Proceedings of the Zoological Institute RAS
Vol. 324, No. 4, 2020, pp. 449–458
10.31610/trudyzin/2020.324.4.449

УДК 597

Vertical distribution, seasonal differentiation and trajectory of movement of zooplankton and pelagic fish of Lake Baikal

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Submitted October 18, 2020; revised November 22, 2020; accepted November 30, 2020.

ABSTRACT

In Lake Baikal, the majority (87%) of fish biomass is generated in the pelagic zone. Two species of *Comephorus*, three species of *Cottocomephorus* and *Coregonus migratorius* inhabit in the pelagic zone of the lake. Currently, only *C. migratorius* is considered a resource species, the harvest of which accounts for about 50% of the total fish harvest. Food items for pelagic fish are copepods *Epischura baikalensis* and pelagic amphipods *Macrohectopus branickii*. The seasonal distribution and formation of zooplankton concentrations determine the food migrations of fish. The patterns of the seasonal distribution of zooplankton and pelagic fish were described by M.M. Kozhov (1954, 1964). Comparative analysis of the abundance of zooplankton in South Baikal over time, showed that during the period of maximum development of *E. baikalensis* in the months of July, August, and October, zooplankton concentration in the decade 1997 to 2007 was twice more than in 1951 (Kozhov 1954; Kiprushina 2010). The distribution of *E. baikalensis* is directly dependent on the water temperature. Yet there is an inverse relationship in the surface layer 0–25 meters. During warming up of the surface water layers, which had been observed in 2002 year *E. baikalensis* left the upper zone and migrated deeper, to a layer of 50–100 meters. In other months of the year, no changes in the average values of the *E. baikalensis* abundance were revealed. At present, when the ecosystem of Lake Baikal is changing, there is a need to restart such complex studies, and to use the results obtained by M.M. Kozhov for comparative analysis.

Key words: *Comephorus*, *Coregonus migratorius*, *Cottocomephorus,* Lake Baikal, pelagic fish, zooplankton

Вертикальное распределение, сезонная дифференциация и траектория перемещения зоопланктона и пелагических рыб озера Байкал

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Представлена 18 октября 2020; после доработки 22 ноября 2020; принята 30 ноября 2020

РЕЗЮМЕ

В озере Байкал большая часть (87%) биомассы рыб создается в обширной пелагиали. В пелагиали озера обитают два вида *Comephorus,* три вида *Cottocomephorus* и *Coregonus migratorius*. В настоящее время из этих видов ресурсным считается только *C. migratorius*, вылов которого составляет около 50% от общего улова рыбы. Корм для пелагических рыб – веслоногие рачки *Epischura baikalensis* и пелагическая амфипода *Macrohectopus branickii*. Сезонное распределение и формирование концентраций зоопланктона определяют пищевые миграции рыб. Закономерности сезонного распределения зоопланктона и пелагических рыб описаны М.М. Кожовым (1954, 1964). Сравнительный анализ численности зоопланктона южного Байкала с течением времени показал, что в период максимального развития *E. baikalensis* в июле–октябре концентрация зоопланктона за десятилетие с 1997 по 2007 гг. вдвое больше, чем в 1951 г.

(Кожов 1954; Кипрушина 2010). Распространение *E. baikalensis* напрямую зависит от температуры воды. Но в поверхностном слое 0–25 м наблюдается обратная зависимость. Во время прогрева поверхностных слоев воды, которое наблюдалось в 2002 г., *E. baikalensis* покидает верхнюю зону и уходит глубже, в слой 50–100 м. В остальные месяцы года изменений средних значений численности *E. baikalensis* не выявлено. В настоящее время, когда происходит изменение экосистемы оз. Байкал, возникла необходимость воспроизведения подобных комплексных исследований и использовать результаты, полученные М.М. Кожовым, для сравнительного анализа.

Ключевые слова: *Comephorus*, *Coregonus migratorius*, *Cottocomephorus,* зоопланктон, оз. Байкал, пелагические рыбы

INTRODUCTION

The ecosystem of Lake Baikal is regarded as an unique source of the biological resources. Their condition, assessment and methods of rational use have always posed a challenge. In the scientific community there is a view that changes in natural ecosystems occur in "catastrophically short time scales." In this regard, there is a need for the availability of sound information about the state of biological resources during the period of stable states of ecosystems. Such data is utilized as background information for comparative analysis and forecasting likely ecological risks during large ecosystems changes.

The ecosystem of Lake Baikal is characterized by a high degree of entropy, a state close to equilibrium. The large pelagic zone, the deepest part of which is characterized by stable environmental conditions, determines the stable functioning of organisms at different trophic levels. The trophic level of mesozooplankton in pelagic zone of Baikal is mainly represented by the species *Epischura baikalensis* (Copepoda), the trophic level of macroplankton – by the species *Macrohectopus branickii* (Amphipoda) (Kozhov 1954, 1964, 1969). Pelagic fish form two trophic levels: the level of five species of cottoid fish (three species of the genus *Cottocomephorus* and two species of the genus *Comephorus*), consume zooplankton and their own juveniles, and the trophic level of predatory fish is represented by one species – *Coregonus migratorius*, feeding on zooplankton and cottoids of the previous level (Sideleva 2003).

In recent years, changes had been noted in the coastal phytobenthic and pelagic phytoplankton communities of Lake Baikal. While there is also a decline in the number of the Baikal omul (*C. migratorius*). Additionally, within the past 50 years, the population of the *Cottocomephorus grewingkii*, has not been able to recover, the commercial harvesting of which was prohibited in 1971 (Khanaev et al. 2016; Sideleva 2020).

Research by M.M. Kozhov (1954, 1964) regarding the relationship between the consumption of zooplankton and the state of pelagic fish population can serve as background data for a comparative assessment of changes in the Baikal ecosystem.

