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MARINE BIOLOGY

Diversity of Macrobenthic Communities in the White Sea Estuaries

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Abstract—The diversity of shallow–water macrozoobenthic communities is described based on materials concerning 11 estuaries of small rivers and streams in the Kandalaksha Bay of the White Sea. Using the Brown–Blanke and cluster analysis techniques, nine types of communities of these estuaries were distinguished depending mostly on the estuary size, salinity, substrate type, water velocity, and depth. In large estuaries, a kind of zonation of the macrobenthic communities along the main estuary axis was observed related to the pronounced salinity gradient; it is described in detail for the Chernaya River estuary, which was the most studied. Such zonation is completely absent in small stream estuaries with polypoikilohaline conditions, where a poor species assemblage of brackish–water amphipods of the *Gammarus* genus dominate. The prevalence of the riverine and lacustrine freshwater species (especially of larvae of Diptera and Trichoptera) in the fauna of small estuaries is shown. In contrast, brackish–water and marine species dominate over the majority of the estuarine communities with respect to abundance, while the role of freshwater species is insignificant.

INTRODUCTION

It is commonly accepted that the fauna of the near-mouth zone and estuaries of rivers at a characteristic salinity of 2–10‰ (mixohaline zones) is strongly impoverished as compared to the adjacent marine and freshwater areas and is mostly represented by marine euryhaline species. This process is considered to be most intensive in the salinity range from 5 to 8‰, which is referred to as "the critical salinity of biological processes" [16] and which cannot be sustained by the overwhelming majority of both marine and freshwater species. The interfaces between the marine and freshwater faunas in various regions and sea basins are confined precisely to this (chorohaline) zone [16]. The poorness of the chorohaline fauna was proved in numerous papers [2, 5, 15, 22], including those concerning the estuary of the Chernaya River estuary on the Karelian coast of the White Sea [3, 11]. Meanwhile, these papers are based on the quantitative data on soft substrates, while the majority of freshwater species (which might be supplied by the rivers to the estuaries and inhabit them) are confined to dense substrates and aquatic plants.

In addition, most of the studies of the estuarine communities explicitly or implicitly underestimate the species of freshwater origin. The approach of the kind "no larvae of Chironomidae and other insects were determined" [5] is either directly claimed in the name of the technique or held back, which becomes evident from an analysis of the results presented [15, 21, 23]. Meanwhile, as was shown in selected special papers devoted to estuarine insects, this group provides from 17 to 54% of the macrobenthic species in the estuaries [25]. Great numbers of insects are delivered by rivers to their estuarine mouths [19]; they, being capable of osmoregulation, should evidently enter the estuarine benthos. Ignoring this group, one cannot obtain a correct estimation of the composition of an estuarine community and compare it with the freshwater and marine analogs. In this paper, we tried to fill this gap by paying special attention to the consideration and determination of minor representatives of the estuarine macrobenthos, mostly diptera larvae and oligochaets.

While discussing the fact of impoverishment of the benthic communities in the brackish waters, the enormous diversity of these communities often eludes the scientists, though it is observed by comparison of both different brackish-water basins and near-mouth areas of different rivers within a single sea basin or even within a single estuary. This is related, first of all, to the complex and diverse organization of the salinity gradient in the near-mouth parts of water flows [17]. The following alternatives of the salinity growth are possible: from the river to the sea; from the intertidal to subtidal zones; with the depth increase, within the subtidal zone; from low to high water within a tidal cycle; from the spring to the summer over seasons; and with the decrease in the desalinating runoff from land. In addition, the salinity may sharply grow during storms when the near-mouth areas are flooded with high waves. In all of these cases, the zone of critical salinity is crossed. The position and extension of the chorohaline zone in estuaries is defined precisely by the combination of the coast outlines and hydrological conditions [17]. In so doing, salinity is not the only factor determining the composition of the fauna in brackish-water basins and the abun-

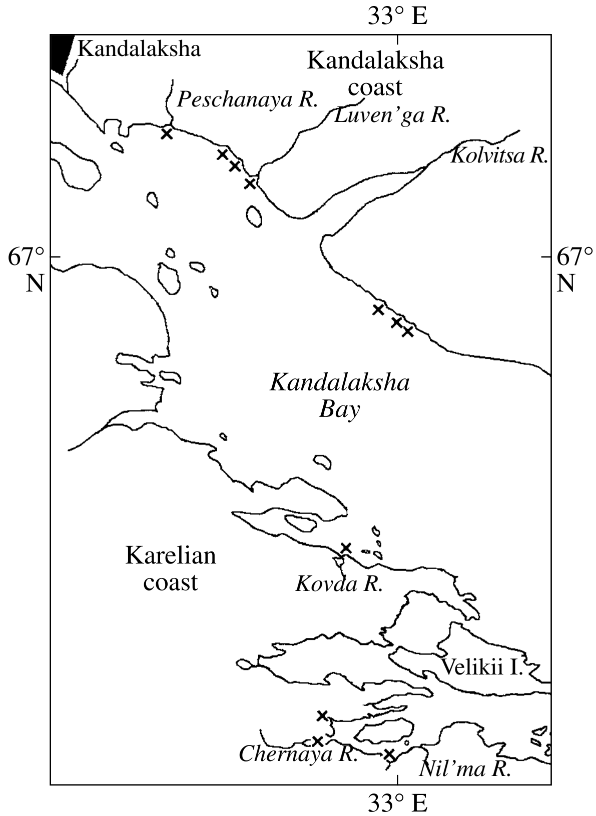

Fig. 1. Location of the estuaries studied in Kandalaksha Bay of the White Sea. The crosses indicate the sites of the estuaries.

dance proportions between the marine and brackish-water species [10]. The comparative analysis of estuarine systems is claimed to be a priority line in the ecology of estuaries [20], though to date it has been restricted to a few local considerations [24, 26].

