Long-term temporal and spatial variation of macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha Bay, White Sea)

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Abstract Despite the dynamic nature of spatial pattern, the temporal variation of spatial structure of marine benthic assemblages is rarely assessed using several temporal scales. We quantified the variability of density and biomass of main benthic species in the intertidal soft-bottom flats at two bights in Chupa Inlet (Kandalaksha Bay, the White Sea). The data cover the 21-year period (1987–2008) of a long-term monitoring survey (1987–present) using a hierarchical sampling design with two temporal (year, season within a year) and three spatial scales (bights—7 km, stations within a bight—10–100 m, and replicate samples—10 s cm apart). We used nested ANOVA to test significance and variance components to compare the relative contribution of different scales of variability of density and biomass of 18 most occurring macrobenthic species. Some species demonstrated high large-scale variability, however, the majority showed high small-scale variability and residual variance. The interactive variability was at least as important as the temporal effects, indicating that the spatial pattern changes through time. The assemblages were more variable at small scales and more stable at larger scales. Potential implications for sampling design are discussed.

Keywords Spatial and temporal scale · Long-term studies · Soft-bottom intertidal assemblages · The White Sea

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Introduction

Variation of the structure and composition of marine benthic assemblages occurs at various spatial and temporal scales (Levin, 1992; Fraschetti et al., 2005). The conclusions about the forces forming a spatial pattern are relevant only with respect to the scale of observations (Butman, 1987; Levin, 1992; Archambault & Bourget, 1996; Bellehumeur & Legendre, 1998; Thrush, 1999; Dulvy et al., 2002). The large-scale variation is likely caused by the physical factors such as topography, currents and winds (Thrush et al., 1997a; Legendre et al., 1997). The small-scale variation may be caused by the environmental heterogeneity (Ysebaert & Herman, 2002) or biotic interactions operating at the same scale (Hall et al., 1994; Turner

et al., 1997). However, the processes shaping the spatial pattern at smaller scales in some cases can influence the large-scale patterns (Thrush et al., 1997b, but see Willis & Whittaker, 2002).

Many of the forces structuring the benthic assemblages have temporal variations either in intensity or frequency, thus the spatial pattern they generate can be viewed as a dynamic picture changing at the multiple temporal and spatial scales (Watt, 1947; Levin, 1992). The most widely reported are the inter-annual and the seasonal variability (Caffey, 1985; Chapman, 2002; Norén & Lindegarth, 2005). Some characteristics of assemblages vary even at shorter time periods—months, weeks, or days (Morrisey et al., 1992b; Jarrett & Pechenik, 1997; Lawrie & McQuaid, 2001; De Biasi et al., 2003; Porri et al., 2006). Large scale, especially seasonal variation is generally related to the impact of climatic factors; however, prominent inter-annual changes often result also from biotic interactions (Lukanin et al., 1986a, b, 1989, 1990; Naumov, 2006). The temporal variation makes the interpretation of spatial patterns harder and ought to be taken into consideration.

Field studies, that explicitly take the scale into account, describe the context in which the ecological processes operate and help to build and test the hypotheses about the structuring forces in benthic assemblages (Butman, 1987; Archambault & Bourget, 1996; Underwood & Chapman, 1996; Underwood et al., 2000). The studies using several spatial and/or temporal scales are an important source of information to choose the relevant scale of observations and optimize sampling effort, in monitoring programs or when assessing environmental changes or anthropogenic impacts (Underwood, 1992; Hewitt et al., 1998, 2007; Thrush et al., 1999; Underwood & Chapman, 2003).

Despite the importance of changes of the spatial patterns over time, the temporal variation of marine benthic assemblages is usually assessed in short-term periods using one temporal scale (for review see Fraschetti et al., 2005). Perhaps the main reason is that the use of several temporal scales comes at the expense of low spatial replication that reduces the confidence in results. Most multi-scale studies use several spatial and single temporal scale (Jenkins et al., 2000; Lawrie & McQuaid, 2001; Edgar & Barrett, 2002; De Biasi et al., 2003; Azovsky et al., 2004; Norén & Lindegarth, 2005; Giménez et al. 2005, 2006; Commito et al., 2006; Sánchez-Moyano et al., 2010). However,

there are few long-term studies using several spatial scales (e.g., Ysebaert & Herman, 2002; Middelboe et al., 2003) and a few studies that combine several spatial and temporal scales simultaneously (e.g., Caffey, 1985; Chapman, 2002; Porri et al., 2006). The information on the interactions of the spatial and the temporal variability at different scales is scarce and there is still a need in the multi-scale studies assessing the both sources of variability.

This article is based on the data of the long-term monitoring survey (1987–present) of the soft-bottom intertidal zone of the two small bights in Chupa Inlet (Kandalaksha Bay, the White Sea). The data were obtained in the region where the anthropogenic influences are minimal: the coast is thinly populated, the boat traffic is low. The pollutants brought by river runoff are deposited by marginal filters—narrow zones where the river and seawater mix and sedimentation of suspended particles and dissolved substances occurs (Lisitzin, 1999; Nemirovskaya, 2004), and the resulting total pollution level is relatively small (Savinov et al., 2001, 2010; Naumov, 2011). On the other hand, the influence of climatic factors is mitigated due to the characteristics of water exchange between the Barents and the White Seas, and daily and seasonal temperature fluctuations affect mainly the intertidal species (Naumov et al., 2009; Solyanko et al., 2011). The data used in this paper cover a 21-year period and combine several temporal (year, season) and spatial scales (bight, station, sample). In this paper, we wanted to quantify the variability of density and biomass of the main macrobenthic species using combination of two temporal and three spatial scales. We checked whether the variability was distributed evenly between the scales or some of the scales were more important than others. We also compared the relative contribution of the spatial, temporal, and interactive variability to the total variability of density and biomass of the main macrobenthic species.

