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# Jellyfish of the Far Eastern Seas of Russia. 3. Biomass and Abundance

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**Abstract**—The biomass and abundance of large jellyfish (Cnidaria: Scyphozoa, Hydrozoa) was estimated and their seasonal and interannual dynamics was studied based on the data of trawl surveys conducted by the Pacific Research Fisheries Center (TINRO Center) in the Sea of Okhotsk, Bering Sea, Sea of Japan, and the Northwestern Pacific Ocean (NWPO) in 1991–2009. Most of the jellyfish biomass (over 95%) in the Sea of Okhotsk, Bering Sea, and NWPO was formed by *Chrysaora* spp., *Cyanea capillata*, *Aequorea* spp., *Phacellophora camtschatica*, and *Aurelia limbata*. The same species along with *Calycopsis nematophora* predominated in abundance in the Bering Sea and NWPO, while *Ptychogena lactea*, *C. capillata*, and *Chrysaora* spp. were most abundant in the Sea of Okhotsk. In the northwestern Sea of Japan, *Aurelia aurita*, *C. capillata*, and *Aequorea* spp. predominated both in abundance and biomass. Generally, the jellyfish abundance reached the highest values in the summer and fall and decreased abruptly in the winter. Meanwhile, the seasonal dynamics proved to be specific for each species and were manifested in some of them by reaching maximum values at various periods of the warm season, whereas the other (*Tima sachalinensis* and *P. lactea*) showed the reverse pattern of seasonal variations, with the highest abundance in cold months. Jellyfish biomass and abundance varied greatly from year to year, which was related to the short lifecycle and alternation between sexual and asexual generations, in which reproductive success was predetermined by various environmental factors. In the fall, year-to-year fluctuations of the relative biomass could increase by ten times. In 1991–2009, it varied from 200 to 2000 kg/km$^2$ in the northern Sea of Okhotsk, from 500 to 4200 kg/km$^2$ in the northwestern Bering Sea, and from 300 to 3700 kg/km$^2$ in the southwestern Bering Sea. Taking the jellyfish abundance estimates into account, along with the vertical distribution and the seasonal dynamics, the overall biomass of large species that occurred in trawl catches in Far Eastern seas and adjacent Pacific waters during the warm season could reach 13.0–15.0 million tons, of which up to about 6.0 million tons would be concentrated in the western Bering Sea and 5.5–6.0 million tons in the Sea of Okhotsk.

**Keywords:** Cnidaria, Scyphozoa, Hydrozoa, jellyfish, biomass, abundance, quantitative composition.

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## INTRODUCTION

A large amount of data from various areas of the World Ocean show that the abundance of gelatinous zooplankton (medusae, ctenophores, salps) may vary significantly from year to year; for the past decades it has had the tendency to grow in many populations [20, 34, 41]. The causes of these variations remain unclear in most cases and can be linked to climatic conditions [19, 20, 23, 24, 32, 33, 39], eutrophication [18, 42, 43, 48], introduction of new species [27, 34, 45, 49], alterations of ecosystems related to fishery [31, 38], forage resources, and other factors [28, 29, 46].

Fluctuations in the abundance of gelatinous zooplankton, which is an important component of pelagic communities, can exert a significant influence on the situation in marine ecosystems. During surges of abundance, its role as a consumer of plankton, spawn, and juvenile fish and squid grows sharply [2, 8, 12, 17, 21, 33, 35, 40, 44], which may greatly affect the state of the resources of commercial species. Hence, estimation of the abundance of jellyfish, and analysis of its seasonal and year-to-year dynamics in order to determine the significance for marine communities in various periods, remains an important field of ecosystem studies.

This work completes the series of articles on jellyfish of Russian Far Eastern seas [4, 5]. It is dedicated to the appraisal of the biomass and abundance of large medusae (Cnidaria: Scyphozoa, and Hydrozoa), which occurred in trawl catches in Far Eastern seas and adjacent Pacific waters in various seasons from 1991 until 2009.

## MATERIALS AND METHODS

This work is based upon the materials of pelagic trawl surveys that the TINRO Center conducted in the Bering Sea, Sea of Okhotsk, Sea of Japan, and in the

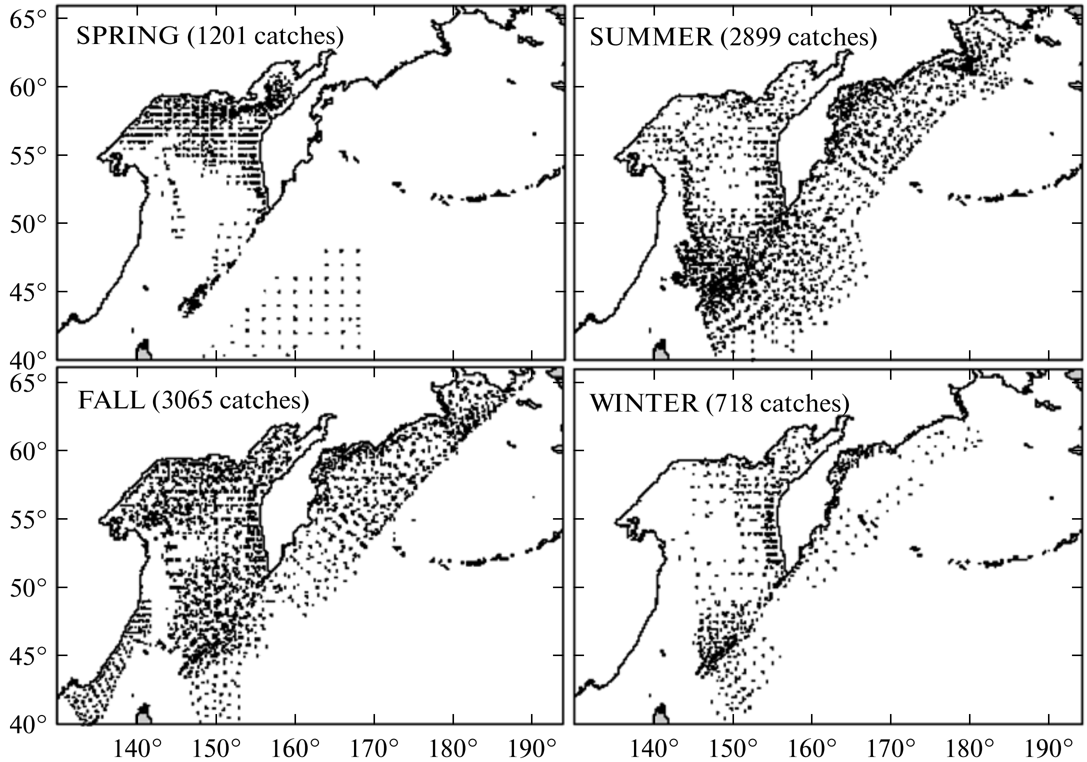


**Fig. 1.** Map of trawl catches in the epipelagic layer of the Far Eastern seas of Russia and the Northwestern Pacific Ocean by seasons.

Northwestern Pacific Ocean (NWPO) in 1991–2009. The technique of data collection and calculation of jellyfish abundance was described thoroughly in the first report of the series [4]. In this part, while estimating the jellyfish biomass and abundance, we paid attention mainly to the epipelagic zone as the most comprehensively studied layer of the water column (almost 90% of all the pelagic trawl catches). The map of trawl catches by season is presented in Fig. 1. It shows the scale and the intensity of the studies that were conducted in several water areas within each of the four seasons.

When studying the factors that account for the dynamics in jellyfish abundance, we used climatic indices, which are the resulting characteristics of the climatic conditions in the North Pacific region:

PDO – The Pacific Decadal Oscillation, and PDOw, PDOs and PDOa are, respectively, mean winter, mean summer, and mean annual values;

NPI – The North Pacific Index;

SAI – The Siberian–Alaskan Index;

SI – The Siberian Index;

AI – The Aleutian Index.

