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MESOPELAGIC FISH COMMUNITY SUPPLIES "BIOLOGICAL PUMP"

Vladimir I. Radchenko
Sakhalin Scientific Research Institute on Fisheries and Oceanography (SakhNIRO), Yuzhno-Sakhalinsk, 693023, Russia

ABSTRACT. **–** Trawl surveys in the Bering Sea and Sea of Okhotsk focusing on the mesopelagic layer (200 - 1000 m), yielded 50 fish species belonging to 43 genera and 28 families in the Bering Sea and 48 fish species belonging to 41 genera and 23 families in the Sea of Okhotsk. The bulk of mesopelagic fish species were represented by two families, Myctophidae and Bathylagidae. Six myctophids and four bathylagids were localized in the Bering Sea, while seven myctophids and four bathylagids were localized in the Sea of Okhotsk, respectively. The body density of mesopelagic fishes decrease during the daytime (when they reside in the deep water layers) and increase during the night time (when active feeding begins). Such dynamics are related with the filling of the fish's stomach (relative density increases) and faecal discharge (relative density decreases). Such feeding habits promote the diurnal vertical migrations of mesopelagic fishes to the upper layers when the body density decreases and sinking when the body density increases. A light-rayed lanternfish specimen can transport 52 mg of food to the deep pelagic layer and excrete about 8.3 mg of faeces. Gross total transport between the ocean layers by the entire light-rayed lanternfish stock in the Bering Sea was estimated at 15,000 tons per day or 5.46 million tons annually. The magnitude of this value is noticeable in comparison with the estimates of the entire matter flux within "marine snow" (detritus, faeces and carcasses of dead animals partly-decomposed by bacteria and ciliates).

KEY WORDS. **–** Mesopelagic fish, feeding migrations, vertical matter transport.

INTRODUCTION

The research focusing on the ecology, assessment of biomass and the role of mesopelagic fishes in pelagic ecosystems developed as a chapter in Russian far-eastern seas ecosystem studies, which began in the 1980s (Balanov & Iljinskiy, 1992; Balanov & Radchenko, 1995). Trawl surveys in the 200 - 1,000 m layer revealed the mesopelagic ichthyofauna to include 50 fish species belonging to 43 genera and 28 families in the Bering Sea and 48 fish species belonging to 41 genera and 23 families in the Sea of Okhotsk. Most families were represented by one or two species. Two fish families, Myctophidae and Bathylagidae, represented the bulk of the mesopelagic fish species in both seas. Six myctophids and four bathylagids were localized in the Bering Sea, while seven myctophids and four bathylagids were localized in the Sea of Okhotsk (Balanov & Radchenko, 1995). The total biomass of mesopelagic fish is estimated at 15 - 20 million tons in the Bering Sea and 15 - 30 million tons in the Sea of Okhotsk (Shuntov et al., 1993).

These abundant fish species play an important role in the trophic structure of the fish community, both as zooplankton resource consumers and as prey for predatory species. Our attention was attracted by the contradiction between initial estimates of mesopelagic fish biomass derived from the trawl catch data during surveys of the upper pelagic layer and the assessment of their consumption by common nektonic species. Mesopelagic fishes make up 7.5 - 8.1% of the diet of walleye pollock (*Theragra chalcogramma*) in the offshore waters of the Bering Sea and 10.0 - 13.6% in the offshore waters of the Sea of Okhotsk (Shuntov et al., 1993). Walleye pollock biomass was assessed at 4.0 million tons in the offshore waters of the Bering Sea and 2.8 million tons in the offshore waters of the Sea of Okhotsk in 1986 - 1987 and a diet ration value of 5.5% of body weight for adult fish (Shuntov et al., 1993). These data assume that the mesopelagic fish consumption by walleye pollock was 1.03 and 1.09 million tons respectively, during the two months of the warm season. These calculations showed that previous estimates of the mesopelagic fish biomass captured by large pelagic rope trawls with a short (15 m) fine-mesh (8 - 10 mm) insert were underestimated. Updated estimates were obtained with pelagic trawls having a fine-mesh insert in half of the conical portion and a cod end of 87.3 m in length.