The mouth zones of streams less than 2–3 m wide entering the sea virtually escaped the attention of hydrobiologists. Commonly, these zones feature a small (less than 100 m) extension; meanwhile, precisely there, the problem of animals settling in the chorohaline zone is the most crucial, since the salinity regularly changes with maximum amplitudes, together with the tidal phases, in tidal seas and with every surf wave in nontidal seas. No steady-state chorohaline zone is observed in this kind of estuary; it is replaced by a polypoikilohaline zone characterized by a permanently changing salinity [17]. The spatial salinity gradient is not expressed explicitly and the zone of this kind of estuary is based on the assessment of the duration of the seawater impact on selected areas rather than on the measurements of salinity values [26]. This represents an extreme case of the salinity dynamics in estuaries. The other extreme case of this sort of dynamics is represented by giant desalinated basins such as the Baltic Sea, where regions with different salinities are large and virtually constant in time.

In this paper, we tried to analyze the macrozoobenthic communities in the estuary of the White Sea in the zones of the critical salinity and close to it (approximately from 1 to 15‰) and the find the reasons for the differences between them. We examined estuaries with typical outlines (located along the axis of the channel and featuring a through-flow character) leaving lagoons and intertidal pools beyond our assessment. The principal attention was paid to the mouth zones of streams and minor rivers less than 10–15 m in width.

MATERIALS AND METHODS

The general conditions of the benthic habitats in the estuaries studied are determined by the features of geography and hydrological of the White Sea. The height of the tides reaches 2 m; therefore, the salinity distribution in the estuaries is, to a great extent, defined by the tidal phase. In most of the areas, the surfs are weak due to the complicated outlines of the coasts with semiclosed bights and bays. The dynamics of the salinity are mostly related to the tidal cycles. In the sea, the salinity equals 24–25‰, while in the water flows from the land, the mineralization is extremely low (0.01–0.04‰) and a lithorheophilic biotope with the corresponding fauna prevails in the waters. The lengths of the estuarine zones studied ranged from 30–50 m to 1–2 km at a width of the water channels entering them from 0.5–1.0 to 8–15 m.

The principal test area for studying macrobenthic communities in the critical salinity zone was the estuary of the Chernaya River (Kandalaksha Bay of the White Sea). The lower boundary of the estuary was regarded to run over the mean salinity level equal to 14–15‰, which coincides with the previously accepted boundary between the marine and brackish-water zones [3]. We used the results of the surveys of the Chernaya River estuary performed along the salinity gradient in July 1995 (one survey) and in June–August 2000 (three surveys) in order to classify the types of communities. The most complete survey of July 2000 was used. In all, 40 qualitative and 122 quantitative samples of macrobenthos in 14 estuary alignments were examined. For the sake of comparison, the data on the macrobenthic fauna of the Chernaya River and on the seaward part of the Chernaya River Bay of the White Sea are also presented. Qualitative samples were collected from various bottom substrates (silts, silty sands, washed sands, detritus, rocks, and macrophytes) in the lower intertidal and upper subtidal (down to sea depths of 0.5 m at low tide) zones. Quantitative samples (four samples down to a depth of 10–15 cm (12 × 12 cm in area) at each of the stations) were collected from the loose sediments of each of the alignments and also from the lower subtidal zone and at the zero depth mark. It should be noted that, in the upper part of the estuary, these levels are hardly distinguishable if the intertidal zone is poorly manifested.

Separation of the types of biocoenoses of the estuaries of the White Sea using the Brown–Blanke method. Mean proportions in the community are presented

Biocoenosis number	1	2	3	4	5	6	7	8	9
Number of stations	4	3	6	5	7	3	3	13	4
Salinity range, ‰	0–5	0–7	3–15	5–17	0–24	5–16	3–15	0–24	0–24
Substrate characteristic	Silts	Silts	Silts, sands	Silts, sands	Silts, sands, rocks	Rocks	Silts, sands, flora	Rocks	Rocks, sands, ailts
Insects									
Glossosoma sp.	0	0	0	0	0	0	0	3	4
Apatania stigmatella	1	0	0	0	0	0	0	10	3
Limnephilus nigriceps	2	5	2	0	3	0	9	5	16
Chironomus salinarius	9	7	8	1	0	0	0	1	1
Stictochironomus sp.	21	0	0	0	0	0	0	0	0
Micropsectra recurvata	14	0	0	0	0	0	0	0	0
Chrysops caecutiens	21	4	7	1	2	0	0	3	0
Crustaceans									
Gammarus oceanicus	0	0	8	0	34	11	0	2	0
Gammarus setosus	0	0	0	0	7	3	12	0	0
Gammarus zaddachi	5	0	0	0	5	0	0	61	5
Gammarus duebeni	0	6	0	0	2	0	0	6	68
Pontoporeia affinis	3	54	5	3	3	0	10	1	1
Jaera ischiosetosa	0	0	1	0	7	1	0	1	0
Mysis relicta	0	0	0	0	0	0	52	0	0
Gasteropod mollusks									
Hydrobia ulvae	0	1	11	52	8	0	0	2	0
Littorina saxatilis	0	0	0	0	13	9	0	0	0
Bivalve mollusks									
Mytilus edulis	0	0	0	0	0	72	0	0	0
Macoma balthica	0	10	44	21	7	0	1	1	0
Mya arenaria	0	0	3	2	2	0	15	0	0
Oligochaets									
Paranais simplex	7	0	0	0	0	0	0	0	0

In order to study the diversity of the near-mouth brackish-water communities, we also used sampling series from the mouths and estuaries of other water flows in the White Sea basin. These are the Luven'ga and Peschanaya rivers, five nameless streams on the northern (Kandalaksha) coast of Kandalaksha Bay, and the Kovda River and two streams on the Karelian coast (Fig. 1). The surveys were performed in July 1990 (the Kovda River estuary), in July 2000 (streams on the Karelian coast), and in June 2002 (flows of the Kandalaksha coast). At the sites listed, qualitative data (with no estimates of the organism densities on the ground) were obtained through full extraction of organisms from the sample with estimation of their quantitative relations. Thus, while assessing the diversity of estuarine communities, we will deal with their species structure rather than with the total biomass and production. The washing of the samples from loose sediments was performed through sieves with a mesh size of 0.5 mm; for samples with rocks, a mesh size of 1 mm was used. The number of samples in each estuary ranged from two to nine depending on its extension.