SEASONAL DISTRIBUTION OF ZOOPLANKTON AND PELAGIC FISH

Winter ice period

Lake Baikal zooplankton was represented mainly by the species *E. baikalensis*, which had a distinct seasonal distribution (Fig. 1). In the sub-ice period from January to March, the number of adult and copepodite stages of crustaceans in the 0–250 meter layer reached 100 000–150 000 ind/m^2 (400–600 ind/m^3), biomass – 7–9 g/m^2 (0.028–0.036 g/m^3) (Kozhov 1954). At this time, about 30% of adults of *E. baikalensis* had been concentrated at the intermediate layer of 150–250 meters. The pelagic amphipod *M. branickii* was concentrated in the 200–300 meter layer, and performed migrations to the surface sub-ice layers of water at night.

Planktivorous fish: *C. migratorius*, *C. grewingkii* and *C. inermis* had been found in wintering grounds, in the area of the submerged coastal slope, at a depth of 200–300 meters near vast shallow waters (Fig. 2). Pelagic *Comephorus* during the ice period were dispersed in the water column, but formed higher population density at a depth of 150–350 meters. During the ice period, *Comephorus* were caught together with omul (*C. migratorius*). The water temperature at this depth had reached 3.5–3.6 °C, which was 2.5 times warmer than at a depth of 50 meters. In March, zooplankton started to move to the surface water layers 0 to 50 meters (Fig. 1).

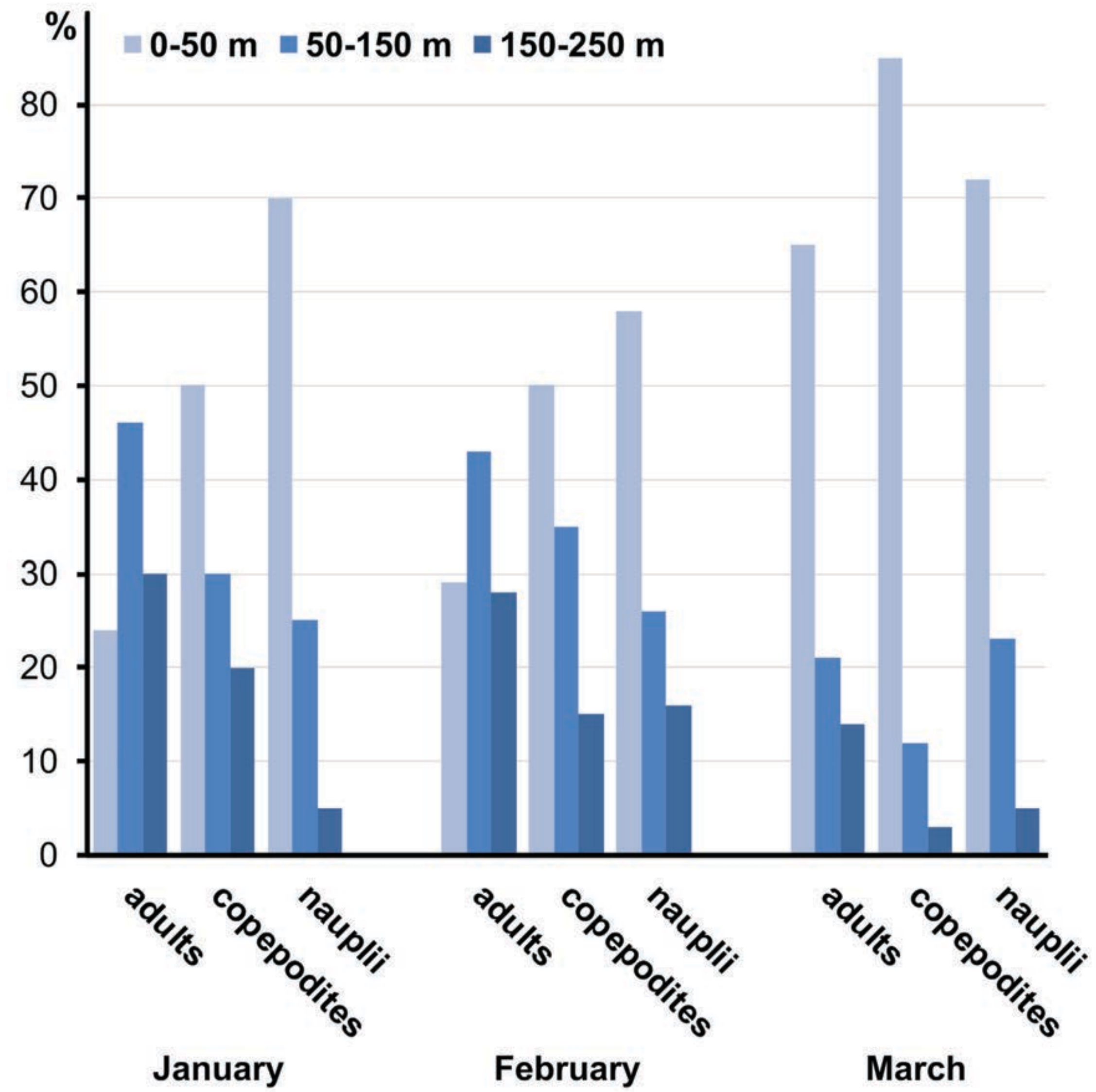

Fig. 1. Vertical distribution of *Epischura baikalensis* in the pelagic zone of South Baikal in winter (under ice) (Kozhov 1954).

Spring period

Under influence of wind and sun, ice of Lake Baikal usually melts in the springtime period from April to May, thus commencing to the spring turnover. Soon, at the end of April and the first half of May, when the temperature in the entire water column of Lake Baikal reaches 3.5 °C, zooplankton accumulates in the surface layer (Fig. 3).