Materials and methods

Study area

The data were obtained during the long term monitoring survey (1987–present) at two small bights of the Chupa Inlet (Kandalaksha Bay, the White Sea). The analysis covers the 21-year period from 1987 to 2008.

Fig. 1 The map of the sampling locations. *Circles* denote sampling stations located along the transects in Seldyanaya and Medvezhya Bights
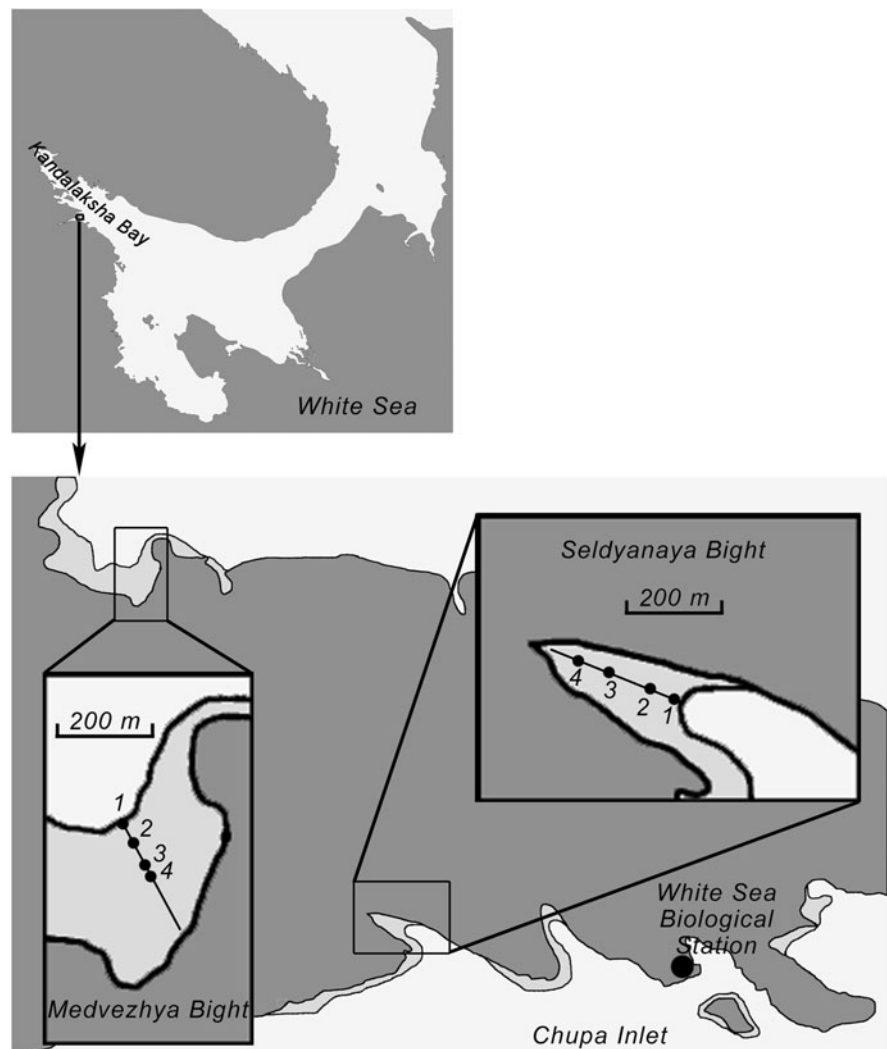
The Seldyanaya and the Medvezhya are small, sheltered bights with the average tidal range of 1.8 m (Fig. 1). The water surface temperature is 14–16°C in summer and −0.9°C in winter. Salinity of the surface water varies from 9 to 23 ppt depending on the rainfall conditions and the tidal phase. There is one small fresh-water stream in the head of the Seldyanaya Bight and there are two streams in the Medvezhya Bight (the larger of them flows in the south-eastern part of the bight). In winter, during low tides salinity of the upper 0.5 m water layer can drop down to 5 ppt due to accumulation of fresh-water runoff under the ice in the

both bights. The ice cover establishes in Medvezhya Bight about a week earlier than in Seldyanaya Bight, because of the lower average salinity. The both bights are covered by ice from October to February until May. During low tide, the ice lays directly upon the surface of sediment. The freezing of the upper sediment layer into the ice was sometimes observed in Seldyanaya Bight. The windy weather during ice melting period in 1988, 1994, 1998, 2002, 2005, 2006 (Naumov, 2007), and 2007 (Naumov, 2012) caused removal of the ice together with frozen sediment from the Seldyanaya Bight. Neither freezing in of sediment,

nor wind-induced ice removal was noticed in the Medvezhya Bight during the whole period of observations.

At the head of the Seldyanaya Bight the tidal flat is covered by semi-liquid silt smelling strongly of hydrogen sulfide because of a great amount of decaying plant material of marine and terrestrial origin. The sediment there has high pore water content (70.50 ± 7.10 vol.%), and low median grain size (0.04 ± 0.02 mm). At the Medvezhya Bight the sediment is more sandy, with moderate pore water content (43.00 ± 3.03 vol.%), and higher median grain size (0.13 ± 0.01 mm). The pore water salinity in the both bights is 24 ppt.

More detailed information on the hydrological regime and the sediment composition of the locations studied can be found elsewhere (Naumov, 2012).