We did not use the data on large extended estuarine systems, the data on the subtidal zone deeper than 0.5 m, and those on the upper and intermediate levels of the intertidal zone. This way, we excluded the influence of the intertidal level and sea depth from our analysis.

We applied the value of the intensity of metabolism as the measure of species abundance, since this value more adequately represents the contribution of a species to the community activity than its abundance or biomass [6]. In order to classify the communities of the estuarine systems studied, we applied the Brown–

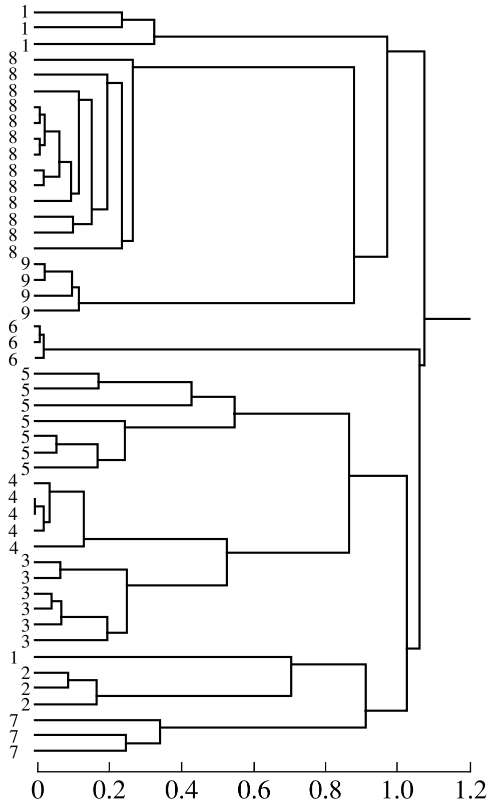

Fig. 2. Similarity dendrogram for 20 macrobenthic species at 48 stations. The numerals denote the types of biocoenoses distinguished by the Brown–Blanke method.

Blanke method [8] and cluster analysis implemented in SYSTAT software (the Pearson correlation coefficient between the abundance proportions of species in the community was used as the measure of similarity).

RESULTS AND DISCUSSION

Types of Estuarine Benthic Communities

In order to classify the communities, various methods are used; we applied two of them: the Brown–Blanke method, which implies a significant creative element produced by the interpreter, and the completely formalized method of cluster analysis.

Brown–Blanke method. We used the most recent version of this method [8]. It is rather widely used for classifying communities in geobotany, where it showed its efficiency; meanwhile, in hydrobiology, it is not popular despite the presence of corresponding problems. We used the table of the proportions of species abundances in the community as the initial table regarding these quantities to be most convenient and adequate. Instead of differentiating the species with respect to their constancy, we selected 20 species whose share in the total abundance was greater than 15% in at least one of the samples. The subsequent computer-based procedure of the analysis followed [8] and included diagonalization of the table of initial data, separation of the active part of the table (differentiating species), rearrangement of the sample columns, and distinguishing biocoenosis types. The result of the classification (partial synergetic table) is presented in the table. Nine types of biocoenoses are distinguished distinctly correlating with the characteristic combinations of environmental factors. In each of the biocoenoses, a species dominating with respect to abundance (or two or three dominating species) is recognized. These species-dominants are used to name the corresponding biocoenoses following the technique suggested by Vorob'ev [7].

(1) Chironomidae–*Chrysops caecutiens* biocoenosis. Loose (silts or silty sands with great detritus contents) grounds of a large estuary in the freshwater–oligohaline zone (average salinity of 0–2‰). This biocoenosis was encountered only in the estuary of the Chernaya River. In all, not including single findings, 18 macrobenthic species were recognized. Larvae of diptera *Stictochironomus* sp. (mean contribution to the community metabolism of 21.4%), *Ch. caecutiens* (21.1), and *Micropsectra recurvata* (14.5) dominate; also characteristic are the oligochaets *Nais elinquis* (5.6), *Paranais* gr. *simplex* (7.0), and *Paranais litoralis* (2.1); the chironomids *Chironomus salinarius* (9.3), *Ablabesmyia* sp. (3.7), *Procladius (Holotanypus)* sp. (3.2), *Cladotanytarsus* gr. *mancus* (3.0), *Stictochironomus* sp. (0.7), and *Tanytarsus* sp. (0.3); the amphipods *Gammarus zaddachi* (4.8) and *Pontoporeia affinis* (3.2); the caddis flies *Limnephilus nigriceps* (2.2), as well as *Bezzia nobilis* (0.7); and the dipterous *Palpomyia rufipes* (0.3) (Ceratopogonidae family) and *Aphrosylus* sp. (2.1) (Dolichopodidae family). This biocoenosis (similar to the following one) is more subject to the seasonal dynamics, in the course of which selected chironomid species replace one another.

(2) *Pontoporeia affinis* biocoenosis. Loose (silty sands) grounds of a large estuary in the oligohaline zone (average salinity of 2–5‰). Twenty species are recognized; the brackish-water amphipod *P. affinis* dominates (54% of the community metabolism); also characteristic are the bivalve mollusk *Macoma balthica* (10.1) and the chironomid *Ch. salinarius* (6.7). Accessory species are represented by the amphipod *Gammarus duebeni* (6.0); the caddis fly *L. nigriceps* (4.8); the diptera *Ch. caecutiens* (4.7), *Pr. (Holotanypus)* sp. (1.3), *Cl.* gr. *mancus* (2.0, at the beginning of the summer 14–20%), *Orthocladius* gr. *saxicola* (0.2), *Paracladopelma camptolabis* (0.1), and *Ephydridae* sp. (0.1); the polychaet *Marezellaria viridis* (3.3); the oligochaets *Tubifex costatus* (3.0) and *P. litoralis* (1.2); the larvae of the beetle *Haemonia mutica* (1.7); and the gasteropod mollusk *Hydrobia ulvae* (0.7). In the survey of June 2000, the chironomids *Paratendipes* gr. *albimanus*, *Polypedilum scalaenum, Cricotopus maritimus*, and *Ceratopogon* sp. were also found.

