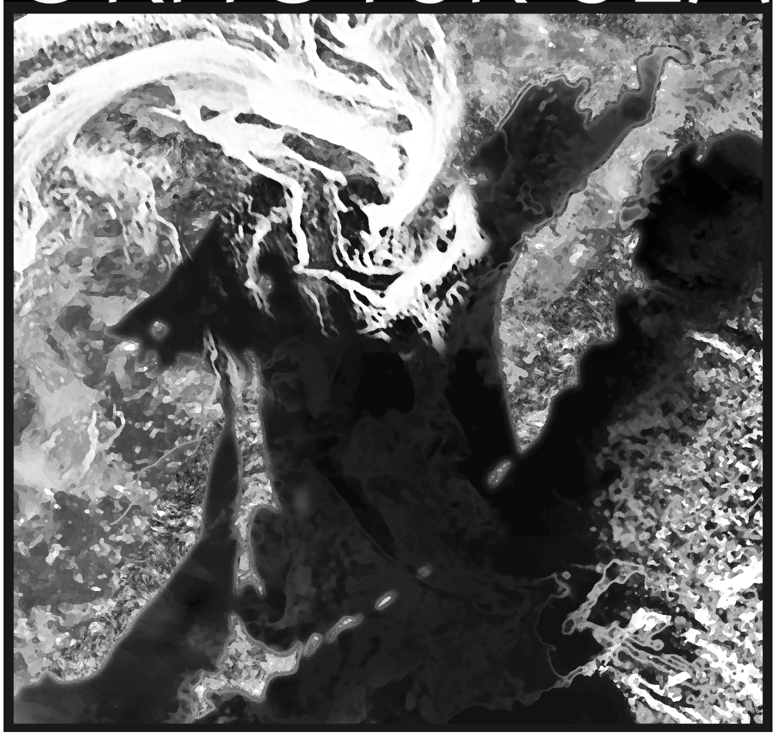
ZOOPLANKTON of the OKHOTSK SEA



A Review of Russian Studies

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Contents

About the Authors

A.J. Paul has been involved in marine biological and biological oceanographic investigations in the North Pacific since 1972. He has been employed both as research staff and faculty of the University of Alaska Institute of Marine Science during that period. In conjunction with colleagues he has authored 102 peer reviewed journal papers and numerous technical reports dealing with a variety of planktonic and benthic organisms.

Alexei Pinchuk is currently a visiting scientist at the University of Alaska Fairbanks. Pinchuk worked on arctic and North Pacific zooplankton research for more than 10 years at the Institute of Biological Problems of the North in Magadan, Russia, and at the Zoological Institute of the Russian Academy of Sciences in St. Petersburg. He has published several papers on zooplankton ecology and biology.

Abstract

The major Russian reports addressing Okhotsk Sea zooplankton published from 1940 to 1999 are reviewed. Topics include a summary of the history of zooplankton research, species composition, zoogeographic zonation, vertical and geographic distribution, abundance and biomass, seasonal and interannual dynamics, and response of plankton communities to global weather change patterns. Distributional maps are presented and summary data on abundance and biomass are tabulated.

Introduction

The Okhotsk Sea supports important fisheries, and its zooplankton and other bioresources have been studied extensively over the last 60 years. Since most of the Okhotsk Sea falls within the Russian Economic Zone (Fig. 1) a great deal of information accumulated is in Russian language reports or data files that are not accessible to most researchers.

To make this information more accessible we reviewed much of the Russian language literature on Okhotsk Sea zooplankton produced during the last 60 years. Zooplankton reports compiled by the Institute of Oceanology, Russian Academy of Sciences (RAN), in Moscow; the Zoological Institute (RAN) in St. Petersburg; the Pacific Research Institute of Fisheries and Oceanography (TINRO) in Vladivostok and its branches in Magadan, Petropavlovsk-Kamchatskiy, and Yuzhno-Sakhalinsk (now Sakhalin Research Institute of Fisheries and Oceanography [SakhNIRO]); and the Russian Academy of Sciences of the Far-East (DVO RAN) have been reviewed to provide an overview of the plankton throughout the Okhotsk Sea. Also, original data collected by author Pinchuk on neritic zooplankton of the northern Okhotsk Sea has been included.

This report is a broad review of zooplankton biology. Most of the previous research on Okhotsk Sea zooplankton has dealt with species and community composition, and spatial, vertical, or seasonal distribution relative to water masses and current patterns. In this publication all geographic and oceanographic names are used in accordance with PICES nomenclature (Nagata and Lobanov 1998).

History of Research

The first data on Okhotsk Sea plankton appeared in Marukawa (1921). A systematic zooplankton survey was later undertaken by the collaborative expedition of TINRO (formerly TIRKh, Vladivostok) and the State Hydrological Institute (GGI, Moscow) on the vessels *Gagara*, *Ara,* and *Plastun* (1930-1933). The detailed results of that survey were never published. However, the specimens were used to produce the first taxonomic key for the calanoids of the far-eastern seas and the polar basin (Brodskiy 1950). Zooplankton samples from the Shantar Islands region were collected by TINRO aboard the vessel *Lebed* in 1935. That data along with 1937 information gathered by TINRO along the western coast of the Kamchatka Peninsula was published by Kusmorskaya (1940).

After World War II Kun (1951) published data on zooplankton distribution (109 samples) and herring diet (127 stomachs) collected in August-September 1949 between Cape Khanyangda and Tauyskaya Bay. In summer 1955, 1,285 plankton samples were collected in Shelikhov Bay, Tauyskaya Bay, and in the vicinity of St. Iona Island (Mikulich 1960).

More than 1,200 summer plankton samples were taken at various depths from the vessel *Vityaz* during 1949 to 1952. Sampling was done at 0-10, 10-25, 25-50, 50-100, 100-200, and 200-500 m depths but the neritic plankton was not sampled. These were the first collections suitable for examining the taxa composition and spatial distribution of phytoplankton and zooplankton on a large scale (Lubny-Gertsik 1959, Smirnova 1959). Also, calanoids, ostracods, and euphausiids were studied

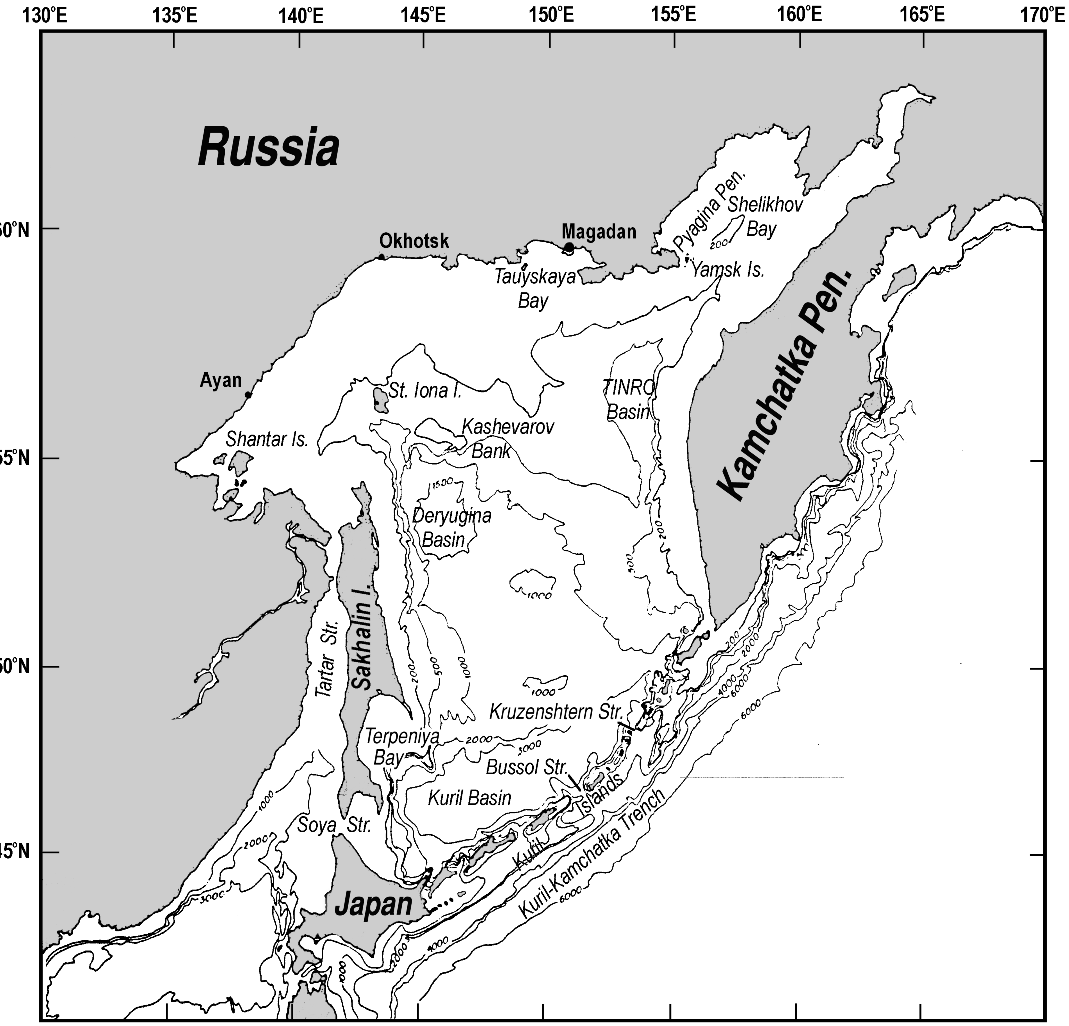

Figure 1. The Okhotsk Sea showing bathymetry (from Alfultis and Martin 1987, modified).

(Brodskiy 1957; Ponomareva 1957, 1959, 1963; Chavtur 1976) in more detail.

Since 1949 TINRO has studied the spring and summer prey populations of commercial fishes, sampling from the surface to 100-200 m depths, rarely to 500-1,000 m. More than 4,600 zooplankton samples were collected during 1949-1982 (Volkov and Chuchukalo 1985). Those studies resulted in a number of publications on biology of euphausiids which are an important fish prey (Zhuravlev 1976, 1977; Afanasiev 1981, 1982). In 1963 the Magadan Branch of TINRO started multiyear monitoring of herring populations in the northern Okhotsk Sea. That project produced a number of plankton papers (Kotlyar 1965, 1966, 1967, 1970; Kotlyar and Chernyavskiy 1970a, 1970b).

During the 1980s-1990s TINRO researchers sampled plankton and published the results in a series of papers and reviews (Gorbatenko 1990; Radchenko et al. 1997a, 1997b; Shuntov 1985; Shuntov and Dulepova 1993; Shuntov et al. 1993b, 1993c, 1998a, 1998b). The cruise reports from those expeditions are archived at TINRO (Vladivostok). During 1987-1996 SakhNIRO conducted zooplankton studies in the southwestern Okhotsk Sea and Tartar Strait (Bragina 1999). In addition, large bibliographies were published (Romanov 1959, Mileikovskiy 1970).

Following is a summary of published Russian information on Okhotsk Sea zooplankton taxonomy, taxa composition, horizontal and vertical distribution, abundance, and wet weight biomass.

Methodological and Taxonomic Clarification

Russian planktologists usually report net mesh size as a mesh number. A brief summary of this system from Kiselev (1969) was presented in Coyle et al. (1996). Most Russian plankton programs in the Okhotsk Sea from 1935 to 1982 used a 34-38 cm diameter Juday net with No. 38 (0.168 mm) mesh (Kusmorskaya 1940, Volkov and Chuchukalo 1985). The data reviewed in this compendium was collected with the above gear type unless otherwise stated.

The names applied to some of the common zooplankton taxa in this report may differ from those used in the original publications due to name changes and Russian application of specific designations. The following explanations clarify this potential confusion.

When zooplankton research began in the Okhotsk Sea, the only *Calanus* species recognized for arctic-boreal waters was *Calanus finmarchicus*. Later, *Calanus glacialis* was separated from *C. finmarchicus* as a sibling species distributed in the North Pacific (Yashnov 1955, 1957a, 1957b). Thus, *Calanus glacialis* was identified as *Calanus finmarchicus* in some earlier works on Okhotsk Sea zooplankton. Later, the genus *Calanus* was divided into *Neocalanus* and *Calanus* (Bradford and Jillett 1974) and the species *Calanus plumchrus* and *Calanus cristatus* were assigned to *Neocalanus*. Russian taxonomists did not generally recognize the distinction and have continued to refer to *plumchrus* and *cristatus* as species in the genus *Calanus*. Thus, *Neocalanus cristatus* and *N. plumchrus* are identical to *Calanus cristatus* and *C. plumchrus* in Russian literature.

Pseudocalanus species in the Russian literature have commonly been assigned to *Pseudocalanus elongatus* and *P. minutus*. Recent literature has often referred to species in this genus as *Pseudocalanus* spp. due to extremely minor differences between them and much uncertainty in species distinction. Frost (1989) described several new species of *Pseudocalanus* and redefined older species designations using biochemical evidence and very minor morphological distinctions. The specific designations used for *Pseudocalanus* in the Russian literature do not necessarily conform to the designations of Frost (1989).

Recent Russian literature has referred to *Sagitta elegans* as *Parasagitta elegans*, and *Centropages mcmurrichi* in the Russian literature is usually designated *Centropages abdominalis*.

Zoogeographic Zonation

According to Kun (1975), the Okhotsk Sea planktonic fauna included over 200 species. The species composition of the epipelagic layer has received the most attention. Little research has been done on the deep fauna, especially below 1,000 m. Based on taxonomic analysis of calanoid copepods, Brodskiy (1955a, 1955b, 1957) and Brodskiy et al. (1983) identified four major groups in the upper pelagic zone of the southern, central, northern (co-arctic), and eastern Sakhalin neritic regions of the Okhotsk Sea (Table 1). Each group had its primary and secondary species. The distribution of these species aggregates was related to hydrographic and seasonal conditions and the boundaries between groups have varied from year to year (Lubny-Gertsik 1959, Volkov and Chuchukalo 1985, Gorbatenko 1990).

The southern Okhotsk Sea faunal group (Table 1) occupied the surface layer to 200 m depth over the Kuril Basin. This region is influenced by water of the northern Sea of Japan and adjacent Pacific water. As a result its faunistic composition included the typical Okhotsk Sea species as well as warm-water *Paracalanus parvus* and subtropical *Candacia bipinnata*. The most remarkable feature of this group was large concentrations of the relatively warm-water North Pacific species *Calanus pacificus* (Brodskiy 1957).

The central Okhotsk Sea group (Table 1), or oceanic temperate cold-water group according to Lubny-Gertsik (1959) (Fig. 2), was common in the upper 200 m layer over the relatively deep central Okhotsk Sea. This group typically contained *Calanus plumchrus*, *C. cristatus*, *Metridia pacifica*, *Eucalanus bungii*, *Pseudocalanus minutus*, and *Parathemisto japonica* as the dominant species.

The northern Okhotsk Sea faunal group (Table 1), or oceanic cold-water group according to Lubny-Gertsik (1959), occurred over the northern and western shelf. It was characterized by partial or total absence of the common warm-water species, especially in winter. The dominant species in the northern Okhotsk Sea group included *Pseudocalanus minutus*, *Calanus glacialis*, *Metridia ochotensis*, and *Parathemisto libellula*. Brodskiy (1957) named it the co-arctic group because of the presence of arctic species such as *Calanus glacialis* and *Jaschnovia tolli* (Brodskiy 1957). Similar groups have been observed in the northern Sea of Japan and Bering Sea by Brodskiy (1957) and Brodskiy et al. (1983) and they probably were connected with arctic faunal groups in the past (Brodskiy et al. 1983).

Table 1. Species composition of faunistic groups of pelagic calanoid copepods in the upper layers of the Okhotsk Sea.

Frequency at the stations	Species	Percent of total population density	Frequency at the stations	Species	Percent of total population density
Southern Okhotsk Sea Group			Northern Okhotsk Sea (co-arctic) Group		
100	*Pseudocalanus minutus*	59.0	100	*Calanus glacialis*	2.5
	Calanus pacificus	20.03		*Pseudocalanus minutus*	65.0
	Metridia pacifica	11.2		*Calanus plumchrus*	<1
	Eucalanus bungii	1.62	75	*Metridia ochotensis*	11.1
75	*Calanus plumchrus*	2.3		*Acartia longiremis*	17.0
50	*Metridia ochotensis*	<1	50	*Metridia pacifica*	2.6
	Calanus cristatus	<1		*Eucalanus bungii*	<1
	Acartia longiremis	<1		*Bradyidius pacificus*	<1
	Acartia clausi	4.1		*Eurytemora pacifica*	<1
	Scolecithricella minor	<1	25	*Jaschnovia tolli*	<1
25	*Pareuchaeta japonica*	<1		*Acartia clausi*	<1
	Centropages abdominalis	<1		*Eurytemora americana*	<1
	Clausocalanus arcuicornis	<1		*Microcalanus pygmaeus*	<1
	Microcalanus pygmaeus	<1		*Acartia bifilosa*	<1
	Candacia columbiae	<1		*Centropages abdominalis*	<1
		100		*Scolecithricella minor*	<1
					100
Neritic (eastern Sakhalin) Group			Central Okhotsk Sea Group		
100	*Pseudocalanus minutus*	98	100	*Pseudocalanus minutus*	88.5
	Epilabidocera amphitrites	<1	75	*Metridia pacifica*	3.5
	Acartia longiremis	<1		*Calanus plumchrus*	2.2
75	*Centropages abdominalis*	<1		*Metridia ochotensis*	4.55
	Calanus glacialis	<1	50	*Eucalanus bungii*	<1
	Tortanus discaudatus	<1		*Calanus cristatus*	<1
50	*Metridia ochotensis*	<1		*Acartia longiremis*	1.02
	Eurytemora pacifica	<1	25	*Pareuchaeta japonica*	<1
	Calanus plumchrus	<1		*Microcalanus pygmaeus*	<1
25	*Acartia clausi*	<1		*Scolecithricella minor*	<1
	Eucalanus bungii	<1		*Neocalanus lighti*	<1
	Scolecithricella minor	<1			100
		100			

Brodskiy et al. 1983.

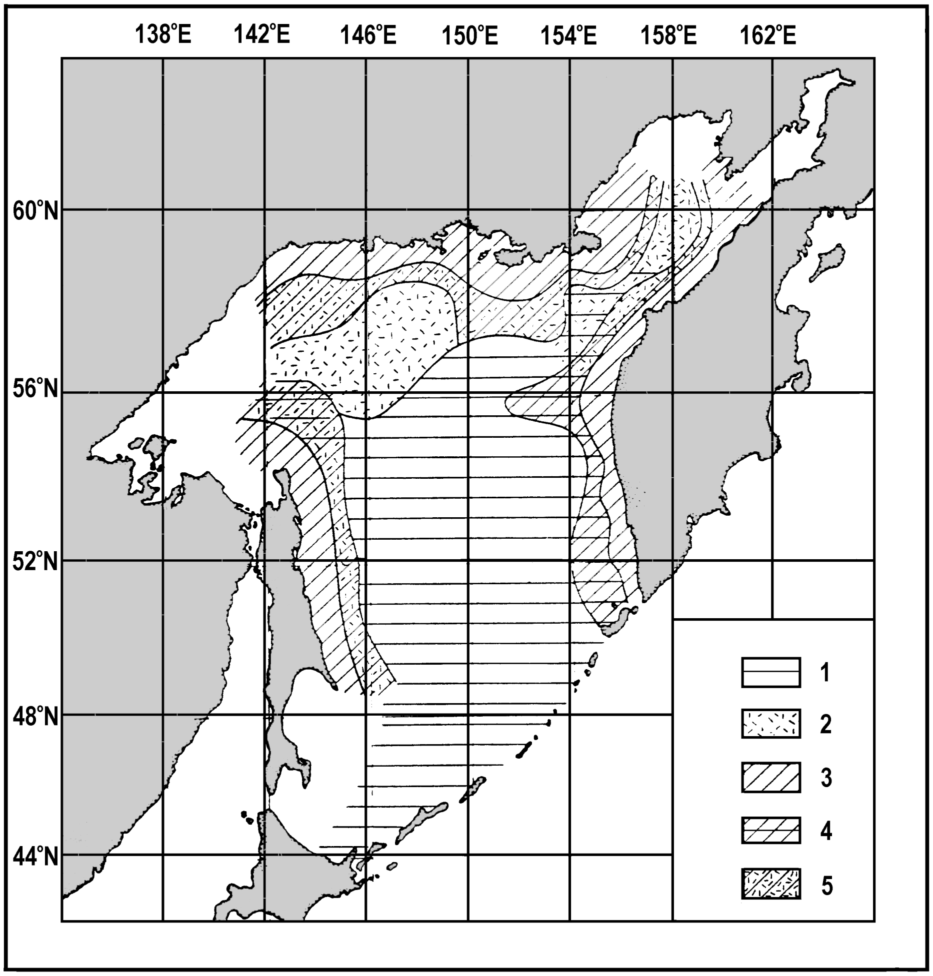

Figure 2. Faunistic groups of zooplankton in the Okhotsk Sea in summer based on samples collected from 1949 to 1952. Zone 1 is the oceanic temperate cold-water group, 2 is oceanic cold-water group, 3 is neritic group, 4 and 5 are transitional zones (from Lubny-Gertsik 1959).

The neritic group, originally described for the eastern Sakhalin region (Brodskiy 1957), occupied the coastal waters in the western, eastern, and northern Okhotsk Sea (Lubny-Gertsik 1959, Volkov and Chuchukalo 1985, Gorbatenko 1990, Pinchuk 1992). The cold coastal water supported species like *Acartia longiremis*, *Centropages abdominalis*, *Tortanus discaudatus*, *Eurytemora hirundoides*, *Podon leuckarti*, *Mysis oculata*, and various polychaetes, echinoderms, decapods, barnacles, and mollusk larvae.

The deepwater calanoid fauna was similar to that of the North Pacific. It was less diverse (35 versus 115 species) with a few endemic species like *Xanthocalanus kurilensis* and *Undinella* spp. (Brodskiy et al. 1983).

Transitional zones with a mixture of species occurred at the boundaries between species groups, indicating mixing. Such transitional regions were commonly observed in the Okhotsk Sea (Lubny-Gertsik 1959, Volkov and Chuchukalo 1985, Gorbatenko 1990).

Vertical Distribution

Reports on vertical zooplankton distribution in the Okhotsk Sea are scarce. Some authors mapped the biomass in the 0-50 and 50-100 m layers (Mikulich 1960, Kotlyar 1970, and others), while a more detailed description was presented by Lubny-Gertsik (1959) and Kotlyar and Chernyavskiy (1970b).

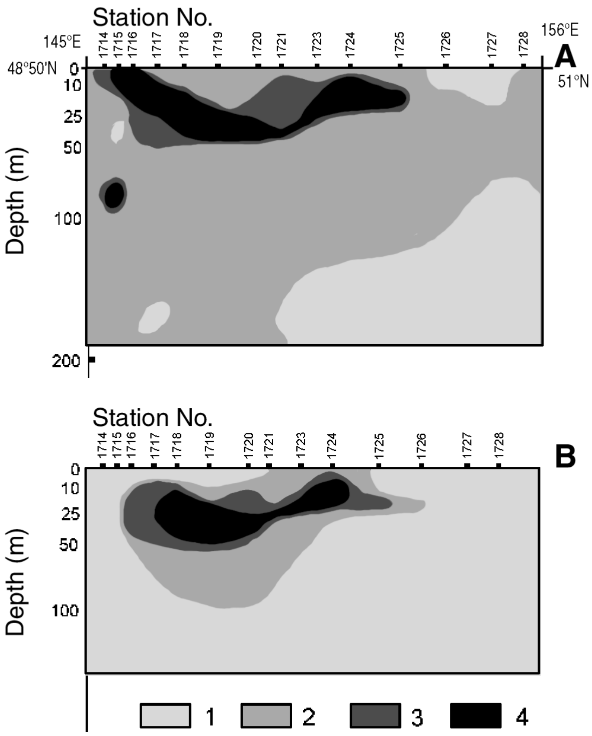

Figure 3. Vertical zooplankton biomass (mg m⁻³) distribution on the profile between Cape Terpeniya (southern Sakhalin) and Kambalnyi Bay (southern Kamchatka) in the upper 0-200 m layer, mesh = 0.168. A = general zooplankton biomass, B = Calanus plumchrus biomass. 1 = <100, 2 = 100-500, 3 = 500-1,000, 4 = >1,000 (from Lubny-Gertsik 1959).