Values of the indices are taken from the web-site of the National Oceanic and Atmospheric Administration (NOAA), USA, http://www.beringclimate.noaa.gov.

## RESULTS AND DISCUSSION

### *The Composition and Correlation of Jellyfish Species*

According to the data of trawl catches, which are generalized for all surveys from 1991 to 2009, the major portion of the jellyfish biomass in the Sea of Okhotsk, western Bering Sea, and NWPO consisted mainly of species of the genus *Chrysaora* (Fig. 2a). Their share in these waters varied within 44–60%. As well, in the Sea of Okhotsk, most significant species were *Cyanea capillata* (34%), which became predominant in biomass in some years, as well as *Aurelia limbata* (15%). In the Bering Sea, in addition to *Chrysaora* spp., a large share of the jellyfish biomass was formed by both species of the genus *Aequorea* (25%) and *C. capillata* (11%). In the NWPO, *Aequorea* spp. (20%) and *Phacellophora camtschatica* (14%) were subdominant. Thus, the jellyfish biomass values in the Sea of Okhotsk, Bering Sea, and NWPO were almost completely (96% to almost 100%) formed by five species and groups of species such as *Chrysaora* spp., *C. capillata, Aequorea* spp., *P. camtschatica*, and *A. limbata*.

In the Sea of Japan, the structure of predominant species differed notably (Fig. 2a). There *Aurelia aurita* prevailed in biomass (50%). Also *C. capillata* (37%) and *Aequorea* spp. (12%) together constituted a large portion. As the information on jellyfish abundance here is based only on one fall survey, the proportions of

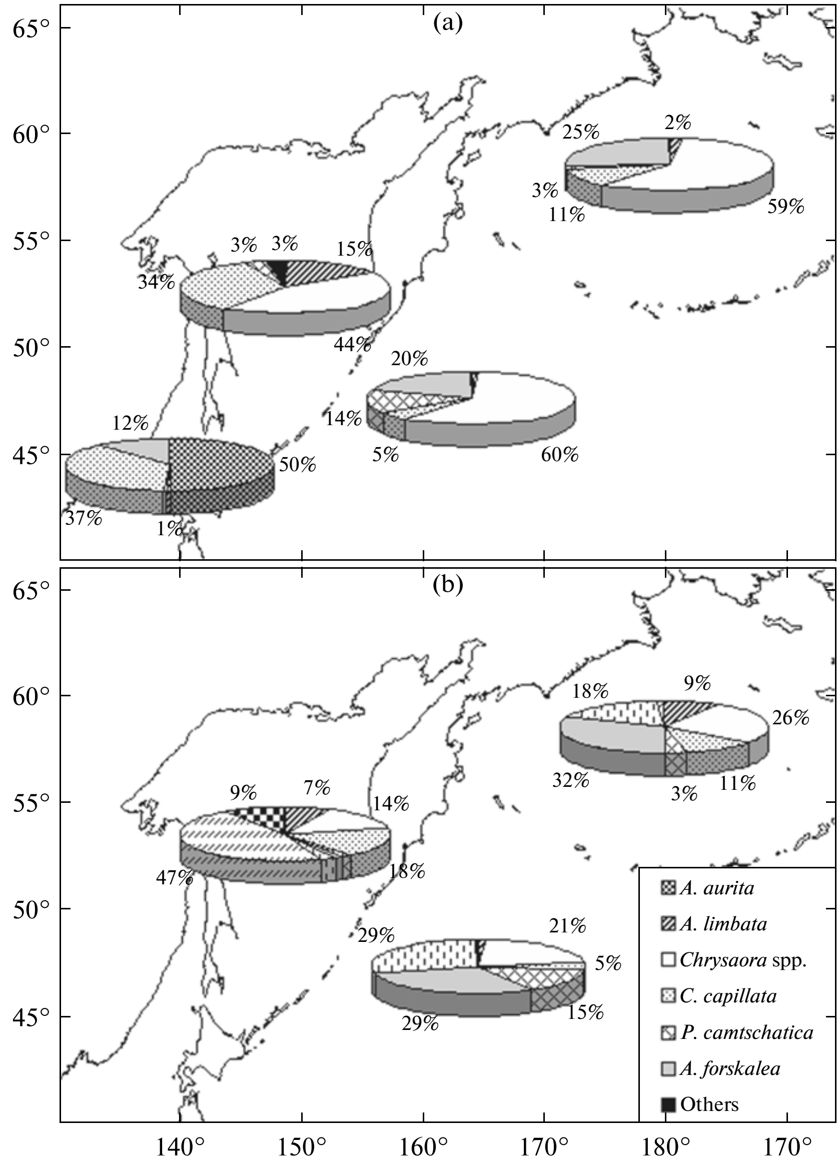


**Fig. 2.** Composition of jellyfish species and proportions of their biomass (a) and abundance (b) in the epipelagic layer of the Far Eastern seas of Russia and adjacent Pacific waters in 1991–2009.

the species may change upon obtaining additional data. However, both the information from the literature and our observations show that these data correspond to the actual quantitative composition of jellyfish, at least concerning the predominant species.

Medusae that formed the general portion of biomass also predominated in abundance or were among the most abundant species (Fig. 2b). In the Bering Sea, these were *Aequorea* spp. (32%), *Chrysaora* spp. (26%), and *C. capillata* (11%). As well, the mesopelagic species *Calycopsis nematophora* also played a major role (18%). In the NWPO, the structure of the species, which prevailed in abundance, was similar to that in the Bering Sea. There the predominant species were *Aequorea* spp. (29%), *C. nematophora* (29%), *Chrysaora* spp. (21%), and *P. camtschatica* (15%). In the Sea of Okhotsk, the mesopelagic species of hydromedusae *Ptychogena lactea* constituted almost half (47%) of the total jellyfish abundance. Also *C. capillata* (18%) and species of the genus *Chrysaora* (14%) had a notable significance. In the Sea of Japan, *Aurelia aurita* (45%) and *Aequorea* spp. (47%) prevailed in abundance. The share of *C. capillata* in the total jellyfish abundance was only 7%, despite the fact that the species predominated in biomass there.

### *The Seasonal Dynamics of the Relative Biomass*

The analysis of seasonal variations in the relative biomass of jellyfish in the epipelagic zone was carried