In the 1990s and 2000s, these estimates were widely used for trophic-structure modeling, calculations of fish productivity and further studies on the functioning of the ecosystem (Shuntov & Dulepova, 1993, 1995). It was generally recognized that mesopelagic fishes play an important role in the pelagic fish community as food

Table 1. Volume of material collected in the Sea of Okhotsk from 28 February 1990 to 6 April 1990.

Species	Number of Samplings	Number of Fish Sampled	Depth Range (m)	Average SL (cm) of Fish Sampled
Dark-rayed lanternfish (*Stenobrachius nannochir*)	43	5,217	200 - 1,000	9.89
Eared blacksmelt (*Lipolagus ochotensis*)	35	4,093	200 - 1,000	11.84
Light-rayed lanternfish (*Stenobrachius leucopsarus*)	27	4,165	200 - 1,000	8.39
Northern smooth-tongue (*Leuroglossus schmidti*)	70	12,973	0 - 1,000	11.42
Total	**175**	**26,448**		

competitors to commercial fishes as well as being food sources themselves. Furthermore, analysis of mesopelagic fish distribution, migration and feeding pattern reveal their important function in vertical transport of living matter in the pelagic zone.

MATERIALS AND METHODS

The data used in this study consisted of length (standard length or SL in mm) and weight (in g) measurements from 26,448 fish specimens belonging to four species: 1) light-rayed lanternfish (*Stenobrachius leucopsarus*); 2) dark-rayed lanternfish (*S. nannochir*), both of the family Myctophidae; 3) Northern smooth-tongue (*Leuroglossus schmidti*) and 4) eared blacksmelt (*Lipolagus ochotensis*), both of the family Bathylagidae (Table 1). Individual weights were calculated by dividing the sample's weight by number of fishes in a sample.

Fish data were collected using specialized trawls with a fine-mesh insert conducted in the epipelagic (9 hauls, 0 - 200 m), middle mesopelagic (47 hauls, 200 - 500 m) and lower mesopelagic (18 hauls, 500 - 1,000 m) layers. The trawl survey was conducted by the research vessel 'MLECHNY PUT' in the Sea of Okhotsk area (which was free of ice cover) between 28 February 1990 and 6 March 1990. Surveys were conducted with midwater trawls, 'RT/TM 108/528' with a horizontal opening of about 50 m and average vessel speed of 2.5 - 3.0 knots. The patterns of mesopelagic fish distribution were analyzed using additional data from three other cruises: 1) from 9 April 1990 to 26 June 1990; 2) from 30 September 1990 to 18 November 1990, in the Bering Sea and 3) from 20 November 1990 to 20 January 1991 in the Sea of Okhotsk. The research vessel and trawl equipment were the same for all of the surveys.

A cable sensor ("Igla-3M") attached to the upper trawl panel registered the density of fish concentrations trawled in the different layers of the water column during stepped trawl hauls. Its signal frequency was 19.7 kHz, depth rating 0.5 to 2,000 m, operating temperature –10 to 40°C. The composition of fish aggregations was identified by using the trawl-catch composition. These concentrations were not registered by ship sonar, likely due to their low density and the significant depth of their residency.

The relative body density for mesopelagic fish was calculated by equation [1]. It is very similar to the well-known Fulton's condition factor formula (Y / X^3), sometimes called "the most primitive solution to remove the size effect" (Garcia-Berthou, 2001).

$$P = BW \times 100 / L_{sl}^3 \quad [1]$$

where P = fish body density (g mm^{-3}); BW = body weight (g); L_{sl} = fish standard length (mm).

The data were partitioned into 1 hour intervals when patterns of the diurnal dynamics of fish-body density were compiled. If several values were obtained for the same time interval, the average values were used for further calculations.

The Northern smooth-tongue (82 individuals) used for body-volume measurements and actual-density calculations were captured in the epipelagic layer during the night in the Southwestern Sea of Okhotsk on 17 July 2003.