The pelagic fish *C. migratorius, C. grewingkii* and *C. inermis* started to migrate to the shallower regions closer to the coast (Fig. 4). Separate flocks migrated along the coast. During the May, *C. grewingkii* spanners in breeding plumage migrated to the littoral of the lake, and spawned in rocky areas.

In the second half of May and June, zooplankton was dispersed throughout the water column of the lake and did not form dense accumulations, which are very important for fish nutrition. In the shallow water, the water started to warm up. Already at the beginning of June, the abundance and biomass of zooplankton in shallow water reached significant values up to 1.6 g/m^3 (Kozhov 1954). This was one of the most important reasons for the mass migra-

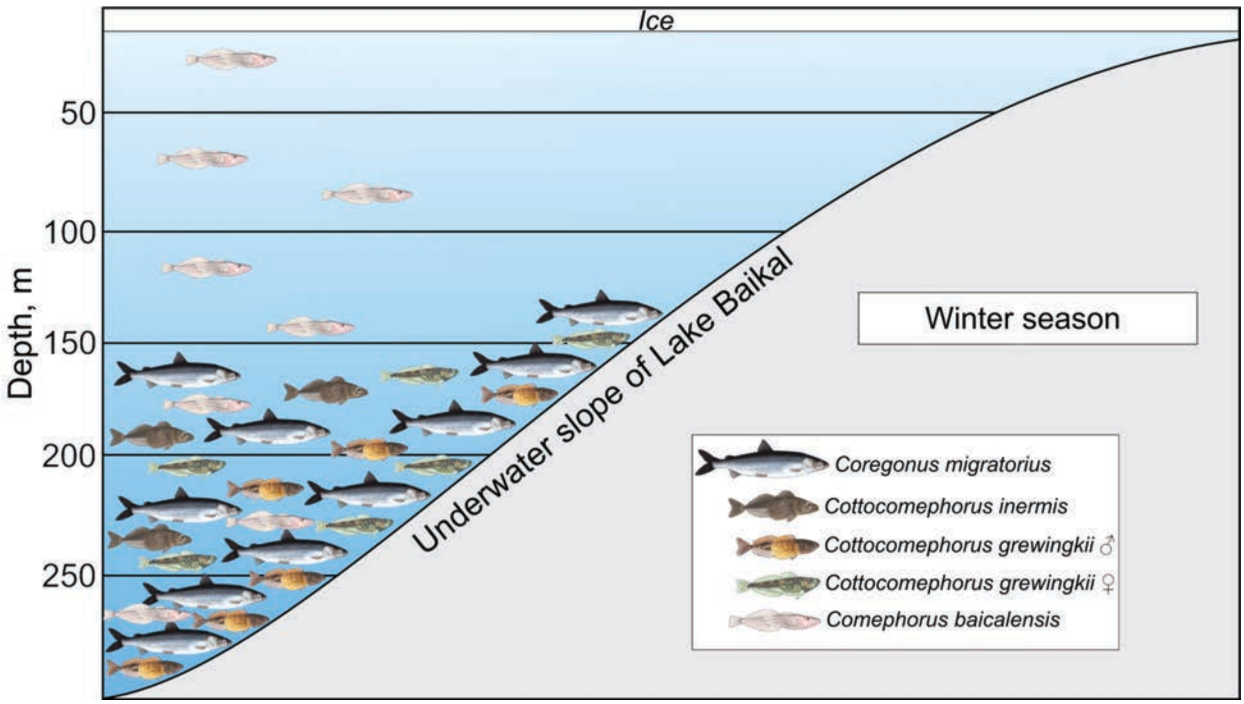

Fig. 2. Distribution of pelagic fish during the ice period in the pelagic zone of Lake Baikal.

tion of the Baikal omul into the littoral of the lake (Fig. 5).

Summer period

In July there was a clear thermal stratification. In the upper layers of the lake, the temperature reached 9 °C. Clear vertical differentiation congruent with temperature has been observed in plankton distribution. The summer reproduction of *E. baikalensis* also started in July. In the upper water layer 0 to 50 meters the number of nauplii was up to 75% (Fig. 6). In total, the layer 0–250 meters contained 1 800 000 ind/m^2 (or 7200 ind/m^3) (Kozhov 1954). In 1947–1949, 1951 years, the number of nauplii reached 4 000 000–6 000 000 individuals. At the end of July, the number of copepodite stage crustaceans increased sharply (Kozhov 1954). The maximum number of copepodites in the 0–250 m layer in 1947–1949 and 1951 was 2 000 000–4 000 000 ind/m^2 (on average 1 250 000–1 450 000 ind/m^2) (Fig. 6). At least 70–80% of crustaceans accumulated in the layer 0 to 50 meters. At the end of July, August and September, the annual maximum development of *E. baikalensis* was observed (Fig. 7). Crustaceans were evenly dispersed over the entire 0–250 meters layer. The total biomass of *E. baikalensis* in this layer was 39 g/m^2 (or 0.16 g/m^3). Currently, the daily vertical migrations of zooplankton were clearly expressed. Macroplankton (*M. branickii*) also had been distributed in the 0–300 meters layer and, following *E. baikalensis*, made vertical diurnal movements.

In the summer, *C. migratorius* moved away from shallow waters to the open areas of the lake, into layers of water rich by zooplankton (Fig. 8). In the darkness, *C. migratorius* stayed closer to the surface than during the day. This was attributed to the vertical migrations of zooplankton into the upper water layers.

Until completion of spawning, *Cottocomephorus* adhered to the coastal area and actively fed upon zooplankton. In July – August larvae of *Cottocomephorus* appeared and migrated as a school along the coast. For *C. migratorius* and adult *Cottocomephorus* larvae had been the main food source at this time. In open areas of the pelagic zone, a high level of zooplankton biomass was sustained till the first half of October. Therefore, the period from mid-July to the end of September was the main feeding period for planktivorous fish in the open pelagic zone of the lake.