(3) *Macoma balthica* biocoenosis. Loose grounds of a large estuary in the chorohaline zone (average salinity

of 5–10‰). Seventeen species were recognized. The marine euryhaline mollusk *M. balthica* (43.7% of the total metabolism) dominates, also characteristic are *H. ulvae* (11.1), *Ch. salinarius* (8.2), *G. oceanicus* (8.1), and *Ch. caecutiens* (7.3). Accessory species are represented by the amphipods *P. affinis* (5.5) and *Gammaracanthus loricatus* (0.5); the oligochaets *P. litoralis* (5.4), *Tubifex costatus* (3.0), and *Enchytraeidae* (0.7); the polychaet *Marenzelleria arctia* (2.5); the chironomid *Pr. (Holotanypus)* sp. (2.2), *Cl.* gr. *mancus* (0.8), and *Cricotopus maritimus* (0.3); the larvae of the beetle *Haemonia mutica* (0.9); the isopod *Jaera ischiosetosa* (0.8); and the mollusk *Mya arenaria* (0.3).

(4) *Hydrobia ulvae* biocoenosis. Loose grounds of a large estuary in the brackish-water zone (average salinity of 8–13‰). Twenty-three species were recognized. The marine euryhaline mollusk *H. ulvae* (52.4% of the total metabolism) dominates, *M. balthica* (21.1) is subdominant. Accessory species are represented by the oligochaets *T. costatus* (5.8), *P. litoralis* (3.6), *Enchytraeidae* (0.6), and *Tubificoides benedeni* (0.2); the amphipods *P. affinis* (3.5) and *Monoculodes borealis* (0.3); the polychaets *Nereis virens* (2.6), *M. arctia* (1.8), *Arenicola marina* (0.7), *Eteone longa* (0.5), *Spio filicornis* (0.3), *Pygospio elegans* (0.3), *Fabricia sabella* (0.3), and *Scoloplos armiger* (0.2); the mollusk *M. arenaria* (1.7); and the diptera *Satchelliella* sp. (1.4), *Aphrosylus* sp. (1.2), *Ch. salinarius* (1.2), *Cricotopus vitripennis* (0.7), and *Ch. caecutiens* (0.6). This biocoenosis is very similar to the intertidal community of silty sands from Kandalaksha Bay proper (at a salinity of 20–25‰) but differs from it by a train of accessory brackish-water species and a very low abundance of a series of characteristic marine species.

(5) *Gammarus oceanicus* biocoenosis. Mixed (rocky–sandy) grounds in the chorohaline zone, often with a great salinity range. Sixteen species were recognized. The most characteristic are *G. oceanicus* (34.2% of the total metabolism), *G. setosus* (6.8), *L. saxatilis* (12.6), *H. ulvae* (8.3), *J. ischiosetosa* (7.2), and *M. balthica* (7.1) with no evident domination of a single species. Accessory species are represented by the amphipods *G. zaddachi* (4.7), *G. loricatus* (3.5), *G. duebeni* (2.3), and *P. affinis* (3.0); the caddis fly *L. nigriceps* (2.6); the diptera *Ch. caecutiens* (2.1); the mollusks *Mya arenaria* (2.4), *Mytilus edulis* (1.0), and *Littorina littorea* (0.2); and the polychaet *N. virens* (2.1).

(6) *Mytilus edulis* biocoenosis. Rocky grounds in the brackish-water zone with strong currents (mussel banks). Eight species were recognized. *M. edulis* strongly dominates often featuring enormous densities (72.3% of the total metabolism). Accessory species are represented by the amphipods *G. oceanicus* (10.7), *G. setosus* (3.0), and *G. loricatus* (0.3); the mollusks *L. saxatilis* (9.3) and *L. littorea* (2.8); and the isopods *J. ischiosetosa* (1.0) and *J. albifrons* (0.3).

(7) *Mysis relicta* biocoenosis. Sandy grounds of large lake-type extensions in the chorohaline zone. Twelve species were recognized. The myside *M. relicta* (52.3) dominates, also characteristic are *M. arenaria* (14.6), *P. affinis* (14.2), and *L. nigriceps* (9.3). Accessory species are represented by the chironomids *Cl.* gr. *mancus* (3.0), *G. setosus* (2.3), *G. loricatus* (1.7), and *G. oceanicus* (0.3); the mollusks *M. balthica* (1.0), *Lymnaea auricularia* (0.7), and *Lymnaea stagnalis* (0.3); and the caddis fly *Oecetis ochracea* (0.7). This type of community was encountered only in the Kovda River estuary.

(8) *Gammarus zaddachi* biocoenosis. Rocky grounds of various (both large and small) estuaries in the polypoikilohaline (salinity range from 0 to 24‰) and oligohaline zones. Twenty species were encountered; the amphipod *G. zaddachi* (61.2% of the total metabolism) dominates. The upper sides of rocks are inhabited by freshwater litholrheophilic species of the caddis flies *Apatania stigmatella* (10.1), *L. nigriceps* (4.8), *Glossosoma* sp. (3.0), and *Hydroptila* sp. (1.2). Under individual stones, species of various origins are encountered: the amphipods *G. duebeni* (6.0), *G. loricatus* (2.3), *G. oceanicus* (2.1), and *P. affinis* (0.9); the diptera *Ch. caecutiens* (3.2), *P. (Holotanypus)* sp. (1.3), *Ch. salinarius* (0.6), and *Micropsectra recurvata* (0.3); the mollusks *H. ulvae* (2.0), *M. balthica* (0.9), and *L. saxatilis* (0.3); the isopod *J. ischiosetosa* (1.2); and the mayflies *Heptagenia sulphurea* (0.4), *Baetis rhodani* (0.3), and *Ephemerella ignita* (0.3).

(9) *Gammarus duebeni* biocoenosis. Mixed grounds of a small estuary in the polypoikilohaline zone (the salinity also veries from 0 to 24‰). Nine species were recognized; *G. duebeni* (67.6) and *L. nigriceps* (15.6) dominate. Accessory species are represented by the amphipods *G. zaddachi* (5.2) and *P. affinis* (0.6)); the caddis flies *A. stigmatella* (3.2) and *Glossosoma* sp. (3.7); the chironomids *Cl.* gr. *mancus* (1.7) and *Ch. salinarius* (1.3); and the polychaet *M. viridis* (1.0).