Sampling design and processing

The samples were taken four times each year: during hydrological spring (end of May–beginning of June), summer (end of July–beginning of August), autumn (end of October–beginning of November), and winter (end of March–beginning of April). At each bight the transect of four sampling stations was established perpendicular to the shore line. The lowest station on each transect was at the hydrographic datum (mean low water spring tide level). In the wider intertidal zone of Seldyanaya bight the rest stations were located approximately at 100 m intervals (0.35, 0.55, and 0.75 m above the hydrographic datum). In the upper part the narrower intertidal zone of Medvezhya bight a boulder field is located, and the use of the same sampling techniques was not possible there, that is why the rest stations were placed at 10 m intervals (0.20, 0.55, and 0.50 m above the hydrographic datum). At each station, three replicate samples were taken 10–30 cm apart. Each sample consisted of the three nested corers inserted into one another (surface areas 0.004, 0.0076, and 0.0153 m^2) and pushed 10–15 cm deep into the sediment. The construction of the corer allowed to estimate the abundance of the small and large organisms simultaneously, avoiding large counts. The sediment from each corer was sieved through the column of sieves (3.0, 1.0, and 0.5 mm). The organisms retained on the 0.5 mm mesh were registered only from the small corer, the fraction on the 1.0 mm sieve—from the small and medium ones, the organisms retained on the 3.0 mm sieve were listed from all three tools. The data obtained from the three corers were analyzed together as a single sample.

The sampled organisms were identified to species level, except for the species of genus *Gammarus*, Nemertini, some species of Algae, Oligochaeta, Opistobranchia and insect larvae. Species of genus *Monoculodes* were not distinguished because of very small size of sampled juvenile specimens. All the organisms were counted and weighted (wet weight) accurate to 0.001 g if their weight did not exceed 1 g and with an accuracy to 0.01 g in other cases. Mollusks were weighted with the shell and mantel fluid, polychaetes—without their tubes.

Data analysis

We estimated spatial variability at three scales: among bights (located at a distance of 7 km), among the stations within a bight (tens m apart), and among replicate samples within a station (10–30 cm apart). In studies like these, any significant variability at a particular scale may be caused by patchiness at any scale between this one and the next smaller scale. Thus, for example, significant variability at the scale of bights may be related to the patchiness at any scales between the stations and the bights. Temporal variability was estimated at two scales: among years, and among seasons within a year. The design was unbalanced because in both localities on several occasions: some of the stations were not sampled or the total number of samples was less than three due to logistic constraints (1,799 samples were analyzed and 217 were missing).