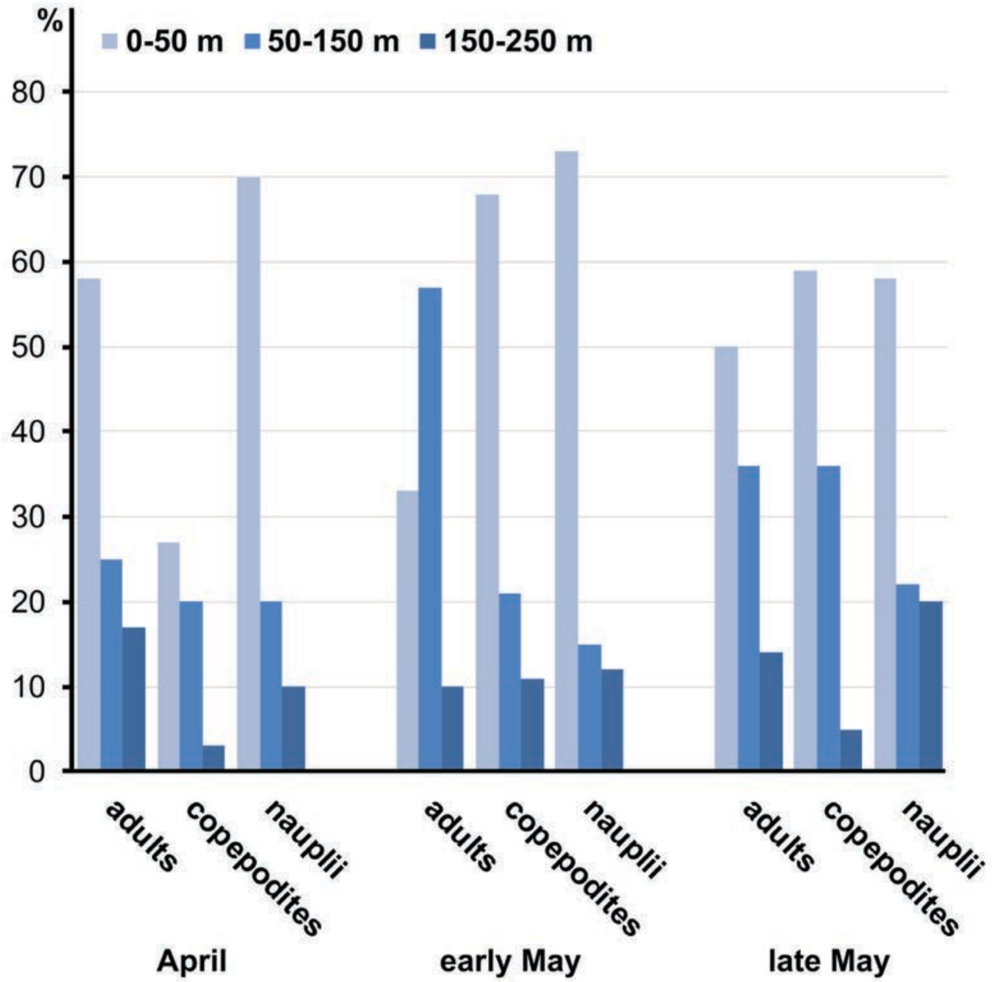

Fig. 3. Distribution of *Epischura baikalensis* in the 0–250 m layer, above a depth of 800 m in spring (Kozhov 1954).

Autumnal period

In autumn, in the second half of October and November, the upper layers of the lake were cooled, the wind circulation intensified, and by the end of November, autumnal homoeothermic regime was established. Plankton scattered and went to the deep zone of 100–500 meters (Fig. 9). *Macrohectopus branickii* migrated to the bottom water layers with fading of vertical migrations.

White-fish *C. migratorius* feeding in the pelagic zone moved closer to the shallow waters. The mass development of zooplankton was gradually dying out (Fig. 10). Closer to the winter period, the part of zooplankton was concentrated at a depth of 150–300 meters. Planktonic *Cottocomephorus* again gathered in the depth of 200–300 m, and remained there for the winter.

In 1947–1949 and 1951, throughout the year, the total number of *E. baikalensis* adults and copepodites varied at 14.5 times, from 100 000 in January to 1 450 000 ind/m^2 in September. The total biomass at this time changed at 5.6 times, from 7 to 39 g/m^2. 50 years later, in the early 2000s, the total number of *E. baikalensis* in the upper layer of 0–25 m changed more than 70 times – from 37 470 to 2 670 200 ind/m^2. The average number of *E. baikalensis* in 1951 was 405 820 ± 59.7 ind/m^2 (Kozhov 1954). This value was two times less than the average long-term value of the abundance of zooplankton in 1997–2007 (Kiprushina 2010).