RESULTS

In the offshore waters of the Sea of Okhotsk, the most significant mesopelagic fish biomass was concentrated in areas adjacent to the continental slope, in particular in the TINRO Basin and Southern Kurile Basin (Fig. 1). In late autumn, bathylagid fishes formed almost the entire fish biomass in the 200 - 500 m layer (90.5% without taking walleye pollock into account since they are a common epipelagic fish that descend from offshore waters to deeper water layers). The predominant species was the Northern smooth-tongue (*Leuroglossus schmidti*), making up 73.2% of the total catch (without walleye pollock). In the 500 - 1,000 m layer, the dense mesopelagic fish aggregations were also restricted to the area above the continental slope. The Northern smooth-tongue contributed 36.9% to the total fish biomass there. In March, catch values and estimated mesopelagic fish biomass were higher in the 500 - 1,000 m layer than in the 200 - 500 m layer. Almost half of the Northern smooth-tongue, > 80% of the eared blacksmelt (*Lipolagus ochotensis*) and 90% of the myctophid biomasses were concentrated in the deeper regions of these selected layers.

Despite differences in species composition, the catch distributions of mesopelagic fishes in the Bering Sea appeared similar. For instance, in the 200 - 1,000 m layer during spring and autumn, the most abundant mesopelagic fish aggregations were restricted to areas adjacent to the continental slope in the Western and Central Bering Sea (Fig. 2). Differences in the catch data between these areas and the offshore zone were especially noticeable in the 200 - 500 m layer. Catch data in the area above the continental slope were five to seven times higher than in the offshore zone. The light-rayed lanternfish (*Stenobrachius leucopsarus*) predominated and contributed to 78.9% of the total fish biomass in the 200 - 500 m layer or 86.9% when walleye pollock were not taken into account. In the 500 - 1,000 m layer, myctophids also predominated, making up 59.0% of the total fish biomass. Half of this biomass was composed of the dark-rayed lanternfish (*S. nannochir*) which is considered a non-migratory species (Iljinskiy, 1998). The bathylagid proportion increased in this layer to 27.8% of the total fish biomass, owing to the higher abundance of *Bathylagus pacificus* (14.4%), *Pseudobathylagus milleri* (5.7%), eared blacksmelt (5.1%) and Northern smooth-tongue (> 2.8%).

The vertical distribution of the common mesopelagic fishes is distinct in the Bering Sea and Sea of Okhotsk. The most common mesopelagic fish of the Sea of Okhotsk, the Northern smooth-tongue, was concentrated in the 210 - 400 m layer in the offshore zone. It also occurred from 270 - 300 m to the bottom above the continental slope which was at depths of 270 - 600 m. These concentrations were in most cases confined to the Okhotsk Upper Intermediate Water and the upper boundary of the steep gradient zone between the modified cold and warm interlayer (the Okhotsk Lower Intermediate Water). Despite the high migratory activity of the Northern smooth-tongue, the diurnal dynamics of the depth layer with the maximum concentrations were only feebly expressed. The dark-rayed lanternfish (*S. nannochir*) were distributed in deeper regions of the water column than the Northern smooth-tongue. They occurred in the 340 - 700 m layer in the offshore zone as well as from 400 - 450 m to the bottom above the continental slope which was at depths of 400 - 930 m. These depths coincided with the lower part of the previously mentioned steep gradient zone and with the upper part of the Okhotsk Lower Intermediate Water. In the Bering Sea, the light-rayed lanternfish (*S. leucopsarus*) concentrations were restricted to the 220 - 500 m layer in the offshore zone as well as at 300 - 500 m near the continental slope during the daytime. These depths coincided with the presence of the warm interlayer with water temperatures of 3.0 - 3.5°C. During the night time, despite the massive migration of light-rayed lanternfish from the upper layers all the way up to the sea surface, residual fish concentrations were fixed at the upper boundary of the warm interlayer.

