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"Unreliable Fish" or Unreliable Hypotheses: What Happens to Nekton in Ocean Waters off the Kuril Islands?

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Abstract—The phenomenon of population waves of nekton in the Kuroshio Current system is discussed using the example of the Japanese sardine *Sardinops melanostictus*, one of the most common species that show the greatest amplitude of abundance fluctuations. So-called "sardine epochs" are distinguished on the basis of the pattern of abundance fluctuations that occur in this species. The last such epoch ended in the first half of the 1990s. Since 2014, the nekton communities in the Pacific waters off the Kuril Islands have again undergone structural changes with the expansion of southern fish and squid species. The rearrangement of the nekton species structure was mainly due to a noticeable increase in abundances of the Japanese sardine and the chub mackerel *Scomber japonicus* and also a noticeable decrease in the abundances of the Japanese anchovy *Engraulis japonicus* and the Pacific saury *Cololabis saira*. The magnitude of these changes allowed Russian fishermen to resume fishing for Japanese sardine and chub mackerel in the Russian exclusive economic zone since 2016. The Japanese sardine catch was increasing steadily from 6700 (in 2016) to 315 500 t (in 2020). Over 5 years, Russian fishermen landed a total of more than half a million tons (531 700 t) of this fish; the chub mackerel landing was 167 900 t. Even in this situation, many Russian forecasters, apparently trusting the formal climatic and hydrological indices too much and without investigating the mechanisms that underlie population waves carefully, suggest this was only a forerunner of the upcoming sardine epoch. The authors of the present publication assume with great confidence that, even with different interpretations, certain epochs (sardine one or other ones) cannot be predicted as being very similar to the previous ones. As well, the authors critically consider some of the previous hypotheses about the causes of the onset and end of Japanese sardine abundance outbreaks and make conclusions about the difficulties of solving the problems of such predictions. Certain mechanisms responsible for the formation of year-class strength and, especially, population waves in Japanese sardine and other fluctuating nekton species, remain poorly understood.

Keywords: nekton, epipelagic layer, Pacific waters off the Kuril Islands, Japanese sardine, chub mackerel, population waves

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INTRODUCTION

Among other areas of the Far Eastern economic zone of Russia, the ocean waters off the Kuril Islands are characterized by the greatest species richness (approximately 400 species) of the pelagic nekton assemblage of fish and cephalopods. However, the species list in the epipelagic layer of the adjacent Kuroshio Current system is much longer, numbering more than 700 species [1, 6, 12, 13]. The greatest species diversity of the southern Kuril waters is provided by subtropical and tropical migrants from the waters of the Kuroshio and the Subarctic Front. These include a noticeable group of fish and squid species with high abundance, of which many are commercially valuable (the Japanese sardine *Sardinops melanostictus*, chub mackerel *Scomber japonicus*, Pacific saury *Cololabis saira*, Pacific flying squid *Todarodes pacificus*, neon flying squid *Ommastrephes bartramii*, etc.). Of these, the Japanese sardine has historically been the most popular species. Among the fluctuating nekton species in the Kuroshio Current system, Japanese sardine shows the greatest amplitude of rises and falls in biomass and abundance. The peaks waves of its abundance exceed the increases of other species. For this reason, apparently, the Japanese sardine was mentioned in the ancient oriental monastic chronicles as an "unreliable fish." It is also not a mere coincidence that alternating so-called "sardine" epochs have been distinguished on the basis of the pattern of abundance fluctuations in this species and named accordingly.

Two major outbreaks (waves) in the Japanese sardine abundance were recorded in the 20th century: in the 1920s–1930s and in the 1970s–1980s. In the scientific literature, they have been considered in sufficient detail, especially for the latter period. According to the calculations published by V.A. Belyaev [1], the total biomass of epipelagic fish in the Kuroshio zone in the 1970s–1980s varied as follows: in 1977, 15 million t were recorded; in 1980, 23 million t; in 1986, 40 million t. In these estimates, Japanese sardine accounted for 53, 78, and 87%, respectively. In the following decade, the abundance of Japanese sardine significantly increased; as a result, the biomass of epipelagic fish in 1994 was not higher than 10 million t with the proportion of Japanese sardine being 10%, as reported by this author. A period of deep depression for this species began in the following years. Naturally, an intriguing question arose: When will the next outbreak of the Japanese sardine abundance occur? Many hypotheses have appeared in the dedicated Russian and foreign literature since then, of which some have not stood the test of time, while others are not supported by convincing evidence. In fact, the depression period for the Pacific and Tsushima populations of Japanese sardine ended in the first decade of the 21st century; its abundance then began to increase. In this regard, the goal of the present review is to critically consider the hypotheses in publications about the causes of this event on the basis of actual data on the changes that took place in the structure of the epipelagic nekton community that take trophic relationships, food availability, and catch data into account.

PERIODICITY AND THE PREDICTION OF POPULATION WAVES

There are a great number of publications on the biology and dynamics of the abundance of Japanese sardine. Many of them consider (often speculatively) the factors that limit the abundance and make attempts to explain the mechanisms underlying the formation of population waves. They are based mainly on a retrospective analysis of series of observation data (primarily fishing statistics) over the past years.

The specific mechanisms responsible for the formation of strength of year-classes and, in particular, population waves of Japanese sardine, remain largely unclear. The same conclusion can be drawn concerning other fluctuating species of nekton. In this regard, the problem of predicting the onset of the next abundance outbreak of this species and the end of the current one is difficult to solve. This becomes evident based on the example of forecasts in the 1980s, as well as in the current century.

During the peak of sardine abundance and landings in the late 1980s, the fisheries organizations in the Russian Far East were naturally concerned how long the commercially valuable runs of this fish to the northern Sea of Japan and the southern Kuril region would continue. The prevailing view expressed at the Pacific Research Institute of Fisheries and Oceanography (TINRO) [16] was that the upcoming abundance and landing decline would occur in the early 1990s, which in fact happened in 1991–1992. However, the landing from the waters off Japan decreased to 1 million t only by 1995. At the same time, experts of the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) based their opinions on the ideas of V.V. Kuznetsov [9, 10] about the "autogenic succession" in the assemblages of Kuroshio fish and their entry into the climax stage since the second half of the 1980s, which would allow the population to maintain a high abundance for another 20–30 years, i.e., during the first decade of the 21st century.

Later, approximately similar periods favorable for the reproduction of Japanese sardine (of the Sea of Japan population) were also reported at TINRO [4, 5]. In this case, the following years with optimum conditions for the reproduction of this fish were indicated: 1972–1976, the 1980s only since 1982, and then in 1993–1998 and 2002–2004. Thus, since 2005, conditions for the Japanese sardine to increase its reproduction were no longer in place, according to Yu.I. Zuenko.

The 1990s and the first decade of the 21st century were shown as a period of steady decline in the abundance and catches of Japanese sardine in the monograph by L.B. Klyashtorin and A.A. Lyubushin [7]. These authors predicted a following increase in its abundance to occur in the 2020s–2030s, with a peak in 2040.