The relative importance of the different temporal and spatial scales of variation in density and biomass of the macrobenthic species was estimated using a hierarchical (nested) ANOVA design. The model included the effects of Year, Season nested in Year, Bight, and Station nested in Bight, and interactions of those factors, namely Year × Bight, Year × Station (Bight), Bight × Season (Year). The residual variation in the model represents the within-station variation. All the factors were considered random. We also estimated the magnitude (variance components) of the effects (Searle et al., 1992; Underwood, 1997). The variance components give an estimate of the relative contribution of factors to variability in the dependent variable (Graham & Edwards, 2001).
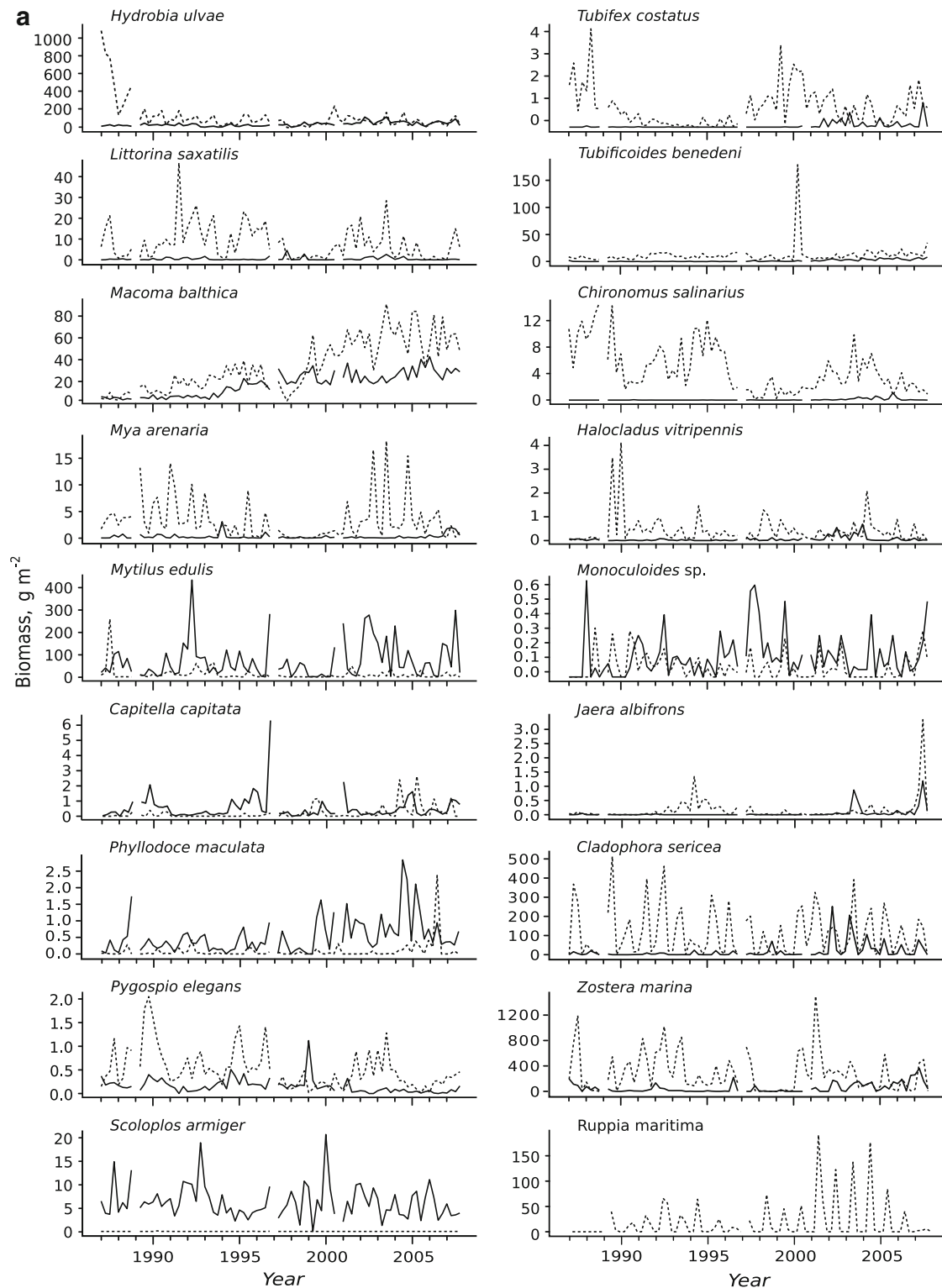
Fig. 2 Changes of the mean biomass (g m^{-2}) (**a**) and density (ind m^{-2}) (**b**) of the 18 species with occurrence percentages higher than 25% in Seldyanaya and Medvezhya Bights over time (1987–2008)
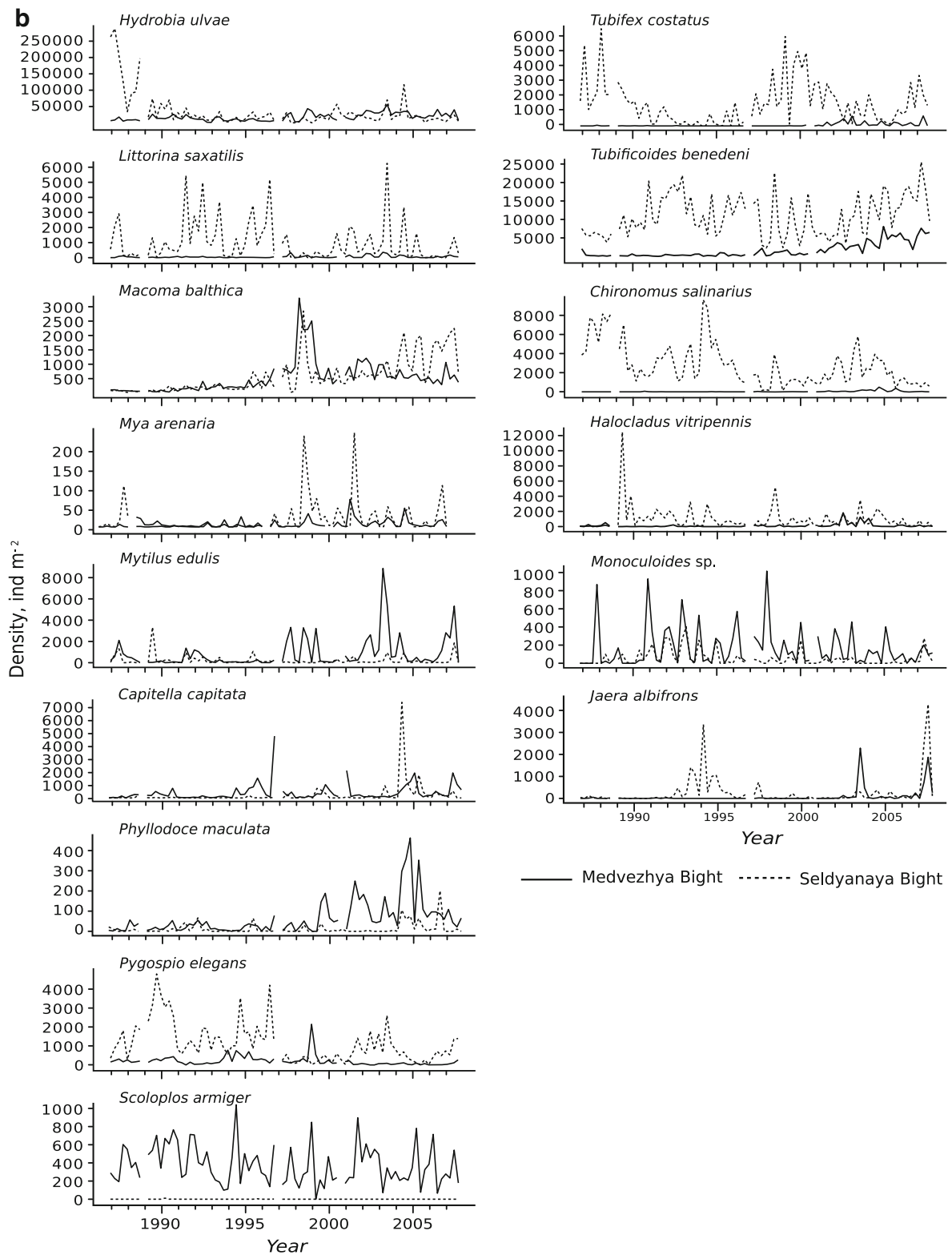
b

Fig. 2 continued

We analyzed density (ind m^{-2}) and biomass (g m^{-2}) of the 18 individual species occurring in more than 25% of samples (about 60% on average). The distribution of the dependent variables differed from normal, so we used the lg($x + 1$)-transformation which improved normality in most cases. However, ANOVA is robust to deviations from the normal distribution (Quinn & Keough, 2002), so analyses were performed despite this violation.