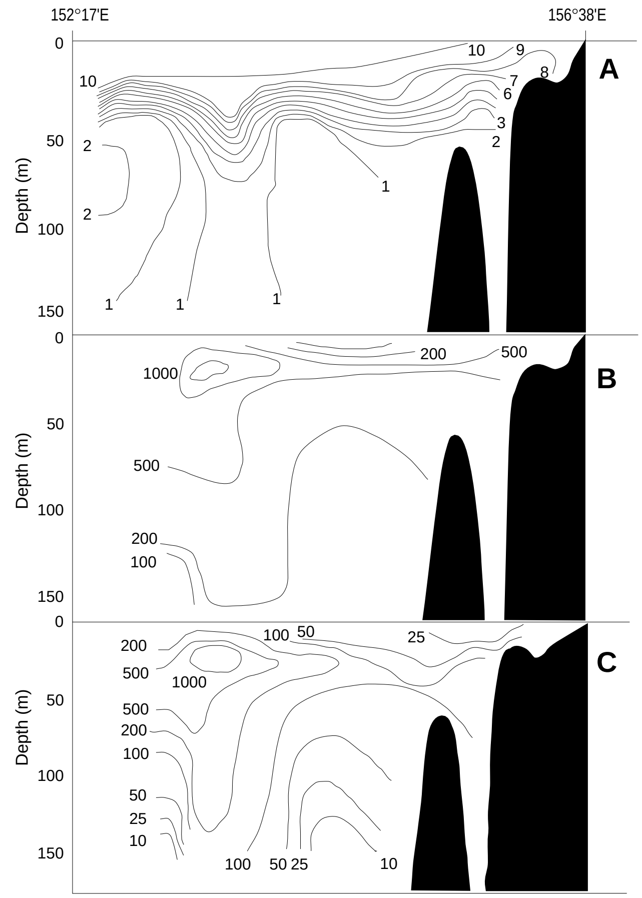

Figure 4. A = vertical distribution of temperature in summer, B = total zooplankton biomass, and C = Calanus plumchrus biomass (mg m⁻³) on the profile along 50°53′ N, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).

The Okhotsk Sea has a subarctic vertical water mass structure (Dobrovolskiy 1962; Moroshkin 1964, 1966) and is formed under the influence of the Pacific water advection, fall-winter cooling, river runoff, water mixing in the regions of intensive dynamics, solar radiation, and the system of currents (Leonov 1960; Luchin 1995, 1996). There are four different water masses in the Okhotsk Sea: the surface layer, the cold intermediate layer, the deep Pacific water mass, and the near-bottom water mass of the Kuril Basin (Leonov 1960, Luchin 1996). The warmer surface layer forms as a result of summer heating and it is distinguishable only during the warm period (Leonov 1960; Moroshkin 1964, 1966; Luchin 1996). The cold intermediate layer with temperatures of –1.7°C first distinguished by Makarov (1884) forms by winter cooling and usually occurs during summer at 50-200 m depth, but currents can result in vertical mixing (Chernyavskiy 1981, Luchin 1996). The cold intermediate layer is also characteristic of the Bering Sea (Leonov 1960). In years of intensive advection of warmer Pacific water by the Western Kamchatka Current into the Okhotsk Sea, the cold layer can be destroyed (Vinokurova 1965), changing the vertical distribution of zooplankton (Kotlyar and Chernyavskiy 1970b).

Between southern Sakhalin Island and the southern tip of the Kamchatka Peninsula *Calanus plumchrus* dominated in dense zooplankton aggregations in the upper 50 m (Fig. 3). Only near the Sakhalin coast was this species replaced by smaller *Pseudocalanus elongatus* and *Oithona similis* with a biomass up to 1,000 mg m⁻³ (Lubny-Gertsik 1959).

A maximum zooplankton biomass of 500-2,000 mg m⁻³ has been observed during summers over the Kamchatka Shelf in areas where oceanic water

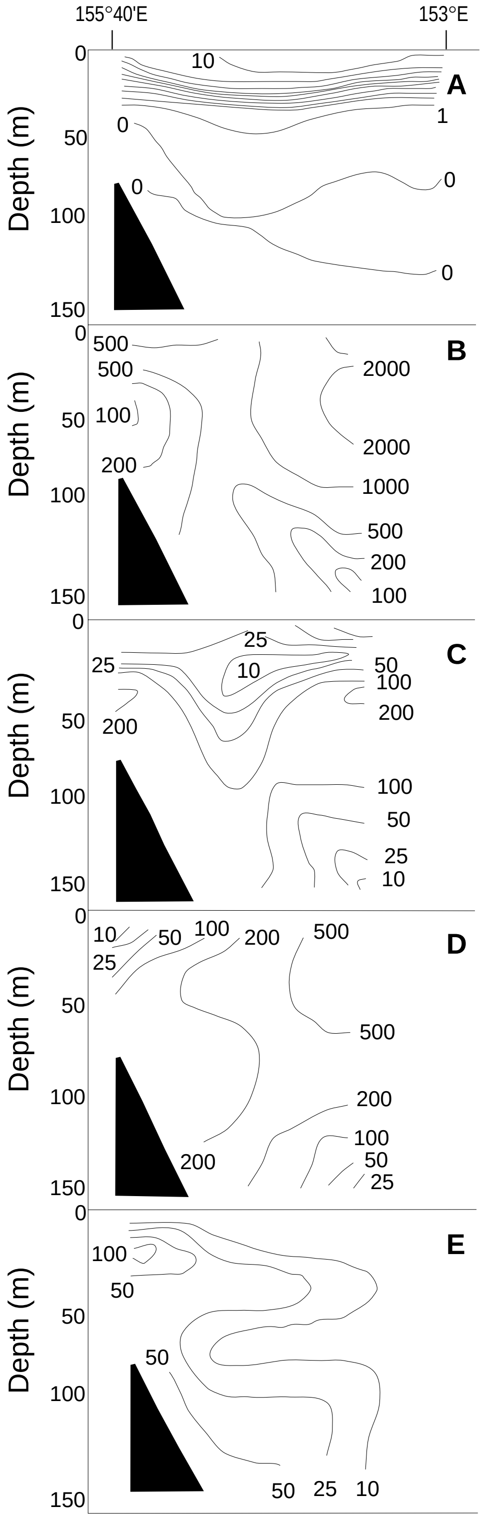

Figure 5. *A = vertical distribution of water temperature, B = total zooplankton biomass, C = Metridia ochotensis biomass, D = Calanus plumchrus biomass, and E = Eucalanus bungii biomass (mg m*$^{-3}$*) on the profile along 54°19′ N in summer 1965, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).*

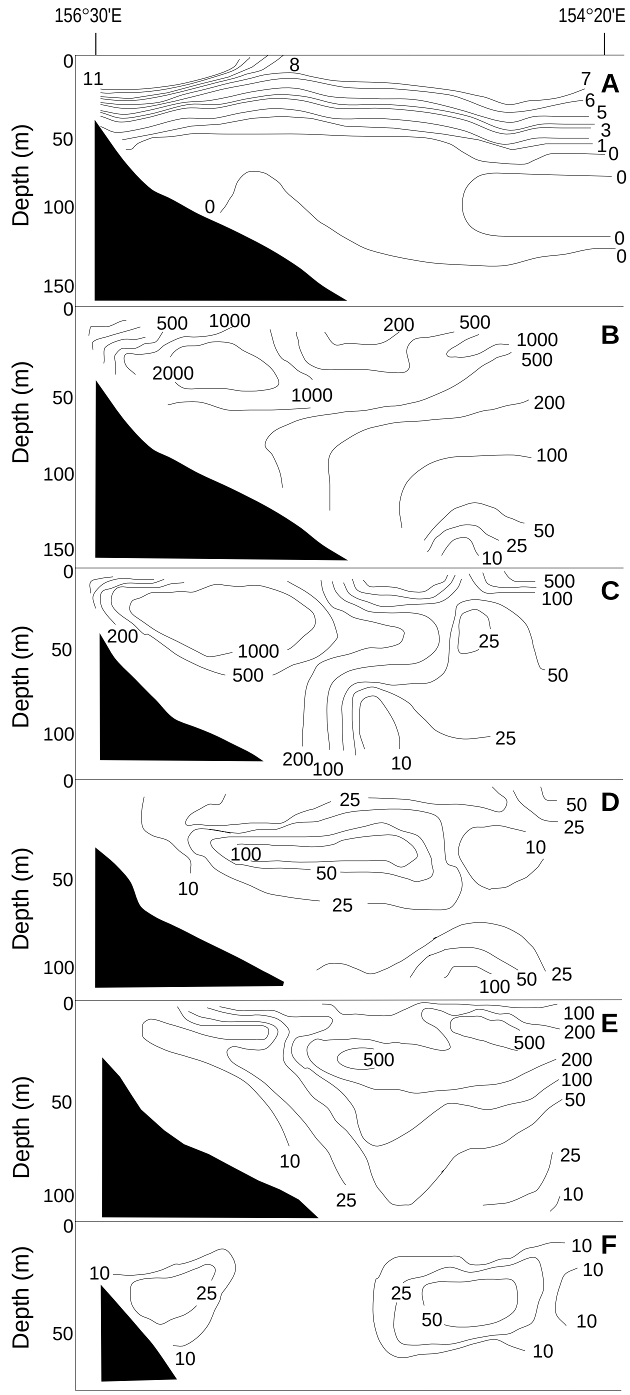

Figure 6. *A = vertical distribution of water temperature, B = total zooplankton biomass, C = Calanus glacialis biomass, D = Metridia ochotensis biomass, E = Calanus plumchrus biomass, and F = Eucalanus bungii biomass (mg m*$^{-3}$*) on the profile along 57°16′ N in summer 1967, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).*

penetrated into the southeastern Okhotsk Sea (Kotlyar and Chernyavskiy 1970b). While zooplankton generally was abundant in the upper 50 m layer, dense patches have often been found in deeper layers (Fig. 4) where Pacific water entered the Okhotsk Sea. This inflow resulted in intensive eddies and disrupted the vertical water column structure causing downwelling. *Calanus plumchrus* dominated the zooplankton in both 0-50 m and 50-100 m layers (Kotlyar and Chernyavskiy 1970b).

Northward between 53° and 53°30′ N the Western Kamchatka Current typically deflects off the Kamchatka coast (Moroshkin 1966). A strong summer thermocline was formed at 15-35 m depth in the region (Kotlyar and Chernyavskiy 1970b). Zooplankton concentrated beneath the thermocline and had a maximum biomass of about 1,000-2,800 mg m^{-3} (Fig. 5) in the upper 50 m. In the deeper layers zooplankton biomass decreased to 100-150 mg m^{-3}. In warmer years *Calanus plumchrus* dominated the community, while in colder years *C. glacialis* prevailed (Kotlyar and Chernyavskiy 1970b).

The area north of 54°N is characterized by a large anticyclonic gyre over the TINRO Basin (Moroshkin 1964) which transforms the vertical structure of water masses. The deep branch of the Western Kamchatka Current was upwelled onto the shelf and into the surface layer, where it mixed with lower salinity shelf water (Kotlyar and Chernyavskiy 1970b). Over the shelf, dense zooplankton aggregations occurred above and below the strong thermocline (Fig. 6). In the open sea the thermocline was weaker, but zooplankton was abundant in the upper 50 m layer (Kotlyar and Chernyavskiy 1970b). *Calanus glacialis* dominated over the shelf in the 10-25 m layer (2,000- 5,000 mg m^{-3}) and was common in the 25-50 m layer, while in the cold layer (50 to 200 m depth) its biomass decreased to 10-25 mg m^{-3} (Fig. 6). *Metridia ochotensis* occurred over the whole area at different depths because it undergoes strong diel vertical migrations (Vinogradov 1954) while *Calanus plumchrus* and *Eucalanus bungii* concentrated near the bottom edge of the thermocline (Fig. 6).

The upper 30 m layer in the northern Okhotsk Sea warms to 11-14°C in summer (Kotlyar and Chernyavskiy 1970b). However, temperatures below the thermocline are about –1.7°C and water at that depth is influenced by weak currents and strong vertical stability (Moroshkin 1966). The zooplankton community in this area was dominated by *Calanus glacialis* and *Metridia ochotensis* which were concentrated in the upper 25 m near the thermocline (1,000-5,000 mg m^{-3}) (Figs. 7, 8). The zooplankton biomass declined from 100-200 mg m^{-3} at 30-50 m depth to 10-25 mg m^{-3} in deeper layers (Figs. 7, 8). The oceanic zooplankton was transported into the area by currents from the central Okhotsk Sea, especially during warm years (Fig. 7E) (Kotlyar and Chernyavskiy 1970b).

South of the Koni Peninsula and Zaviyalov Island, roughly between 57°50′ N and 58°30′ N and between 150°20′ E and 151°20′ E, the convergence of the cold Yamsk Current and the warmer Northern Branch Current produce a strong seasonal oceanographic front, which is characterized by downwelling with numerous eddies in the middle of the convergence zone and along its boundary (Chernyavskiy 1970a). Large patches of zooplankton, mostly of *Metridia ochotensis* (200-500 mg m^{-3}) occurred in the upper 0-50 m primarily below the thermocline (Fig. 9). *Calanus glacialis* was abundant in the surface 0-10 m (Kotlyar and Chernyavskiy 1970b).

Counter currents influence the entrance of Shelikhov Bay. A branch of the Western Kamchatka Current enters along the Kamchatka coast and the cold Yamsk Current flows out near the Piyagina Peninsula resulting in upwelling in the divergence zone and coastal downwelling (Kotlyar and Chernyavskiy 1970b). In the upwelling zone zooplankton was distributed uniformly in the 25-100 m layer (200-500 mg m^{-3}) (Fig. 10) and consisted mostly of *Calanus glacialis* and *Metridia ochotensis* (Kotlyar and Chernyavskiy 1970b). Off the Kamchatka coast, zooplankton biomass was 500-5,000 mg m^{-3} with dense aggregations of *Calanus plumchrus* found in the 10-25 m depth layer (Kotlyar and Chernyavskiy 1970b). Zooplankton was scarce in the upper 0-50 m layer of the Yamsk Current (25-50 mg m^{-3}) (Kotlyar and Chernyavskiy 1970b).

Another upwelling zone is located near St. Iona Island in the northwestern Okhotsk Sea. The upwelling is caused by a branch of the Western Kamchatka current which flows over the slope breaking up the cold intermediate layer and penetrating to the surface layer (Chernyavskiy et al. 1981). Zooplankton biomass was uniform (over 500 mg m^{-3}) from 200 m depth up to the surface in this area (Fig. 11). The dominant copepods were *Metridia ochotensis*, *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii,* and other oceanic species (Lubny-Gertsik 1959).

The above review indicates that most zooplankton in the Okhotsk Sea was concentrated in the upper 0-50 m during summer with fewer individuals in the cold intermediate layer. However, considerable concentrations of zooplankton have been found in deeper layers where vertical mixing occurred.

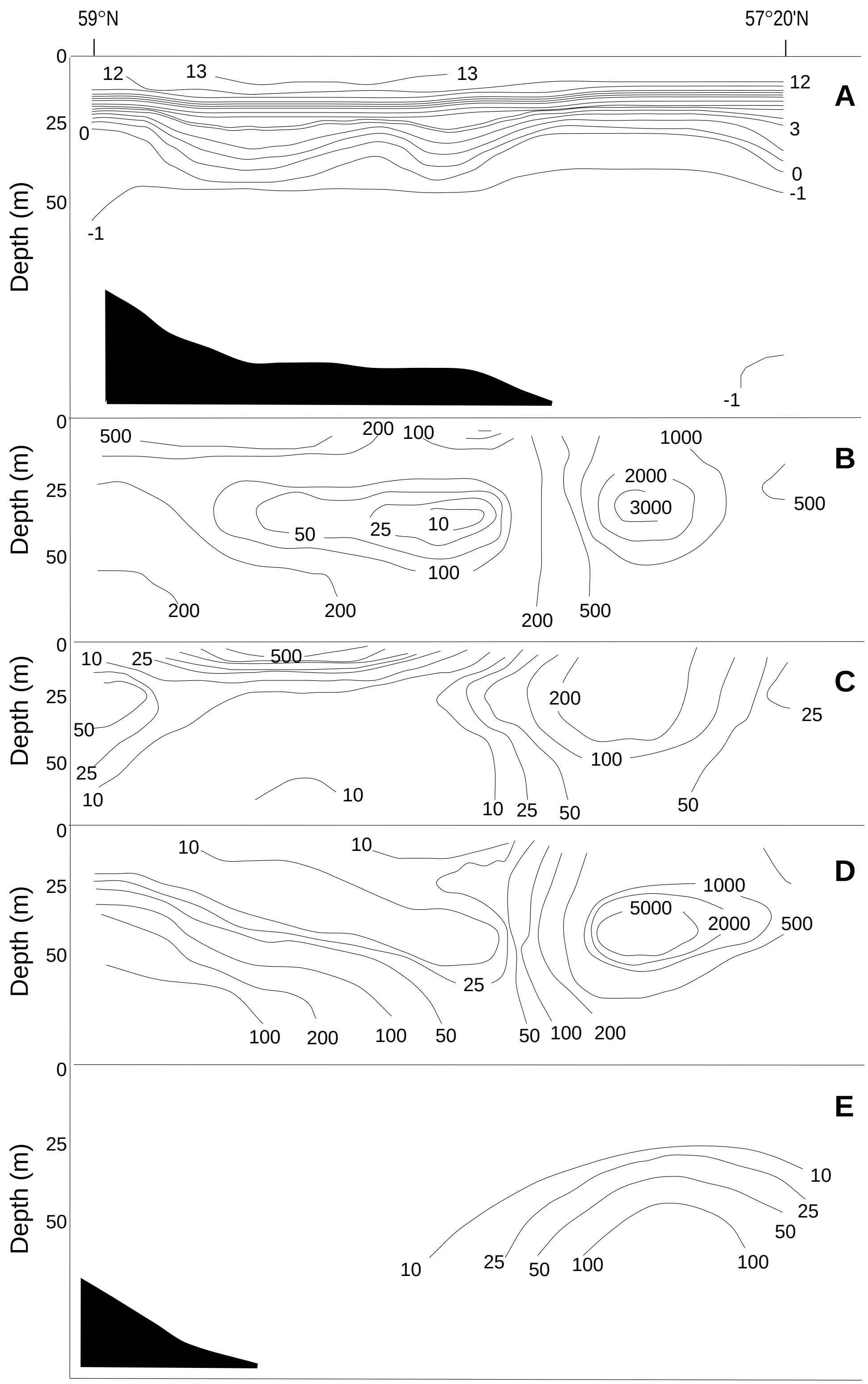

Figure 7. *A = vertical distribution of water temperature, B = total zooplankton biomass, C = Calanus glacialis biomass, D = Metridia ochotensis biomass, and E = Calanus plumchrus biomass (mg m⁻³) on the profile along 147°33′ E in summer 1964, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).*

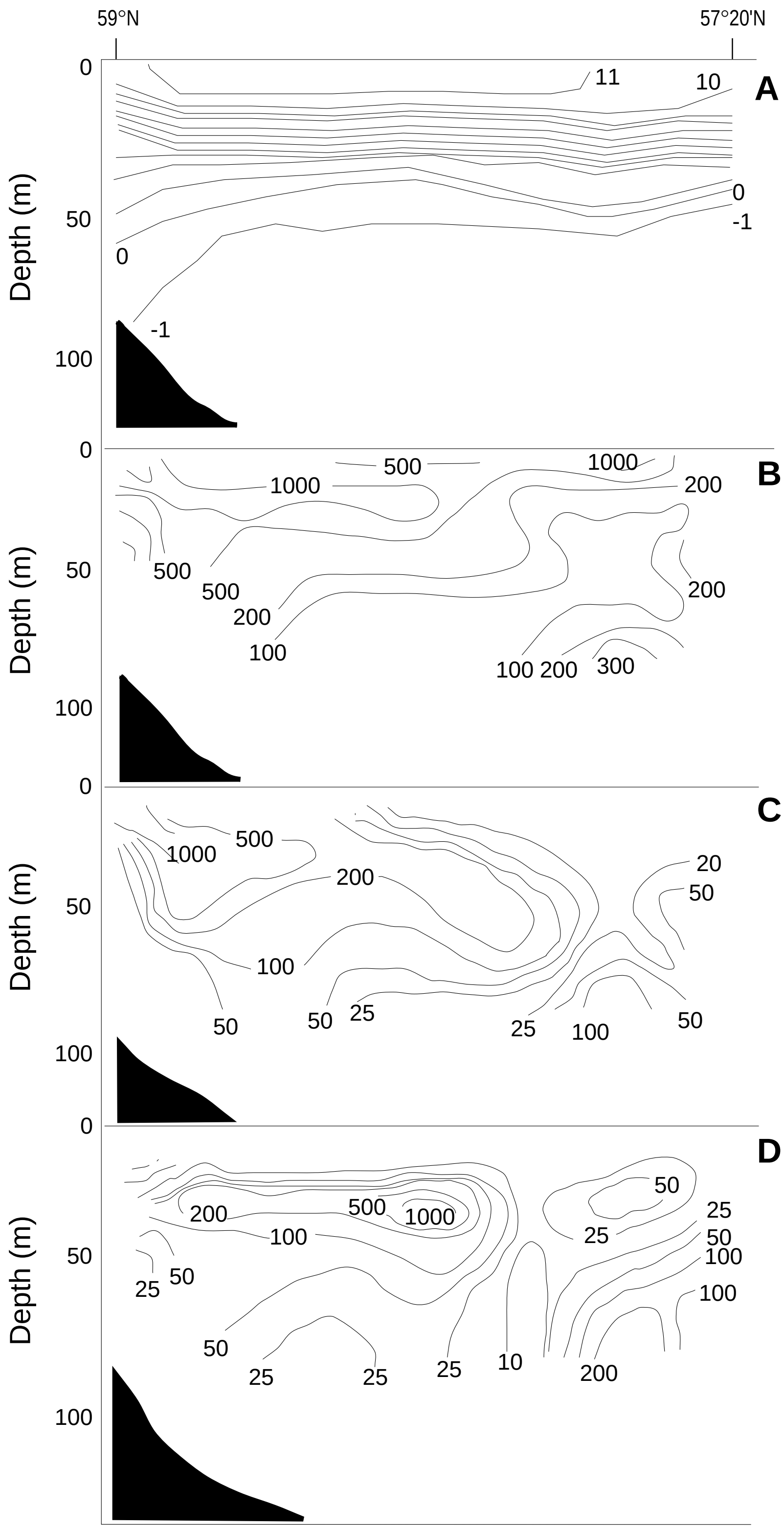

Figure 8. A = vertical distribution of water temperature, B = total zooplankton biomass, C = Calanus glacialis biomass, and D = Metridia ochotensis biomass (mg m^{-3}) on the profile along 147°35′ E in summer 1967, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).