However, as often happens in ecology with a lack of understanding of the cause and effect mechanisms of natural processes, events actually develop via a different scenario, i.e., contrary to the predictions. In this case, the onset of increase in the Pacific and Tsushima Japanese sardine populations was recorded from the waters off Japan in the middle of the first decade of the 21st century[1]

In the early 2000s, the biomass of the Pacific population of Japanese sardine decreased to 0.10 million t; in 2014, it already exceeded 1.0 million t; and in 2018, it was 3.48 million t. The abundance of the Tsushima population began to increase since 2004. Its commercial harvesting began, but the rate of population growth was still slower than in the Pacific Ocean. Since 2016, the Russian Japanese sardine fishery (along with the chub mackerel fishery) resumed in the Russian economic zone (Pacific waters off the Kuril Islands) and was steadily increasing from 6700 (in 2016) to 315 500 t (in 2020). Over 5 years, Russian fishermen landed a total of more than half a million tons (531 700 t) of this fish (and 167 900 t of chub mackerel). In 2019, the Japanese catch of Japanese sardine reached 525 000 t; in 2020 (over 12 months), according to preliminary data (kindly provided by V.V. Tsygir), the amount of Japanese sardine unloaded at the ports

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[1] Data on the status of biological resources in the waters of Japan are annually sent to TINRO within the framework of the long-term scientific and technical cooperation between Russia and Japan [34–36]

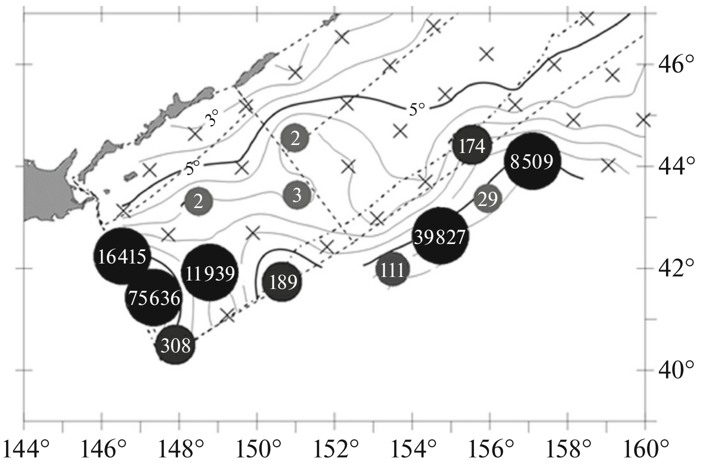

Fig. 1. The distribution of Japanese sardine in the northwestern Pacific Ocean, May 30–July 14, 2018. Values in circles are actual catch (fish/h trawling); contour lines (here and below) are sea surface temperature isotherms.

of Japan alone made up 604800 t. The Russian landing in 2019 was 133000 t; in 2020, it was 315500 t[2]

The scale of feeding migrations of Japanese sardine to temperate waters depends on its total abundance. In 1991 and 1993, when the previous population outbreak rapidly subsided, the species accounted for only 2.2 and 0.8%, respectively, in the nekton of the upper epipelagic layer in the ocean waters off the southern Kuril Islands in the summer. In 2012, during a scheduled pelagic survey conducted by TINRO, Japanese sardine constituted 0.2% [15]. However, in the summer of 2014, the sardine biomass here was estimated at 365000 t as a result of another TINRO survey; in the early summer of 2015, at 289000 t; and in July and August 2015, at 736000 t. In the same years, the abundances of the Japanese and South Asian populations of the blue mackerel, *Scomber australasicus*, also increased. More correctly, their growth began, as during the previous outbreak [1], a few years earlier than that of the Japanese sardine. In 2012, they accounted for 8.9% in the upper epipelagic nekton. In 2014, the biomass of both mackerel populations was estimated at 1274000 t.

The increase in migration of southern fish and squid species to the waters off the Kuril Islands caused noticeable rearrangements in the structure of nekton communities. Due to the steady reduction in the scale of marine vessel-based monitoring of bioresources by fisheries science (first, the integrated TINRO expeditions) in the second decade of the current century and the decrease in the potential of this monitoring in general, it proved to be impossible to quantify the changes that occur at all stages of the extensive pelagic layer. However, it became possible to continue the annually conducted standard summer surveys of the upper epipelagic layer in the ocean waters off the Kuril Islands over an area of approximately 1 million km^2. The major goal of those surveys was to assess the Pacific salmon migrations from the ocean to the Sea of Okhotsk at this time. Therefore, trawling stations covered only the upper "salmon" layer, 0–50 m.

Information on the structure of nekton communities, biomasses, and abundances of species, and also about the density of concentrations for the 1990s and early 2000s, in addition to numerous articles, is published in the monographs of the first author [15, 19].

Tables 1–3 show the situation in the waters off the Kuril Islands in the second half of the 2010s, which indicates certain trends in rearrangements in the nekton communities of the area. Since the traditional objective of these surveys was total assessment of salmon near the Kuril Islands, it should be noted that the surveys clearly revealed a high abundance of these fish (especially pink salmon in 2018) migrating to the Sea of Okhotsk.

The surveys of sardine and both mackerel species confirmed the development of population waves. In the recorded biomass of these species, juveniles constituted a substantial proportion. However, the abundance of Japanese anchovy and Pacific saury decreased.

For the patterns of distribution of Japanese sardine and mackerel in early summer (Figs. 1–4), the fact that in all cases only the head part of their concentrations entering the Kuril waters for feeding is contoured is of particular attention. The dislocation of major aggregations also varies between different years, which is determined by the distribution of various gyre formations and frontal zones.

The results of autumn surveys of post-smolt juvenile salmon in the Bering Sea and the Sea of Okhotsk, conducted by TINRO, first, in 2018, and then in 2020

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[2] Data on the status of biological resources in the waters of Japan are annually sent to TINRO within the framework of the long-term scientific and technical cooperation between Russia and Japan [34–36].

Table 1. The major species and total biomass of nekton and jellyfish in the upper epipelagic layer of the ocean waters off the Kuril Islands, May 31–July 7, 2016

Species, group	$\times 10^3$ t	%
Lamna ditropis	18.6	0.7
Sardinops melanostictus	663.3	24.5
Leuroglossus schmidti	12.0	0.4
Oncorhynchus gorbuscha	289.7	10.7
Oncorhynchus keta	138.3	5.1
Notoscopelus japonicus	204.2	7.6
Symbolophorus californiense	175.1	6.5
Theragra chalcogramma	10.1	0.4
Cololabis saira	14.4	0.5
Scomber japonicus, *S. australasicus*	958.8	35.5
Other fishes	67.6	2.5
Total for fish	**2552.1**	**94.4**
Watasenia scintillans	18.2	0.7
Boreoteuthis borealis	109.1	4.0
Okutania anonycha	12.6	0.5
Todarodes pacificus	3.4	0.1
Other squid	8.8	0.3
Total for squid	**152.1**	**5.6**
Total for nekton	**2704.2**	**100**
Jellyfish	**406.1**	

(Tables 4, 5), are another indicator of the increasing sardine abundance. Juvenile Japanese sardine in 2018 entered the Commander Basin of the Bering Sea. South of the Commander Islands, in the open ocean waters east of Kamchatka, significant concentrations of this fish were also observed in that year. In 2018, sardine also entered the Sea of Okhotsk in significant numbers for feeding. Unfortunately, no observations were conducted here in the summer; however, in the second half of October, about 30000 t of this fish, already moving to the Pacific Ocean, were recorded from the southern part of the sea. In October 2020, the TINRO salmon expedition recorded 673000 t of sardine by opportunistic surveys in the southern Sea of Okhotsk (data provided by A.Yu. Sheibak and A.N. Starovoitov).