Because the data were unbalanced they were fitted to a random linear model using the general linear model with type III sums of squares to compute the F tests of effect significance (Quinn & Keough, 2002). Variance components were estimated using restricted maximum likelihood method (MIXED procedure of SPSS Statistics, Release 17.0.0, SPSS Inc., 2008, Chicago, IL, USA). When the fitting algorithm has not been able to produce an acceptable solution, the maximum number of the scoring steps or the number of iterations was increased, or the accuracy of the solution was reduced by increasing the parameter convergence value. Finally, the iteration history was examined to find out whether the parameter estimates of the model have converged.

Results

General characteristics of the assemblages

Approximately one-hundred taxa were registered during the study: 92 were identified to species level (belonging to Porifera, Cnidaria, Annelida, Priapulida, Arthropoda, Mollusca, Bryozoa, Echinodermata, Tunicata, Chlorophyta, Rhodophyta, Phaeophyta, and Angiospermae), 12 taxa—to genus level (one species of Diptera, two species of Oligochaeta, two species of Gammaroidea, two species of Nemertini, one species of Enteropneusta, 4 species of Algae), 4 taxa—to family level (Enchytraeidae and larvae of Diptera), two taxa—to order level (one species of Opistobranchia and some Diptera), and one taxon—to classis level (Oligochaeta). The majority of the taxa occurred in the both bights. Mean number of taxa per station varied from 9.7 to 19.9 with an average of 15.2 taxa. Plots of the mean biomass and density of the 18 species occurring in more than 25% of samples are shown in Fig. 2. Three of them were equally common at both bights: *Hydrobia ulvae* (Pennant, 1777), *Macoma balthica* (Linnaeus, 1758), and *Tubificoides benedeni* (Udekem, 1855). Ten species were common for Seldyanaya Bight and were relatively rare or absent in Medvezhya Bight: *Pygospio elegans* Claparède, 1863, *Littorina saxatilis* (Olivi, 1792), *Tubifex costatus* (*Claparède*, 1863), *Mya arenaria* Linnaeus, 1758, *Chironomus salinarius* Kieffer, 1915, *Halocladius vitripennis* (Meigen, 1818), *Cladophora sericea* (Hudson) Kützing, 1843, *Zostera marina* Linnaeus, 1753, *Jaera albifrons* Leach, 1814, and *Ruppia maritima* Linnaeus, 1753. Five other species were more common in Medvezhya Bight: *Scoloplos armiger* (O.F. Müller, 1776), *Mytilus edulis* Linnaeus, 1758, *Capitella capitata* (Fabricius, 1780), *Phyllodoce maculata* (Linnaeus, 1767), and *Monoculodes* sp. High year-to-year and seasonal variation of density and biomass was observed for most of the species.

Spatio-temporal variation of biomass and density

Variance components for biomass and density indicated different patterns for different species (Fig. 3). Relative contribution of spatial components to the total variation of biomass and density varied considerably (6–80%) and was especially high for some species (e.g., for *Scoloplos armiger*, *Tubificoides benedeni*, *Chironomus salinarius*, and *Tubifex costatus* ranging from 56 to 80%). The proportion of variance associated solely with temporal components was relatively small (0–24%) for density and biomass of all the species. The variance associated with the interactions of spatial and temporal scales ranged from 3 to 33%. For most species the interaction of temporal and spatial variability contributed to the total variance more than temporal components.