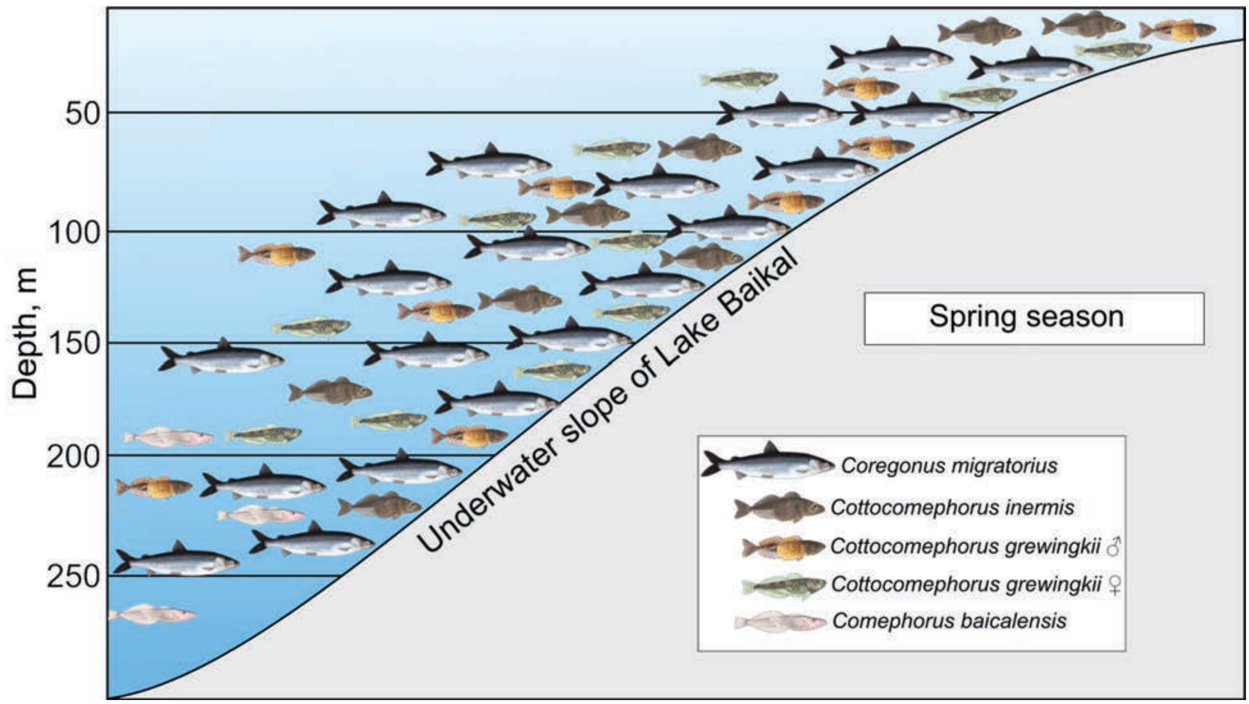

Fig. 4. Spring migration of pelagic fish to the coastal area of the lake.

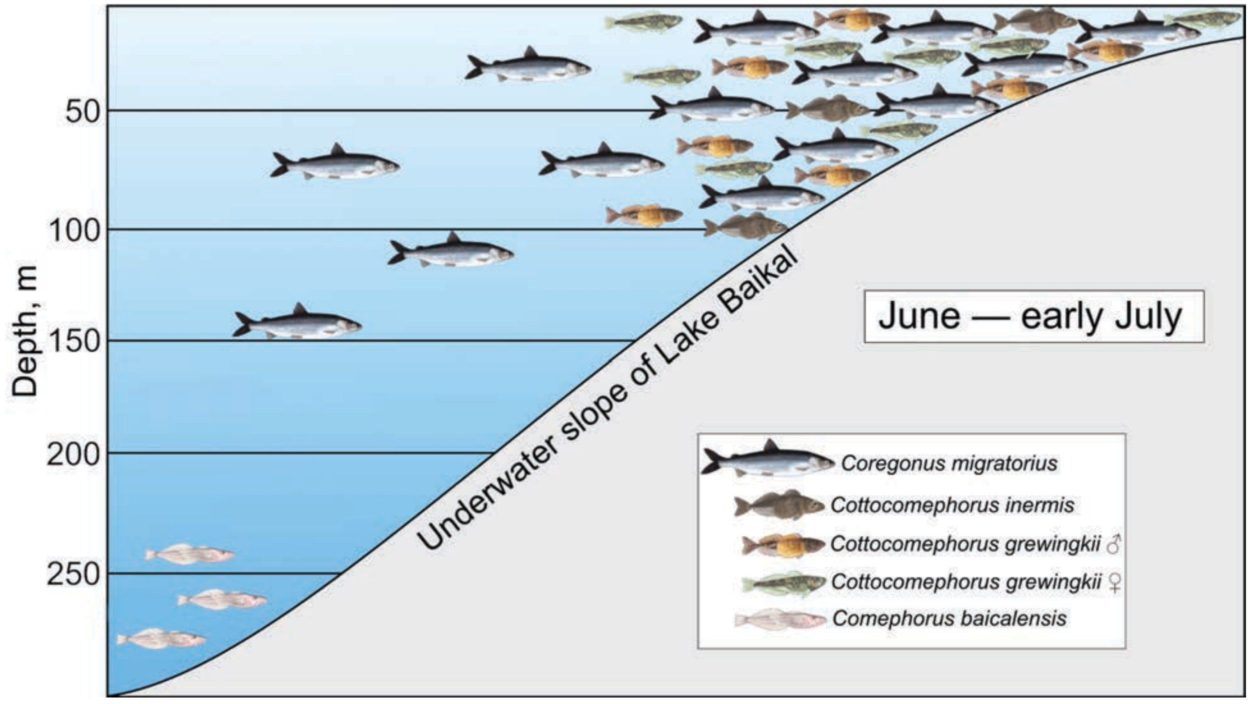

Fig. 5. Concentration of pelagic fish in the coastal zone of Lake Baikal – “halt”.