The Russian landing in 2019 was 133000 t of Japanese sardine and 86600 t of chub mackerel; the Japan's landing was 525000 and 400000 t, respectively. Based on data on increase in abundance of both species, the TINRO forecast for 2020 set a level of Japanese sardine landing by Russian fishermen of 245000 t on and a level of chub mackerel landing of 240000 t [36]. In 2020, the actual Russia's landing of Japanese sardine exceeded the forecast by more than 20% (315500 t) and the actual chub mackerel landing by more than 60% (81400 t).

Despite the extensive information about the growth of sardine and mackerel abundance obtained annually by Japanese researchers from the breeding grounds and by Russian expeditions from the feeding grounds of these fish, and also despite the successful fishing, a recently published work by VNIRO experts [8] states that another "mackerel era" will "begin soon" and will last for at least 20 years. The conclusions of these authors about the current status and prospects of the population dynamics of the Japanese sardine are even more astonishing [2, 8]. They believe that the significant increase in its abundance in the second decade of this century (which has not been recognized by VNIRO for several years) is only a precursor of the upcoming "sardine era," which they called a run-up to the new sardine era (the run-up was not bad: over the past 2 years, the sardine landing by Russian fishermen was 448500 t). However, in their opinion, there will be initially a sharp abundance decline in the near future, and the new era is to begin no earlier than in 10 years: from the late 2020s to the mid-2030s (according to their scenario, the Russian landing in 2035 will reach 800000 t).

Judging by the patterns of the two previous outbreaks of the Japanese sardine abundance, it (as well as the chub mackerel abundance) is most likely to decrease or even end by the time of the peak in the 2030s predicted by the VNIRO experts. Of course, the question arises of why the modern multifold increase in the sardine and mackerel abundance is considered beyond the upcoming sardine era? This is largely due to a simplified approach, with the analysis based on formal atmospheric, climatic, and hydrological indicators (indices) and epochs (such as the famous El Niño effects in the far Southern Hemisphere), rather than on the actual characteristics of the ecology of fish and the factors that limit their abundance (especially at the stages of reproduction and early juveniles). This means that modern VNIRO experts continue to automatically follow the methodological approaches of the popular monograph by Klyashtorin and Lyubushin [7] concerning the related cyclical changes in fish capacity and climate, without carefully investigating the mechanisms of the formation of population waves. The cited authors attach particular importance to the 60-year cycle of atmospheric circulation over the North Pacific, with the development and position of the Aleutian Low accepted as the initial indicator. In this scheme, another surge of the Japanese sardine abundance is predicted to occur in the 2030s–2040s [7].

ON THE MECHANISMS OF FORMATION OF YEAR-CLASS STRENGTH

The incredible discrepancies in views on abundance fluctuations in year-classes of various nekton species are explained, of course, by the extreme complexity of this problem. This is determined largely by the multifactor impact of biotic and abiotic conditions on populations and communities (hence, resulting in many scenarios), which, in turn, makes it difficult to identify the mechanisms responsible for the reproduction success. The fascination with formal approaches, where various indices are used in the search for active factors and certain causes, and a unidirectional or alternative relationship of abundances or commercial catches with them accepted as proof, also negatively affects the cognition process.

When considering Russian publications, we cannot help but note the weak awareness of their authors about the results of direct observations not only in other countries (in this case, first, in Japan and South Korea), but also in Russia. The latter becomes clearly evident, in particular, in a recent review on the prospects of Russian fisheries until 2035 [8].

A common weakness of researchers who study fish fluctuations is their almost absolute focus on the quality of environmental conditions (although mostly through the warm–cold dilemma) and the completely insufficient attention paid to the quality of fish groups and populations. Body size and growth rate are usually accepted as the criteria for the physiological condition (viability). These, of course, are not enough to diagnose the biotic potential of certain groups.

In the second volume of the *Biology of the Far Eastern Seas of Russia* [15], which was written by V.P. Shuntov when the current sardine epoch was only beginning, the author overviewed the latest publications of Japanese and South Korean scientists on the breeding biology and the factors responsible for fluctuations in the major commercial pelagic fishes of the subtropical complex. These publications preserved the preference for the approaches used since the previous abundance outbreaks in Japanese sardine and other associated species. In recent years, monitoring at breeding grounds of these species (mainly in Japanese waters) has been extended, which allows collection reliable data on reproduction success and dynamics in sizes of stock and recruitment. These data are updated by Russian studies at the feeding grounds of southern fish in waters off the Kuril Islands. However, it is a characteristic fact that, among the factors that determine status of populations, all the same factors are now listed that were repeatedly mentioned in previous times. As before, the possible impact of fishing pressure in some periods, e.g., in the 1990s and early 2000s, which hinders the recovery of sardine and mackerel stocks, is not rejected as well [21, 33]. However, no convincing evidence of overfishing is adduced. Most likely, this is a tribute to tradition, because a natural decline after a population wave is observed in any fluctuating species.

Table 2. The major species and total biomass of nekton and jellyfish in the upper epipelagic layer of the ocean waters off the Kuril Islands, June 1–July 1, 2017

Species, group	$\times 10^3$ t	%
Lamna ditropis	75.5	0.8
Sardinops melanostictus	3214.3	32.0
Leuroglossus schmidti	40.9	0.4
Oncorhynchus gorbuscha	330.2	3.3
Oncorhynchus keta	144.9	1.4
Notoscopelus japonicus	3104.6	30.9
Symbolophorus californiense	80.9	0.8
Theragra chalcogramma	181.2	1.8
Scomber japonicus, *S. australasicus*	1432.9	14.3
Other fishes	57.2	0.6
Total for fish	**8662.6**	**86.3**
Watasenia scintillans	3.7	+
Onychoteuthis borealijaponica	11.9	0.1
Boreoteuthis borealis	218.6	2.2
Gonatus kamtschaticus	12.9	0.1
Okutania anonycha	1080.4	10.8
Todarodes pacificus	46.1	0.5
Other squid	1.1	+
Total for squid	**1374.7**	**13.7**
Total for nekton	**10037.3**	**100**
Jellyfish	**146.5**	

Table 3. The major species and total biomass of nekton and jellyfish in the upper epipelagic layer of the ocean waters off the Kuril Islands, May 31–July 7, 2018