Residual variation of biomass and density varied from 13 to 80% (Fig. 3). High residual variation recorded for most species suggested patchy distribution at the scales smaller than station. For 8 of the 18 species residual variation exceeded 50% of total variability of either biomass or density (*Macoma balthica*, *Mya arenaria*, *Mytilus edulis*, *Capitella capitata*, *Halocladius vitripennis*, *Monoculoides* sp., *Phyllodoce maculata*, *Jaera albifrons*). Relatively low residual variation was observed for *Tubificoides*
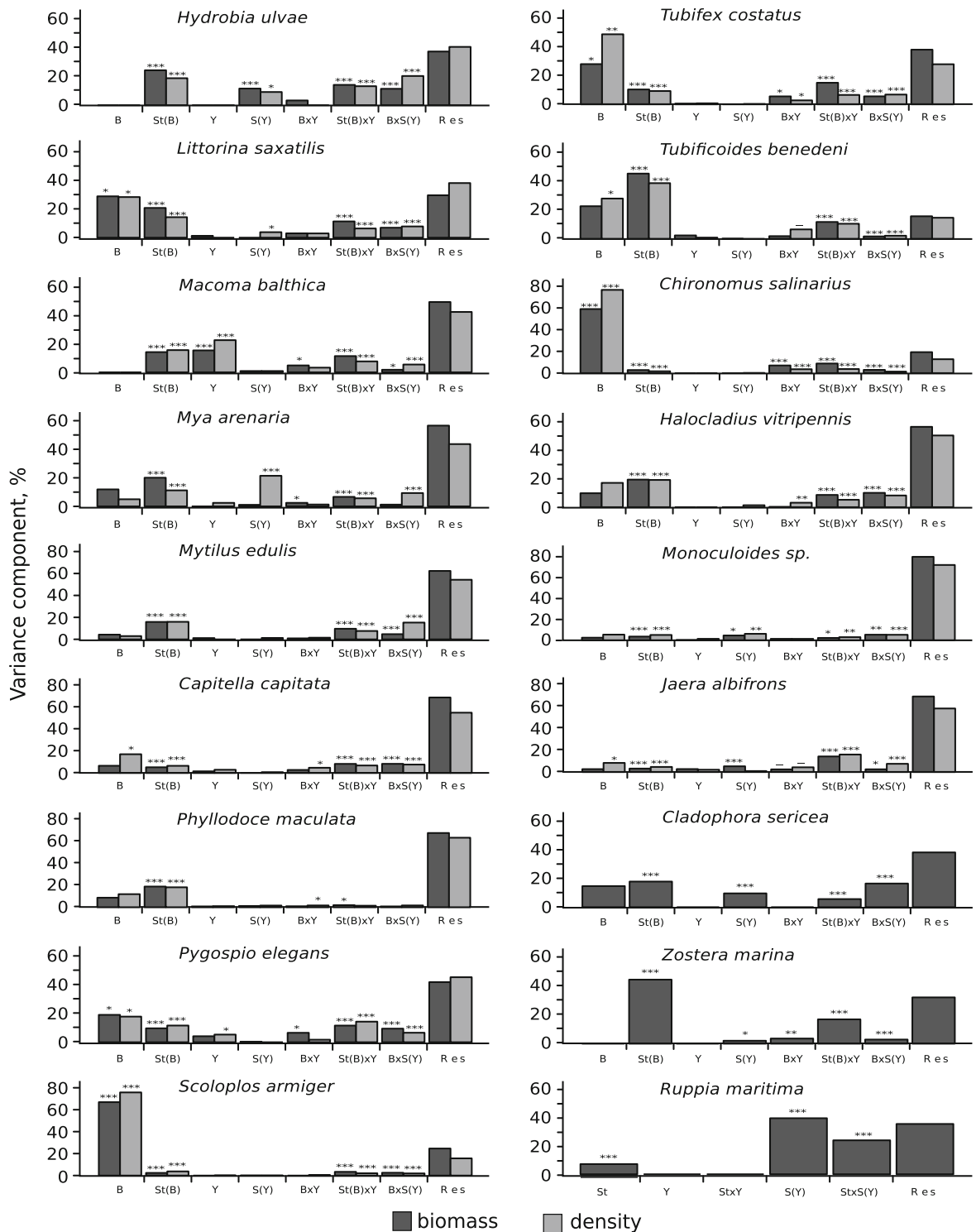
Fig. 3 Variance components for biomass and density of the 18 species with occurrences higher than 25%. Factors are: Y = Year; S (Y) = Season (Year); B = Bight; St (B) = Station (Bight); Y × B = Year × Bight; Y × St (B) = Year × Station (Bight); B × S (Y) = Bight × Season (Year); Res = residual. A *dash over a bar* denotes the variance component which estimation had not converged. *Scales* of significant variation from the nested ANOVA analyses: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

benedeni, *Chironomus salinarius*, and *Scoloplos armiger* (13–25%).

Scales of spatial variation

Both biomass and density varied between bights for *Scoloplos armiger*, *Chironomus salinarius*, *Tubifex costatus*, *Littorina saxatilis*, and *Pygospio elegans* (Fig. 3). For these species the between-bight variability of density was higher than within-bight one. The variation between bights was particularly strong for *Scoloplos armiger* and *Chironomus salinarius* (67 and 59%, respectively, for biomass and 76% for density of each species). For the other species variation was moderate (18–28% for biomass and 8–47% for density). Density but not biomass varied significantly between bights for *Tubificoides benedeni*, *Capitella capitata*, and *Jaera albifrons* (8–28%).

Variability at the station scale was significant for all the species (Fig. 3). The Station (Bight) effect was strong for biomass and density of *Tubificoides benedeni* (45 and 38%, respectively) and *Zostera marina* biomass (44%), and was lower for the rest species ranging from 1 to 24% for biomass and from 2 to 18%. Between-station variability in Seldyanaya Bight was also significant for biomass of *Ruppia maritima* and it accounted for 7% of the total variation.

Scales of temporal variation

Significant inter-annual variation of biomass and density was found for *Macoma balthica* and it explained 16 and 24% of the total variance, respectively (Fig. 3). Density of the polychaete *Pygospio elegans* also varied from year to year, accounting only for 5% of the total variance.

Seasonal variation of both biomass and density was significant for *Hydrobia ulvae* (11 and 9%, respectively) and *Monoculoides* sp. (5 and 6%, respectively). Seasonal variation of biomass was also the case for the isopod *Jaera albifrons* (5%) and all the algae and plant species—*Ruppia maritima* (37%), *Cladophora sericea* (9%), and *Zostera marina* (2%, respectively). Only density but not biomass varied seasonally for *Mya arenaria* and *Littorina saxatilis*. Seasonal changes accounted for 21% of the total variance for the former species and only 4% for the latter.

Interactions of temporal and spatial variation

For the most species both year-to-year and seasonal variations tended to be different between the bights and/or between the stations so that the pure effects were masked by the interactions for the majority of the species (Fig. 3). The inter-annual changes were more pronounced at the station scale than at the bight scale. There were more significant Station (Bight) × Year interactions then Year × Bight effects and they were stronger in most cases. At the bight scale inter-annual variation was significant for both biomass and density of *Chironomus salinarius*, and *Tubifex costatus* (3–7%), while for several other species either biomass or density variations were significant (*Pygospio elegans*, *Macoma balthica*, *Zostera marina*, *Mya arenaria*, *Jaera albifrons*, *Capitella capitata*, *Halocladius vitripennis*, and *Phyllodoce maculata* (2–6%). As for the station scale, inter-annual variation was significant for both biomass and density of majority of species (2–17%) except *Phyllodoce maculata* where only biomass varied significantly (2%).