The presence of the mesopelagic fish residence layers where they are found in higher concentrations in stratified water layers is probably correlated with the buoyancy maintenance with the least energy expenditures (Rodin, 1990). As it has been shown by underwater observations at depths of 300 - 350 m, the Northern smooth-tongue individuals are lethargic during the day, hovering head-down in the pelagic zone (Orlov, 1990). Thus, each fish species probably has its own preferred ranges of water densities which usually increase with depth and change discontinuously at the boundaries between different water masses. The preferred ranges of densities could be determined by the linear dimensions and other physical properties of the fish's body.

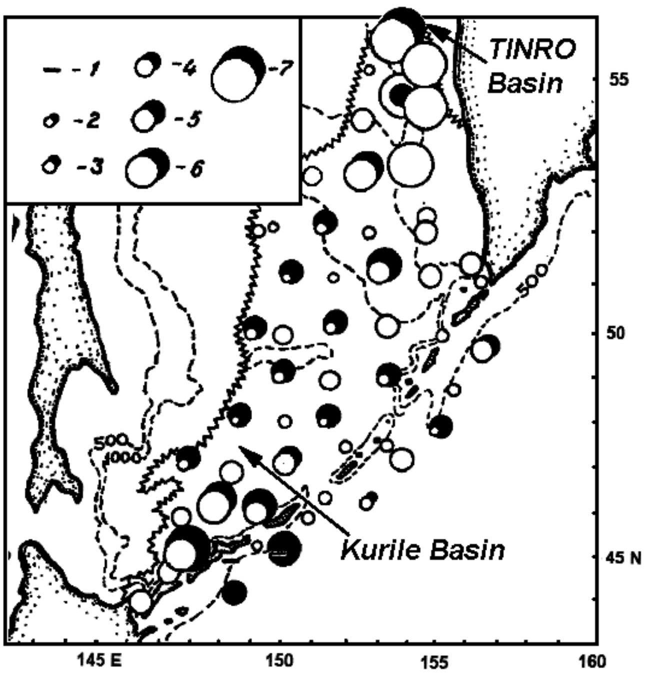

Fig. 1. Mesopelagic fish catch distribution in the Sea of Okhotsk from March to April 1990 in kilogram per hour of trawl haul. hollow circles = catches in upper mesopelagic layer (200 - 500 m); solid circles = catches in lower mesopelagic layer (500 - 1,000 m); 1 = no catch; 2 = < 5; 3 = 5 - 24; 4 = 25 - 49; 5 = 50 - 249; 6 = 250 - 500; 7 = > 500.

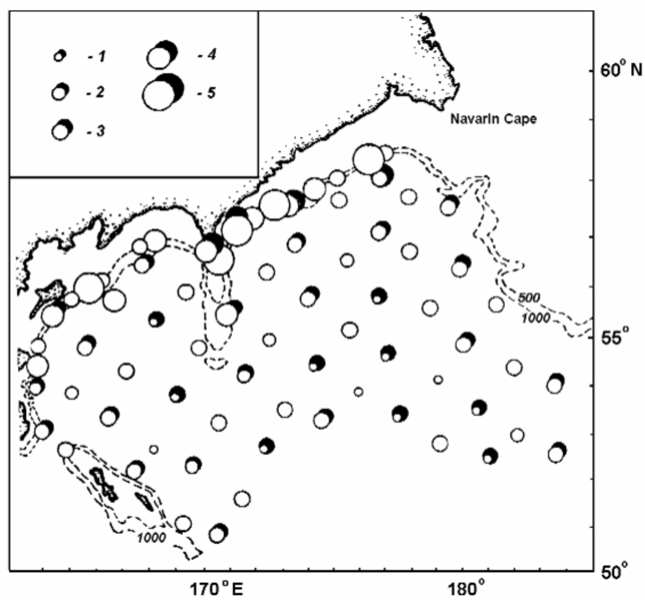

Fig. 2. Mesopelagic fish catch distribution in the Bering Sea in April to June of 1990 in kilogram per hour of trawl haul. hollow circles = catches in upper mesopelagic layer (200 - 500 m); solid circles = catches in lower mesopelagic layer (500 - 1,000 m); 1 = 5 - 24; 2 = 25 - 49; 3 = 50 - 249; 4 = 250 - 500; 5 = > 500.