Species, group	$\times 10^3$ t	%
Lamna ditropis	14.2	0.1
Sardinops melanostictus	666.4	7.2
Oncorhynchus gorbuscha	913.4	9.9
Leuroglossus schmidti	15.8	0.2
Oncorhynchus keta	179.7	2.0
Lipolagus ochotensis	8.6	0.1
Gasterosteus aculeatus	138.2	1.5
Diaphus theta	14.3	0.1
Notoscopelus japonicus	4913.4	53.4
Stenobrachius leucopsarus	17.7	0.2
Symbolophorus californiense	112.7	1.2
Cololabis saira	51.2	0.6
Scomber japonicus, *S. australasicus*	1931.3	21.0
Other fishes	57.1	0.6
Total for fish	**9034.0**	**98.1**
Boreoteuthis borealis	124.9	1.4
Watasenia scintillans	33.4	0.4
Onychoteuthis borealijaponica	7.4	0.1
Moroteuthis robusta	3.6	0
Todarodes pacificus	2.2	0
Other squid	3.2	0
Total for squid	**174.7**	**1.9**
Total for nekton	**9208.7**	**100**
Jellyfish	**822.1**	

However, the major emphasis in the search for patterns of population dynamics and, first of all, the formation of year-class strength, is on the variability of the climatic and oceanological background (climatic epochs and so-called regime shifts), on the transport of fish in early developmental stages by currents to the nursery zones of water mixing, and also on the conditions in them for the increase in food supply for larvae and fry, consisting of microplankton (phyto- and zooplankton) [21, 22, 24, 25, 27–33]. Much attention is paid also to the intensity and geographical location of the Aleutian Low and the winter monsoon. With their strengthening, the Tsushima Current weakens and the transport of its waters from the northern East China Sea to the Kuroshio Current, running to the ocean coast of the Japan islands, increases. The vertical mixing of water increases and temperatures in the upper epipelagic layer decrease, which contributes to an increase in the entry of nutrients to the photosynthesis layer and, consequently, to the growth of primary production. This situation is considered favorable for strong year-classes of Japanese sardine to form.

With the weakening of the winter monsoon and the Aleutian Low, a warmer hydrological regime is formed, the inflow of water with the Tsushima Current increases, and the phytoplankton and zooplankton production is reduced. This regime is considered favorable for Japanese anchovy, which breeds somewhat later than sardine. Moreover, being somewhat more thermophilic, the anchovy continues to spawn during feeding migrations to temperate latitudes.

The variation in the flow intensity of the Tsushima and Kuroshio currents under the effect of northerly winds, besides the formation of corresponding hydrological scenarios for the reproduction of pelagic fish in winter and spring, is important also in another sense. In these currents, the amount of eggs, larvae, and early fry transported from breeding grounds near the southern coasts of Japan and South Korea to the Sea of Japan and the Pacific Ocean varies depending on the expression of the currents. In the Pacific Ocean off the eastern Japan coast, the success of transport of offspring to the nursery ground also depends on the position of the main Kuroshio Current and, in particular, on the expression of its meander off the southern Honshu coast [22, 25, 27, 28, 31].

All or almost all of the above conclusions or assumptions about the pattern of the effect of background factors on the formation of abundance of fluctuating subtropical fish have a right to exist. Nevertheless, some doubts arise concerning their full credibility. The fluctuating nekton species being discussed and certain of their populations live under the same global factors. However, unidirectional responses to them are rare and, in some cases, even antiphase. This may be related with the sharply different ecological profiles of the species. In this sense, it is enough to compare saury with sardine, mackerel, and anchovy that spawn throughout a year in vast oceanic and marine waters and breed seasonally at local grounds on the margins of the seas and the ocean.

The Sea of Japan and the Pacific waters off the Japan coast are connected via the Kuroshio circulation system and its large branch, the Tsushima Current. The redistribution of fish in the early developmental stages during their transport with the waters of the Kuroshio (to the Pacific Ocean) and the Tsushima Current (to the Sea of Japan) was mentioned above. This probably makes some contribution to the differences in the population dynamics of some fish in the Sea of Japan and in the Kuroshio zone. In ocean waters, the Japanese sardine, which has had a significant abundance for several years and is currently successfully harvested, already entered the Bering Sea during feeding seasons. Sardine stranding events (up to 100 t) were documented from the northern Sea of Japan, the southwestern coast of Sakhalin, in October 2011. However, no regular and noticeable migrations of this fish to the northern Sea of Japan have formed to date. As noted above, the Tsushima population is

