Current Status and Tendencies in the Dynamics of Biota of the Bering Sea Macroecosystem

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Abstract: In the analysis of the long-term changes in the biota of the macroecosystems of the Bering Sea, many researchers focus on a) global greenhouse warming, b) decadal changes in climate and oceanological regimes, and c) cascading changes at different trophic levels. We think that the association of the majority of significant biological events in the Bering Sea with irreversible greenhouse warming is not justified. The relation between the dynamic processes in the populations, communities and ecosystems of the sea with the decadal changes in the climate regime is obvious. However, due to the sheer complexity of natural events, no identical recurrence of such changes has been observed, even during time periods with similar climatic conditions. Up until now, the cause-and-effect mechanisms of the transformations in populations and communities remain insufficiently studied. Here we present a critical assessment of the hypotheses of cascade transformations, including the chain of events following the overharvest of whales. In the 1990s–2000s, a significant amount of information has been collected on the biota in the Bering Sea, representing middle and higher trophic levels (zooplankton, zoobenthos, nekton, nektobenthos, sea birds and mammals). The abundance and biomass assessments of the majority of these animals, with few exceptions, suggest that they are at medium or high multi-annual levels. We conclude that normal functioning of the biota in the Bering Sea macroecosystem ensures its ability to support both biological and fish productivity at a high level.

Keywords: ecosystem, global warming, regime shift, pelagic and bottom communities, trophic relationships

INTRODUCTION

Important changes in Bering Sea biota have resulted in the expansion of ecosystem investigations there. Today there are literally hundreds of references that discuss the complex nature of the Bering Sea, in general, and the ecology of its populations, communities and ecosystems, in particular. This research is often characterized by a variety of viewpoints, particularly when it comes to interpretations of cause-and-effect mechanisms within the dynamics of Bering Sea ecosystems. Further, this research has led scientists into a wide range of subject areas including studies on the effects of global warming, research on the cyclic dynamics of climate-oceanologic factors that influence biota, and studies of anthropogenic influences on marine ecosystems.

Since the late 20th century, an underlying theme of many publications on the changes in the biota of either ecosystems, communities, or and individual species has been an assumption of some (often negative) relation to global warming caused by the greenhouse effect. In some studies on the Bering Sea and adjacent waters, modern events have been related to global warming, and forecasts have been made of their influence on Pacific salmon (*Oncorhynchus* spp.) un-

til the end of the 21st century. Such predictions have included the abundant bloom of coccolithophorids (*Emiliania hyxleyi*) in the late 1990s on the eastern shelf of the Bering Sea, the mass mortality of puffins (*Puffinus tenuirostris*) in the same area in 1997, the multi-year decrease in abundance of sea lions (*Eumetopias jubatus*) and fur seals (*Callorhinus ursinus*), increased mortality and the redistribution of gray whales (*Eschrichtius robustus*) to the Arctic, significant changes in phytoplankton community structure, a decrease in primary production, and other negative effects.

At the same time, it has been emphasized (and we agree) that the negative effect(s) of warming can be seen, first of all, not in temperature *per se*, but in "secondary effects" (a decrease in the forage base, ice reduction, e.g.) (Sukhanova and Flint 1998; Bering Ecosystem Science Study Plan 2004; Macklin and Hunt 2004; PICES 2004; Grebmeier et al. 2005; Hare et al. 2007; Shuntov and Temnykh 2008a).

We do not, however, share the opinion that there is a prevailing influence of the greenhouse effect on the dynamics of the modern climate and/or the world ocean regime. No clear global tendencies can be tracked in any of the large number of publications on the multiannual dynamics of the climate-oceanological conditions in the Bering Sea or the

North Pacific Ocean, including the most recent work (Luchin et al. 2002; Minobe 2002; Khen et al. 2004, 2006; Ponomarev et al. 2007; Darnitskiy and Ishchenko 2008). Further, in addition to the obvious interannual variations, cyclicity in climate patterns for periods from several years to several dozen years has been acknowledged for decades.