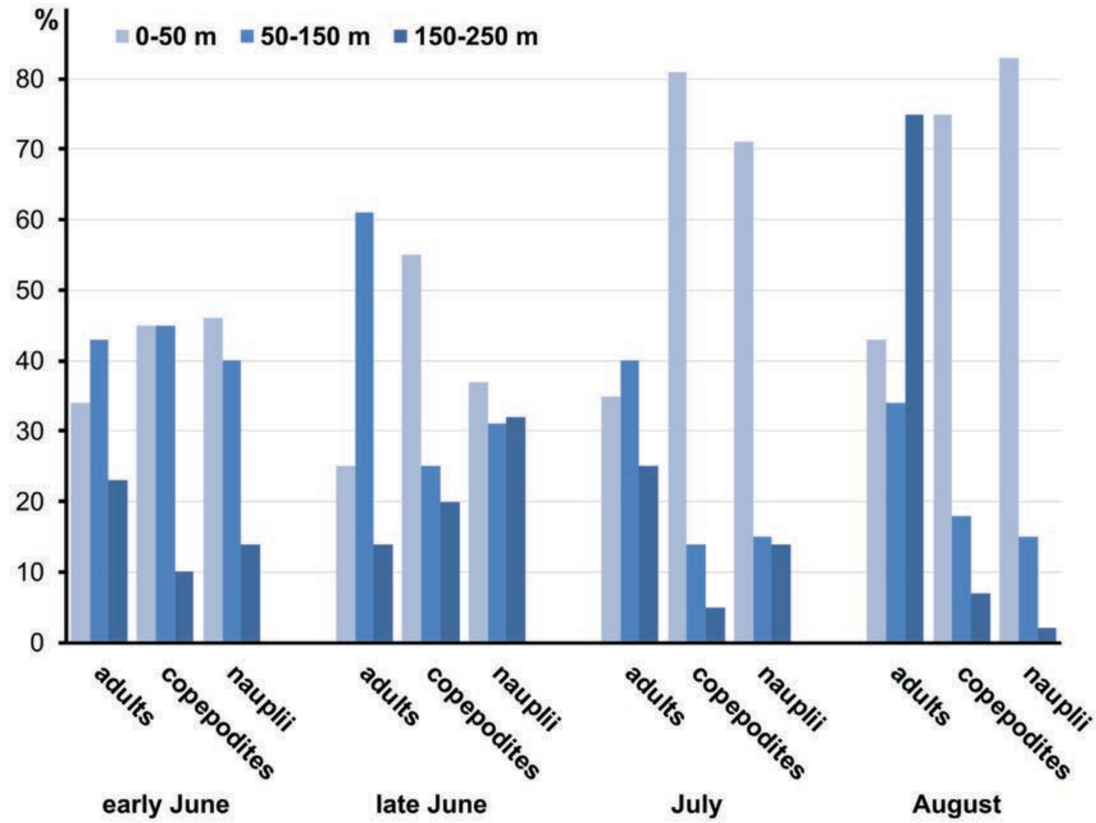

Fig. 6. Maximum numerical and uniform distribution of zooplankton in the water column in summer (Kozhov 1954).

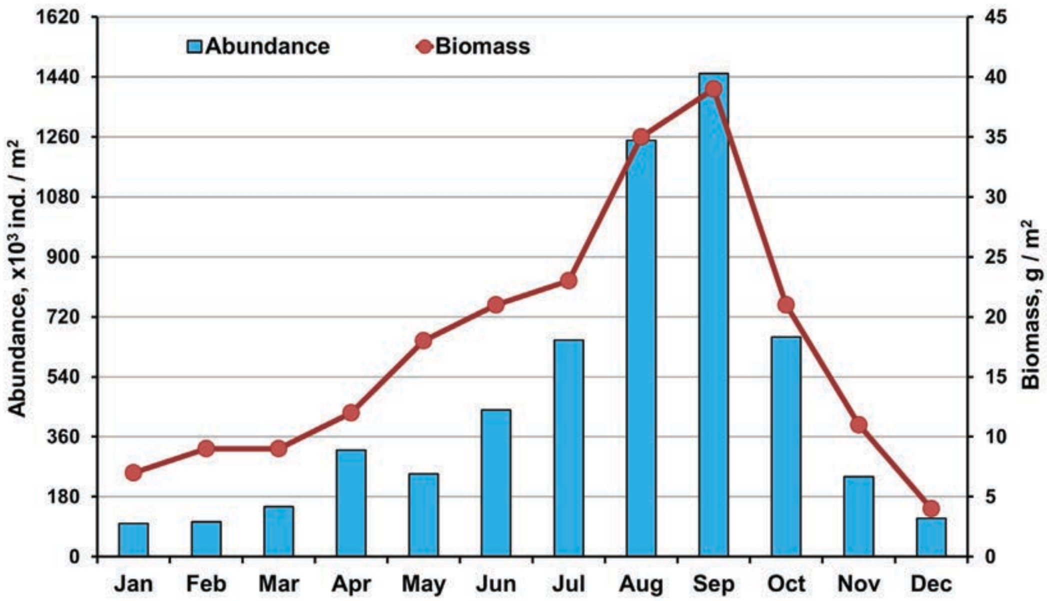

Fig. 7. Dynamics of seasonal changes in the abundance and biomass of zooplankton in the open pelagic zone of Lake Baikal (Kozhov 1954).