Table 2. Mesopelagic fish biomasses estimated for the middle (200 - 500 m) and lower (500 - 1,000 m) pelagic layers in the Bering Sea and Sea of Okhotsk based on trawl survey data collected from February to June 1990.

Species	Fish Biomasses (thousands of metric tons)			
	Bering Sea		Okhotsk Sea	
	200 - 500 m	500 - 1,000 m	200 - 500 m	500 - 1,000 m
Dark-rayed lanternfish	14.0	1,382.7	38.6	1,025.0
Eared blacksmelt	34.5	164.6	349.7	1,434.4
Light-rayed lanternfish	2,737.6	3,752.3	57.6	42.9
Northern smooth-tongue	42.4	237.4	1,477.7	2,167.7
Pacific viperfish	45.3	203.0	2.0	83.5
Other myctophids	55.0	52.2	9.4	77.5
Other bathylagids	22.3	650.1	0.3	632.4

Therefore, it can be summarized from these observations that the mesopelagic ichthyofauna in the Bering Sea and Sea of Okhotsk are generally characterized by close numerical indices of specific diversity and quantitative distribution (Table 2). However, two distinct families of mesopelagic fish dominate in each Sea. While the abundant myctophid (light-rayed lanternfish) represents the "typical" (i.e. abundant, highly-migratory in the diurnal aspect, important in the pelagic food web) mesopelagic fish in the Bering Sea, the equally abundant bathylagid (Northern smooth-tongue) plays the same role in the Sea of Okhotsk ecosystem. Another common myctophid, the dark-rayed lanternfish, dwells in deeper layers in the Sea of Okhotsk than the Northern smooth-tongue and can be regarded as non-migratory (at least, in the vertical aspect). However, like its Bering Sea congener, it also dwells in the warm interlayer. Aggregation in the warm interlayer can be an important feature of biology for this genus. Furthermore, the close relationship between the light-rayed lanternfish concentrations and water of sub-Arctic structure (with well-expressed cold and warm interlayers and a thermocline zone between them) was previously found for the Pacific Ocean off the Kurile Islands (Radchenko & Ivanov, 1997).

The Northern smooth-tongue concentrates in the Okhotsk Upper Intermediate Water layer and are able to migrate through the cold interlayer (with sub-zero water temperatures) up to the sea surface during the night. The Sea of Okhotsk is the only water body in the world with such well-expressed bathylagid fish domination in its mesopelagic fauna, whereas myctophids predominate in most other North Pacific regions. The sub-zero water temperatures of the cold interlayer can be too severe for migrating myctophids. The Okhotsk Upper Intermediate Water is also colder (0.5 - 2ºC) than the warm interlayer in the Bering Sea. The Okhotsk Lower Intermediate Water (of Pacific origin) is warmer (2 - 3ºC) and saltier than the overlying water but probably lies too deep (500 - 2,200 m) for the daily migrations of mesopelagic myctophids. It can be concluded that environmental conditions within the Sea of Okhotsk's mesopelagic waters contribute to the phenomenon of bathylagid fish domination.

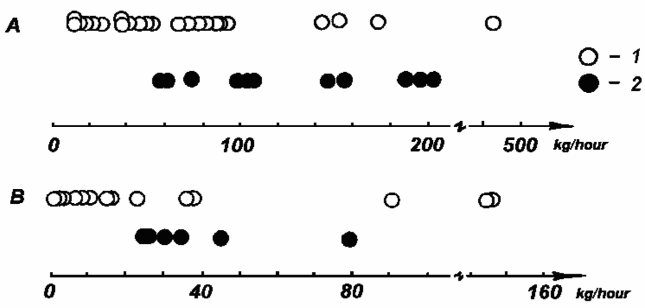

Fig. 3. Values of trawl catches in the mesopelagic layer (200 - 500 m) in the day and night time: A) Sea of Okhotsk, B) Bering Sea. 1 = daytime (0800 – 1600 hours); 2 = night (2000 – 0400 hours).