In addition to the species listed, a series of species were found only in minor amounts in the qualitative samples collected from the dense substrate in the oligohaline zone of the Chernaya River estuary. These are the caddis flies *Polycentropus flavomaculatus, Lepidostoma hirtum, Grammotaulius atomarius, Potamophylax stellatus, Limnephilus politus,* and *Oxyethira* sp.; the larvae of the beetles *Coelambus* sp., *Elmis maugetii*, and *Oulimnius tuberculatus*; the chironomid *Rheotanytarsus* sp.; the isopod *Asellus aquaticus*; and the mollusk *Anisus draparnaldi.*

Cluster analysis. The results of the cluster analysis at the 0.5–0.6 similarity level (Fig. 2) revealed the same principal groups of communities that were distinguished with the Brown–Blanke method. Only a single station from biocoenosis 1 separated in the cluster field and formed its own assemblage. In addition, the cluster diagram shows different levels of the internal uniformity of the groups: the samples from biocoenoses 4, 6, 8, and 9 are quite similar due to the domination of a single species, while biocoenoses 1, 5, and 7, on the contrary, are rather heterogeneous in their structure and two or three different species may play the role of the first dominant.

Naturally, in each specific estuary, the set of biocoenoses include only a part of the nine types listed. The estuaries studied by us contained from seven (the Chernaya River estuary) to one (a series of stream estuaries) biocoenoses.

ZONATION AND DIVERSITY OF THE COMMUNITIES IN INDIVIDUAL ESTUARIES

Chernaya River (Karelian coast). The river is 7–10 m wide and its estuarine zone extends over about 2.5 km forming two long reaches up to 500–600 m wide and three restrictions with a width of 30–100 m. On the reaches, the current is almost absent and the floor is composed of rocks and sands. The mouth of the Chernaya River is represented by a high threshold making difficult tidal water motions. Seven of the above-described nine types of macrobenthic biocoenoses are found in the estuary; the most developed are biocoenoses 1, 2, 3, and 4, consequently changing for one another on the soft substrates along the mean salinity gradient. These biocoenoses corresponding to different salinity ranges have been distinguished and described earlier [11, 12]; our data allow us to make important corrections in their descriptions.

The freshwater (near-mouth) zone of the estuary (up to 400 m from the mouth of the river) is mostly occupied by the Chironomidae–*Chrysops caecutiens* biocoenosis. In this zone, there exists a permanent weak current from the river, which is distorted by the echo of the tidal wave during the high tide phase. As a rule, the salinity does not exceed 2‰. This area is characterized by enhanced species diversity due to the freshwater species delivered from the river, which settle mostly on the rocks and macrophytes in the channel; meanwhile, as compared to the river proper, the freshwater community is significantly poorer.

In the oligohaline zone (the subsequent 500 m from the mouth), silty grounds are also observed and *P. affinis* biocoenosis prevails. The estuary has a characteristic width of 50–120 m, which allows retaining a permanent though weak current. Salinity ranges from 0 to 7‰ being about 2‰ on the average. The general species diversity falls due to the elimination of the majority of rheophilic species.

The chorohaline zone (subsequent 1000–1200 m) is occupied by the *M. balthica* biocoenosis. On the average, the salinity grows up to 5–7‰ ranging from 0 to 16‰. The brackish-water species (*M. arctia, T. costatus,* and *J. ischiosetosa*) are combined with marine euryhaline species (*H. ulvae, M. balthica*, and *M. arenaria*), while the majority of chironomids disappear. This area is completed by a restriction of the estuary, where rocky grounds with the *G. oceanicus* community prevail and, one, for the last time, encounters lithophilic species of freshwater origin—the caddis fly *L. nigriceps* and the chironomid *Orthocladius* gr. *saxicola*; meanwhile, the typical marine lithophilic species *L. saxatilis* and *M. edulis* appear. No freshwater fauna can penetration across this boundary.

The brackish-water zone abrasive (700–800 m long) is represented by a wide shallow-water reach with a silty bottom and an *H. ulvae* community (biocoenosis 4). The average salinity increases up to 11.5‰, oscillating from 2.5 to 19‰. Keeping its small species diversity, this community sharply increases its biomass, mostly due to the mollusks *H. ulvae* and *M. balthica.* This portion of the estuary is bound by a rather steep threshold with lithorheophilic conditions where the *M. edulis* community is developed. Below this threshold, where the average salinity is 14.6‰ and it never falls below 8.3‰, a community typical of Kandalaksha Bay with a prevalence of *H. ulvae, M. arenaria, M. balthica, A. marina,* and *T. benedeni* is formed over the soft grounds of the intertidal zone [18].

It is interesting to follow the changes in selected integral characteristics of the pelophilic community along the salinity gradient in the estuary. The total abundance of benthos, ranging from 6000 to 15000 ind./m^2, features virtually no regular changes along the estuary, though selected surveys suggested the presence of tendencies both to its increase [13] and decrease [14] down the estuary. These tendencies are mostly of a seasonal character and are related to the peculiar features of the reproduction (and precipitation of larvae) of marine species and flights of insects (see below). On the contrary, the total biomass continuously grows from the river mouth to the sea with no significant fluctuations. On the average, it is 5.5 g/m^2 in the freshwater zone, 6–9 g/m^2 in the oligohaline zone, from 15 to 40 g/m^2 in the chorohaline zone, and from 51 to 96 g/m^2 in the brackish-water zone (in the marine part of Chernaya River Bay, it is 115–160 g/m^2, at places reaching 600 g/m^2). The total metabolism of the concentration changes in a similar manner. This is related to the increase of the share of large species in the community, first of all, of the mollusks *H. ulvae* (with a mean body mass of 4.5 mg) and *M. balthica* (24.5 mg). They replace the significantly smaller chironomids and oligochaets with a characteristic body mass from 0.2 to 1.2 mg. Down the estuary, the average body mass of the organisms almost linearly grows with the distance from the mouth from 0.55 to 7.40 mg.