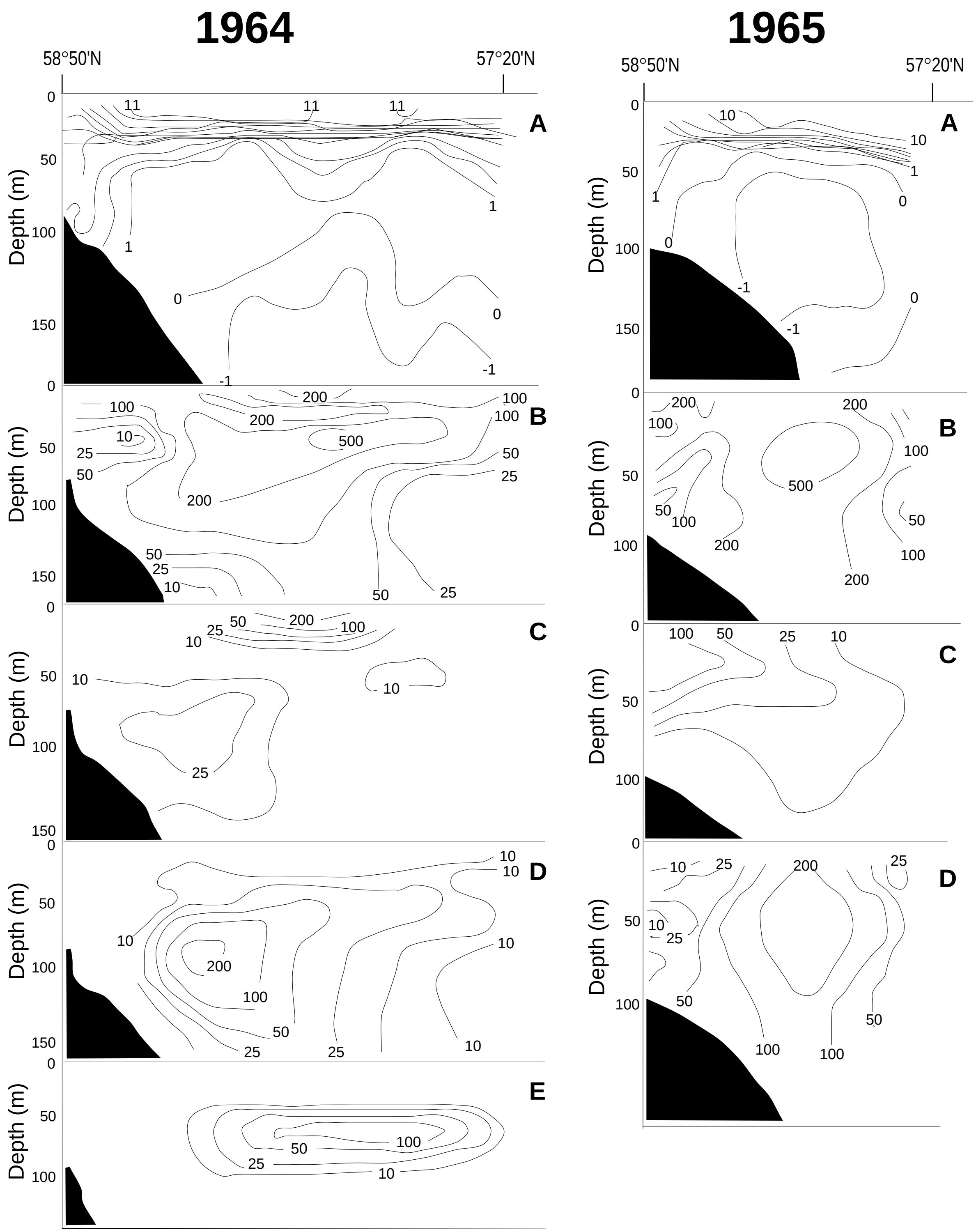

Figure 9. *A = vertical distribution of water temperature, B = total zooplankton biomass, C = Calanus glacialis biomass, D = Metridia ochotensis biomass, and E = Calanus plumchrus biomass (mg m⁻³) on the profile along 151°20′ E in summers 1964 and 1965, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).*

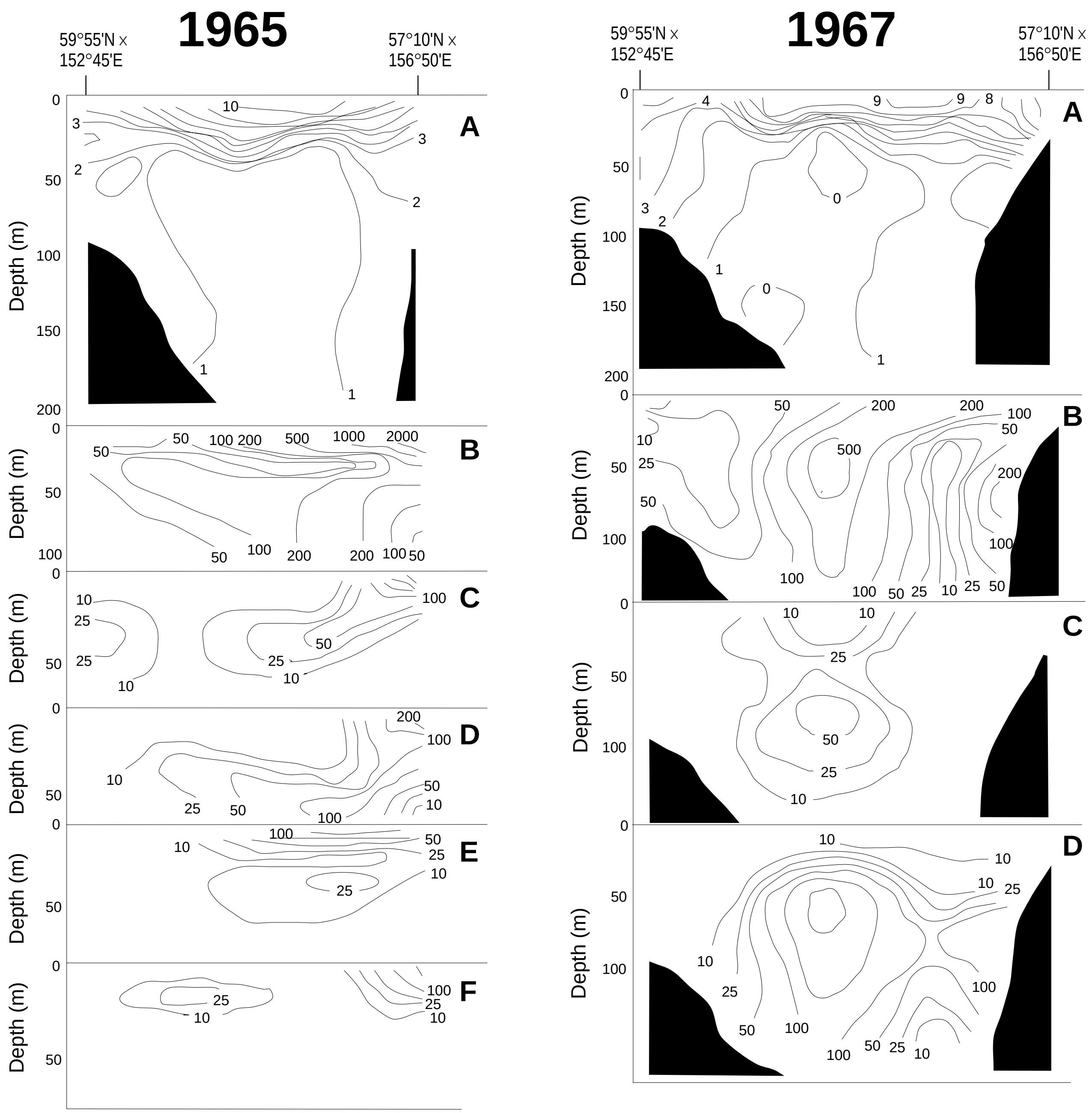

Figure 10. A = vertical distribution of water temperature, B = total zooplankton biomass, C = Calanus glacialis biomass, D = Metridia ochotensis biomass, E = Calanus plumchrus biomass, and F = Eucalanus bungii biomass (mg m⁻³) between Cape Evreinov and Cape Hayryuzov in summers 1965 and 1967, mesh = 0.168 (from Kotlyar and Chernyavskiy 1970b).

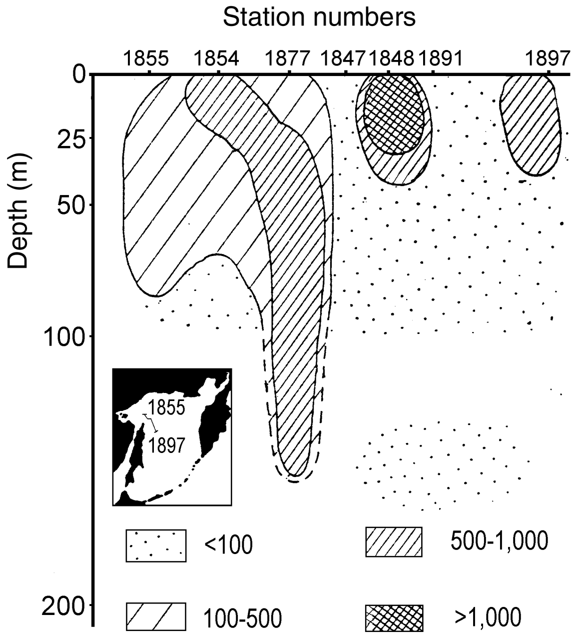

Figure 11. Vertical zooplankton biomass distribution (mg m⁻³) over the trough between Sakhalin and St. Iona islands in the upper 0-200 m. 1 = <100, 2 = 100-500, 3 = 500-1,000, 4 = >1,000, mesh = 0.168 (from Lubny-Gertsik 1959).

Geographic Distribution of Zooplankton

Northern Okhotsk Sea

The first zooplankton report for the northern Okhotsk Sea summarized TINRO expeditions of 1935 and 1937 (Kusmorskaya 1940). Plankton samples were taken in two regions: Shantar Islands in September 1935, and the northwestern coast of Kamchatka near Cape Khayryuzov in May-August 1937. The colder Shantar Islands water was characterized by one phytoplankton bloom and by domination of *Pseudocalanus elongatus* and nauplii of neritic copepods together with numerous meroplankton. The oceanic vertical migrant *Metridia ochotensis* occurred at two stations sampled at night, bringing the total biomass to 1,755 mg m^{-3}. *Calanus finmarchicus* and *Metridia ochotensis* were primarily in the late copepod stages.

The northeastern Okhotsk Sea had two phytoplankton blooms: the first in May dominated by diatoms of the genera *Thalassiosira* and *Chaetoceras*, and the second bloom in August characterized by *Ceratium* spp. and *Peridinium* spp. *Calanus plumchrus* dominated the zooplankton community in May along with polychaete larvae. In June and July meroplankton and euphausiid larvae dominated, while oceanic *Metridia pacifica*, *Metridia ochotensis*, and *Eucalanus* spp. increased in abundance during July. In August *Calanus finmarchicus* was more common than the oceanic species, with small amounts of neritic larval zooplankton present. Oceanic *Calanus plumchrus* was distributed in open sea areas influenced by Pacific water where dinoflagellates were common. *Calanus finmarchicus* had an offshore distribution in areas with few diatoms.

Kun (1951) reported on zooplankton distribution in August-September 1949 for the area from Cape Khanyangda to Tauyskaya Bay. Cold-water *Metridia* sp., *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Acartia longiremis*, and *Parathemisto libelulla* formed dense patches (1,000-500 mg m^{-3}) between the Lisyanskiy Peninsula and Cape Moskvitin 100-150 km offshore to the south, and in the vicinity of Cape Khanyangda.

In May-September 1955 TINRO surveyed plankton in Shelikhov Bay, Tauyskaya Bay, and the St. Iona Island region while studying herring (Mikulich 1960). In Shelikhov Bay, the dominant species were *Limacina helicina*, *Sagitta elegans*, *Parathemisto libellula*, *Thysanoessa raschii*, *Metridia ochotensis*, *Calanus plumchrus*, *C. glacialis*, *Pseudocalanus elongatus*, larval barnacles, decapods, polychaetes, and echinoderms. During August-September the neritic species *Evadne nordmanni*, *E. spinifera*, *Podon leuckarti*, *Centropages mcmurrichi*, and larvae of holoturians, starfish, and bivalves appeared. The distribution of zooplankton biomass collected with ichthyoplankton nets (diameter 80 cm, 0.569 mesh) in the upper 50 m layer was patchy in May to June and even more so in August to September. The highest average biomass was 653 mg m^{-3} in June and 474 mg m^{-3} in May; the lowest biomass was 113 mg m^{-3} in August and September (Fig. 12). The highest biomass concentrations in the inner bay were formed by *Limacina helicina* between July and August. In the center of Shelikhov Bay *Sagitta elegans*, *Parathemisto libellula*, *Calanus glacialis*, *Metridia ochotensis*, *Thysanoessa raschii*, *Pseudocalanus elongatus*, and barnacle larvae were common. In the outermost part of the bay oceanic *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii*, *Metridia pacifica*, *Thysanoessa longipes*, *Undinopsis pacificus,* and *Parathemisto japonica* were common. The neritic species were observed both in the inner bay and near its entrance where strong tidal currents prevailed.

The patterns of zooplankton biomass distribution in the 50-100 m layer were similar to those in the upper layer (Fig. 13). The average biomass in this layer was 203 mg m^{-3} in May, 403 mg m^{-3} in June, and 201 mg m^{-3} in August. The key feature of the area was the lack of any sharp decrease of zooplankton biomass in the 50-100 m layer which was common in other parts of the Okhotsk Sea.

Population analysis of the dominant species showed intensive reproduction of *Sagitta elegans*, *Thysanoessa raschii,* and *Calanus glacialis* in May-June. *Calanus plumchrus* reproduced in July, and younger stages of *Pseudocalanus elongatus* occurred throughout the survey area.

The distribution of zooplankton collected by ichthyoplankton nets in Tauyskaya Bay in July 1954 and 1955 was similar, with highest concentrations in areas influenced by freshwater runoff (Fig. 14). The highest biomass was recorded for the warm 0-50 m layer, while in the colder 50-100 m layer zooplankton biomass declined. Cold-water *Metridia ochotensis*, *Parathemisto libellula*, *Calanus glacialis*, *Thysanoessa raschii*, *Sagitta elegans,* and *Pseudocalanus elongatus* dominated over the area. Oceanic *Calanus plumchrus*, *Thysanoessa longipes*, *Metridia pacifica*, *Eucalanus bungii*, *Calanus cristatus*, and *Oikopleura* sp. were common at open-sea stations.

Plankton samples were taken near St. Iona Island, which is in the northwestern Okhotsk Sea, during July 1955. The distributions of seston biomass (mostly zooplankton) collected in the 0-50 m and 50-100 m layers for the St. Iona Island region, and zooplankton biomass estimated with ichthyoplankton nets in the 0-50 m layer are presented in Figs. 15 and 16. Both cold-water *Metridia ochotensis*, *Parathemisto libellula*, *Sagitta elegans*, *Pseudocalanus elongatus*, *Thysanoessa raschii*, and *Limacina helicina*, and oceanic *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii*, *Metridia pacifica*, *Thysanoessa longipes*, and *Parethemisto japonica* formed the bulk of the biomass with an average value of 514 mg m^{-3}. The lowest biomass was found in the southeastern area where there was localized upwelling and surface temperatures of 2-3°C. Zooplankton biomass increased in the areas around the upwelling (Mikulich 1960).

In 1956 TINRO surveyed southwestern Kamchatka Peninsula zooplankton. Maps of zooplankton biomass, based on analysis of 340 samples, were published by Mesheryakova (1959) (Fig. 17). Most of the biomass consisted of *Calanus plumchrus* and *Metridia pacifica*. The presence of *C. glacialis* near the shore was interpreted as evidence that a cold southward current existed along the western Kamchatka coast. Many of the zooplankton species in the southern part of the area started to reproduce considerably earlier than in the north. The lower biomass in the south in July-September appeared to be caused by herring predation.

Makarov (1969) reported zooplankton biomass distribution in the upper 50 m layer along the western coast of the Kamchatka Peninsula during June-July in 1962 and 1963 (Fig. 18). The highest biomass occurred in the north of the study area and consisted primarily of *Calanus glacialis*. *Calanus plumchrus* and *C. glacialis* were mutually exclusive in distribution. *Acartia longiremis* was abundant in the neritic community. There tended to be higher biomass near river mouths. Young *Sagitta elegans* formed dense patches in areas of high concentrations of *Acartia longiremis*, while older stages co-occurred with *Calanus glacialis* and *C. plumchrus*.

Another Shelikhov Bay plankton survey was done in herring feeding areas by the Magadan branch of TINRO in June 1963 (Kotlyar 1965). That survey collected 156 zooplankton samples from 103 stations in the 0-50 m layer. The zooplankton patches with highest biomass were populated by cold-water and oceanic copepods like *Calanus glacialis*, *C. plumchrus*, *C. cristatus*, *Eucalanus bungii*, *Metridia ochotensis*, *M. pacifica*, and *Themisto libellula*. The cold-water species *Calanus glacialis* was abundant in the northwestern part of the bay, where an outgoing cold current existed (Fig. 19). Oceanic copepods like *Calanus plumchrus* and *C. cristatus* were observed in the deep central part of the bay and near the Kamchatka coast where there was warmer Pacific water (Fig. 20). Neritic species occurred throughout the area. The high abundance of planktonic larvae marked June 1963 as a spring-like reproductive period. The zooplankton distribution was patchy (Fig. 21) with maximal values of 2,747 mg m^{-3} near Cape Utkolokskiy and minimal values of 65 mg m^{-3} in the northernmost part of Shelikhov Bay. Also, dense zooplankton patches were observed near the Pyagina Peninsula and Yamsk Islands. The average zooplankton biomass in Shelikhov Bay in June 1963 was 712 mg m^{-3}.

In August of 1964 TINRO did a zooplankton survey in the northern Okhotsk Sea and collected 259 samples (Kotlyar 1967). The maximal biomass was 9,054 mg m^{-3} seen in the western part of the study area; the minimal value of 102 mg m^{-3} was found near the Pyagina Peninsula in a coastal downwelling area influenced by the cold Yamsk Current (Fig. 22). Patches of higher zooplankton biomass were recorded in a frontal zone characterized by

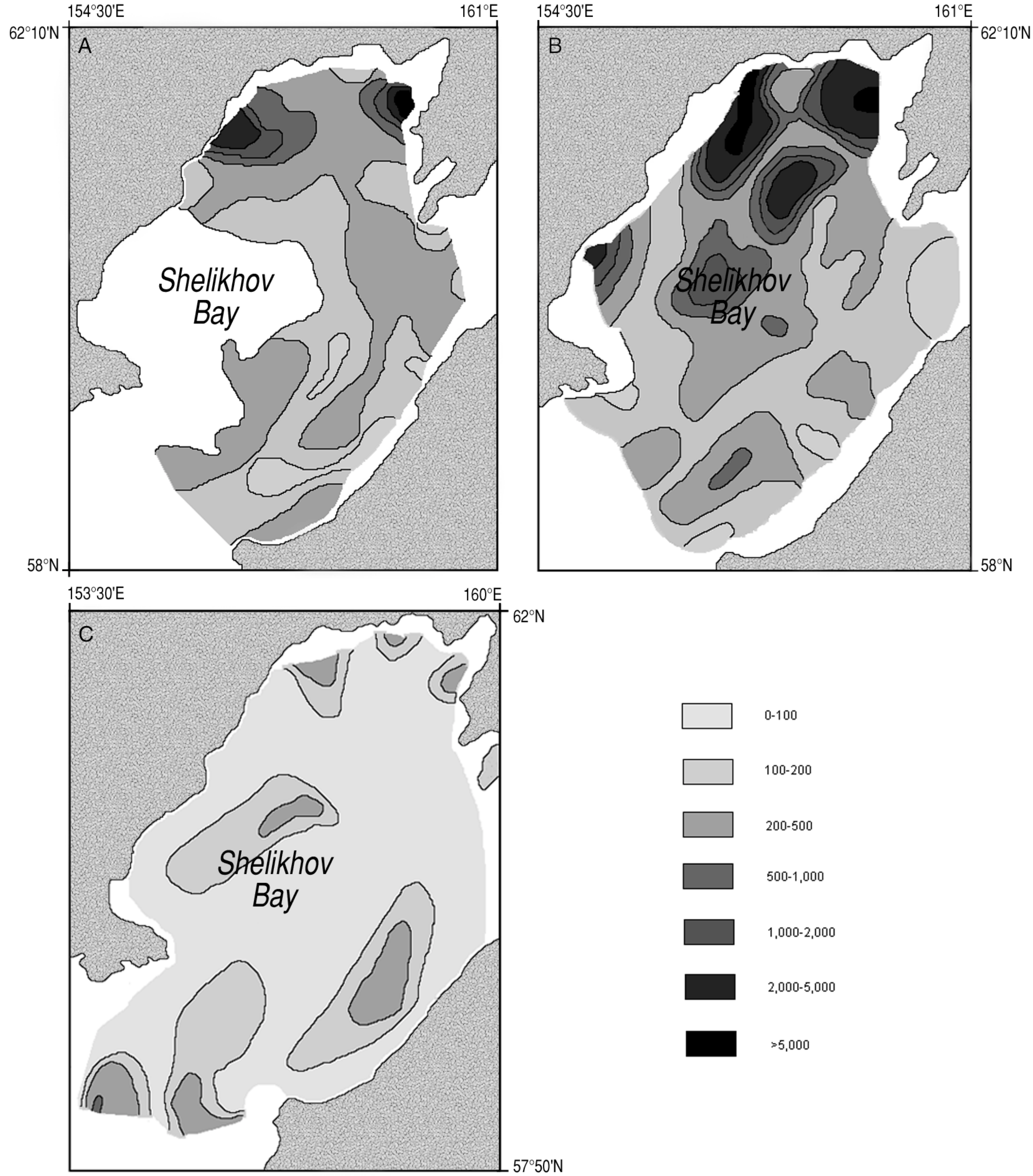

Figure 12. Distribution of zooplankton biomass (mg m⁻³) collected by an ichthyoplankton net (0.168 mesh) in Shelikhov Bay in the 0-50 m layer in 1955. A = May, B = June, C = August-September (from Mikulich 1960).

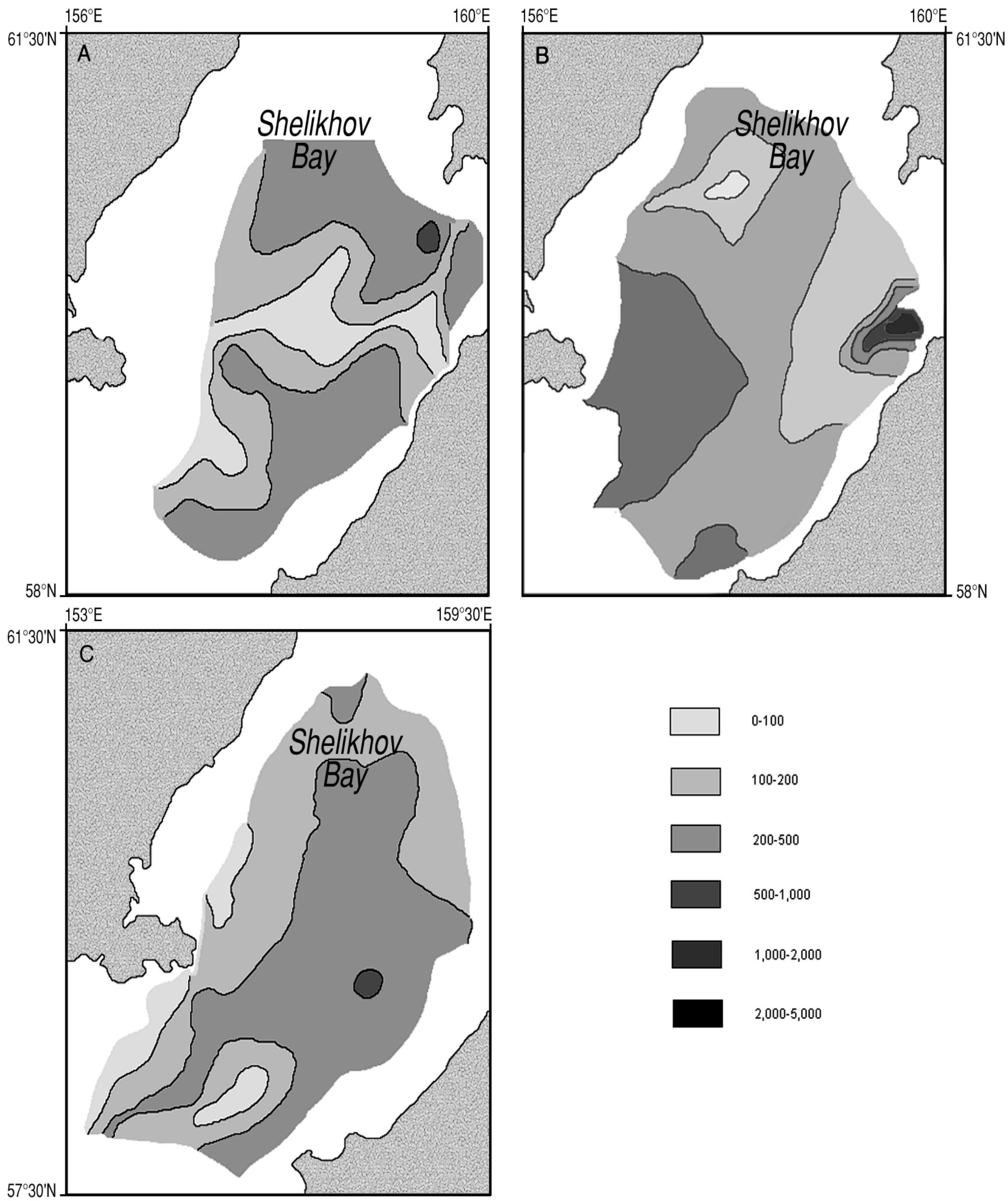

Figure 13. Distribution of zooplankton biomass (mg m⁻³) in the 50-100 m layer in Shelikhov Bay in 1955. A = May, B = June, C = August-September (from Mikulich 1960).