Diurnal vertical migration from deeper daytime water depths to near the surface is inherent for the most abundant mesopelagic fish species, including the Northern smooth-tongue, eared blacksmelt and light-rayed lanternfish. It was noted that the fishes rise into the epipelagic layer at night. The average indices of stomach fullness noticeably increase in the morning (Balanov & Gorbatenko, 1995). In the mesopelagic layer, the average stomach fullness index for these fish species changes little during a 24 hour period. This confirms the idea that the fishes found in this layer do not do much feeding but are instead digesting food consumed earlier in the upper layers.

Thus, mesopelagic fishes are widely-dispersed in the pelagic zone, preserving more or less dense concentrations only in the initial layer of residence. This is confirmed by the diurnal dynamics of trawl catch value of mesopelagic fishes in the upper mesopelagic layer. During the night, biomass of the catch is more stable and characterized by average values comparable to daytime values (Fig. 3). The biomass of daytime catches of mesopelagic fishes depends more on the degree to which the layer where they concentrated was sampled.

DISCUSSION

The 24 hour retention of high concentrations of mesopelagic fish in deep layers assumes that many of these fish do not migrate vertically to the epipelagic layer during night. It could be that the depth of occurrence, the speed and the direction of the movement between oceanic layers during night for these individual fishes may vary in magnitude and timing. Those fishes succeeding in finding food sources in the deeper layers could begin to migrate vertically later in the evening and accomplish their rise more slowly. Other individuals could have already descended at this time after filling their stomachs near the sea surface, where about 75.2 - 78.7% of the zooplankton biomass (in the layer 0 - 1,000 m) is concentrated at night (Volkov, 1995). A portion of the mesopelagic fish assemblage obviously remains in their layer of residence. There is also the assumption of their non-daily nourishment (Gorelova, 1985).

The migratory behaviour of mesopelagic fishes draws attention to the relationship of their possible contribution to transporting living matter to the deep waters. This relationship became evident from the diurnal dynamics of fish-body density. It was found the body density decreased in the deep layers during the day and increased with the beginning of active night feeding (Figs. 4 & 5). In Figure 4 and 5, points reflecting time vs. body density dependence are shaped like a parabola. Judging from the R^2 values, the parabolic fit agrees with the data sets reasonably well. The order of diurnal variability of the fish-body density can be roughly assessed using equations of correspondent polynomial of second degree. Such dynamics are probably related to the changes in the fullness of the fish's stomach and faeces being excreted. Compressed food lumps in the fish's stomach and gastrointestinal tract are likely more dense than the watery tissues of the fish's body. Therefore, it can be supposed that body density increases with stomach filling indices. These indices reached a maximum value at the end of the diurnal feeding route, decreased during the food digestion process and attained a minimal level after excretion. Such feeding habits promote the diurnal vertical migrations of mesopelagic fishes to the upper layers when the body density becomes minimal and decreases when the body density increases. The same pattern of body density diurnal dynamics was observed in all the examined fishes, even for the dark-rayed lanternfish (Fig. 5). The dark-rayed lanternfish's body density dynamics argues in favour of the assumption that this species also migrates vertically. Since this species occupies deeper layers than other mesopelagic fishes, they do not reach the sea surface, but probably migrate up to the boundary between inhabited water masses. The boundary layers between water masses also concentrate interzonal zooplankton to some degree. In this manner, the diurnal migration of common mesopelagic fishes represents a functional "biological pump" of organic matter into the deeper pelagic layers.

It is impossible to estimate from our data how large a change in weight can occur in the fish's body. There were differences in density of 60 mg cm^{-3} among the Northern smooth-tongue size groups measured just after extraction from the water, which were taken from night hauls in the near-surface layer (Table 3). However, notable distinctions in migratory behavior were not restricted to the different size groups. This suggests more significant diurnal changes in the body density during vertical feeding migrations than in the process of somatic growth.