The assumption that known climate changes have a natural cyclic pattern seems substantially more convincing. Based on this assumption, the modern climate state is a "common link" in the chain of the cycle of other planetary events, in which the nature epochs come to replace each other sequentially, with a different periodicities, in a wave-like manner. The statements regarding the essential role of geophysical and cosmo-physical factors provide a reliable, fundamental basis for the cyclic changes in the atmosphere, hydrosphere and biosphere (Sidorenkov 2004; Elizarov 2005; Monin and Sonechkin 2005; Kasimov and Klige 2006a, b). Here, the instability in the slope and the rotation rate of the earth, the activity of the gravitational forces of the moon, sun and planets (the "generic tides" which direct the processes in all parts of the earth), as well as the dynamics of solar activity, are also taken into consideration.

Beginning in the late 20th century, special attention has been paid to the influence of the decadal variability in climate-oceanological processes on biota. This cyclicity has been well tracked using atmospheric and hydrological parameters. The term "regime shift" (meaning a rather sudden change in climate processes) has become very common in the scientific literature. In particular, the years 1976/77, 1988/89 and 1998/99 have been recognized as such historical milestones. At the same time, it has been emphasized that in the different areas of the North Pacific, climate and hydrobiological events within regimes can also occur with specific differences, sometimes in the opposite direction (Bakun and Broad 2001; Hunt and Stabeno 2002; Macklin and Hunt 2004; King 2005).

In light of the above-mentioned approaches and results, nevertheless, it is difficult to agree with much of the published literature. For example, the recently developed concept of regime shifts may result in changes in our previous views on the stability of marine ecosystems. However, ecosystems have never been stable. In fact, nearly all publications (including those cited above) on changes (especially the sudden ones) in climate regimes speak about the ecosystem response to such changes in the form of different transformations. Further, all such examples refer only to the individual components of an ecosystem rather than populations or communities.

Natural communities are not rigidly integrated systems. They are characterized by multi-annual dynamics and abundance fluctuations. In fact some species can enter a community and leave it without any significant consequences. The varying cyclicity in the abundance dynamics of different populations and species living within the same ecosystem supports the idea that relationships within communities are

flexible. As a result, not all events will necessarily develop according to a "falling dominoes" principle (an example of such a cascade in the ecosystem of the Bering Sea: killer whales (Orcinus orca) switch from feeding whales to sea lions and after that to the sea otters - resulting in a decrease in the number of the sea otters (Enhidra lutris); an increase in the number of the sea urchins (Strongylocentrotus spp.); a destruction of algae; essentially the destruction of the nearshore ecosystem) (Estes et al. 1998). To describe the response of communities to the environmental changes, Shuntov (2000) suggested the example of a chess game, where a limited set of rules exists but with a very large number of possible results. In such an example, the reaction of biota to the same climate influence can be different in different regions. In other words, each has it own individual chess game. This is the essence of the "provinciality" principle described in the middle of the 20th century by the Russian fisheries scientist G.K. Izhevskiy (1961, 1964). The dynamics in the abundance and state of the population of each species in the ecosystem is a result of the complex activities and the influence of various factors, including the cosmo-physical, climate-oceanological, and biological. All these factors are constantly overlapping each other and can act in different combinations. Each group of factors at certain stages can either enhance or neutralize the action of others. Because it is difficult to estimate the total influence of all factors, variations in population abundance are generally unpredictable. Therefore, because of the lack of reliable population data, it is possible to speak only about the 'tendencies' in the dynamics in abundance of populations (Shuntov et al. 1993). It looks like 'the effect of the black box' works there as well.

Regrettably, we think that there are very few sufficiently thorough investigations of the structure and functioning of marine macroecosystems over vast sea and ocean territories. This is because it is much easier to study individual components of ecosystems rather than the ecosystem itself. We also emphasize that almost everywhere the lower trophic levels (phytoplankton, bacteria and protozoa), the production of which is many times larger than the total production at higher trophic levels, have been poorly studied and rarely quantitatively estimated.