On the whole, without considering single findings in the near-mouth area, 67 macrobenthic species (the actual number of species is somewhat greater since we failed to determination some species of Chironomidae and Oligochaeta) were recognized in the Chernaya River estuary (above the salinity boundary of 14–16‰). The greatest diversity is characteristic of the larvae of diptera (22 species, mostly of Chironomidae). Taking into account the earlier studies, including those concerning the subtidal zone with sea depths down to 12 m [11, 12], the list of the macrobenthic species of the region under consideration contains 91 species. This number is somewhat smaller than the number of species encountered in the Chernaya River proper (about 120 species), though it exceeds the number of species known in the marine part of the Chernaya River Bay (approximately 80). Three species of fish are also abundant in the estuary: the sticklebacks *Pungitius pungitius* and *Gasterosteus aculeatus* and the plaice *Liopsetta glacialis*; the stickleback juveniles are so numerous that are always encountered in benthic samples.

The species richness of the macrobenthos on soft substrates features no directed changes along the estuary, ranging from 14 to 20 species per alignment. It is interesting that the earlier studies of this estuary [3, 11], when chironomids and oligochaets were not determined to species, reported a sharp decrease in the species richness from the seaward part of the estuary toward its freshwater part. The same tendency is also characteristic of many other studies in other estuaries [5, 15, 23], which did not take into account the diversity of the insect larvae and oligochaets.

On the whole, our data prove the regularities obtained earlier on the changes in the integral characteristics of the benthic community in the estuary under consideration [1], though with a single exception. Our data revealed no sharp variations in the total abundance values described in [1] for the ecotons between the distinguished areas of the estuary. These variations were interpreted as the reflection of the ecoton (boundary) conditions between different types of communities. In our survey, only a single sign of an ecoton at the interface between the chorohaline and brackish-water zones may be recognized; it is related to the sharp decrease in the *M. balthica* density resulting in the decreased total biomass, metabolism, mean individual weight, and domination. However, judging from the materials of a single alignment, one can hardly ascertain that this is precisely an ecoton-related effect.

SEASONAL SALINITY GRADIENT AND SEASONAL CHANGES IN THE COMMUNITY OF THE CHERNAYA RIVER ESTUARY

Due to the decrease in the riverine runoff to the estuary during the summer, the mean salinity in it significantly grows from July to August. As has been shown before [12], macrobenthos responds to this process by a gradual penetration of marine and brackish-water species inside the estuary. In so doing, the boundaries between individual zones related to the salinity gradient partly disappear. Meanwhile, our data allow one to note some additional aspects of the seasonal changes in the community.

During the summer, the larvae of diptera, especially Chironomidae, which dominate over the more freshwater parts of the estuary, proved to be the most variable group of organisms. In June (during the maximum desalination), the freshwater species *Cl.* gr. *mancus, Paratendipes* gr. *albimanus*, and *Polypedilum scalaenum* prevail in the oligohaline and chorohaline areas. As early as in June, these species pupate and fly away from the basin. In July, they are changed for another chironomid species—euryhaline *Ch. salinarius*; probably, it migrates from the subtidal zone and its larvae rest in the intertidal zone throughout the summer. The life cycles of the freshwater species in the estuary seem to adapt in such a way that the rapid growth of larvae coincides with the season of the maximum desalination (the end of the spring–beginning of the summer), while the imago and egg stages, which do not depend on the salinity in the basin, are confined to the period of enhanced salinity. In June, the cadis flies (including *L. nigriceps* inhabiting the entire chorohaline zone) fly away in a similar way.

GROUND TYPES AND THE "CRITICAL SALINITY" BOUNDARY IN THE CHERNAYA RIVER ESTUARY

As one can see, the fauna of the Chernaya River estuary (especially in its upper part) is extremely rich in species of freshwater origin, both rheophilic supplied with the riverine waters and limnophilic (on the whole, 30 freshwater species against 37 marine and brackish-water species). In so doing, the domination of marine or freshwater groups evidently depends on the substrate type. In the areas with soft grounds (occupying the greater part of the area of the floor), marine species penetrate closer to the river mouth, while freshwater species disappear relatively rapidly, evidently not crossing the "critical salinity" boundary. On the contrary, in the areas with a rocky floor, species of a freshwater origin dominate over the major part of the estuary; they reach waters with a mean salinity of 7.6‰, that is, they overcome the "critical salinity." Over hard substrates, marine species are less developed, though salinities of 7.6‰ are also reached. This seems to be related to the fact that, due to the retention of salts by silty particles, the actual salinity in silty grounds may be significantly higher and more stable than at the rock surfaces washed by the currents. On the other hand, the species diversity of the lithophilic estuarine communities is low and everywhere (except for the uppermost near-mouth area) is smaller than that in the pelophilic communities. In addition, in the wide silt-covered estuarine reaches, areas of hard grounds are rare and pelophilic species strongly dominate the phytophilic species in abundance.

Kovda River (Karelian coast). The river is 7–15 m wide; the estuarine zone is about 1.2 km in length and includes a lake with a width of about 1.5 km and a depth up to 5–8 m without noticeable currents and with a constant vertical salinity gradient (from 0–5‰ at the surface to 3–18‰ in the near-bottom layers). In addition to the lake, the estuarine zone includes a channel below it with a strong current. In the riverine part of the area and in the intertidal zone, rocky grounds are developed, while the subtidal zone and the bays of the lake feature a silty floor. The estuary was surveyed at nine stations; four types of macrobenthic communities were found. The major part of the lacustrine shallow-water area refers to the oligohaline zone and is occupied by the *P. affinis* community with a significant admixture of freshwater species (*Limnephilus nigriceps* and *Lymnaea auricularia*). At a depth of about 0.5 m, brackish-water species dominate (*M. relicta* community). In the mainstream part below the lake, the polypoikilohaline zone with the *G. zaddachi* community is encountered, while further downstream, one finds the *M. edulis* community.