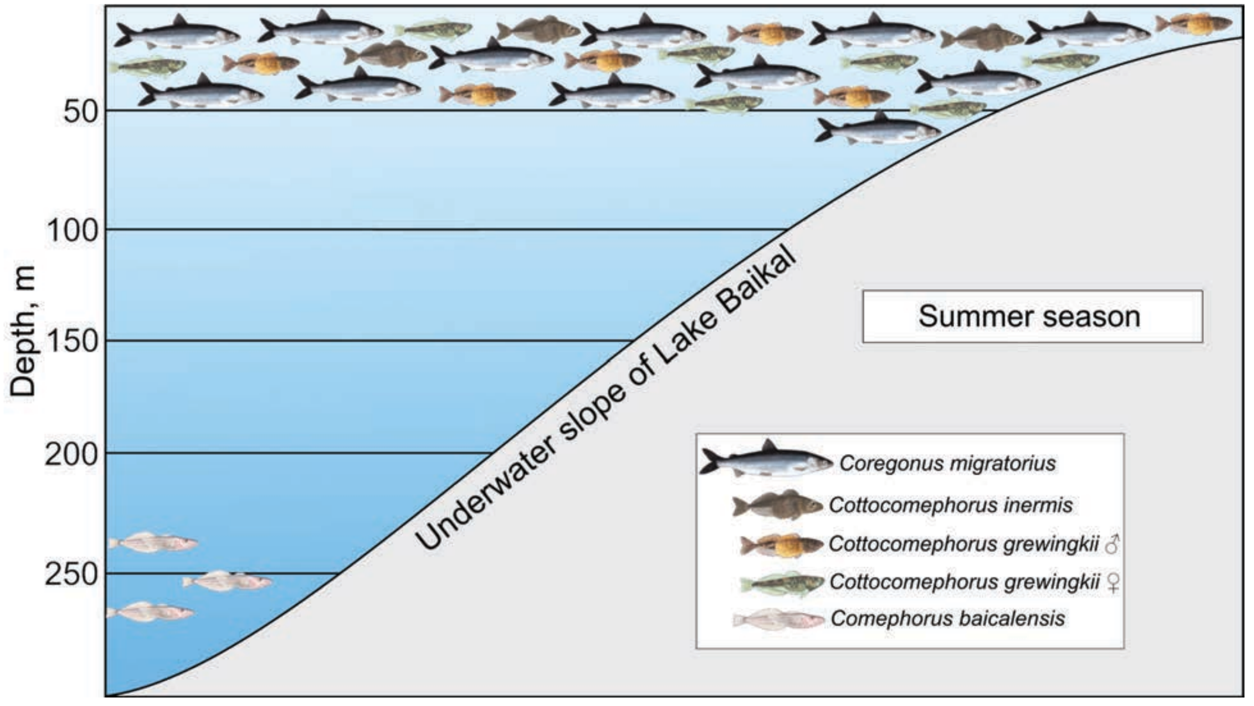

Fig. 8. Dispersion of omul (*Coregunus migratorius*) in the upper layers of the pelagic zone in summer.

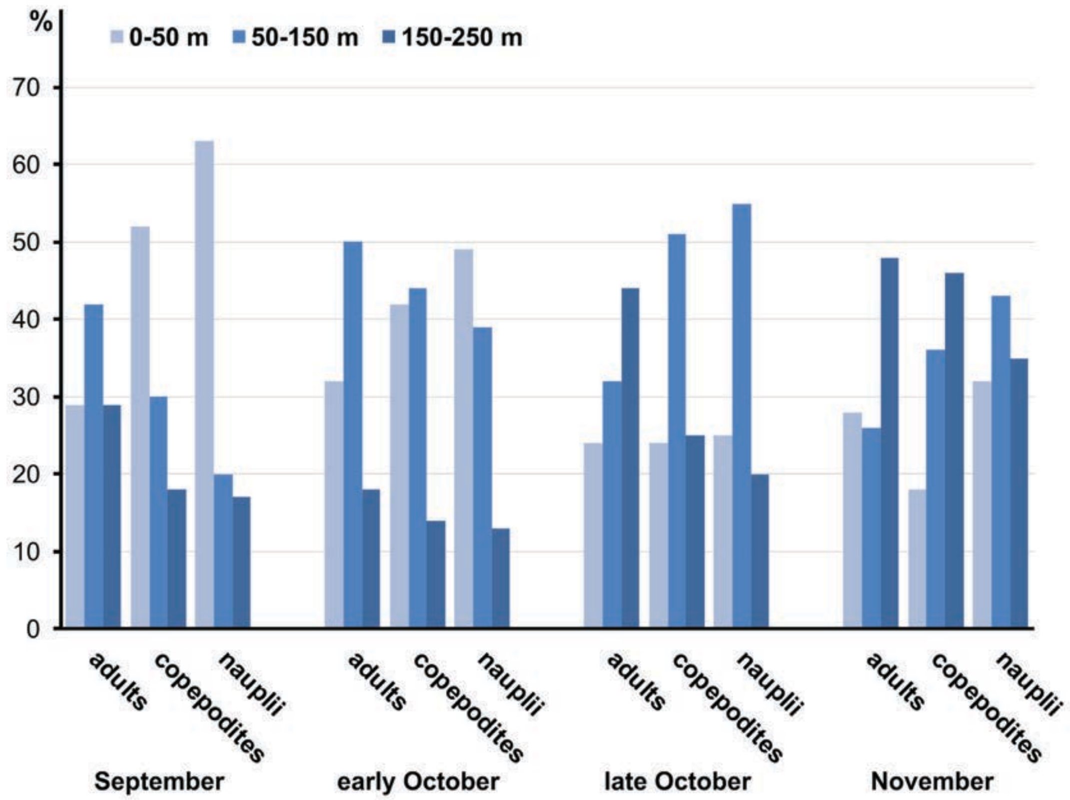

Fig. 9. Distribution of zooplankton in autumn (Kozhov 1954).