The effect of season was tested only at the bight scale where it was often higher than between-year variation at this scale (Fig. 3). Seasonal variations at the bight scale were found for both biomass and density of most species (1–20%). The two exceptions were *Mya arenaria* where only density varied significantly (9%) and *Phyllodoce maculata* where no significant variations occurred.

Seasonal variations of biomass at the station scale were also found for *Ruppia maritima* in Seldyanaya Bight and accounted for 24% of the total variance.

Discussion

The relative contribution of the spatial, temporal, and the interactive variability

In our study, the composition of the scales of significant heterogeneity and their contribution varied from species to species, which is often the case in the marine benthos (for review see Fraschetti et al., 2005). Yet the significant heterogeneity in the studied assemblages was observed at all the spatial and temporal scales. The most frequently significant effects were the spatial variability at the station scale

and the interactions of the temporal and spatial scales. For the majority of species studied the relative importance of the spatial components was higher than the temporal ones. These results suggest that the species distribution in the studied assemblages was mainly spatially structured, especially at small scale. High importance of the small-scale spatial variation (meters—tens of meters) is often reported in marine communities (Thrush et al., 1989; Morrisey et al., 1992a; Jenkins et al., 2000; Olabarria & Chapman, 2001; Ysebaert & Herman, 2002; Anderson et al., 2005; Dethier & Schoch, 2005; Fraschetti et al., 2005; Chapman et al., 2010; but see Kendall & Widdicombe, 1999; Edgar & Barrett, 2002).

The spatial pattern changes through time (Watt, 1947; Levin, 1992; Wu & Loucks, 1995). We found that interactions of temporal and spatial variability often contributed to the total variance more than temporal components, thus the dynamics of the spatial pattern was different between the stations or bights. High importance of interactive variability was reported from the other multiscale studies (Morrisey et al., 1992b; Jenkins et al., 2000; Olabarria & Chapman, 2001; Norén & Lindegarth, 2005), still, no detailed account was given to its sources. In our study both the year-to-year and the seasonal changes of density and biomass of most species were different among the bights or the stations. However, the small scale spatial pattern appeared to be less stable than the large scale one. The inter-annual changes at the station scale were more frequent and strong than at the bight scale. The seasonal variation at the bight scale was often higher than between-year variation at that scale. Our results support the statement that non-equilibrium dynamics at smaller scales can lead to quasi-equilibrium at a higher level (O'Neill et al., 1989; Turner et al., 1993; Wu & Loucks, 1995).

Our data suggest that pattern of spatial variation changes considerably over time, and the generality and persistence of the pattern can be verified in long term studies. Unfortunately, we can only suggest the processes that led to changes of spatial pattern through the period of the study, because of the absence of the full spatio-temporal replication of environmental measurements. In the further studies it is important to get quantitative data at scales where variation occurs, because it can help to uncover the ecological processes that determine the patterns of distribution and abundance (Chapman et al., 2010).

Spatial variability

We observed small scale variation of the density and biomass of most species whereas the large scale heterogeneity was registered only for a few species. The small-scale spatial variation is widespread and may be considered the important property of the benthic communities (for review see, Fraschetti et al., 2005). The possible causes of the small-scale variability may vary between the species and locations, however, there may be two major groups of factors—the environmental heterogeneity at the same scale (Ysebaert & Herman, 2002) or biotic interactions operating at these small scales (Hall et al., 1994; Turner et al., 1997; Commito et al., 2006; Naumov, 2006). In our study the distribution of the density and biomass of most species differed at the station scale (10–100 m), likely as a result of different physical conditions related with differences in emersion times between the stations. The remaining unexplained variance (the within station variation) was high for most species, this can indicate the substantial heterogeneity at the scales even smaller than station (10–30 cm). However, this variability may also result from the random processes acting on individual animals. The residual variation was higher than 50% for biomass and density of the motile species (Monoculoides sp., *Phyllodoce maculata*, *Jaera albifrons*), large mollusks (*Mytilus edulis*) and patchy-resource-exploiter *Capitella capitata*. For *Mya arenaria*, *Macoma balthica*, and *Halocladius vitripennis* high residual variation was found only for biomass, but not for density. This can happen, for example, if the individuals of different age/weight categories had different distribution. The negative correlation between densities of adult and juvenile *Macoma balthica* was reported in the Baltic (Bergström et al., 2002) and the White Sea (Burkovsky et al., 1997).

Only for a few species the high importance of the spatial components of variation was caused mainly by the large-scale heterogeneity. For *Pygospio elegans*, *Chironomus salinarius*, *Scoloplos armiger*, *Littorina saxatilis*, and *Tubifex costatus* the importance of the Bight effect was higher than within-bight differences. One possible explanation is that these species could respond to the differences in physical conditions between locations, which is often the case for the large-scale (>100 m) variation (Legendre et al., 1997;

Thrush et al., 1997a; Ysebaert & Herman, 2002; Giménez et al., 2005; Sánchez-Moyano et al., 2010).

Temporal variability

Often in spatially structured assemblages the whole pattern changes through time, as evidenced by the high importance of the interactions of the spatial and temporal scales in multiscale studies (Morrisey et al., 1992b; Jenkins et al., 2000; Olabarria & Chapman, 2001; Norén & Lindegarth, 2005). We also found that the "pure" seasonal and inter-annual variability was significant only for several species, whereas significant interactive variability was present in most species. Possible causes of temporal variability differed from species to species.