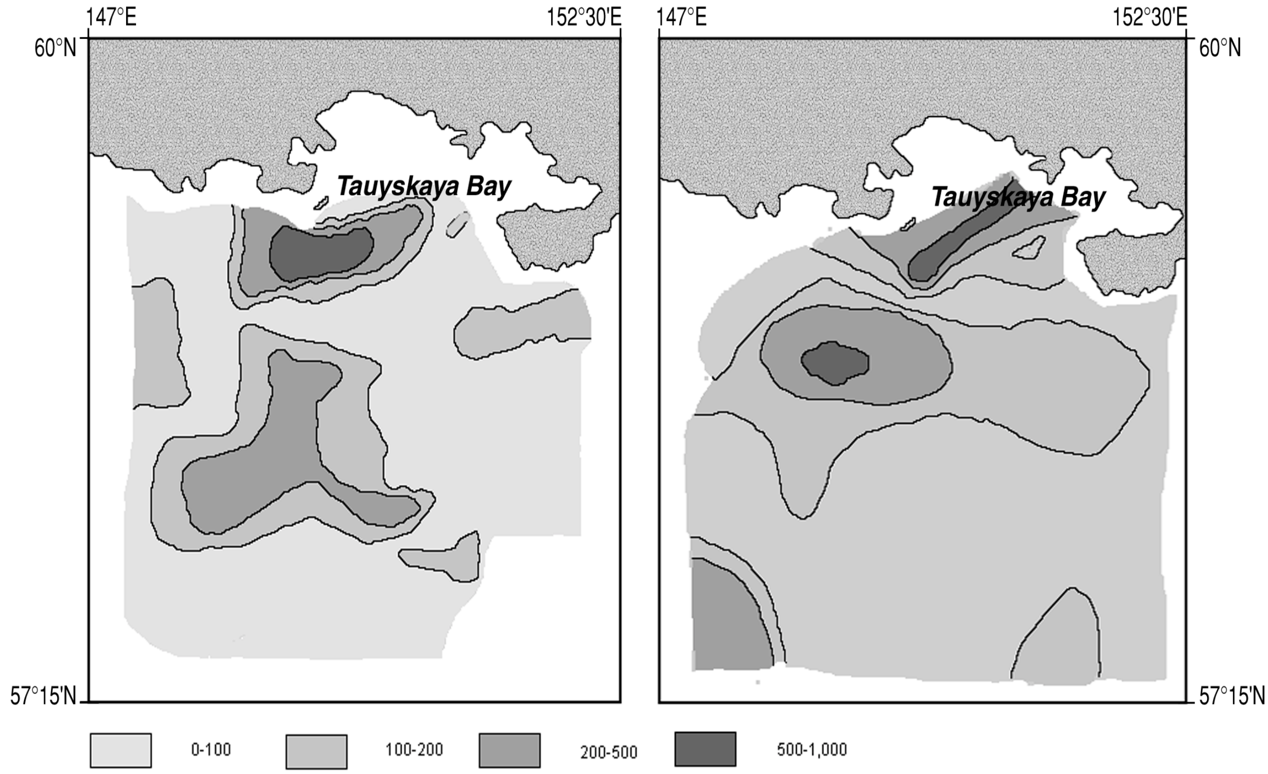

Figure 14. Distribution of zooplankton biomass (mg m⁻³) collected by an ichthyoplankton net in Tauyskaya Bay in the 0-50 m layer. A = June 1955, B = July 1954 (from Mikulich 1960).

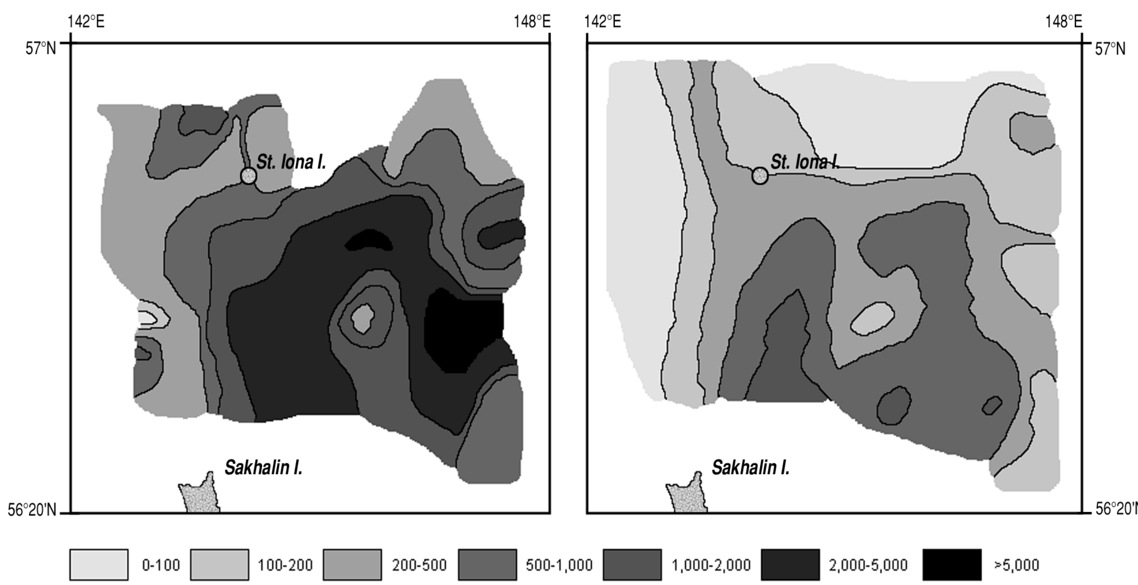

Figure 15. Distribution of seston biomass (mg m⁻³) (0.168 mesh) near St. Iona Island during July 1955. A = in the 0-50 m layer, B = in 50-100 m layer (from Mikulich 1960).

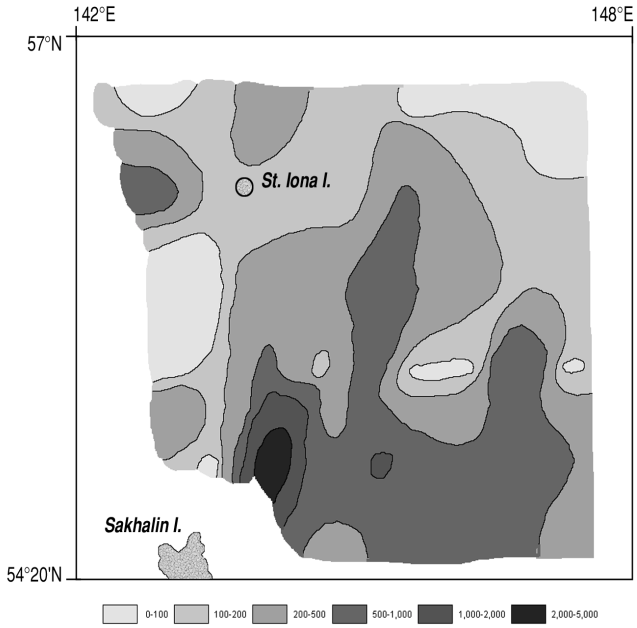

Figure 16. Distribution of zooplankton biomass (mg m^{-3}) collected by an ichthyoplankton net near St. Iona Island in the 0-50 m layer during July 1955 (from Mikulich 1960).

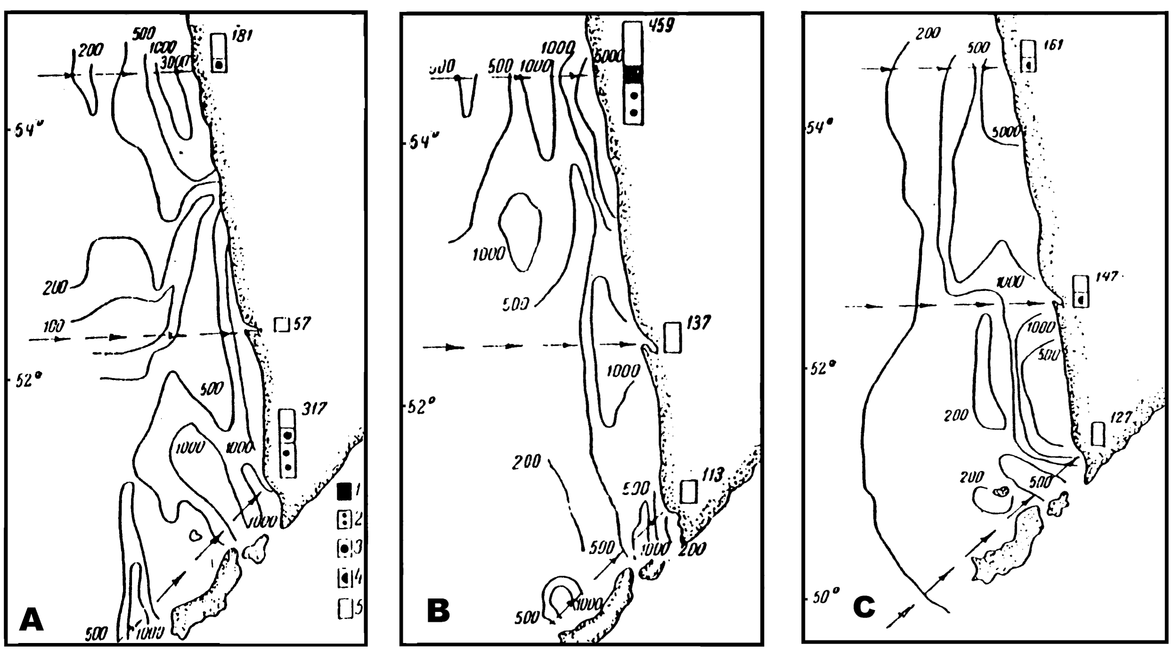

Figure 17. Distribution of zooplankton biomass (mg m^{-3}) near southwestern Kamchatka in 1956 (0-100 m, 0.168 mesh). A = July, B = August, C = September. 1 = Calanus glacialis, 2 = Metridia pacifica, 3 = Calanus cristatus, 4 = Pseudocalanus elongatus, 5 = others. Arrows indicate major transects; numbers are the average total biomass on the transects (from Meshcheryakova 1959).

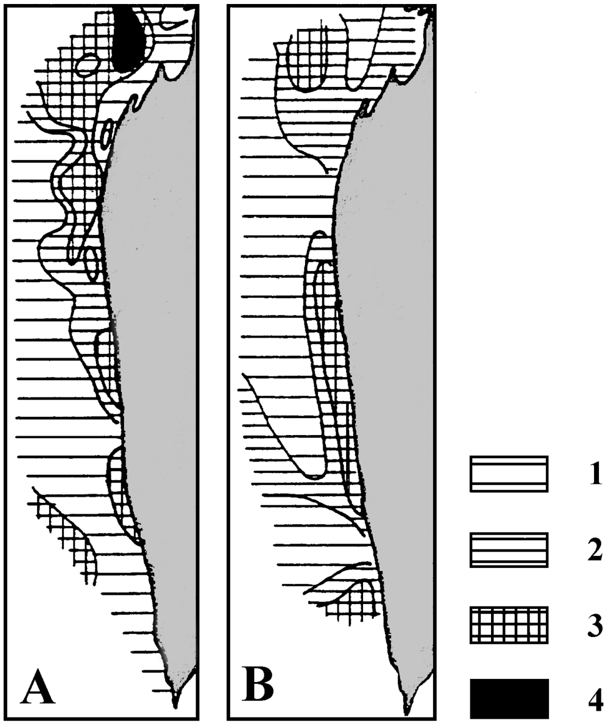

Figure 18. Distribution of zooplankton biomass (mg m⁻³) near the western coast of Kamchatka in the 0-50 m layer: 1 = 100-500, 2 = 500-1,000, 3 = 1,000-3,000, 4 = >3,000. A = June 1962, B = June-July 1963 (from Makarov 1969).

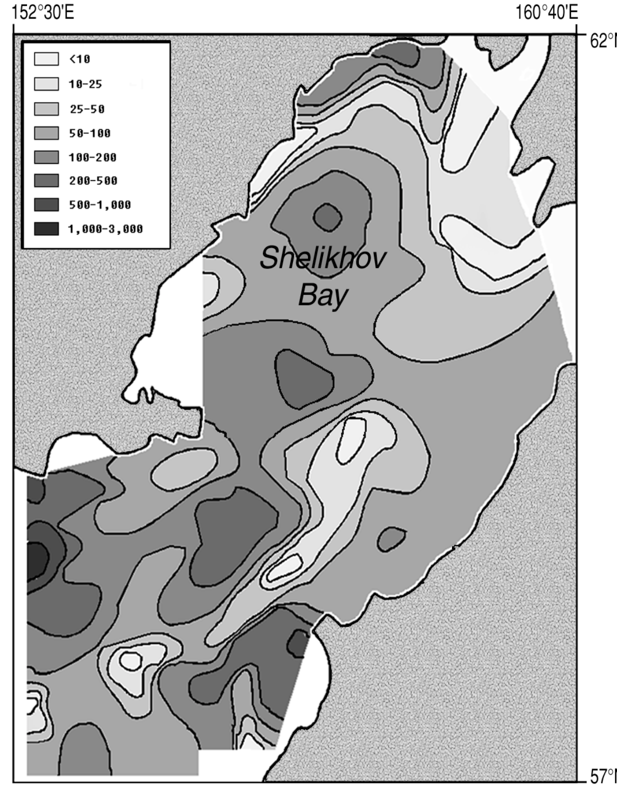

Figure 19. Distribution of Calanus glacialis biomass (mg m⁻³) in the 0-50 m layer in Shelikhov Bay during June 1963 (from Kotlyar 1965).

intensive upwelling in the middle of the entrance to Shelikhov Bay. They were also seen in regions influenced by freshwater runoff near Tauyskaya Bay and along the Kamchatka coast. Downwelling caused by an anticyclonic eddy was observed over the TINRO Basin with lower biomass in the eddy's center and higher biomass beyond it. The average biomass in a 0-100 m layer in August 1964 was 1,008 mg m^{-3}. Zooplankton biomass was higher in the upper 0-50 m with a sharp decline in the 50-100 m layer below 0°C in the western part of the studied area. Waters to the east did not have strong vertical temperature gradients and the zooplankton biomass did not exhibit notable vertical aggregations.

Most of the biomass consisted of cold-water *Metridia ochotensis* (Fig. 23) and *Calanus glacialis* (Fig. 24). The distribution of these species corresponded to those of cold waters in a frontal upwelling zone and to the west. In areas influenced by warmer Pacific water oceanic *Calanus plumchrus* (Fig. 25), *Eucalanus bungii* (Fig. 26), and *Metridia pacifica* were numerous.

The interannual zooplankton distribution patterns were described by Kotlyar (1970) for 2,317 northeastern Okhotsk Sea samples collected at 607 stations by TINRO in June-August 1964-1967 (Fig. 27). The interannual fluctuations in zooplankton distribution corresponded to oceanographic changes related to winter atmospheric circulation patterns (Vinokurova 1965). The northern Okhotsk Sea was characterized by the presence of a cold intermediate layer with a minimum temperature of –1.7°C forming after the winter cooling. In the autumn-winter period of maximum convection the cold layer's core approached the surface, and in spring the cold core became the subsurface layer. Summer warming and the warmer Pacific water entering the Okhotsk Sea destroyed the cold core during summer. The extent of this destruction depended on the intensity of the Western Kamchatka Current transporting warm Pacific water northward into the Okhotsk Sea, which, in turn, depended on the intensity of winter atmospheric circulation (Vinokurova 1965). The years with intensive penetration of warmer Pacific

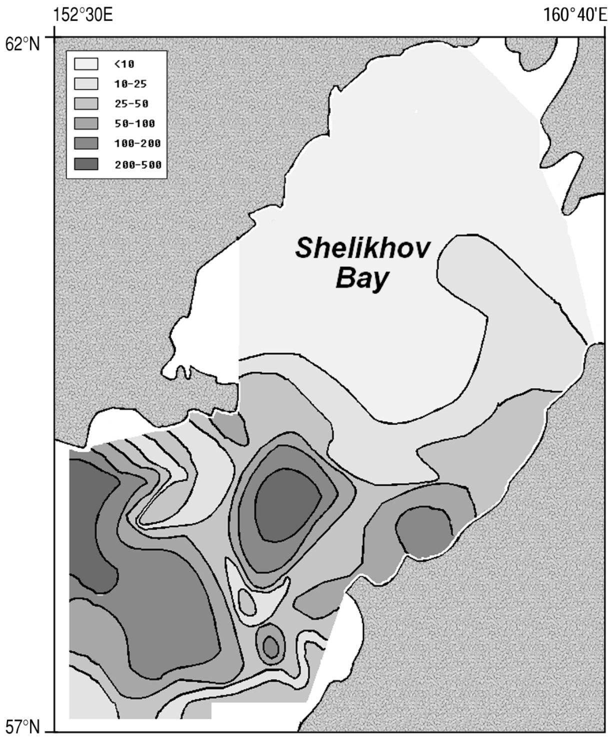

Figure 20. Distribution of Calanus cristatus biomass (mg m^{-3}) in the 0-50 m layer in Shelikhov Bay during June 1963 (from Kotlyar 1965).

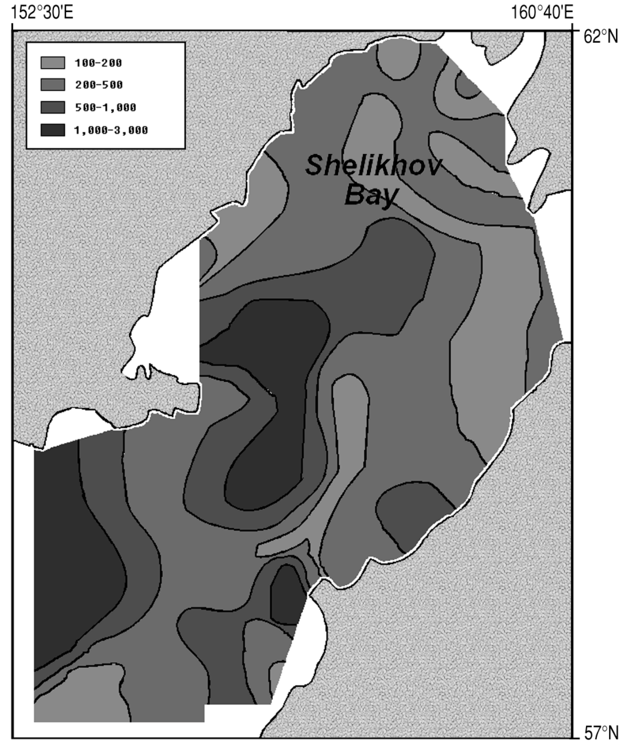

Figure 21. Distribution of zooplankton biomass (mg m^{-3}) in the 0-50 m layer in Shelikhov Bay during June 1963 (from Kotlyar 1965).

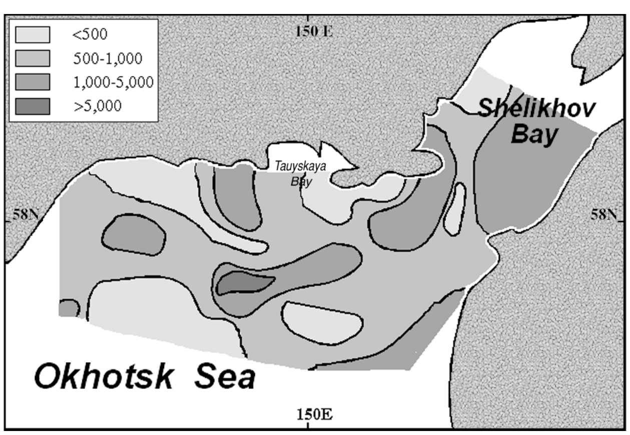

Figure 22. Distribution of zooplankton biomass (mg m^{-3}) in the 0-100 m layer in the northern Okhotsk Sea during August 1964 (from Kotlyar 1965).

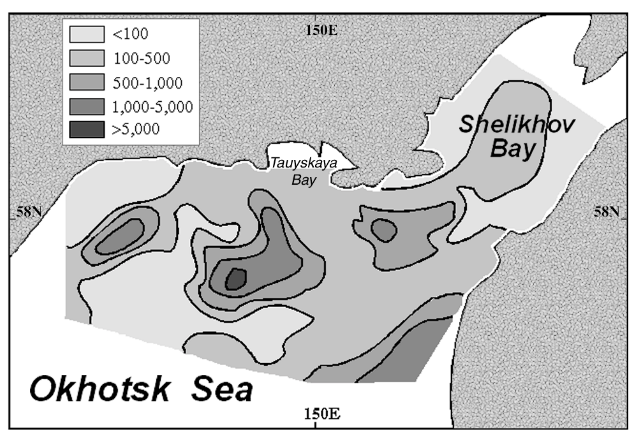

Figure 23. Distribution of Metridia ochotensis biomass (mg m^{-3}) in the 0-100 m layer in the northern Okhotsk Sea during August 1964 (from Kotlyar 1965).

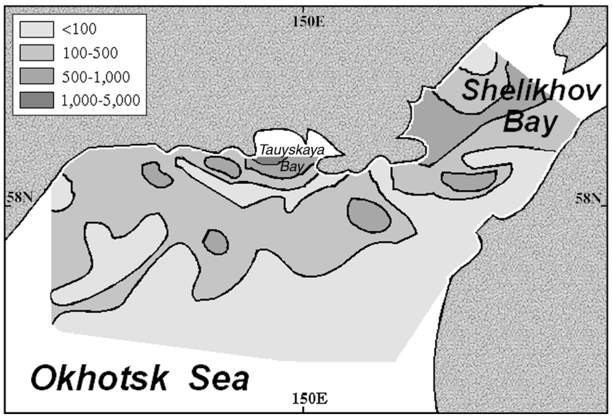

Figure 24. *Distribution of Calanus glacialis biomass (mg m⁻³) in the 0-50 m layer in the northern Okhotsk Sea during August 1964 (from Kotlyar 1965).*

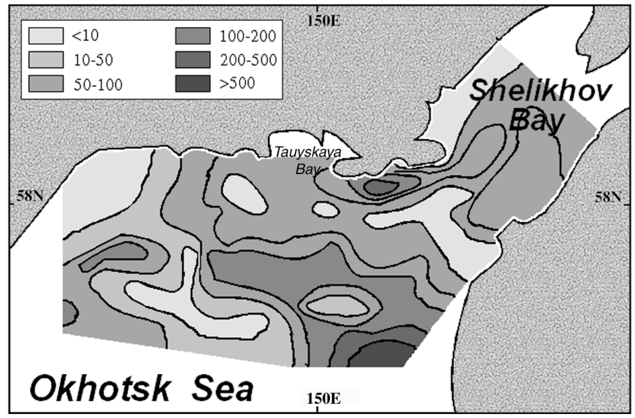

Figure 25. *Distribution of Calanus plumchrus biomass (mg m⁻³) in the 0-100 m layer in the northern Okhotsk Sea during August 1964 (from Kotlyar 1965).*

waters were characterized by fewer cold core areas (Chernyavskiy 1970a). Such years were considered "warm." In "cold" years there was low Western Kamchatka Current intensity and the cold core was prominent, expanding over the shelf and leading to small horizontal temperature gradients on the surface. Between these two extremes were a number of "intermediate" years with slightly positive or negative temperature anomalies (Kotlyar and Chernyavskiy 1970a). The intermediate year of 1964 had a slight positive temperature anomaly, 1965 was intermediate with slight negative temperature anomaly, and 1966 and 1967 were cold years. During all those observations, high zooplankton biomass was observed near the southern tip of the Kamchatka Peninsula where there was Pacific water influence, around the anticyclonic gyre over TINRO Basin, along the northern Kamchatka shelf, in the outermost Shelikhov Bay, and along the oceanographic front off the Shelikhov Bay entrance (Fig. 27).

During biological spring in the area in June the average zooplankton biomass along the western Kamchatka coast was 700-850 mg m^{-3} in intermediate years with dominance of *Calanus plumchrus*, and half the biomass in cold years with *Metridia ochotensis* most common. In Shelikhov Bay interannual zooplankton biomass fluctuations showed a similar pattern with minimal values of 430 mg m^{-3} in the cold year of 1966 and 1,300-800 mg m^{-3} in warmer years. *Calanus glacialis* dominated the zooplankton biomass in cold years, while *Metridia ochotensis* was the predominant species in other years. In the northern waters higher than average biomass (1,200 mg m^{-3}) were observed in intermediate temperature years like 1965, while the lowest values of 900 mg m^{-3} were recorded in the cold year of 1967. *Metridia ochotensis* dominated during all those years.

In summer along the western Kamchatka coast the highest average biomass of zooplankton was observed in intermediate temperature conditions of 1965 and the cold year of 1967 (3,716 mg m^{-3} and 2,740 mg m^{-3} respectively) with a dominance of *Calanus plumchrus* in intermediate temperature years and *Calanus glacialis* during the cold years. In Shelikhov Bay the average zooplankton biomass was higher in the cold year of 1967 (2,370 mg m^{-3}) and lower in the intermediate temperature years of 1964 and 1965 (780 mg m^{-3} and 1,903 mg m^{-3} respectively). *Metridia ochotensis* was most common during the warmer 1964 and *Calanus glacialis* was common in the colder 1965 and 1967 sampling periods. In the northern part of the area the highest zooplankton biomass was observed in the cold year of 1967 (1,425 mg m^{-3}) with the dominance of *Calanus glacialis*, while in the warmer years *Metridia ochotensis* dominated. The dominant copepod species reproduced earlier in the intermediate years of 1964 and 1965 compared to the cold years of 1966 and 1967.