In the Sea of Okhotsk, the mesopelagic nekton with an estimated average biomass of 27.8 million tons consume about 140 million tons of zooplankton annually (Iljinskiy & Gorbatenko, 1994; Iljinskiy, 1998). In the Bering Sea, annual

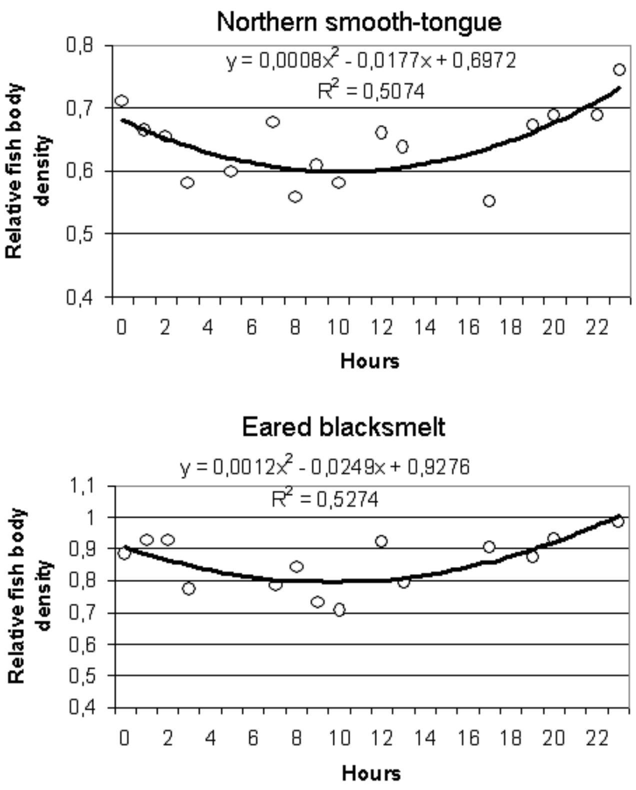

Fig. 4. Diurnal dynamics of the Northern smooth-tongue (*Leuroglossus schmidti*) and eared blacksmelt (*Lipolagus ochotensis*) in terms of "relative fish-body density" in the Sea of Okhotsk, March 1990.

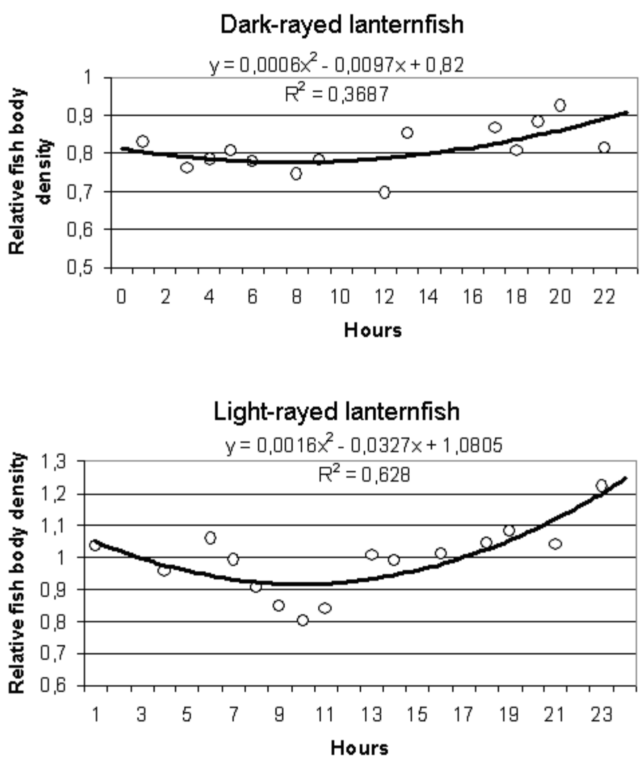

Fig. 5. Diurnal dynamics of the dark-rayed (*Stenobrachius nannochir*) and light-rayed (*S. leucopsarus*) lanternfish in terms of "relative fish-body density" in the Sea of Okhotsk, March 1990.

Table 3. Length to volume dependence in different size groups of the Northern smooth-tongue (*Leuroglossus schmidti*).