The seasonal variability in the intertidal communities can be very big (e.g., Beukema, 1982; Möller, 1986). However, in our study, the importance of the "pure" seasonal changes was relatively low in most cases. On the other side, the interaction with the Bight effect was significant for almost all the species and its contribution was higher than the pure seasonal effect (except for the density of *Mya arenaria*). This suggests that the seasonal fluctuations of the density and biomass of the studied species were asynchronous between the bights. The seasonal changes were significant for several species (density and biomass of *Hydrobia ulvae*, and *Monoculoides* sp.; density of *Mya arenaria*, *Littorina saxatilis*, and *Phyllodoce maculata*; biomass of *Jaera albifrons*, *Cladophora sericea*, *Ruppia maritima*, and *Zostera marina*). For the animal species all the registered peaks in density and biomass were in summer and thus may result from the seasonal recruitment of juveniles and growth of the younger adults. The seasonal effect observed in the plant species was possibly related to the winter degeneration of their shoots and thalli.

Only two species (*Macoma balthica* and *Pygospio elegans*) displayed significant inter-annual variability, yet the interactions with the spatial scales were also present. The density of *Pygospio elegans* also fluctuated significantly between years, although the changes differed between stations. No apparent synchronicity between bights was observed despite the non-significant interaction with the Bight factor, so this pattern is unlikely to be explained by inter-annual variation of large-scale climatic factors. The variations of density of *Pygospio elegans* may rather be explained by some factors with the spatial variation at smaller scales.

The density and biomass of *Macoma balthica* gradually increased during the second half of the study after the peak in 1998. The changes were similar at the both bights, so the Year effect was not totally masked by the Bight effect like in the other species. The synchronicity of year-to-year dynamics at the large spatial scale was registered for *Macoma balthica* in the other studies (e.g., Ysebaert & Herman, 2002). This can likely be explained by good dispersal abilities of its juveniles (Beukema & de Vlas, 1989) and the relatively long life span of this species (from 3 to 8 years in the White Sea according to Maximovich et al., 1991, 1992, 1993).

On the other side, large scale synchronicity of the changes of density and biomass can be regulated by climatic factors acting at large spatial scale. In the temperate seas, many shallow water species are temperature-sensitive and heavy mortality in exceptionally cold winters (Crisp, 1964; Beukema, 1992) sometimes is compensated by the better recruitment in the following season (Beukema et al., 1998). However, we could not relate the increase of *Macoma balthica* density and biomass to enhanced reproduction after cold winters. The correlation of average weight of *Macoma balthica* in summer with the average surface water temperatures in previous winter was weak and non-significant ($r = -0.3$). The absence of this effect is not surprising, given that the shore-fast ice that covers most of the White Sea shores every winter protects intertidal species from temperature fluctuations during low tide like a thermostat (Kuznetsov, 1960). Under the shore-fast ice the thermal conditions are determined mainly by the surface water temperature which is stable and close to $-1°C$ at the studied locations. The minor differences in temperature under such conditions may become less important than many other factors describing the "harshness" of the winter (the length of the ice period, the month of the ice formation).

Seaward winds in some years can remove the ice from the bight together with frozen sediment, however, the density and biomass increase of *Macoma balthica* could not be related to increased reproduction after the wind induced ice removal either. The highest density increase was observed in 1998, the year when wind induced ice removal happened in Seldyanaya Bight. However, the density and biomass did not increase in many other years when this occurred which were 1988, 1994, 2002, 2005, 2006 (Naumov, 2007),

and 2007 (Naumov, 2012). Moreover, in 1998 the density and biomass of *Macoma balthica* increased not only in Seldyanaya Bight, but also in Medvezhya Bight, where neither wind induced ice removal nor freezing of the sediment into the ice have ever been observed (Naumov, 2007).

Conclusion

The studied assemblages were mainly spatially structured, however, the interactions between the spatial and temporal scales were at least as important as the pure temporal effects which is often reported from the other multiscale studies (Morrisey et al., 1992b; Jenkins et al., 2000; Olabarria & Chapman, 2001; Norén & Lindegarth, 2005). Our data demonstrate that pattern of spatial variation changes considerably over time often asynchronously between locations. It suggests that the enhanced large scale temporal and spatial replication is needed when studying spatial pattern dynamics. High importance of interactive variability indicates that extrapolation across scales should be done with caution. However, the need to interpret results within the context given by study scale is often neglected (Underwood & Chapman, 1996; Underwood et al., 2000).

We found that the spatial pattern in the studied assemblages was more variable at small temporal and spatial scales and more stable at the larger scales, as indicated by the pattern of interactive variability. Spatial patchiness and temporal variation may reduce the power of statistical tests, so it is important to optimize sampling programs in patchy and dynamic assemblages (Thrush et al., 1994; Underwood & Chapman, 2003). It suggests that enhanced replication at small scales is essential when taking surveys in the assemblages like these. In our study the importance of different spatial and temporal scales of variation varied from species to species. Some of the species showed high contribution of large-scale variability, however, the majority showed high small-scale variability. It suggests that the ways of sampling optimization may depend on the species on which the study is focused.

The dynamics of spatial pattern in marine benthic assemblages has long been a focus of research; however, the need remains in the properly replicated multiscale hierarchical analyses of spatial and temporal variability. Such studies can provide clues to choosing the relevant scale of observations, optimizing sampling effort, and help to build hypotheses about the structuring forces in benthic assemblages (Zajac et al., 1998; Hewitt et al., 1998, 2007; Thrush et al., 1999; Underwood et al., 2000; Underwood & Chapman, 2003).

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