Based on the same data sets used by Kotlyar (1970), the spatial distribution of some common copepods were reviewed by Kotlyar and Chernyavskiy (1970a). The copepods *Calanus glacialis* and *Metridia ochotensis* were found in the cold currents in the northern Okhotsk Sea. The oceanic *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii,* and *Metridia pacifica* were distributed in regions

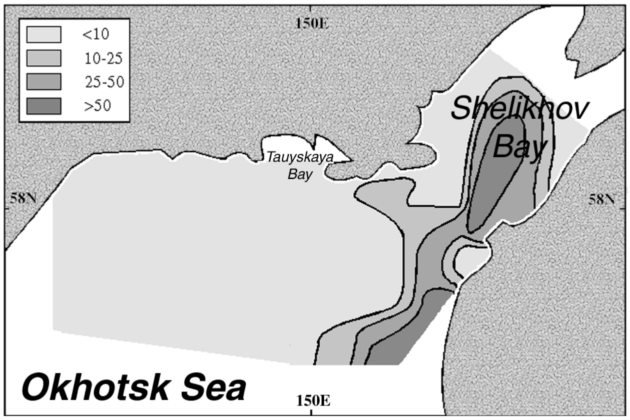

Figure 26. Distribution of Eucalanus bungii biomass (mg m⁻³) in the 0-100 m layer in the northern Okhotsk Sea during August 1964 (from Kotlyar 1965).

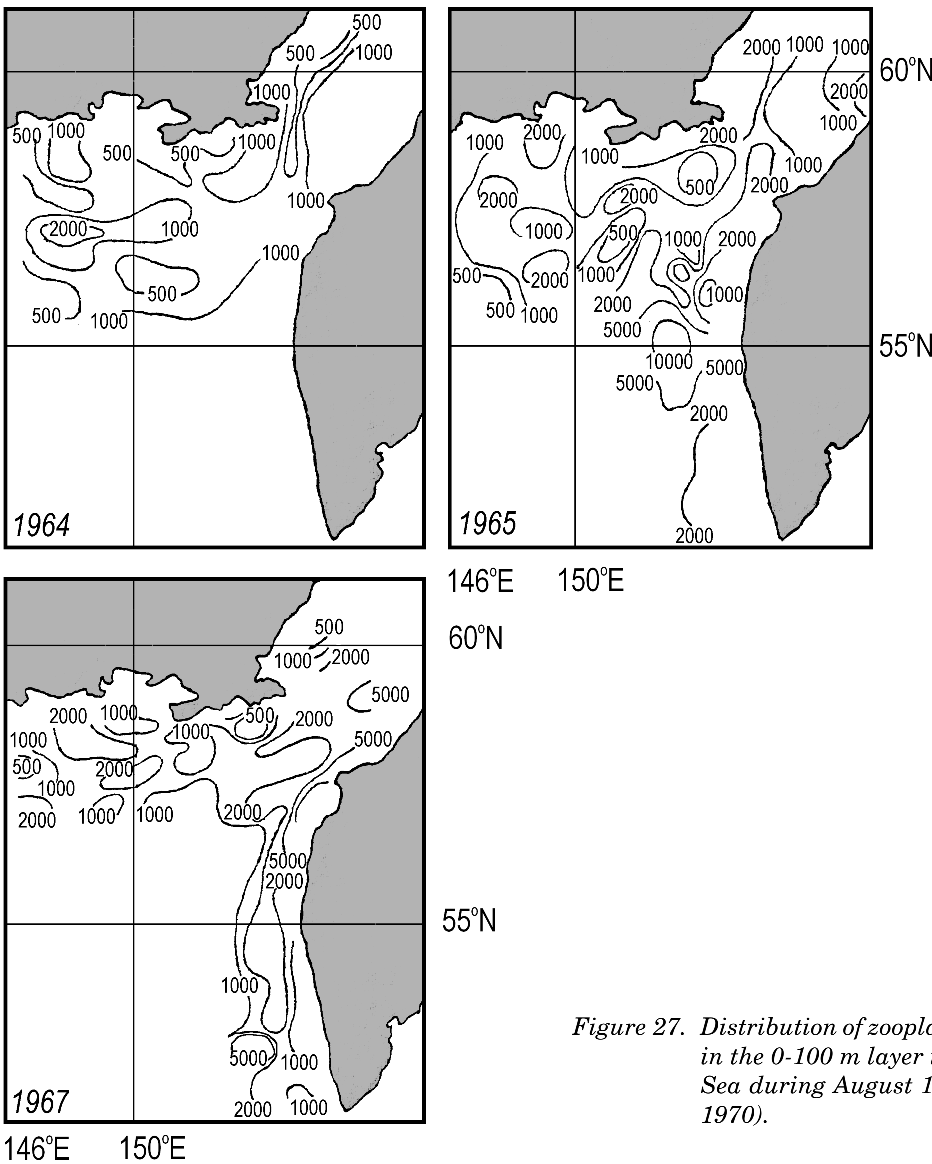

Figure 27. Distribution of zooplankton biomass (mg m⁻³) in the 0-100 m layer in the northern Okhotsk Sea during August 1964-1967 (from Kotlyar 1970).

where Pacific water mass occurred. The cold-water species were distributed over larger areas in the cold year, while oceanic species had broader distribution in intermediate temperature years.

In August 1968 and 1969 TINRO conducted a herring feeding study in the northwestern Okhotsk Sea collecting 200 zooplankton samples in the 0, 10, and 25 m layers. The zooplankton distribution patterns in the upper 0-25 m layer were similar for those years (Guryeva 1973) (1968 results are shown in Fig. 28). An important oceanographic feature of the area was the cyclonic Ayansk Gyre around which the maximal zooplankton biomass (1,000 mg m^{-3}) was observed. The minimal biomass (25 mg m^{-3}) occurred offshore. The average biomass in 1968 was less than in 1969 (378 mg m^{-3} and 810 mg m^{-3} respectively). The zooplankton types in 1968 were neritic *Acartia longiremis*; cladocerans; barnacle and bivalve larvae; and *Pseudocalanus minutus*, while in 1969 *Metridia ochotensis*, *Calanus glacialis,* and *C. plumchrus* were abundant.

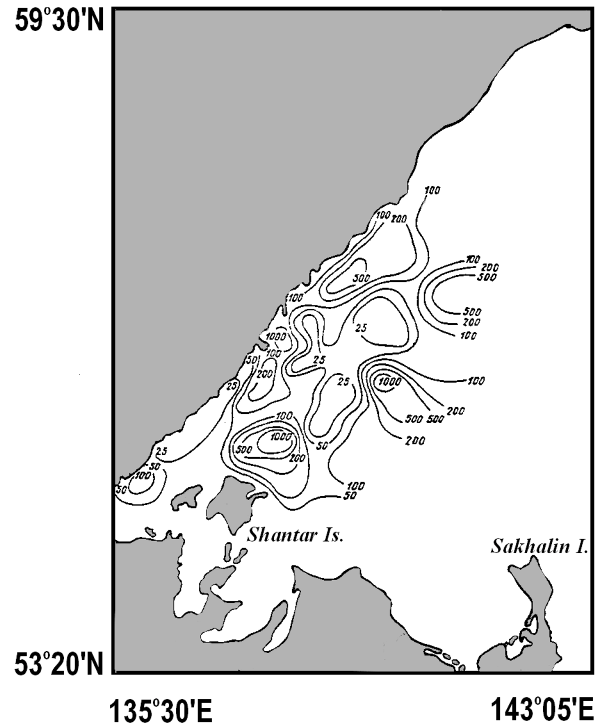

Figure 28. Distribution of zooplankton biomass (mg m^{-3}) in the 0-25 m layer in the northwestern Okhotsk Sea during August 1968 (from Guryeva 1973).

Neritic Zone

The Okhotsk Sea's nearshore pelagic ecosystems remain poorly described, even though the neritic zooplankton is important prey for larval fish reared in bays and inlets (Bailey et al. 1975, Maksimenkov 1982, Murphy et al. 1988).

The Institute of Biological Problems of the North, Magadan, studied nearshore zooplankton in the northern Okhotsk Sea in 1988-1989 (Pinchuk 1992, and unpublished). Forty-eight samples (0.168 mesh) were taken at 15 inshore stations of Motykleisky Bay and adjacent offshore waters in July and September 1988, and in May 1989 (Fig. 29).

The number of zooplankton taxa varied from 35 during May to July, to 42 in September. The importance of meroplankton was similar in all seasons; however, the species composition changed with the season. In May the early developmental stages like eggs, nauplii, and zoeae were common. Euphausiid eggs, and majid and lithodid crab zoeae disappeared from the samples by July, while euphausiid calyptopis and furcilia increased. In September no crustacean nauplii except barnacle nauplii were found, and only the older stages of euphausiids and echinoderm larvae of Asteroidea, Ophiuroidea, and Echinoidea were common.

The lowest average values for zooplankton abundance and biomass during the neritic sampling occurred in May (Table 2) with the lowest value being 57.9 mg m^{-3} at station 15. In July and September average abundance and biomass were higher (Table 2). The maximal abundance and biomass values were observed at Station 10 in September (50,180 individuals m^{-3}, 1,935 mg m^{-3}). There were significant differences between both population and biomass values in May and other months, but not in July and September. The average zooplankton diversity in the area was minimal in May and similar during July and September (Table 2).

In May the overwhelming abundance of meroplankton (Figs. 30a, 31a) made it impossible to classify zooplankton communities clearly. In July numerical classification determined that there were two distinct communities. Community A, in the outermost part of the study area beyond station 10, was dominated by oceanic and eurybiontic species like *Metridia pacifica*, *Calanus glacialis*, *C. plumchrus*, *Pseudocalanus* spp., and *Acartia longiremis* (Figs. 30b, 31b). While population and biomass of community A had not changed much in September (Table 2), the composition was very different. The oceanic species were poorly represented, the brackish water cladocerans *Podon leuckarti* and *Evadne nordmanni* dominated with subdominant eurybiontic *Pseudocalanus* spp. and *Acartia longiremis* also observed (Figs. 30c, 31c).

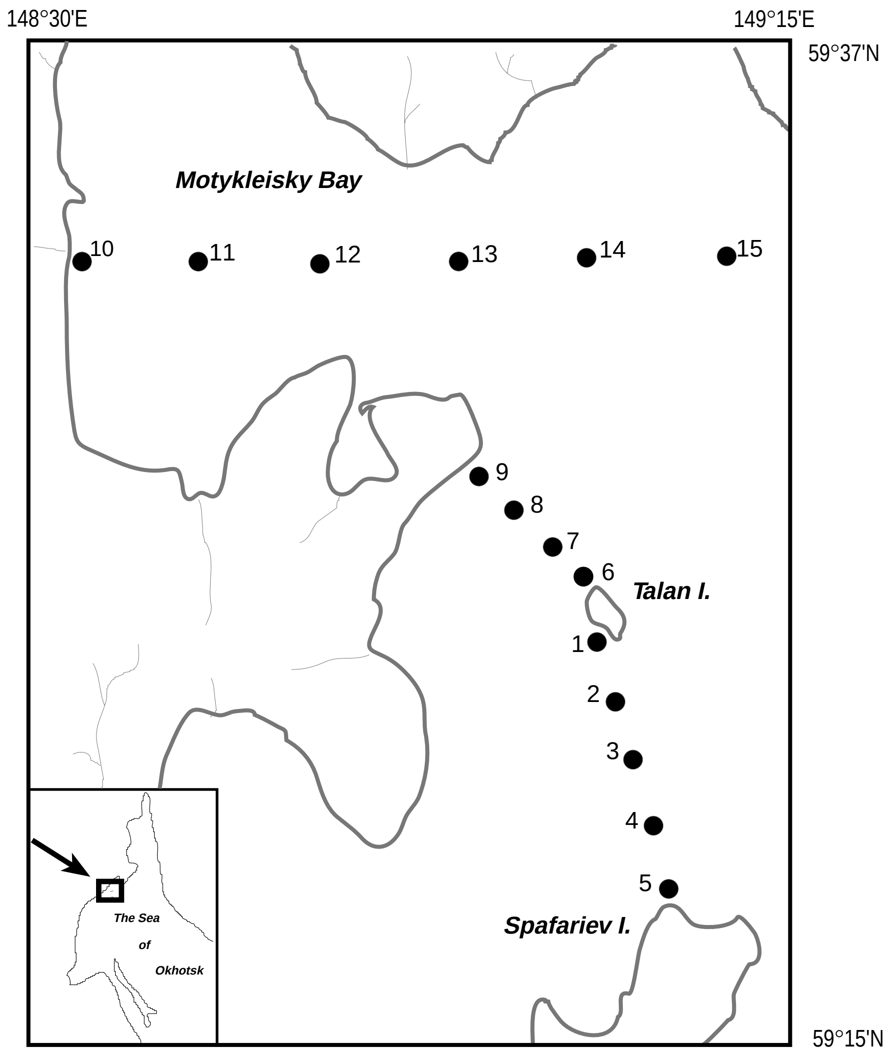

Figure 29. The location of sampling stations in Motykleisky Bay, northern Okhotsk Sea, 1988-1989 (Pinchuk, unpublished).

Table 2. Characteristics of communities A and B and average for Motykleisky Bay, 1988-1989.

Parameter	July 1988	September 1988	May 1989
Abundance A, ind. m^{-3}	3,308 (443)	4,259 (633)	–
Abundance B, ind. m^{-3}	3,494 (1,401)	12,670 (8,077)	–
Average abundance, ind. m^{-3}	3,323 (399)	5,597 (1,394)	2,897 (291)
Biomass A, mg m^{-3}	188 (18)	180 (19)	–
Biomass B, mg m^{-3}	170 (87)	574 (360)	–
Average Biomass, mg m^{-3}	186 (16)	243 (59)	77 (3)
Shannon Index of diversity A, bits	2.30 (0.11)	2.47 (0.07)	–
Shannon Index of diversity B, bits	1.60 (0.17)	1.44 (0.22)	–
Average Shannon Index, bits	2.23 (0.12)	2.16 (0.17)	1.0 (0.33)

(SE = standard error.) From Pinchuk, unpublished. Figs. 30B,C and 31B,C show species composition of communities A and B.

Community B was found in the innermost part of Motykleisky Bay at Station 10 in July, and was dominated by the inshore species *Acartia hudsonica* with few other taxa (Figs. 30c, 31c). Although the average values of abundance and biomass did not differ much between the communities, the species diversity estimated by the Shannon Index (Shannon and Weaver 1963) of community A was considerably higher (Table 2). In September community B reached the middle of the bay (between Station 12 and 13), with higher abundance and biomass values (Table 2). Cladocerans showed a subdominant position with *Acartia hudsonica* dominating as they were in July (Figs. 30c, 31c). The diversity of both communities did not change markedly with time (Table 2).

The spatial distribution of the closely related species *Acartia hudsonica* and *Acartia longiremis* differed. While *Acartia hudsonica* showed high abundance and biomass at the innermost stations, *Acartia longiremis* was more abundant in the outer bay. The boundary of these species was between Stations 12 and 13 in September (Fig. 32).

The community indicator species, *Acartia hudsonica*, was typically more abundant in the enclosed inlets of Japan, and it was replaced by *Acartia omori* in offshore areas (Ueda 1987, 1991). In Avachinsky Bay, Kamchatka, *Acartia hudsonica* was abundant in the inner bay and was replaced by *Acartia longiremis* offshore (A. Somatov, Institute of Marine Biology, Vladivostok, pers. comm.), a similar distribution pattern to that in the northern Okhotsk Sea.

Low food concentrations in offshore areas were the main delimiting factor for *Acartia tonsa*, for which the distribution was restricted to the nearshore environment (Paffenhöfer and Stearns 1988). This same factor may have been responsible for the distribution of *Acartia hudsonica* (Ueda 1991).

Previous large-scale studies examined the offshore zooplankton community (Gorbatenko 1990). These studies were conducted at bottom depths ≥40 m. The dominance of *Thysanoessa* spp., *Pseudocalanus minutus*, *Metridia ochotensis*, *Acartia longiremis*, and numerous meroplankton in those samples (Gorbatenko 1990) suggested that community A was part of this offshore group.

The most important seasonal changes in the zooplankton community structure were changes of relative abundance of oceanic and neritic species, and changes in the area occupied by inshore community B. These changes were related to oceanographic patterns. Two main oceanographic features influenced the region: the northern Okhotsk Sea seasonal oceanographic front, and freshwater runoff (Chernyavsky 1970a, Chernyavsky et al. 1981). The seasonal front occurred as a result of the convergence of warmer shelf water and the colder upwelled Yamsk Current flowing from the northeastern Okhotsk Sea southwest along the coast. The front usually developed with atmospheric warming in July and was maximal in September, resulting in higher horizontal and vertical density gradients (Chernyavsky 1970a). It seemed that the front isolated the nearshore environment from the penetration of oceanic water. As a result freshwater runoff had a stronger influence than it did in other months when the front was not present. These processes created a brackish water habitat suitable for neritic species in closed and semi-closed bays.

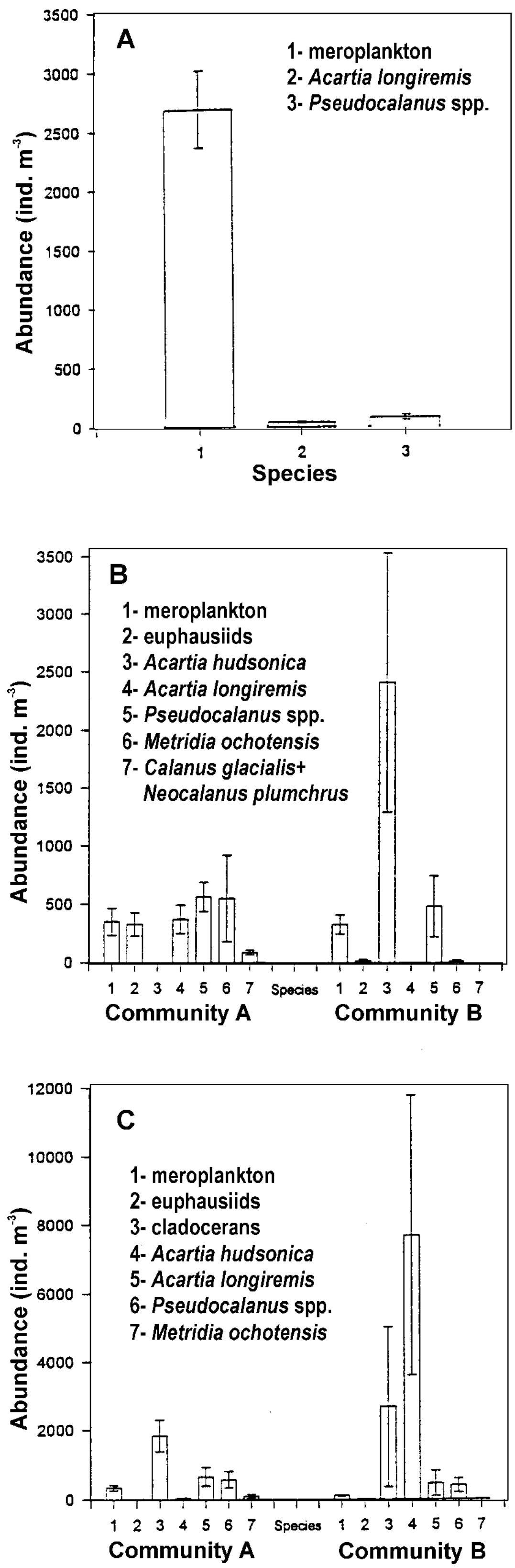

Figure 30. Abundance of the dominant zooplankton taxa in the northern Okhotsk Sea. A = May 1989, B = July 1988, C = September 1988.

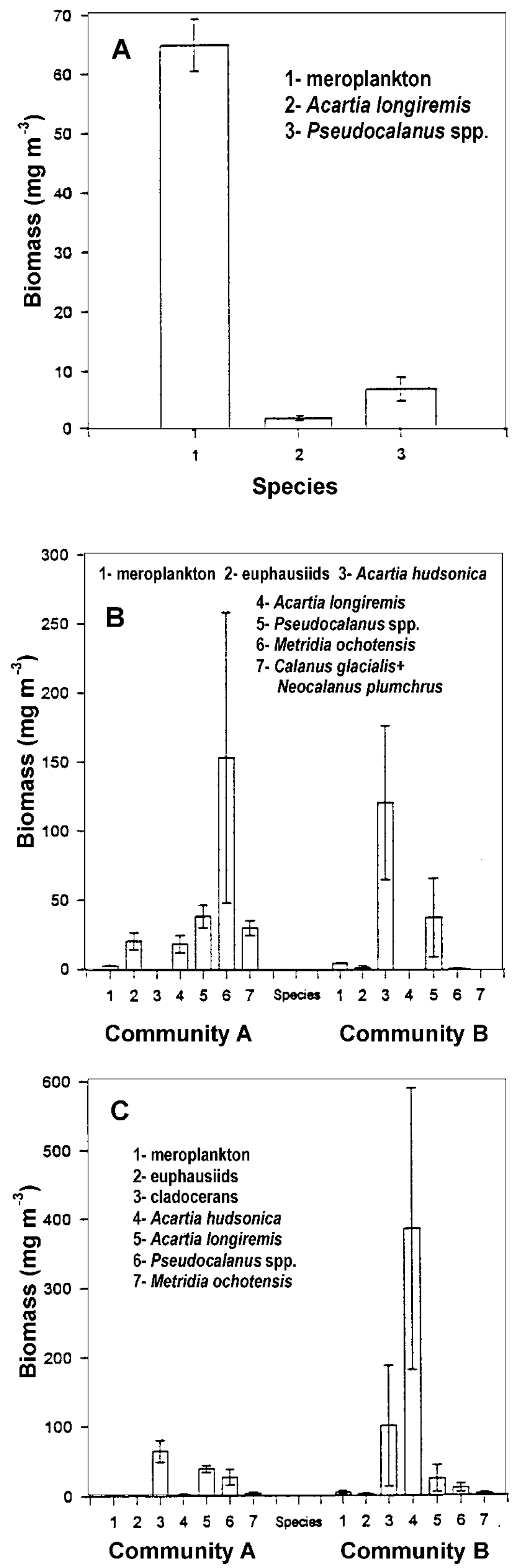

Figure 31. Biomass of the dominant zooplankton taxa in the northern Okhotsk Sea. A = May 1989, B = July 1988, C = September 1988.

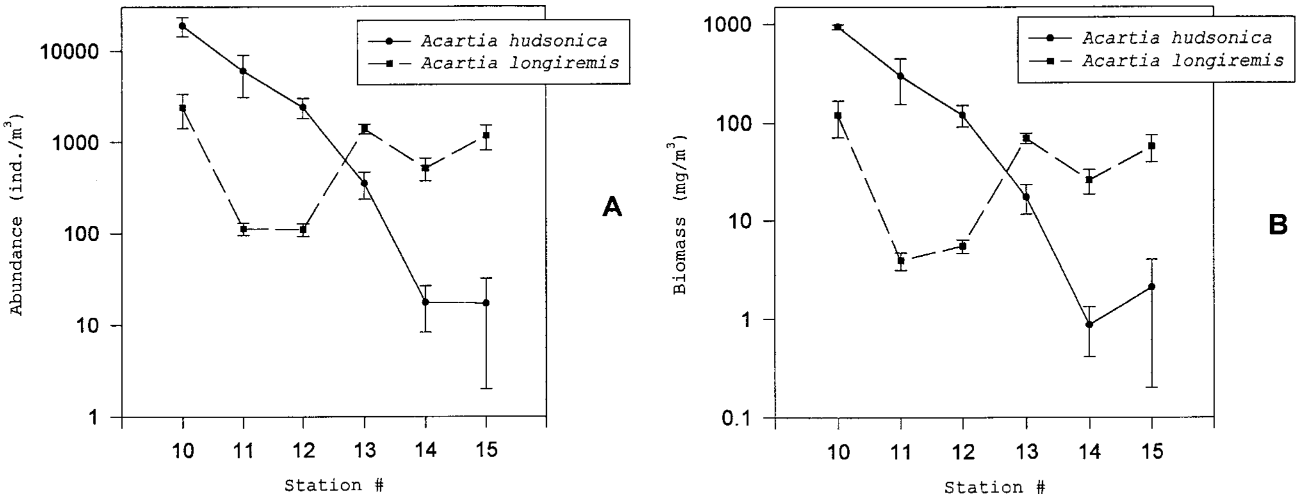

Figure 32. Acartia hudsonica and Acartia longiremis abundance (A) and biomass (B) in Motykleisky Bay during September 1988.