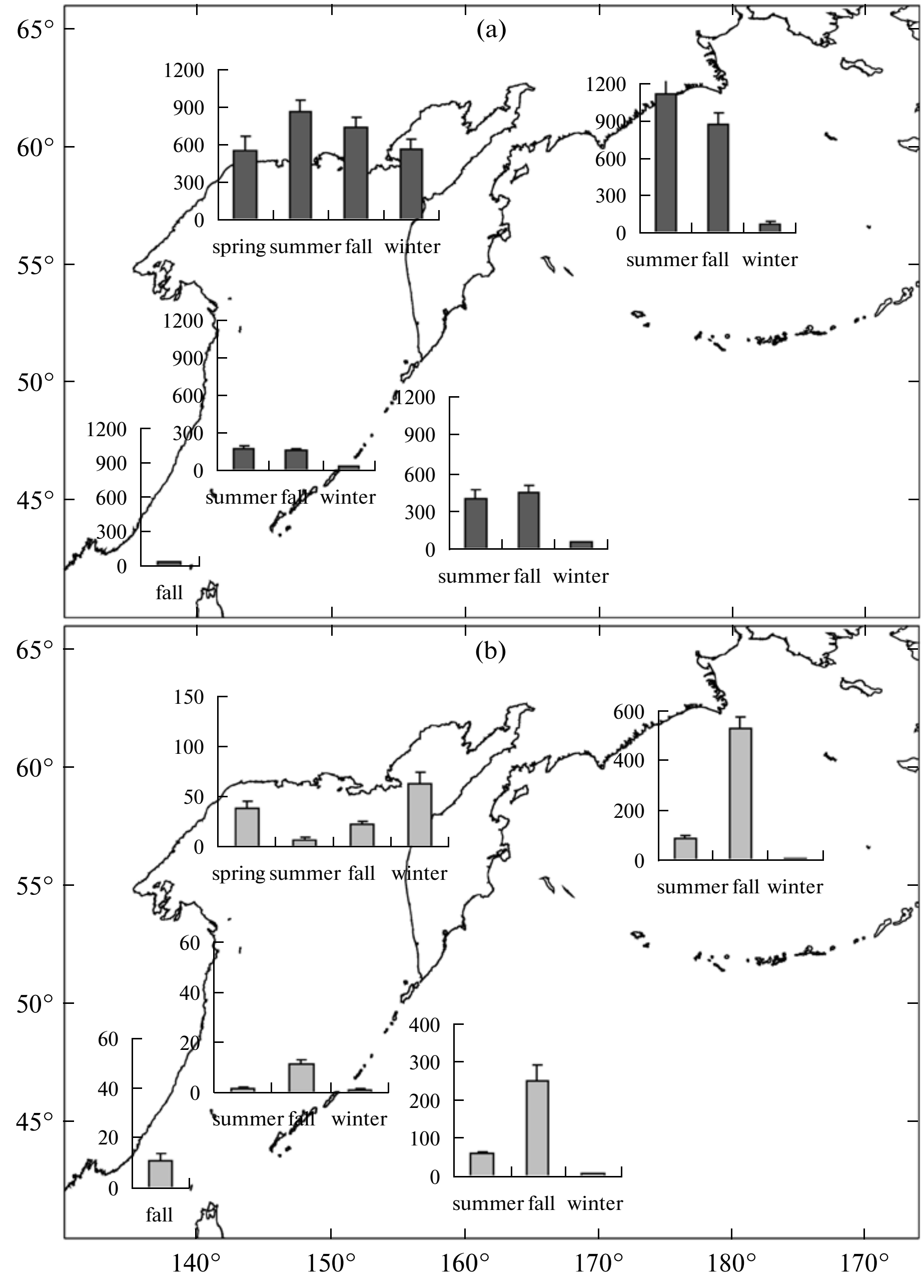


**Fig. 3.** Seasonal dynamics of relative biomass (kg/km$^2$) of scyphomedusae (a) and hydromedusae (b) in the epipelagic layer of the Far Eastern seas of Russia and adjacent Pacific waters in 1991–2009. Bars with lines are the mean values and standard errors.

out within the following vast areas: western Bering Sea, northern Sea of Okhotsk, southern Sea of Okhotsk, and the NWPO. Data of the fall survey in the northwestern Sea of Japan are also submitted for comparison. The Sea of Okhotsk was divided into two regions via differences in the bathymetry and thermal conditions. The NWPO area was restricted to the exclusive economic zone of Russia with adjacent waters; also the data of surveys within the zone of the Subarctic Front east of 172°E were not included, since works there were episodic and performed mainly in the winter and spring (see Fig. 1).

The seasonal dynamics of the relative biomass of scyphomedusa had a similar pattern in all the studied areas (Fig. 3a). The highest relative biomass of jellyfish was observed in the summer and fall. In the winter, it declined abruptly. In the Bering Sea, NWPO, and the southern Sea of Okhotsk, the biomass decreased by approximately one order of magnitude (Fig. 3a, Tables 1–3). Judging by the available data, the decline in the northern Sea of Okhotsk was not so significant (Fig. 3a, Table 4). The biomass of Scyphozoa dropped by one and a half times in the cold season. Such weak differences in the estimates of relative biomass of scy-

**Table 1.** The relative biomass of jellyfish in the epipelagic layer of the western Bering Sea by seasons ($M \pm SE$), kg/km$^2$

| Class, species | Summer | Fall | Winter |
|---|---|---|---|
| *Scyphozoa* | 1116 ±182 | 871 ± 93 | 75 ±15 |
| *Aurelia limbata* | 2 ± 1 | 50 ± 16 | – |
| *Chrysaora* spp. | 1054 ±181 | 547 ± 84 | 51 ±14 |
| *Cyanea capillata* | 30 ±7 | 230 ± 33 | 1 ± 1 |
| *Phacellophora camtschatica* | 28 ± 2 | 42 ± 3 | 16 ± 7 |
| Hydrozoa | 86 ±12 | 530 ± 46 | 6 ± 2 |
| *Aequorea* spp. | 85 ±12 | 527 ± 46 | 5 ± 2 |
| Number of trawl catches | 868 | 1074 | 80 |

**Table 2.** Relative biomass of jellyfish in the epipelagic layer of Pacific waters off the Kuril Islands and East Kamchatka by seasons ($M \pm SE$), kg/km$^2$

| Class, species | Summer | Fall | Winter |
|---|---|---|---|
| Scyphozoa | 402 ± 61 | 451 ± 47 | 52 ± 9 |
| *Chrysaora* spp. | 317± 60 | 308 ± 45 | 31 ± 8 |
| *Cyanea capillata* | 13 ± 6 | 58 ± 11 | 2 ± 1 |
| *Phacellophora camtschatica* | 70 ± 7 | 73 ± 9 | 10 ± 2 |
| Hydrozoa | 59 ± 7 | 250 ± 43 | 7 ± 2 |
| *Aequorea* spp. | 59 ± 7 | 248 ± 43 | 6 ± 1 |
| Number of trawl catches | 903 | 295 | 130 |

phomedusa in the northern Sea of Okhotsk between various seasons can be explained by the discontinuance of studies for the coldest months, viz., January, February, and March, when most of the area is covered with ice, the abundance of jellyfish is the lowest; the surveys skip this period.

The biomass of hydromedusae was much less than that of scyphomedusae (Fig. 3b). The levels of the biomass of Hydrozoa and Scyphozoa were comparable only in the Bering Sea and NWPO because of the large quantity of large hydromedusae of the genus *Aequorea*. The seasonal dynamics of the hydromedusae in the Bering Sea, NWPO, and southern Sea of Okhotsk were similar and had a pronounced maximum of the biomass in the fall and a minimum in the winter. In these areas, the value of overall hydromedusae biomass depended on one predominant group of species, viz., *Aequorea* spp. (see Tables 1–3). In the northern Sea of Okhotsk, in contrast, the lowest relative biomass was observed during the warm time of the year, and it grew significantly in cold seasons. Other species, viz., *P. lactea* and *Tima sachalinensis*, predominated there (see Table 4).