Luven'ga River (Kandalaksha coast). The river is 7–10 m wide; the estuarine zone is about 300 m in length without noticeable reaches; it features a strong current and rocky ground over its entire extension. At low water, complete desalination over the entire length of the estuary is observed; at high water, the water salinity is generally high, while its distribution is extremely irregular (fresh water overrides the marine water propagating over the floor). On the whole, the estuary represents a polypoikilohaline zone with clearly manifested tidal and poorer expressed spatial salinity gradients. The estuarine zone is examined at five alignments; in all, 19 species and two community types of macrobenthos were distinguished. In the upper and middle parts of estuary, the *G. zaddachi* biocoenosis is developed; in the upper part, it is enriched with lithorheophilic larvae of the caddis flies (*Apatania stigmatella*, *Glossosoma* sp., *Silo pallipes, Rhyacophila fasciata*, and *Hydroptila* sp.), while in the middle part, the biocoenosis is reduced to three species—*G. zaddachi* (dominant), *A. stigmatella*, and *J. ischiosetosa.* In the lower part, the *G. oceanicus* community is developed; its diversity is enhanced due to the eurihaline amphipods *G. oceanicus, G. setosus*, and *P. affinis.*

Peschanaya River (Kandalaksha coast). The river is 4–6 m wide; the estuarine zone is about 100 m in length without noticeable reaches. The estuary features a strong current and rocky ground and also represents a polypoikilohaline zone. In the estuary, nine macrobenthic species (five freshwater, three brackish-water, and one marine) and two types of biocoenoses are encountered. In the upper and middle parts of the estuary, *G. zaddachi* dominates; the upper part is characterized by freshwater insect larvae (*A. stigmatella, Baetis rhodani*, and *Simuliidae* spp.), while the middle part features brackish-water species (*G. duebeni* and *J. ischiosetosa*). In the lower part, *L. saxatilis* and *G. oceanicus* dominate.

Streams. The mouths of five streams on the Kandalaksha coast and two streams on the Karelian coast from 0.5 to 1.5 m wide were examined. All of them feature a polypoikilohaline character; at low tide, the salinity is close to 0‰ (freshwater runoff with the absence of seawater), while at high tide, it is close to the normal sea salinity value equal to 24–25‰ (a southwest inflow suppresses the stream runoff). Two types of biocoenoses were found, both with the domination of the brackish-water amphipods *G. zaddachi* (more often, under the flow-through conditions over rocky grounds) or *G. duebeni* (in the areas with more silty grounds). Freshwater and marine species play a subordinate role; frequently, the community is represented only by the species of the *Gammarus* genus. In addition, at the places with slow currents, the sticklebacks *Pungitius pungitius* and *Gasterosteus aculeatus* are regularly encountered.

FACTORS DEFINING THE DIVERSITY OF ESTUARY COMMUNITIES

The diversity of the estuarine macrobenthic communities studied by us is mostly described by four factors: the size of the estuarine system proper, the flow properties and type of the bottom sediment, the depth, and the salinity.

Size of the estuary. This characteristic is rarely regarded as a factor defining the composition of the benthic community [26]. Meanwhile, according to our results, it represents a key factor. One (with domination of *G. duebeni*) of the nine biocoenoses distinguished by us is developed only in the smallest estuaries less than 50–100 m long formed by streams with a width of 0.3–2 m. Seven biocoenoses refer to larger estuaries of rivers from 3–5 to 10–12 m in width. Finally, one type (*G. zaddachi*) was encountered in estuaries of all sizes. On the whole, stream estuaries are characterized by the sharp domination of the brackish-water amphipods of the *Gammarus* genus (*G. zaddachi* or *G. duebeni*; commonly, a single species dominates over the entire length of the estuary). In larger estuaries, these species play subordinate roles. The principal reason for the particular features of small estuaries lies in the polypoikilohaline conditions, which eliminate all the species except for those adjusted to the rapid changes in salinity over a wide range. It is interesting that no species of this kind are encountered among marine euryhaline species, which, in the opinion of Khlebovich [17], should dominate under the polypoikilohaline conditions. In our case, here, the amphipod species, regardless of their marine origin not characteristic of fully saline waters, prevail.

The species richness of macrobenthos rapidly increases with the increase in the estuary sizes from 6–9 species in the estuaries of streams to 67 in the estuary of the Chernaya River. In so doing, the number of marine and freshwater (that is, relatively stenohaline) species grows at a greater rate than that of brackish-water species (adjusted to rapid salinity changes).

Currents and types of sediments. These factors are closely interrelated and are commonly regarded as the leading factors when classifying freshwater bottom biocoenoses [4]. They play the key roles in the distribution of the estuarine benthos as well. Among the nine types of bottom biocoenoses distinguished (table), five refer to silty–sandy grounds with the absence of currents; two (*G. oceanicus* and *G. duebeni* biocoenoses) are observed over mixed substrates composed of rocks, sands, and silts with a noticeable current; and two more (biocoenoses *M. edulis* and *G. zaddachi*) are developed over rocky grounds at the places with strong (though not permanent) currents.

The mechanisms of the influence of the sediment type on the estuarine fauna are diverse. First, the ground type influences directly: most of the dominating benthic species are adjusted to a certain substrate type (commonly, to rocky or silty–sandy grounds). Only a few species such as the amphipods of the *Gammarus* genus are adapted to dwelling over various grounds. Second, the current regime and the characteristic of the sediments in the estuary are closely related to the salinity regime in it, because both of these parameters, in their turn, depend on the geometry of the basin (mostly, on the relation between the cross section of the estuary and the incoming water flow). In the estuaries with string currents (narrow and shallow, with intensive water exchange), a complete desalination over the entire extension is observed at low water tides. In this kind of system, marine species are almost completely absent, brackish-water species (especially *G. zaddachi*) dominate, and over great areas of the estuary, selected freshwater forms (caddis flies *A. stigmatella* and *Gossosoma* sp.) are encountered. The smaller the water exchange and the greater the distribution of loose sediments, the more stable the salinity regime and the better manifested the longitudinal zonation of the benthos.

Depth. This factor almost did not vary in the database used by us (from the lower intertidal zone to a depth of 0.5 m). Only the biocoenosis *M. relicta* differs from the other types in the depth of its habitat (it starts from a depth of 0.3–0.5 m and deeper). Other biocoenoses are characteristic of the zero depth mark and adjacent levels. It is very necessary to note that most of the infauna species dominating over soft substrates (*M. balthica, H. ulvae*, and others) also inhabit the lower intertidal and the upper subtidal zones, while the epifauna representatives dominating over rocky grounds (*M. edulis*, species of the *Gammarus* genus) evidently gravitate to the subtidal zone and sharply decrease their abundance above the zero depth mark.