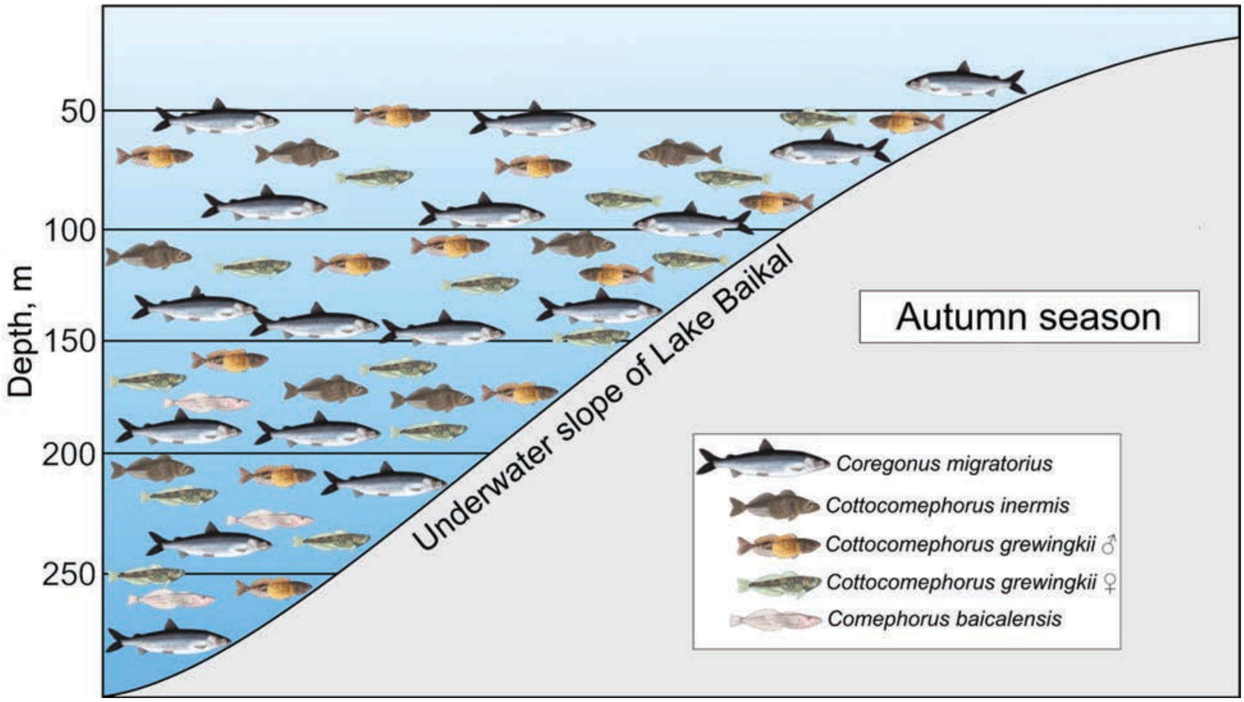

Fig. 10. *Coregunus migratorius* and *Cottocomephorus* in the coastal pelagic part of Lake Baikal in autumn.

CONCLUSION

One of the main food items for pelagic fish of Lake Baikal is the copepod *Epischura baikalensis*. In the summer, its biomass reached 74–100% of the total zooplankton biomass of the lake. In shallow waters, and sometimes in the open areas of the lake, *Cyclops kolensis* had been found together with *E. baikalensis*. In the deep-water pelagic zone of the lake, the pelagic amphipod *Macrohectopus branickii* was a valuable food item for fishes.

It was shown in the experiment that *C. migratorius* actively fed when number of copepodite stages reached 30–35 specimens per liter (Potakuev 1954). Such concentrations of zooplankton were formed in spring and summer at night, when 60–70% of crustaceans gathered in the surface water layer 0 to 5 meters. The abundance of copepodite stages of *E. baikalensis* in these layers could reach 150 to 300 specimens per liter. In addition to *E. baikalensis*, the omul fed on pelagic amphipods *M. branickii*, which able to catch in individual specimens, regardless of concentration. An assessment of the forage base of Lake Baikal showed that the main fish production was formed in the pelagic zone. In addition to omul, two species of *Comephorus* and 3 species of sculpins genus *Cottocomephorus* could be found in the pelagic zone of Lake Baikal, which are able to use lower concentrations of zooplankton than omul (*C. migratorius*).

Comparative analysis of the abundance of zooplankton in Southern Baikal in different years showed that during the period of maximum development of *E. baikalensis* in July, August, and October, its number in 1997–2007 was twice more than in 1951 (Kozhov 1954; Kiprushina 2010). The distribution of *E. baikalensis* was related to water temperature, and in the surface layer from 0 to 25 meters had an inverse relationship. During the warming up of the surface layers of water, which was observed in 1947–1949, 1951 and some years of the last decade, *E. baicalensis* left the upper zone and went deeper, to a layer of 50–100 meters. In other months of the year, no changes in the average values of the *E. baikalensis* abundance were revealed (Kozhov 1954).

Review of research from 1948 to 2007 showed that the life strategy of pelagic fish of Lake Baikal, including vertical distribution, seasonal differentiation, and trajectories of movement, had been associated with seasonal redistribution and concentrations of food items.

The study of M.M. Kozhov involved an integral approach to solve the problem of the relationship between aquatic organisms in the pelagic zone of Lake Baikal. In one complex had been studied the annual dynamics of the vertical distribution of zooplankton; relationship between clusters of zooplankton and pelagic fish (*Coregonus migratorius, Cottocomephorus* and *Comephorus)*; feeding of pelagic fish. In the experimental conditions of the aquarium in the village of Bolshiye Koty, an abundance of *Epischura baikalensis* per liter was determined, at which an adult omul started to feed on. The feeding coefficients were experimentally determined and showed the quantity of food which was necessary for the greatest increase in omul biomass. M.M. Kozhov was able to combine, compare and generalize all results obtained from a system of relationships between zooplankton and pelagic fish. The revealed relationships can explain the seasonal distribution and trophic migrations of fish, they are stable every year, and can be called regular. After M.M. Kozhov, no one has repeated such complex studies. At present, when the ecosystem of Lake Baikal is changing, the need arose to start such complex studies, and to use the results obtained by M.M. Kozhov for comparative analysis.

ACKNOWLEDGEMENTS

The text of the manuscript was checked by a native English speaker Aleksander Sidelev. The study was supported by a State research topic AAAA–A17–117030310197–7. My thanks go to Zakhar Zhidkov (Saint Petersburg State University) for the care in the creation of this paper.

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