Seasonal variations in scyphomedusae abundance were generally similar to biomass variations. The largest quantities of jellyfish occurred in catches during

**Table 3.** Relative biomass of jellyfish in the epipelagic layer of the southern Sea of Okhotsk and in the Sea of Japan by seasons ($M \pm SE$), kg/km$^2$

| Class, species | Sea of Okhotsk | | Sea of Japan | |
|---|---|---|---|---|
| | Summer | Fall | Winter | Fall |
| Scyphozoa | 174 ± 20 | 163 ± 15 | 30 ± 7 | 36 ± 6 |
| *Aurelia aurita* | – | 1.0 ± 0.3 | 2 ± 2 | 19 ± 4 |
| *Chrysaora* spp. | 118 ± 16 | 61 ±10 | 6 ± 2 | – |
| *Cyanea capillata* | 50 ± 8 | 91 ± 11 | 15 ± 5 | 14 ± 4 |
| *Phacellophora camtschatica* | 3.0 ± 0.4 | 8 ± 2 | 7 ± 2 | – |
| Hydrozoa | 2 ± 1 | 12 ± 2 | 1.0 ± 0.3 | 11 ± 3 |
| *Aequorea* spp. | 2 ± 1 | 11 ± 2 | 1.0 ± 0.3 | 5 ± 2 |
| Number of trawl catches | 585 | 411 | 158 | 162 |

**Table 4.** Relative biomass of jellyfish in the epipelagic layer of the northern Sea of Okhotsk by seasons ($M \pm SE$), kg/km$^2$

| Class, species | Spring | Summer | Fall | Winter |
|---|---|---|---|---|
| Scyphozoa | 558 ± 111 | 867 ± 91 | 742 ± 77 | 565 ± 82 |
| *Aurelia limbata* | 17 ± 4 | 2 ± 1 | 119 ± 42 | 6 ± 3 |
| *Chrysaora* spp. | 176 ± 19 | 797 ± 90 | 291 ±48 | 202 ± 38 |
| *Cyanea capillata* | 362 ±109 | 64 ± 20 | 290 ± 34 | 212 ± 49 |
| *Phacellophora camtschatica* | 2 ± 1 | 4 ± 1 | 31 ± 7 | 55 ±19 |
| Hydrozoa | 39 ± 7 | 7 ± 2 | 23 ± 3 | 63 ±13 |
| *Ptychogena lactea* | 22 ± 7 | 2 ± 1 | 6 ± 1 | 10 ± 5 |
| *Tima sachalinensis* | 14 ± 3 | 5 ± 2 | 11 ± 2 | 42 ±12 |
| Number of trawl catches | 998 | 540 | 1310 | 352 |

warm seasons, viz., in the summer and fall (Fig. 4a), and the fall abundance was slightly higher. One more peak of jellyfish abundance in the northern Sea of Okhotsk in the spring deserves special attention. Unfortunately, there are no data on jellyfish abundance for this season in other water areas, therefore we cannot say for sure if this pattern of seasonal dynamics was typical for all the studied areas or it was related to the peculiarities of surveys in this area, mentioned above.

Seasonal dynamics of hydromedusae abundance completely coincided with those of their biomass. In the Bering Sea, NWPO, and southern Sea of Okhotsk, the largest quantities of jellyfish were observed in the fall (Fig. 4b). In the northern Sea of Okhotsk, the maximum abundance was in the winter and spring.

The highest biomass and abundance of Scyphozoa and Hydrozoa were recorded in the western Bering Sea (see Figs. 3 and 4). Scyphomedusae were also abundant in the northern Sea of Okhotsk, and hydromedusae, in the NWPO. In these areas, their biomass was comparable to that in the Bering Sea.

Seasonal dynamics differ in various jellyfish species. Species of the genus *Chrysaora* had the highest values of biomass in all the areas during the summer (see Tables 1–4), while the remaining mass jellyfish species (*A. limbata, C. capillata, P. camtschatica, Aequorea* spp.) reached the highest biomass mainly in the fall. However the second peak of biomass in *C. capillata*, observed in the Sea of Okhotsk in spring, surpassed the first one in the fall by magnitude (Table 4). *P. camtschatica* was also abundant in the winter (see Tables 1–4), when its biomass in the northern Sea of Okhotsk even exceeded the one in the fall (Table 4).

*P. lactea* and *T. sachalinensis*, which were predominant among hydromedusae in the Sea of Okhotsk, also differed in the pattern of seasonal abundance variations. Both species showed higher abundance values during the cold period, but *T. sachalinensis* was the most abundant in the epipelagic zone in the winter, while *P. lacteal* reached the maximum abundance in the spring (Table 4).

### *The Interannual Dynamics of the Relative Biomass*

Biomass of jellyfish varies significantly from year to year. In the northern Sea of Okhotsk, the jellyfish relative biomass varied from 200 to 2000 kg/km$^2$ in the falls of 1994–2009 (Fig. 5a). Its maximum value was recorded in 2009. Higher values of relative biomass also occurred in 1994 and 1999 (1750 and 1400 kg/km$^2$, respectively). The lowest levels of jellyfish biomass that did not exceed 300 kg/km$^2$ were observed in 2007, 2001, and 2002.

In the springs of 2004–2009, the jellyfish biomass in the Sea of Okhotsk had cyclic oscillations from the minimum to the maximum with a periodicity of 2 years (Fig. 5b). This was caused by abrupt year-to-year variations in the abundance of *C. capillata*, the predominant species in this season. According to the results of the spring survey of 2010, whose data were not included in this work, the relative jellyfish biomass was estimated at a medium level for the spring season (about 500 kg/km$^2$), while the biomass of *C. capillata* was the minimum and reached only 5 kg/km$^2$, which meant that the 2-year cycle of dynamics of this jellyfish species continued. It should be noted that no similar cyclic biomass variations were observed in the Sea of Okhotsk in the fall.

In the shallow northwestern Bering Sea, jellyfish biomass gradually declined from the early to the late 2000s (Fig. 6a). This was related mainly to the decrease in abundance of *Chrysaora melanaster*, one of the predominant species, whose relative biomass dropped from 3700 kg/km$^2$ (in 2000) to 300 kg/km$^2$ (in 2009). In years of high abundance of *Aequorea forskalea* in central areas of the Bering Sea (in 2003 and 2004), a major portion of this jellyfish was brought to the northern shelf with currents, and, as a result, its share in the overall jellyfish biomass grew significantly in these years. As in the Sea of Okhotsk in the spring, the biomass of *C. capillata* oscillated with a 2-year