On the whole, depth is mostly an indirect ecological factor defining the presence of a vertical salinity gradient. In many rather large estuarine systems, water masses are known to be stratified with respect to salinity and benthic communities manifest vertical zonation; in so doing, freshwater and brackish-water species occupied the upper layers, while the lower layers were inhabited by marine species [9]. Among the areas studied by us, this kind of distribution pattern was recognized in the Kovda River estuary.

Salinity. Salinity is the most evident factor of the benthos distribution in the estuaries; its examination is described in numerous publications [2, 3, 9, 16]. Commonly, in the aquatic areas studied, longitudinal zonation is assessed; it includes from three to five types of benthic communities (from the river mouth toward the sea freshwater, brackish-water, and marine species assemblages subsequently replace one another).

In the areas studied by us, salinity represents the key factor of the benthos distribution in larger estuarine systems over soft substrates, where a relatively stable longitudinal salinity gradient is formed. Here, with the salinity growth, a series of subsequently changing biocoenoses with domination of Chironomidae—*Ch. caecutiens, P. affinis, M. balthica*, and *H. ulvae* are formed. Over rocky and mixed grounds, this kind of zonation is poorer expressed and includes the replacement of the *G. zaddachi* biocoenosis in the oligohaline zone by the *M. edulis* and *G. oceanicus* biocoenoses in the brackish-water zone.

In the smallest estuaries, salinity strongly varies with time almost over all the area; therefore, it does not represent a factor of the benthos distribution, since all the benthic organisms dwelling here are forced to adjust to the maximum range of the salinity changes. Here, the longitudinal zonation is restricted to the delivery of freshwater species to the upper part of the estuarine zone. These species are not adapted to salinity rises and seem to be eliminated during the high tidal phase.

CORRELATION BETWEEN THE BRACKISH-WATER, MARINE, AND FRESHWATER SPECIES ASSEMBLAGES IN ESTUARIES

While characterizing species, we regard the species developed in the fresh waters of the region as freshwater species, the species characteristic of the shallow-water areas off the open and slightly desalinated coast of Kandalaksha Bay as marine species, and those characteristic only of the estuaries as brackish-water species. Among the latter species, we will distinguish the species of marine (thalassogenous) and freshwater (limnogenous) origins. Among the 76 species found by us in the estuaries, there are 23 (30%) marine species, 16 (21%) brackish-water species, and 37 (49%) freshwater species. Six and ten brackish-water species are of marine (mostly amphipods) and freshwater (oligochaets and various diptera larvae) origins, respectively. Thus, the contribution of freshwater species to the formation of the estuarine fauna in the White Sea is greater than that of marine and brackish-water species. Moreover, the leading role in the formation of the assemblage of the estuarine species proper also belongs to freshwater species.

We conventionally subdivide freshwater species into riverine, characteristic of the water flows entering the estuary, and lacustrine, inhabiting adjacent stagnant basins. Among the 37 freshwater species found in the estuaries, riverine species (mostly larvae of caddis flies) comprise about half (19 species) and approximately the same number (18 species) refer to the lacustrine group (larvae of diptera, caddis flies, and mollusks). Thus, the freshwater species assemblage in the estuaries is formed not only due to the animal supply by the flows from land but also through their active settling in the estuaries. The share of lacustrine species grows in larger estuaries with weak currents (for example, the Chernaya River estuary), where environmental conditions are similar to those of lakes and ponds. On the contrary, in the estuaries with strong currents (Luven'ga and Peschanaya rivers) with lithorheophilic conditions, no lacustrine species were found.

A completely different pattern is observed from the assessment of the species abundance. Only a single type of biocoenosis (Chironomidae–*Ch. caecutiens*) is characterized by the domination of freshwater (lacustrine) species. Of the remaining eight types of biocoenoses, four feature prevalence of brackish-water species and four others are characterized by the domination of marine species. On the whole, brackish-water species dominate in the polypoikilohaline and oligohaline zones, while, in the chorohaline and all the more in the brackish-water zone, they are replaced by marine invaders. It is interesting that all the freshwater dominants in the estuaries are represented by the larvae of diptera (*Stictochironomus* sp. and *Micropsectra recurvata*), all the brackish-water dominants refer to crustaceans (*G. zaddachi, G. duebeni, P. affinis*, and *M. relicta*), and all the marine dominants are mollusks (*H. ulvae, M. balthica*, and *M. edulis*).

Our data contradict the commonly accepted opinion that the greater part of the estuarine benthos diversity is provided by euryhaline marine species, while the role of more abundant but less diverse brackish-water species is small and the role of freshwater species is insignificant with respect to both diversity and abundance [5, 10, 15]. Probably, this opinion is based on a direct underestimation of the small organisms of a freshwater origin (mostly insect larvae and oligochaets). In the earlier studies of the benthos of the Chernaya River [3, 11], where neither chironomids nor oligochaets were determined, the content of freshwater species is also underscored. The larvae of small insects in the estuaries are undercounted due to the difficulties in their identification and the seasonal changes in their abundance and species composition. In this study, we could not determine the species of all of the insects and their observed diversity proved to be lower than that estimated in the special research on this issue [26]. Nevertheless, on the whole, insects contribute about 53% (40 species) of the estuarine macrobenthos, which is close to the results obtained in the estuaries of Great Britain and Canada presented in the papers by Williams and coauthors [25, 26].

In the chorohaline zone proper with a characteristic salinity of 5–8‰ (biocoenoses *M. balthica, G. oceanicus*, and *M. relicta*), 32 macrobenthic species were found; of them, 10 species are marine, 13 species are estuarine, and 9 species are freshwater (among them, eight are lacustrine and only one is riverine). Thus, here, no sharp impoverishment of the species richness of the community is observed and the contributions of marine, brackish-water, and freshwater assemblages to the fauna formation are approximately equal. Meanwhile, in terms of abundance, marine and estuarine species dominate over all of the biocoenoses, while all the freshwater invaders play a subordinate role.

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