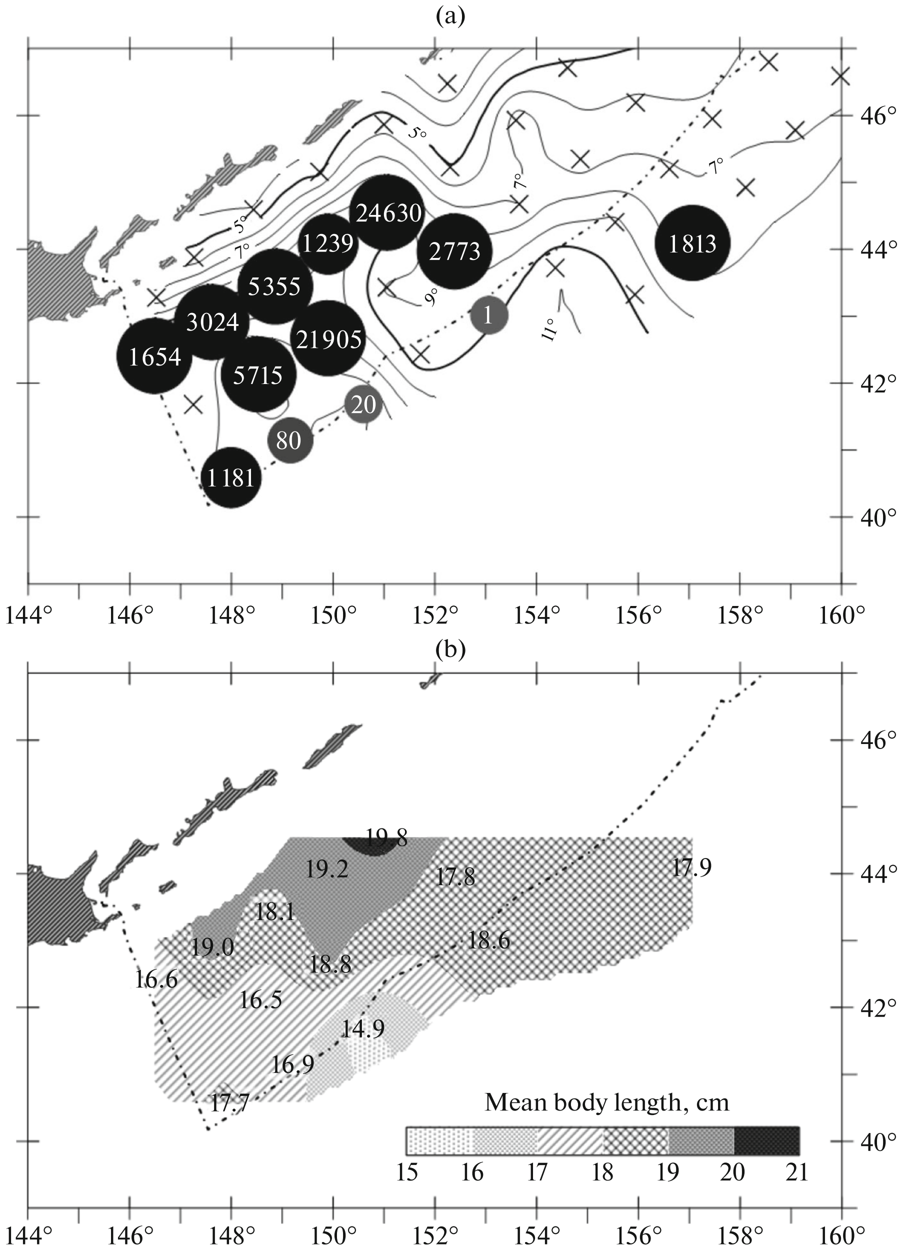

Fig. 2. The spatial distribution of catches (a) and mean body length (b) for Japanese sardine in the northwestern Pacific Ocean, May 28–June 20, 2019. Values are catch in fish/h trawling (a) and mean body length in cm (b).

gradually increasing, but at a lower rate than in the ocean.

The actual abundance of chub mackerel is even more contrasting: high in the Pacific Ocean and low in the Sea of Japan. Consequently, in this case, the effect of global background factors is mitigated by provincial (local) conditions.

In recent years, studies at breeding grounds of pelagic fish in the Kuroshio zone pay increasingly more attention to the ranking of factors that limit fish survivability at the early life history phases [21, 24, 28, 32, 33]. It has been convincingly shown that the development of the food supply for larvae and juveniles at the nursery ground on the northern side of the main Kuroshio Current in the winter–spring period depends on the thickness of the upper mixed layer. This is the upper epipelagic layer, i.e., the zone of intensive photosynthesis. With a growth of the thickness of the mixed layer, the supply of nutrients increases and, therefore, the primary production, which is the basis of the food supply for larvae and fry, also grows. However, the above-cited publications additionally show that these assessments of the environment are not enough to understand the dynamics

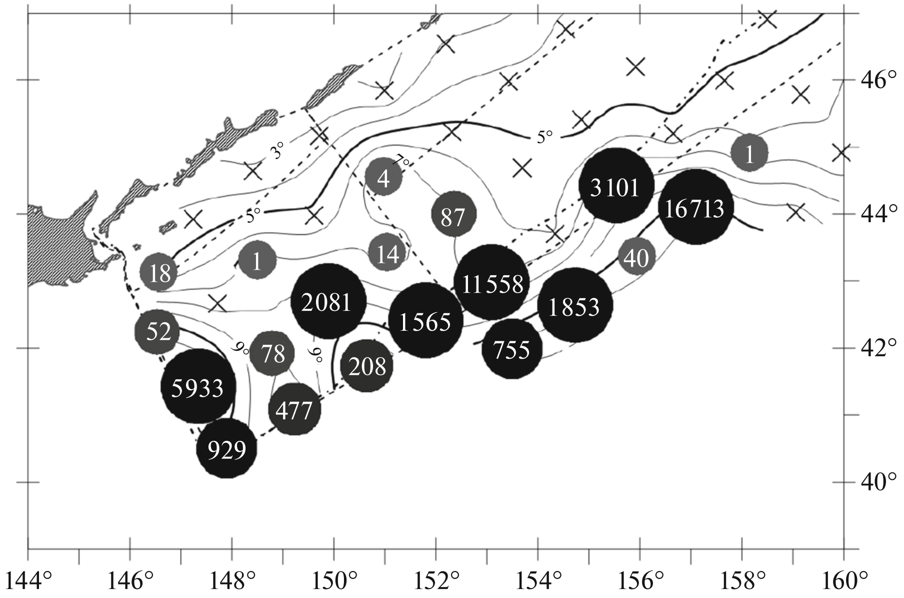

Fig. 3. The distribution of chub mackerel in the northwest Pacific Ocean, May 30–July 14, 2018. Values in circles are actual catch (fish/h trawling).

in abundance of even satisfactorily studied common commercial species. Other factors also have a significant influence on this general pattern. In the above-cited works, the authors show that the strength of a certain year-class can depend, e.g., on the water temperature even with sufficient food availability. At an elevated temperature, eggs, and then larvae and fry, develop faster. Thus, the overall period with the highest mortality rate, which is generally observed in any species, is shortened [24].

The corresponding influence on the formation of strength of the following year-class is exerted by the abundance and state of the population at the moment. Furthermore, this topic seems to have even more unexpected nuances. For example, the intraspecific density factor during maturation and spawning of sardine is assumed to have a significant effect on the formation of year-class abundance, but a weaker effect on the development of larvae. In the Japanese anchovy, the density factor, on the contrary, is observed to have a strong effect at the larval stage [32].

INTERSPECIFIC COMPETITION AND OTHER BIOTIC FACTORS

Patterns of interspecific feeding interactions are also not sufficiently understood, despite the many years of research. Interactions between sardines and anchovies and also between sardines and mackerel at different stages of ontogeny are discussed in the usual and habitual manner. For the sardine–mackerel pair, their competition at the early life-history phases is unambiguously recognized [25]. However, the anti-phase pair sardine–Japanese anchovy is compared more frequently. There are opposite opinions on this issue. Apparently, absolutely different situations occur there. However, most likely, no fierce competition exists between these species. Sardine and anchovy have significantly different diets and are usually separated spatially [21]. The cited authors in this case draw attention to the fact that numerous mesopelagic fish and jellyfish can be competitors for both sardines and anchovies at different stages. We would also mention squid and, for waters of the shelf and continental slope, and juveniles of benthic fish and large invertebrates.

Despite the large number of publications [1, 15] on rearrangements in nekton communities and cause-and-effect relationships in the pattern of abundance dynamics of commercial species in subtropical waters of the northwestern Pacific Ocean (NWPO) and the Sea of Japan, a significant part of their conclusions can only be considered as hypotheses. There is a significant scarcity of quantitative data in the form of long series of observations on the production of various items of food supply (from larvae to adults) and the distribution of energy fluxes over trophic levels. Without such data, the ecological capacity of biotopes and landscapes at breeding, migration, and feeding grounds cannot be determined.

Of course, biological processes in this case should be considered with the climatic and oceanological background taken into account. However, this should be done, first of all, taking the periods between regime shifts into account, i.e., the epochs between them (from decades and longer periods), rather than the regime shifts proper (which are short time spans).