Much more reliable information has been collected on the composition and qualitative characteristics of biota at the middle and higher trophic levels. For some of them, i.e. meso- and macro-zooplankton, as well as nekton (fish and squids), the studies included in the BASIS program achieved good results. During the same years, the new information on zoobenthos and nektobenthos (bottom fish and commercial invertebrates) obtained as a result of the national research programs of Russia and the USA, has been added to the database.

The results of 20 years of ecosystem observations allow us to evaluate the current state of the pelagic and bottom communities in the Bering Sea taking into consideration inter-annual and multi-annual dynamics. We will be able to

determine regularities in the dynamics of these communities of the Bering Sea and to define the functional characteristics of these communities in the 1980–2000s, during which several so-called regime shifts occurred.

MATERIALS AND METHODS

Due to the significant differences in the methods of collection and treatment of zooplankton and nekton, the data from expeditions of different research institutions and countries, as well as those obtained in different years, are often difficult or even impossible to compare (Shuntov et al. 2007a).

For this reason, the materials of 160 expeditions of TINRO-Centre in the far-eastern seas, beginning 1980, were used. In addition to the data on the benthos (1000 stations) and bottom fish (13,000 trawls), the database of new information at TINRO-Centre on the macroecosystem biota during 1980-2000 includes the results of about 25,000 trawls (out of them about 4000 trawls were conducted in the Bering Sea). These data were systematized and combined in a series of catalogs on the composition and quantitative distribution of nekton in the far-eastern seas and the northwest Pacific Ocean (Shuntov 2003, 2004, 2005, 2006). These data as well as data from 10,000 plankton stations (> 2600 in the Bering Sea) were used for the study of multi-year trends in the nekton and plankton communities of the far-eastern seas (including the western Bering Sea) during the last 25 years. Data on average plankton and nekton biomass were systematized for the far-eastern seas, for the years 1980–1990, 1991–1995, 1996–2006), 48 standard statistical regions, and three different topographic zones (inner shelf, outer shelf, deep-water basins) (Shuntov and Temnykh 2008b; Volkov 2008).

RESULTS

Status and Multi-annual Dynamics of the Zooplankton Community

The mean multi-annual total biomass of zooplankton is approximately one-and-one-half times less in the Bering Sea than in the Okhotsk Sea: 755 mg/m³ and 1,106 mg/m³, respectively (Shuntov et al. 2007b). The concentration of macroplankton (the main food source of nekton older than those at the fry stage) in those seas is approximately the same.

Inter-annually, the average total biomass of zooplankton in the Bering Sea and other comparable regions normally varies by not > 1.5–2 times (Volkov et al. 2007). In total, no distinct differences in the biomass of zooplankton in either 'warm' or 'cold' years were observed. However, an increased biomass was more often observed in colder years. As a rule, in the absence of the growth spurts and significant decreases in the zooplankton biomass in individual years in the western Bering Sea, plankton stocks do not differ much in different periods of years (Table 1).

Therefore, over 20 years, the zooplankton resources in the western Bering Sea, in general, and macroplankton, in particular, remained at a high and relatively stable level.

In contrast to the relative stability of the total zooplankton stock, the ratio of different plankton species and groups can differ distinctly in different years. For example, inverse tendencies in the dynamics of copepod biomass on the one hand, and euphausiid and arrow worm biomass on the other, are observed (Volkov et al. 2004, 2007). However, data on the abundance of specific zooplankton species or groups in the Bering Sea are lacking, such that in most cases conditions (whether favourable or limiting) for successful reproduction are unknown. In particular, no sufficient explanation has been found for the significant decrease in macroplankton abundance in the early 2000s on the eastern shelf of the Bering Sea, or the recent increase in density beginning in 2006 (Volkov et al. 2007).