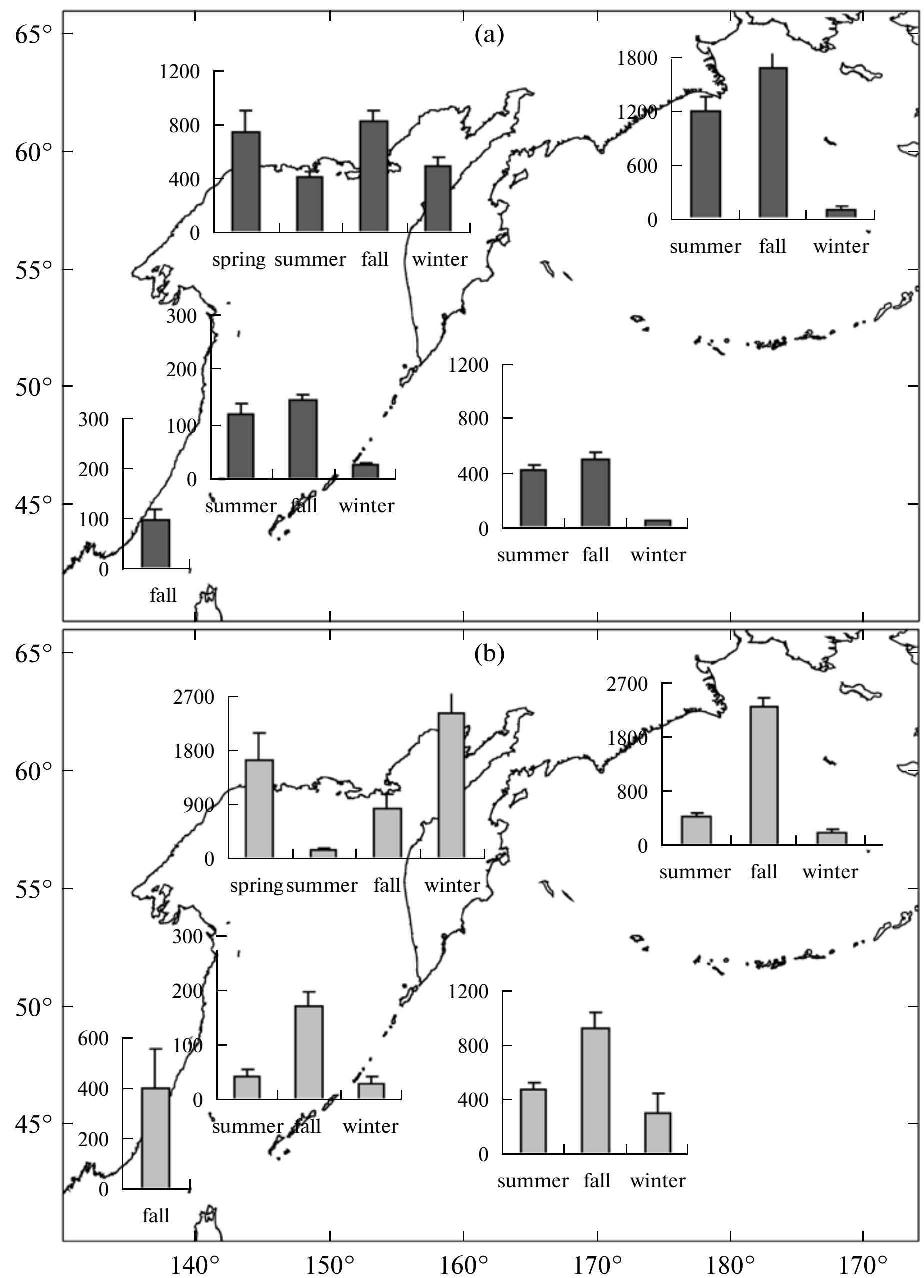


**Fig. 4.** Seasonal dynamics of abundance (ind./km$^2$) of scyphomedusae (a) and hydromedusae (b) in the epipelagic layer of the Far Eastern seas of Russia and adjacent Pacific waters in 1991–2009. Bars with lines are the mean values and standard errors.

cycle here. An interesting fact was discovered from data and materials of the summer survey 2005: a shift in cycles from maximums in even years to maximums in uneven years took place in 2004–2005, which is seen in Fig. 6a.

In the deep-water southwestern Bering Sea, the jellyfish biomass grew from the 1990s to the middle 2000s and decreased abruptly again by 2008–2009 (Fig. 6b). The variations that were observed were linked mainly to the fluctuations in the abundance of *A. forskalea*. In the fall of 2004 this species had the largest biomass, which was estimated at about 3000 kg/km$^2$.

In the NWPO, the maximum jellyfish biomass was recorded in the first half of the 1990s (Fig. 7). In 2004–2009, its level was notably lower. However in the 2000s, surveys were conducted here in June and July, and in the 1990s, mostly in July and August, when the jellyfish biomass became significantly larger because of the somatic growth and the inflow from shelf areas with currents; therefore, the difference in biomass between these years was probably not so large. In 1993

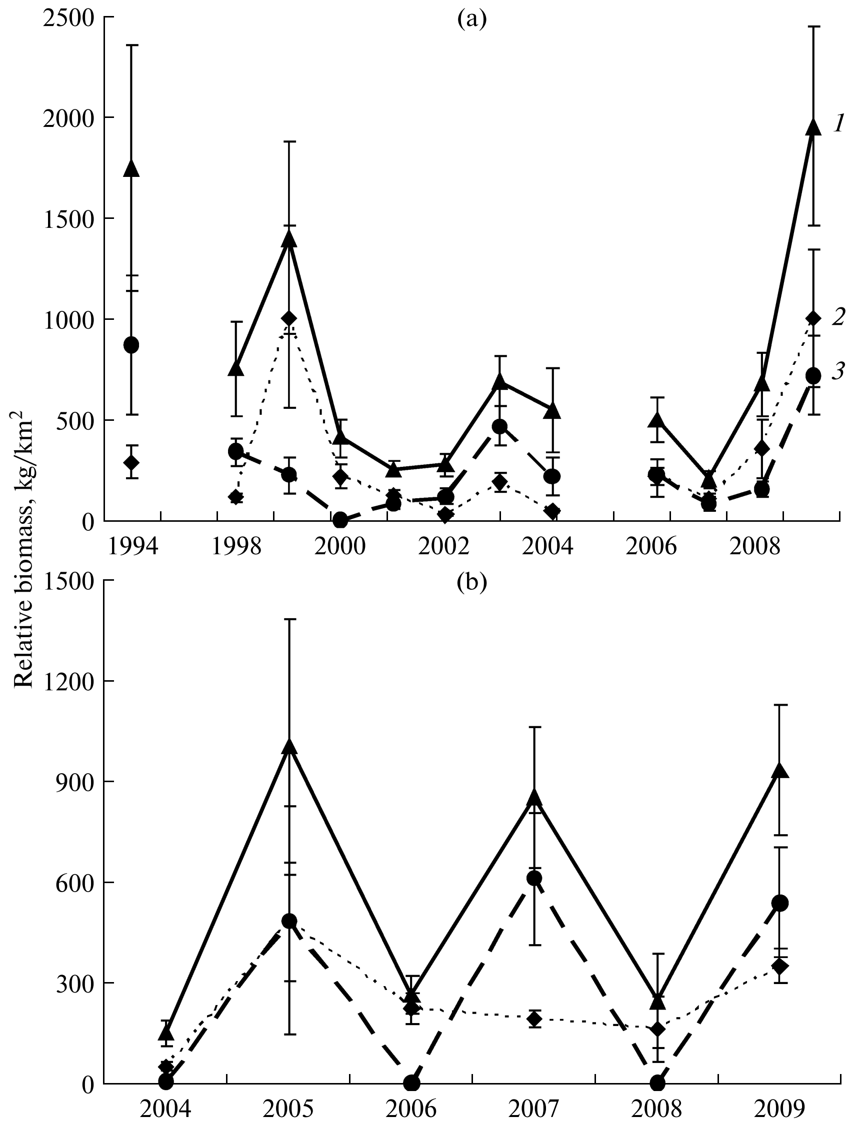


**Fig. 5.** Year-to-year dynamics of the jellyfish relative biomass (kg/km$^2$) in the epipelagic layer of the northern Sea of Okhotsk in the fall (a) and spring (b): *1*, all jellyfishes; *2*, *Chrysaora* spp.; *3*, *Cyanea capillata*. Vertical lines are the standard errors.

and 1995, *Chrysaora* spp. constituted most of the jellyfish biomass. In 2004–2009, the predominant species were mainly those of the genus *Aequorea*.

The interannual dynamics did not match in the predominant species, viz., *C. capillata, Chrysaora* spp. and *Aequorea* spp. Synchronous biomass variations were observed only in recent years (2002–2009) in pairs of species, viz., *C. capillata* and *Chrysaora* spp. in the Sea of Okhotsk and *Chrysaora* spp. and *Aequorea* spp. in the Bering Sea. in the fall (see Figs. 5a and 6b). While the jellyfish biomass in the Sea of Okhotsk steadily rose, that in the Bering Sea declined. The "antiphase" effect of jellyfish biomass variations was noted in these seas in other years as well. Thus, in the 1990s, the jellyfish biomass in the Bering Sea was at a low level (Fig. 6b), while in the Sea of Okhotsk it reached one of the highest values for the entire period of studies (see Fig. 5a).