Size Group (cm)	Average Length (cm)	Weight Range (g)	Average Weight (g)	Volume (cm^3)	Density (g cm^{-3})	Sample Size (n)
9 - 12	11.8	4 - 8	6.0	6.1	0.98	30
11 - 14	12.7	6 - 15	10.2	11.0	0.93	31
13 - 16	14.6	12 - 22	16.8	18.3	0.92	21

zooplankton consumption by mesopelagic fish can be estimated at 80 million tons with the assumption of the total mesopelagic fish biomass of 17.5 million tons. These estimates reach 4.7% and 2.1% of the total zooplankton production, respectively (Shuntov & Dulepova, 1993, 1995). Among planktivorous fishes, such levels of zooplankton consumption were very significant with respect to the transport of living matter to higher trophic levels. Zooplankton predators consume up to 84.4% of the total zooplankton production in the Bering Sea epipelagic layer (Radchenko, 1994).

Balanov & Gorbatenko (1995) have estimated daily food intake at 1.5% of body weight for the light-rayed lanternfish, 0.8% for the dark-rayed lanternfish, 1.0% for the Northern smooth-tongue and 1.1% for the eared blacksmelt. According to this study, one light-rayed lanternfish specimen held 52 mg of food which it could potentially transport to the deep pelagic layer and subsequently excreted about 8.3 mg of faeces. The assumption made is that the proportion of consumed food egested is about 0.16, as with another planktivorous fish, the Pacific herring (Megrey et al., 2002). These estimates agree with those reported for other freshwater and marine fishes. One Northern smooth-tongue specimen consumed about 177 mg of food and excreted about 28.3 mg of faeces.

The Northern smooth-tongue stocks in the Sea of Okhotsk consist of 2.2×10^{12} individuals and the light-rayed lanternfish stocks in the Bering Sea consist of about 2.4×10^{12} individuals. It remains unclear what proportion of the total mesopelagic fish numbers migrate to the upper layer every night. If half of the total population feed in the epipelagic layer at night, then the Northern smooth-tongue can deliver 31,300 tons of digested material per day, or 11.4 million tons per annum, to the deep oceanic layers. Gross total transport between the ocean layers by the entire light-rayed lanternfish stock in the Bering Sea can be estimated at 15,000 tons daily or 5.48 million tons annually, if just 75% of these fish migrated every night.

It is generally recognized that life in deep oceanic layers is supported by "marine snow" or "dead body rain" which consists of detritus, faeces and carcasses of dead animals partly decomposed by bacteria and ciliates. According to mass-balance models, about 10% or about 300 million tons come from detritus of the total euryphagous zooplankton production in the Bering Sea (Shuntov & Dulepova, 1995). On average, zooplankton faecal pellets comprise 11 - 37% of particulate organic and vertical carbon flux, estimated over the Nordvestbanken on the Northern Norwegian shelf (Wassmann et al., 1999). These values show a seemingly low contribution of mesopelagic fish faeces in the total marine snow flux. However, as this material is egested in layers of the mesopelagic fish residence, it is being spread out. The level of dissolved nutrients increases from fish faeces after their mineralization by bacteria in layers relatively close to the surface of the sea. These nutrient supplies can be easily recycled by vertical water movements in the slope-eddies system (Radchenko et al., 1991). The pelagic residence time of zooplankton faecal pellets in the upper 100 m of the water column is estimated at 1.3 - 8.3 days (Wassmann et al., 1999) which is adequate time to reach the abyssal depths. The same phenomenon was observed for crustacean carcasses found at depths of 5,500 m in the South Atlantic and Arctic Oceans (Sokolova, 1994; Klages et al., 2001). Surface waters lack the stock of nutrients because the not-readily-soluble zooplankton faeces and dead matter tend to settle to the ocean bottom.

CONCLUSION

The abundant mesopelagic fish community plays an important role in ecosystem functioning at the microbial and other lower trophic levels. Their migratory and feeding behaviour supports a "biological pump" mechanism for delivering organic matter to mesopelagic layers through the stratified water column. Further transformation of this material makes provision for its involvement into nutrient recycling in the active ocean layer.

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