Multi-annual Dynamics of Benthos

Regular monitoring of the status and quantitative distribution of benthos from the 1950s to the 2000s has been conducted only in the western Bering Sea. From the 1950-1960s to the 1980s no appreciable changes or transformations in the composition of benthic communities were observed (Shuntov 2001; Dulepova 2002). Of course, this conclusion does not exclude the presence of some differences in biomass distribution, the configuration of the borders of bottom communities, the level of total benthos biomass and/or the ratio of different taxa within them. We assumed that these differences were within the range of the natural dynamics that is typical for relatively stable communities. In the 2000s, the TINRO benthos surveys on the shelf of the western Bering Sea were repeated (Nadtochiy et al. 2008). In general, the new data confirmed our previous conclusions on the stability of the benthic communities at a macroecosystem scale (Fig 1).

Table. 1. Total biomass of zooplankton/macroplankton (millions of tons) at night in the upper epipelagic layer of the western Bering Sea during different time periods (Shuntov and Temnykh 2007).

Year	Inner shelf	Outer shelf	Deep-water regions	Total
1986-1990	7.87/5.23	20.75/14.56	61.21/49.99	89.83/69.87
1991-1995	2.64/1.9	19.63/14.8	63.81/52.35	86.08/69.06
1996-2006	6.74/5.16	19.52/16.58	70.08/53.65	96.34/81.39

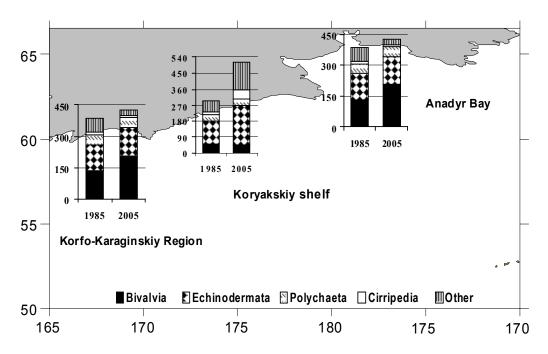


Fig. 1. Composition and biomass (g/m²) of macrozoobenthos in the western Bering Sea from 1980–2000 (Nadtochiy et al. 2008)

Based on the data collected in all the three areas of the western Bering Sea, it is possible to say that the general appearance and location of the benthic population on the shelf of the Bering Sea have remained consistent over several decades.

Status and Multi-annual Dynamics of the Nektobenthic Community

The biomass of benthic fish species increased from the 1980s to the 2000s on the western Bering Sea shelf (Fig. 2). Some changes have also been observed in the structure of nektobenthic communities over the last 20 years. The most typical feature of the structure of the bottom communities in the western Bering Sea in the 1980s was the absolute predominance of cod – almost 70% in Anadyr Bay and about 83% on the Koryakskiy Shelf (Borets 1997). A dramatic increase in the abundance of this species, combined with an increase in reproduction, beginning in the late 1970s, occurred in many parts of the far-eastern seas, including the eastern Bering Sea (Fig. 3). Up until now, cod, together with flatfish and sculpins, remain the main species contributing to the biomass. Based on data discussed above, it can be assumed that 'modern' levels of bottom fish abundance in the western Bering Sea should be considered relatively high.

The biomass dynamics of the main commercial bottom fish species from the 1980s to 2007 in the eastern Bering Sea are shown in Fig. 3. In that area, monitoring the status and dynamics of the populations of bottom fishes and crabs is conducted more systematically and regularly. One of the main conclusions based on those assessments is that in the 1980s–2000s the abundance of bottom fishes on the shelf of

the eastern Bering Sea was similar to levels in the 1960s–1980s. In the 2000s, a gradual decrease in abundance was seen only for cod (*Gadus macrocephalus*) and Greenland turbot (*Reinhardtius hippoglossoides*). Other important species in bottom communities have remained at high levels in recent years (about the same as levels in the 1980s.).

State and Multi-annual Dynamics of Nektonic Communities

Figure 4 shows changes in nekton density in 48 statistical areas of the northwestern Pacific Ocean. In the 1980s nekton density in the epipelagic zone of most areas was very high. In the early 1990s it decreased, and since the middle of the 1990s it has begun to increase again, but still has not reached the 1980s values. The very high abundance of nekton in the 1980s was the result of a massive decrease in populations of walleye pollock in northern boreal waters and the western Pacific sardine in southern boreal waters. In the early 1990s, the decrease in abundance of these fish, especially the western Pacific sardine, was so significant and sharp that it could not be compensated by an increase in abundance of a large number of fish and squid species - such as herring, Pacific saury, Pacific salmon, Japanese anchovy, Atka mackerel, Pacific squid and others.