### *Information on Seasonal Jellyfish Biomass Variations from the Literature*

Unlike the biomass and abundance of many other large aquatic organisms, those of jellyfish in which the lifespan lasts usually for under 1 year are subjected to strong seasonal variations. The dynamics in the abundance of jellyfish are predetermined by its lifecycle. Generally, in most of Scyphozoa and Hydrozoa, registered in trawl catches, they have the following pattern [13, 14]: from winter and, probably, up to summer, polyps (called "scyphistoma" in Scyphozoa) that live on the bottom actively produce juvenile medusae. The latter grow during the warm period and reach the high-

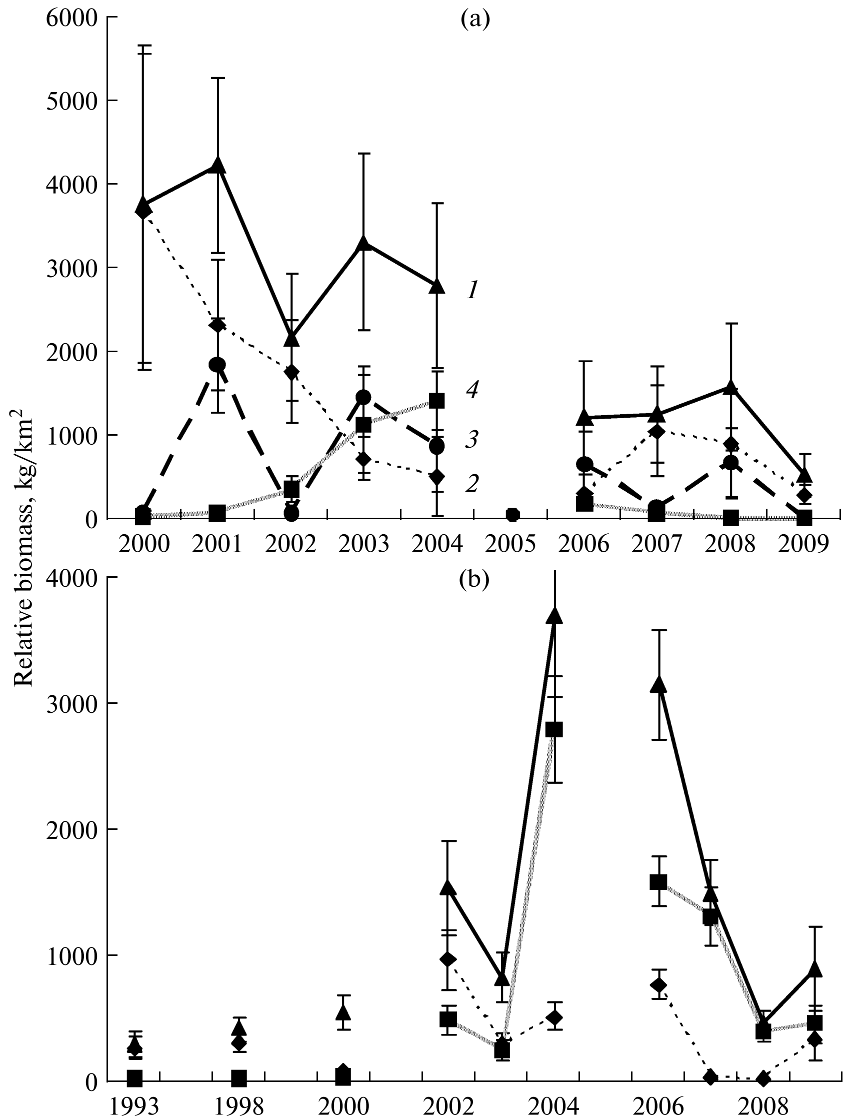


**Fig. 6.** Year-to-year dynamics of the jellyfish relative biomass (kg/km$^2$) in the epipelagic layer of the northwestern (a) and southwestern (b) Bering Sea in fall: *1*, all jellyfishes; *2*, *Chrysaora* spp.; *3*, *Cyanea capillata*; *4*, *Aequorea* spp. Vertical lines are the standard errors. The value of biomass of *C. capillata* in the summer 2005 is designated as a black spot in part (a).

est biomass in the summer and early fall. After spawning, which occurs at different times for different species, they die and their abundance in the pelagic zone drastically drops.

This agrees well with our data (see Figs. 3 and 4, Tables 1–4), which show that jellyfish have the highest biomass, as a rule, in the summer and fall and it significantly decreases in the winter. At the same time, seasonal dynamics in every particular jellyfish species have specific features, which are manifested by reaching maximum abundance values in different periods of warm season. Thus, species of the genus *Chrysaora* had the largest biomass in the summer, and then their quantities declined in the fall after spawning, which lasts mainly for August and September (Tables 1–4). The biomass peaks in *C. capillata* and *A. limbata* occurred mostly in the fall. Similar dynamics were found in *C. capillata* in the southern North Sea [22]. *P. camtschatica* is usually the most abundant in the fall and early winter. But some species show the reverse pattern of seasonal variations. The largest quantities of *T. sachalinensis* and *P. lacteal* in the epipelagic zone were recorded in cold seasons.

Because of the extended period of asexual reproduction and that fact that several generations probably exist at least in some of the species during the year [17, 12, 37], a significant portion of the medusae do not reach sexual maturity by the fall and early winter and travel to deeper layers in order to winter. In the Sea of Okhotsk, this was clearly seen as an increase in the abundance of jellyfish (*C. capillata, Chrysaora* spp., *A. limbata, P. camtschatica*) in the mesopelagic layer in

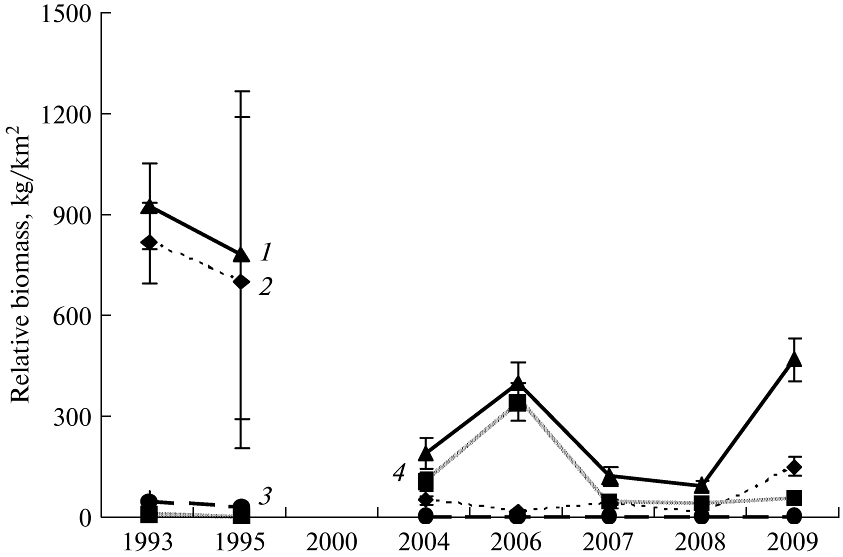


**Fig. 7.** Year-to-year dynamics of the jellyfish relative biomass (kg/km$^2$) in the epipelagic layer of Pacific waters off the Kuril Islands and East Kamchatka in the summer: *1*, all jellyfishes; *2*, *Chrysaora* spp.; *3*, *Cyanea capillata*; *4*, *Aequorea* spp. Vertical lines are the standard errors.

cold seasons [6]. The existence of wintering jellyfish was proven with yearly catches of large (up to 50 cm) individuals, sometimes in large quantities, in the epipelagic layer of the Sea of Okhotsk during spring surveys conducted by the TINRO Center.

A detailed analysis of the seasonal variations in the abundance and size structure of jellyfish from June until October was performed for the western Bering Sea [7]. The biomass of most species, except for *Chrysaora melanaster*, was shown to grow from the summer to the fall. The mean size of jellyfish also increased; however, large quantities of small medusae, which would probably spawn the following year, were observed along with large ones during the entire period of studies, including fall. The same was typical for fall surveys in the Sea of Okhotsk, where jellyfish with the diameter of several centimeters to over half a meter was observed from September to November [11].