Southern Okhotsk Sea

TINRO surveyed zooplankton in the Sakhalin-Kuril region in the summer of 1991 (Shuntov et al. 1993c). They sampled 138 hydrographic and plankton stations, and undertook nekton trawling in 10 areas (Fig. 33). The sampling sites were similar to previous expeditions (Shuntov et al. 1988, 1990; Gorbatenko and Cheblukova 1990). The zooplankton were divided into three size categories, (small <1.2 mm, medium 1.2-3.5 mm, and large >3.5 mm) using screens as described in Volkov (1988). Macroplankton was predominant in all areas, contributing up to 90% of the total biomass. The small size fraction accounted for 5-21% of the total plankton biomass, which averaged 76-206 mg m^{-3}. The biomass of the medium fraction was approximately half that (28-111 mg m^{-3}). The average biomass of macroplankton in waters of the vast region adjoining the Kuril Islands (areas 1, 2, and 6) (Fig. 33) was 263.8-364.8 tons km^{-2} (Table 3). That was comparable to the macroplankton density in the very productive areas of the northern Okhotsk Sea (Shuntov et al. 1990). The oceanic waters appeared to be rich with macroplankton when compared with the deepwater areas of the Okhotsk Sea.

Oceanographic conditions in the Sakhalin-Kuril region were characterized by great heterogeneity (Shuntov et al. 1993c). This resulted from intensive water dynamics and intrusion of warm subtropical waters via the Soya Current from the Sea of Japan and via the Kuroshio Current branches into the southern parts of the region southeast of the South Kuril Islands. The study area supported large-scale pelagic fisheries. The diversity of food organisms in this region was related to its high productivity (Shuntov et al. 1993c), but the stock density was determined by variable oceanographic conditions. When the Kuril front passed close to the islands (Kosaka 1986, Filatov 1989) there was increased plankton abundance. In the summer of 1991 the frontal zone was parallel to the Kuril Islands and between the Kuril Current and Oyashio Countercurrent.

General Patterns of Zooplankton Distribution

The first zooplankton survey that covered the entire Okhotsk Sea was conducted by the Institute of Oceanology on the vessel *Vityaz* in 1949 and 1952 (Lubny-Gertsik 1959). Based on this survey of zooplankton biomass in the 0-100 m layer (Fig. 34), the Okhotsk Sea was subdivided into five areas:

1. The southern Okhotsk Sea with over 1,000 mg m^{-3}, mostly oceanic species.

2. The central Okhotsk Sea with the lowest biomass of 130-160 mg m^{-3}.

3. The northeastern Okhotsk Sea with 1,000 mg m^{-3} over most of the area, but exceeding 6,000-9,000 mg m^{-3} in some localities.

4. The shallow northern Okhotsk Sea with only 200-500 mg m^{-3}.

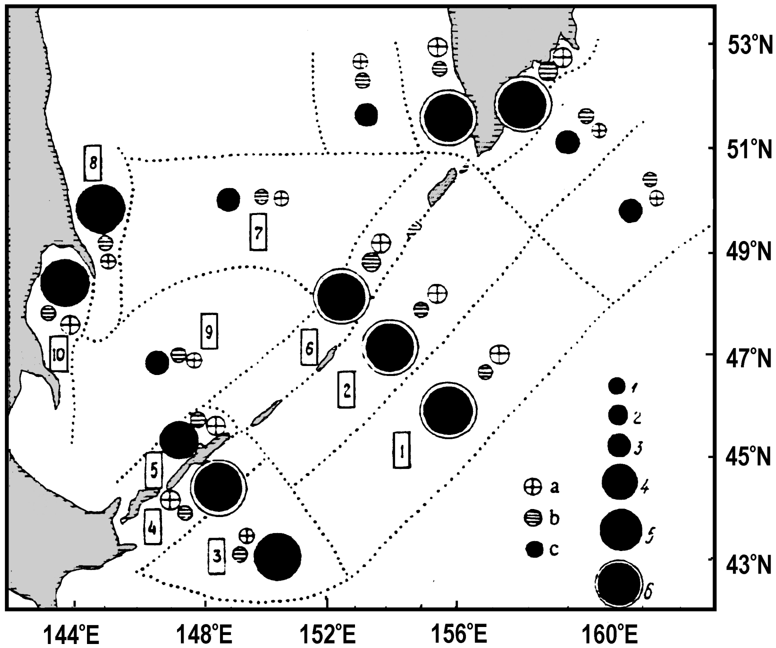

Figure 33. Average biomass (mg m^{-3}) of small (a), medium (b), and large (c) zooplankton fractions by area in summer 1991. Biomass: 1 = <100, 2 = 100-300, 3 = 300-500, 4 = 500-750, 5 = 750-1,000, 6 = >1,000. Mesh size = 0.168. Dotted lines represent boundaries of areas of averaged biostatistical information; figures in rectangles are numbers of areas (from Shuntov et al. 1993c).

Table 3. Density and biomass of macroplankton in the Sakhalin-Kuril region July 18-August 14, 1991.

	Density, tons km^{-2}						Biomass
Areas	Euphausiids	Amphipods	Copepods	Chaetognaths	Others	Total	10^6 tons
1	63.4	10.2	47.2	126.8	16.8	264.4	64.07
2	50.2	6.2	78.2	122.2	7.1	263.9	39.5
3	39.6	8.8	34.0	113.6	2.4	198.4	19.14
4	63.1	7.2	44.1	36.8	5.8	157.0	6.05
5	70.4	3.2	20.4	22.0	6.6	122.6	3.0
6	208.6	11.2	71.6	72.8	0.6	364.8	26.81
7	22.2	4.4	36.4	23.8	1.4	88.2	9.99
8	140.2	2.5	10.4	21.3	0.6	175.0	4.02
9	50.6	2.4	22.6	21.6	0.8	98.0	15.09
10	65.3	8.8	8.3	15.5	0.7	98.6	5.53

From Shuntov et al. 1993c.

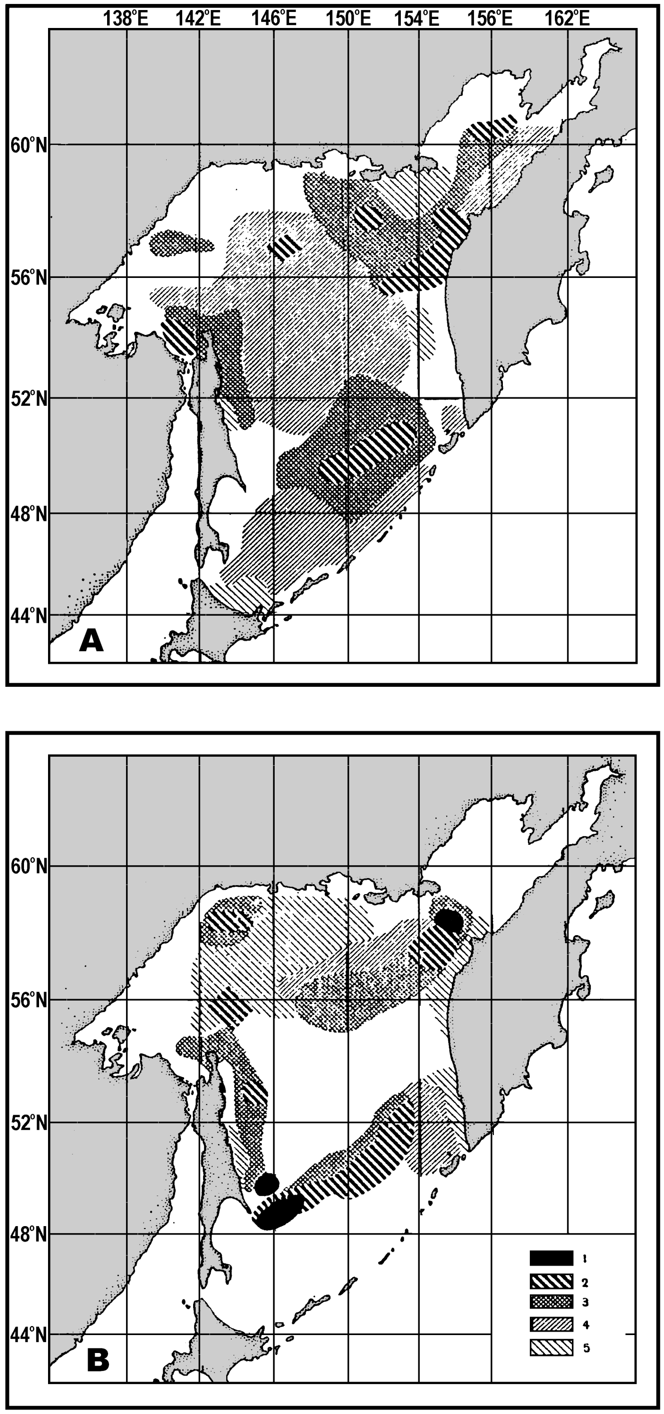

Figure 34. Zooplankton biomass distribution in the 0-100 m layer (mg m⁻³). A = August-November 1949, B = September-November 1952. 1 = >1,000, 2 = 500-1,000, 3 = 200-500, 4 = 100-200, 5 = <100 (from Lubny-Gertsik 1959).

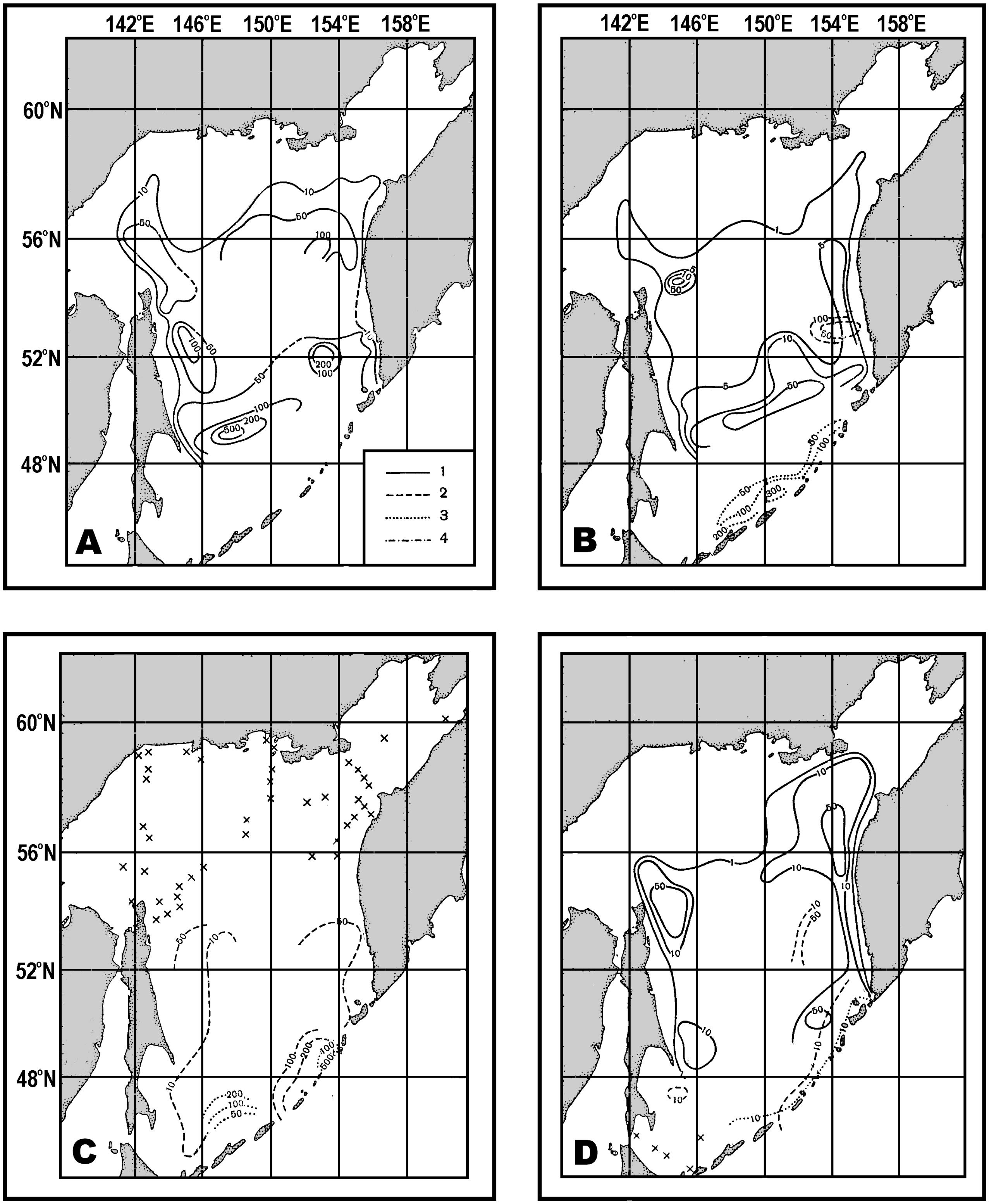

Figure 35. Biomass distribution in the 0-100 m layer. A = Calanus plumchrus, B = Calanus cristatus, C = Eucalanus bungii, D = Metridia pacifica. 1 = September-October 1952, 2 = June-July 1951, 3 = June-July 1950, 4 = August-September 1949 (from Lubny-Gertsik 1959).

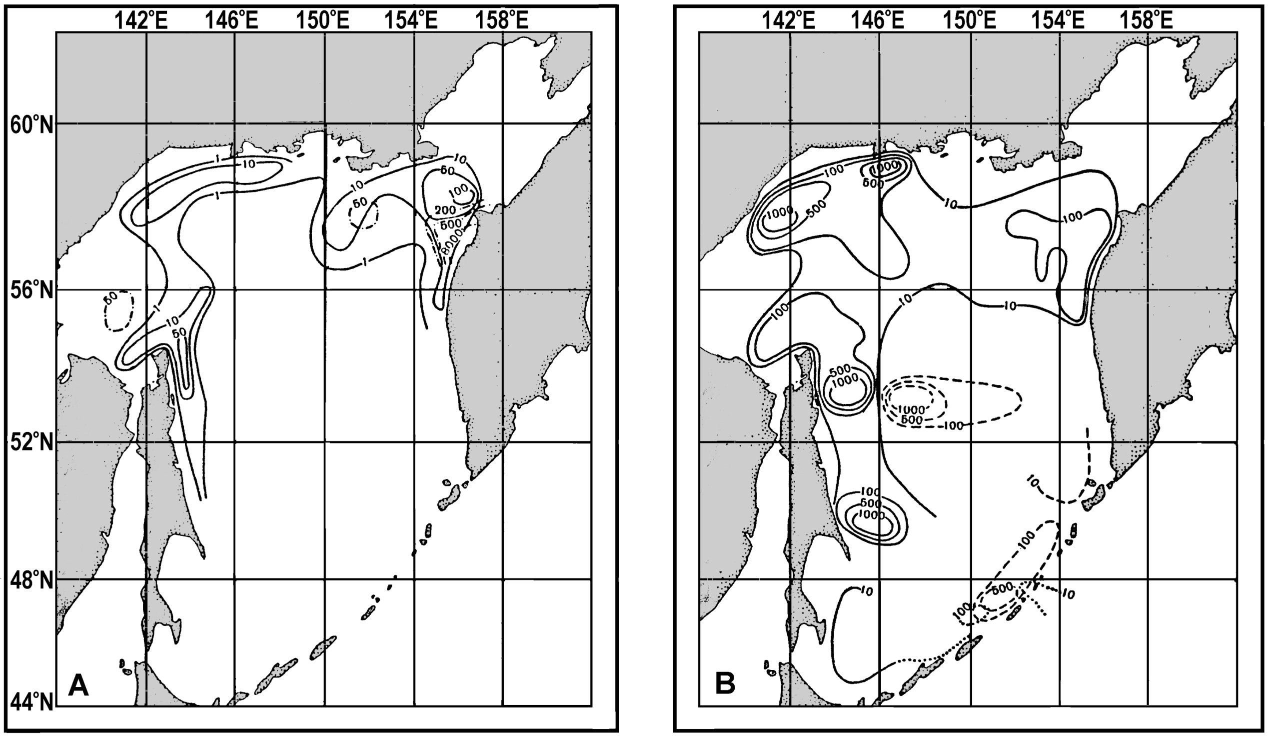

Figure 36. Biomass distribution in the 0-100 m layer. A = Calanus glacialis, B = Metridia ochotensis. 1 = September-October 1952, 2 = June-July 1951, 3 = June-July 1950, 4 = August-September 1949 (from Lubny-Gertsik 1959).

5. The northwestern Okhotsk Sea including St. Iona Island and northern Sakhalin Island regions with 1,000 mg m^{-3}, dominated by *Metridia ochotensis*.

The average zooplankton biomass for the summer-fall season over the Okhotsk Sea in the 0-100 m layer was estimated to be 340-350 mg m^{-3}. The maximal value of 9,000 mg m^{-3} was observed in the 0-70 m layer in the northeastern Okhotsk Sea. The copepod biomass distribution maps show the concentration of oceanic species in the south (Figs. 35, 36).

Others have attempted to assess plankton stocks and distribution over the entire Okhotsk Sea. Kun (1975) pooled data on the mesoplankton from two surveys, taken in different regions of the sea in different years. Markina and Chernyavskiy (1984) pooled information, primarily from the previous 25 years, and averaged the biomass from net-caught phytoplankton and zooplankton to obtain general Okhotsk Sea distributions. The distribution scheme was based on data collected in the upper 100 m, and the technique for averaging the data was recorded in Markina and Chernyavskiy (1984). Their composite estimates of biomass were higher than earlier calculations, both in the coastal regions and off the shelf. The authors emphasized that their plankton distribution patterns generally corresponded with the locations of cyclonic and anticyclonic eddies and gyres and other Okhotsk Sea current patterns (Figs. 37, 38, 39). The highest plankton biomass, up to 30,000 mg m^{-3}, was recorded for the northeastern Okhotsk Sea and was related to complicated oceanographic patterns which featured the Western Kamchatka Current divergence, the anticyclonic gyre over the TINRO Basin, divergence between the Yamsk and North Branch currents, coastal transformation of Yamsk Current water, and a seasonal oceanographic front resulting from convergence of North-Okhotsk and Yamsk currents.

In the northwestern Okhotsk Sea, another productive region was formed by the Ayansk cyclonic gyre with transformed water from the Shantar Islands region, the brackish Amur Current, upwelling near St. Iona Island, and the cyclonic gyre over Kashevarov Bank. The plankton biomass exceeded 20,000 mg m^{-3} in that area. Generally high

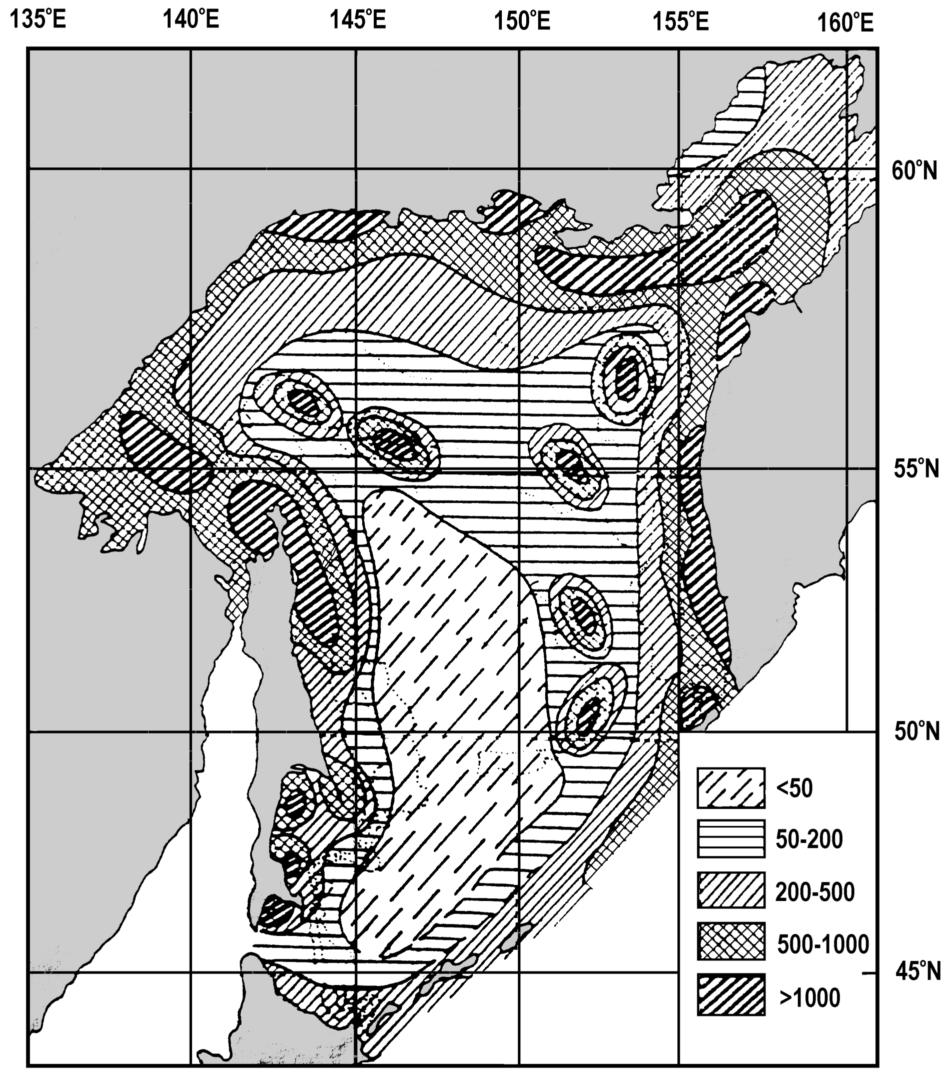

Figure 37. Generalized summer phytoplankton biomass distribution (mg m^{-3}) in the 1-100 m layer (from Markina and Chernyavskiy 1984).

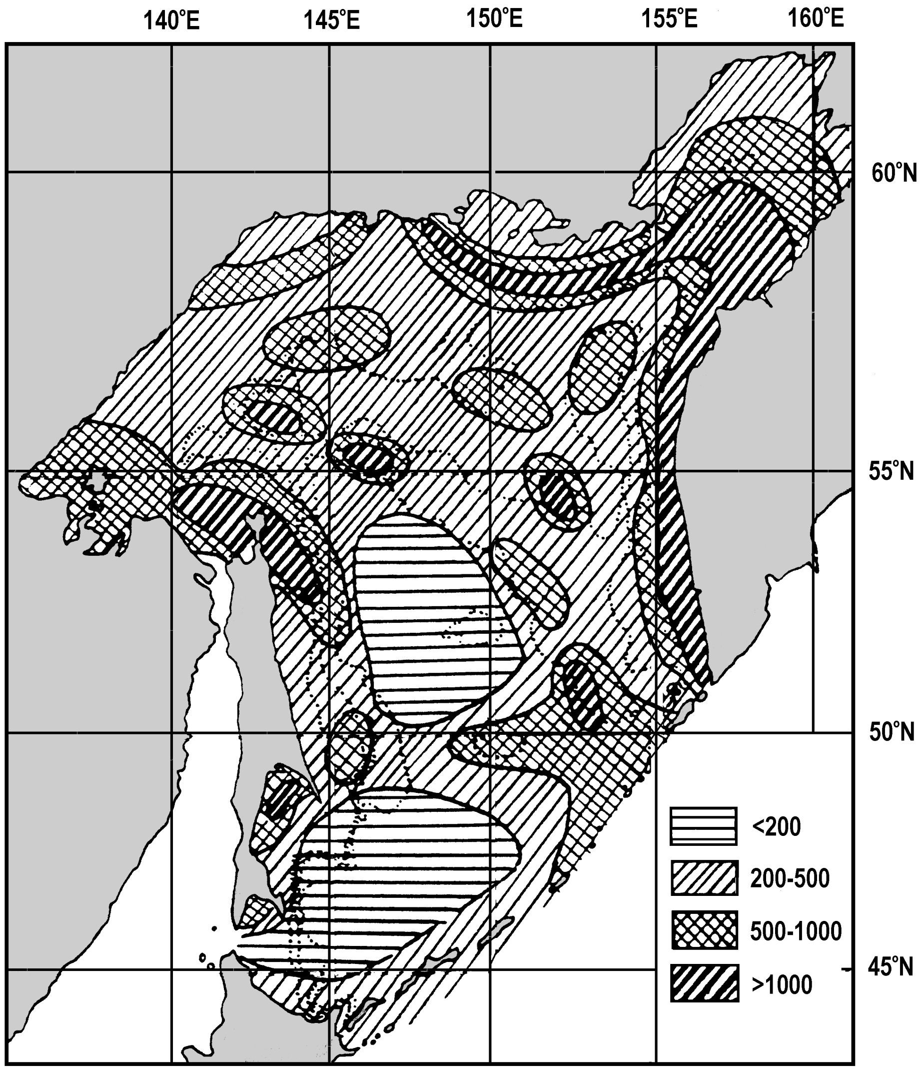

Figure 38. Generalized summer zooplankton biomass distribution (mg m^{-3}) in the 1-100 m layer (from Markina and Chernyavskiy 1984).

