, on the presence of other food sources (hyperiids and pteropods), and on the time of day. Thus, during our studies in autumn 2004 in deepwater regions, the biomass of euphasiids during the day in the 0–50 m layer did not exceed 6 mg/m^3, although in the 50–200 m layer it was greater. At night, however, the number was one or two orders of magnitude higher (Table 2). This is why pink and chum salmon preyed most heavily on euphausiids at twilight, when euphausiids moved toward the surface (Figs. 3 and 4). The food base for coho and chinook was nekton, fish and squid, however, for coho, there was also a large proportion of zooplankton, particularly hyperiids and euphausiids (Figs. 6 and 7).

Investigation of the diurnal feeding habits of juvenile Pacific salmon (pink, chum, sockeye, coho, and chinook salmon) over 24 hours conducted in the western Bering Sea and adjacent waters has revealed the uniformity of their feeding rhythms regardless of whether nekton or zooplankton were the dominant components in the food. These salmon species, being visual predators, consume food predominantly during the daytime. At night they digest the food, with the food generally being totally digested by dawn. Taking into

Table 2. Zooplankton biomass (mg/m³) of the large fraction in the western North Pacific Ocean (WP) and Bering Sea (WB) during day (d) and night (n). Sampling areas are indicated in Fig. 2.

Zooplankton	Layer (m)	Biomass (mg/m³) 5p (WP) d	5p (WP) n	6p (WP) d	6p (WP) n	8 (WB) d	8 (WB) n	12 (WB) d	12 (WB) n
Copepoda	0-50	119.4	233.6	148.7	290.8	43.7	34.9	64.6	102.1
	50-200	89.1	72.5	102.0	77.5	32.7	46.5	68.7	29.0
Euphausiacea	0-50	5.4	51.3	2.1	168.7	3.0	151.6	0.4	150.1
	50-200	5.5	32.1	6.4	168.1	76.3	147.1	16.7	101.8
Amphipoda	0-50	8.2	41.5	6.9	32.9	9.8	7.9	10.2	26.5
	50-200	4.9	21.1	13.5	19.2	9.0	15.3	5.8	6.1
Pteropoda	0-50	0.2	0.8	1.1	0.5	0.1	0.0	0.0	0.0
	50-200	0.3	1.3	0.1	0.3	0.3	0.3	0.3	2.1
Sagitta	0-50	167.9	224.5	114.2	254.3	305.4	206.5	234.0	376.3
	50-200	136.4	46.4	110.8	77.1	55.7	102.4	152.6	85.0
Coelenterata	0-50	1.6	30.4	1.1	17.2	3.6	18.6	3.8	28.9
	50-200	22.4	11.3	11.1	1.9	20.4	30.5	13.1	6.8
Other	0-50	1.8	22.3	0.6	5.4	0.2	3.7	1.1	14.0
	50-200	3.9	6.2	9.6	1.7	4.3	3.4	6.0	1.7

Table 3. Zooplankton composition in the 0-200 m layer of the western North Pacific Ocean (WP) and Bering Sea (WB) during day (d) and night (n). Sampling areas are indicated in Fig. 2.

Zooplankton	Layer (m)	Composition (%) 5p (WP) d	5p (WP) n	6p (WP) d	6p (WP) n	8 (WB) d	8 (WB) n	12 (WB) d	12 (WB) n
Copepoda	0-50	39.2	38.7	54.1	37.8	12.0	8.3	20.6	14.6
	50-200	33.9	38.0	40.2	22.4	16.5	13.5	26.1	12.5
Euphausiacea	0-50	1.8	8.5	0.8	21.9	0.8	35.8	0.1	21.5
	50-200	2.1	16.8	2.5	48.6	38.4	42.6	6.3	43.8
Amphipoda	0-50	2.7	6.9	2.5	4.3	2.7	1.9	3.3	3.8
	50-200	1.9	11.0	5.3	5.6	4.5	4.4	2.2	2.6
Pteropoda	0-50	0.1	0.1	0.4	0.1	0.0	0.0	0.0	0.0
	50-200	0.1	0.7	0.1	0.1	0.1	0.1	0.1	0.9
Sagitta	0-50	55.1	37.1	41.6	33.0	83.5	48.8	74.5	53.9
	50-200	52.0	24.3	43.7	22.3	28.0	29.6	58.0	36.5
Coelenterata	0-50	0.5	5.0	0.4	2.2	1.0	4.4	1.2	4.1
	50-200	8.5	5.9	4.4	0.6	10.3	8.8	5.0	2.9
Other	0-50	0.6	3.7	0.2	0.7	0.0	0.9	0.4	2.0
	50-200	1.5	3.2	3.8	0.5	2.1	1.0	2.3	0.7

account the daytime feeding habits of salmon, quantitative estimations of the plankton share of the diet should be calculated using the plankton community that lives in the 0–50 m layer in the daytime.

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