The above-mentioned dynamics in nekton density are typical for the entire far-east region, including the western Bering Sea. Throughout the area nekton density showed a sharp decrease in all zones in the first half of the 1990s. In the following decade, it did not change appreciably in either the outer shelf or shelf edge waters of the Bering Sea (Fig. 4, Table 2).

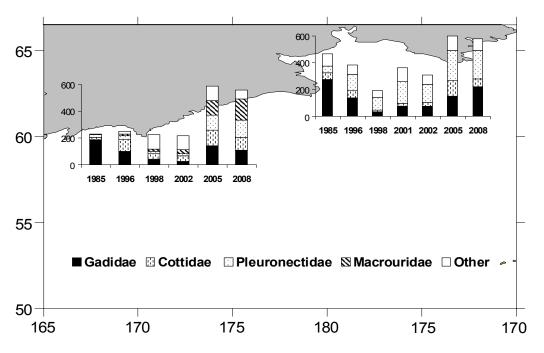


Fig. 2. Composition and biomass (thousand tons) of benthic fishes in the northwestern Bering Sea during 1985–2002.

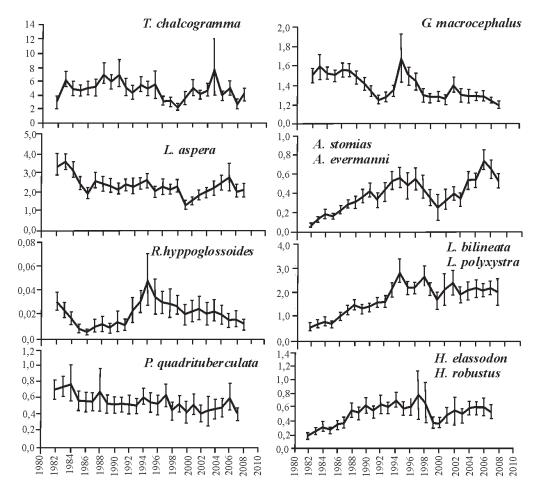


Fig. 3. Biomass dynamics (million tons) of major commercial fish species on the shelf of the eastern Bering Sea during 1982–2007 (Lauth 2007).