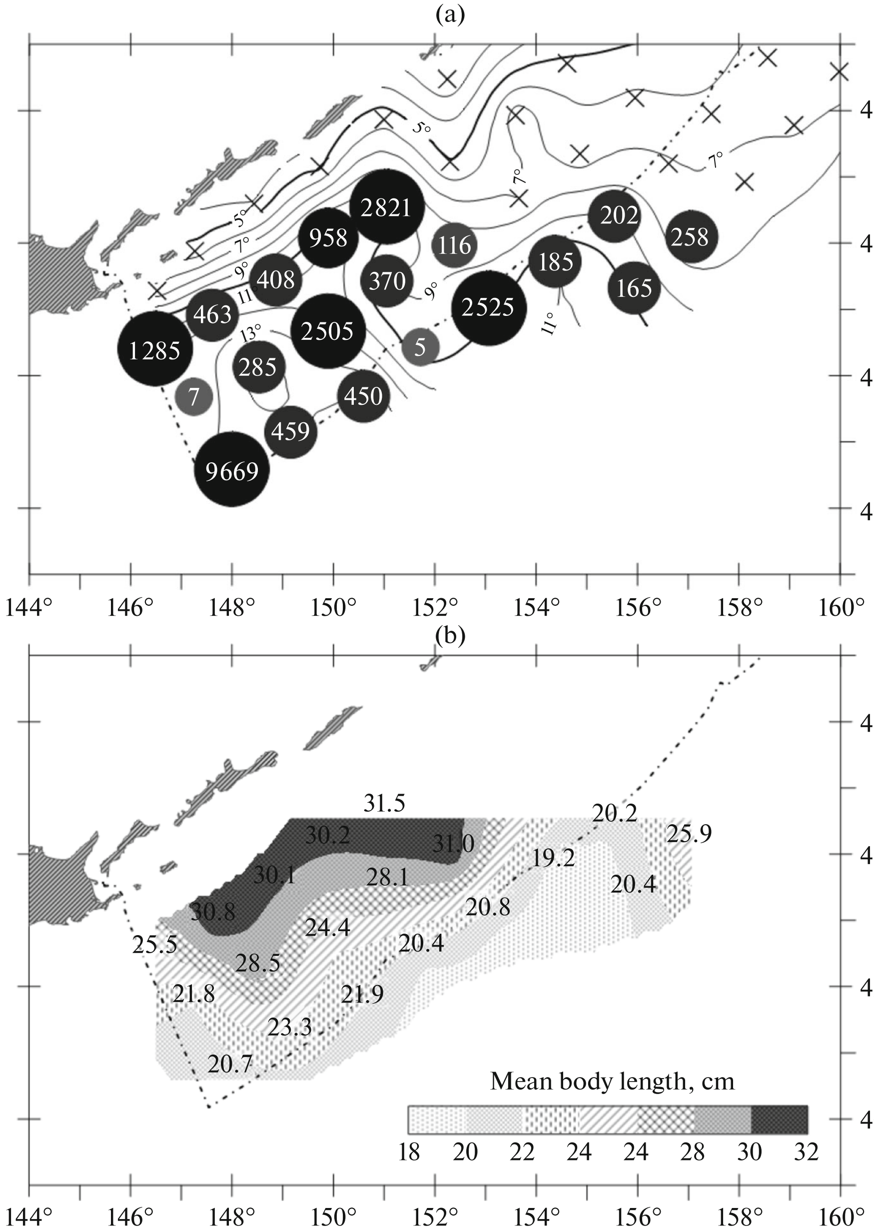

Fig. 4. The spatial distribution of catches (a) and mean body length (b) for chub mackerel in the northwestern Pacific Ocean, May 28–June 20, 2019. Values are catch in fish/h trawling (a) and mean body length in cm (b).

Based on accumulated data, even with their different interpretations, we can now suggest with great confidence that certain (sardine and other) epochs cannot be predicted as absolutely similar to the previous ones [26]. In addition to the fundamental global factors, various specific circumstances, both background (abiotic) and biotic, influence the formation of population waves. Regular comprehensive surveys of juveniles, recruitment, and spawners can be helpful for several more years and even are fundamental to prevent large surprises in forecasts for the future. At the same time, for identifying the causes (and consequences) of formation of population waves, it is necessary to clearly understand that quantitative estimates of eggs, juveniles, and spawners are not enough. Data on their physiological quality, i.e., their viability, are also needed. Fish hatcheries have accumulated a substantial range of criteria for assessing the viability of juvenile fish, which determine their so-called biotic potential to resists environmental impacts. Concerning fish and other aquatic organisms, the criteria, in this sense, are mainly limited to size and growth rate, which are not enough. The mechanism of emergence and accumulation of individuals with reduced viability in populations can apparently be interpreted as follows. The onset and continuation of population waves

Table 4. The \major species and total biomass of nekton and jellyfish in the upper epipelagic layer of the southwestern Bering Sea, September 29–October 11, 2018

Species, group	$\times 10^3$ t	%
Lamna ditropis	8.0	1.3
Clupea pallasii	112.8	18.0
Sardinops melanostictus	6.4	1.0
Oncorhynchus gorbuscha (underyearlings)	76.4	12.2
Oncorhynchus keta	78.9	12.6
Oncorhynchus nerka	38.0	6.0
Stenobrachius leucopsarus	165.8	26.5
Theragra chalcogramma	3.7	0.6
Gasterosteus aculeatus	66.5	10.6
Pleurogrammus monopterygius (underyearlings)	10.0	1.6
Other fishes	8.8	1.4
Total for fish	**575.3**	**91.8**
Berryteuthis magister	42.5	6.8
Gonatus kamtschaticus	7.0	1.1
Total for squid	**51.5**	**8.2**
Total for nekton	**626.8**	**100**
Jellyfish	**684.8**	

The number of underyearling pink salmon was 996.20 million fish; saury, 5.40 million fish; Pacific pomfret, 0.14 million fish.

Table 5. The major species and total biomass of nekton and jellyfish in the upper epipelagic layer of the Sea of Okhotsk, October 14–November 2, 2018

Species, group	$\times 10^3$ t	%
Lamna ditropis	34.4	5.5
Sardinops melanostictus	30.6	4.9
Leuroglossus schmidti	136.3	21.6
Oncorhynchus gorbuscha (underyearlings)	124.9	19.8
Oncorhynchus keta	141.0	22.4
Oncorhynchus kisutch	10.2	1.6
Oncorhynchus masou	8.9	1.4
Oncorhynchus nerka	22.1	3.4
Mallotus villosus	31.9	5.0
Stenobrachius leucopsarus	25.6	4.1
Theragra chalcogramma	21.2	3.4
Scomber japonicus	2.9	0.5
Other fishes	13.5	2.1
Total for fish	**603.5**	**95.7**
Boreoteuthis borealis	26.3	4.2
Total for squid	**27.2**	**4.3**
Total for nekton	**630.7**	**100**
Jellyfish	**1204.3**	

The number of underyearling pink salmon was 677.8 million fish.

in the first stages undoubtedly occur in breeding conditions favorable for survival. Consequently, the survival rate of weak individuals increases, they are recruited in reproduction and, thus, weaken the potential of spawners. As the following period with unfavorable conditions occurs, weak individuals are eliminated first. However, surviving individuals, even in reduced numbers, give rise to another outbreak of abundance with the onset of the following period that is favorable for reproduction.