### *Factors that Determine Jellyfish Biomass*

Strong year-to-year variations in biomass are typical for jellyfish due to their short lifecycle and the alternation between generations with two types of breeding in most of the mass species, viz., sexual and asexual, in which success depends on different environmental conditions. In the eastern Bering Sea, the jellyfish biomass grew by 100 times from 1975 to 2000 and drastically fell after 2000 [23]. In the waters of the Benguela Current off the southwestern coast of Africa, which was previously known for high fish productivity, a rapid increase in jellyfish quantity has occurred in recent years. Formerly, the biomass of large jellyfish there was lower as compared to that of fish, and for the past decade the jellyfish biomass has exceeded that of fish by three to four times and reached about 12 million tons [31]. Regular blooms of gelatinous zooplankton have been observed off the coast of Japan [30, 47]. In the Sea of Okhotsk and Bering Sea, the jellyfish biomass also varied greatly from year to year [7, 9, 10].

Taking the serious consequences of blooms in jellyfish abundance for fishery, industry, and tourism into account, revealing the key factors that account for its dynamics can be considered to be an important field in the modern studies of jellyfish. The influence of climate on gelatinous zooplankton is studied most actively. The dependence between jellyfish abundance and various climatic indices that characterize climatic trends at the levels of the globe, hemisphere, and regions, has been described in many works [23, 24, 26, 32, 36, 39], and conclusions about the probable dynamics in communities of gelatinous zooplankton were made on forecasted climatic variations [23, 32].

The correlation analysis of jellyfish abundance in the Sea of Okhotsk, western Bering Sea, and NWPO, based on our data, and several primary climatic indices, characterizing climatic conditions in the Northern Pacific Ocean (PDO, NPI, SAI, SI, AI)[1], did not reveal any steady links between these parameters. Significant correlations ($p < 0.05$) between the biomass of predominant jellyfish species and climatic indices were found in only 10% of the cases and they were manifested most frequently in *C. capillata* in the Bering Sea and NWPO (Table 5).

The analysis of the relationships between jellyfish abundance in the Sea of Okhotsk and Bering Sea and

[1] According to data by NOAA, USA. http://www.beringclimate.noaa.gov.

**Table 5.** Pearson's coefficients of correlation between climate indices and jellyfish biomass in the Bering Sea and Sea of Okhotsk in the fall and in the NWPO in the summer

| Species | | Climatic indices | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | PDOw | PDOs | PDOa | NPI | SAI | SI | AI |
| Northwestern Bering Sea | | | | | | | | |
| All jellyfishes | r | 0.24 > | –0.11 > | 0.18 > | –0.73 | –0.40 > | –0.09 > | 0.60 > |
| | *p* | *0.10* | *0.10* | *0.10* | *0.07* | *0.10* | *0.10* | *0.10* |
| *Chrysaora* spp. | r | –0.44 > | –0.44 > | –0.29 > | –0.08 > | 0.24 > | 0.37 > | –0.03 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *C. capillata* | r | **0.72** | 0.02 > | 0.24 > | –0.72 | –0.70 | –0.42 > | **0.78** |
| | *p* | ***0.03*** | *0.10* | *0.10* | *0.07* | *0.06* | *0.10* | ***0.02*** |
| *Aequorea* spp. | r | 0.63 | 0.63 | **0.75** | –0.46 > | –0.52 > | –0.48 > | 0.40 > |
| | *p* | *0.07* | *0.07* | **0.02** | *0.10* | *0.1* | *0.10* | *0.10* |
| *N* | | 9 | 9 | 9 | 7 | 8 | 8 | 8 |
| Southwestern Bering Sea | | | | | | | | |
| All jellyfishes | r | 0.19 > | 0.05 > | 0.10 > | 0.48 > | –0.03 > | –0.03 > | 0.01 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *Chrysaora* spp. | r | 0.19 > | 0.16 > | 0.33 > | 0.28 > | –0.40 > | –0.23 > | 0.39 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *C. capillata* | r | 0.17 > | –0.08 > | 0.01 > | 0.23 > | 0.44 > | **0.69** | 0.06 > |
| | *p* | *0.10* | *0.10* | *0.10* | *0.0* | *0.10* | ***0.04*** | *0.10* |
| *Aequorea* spp. | r | 0.15 > | 0.04 > | 0.01 > | 0.45 > | 0.00 > | –0.12 > | –0.12 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *N* | | 10 | 10 | 10 | 8 | 9 | 9 | 9 |
| Northern Sea of Okhotsk | | | | | | | | |
| All jellyfishes | r | –0.06 > | –0.13 > | –0.26 > | 0.21 > | –0.10 > | –0.21 > | –0.03 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *Chrysaora* spp. | r | –0.41 > | –0.40 > | –0.57 | 0.24 > | 0.37 > | 0.08 > | –0.46 > |
| | *p* | *0.10* | *0.10* | *0.05* | *0.10* | *0.10* | *0.10* | *0.10* |
| *C. capillata* | r | 0.34 > | 0.25 > | 0.18 > | 0.01 > | –0.49 > | –0.33 > | 0.41 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *Aequorea* spp. | r | –0.12 > | –0.31 > | –0.27 > | –0.07 > | 0.33 > | 0.22 > | –0.28 > |
| | *p* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* | *0.1* |
| *N* | | 12 | 12 | 12 | 10 | 11 | 11 | 11 |
| *Pacific Northwest* | | | | | | | | |
| All jellyfishes | r | –0.01 > | **0.78** | **0.76** | – | –0.57 > | 0.19 > | **0.92** |
| | *p* | *0.10* | ***0.04*** | ***0.05*** | – | *0.10* | *0.10* | ***0.01*** |
| *Chrysaora* spp. | r | –0.06 > | **0.79** | **0.76** | – | –0.63 > | 0.04 > | **0.84** |
| | *p* | *0.10* | ***0.04*** | ***0.05*** | – | *0.10* | *0.10* | ***0.04*** |
| *C. capillata* | r | 0.06 > | **0.81** | **0.78** | – | –0.67 > | –0.03 > | **0.83** |
| | *p* | *0.10* | ***0.03*** | ***0.04*** | – | *0.10* | *0.10* | ***0.04*** |
| *Aequorea* spp. | r | 0.58 > | –0.17 > | –0.04 > | – | 0.39 > | 0.40 > | –0.13 > |
| | *p* | *0.1* | *0.1* | *0.1* | – | *0.1* | *0.1* | *0.1* |
| *N* | | 7 | 7 | 7 | | 6 | 6 | 6 |

Note: r is the correlation coefficient; p is the significance level; *N* is the number of years. Correlation coefficients with the significance level of up to 0.05 are highlighted in bold, and those from 0.05 to 0.10 are underlined. PDOw, PDOs, and PDOa are the mean winter, mean summer and mean annual PDO indices, respectively.

mean ice condition in the winter [15] as an integral characteristic of thermal water conditions showed a weak and moderate negative dependence between these two parameters in most cases. High and significant negative correlation coefficients were noted only twice in the northern Bering Sea, viz., for *C. capillata* and *Aequorea* spp. These data showed that among the three predominant jellyfish species, *C. capillata* was influenced by climatic conditions probably most of all, as reproduction in this species was connected to shelf waters, which are more subjected to climatic changes.