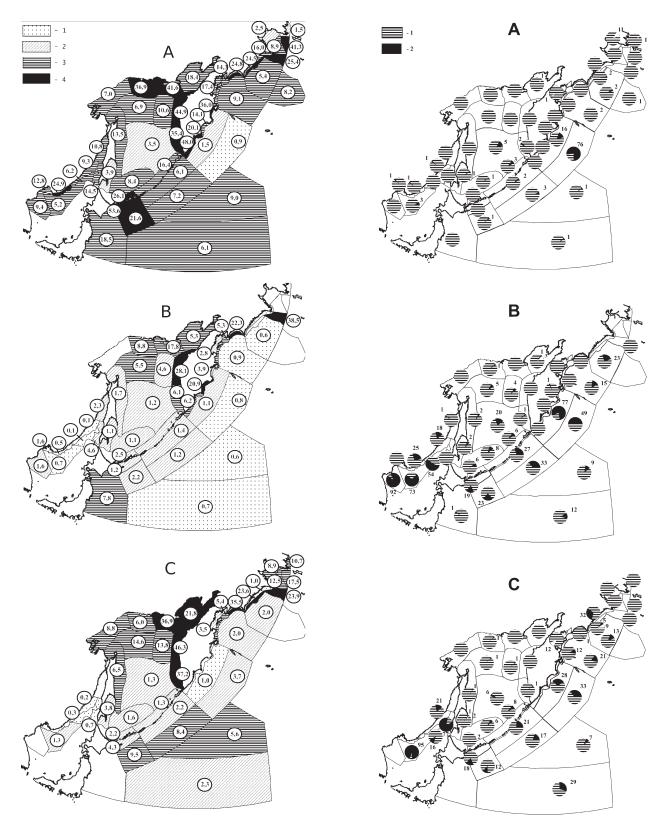


Fig. 4. Average biomass (tons/km²) of nekton species in the epipelagic layer of biostatistical areas of the far-eastern seas and adjacent Pacific waters in 1979–1990 (A), 1991–1995 (B) and 1996–2004 (C). 1 = up to 1, 2 = 1.1-5.0, 3 = 5.1-20.0, 4 = over 20 t/km², circled numbers = average biomass in the biostatistical area (Shuntov et al. 2007b).

Fig. 5. Ratio of different nekton components in the epipelagic layer of different biostatistical areas of the far-eastern seas and adjacent Pacific waters in 1979–1990 (A), 1991–1995 (B) and 1996–2004 (C). 1 = fishes, 2 = squids, numbers = percentage of squids and crustaceans (Shuntov et al. 2007b).

Table. 2. Dynamics in relative biomass averages (tons/km²) of nekton species in upper epipelagic layer of the far-eastern seas and northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2008b).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	9.3	2.8	6.0
Outer shelf and the shelf edge	23.2	22.0	19.7
Deepwater regions	7.6	0.8	2.0
Far-eastern region*			
Inner shelf	13.0	4.5	8.1
Outer shelf and the shelf edge	23.4	8.4	15.8
Deepwater regions	8.1	1.5	3.3

^{*}Hereafter within the borders of the biostatistical areas in Fig. 4.

In the epipelagic zone in both the western and eastern regions, walleye pollock was always dominant. At present, its population density still continues to remain relatively high.

At present, the total nekton biomass in the Bering Sea is slightly lower when compared with levels in the 1980s, mainly due to the decrease in the abundance of walleye pollock. The abundance of the walleye pollock stocks in both the western and eastern Bering Sea is low. The 'shortage' of this species in the total nekton biomass seems to be within the range of 5–10 million tons. However, in the nekton community there are at least two groups, squids and Pacific salmon, with abundance levels that are now higher than in the 1980s.

In the 1980s, fish were dominant in nekton communities of the epipelagic zones almost everywhere (with the exception of Pacific waters off Kamchatka) (Fig. 5). However, in the 1990s and 2000s, the squid share increased significantly. The squid biomass increased several times in the second half of the 1990s and 2000s (Fig. 5). These changes cannot be explained simply by a decrease in the abundance of consumers (primarily fish). Most probably, the changes are a result of the combined effects of many different factors, among which may be favorable conditions for reproduction for at least some squid species (Shuntov et al. 2007b). As a rule, the majority of squids are beyond the edge of the inner shelf (Table 3). However, in the second half of the 1990s and 2000s biomass of squids increased noticeably in the inner shelf waters as young squid are carried there by the currents.

Abundance of salmon in nekton communities of the fareastern seas has increased more than three times in comparison with the 1980s. For example, in the summer of 2003 up to 1 million tons of all salmon species (chum predominated) were observed in the Russian zone of the Bering Sea In recent years, the biomass of the salmon feeding in the North Pacific Ocean has been estimated to be as high as 3.5–4.5 million tons. However, as it has been noted above, the rise in abundance of these species did not compensate for the reduction in nekton biomass in the mid-1990s.

DISCUSSION

After examining the multiannual tendencies and trends in the changes occurring in both the pelagic and bottom communities of the western Bering Sea over 20 years, it is possible to come to a number of conclusions.