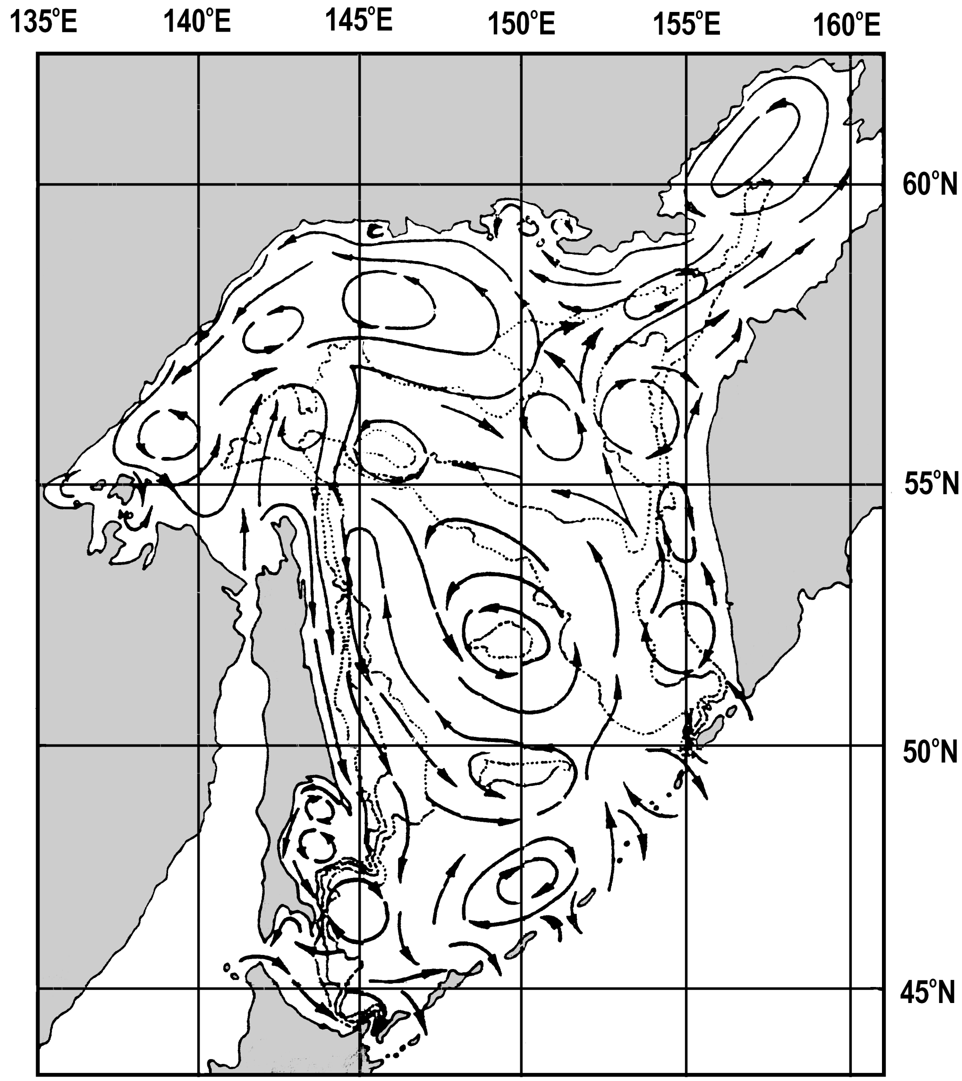

Figure 39. Generalized scheme of summer currents in the 0-200 m layer (from Markina and Chernyavskiy 1984).

Table 4. Average multiyear biomass (10^6 tons) and annual production (10^6 tons) of phytoplankton and zooplankton for different regions of the Okhotsk Sea.

Region	Area, $km^2 \times 10^3$	Phytoplankton biomass	Phytoplankton production	Zooplankton biomass	Zooplankton production
Northern shelf	467	157	23,700	107	1,070
Western Kamchatka shelf	64	23	4,800	21	215
Eastern Sakhalin shelf	83	21	3,600	13	136
Kuril-Hokkaido shelf	33	7	1,500	4	36
All shelf waters	648	208	33,600	145	1,460
Deep sea water	925	48	8,700	61	607
Entire Okhotsk Sea	1,573	256	42,300	205	2,070

From Shuntov 1985, p. 170, modified.

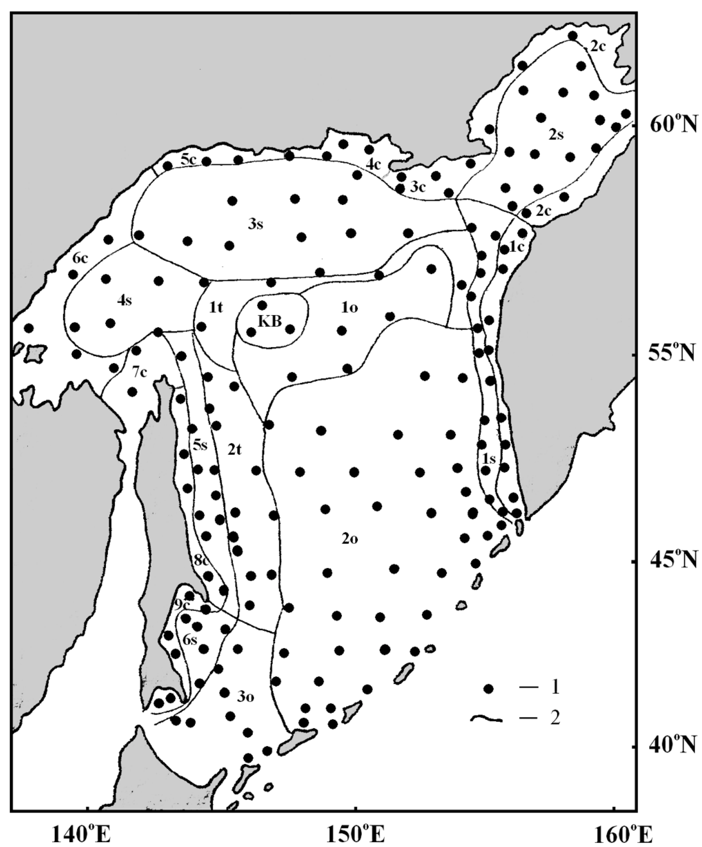

Figure 40. Plankton communities and topographic regions in the Okhotsk Sea. 1 = sampling localities, 2 = boundaries of plankton communities, 1c = Western Kamchatka, 2c = Shelikhov, 3c = Yamsk, 4c = Tauyskaya, 5c = Okhotsk-Lisyanskiy, 6c = Shantar, 7c = North Sakhalin, 8c = South Sakhalin, 9c = Terpeniya Bay, 1s = Western Kamchatka, 2s = Shelikhov, 3s = North Okhotsk, 4s = Shantar, 5s = Sakhalin, 6s = Terpeniya Bay, 1o = Northern, 2o = Central, 3o = Southwestern, KB = Kashevarov Bank, 1t = Northern, 2t = Western (from Gorbatenko 1990).

Table 5. Biomass of zooplankton size fractions, and percent of total, in the Okhotsk Sea, summer 1986.

Region	Depth (m)	Small	Medium	Large	Total	Phyto-plankton	Euphausiids	Hyperiids	Copepods	Chaeto-gnaths	Others
Coastal Community											
1c	95	246.0 5.9	61.0 1.5	3,872.4 92.6	4,179.4	220	2,905 75.1	13.3 0.3	373.3 9.6	53.0 13.7	50.8 1.3
2c	61	364.4 24.4	158.5 10.6	968.0 65.0	1,490.9	181	385 39.8	3.3 0.3	331.1 34.2	216.7 22.4	31.9 3.3
3c	104	120.5 9.3	186.4 14.4	988.7 76.3	1,295.6	153	561.5 56.8	24.5 2.5	372.0 37.6	25.0 2.5	5.8 0.6
4c	107	193.3 38.6	146.9 29.3	161.2 32.1	501.4	+	125.0 77.5	3.0 1.9	30.1 18.6	3.0 1.9	0.1 0.1
5c	100	285.5 21.6	583.3 44.0	456.5 34.4	1,325.3	+	260.7 57.1	5.0 1.1	36.1 7.9	121.0 26.5	33.7 7.4
6c	103	225.5 28.9	226.7 29.0	329.0 42.1	781.2	88	121.7 37.0	59.3 18.0	90.5 27.5	46.3 14.1	11.2 3.4
7c	64	59.7 2.6	53.1 2.3	2,222.5 95.1	2,335.3	375	2,135.0 96.1	5.0 0.2	77.0 3.5	–	5.5 0.2
8c	89	80.9 5.0	44.5 2.8	1,486.5 92.2	1,611.9	140	797.5 33.7	150 10.1	299 20.1	240 16.1	–
9c	52	130.7 7.2	42.6 2.4	1,631.4 90.4	1,804.7	+	1,186.7 79.7	20.0 1.2	149.4 9.2	270.0 16.6	5.3 0.3
Average	81	208.6 12.7	142.6 8.7	1,291.6 78.6	1,642.8	160.7	881.4 68.2	33.7 2.6	189.5 14.7	168.9 13.1	18.1 1.4
Shelf Community											
1s	155	496.3 22.4	212.8 9.6	1,503.3 68.0	2,212.4	+	280.0 18.6	188.0 12.5	908.7 60.4	126.4 8.4	0.2 0.01
2s	178	324.3 15.8	292.2 14.2	1,438.8 70.0	2,055.3	9.2	554.8 38.6	189.8 13.2	514.0 35.7	161.8 11.2	18.4 1.3
3s	199	295.2 13.5	427.0 19.5	1,463.4 67.0	2,185.6	1.0	1,096.2 74.9	37.0 2.5	268.5 18.4	51.0 3.5	10.7 0.7
4s	188	194.3 26.4	75.4 10.2	467.7 63.4	737.4	21.0	127.0 27.1	8.7 1.9	332.0 71.0	–	–
5s	390.2	122.8 8.3	41.0 2.8	1,321.9 88.9	1,484.7	79.2	403.6 30.5	225.0 17.0	687.0 52.0	4.0 0.3	2.3 0.2
6s	150.0	163.2 11.7	203.0 14.6	1,026.0 73.7	1,392.2	6.7	29.0 2.8	10.0 1.0	817.0 79.6	170.0 16.6	–
Average	197.6	295.2 15.6	223.1 11.8	1,373.0 72.6	1,891.3	15.4	529.0 38.5	139.1 10.1	595.9 43.4	101.3 7.4	7.7 0.6
Open Sea Community											
1o	670	124.8 8.1	17.2 1.1	1,398.8 90.8	1,540.8	80	70.3 5.0	40.2 2.9	848.3 60.7	420.0 30.0	20.0 1.4
2o	1496	166.6 11.0	108.9 7.2	1,234.2 81.8	1,509.7	903	113.5 9.2	56.1 4.5	876.2 71.0	183.8 14.9	4.6 0.4
3o	1975	80.3 4.9	104.0 6.4	1,441.0 88.7	1,625.3	133	481.5 33.4	54.6 3.8	858.4 59.5	40.0 2.8	6.5 0.5
Average	1509	149.7 9.9	103.8 6.9	1,254.7 83.2	1,508.2	716	131.6 10.5	55.1 4.4	873.5 69.6	188.9 15.1	5.6 0.4
KB[a]	115	14.0 1.6	97.6 11.2	762.0 87.2	873.6	1152	570.0 74.8	12.0 1.6	172.0 22.6	8.0 1.0	–

Table 5. (Continued.)

Region	Depth (m)	Small	Medium	Large	Total	Phyto-plankton	Euphausiids	Hyperiids	Copepods	Chaeto-gnaths	Others
Transition Zone											
1t	775	98.0 5.7	32.0 1.8	1,651.9 92.5	1,731.9	17.1	8.9 0.5	52.1 3.2	1,504.4 91.1	85.0 5.1	1.5 0.1
2t	502	101.0 7.5	64.4 4.8	1,178.5 87.7	1,343.9	6,340	488.5 41.4	17.5 1.5	530.0 45.0	142.5 12.1	–
Average	693	98.9 6.5	41.2 2.7	1,389.5 90.0	1,529.6	1,914	199.0 14.3	38.4 2.7	1,061.4 70.4	89.7 6.5	1.0 0.1

[a] KB = Kashevarov Bank

Units = mg m^{-2}/% of total. From Gorbatenko 1990.

plankton biomass (500-20,000 mg m^{-3}) characterized the zone of intensive vertical mixing between the warmer Western Kamchatka Current and the cold water of the central Okhotsk Sea. There are some hints of the existence of a productive zone in the central and southwestern Okhotsk Sea, but insufficient hydrobiological data existed to verify it.

Markina and Chernyavskiy (1984) determined the average biomass and total stock of phytoplankton and zooplankton for various regions separately. These results produced maximum net-caught phytoplankton and zooplankton biomass estimates of 1,200 and 2,500 mg m^{-3} over the Western Kamchatka Shelf, with an average for the entire Okhotsk Sea of 510 and 985 mg m^{-3} and total estimated stocks of 8.53×10^7 tons and 1.537×10^8 tons. The nanoplankton component of the phytoplankton and the micro- and macrozooplankton components were not included in the above estimates. Shuntov (1985) revised these calculations and estimated annual production for different regions of the Okhotsk Sea as well (Table 4).

Another assessment of plankton distribution was attempted by Volkov and Chuchukalo (1985), who averaged data on biomass from net-caught phytoplankton and zooplankton for the entire Okhotsk Sea collected by TINRO during the previous 30 years. Their data set included about 4,600 samples collected during several seasons. They found that during biological spring (April-June) the average seston biomass reached about 1,600 mg m^{-3} and consisted mostly of phytoplankton. The general pattern of biomass distribution during biological summer (July-September) was similar to that during spring, although the values were somewhat lower (about 700 mg m^{-3} with range of 300-2,100 mg m^{-3}). Only 14 zooplankton species achieved an average density greater than 100 individuals m^{-3}. The northern Okhotsk Sea had lower biomass of seston (500-1,000 mg m^{-3} in spring and 200-500 mg m^{-3} in summer). Low biomass was also encountered in the southern Okhotsk Sea near Sakhalin Island. The central Okhotsk Sea had higher biomass, probably related to an upwelling in the divergence zone of the Western Kamchatka Current and the cyclonic gyre located at 52°N×150°E. The neritic zone was not surveyed. The total seston biomass over the upper 100 m in the Okhotsk Sea during spring was 2.5×10^8 tons, and 1.1×10^8 tons during summer. These values were close to previous estimates (Markina and Chernyavskiy 1984).

In June-September 1986 TINRO undertook a large-scale survey of the entire Okhotsk Sea, collecting samples from 180 locations with vertical tows from 100 m depth to the surface or from the bottom at shallower stations. The results were presented by Gorbatenko (1990). The author divided the sea into neritic, shelf, open ocean, and intermediate zones. Each zone was further divided into subregions based on zooplankton species composition and abundance (Fig. 40). The following data were tabulated for each region: phytoplankton biomass, total zooplankton biomass, zooplankton biomass by size fraction, and total biomass for various taxonomic categories (Table 5). The biomass of the small zooplankton size fraction was less than 10% of total zooplankton biomass in the open ocean, 15.6% on the shelf, and 12.7% in the neritic zone. The large fraction biomass increased from 78.6% at neritic sites and 72.6% over shelf waters to more than 80% in oceanic waters. The highest total biomass occurred on the shelf (1,373 mg m^{-3}).

In November-December 1990 TINRO conducted plankton surveys at 86 stations over the Okhotsk Sea. The winter distribution of *Metridia pacifica* was reported by Shebanova (1994). It was found

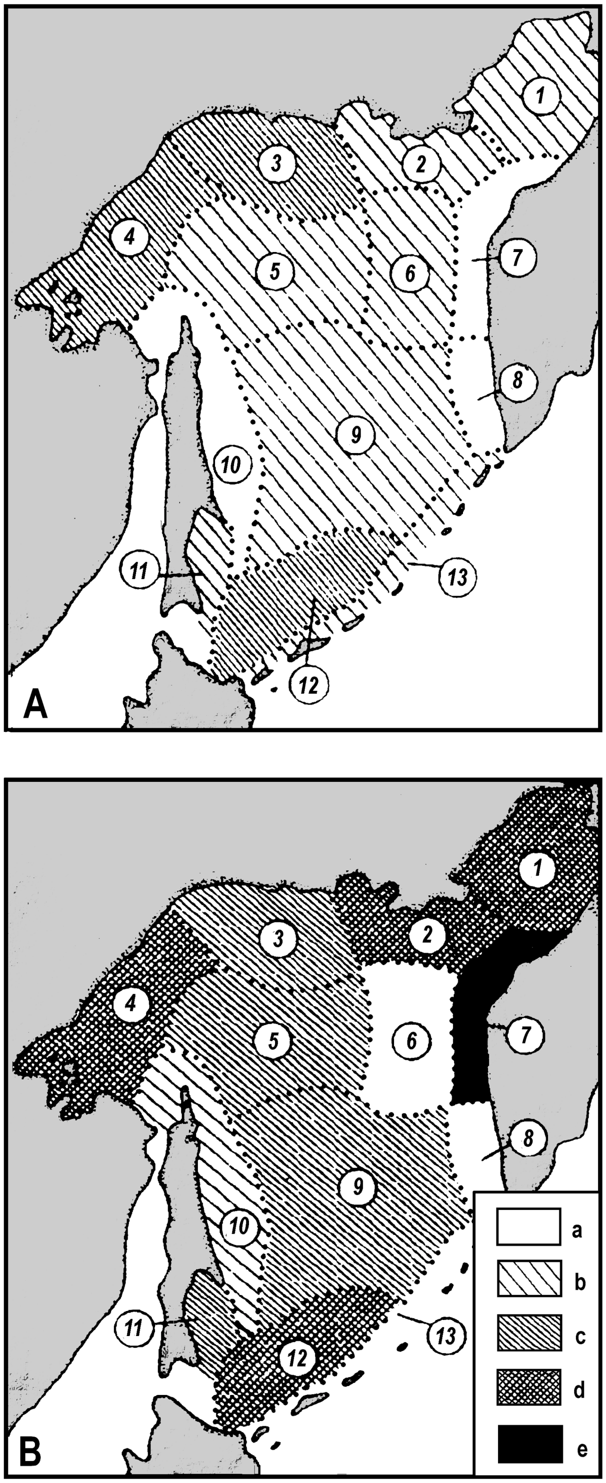

Figure 41. Distribution of zooplankton production (g m^{-2}) in the Okhotsk Sea in the 0-200 m layer in autumn (A) and in summer (B). a = <1, b = <100, c = 150-300, d = 300-800, e = >800. Regions: 1 = Shelikhov, 2 = Yamsk-Tauyskaya, 3 = Okhotsk-Lisyanskiy, 4 = Ayano-Shantar, 5 = Iona-Kashevarov, 6 = TINRO Basin, 7 = North Kamchatka, 8 = South Kamchatka, 9 = Central Trough, 10 = Sakhalin, 11 = Terpeniya Bay, 12 = Southern Deep Water, 13 = Kurils (from Dulepova 1994).

Table 6. Biomass and production of elements of zooplankton communities in the epipelagic layer of the Okhotsk Sea.

	Nonpredatory				Predatory			
	Summer 1989		Autumn 1986		Summer 1989		Autumn 1986	
Region	B	P	B	P	B	P	B	P
1	134	1206	170	287	83	323	98	78
2	254	819	191	173	11	35	47	32
3	160	302	175	284	20	41	68	54
4	297	445	229	206	4	14	34	27
5	134	374	129	87	22	76	33	26
6	212	657	70	125	82	278	23	20
7	435	2699	99	180	106	372	88	79
8	160	481	77	100	77	293	66	51
9	342	1267	89	187	65	247	50	35
10	90	388	61	151	46	165	80	72
11	115	437	71	141	21	77	23	16
12	174	785	81	169	34	93	69	49
13	164	802	97	192	108	336	45	63

B = biomass, g m^{-2}; P = production, g m^{-2}. See Fig. 41 for region locations. From Dulepova 1994.

that the species distribution was rather uniform with an average biomass of 50-100 mg m^{-3}. The highest concentrations, which consisted predominantly of copepodid stages III-V, were seen off the western Kamchatka and eastern Sakhalin Island coasts in the central deepwater part of the Okhotsk Sea. Since copepodid stage IV accounted for 86% of the population, copepodid stages III and V made up only 5% total of the individuals, and about 3% of the population overwintered as mature females, it was concluded that *Metridia pacifica* did not reproduce during the winter.

Data from zooplankton surveys carried out between 1984 and 1990 were used by Dulepova (1994) to analyze the trophic structure of zooplankton communities and to calculate their production. The author divided the Okhotsk Sea into regions based on hydrological characteristics (Fig. 41). The zooplankton was divided into two trophic groups: predatory and nonpredatory. These two groups were further subdivided into three size fractions (Volkov 1988). Reported data on specific production of dominant taxa (Andreeva 1977, Zaika 1983, Shushkina 1977, Shushkina and Vinogradov 1987) and data on taxonomic composition and biomass of each category were used to determine the levels of their specific daily production as:

$$P_{cat} = \sum_{i=1}^{n} C_i \overline{B}_i$$

where P_{cat} is daily production of a category, C_i is specific production of species *i*, $\overline{B}_i$ is mean biomass of species *i*, and *n* is number of species (Dulepova 1991, 1993). Then production values of categories within each trophic group were summed to obtain the group production estimate. Then the average seasonal production was computed from biomass estimates and the length of seasons (Table 6). That technique relied upon a large number of assumptions for both biomass and production estimates, so those results were only rough estimates which must be used with caution (Alimov 1989, Shuntov et al. 1990).

Interannual Variability of Zooplankton and Recent Changes in the Community Structure

Results of recent extensive TINRO studies in the Okhotsk Sea indicated a shift in zooplankton community structure presumably related to a climatic change in the area in the early 1990s (Klyashtorin 1995, Klyashtorin and Sidorenkov 1993, Klyashtorin and Smirnov 1994, Shuntov et al. 1990, Shuntov 1994). The shift was especially well pronounced in the southern Okhotsk Sea, including the Sakhalin-Kuril region (Shuntov et al. 1998b), and it was

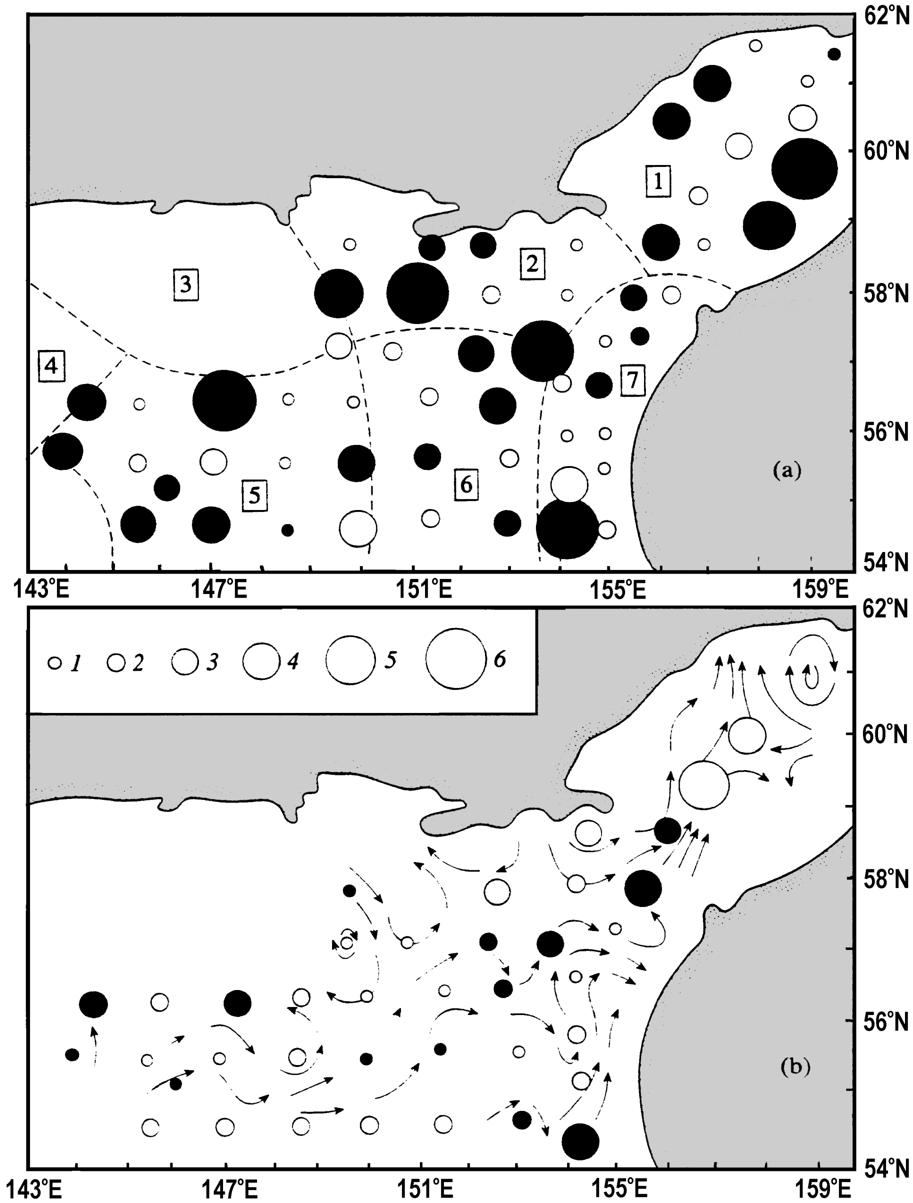

Figure 42. Distribution of biomass of large zooplankton in the 0-50 m (a) and 50-200 (bottom) m layer (b) in fall 1994 in the northern Okhotsk Sea. White (daytime sampling) and black (nighttime sampling) circles correspond to biomass (mg m^{-3}): 1 = < 200, 2 = 201-500, 3 = 501-1,000, 4 = 1,001-2,000, 5 = 2,001-3,000, 6 = >3,000. Dashed lines and numbers indicate areas; arrows indicate main surface currents (from Radchenko et al. 1997b).