In large populations of fluctuating nekton species, the formation of population waves is determined not only at certain breeding grounds. The changing conditions for the transport of larvae and fry to nursery grounds, where food availability depends on global and provincial climatic, oceanic, and hydrobiological conditions (food composition, competitors, and predators), are also of great importance. Unidirectionality and strict periodicity of the dynamics of all these factors in different parts of the range are unlikely. This is another factor responsible for the differences in population waves between different periods.

In a recent article by O.A. Ivanov and A.A. Khoruzhiy [23] on the variability of the integral characteristics of the epipelagic fish community in waters off the Kuril Islands during the current sardine and mackerel expansion, the authors emphasize that there is a high degree of uncertainty in predicting the development of further events due to the complexity of the processes in functioning marine ecosystems (with the properties of dynamism and self-regulation). Therefore, at the current stage, it is necessary to follow the proven approach: to continue monitoring the environment and the communities with fluctuating species that compose them. For monitoring, the above-cited authors state that “so far we have to be satisfied with little.” Continuous and comprehensive monitoring is not as easy to organize. This is very costly and requires the efforts of integrated teams of specialists. Although it is already being conducted at breeding and feeding grounds, it has a limited scale and, of course, requires expansion. Currently, the predominant contribution of Japanese researchers to these studies is also unquestionable.

Above, we evaluated the formal and far-from-realistic conclusions of VNIRO experts on the status of populations of the major fluctuating fish species in the Far Eastern seas and the Kuroshio zone [2, 8]. In addition to them, we can consider the views of A.Ya. Velikanov [3], an expert from the Sakhalin Research Institute of Fisheries and Oceanography (SakhNIRO), on the dynamics of abundance of Japanese sardine and its migrations to Sakhalin waters. Objections to his ideas were expressed earlier [17]. Below, we will focus on the main ones.

As in his previous reports, Velikanov [3] invariably refers to the regular arrival of southern species (including sardines) in temperate waters during the periods of warming as natural phenomena. He suggests that the sea surface temperature (the warmer, the better) is a determinative guiding factor in the timing of migration and feeding. Southward migrations are associated only with cooling. However, it has long been shown that individuals and schools that have accumulated sufficient fat reserves begin moving southward even before the onset of noticeable cooling of waters [14].

Velikanov [3] attempts to relate migrations of Japanese sardine and some other fishes with the condition of ecosystems. Based on this relationship, he concludes that sardines, capelins, and Japanese anchovies are important indicator species of the epipelagic fish community in the Sea of Japan. This means that the three species demonstrate the status of communities in the sea. The Sea of Japan is home to up to 1000 fish species. Thus, the following question inevitably arises: What is the role of the other more than 900 species in the ecosystem? Velikanov also believes that the Japanese sardine abundance breaks out after each shift in the climate regime. If this were true, then there would be no any serious problems with predicting the population dynamics of Japanese sardine and other fluctuating fishes. The sardine has already reached the waters off Kamchatka and even the Bering Sea, while still having low abundance in the Sea of Japan.

Velikanov wrote most of [3] in a confident style, but in conclusion he, nevertheless, stated that the migration of sardines is "a complex multicomponent and multi-layered biological process." Its formation is influenced by "many factors of different origins and levels of effect." This incredible turn corresponds to the original conclusion that sardine migrations "are also part of the general phenomenon of periodic seasonal movements of low-latitude fish."

We have briefly considered the views of some Russian experts on the dynamics of fluctuating subtropical nekton species, related with the fishery for these objects in the NWPO that was launched a few years ago, in order to demonstrate the actual difficulties in professionally interpreting the situations that emerge in the operational and long-term prediction for these objects.

In discussions about the simultaneous use of the food supply by nekton communities in the feeding biotopes in the Kuroshio area and its frontal zone (including larvae and juveniles), and also in the waters off the Kuril Islands where large juveniles and adults are found the following pairs of species are usually compared: sardine–Japanese anchovy and sardine–chub mackerel, i.e., mainly the key commercial species. As noted above, the possibility of food competition in the early ontogeny stages is most often (and reasonably) emphasized. We can agree with this, but, at the same time, another important issue should be taken in consideration. Commercial nekton species have a significant or noticeable abundance. However, in the waters off the Kuril Islands, there are a number of nontarget species and groups that are not quantitatively inferior to commercial ones. According to the average long-term data [15, 18], the nekton biomass in the ocean waters off the Kuril Islands is estimated at 27 million t (24 t/km^2), including 9 million t in the epipelagic (0–200 m) and 18 million t in the mesopelagic layers (200–1000 m). For fish, the epipelagic zone is dominated by fluctuating pelagic species (sardine, saury, Japanese anchovy, chub mackerel, and walleye pollock *Theragra chalcogramma*); the mesopelagic layer is dominated by the California headlightfish *Diaphus theta*, northern lampfish *Stenobrachius leucopsarus*, northern smoothtongue *Leuroglossus schmidti*, and fluorescent lampfish *Notoscopelus japonicus*, which has been the most abundant among them in recent years (Tables 1–3). At night, these fish ascend even to the upper epipelagic layer in significant numbers, where they are not quantitatively inferior to epipelagic species. In some years, abundance of squid—the Pacific flying squid, firefly squid *Watasenia scintillans*, and *Okutania anonycha*, as well as gelatinous organisms, increases sharply and significantly here.

All members of these groups generally have feeding relationships with the common species of zooplankton (and also with phytoplankton in the case of sardine). In certain areas of the feeding grounds, competitive interactions for food may apparently become more severe. However, they are unlikely to reach critical values at high and elevated concentrations of plankton and with the high mobility of most of the nekton migrants redistributing over vast areas of the NWPO. Some of them enter the Sea of Okhotsk and Bering Sea. Nevertheless, the issue of food scarcity (the interspecific competition and the density factor in intraspecies competition) was almost always mentioned, especially in the past, in many publications [1, 11, etc.]. In 2015, i.e., at the beginning of the formation of the modern sardine abundance and its significant runs to the southern Kuril region, this issue arose in the operational analysis of the unsuccessful pink salmon fishing season in Sakhalin and the southern Kuril Islands. With the forecast of 147 000 t, the actual total catch of this salmon was only 50 700 t. According to some of TINRO experts, one of the possible explanations for the pink salmon under-catch was the abundance of southern migrants, including Japanese sardine, which supposedly depleted the food supply for pink salmon. As a refutation of this idea, the annual salmon bulletin provided detailed quantitative data on the structure of plankton and diet of fish [20] collected in the southern Kuril region by the TINRO expedition in the summer of 2015.