A distinct effect of climate on jellyfish abundance is thought to become evident during climatic shifts, i.e., abrupt changes in conditions [23–25, 34, 39]. According to our data, this was observed in the Sea of Okhotsk in the late 1990s and early 2000s. A drastic decline in the biomass of all jellyfish species (see Fig. 5a) occurred after the abnormally cold period of 1998–2001 [3]. However, the mechanism of influences like these remains unknown. It is still unclear whether it's a result of the direct impact on the efficiency of breeding and growth in jellyfish, or if there is a mediated effect through the forage base, competitors, or predators. An analysis of the data on the forage base of jellyfish showed that no significant relationships between the dynamics in its biomass and variations in the quantities of meso- and meroplankton (according to A.F. Volkov [1] and survey reports) were found in Far Eastern seas. This is quite explicable, because the level of abundance of adult medusae that are found in trawl catches is probably determined earlier, viz., at the of polyp or ephyra phases [23, 29], and has very weak links to the amount of food that is available at the time of their catches.

In his review, which analyzed about two dozen works on gelatinous zooplankton, Purcell [39] showed that the abundance of most jellyfish species in temperate latitudes depended on temperature conditions. At relatively higher temperatures, population size and rates of sexual and asexual reproduction grow. In northern areas of the Sea of Okhotsk and Bering Sea, with their typically harsh climatic conditions, the effect of a decrease in jellyfish survivability and growth at lower temperatures is probably significant. At the same time, opposite examples were recorded. In the eastern Bering Sea, the biomass of the locally predominant species *C. melanaster* was at a low level in warm years (1980–1989 and 2001–2005) and grew during the period when temperatures were closer to average ones (1990–2000) [23]. It should be added that, according to NOAA (http://access.afsc.noaa.gov), the trend towards growing jellyfish abundance arose due to the arrival of the next cold period.

In addition to thermal conditions, water salinity may also exert an influence on jellyfish abundance. However, this factor plays a notable role only in marine areas exposed to significant desalination [39]. Also the dependence of the abundance of polyps and medusae produced by them on the level of dissolved oxygen was noted [28, 29, 46]. In the recent decades, the role of anthropogenic impact, including eutrophication [18, 43, 48], introduction of new species [27, 34, 45, 49], and fishery [31, 38], has grown considerably. In Far Eastern seas, only the latter factor may have any considerable, either direct or indirect, effect on the abundance of jellyfish.

It should be added that analysis of the factors that affect jellyfish abundance, could probably be more reasonable if studies covered more restricted areas rather than vast ones, like those described in the article. Due to the principle of provincialism, oceanological, foraging, and other conditions in different parts of large water bodies vary non-simultaneously, with some time lag, and even can become antiphased, which was repeatedly observed in Far Eastern Seas [16]. Obviously, this may affect the estimates of the relationships between dynamics in outer conditions and jellyfish abundance. The areas were not divided into smaller ones in this work because it was aimed at determining the overall jellyfish abundance in Far Eastern seas. Thus, this is a topic for following and more narrowly specified studies.

### *Appraisal of the Overall Jellyfish Biomass in Far Eastern Seas*

The data on the values of jellyfish biomass in various pelagic layers of the Far Eastern seas and its seasonal and annual variability that have been obtained by the present time, allow one to estimate the total biomass of jellyfish. In the pelagic zone of the western Bering Sea, the overall biomass of large medusae in the fall of 2004 was as large as 5 million tons [5]. About 50% of this amount was located in the upper epipelagic layer and about 70% of the overall biomass was in the entire epipelagic zone. Taking into account the low biomass of *C. melanaster*, one of the predominant species, in the Bering Sea in 2004 and the underestimation of jellyfish in the coastal 12-mile zone, the overall jellyfish biomass in the pelagic layer of Russian waters of the Bering Sea may come to 6 million tons.

According to estimates of jellyfish in the Sea of Okhotsk [9, 11], its biomass in the epipelagic zone of the northern part of the sea reached 3 million t; in the upper epipelagic zone of the southern part it was 1 million t. Taking the vertical distribution of jellyfish and the strip of coastal waters that were omitted from surveys into account, the overall biomass of jellyfish in the pelagic zone of the Sea of Okhotsk in the years of its high abundance could be 5.5 to 6.0 million t.

According to the data of trawl catches in the upper epipelagic zone of NWPO in the 2000s that were performed in waters off the Kuril Islands, the maximum estimated values of jellyfish biomass were 0.4 million t. Taking waters of the Kamchatka and Commander Islands area into account, which were not covered by studies, the vertical distribution of jellyfish in the water column, as well as the fact that the surveys were conducted in the early summer when medusae were relatively scarce there, the overall jellyfish biomass could reach 2 million t.

In the Sea of Japan, the only large-scale survey that also recorded jellyfish was conducted in the late fall of 2003. By that time, most of the jellyfish had already completed spawning and died; consequently, the recorded biomass was only 0.02 million t [11]. Considering that here the jellyfish biomass had the lowest values as compared to other studied areas (see Fig. 3a), and was high enough in the southern part of the sea in the summer, we can suppose that the overall jellyfish biomass in the Russian waters of the Sea of Japan does not exceed 0.2–0.5 million t.

Thus, based on the estimations above, the overall biomass of large jellyfish in the pelagic zone of the Russian waters of Far Eastern seas may reach 13–15 million tons.

## CONCLUSIONS

The major portion of the biomass of large jellyfish in the Sea of Okhotsk, western Bering Sea, and NWPO consists of *Chrysaora* spp., *C. capillata, Aequorea* spp., *P. camtschatica*, and *A. limbata*. Together they constitute from 96% to nearly 100% of the total. The same species, along with *C. nematophora*, predominate in abundance in the Bering Sea and NWPO, while *P. lactea, C. capillata* and *Chrysaora* spp. are most abundant in the Sea of Okhotsk. In the northwestern Sea of Japan, *A. aurita, C. capillata*, and species of the genus *Aequorea* prevail in abundance and biomass.

The estimates of biomass and abundance of jellyfish presented above reveal the generalized pattern of variations in its quantities during the year and also give some idea about the role that this group of aquatic organisms plays in marine ecosystems in various seasons. Generally, jellyfish reach the highest biomass in the summer and fall and drops abruptly in the winter. At the same time, seasonal dynamics in every particular jellyfish species have specific features, which are manifested in reaching maximum values in different periods of the warm season, but some of these species also demonstrate a reverse pattern of seasonal variations, with the highest abundance in cold seasons (like *T. sachalinensis* and *P. lacteal*). The occurrence of significant quantities of large scyphomedusae and hydromedusae in catches in the spring indicates that a portion of them travel to lower areas to spend the winter in deeper layers.

Jellyfish abundance varies strongly from year to year, which is related to their short lifecycle and alternation between sexual and asexual generations, in which the breeding success is conditioned by environmental factors. In the fall season, the range of year-to-year fluctuations in jellyfish biomass can increase tenfold. In 1991–2009, it varied from 200 to 2000 kg/km$^2$ in the northern Sea of Okhotsk, from 500 to 4200 kg/km$^2$ in the northwestern Bering Sea, and from 300 to 3700 kg/km$^2$ in the southwestern part of the sea.

Judging by the available estimates of the abundance of jellyfish and taking into account its vertical distribution and seasonal dynamics, the overall biomass of large species of Scyphozoa and Hydrozoa, which occur in trawl catches, may reach 13–15 million tons in Far Eastern seas and adjacent Pacific waters in the warm season. The largest portion of jellyfish is concentrated in the western Bering Sea (up to 6.0 million t in periods of high abundance) and the Sea of Okhotsk (up to 5.5–6.0 million t). In the Russian waters of the Sea of Japan, the total jellyfish biomass is the lowest and probably does not exceed 0.5 million t.

Thus, in this series of reports, which are based upon a large databank that was collected by the TINRO Center during almost 20 years of surveys and covered a vast water area of about 7 million km$^2$, the species composition and spreading were studied [4], vertical distribution and migrations analyzed [5], and the biomass and abundance of large scyphomedusae and hydromedusae were estimated in the Far Eastern seas of Russia and the Northwestern Pacific Ocean.

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