Table 7. Nighttime estimates of zooplankton biomass (t km^{-2}) in the northern Okhotsk Sea in September-October 1994.

Area	Ave. trawling depth, m	Depth	Size			Composition of large zooplankton					Total
			Small	Medium	Large	Euphausiids	Amphipods	Copepods	Chaetognaths	Pteropods	
1		0-50 m	35.5	21.2	95.1	50.8	14.8	7.2	21.8	0.4	152
	115	50-200 m	15.5	1.6	33.7	14.0	0.1	9.0	10.5	0	51
2		0-50 m	10.4	24.0	90.6	67.1	0.6	17.5	3.9	0.6	125
	145	50-200 m	1.4	1.9	1.4	0	0	1.0	0	0.5	5
5		0-50 m	21.5	15.1	77.2	48.0	10.2	14.9	4.0	0	114
	200	50-200 m	12.9	4.5	53.3	27.0	8.7	15.2	2.4	0	71
6		0-50 m	21.9	22.5	76.8	9.8	11.8	50.4	4.5	0.3	121
	200	50-200 m	5.2	9.0	45.8	11.2	23.7	8.0	2.2	0	60
7		0-50 m	35.6	29.0	67.2	22.0	2.6	32.2	9.9	0.1	132
	150	50-200 m	10.5	26.7	125.5	105.2	6.2	8.4	1.9	0	63

Bottom depth = 200 m. From Radchenko et al. 1997b.

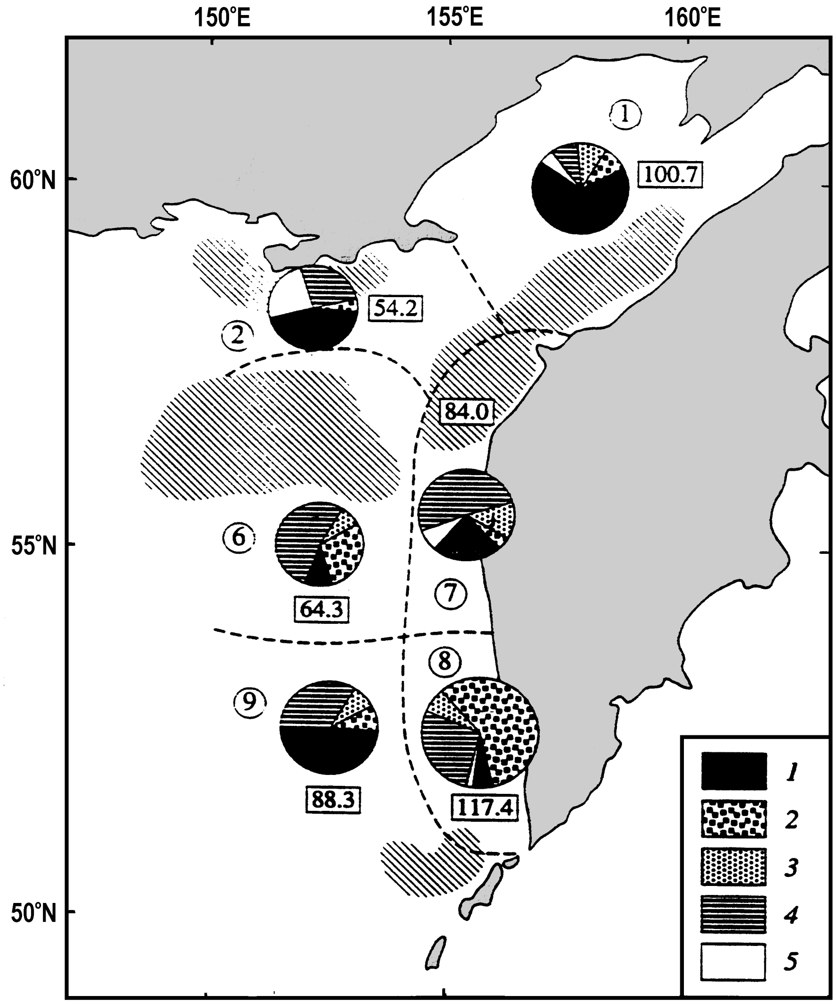

Figure 43. Mean zooplankton biomass (g m^{-2}) and the composition of macroplankton at 0-200 m in the northern Okhotsk Sea in June-July 1995. 1 = chaetognaths, 2 = euphausiids, 3 = amphipods, 4 = copepods, 5 = other. Dashed lines and numbers in circles indicate areas; numbers in rectangles indicate total zooplankton biomass (from Shuntov et al. 1998a).

Table 8. Composition and biomass of zooplankton (g m^{-3}) in the epipelagial of the northern Okhotsk Sea in June and July 1995.

	Size			Composition of large zooplankton					Total
Areas	Small	Medium	Large	Euphausiids	Amphipods	Copepods	Chaetognaths	Others	zooplankton
1	22.0	11.3	67.4	5.4	5.5	6.3	47.6	2.6	100.7
2	14.4	8.1	31.7	1.8	0.1	8.9	12.9	8.0	54.2
6	10.9	10.1	43.3	10.9	3.3	23.8	5.2	0.1	64.3
7	21.4	7.2	55.4	1.2	6.2	31.2	12.6	4.2	84.0
8	9.8	3.1	104.5	61.7	8.8	28.4	4.9	0.7	117.4
9	14.2	7.7	66.4	7.1	5.0	21.2	32.9	0.2	88.3

Mesh size = 0.168. See Fig. 43 for area locations. From Shuntov et al. 1998a.

analogous to a transitional period between the warm epoch of the 1920s-1930s and the epoch of 1940s-1960s (Shuntov et al. 1993b, Shuntov 1994). In the early 1990s a circulation shift was observed which was characterized by a few specific features that repeated from year to year and differed from the previously known circulation pattern (Moroshkin 1966, Chernyavskiy 1981). Those were the weaker advection of Pacific water through the northern Kuril straits and the enhanced advection of the warm, saline Soya Current water from the Sea of Japan (Radchenko et al. 1997a). The latter led to intensive front formation over the southwestern Kuril Basin and to the appearance of a current directed through the Kuril Basin toward the northwest and farther north (Radchenko et al. 1997a). This current brought warmer waters to the TINRO Basin and resulted in changes of the cyclonic circulation in the deepwater zone of the Okhotsk Sea to anticyclonic (Radchenko et al. 1997a). These features were especially well-pronounced in 1992 and 1994, while in 1991 a displacement of the cyclonic circulation into the northeastern Kuril Basin and the development of the warm stream along the southwestern boundary of the Kuril Basin, as well as the penetration of Pacific water into the Okhotsk Sea via Friza Strait, were observed (Shuntov et al. 1993a, Radchenko et al. 1997a).

In the 1990s, the pelagic community was considered to be in transition (Shuntov and Dulepova 1996). In the early 1990s in the southern Okhotsk Sea the biomass of predatory zooplankton such as chaetognaths and euphausiids increased while the copepods declined, possibly due to high numbers of planktivorous walleye pollock and sardines (Shuntov and Dulepova 1996, Shuntov et al. 1998b). The maximum development of chaetognaths was recorded in 1992, when they constituted 46% of total zooplankton biomass (Dulepova 1996). In 1994, this tendency was observed only near western Kamchatka (Shuntov et al. 1998a), while in the other areas the euphausiid biomass remained high and biomass of copepods increased and chaetognaths declined (Shuntov and Dulepova 1996). These shifts may reflect the onset of stabilization of the composition and structure of the zooplankton communities under new climatic conditions (Shuntov and Dulepova 1996).

A plankton and oceanographic survey of the northern Okhotsk Sea was carried out by TINRO from July to October 1994 (Fig. 42). It also revealed a possible transition state of the zooplankton communities (Radchenko et al. 1997b). Southerly and ocean-shifted trajectories of storm movements and an intense input of warm waters of the Soya Current toward Shelikhov Bay considerably prolonged the warm season in the upper layers (Radchenko et al. 1997b).

The group of small zooplankton was not abundant in all areas (Table 7) and was dominated by *Pseudocalanus* spp. The occurrence of nauplii and early copepodites of *Metridia ochotensis*, *Pareuchaeta japonica,* and juvenile *Limacina helicina* suggested their reproduction continued (Radchenko et al. 1997b). Medium-sized zooplankton was dominated by *Metridia ochotensis* and *Pseudocalanus* spp. copepodites as well as 0.5-1 mm long *Limacina helicina*. The latter formed large aggregations in Shelikhov Bay with biomass up to 170 mg m^{-3} (Radchenko et al. 1997b). The group of large zooplankton was dominated by *Thysanoessa raschii* over the shelf and *T. longipes* in deeper areas, as well as by *Neocalanus cristatus* and *N. plumchrus* in areas 6 and 7 (Fig. 42). *Calanus glacialis* dominated over the shelf in areas 1 and 2 with biomass up to 650 mg m^{-3}. This species can be found along

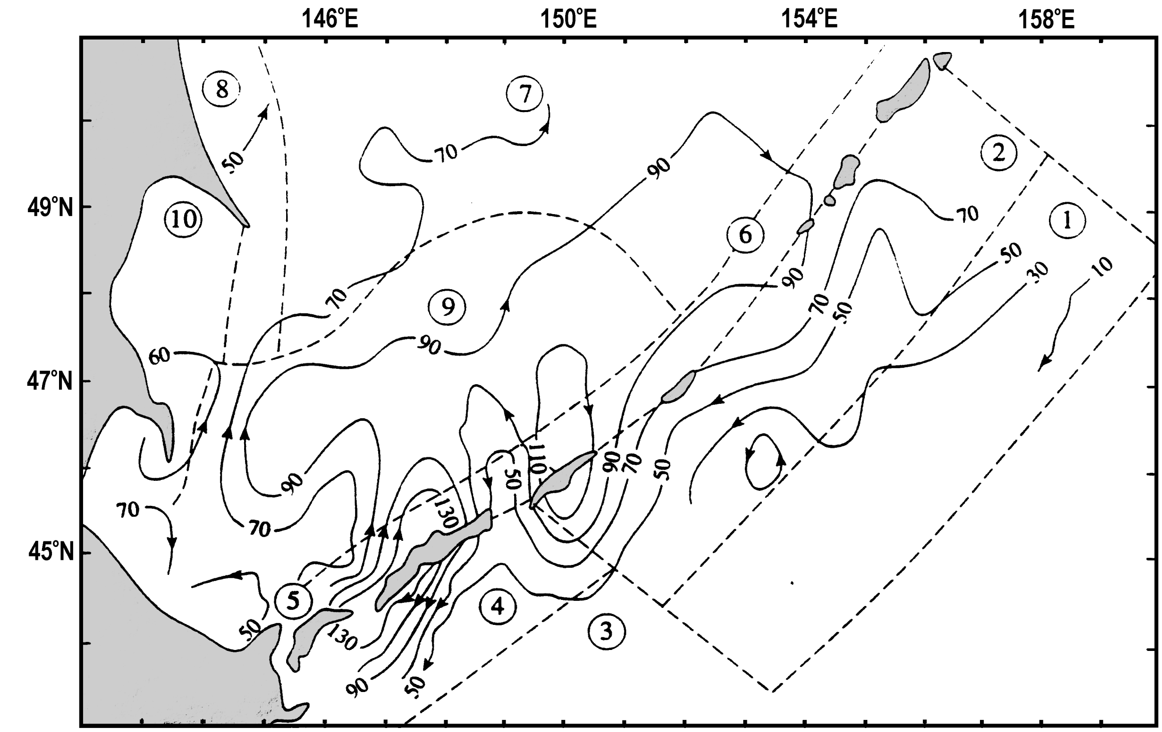

Figure 44. Southern Okhotsk Sea (Kuril Islands region) showing an area surveyed in summer 1994. Dashed lines with circled numbers indicate areas referred to in Table 9. Also shown is the dynamic topography (0-500 dB) (from Radchenko et al. 1997a).

the coast of the Kamchatka Peninsula as far as 51°30′N (Safronov 1984). In 1994 the southern boundary of the *C. glacialis* range was shifted northward to 55°30′N (Radchenko et al. 1997b). In general, the structure of zooplankton communities with euphausiids dominating shelf areas and copepods dominating near slope waters is fairly typical for the fall in the Okhotsk Sea (Volkov 1986, Gorbatenko and Cheblukova 1990).

A similar survey was undertaken by TINRO in the northern Okhotsk Sea during the summer of 1995 (Fig. 43) (Shuntov et al. 1998a). The summer of 1995 was moderately warm (Shuntov et al. 1998a). The major oceanographic features were stronger development of the West Kamchatka Current, a well pronounced northeastern movement of surface water from the southwestern Okhotsk Sea, and a shift of the cold Yamsk Current to the south from the Yamsk upwelling (Shuntov et al. 1998a). As in previous years (Shuntov et al. 1993b) most of the zooplankton biomass was contributed by macrozooplankton (Table 8). While the biomass distribution was rather uniform over the study area, the dominant groups differed spatially.

Zooplankton in areas 1, 2, and 9 was dominated by chaetognaths; in areas 6 and 7 by copepods; and in area 8 by euphausiids (Fig. 43). The higher biomass of chaetognaths in the north of the study area (up to 50% of total zooplankton biomass in 1995 versus 20-25% in 1994) stresses the complicated local patterns of interannual community changes and may be partially explained as a result of transitional conditions in the communities (Shuntov 1995, Radchenko et al. 1997b, Shuntov et al. 1998a).

A zooplankton and oceanographic survey was done by TINRO in 1994 within the framework of multiyear fishery investigations in the southern Okhotsk Sea (Nesis 1994; Shuntov 1993; Shuntov et al. 1993c, 1994; Radchenko et al. 1997a). The survey covered an area of 815,000 km^2 with 100 stations (Fig. 44). The distribution of the total plankton biomass appeared to be similar, as observed in the late 1980s (Gorbatenko 1990, Radchenko et al. 1997a). The biomass of small zooplankton varied slightly throughout all regions (Table 9), being 132-270 mg m^{-3} in the upper 0-50m and 15-60 mg m^{-3} in 50-200 m (Radchenko et al. 1997a). It was dominated by *Oithona similis* and

Table 9. Nighttime estimates of zooplankton biomass (t km^{-2}) in the southern Okhotsk Sea in August-September 1994.

Area	Depth	Size			Composition of large zooplankton					Total
		Small	Medium	Large	Euphausiids	Amphipods	Copepods	Chaetognaths	Others	
5	0-50 m	7.0	50.0	130.4	70.8	7.9	28.4	23.3	<0.05	187.4
	50-200 m	7.5	7.4	215.0	170.0	18.4	20.8	5.6	0.2	229.9
6	0-50 m	9.0	1.0	50.4	1.6	0.5	25.9	22.4	0	60.4
	50-200 m	4.6	12.0	45.4	21.0	1.8	22.0	0.3	0.3	62.0
7	0-50 m	13.0	1.8	73.8	12.5	5.5	40.4	15.4	0	88.6
	50-200 m	6.8	3.3	91.7	13.1	16.2	20.1	40.2	2.1	101.8
8	0-50 m	6.8	1.5	66.7	61.8	1.1	3.0	0.8	0	75.0
	50-200 m	1.5	0.8	21.6	4.3	1.0	8.0	7.2	1.1	23.9
9	0-50 m	11.5	5.6	156.2	66.4	2.6	80.0	7.2	0	173.3
	50-200 m	5.1	4.4	95.4	37.6	5.8	26.1	24.4	1.5	104.9
10	0-50 m	6.6	1.8	62.1	39.2	13.3	8.7	0.9	0	70.5
	50-200 m	0.8	0.4	9.2	0.0	0.0	0.8	8.4	0	10.4

Bottom depth = 200 m. Areas are shown in Fig. 44. From Radchenko et al. 1997a.

Table 10. Composition and biomass of zooplankton (g m^{-3}) in the epipelagial of the southern Okhotsk Sea in July 1995.

	Size			Composition of large zooplankton					Total
Areas	Small	Medium	Large	Euphausiids	Amphipods	Copepods	Chaetognaths	Others	zooplankton
9	15	25	529	277	37	121	67	27	569
10	17	114	913	418	62	360	70	3	1,044
11	25	7	84	45	6	13	18	2	116
12	24	27	124	21	14	49	38	2	175
13	27	10	81	27	1.3	31	20.4	1.3	118

Areas are shown in Fig. 45. Mesh size = 0.168. From Shuntov et al. 1998b.

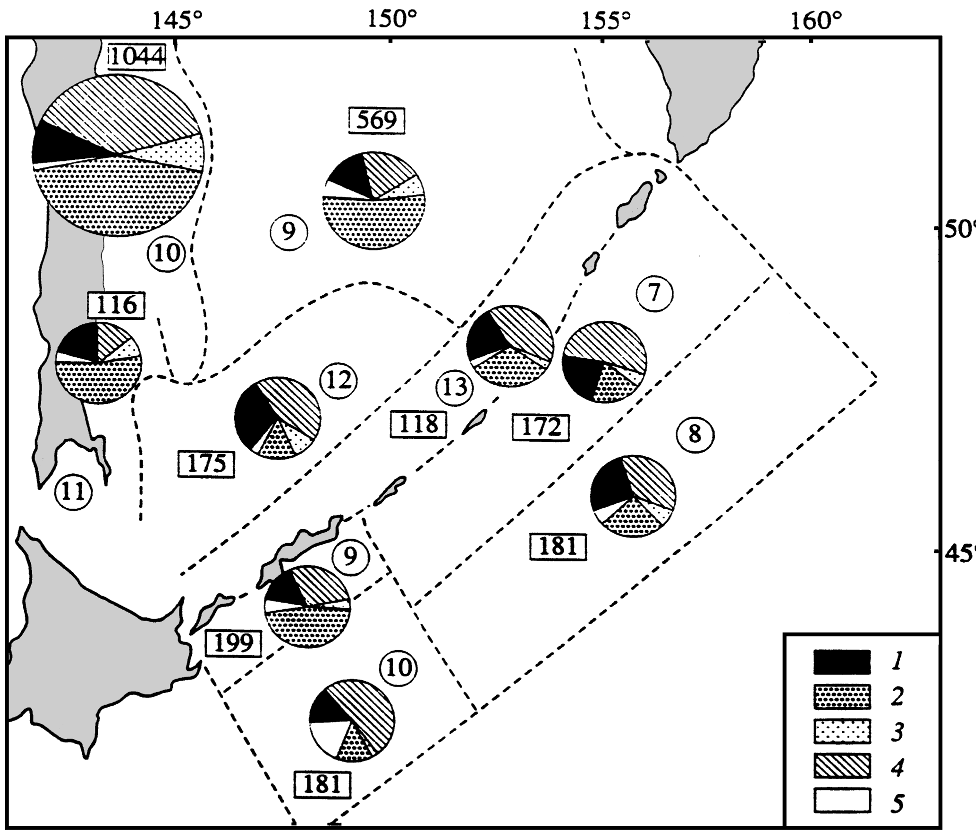

Figure 45. Mean zooplankton biomass (g m^{-2}) and the composition of macroplankton at 0-200 m in the southern Okhotsk Sea in July 1995. 1 = chaetognaths, 2 = euphausiids, 3 = amphipods, 4 = copepods, 5 = other. Dashed lines and numbers in circles indicate areas, numbers in rectangles indicate total zooplankton biomass (from Shuntov et al. 1998b).

Table 11. Percent of predatory zooplankton (mostly chaetognaths) in the epipelagic zooplankton communities of the far-eastern seas in summers of 1986-1995.

Region	1986-1990	1991	1992	1993	1994	1995
Shelikhov Bay	23.5-38.2	–	–	–	23.5	53.0
Northwestern Kamchatka	15.5-22.6	23.0	31.0	–	42.0	22.6
Southwestern Kamchatka	21.0-32.0	41.0	26.0	27.0	56.0	17.7
Eastern Kamchatka	–	54.0	–	45.9	–	24.4
Southwestern Bering Sea	–	54.4	–	56.6	–	33.9
Southern Okhotsk Sea	16.0-22.0	21.0	45.0	34.0	23.0	19.0
Pacific side of the Kurils	–	48.6	47.4	56.7	45.0	27.6

From Shuntov et al. 1998b.

Pseudocalanus spp., except for the southernmost area 5, where *Paracalanus parvus* was abundant (Radchenko et al. 1997a). Medium-sized zooplankton consisted of adults of *Pseudocalanus* spp., copepodites of *Metridia pacifica*, *Calanus pacificus*, *Neocalanus plumchrus,* and *Metridia ochotensis,* and its biomass was smaller than the other size groups (Table 9). Euphausiids including *Thysanoessa raschii* dominated the large fraction of zooplankton in the Kuril Basin, while the overall biomass of euphausiids in the study area decreased compared to 1993 due to low abundance of *Thysanoessa longipes* (Shuntov et al. 1994, Radchenko et al. 1997a). As opposite, the biomass of *Neocalanus plumchrus* dramatically increased with a maximum of 2,000 mg m^{-3} in the upper layer (Radchenko et al. 1997a). The biomass of chaetognaths decreased considerably compared to 1992 and was close to mean values for the late 1980s (Radchenko et al. 1997a).

Another survey was done by TINRO using the same standard techniques in the southern Okhotsk Sea in summer 1995 (Fig. 45) (Shuntov et al. 1998b). While the circulation pattern remained essentially the same as that in 1991-1994, the Western Kamchatka Current was stronger due to a well-pronounced penetration of Pacific water into the Okhotsk Sea through the Chetvertiy Kuril Strait (Shuntov et al. 1998b). The strong input of warm, saline Soya Current water resulted in a shift of the Eastern Sakhalin Current northward and water transport from the southwestern Okhotsk Sea toward northern Kamchatka, as it was observed in the summer of 1994 (Radchenko et al. 1997a, 1997b; Shuntov et al. 1998b). Macroplankton dominated the biomass in all study areas, while small and medium zooplankton was abundant near eastern Sakhalin (Table 10). Small zooplankton was dominated by *Oithona similis*, *Pseudocalanus* spp., and early copepodites of *Metridia* spp. and *Neocalanus plumchrus* (Shuntov et al. 1998b). *Pseudocalanus* spp., copepodites of *N. plumchrus*, *Metridia* spp., and *Eucalanus bungii* dominated the medium-sized zooplankton fraction (Shuntov et al. 1998b). Macroplankton in the southern areas was dominated by copepods *Metridia pacifica* and *Neocalanus plumchrus*, while in areas 9,10, and 11 euphausiids *Thysanoessa longipes* and *T. raschii* were predominant (Table 10, Fig. 45) (Shuntov et al. 1998b). The total biomass of zooplankton in the southern Okhotsk Sea increased, compared to 175-245 g m^{-3} in the late 1980s and early 1990s, and averaged 340 g m^{-3} (Shuntov et al. 1998b).

In 1995 chaetognath biomass was restored to the values seen in the 1980s (Table 11). This phenomenon may be accounted for by a regulatory response of the zooplankton community to an excess density of predators, although it probably involves normal interannual fluctuations in the zooplankton species abundance (Shuntov et al. 1998b). However, the higher biomass of chaetognaths in the northeastern Okhotsk Sea was observed two to three years later than in other areas (Table 11). At the same time, the northern Okhotsk Sea walleye pollock retained higher density through 1990-1994, starting to decrease in 1995, while in the other areas a sharp decrease in planktivorous fish abundance took place in the very early 1990s (Shuntov et al. 1998a, 1998b).

The mechanisms of these alterations are not well understood so far and require additional research efforts (Radchenko et al. 1997, Shuntov et al. 1998b).

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[Note: "In Russian" means the reference is only available in Russian. All others are in English.]

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INDEX

Page numbers in italics indicate figures and tables. Boldface numbers indicate main headings. Okhotsk Sea is abbreviated OS. Dates indicate years of research, not publication.

D

E

T

U

V

W

X

Y

Z