The stability of the plankton and benthos biomass in the western Bering Sea (as well as in all the far-eastern seas) over the long term illustrates a relative stability in the plankton and benthic communities commensurate with the observed dynamics in climate-oceanological conditions and changes in the biomass of the main consumers of plankton and benthos. This conclusion is significant, especially because of the regularly emerging assumptions about both the shortage of food and the severe competition for food in both the pelagic and bottom communities. For example, at the end of the 20th century, this subject was discussed widely in relation to the increase in salmon abundance. The conclusions about the limited carrying capacity of the sub-Arctic epipelagic zone for salmon were based on deductions about the effect of density factors on the salmon food supply (Ishida et al. 1993; Bigler et al. 1996; Volobuev 2000; Klovatch 2003). Such deductions were often based on the indirect assessments rather than actual data on the quantitative assessments of the biomass of plankton and its main consumers.

In accordance with the results of our assessments, in the 1980s, the zooplankton biomass in the Bering Sea comprised about 600 million tons in summer. The annual zooplankton consumption by nekton comprised only about 50% of the total biomass (Shuntov et al. 1993). Although plankton consumption by all nekton species in the ecosystem in general is quite large, it does not look very significant and probably does not exceed 10% of plankton production. For about the last 15 years, the total nekton abundance has decreased and zooplankton abundance remains at the mean multi-annual level. This allows us to conclude that only a few per cent of zooplankton production are consumed by nekton (Shuntov and Temnykh 2004). In the western Bering Sea specifically, zooplankton consumption by nekton comprised not more than 11% of the total zooplankton biomass in the 2000s. Consumption of zooplankton by salmon was not more than

Table. 3. Dynamics of relative biomass averages (kg/km²) of squids in the upper epipelagic layer of the far-eastern seas and northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2008b).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	0.9	< 0.1	77
Outer shelf and the shelf edge	88.2	9.7	465
Deepwater regions	122	125	340
Far-eastern region			
Inner shelf	6.4	32	60
Outer shelf and the shelf edge	93	68.2	365
Deepwater regions	128	319	483

1% of the total zooplankton biomass (Naydenko 2007)

In addition to the above-mentioned data on plankton, the conclusions of sufficient food provision of the nekton in the upper epipelagic zone are also confirmed by our data on the density and stocks of small-sized nekton (young and small fish and squid < 50 mm length) (Table 4). The concentration densities of food objects represented by small nekton (5–10 g/m²) in the epipelagic zone is an order of magnitude lower than the total macroplankton biomass; however, it is comparable to the density of hyperiids (2–8 g/m²), an important component of the fish forage base.

Salmon are not very important in the trophic relationships of nekton species. In the mid-1990s their share was 5% of the total nekton biomass in the epipelagic layers of the far-eastern seas, in the 2000s, 6%. Salmon biomass is appreciable outside shelf areas. For example, in the 2000s in the western deepwater areas of the Bering Sea their share averaged about 50% of the total nekton biomass. For most of their marine life, salmon are spatially separated from mass nekton consumers (including walleye pollock) on the shelf and at the shelf edge. Thus the pressure on forage resources decreases. However, because there is usually an adequate food supply does not necessarily mean that competition for food does not exist from time to time. For many years there have been descriptions in the literature of a decrease in salmon growth rates when abundance is high. However, a decrease in the growth rate does not necessarily indicate a strict regulation of abundance, especially by means of an increase in mortality due to a serious food shortage. The vast literature on the feeding of nekton and nektobenthos generally confirms our conclusions. Competition for food in pelagic and bottom communities does not reach levels at which abundance becomes limited (Napazakov 2003; Kuznetsova 2005; Chuchukalo 2006; Shuntov et al. 2007b).

These conclusions do not exclude the possibility of the limitation of a number of larval and fry stages of fish and commercial invertebrates when both pelagic and the majority of the benthic species in the early stages of development are found together in pelagic growth zones and layers. In these growth zones, the early life stages are more dependent

on each other when their ability to maneuver vertically, and especially horizontally, is limited.

Predators are the main factors in the functioning of marine pelagic and bottom communities. A significant amount of information on the rate of losses due to predators has been accumulated over the years, which allows us to consider the quantitative effects of predation. Table 5 shows the loss rate of walleye pollock from predators and cannibalism.