As can be seen in Fig. 5, zooplankton concentrations in June 2015 were at a level close to average. In the upper epipelagic layer, where both salmon and common southern migrants were concentrated at that time, the zooplankton biomass exceeded 1000 mg/m^3. It is important to emphasize that in the waters off the

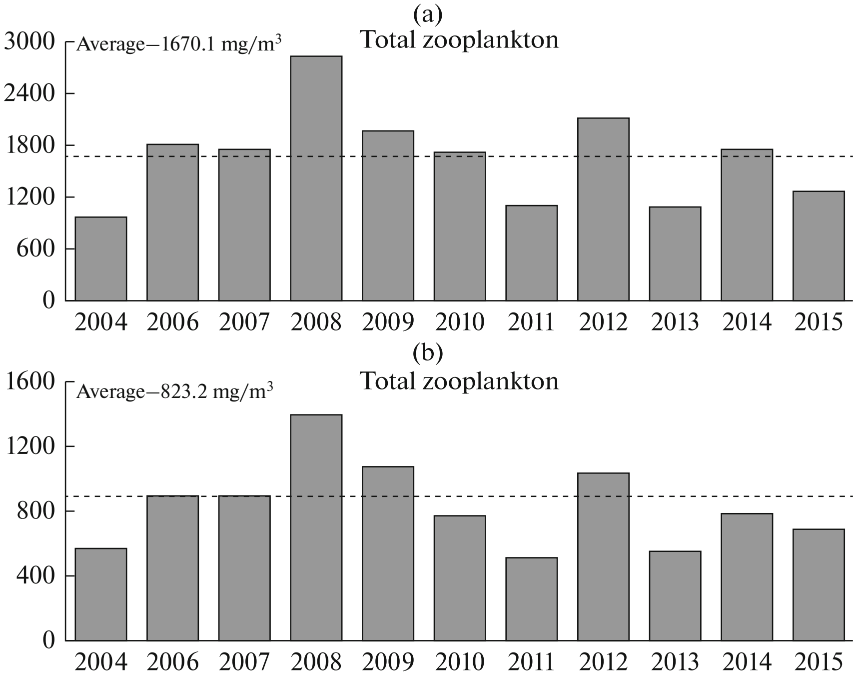

Fig. 5. The rear-to-ear variations in zooplankton concentrations in the Pacific waters off the Kuril Islands during summer: (a) in the layer 0–50 m; (b) in the layer 0–200 m [20].

Kuril Islands, the salmon that migrate from the ocean are mostly isolated from the southern nekton spatially and in time. When the mass entry of southern species begins, the major part of, e.g., pink salmon occurs in the Sea of Okhotsk.

The extensive materials on the diets of fish were also illustrative. In addition to the situation in June (Table 6), data is also provided for July and August, when there are already few salmon here (Table 7). A partial overlap in the food spectra of different species can be seen. Signs of selective feeding of all species are also evident. In sardines, a significant portion of the diet is comprised of phytoplankton; in chum salmon, gelatinous zooplankton; and in chub mackerel, fish. Amphipods and pteropods are mainly items in the diets of pink and chum salmon. Finally, the average and high stomach fullness indices show satisfactory or good food availability for all species. As for the signif-

Table 6. The feeding intensity and structure (%) of the diets of pink salmon, chum salmon, chub mackerel, and Japanese sardine in the waters off the Kuril Islands, June 1–July 1, 2015 [20]

Food item	Pink salmon 40–50 cm	Chum salmon		Chub mackerel 20–30 cm	Japanese sardine 10–30 cm
		40–50 cm	50–60 cm		
Euphausiids	**28.8–45.4**	**41.6–45.5**	**30.8–54.5**	0.0–13.7	4.3–17.7
Amphipods	**21.0–30.2**	**37.3–38.5**	**9.6–22.0**	**10.7–20.3**	0–5.0
Copepods	**9.6–29.9**	1.2–12.5	0.6–1.4	**67.6–77.1**	**82.3–95.7**
Pteropods	4.1–13.7	0.4–5.1	3.3–10.4	0–4.5	0–3.0
Arrowworms	2.9–14.2	0	0	0–1.2	0
Gelatinous zooplankton	0–0.2	2.1–11.6	18.7–47.8	0	0
Squid	0–0.5	0–1.0	0	0	0
Fish	1.9–6.7	0	0	2.4–2.6	0
SFI, ‱	**70.0–77.7**	**41.9–56.7**	**42.9–56.7**	**107.5–135.7**	**18.2–76.6**
Number, ind.	**642**	**267**	**81**	**320**	**139**

In Tables 6 and 7, the minimum and maximum average values of the parameters for different regions are presented.

Table 7. The feeding intensity and structure (%) of the diets of pink salmon, chum salmon, chub mackerel, and Japanese sardine in the waters off the Kuril Islands, July 22–August 17, 2015 [20]

Food item	Pink salmon 40–60 cm	Chum salmon 50–60 cm	Chub mackerel		Japanese sardine 13–25 cm
			20–30 cm	30–40 cm	
Euphausiids	**2.3–49.8**	**7.9–52.6**	**0.5–59.6**	**12.0–22.5**	0–9.3
Amphipods	**16.2–50.3**	2.2–29.8	0.2–5.5	3.0–4.4	0–7.6
Copepods	**2.7–52.5**	0–11.0	**16.7–77.4**	7.5–13.4	**5.3–77.0**
Decapods	0–0.9	0–2.1	0	0	0
Pteropods	1.3–28.9	0–35.9	0–1.2	0–6.2	0
Oikopleurans	0	0	**1.0–21.9**	0–3.2	**1.3–31.8**
Arrowworms	0–0.2	0–8.5	0–2.7	0–0.5	0
Gelatinous zooplankton	0	**3.2–47.9**	0	0–2.7	0
Squid	0–31.8	0–21.7	0–2.3	0–35.1	0
Fish	0.7–2.5	0–25.6	**5.5–20.6**	**31.1–67.0**	0
Phytoplankton	0	0	0	0	**2–90**
SFI, *‱*	**24–107**	**6–75**	**65–122**	**85–112**	**30–179**
Number, ind.	**86**	**57**	**532**	**219**	**312**

icant under-catch of pink salmon relative to the forecast, this was the result of, first, an incorrect interpretation of the data on the downstream migration of its young and, second, the use of an imperfect formal model [20].

CONCLUSIONS

The fact that the dramatic changes occurred in communities of the epipelagic nekton in the Pacific Ocean waters off the Kuril Islands in the second decade of the 21st century is indisputable. The significant increase in the abundance of Japanese sardine and Japanese chub mackerel and a significant decline in the abundance of Japanese anchovy and Pacific saury formed a new structure of the community. In 2020, the Japanese sardine landing by Russian and Japanese fishermen approached the level of 1 million t. The fact that this subtropical species has spread to the Bering Sea and the Sea of Okhotsk clearly shows the continuation of its population wave. In terms of growth rate, the current outbreak of the Japanese sardine abundance is still inferior to the sardine era of the 1970s–1990s, but it cannot be absolutely identical. In modern conditions, to confidently predict the population dynamics of Japanese sardine and other common pelagic species, it is necessary to continue the existing monitoring, including annual quantitative surveys during breeding and feeding migrations. A confident prediction of the onset and subsidence of population waves will become possible only with adequate assessment of the biotic potential of populations, with which the viability of individuals is associated.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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