According to the data collected by TINRO expeditions in the 2000s, the number of generations of pink salmon in the Okhotsk and Bering seas on average decreases by one-third over seven months (November–June) (Shuntov and Temnykh 2008b).

Recent studies have confirmed previous conclusions that strict control of the abundance of commercial crustaceans, crabs and shrimps, occurs from the 'top down'. In 1998-2002 in the western Bering Sea, bottom fish with a biomass of about 700,000 tons consumed 25,000 tons of shrimp and snow crabs per month (Napazakov 2003). From the 1980s until now (see above), the biomass of bottom fish has doubled, which means that the rate of consumption of crustaceans has also doubled. Considering the above-mentioned significant consumption rate of commercial crustaceans, it should be noted that with the exception of cod, walleye pollock and halibut, no other predatory species (grenadiers, sculpins, lords, skates, e.g.) are caught for commercial purposes. By approximate calculations, even a 10% harvest of these fishes will result in about a 10% increase in the number of the unconsumed crabs and shrimp compared with their present total allowable catches (Chuchukalo 2006; Shuntov and Temnykh 2007c). As we know, current fisheries management practices are based on approaches that are very different from ours. They are concerned with a targeted impact on communities with the goal of producing changes in the ratios of species and groups. Modern fisheries management is traditionally based on two concepts – the determination of allowable catch quotas for specific populations and the conservation of resources (Shuntov 2004).

In summary, it is possible to make two general conclusions about the structure, dynamics and function of the biota

Table. 4. Dynamics of relative biomass averages (g/m²) of small-size nekton species (fishes and squids) in the upper epipelagic layer of the far-eastern seas and the northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2007).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	3.9	2.1	1.9
Outer shelf and the shelf edge	3.7	0.1	1.9
Deepwater regions	0.3	0.2	0.5
Far-eastern region			
Inner shelf	2.4	1.4	1.7
Outer shelf and the shelf edge	1.8	0.4	1.1
Deepwater regions	1.2	0.8	1.2

Table. 5. Annual consumption (million tons) of walleye pollock in the Okhotsk and Bering seas in the 1980s (Shuntov and Dulepova 1993).

Cause of mortality	Okhotsk Sea	Bering Sea
Large walleye pollock (cannibalism)	0.6	0.9
Other predatory fish	2.2	4.5
Marine mammals and birds	0.4	1.5
All predators	3.2	6.9
Commercial catch	1.8	2.0*
Walleye pollock production	5.0-7.5	10.0–12.5

in the Bering Sea:

- a) At present the vast ecosystem of the Bering Sea is capable of sustaining a high level of biological and fisheries production;
- b) Natural events (climate-hydrological, community and population factors) are the most important factors influencing the dynamics of marine biota. At present, anthropogenic influences and even fisheries do not play a key role in determining trends in the abundance dynamics of the majority of the populations or in the structural transformations of the communities of the Bering Sea.

CONCLUSION

As we begin the 21st century, it is clear that significant progress has been achieved in our understanding of the functioning of marine ecosystems, including that of the Bering Sea. However, as we have discussed, our understanding of the cause-and-effect mechanisms impacting the dynamics of natural events and processes is mainly based on retrospective analyses. There have been few (or no) successful predictions of future events based on theoretical knowledge. This illustrates the unreliability of hypotheses and suggestions. Nevertheless, despite the complexity of functioning of populations, communities and ecosystems, we can be assured that future studies in the areas that have been defined in recent years will bring good results. At the same time, however, there are doubts regarding the sufficiency of traditional methods and approaches (Shuntov et al. 2007a). Doubts emerge from the fact that significant changes in communities are mainly caused by the dynamics of limited number

of species (such as walleye pollock or Pacific sardine). The contribution of the majority of species to dynamics of communities is imperceptible. Even neighbouring populations of the same species can 'behave strangely' in the similar situations. Dramatic and considerable increases or decreases in abundance of certain species or populations as a rule occur suddenly for investigators. In our opinion, obvious progress in understanding the mechanisms of reorganization of biota will be connected only with the advent of new "nonconventional" hypotheses.

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