

Marina A. Varfolomeeva

Biotic Interactions,
Structure,
and Long-term Changes
in Marine Benthic
Assemblages

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ABSTRACT

Predicting spatial distribution of organisms still remains a challenge of ecology. Small-scale variation is high in most marine benthic communities. Our long-term observations on soft-sediment intertidal assemblages revealed high level of small-scale spatial variation, and most temporal variation was also associated with this scale. As biotic interactions often drive small-scale patterns, we focused on the communities with multiple foundation species where they are understudied. We assessed overgrowth and feeding interference between co-dominating foundation species, long-term recruitment variation in their populations, and their effect on the rest of assemblage. Our observations and experiments indicated that large suspension-feeders develop a facilitation cascade in the White Sea shallow subtidal, boosting species diversity and driving patch dynamics on mixed sediments.

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LIST OF FIGURES

- FIGURE 1 Spatial and temporal scales of natural disturbances in soft-sediment habitats. Small-scale processes, including biotic interactions, happen over shorter time scales. Large-scale processes are slower and take longer time to develop. After Zajac et al. (1998; Fig. 1) with kind permission from Springer Science and Business Media
- FIGURE 2 Spatial and temporal scales of the systems are correlated. To predict spatial pattern correctly the study need to be conducted near the space-time scaling of the system. When appropriate scaling is unknown, multi-scale studies are a possible decision. After Wiens (1989; Fig. 3)
- FIGURE 3 Relative importance of factors controlling successional dynamics as predicted for disturbance at different scales. Effects of biotic interactions are most prominent at small scale, life history events control processes at meso- to large scales, while environmental factors influence multiple scales. After Zajac et al. (1998; Fig. 4) with kind permission from Springer Science and Business Media.

CONTENTS

ABSTRACTS

ACKNOWLEDGEMENTS

LIST OF FIGURES

CONTENTS

LIST OF INCLUDED ARTICLES

1	INTRODUCTION.....	13
2	BRIEF DESCRIPTION OF RESULTS.....	17
3	DISCUSSION	21
3.1	Long-term dynamics of spatial structure.....	21
3.2	Role of multiple coexisting foundation species in small-scale pattern generation.....	22
3.3	Recruitment variation of two foundation species with differing life histories	23
3.4	Interactions between coexisting foundation species	24
3.4.1	Feeding interference in horse mussels and ascidians	24
3.4.2	Overgrowth in barnacles and ascidians.....	25
	Conclusion	26
	REFERENCES	28

INCLUDED ARTICLES

LIST OF INCLUDED ARTICLES

- PI Varfolomeeva, M. A., Naumov, A. D., 2013. Long-term temporal and spatial variation of macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha Bay, White Sea). *Hydrobiologia* 76, 175–189.
- PII Yakovis, E. L., Artemieva, A. V., Shunatova, N. N., Varfolomeeva, M. A., 2008. Multiple foundation species shape benthic habitat islands. *Oecologia* 155, 785–795.
- PIII Yakovis, E. L., Artemieva, A. V., Fokin, M. V., Varfolomeeva, M. A., Shunatova, N. N., 2007. Effect of habitat architecture on mobile benthic macrofauna associated with patches of barnacles and ascidians. *Marine Ecology Progress Series* 348, 117–124.
- PIV Yakovis, E. L., Artemieva, A. V., Fokin, M. V., Varfolomeeva, M. A., Shunatova, N. N., 2013. Synchronous annual recruitment variation in barnacles and ascidians in the White Sea shallow subtidal 1999–2010. *Hydrobiologia* 706, 69–79.
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- PVI Varfolomeeva, M. A., Artemieva, A. V., Shunatova, N. N., Yakovis, E. L., 2008. Growth and survival of barnacles in presence of co-dominating solitary ascidians: growth ring analysis. *Journal of Experimental Marine Biology and Ecology* 363, 42–47.

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- AVI Artemieva A. V., Fokin M. V., Nikolaeva M. A., Shunatova N. N., Yakovis E. L., 2006. Possible role of habitat complexity in structuring of motile benthic fauna by patches of barnacles and ascidians. Benthic Ecology Meeting, 8 – 12 March 2006, Quebec, Canada, 47.
- AVII Nikolaeva M., Shunatova N., Khalaman V., Belyaeva D., Yakovis E., 2006. On substrate choice of ascidian larvae *Styela rustica* (L.). VII scientific session of Marine Biological Station of Saint-Petersburg State University. Theses, 68-69. [in Russian]
- AVIII Khalaman V., Belyaeva D., Nikolaeva M., Shunatova N., Yakovis E., 2006. Substrate preferences of solitary ascidians *Styela rustica* (Linnaeus). VII scientific session of Marine Biological Station of Saint-Petersburg State University. Theses, 79-80. [in Russian]

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- AXI Artemieva A. V., Grishankov A. V., Nikolaeva M. A., Fokin M. V., Shunatova N. N., Yakovis E. L., 2004. Role of predatory boring snails in benthic community: prey shells as a source of information. V scientific session of Marine Biological Station of Saint-Petersburg State University. Theses, 37–38. [in Russian]
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1 INTRODUCTION

The distribution of living organisms varies in space and time. Understanding the forces that determine such variations is one of the main challenges in ecology. Spatial pattern results from interaction of several forces: environmental heterogeneity (Ysebaert and Herman 2002), physical factors (Thrush et al. 1997; Legendre et al., 1997) and biological processes (Hall et al. 1994; Turner et al. 1997) acting at their specific scale (Levin 1992).

Small-scale processes often scale up and their results are displayed at higher levels. This is demonstrated by cellular automata models (Wootton 2001), and supported by examples from marine systems (Thrush et al. 1997; Irving et al. 2004) and terrestrial biomes (reviewed by Wisz et al. 2012). If we look how variation is distributed among different scales, in general, the result depends on the system studied. However, the small-scale variation is common, and sometimes even considered as a fundamental property of marine benthic assemblages with a very few exceptions (Fraschetti et al. 2005). Understanding relationships of variability at different scales is important when generating hypotheses about structuring processes (Underwood et al. 2000).

Spatial structure can vary annually or seasonally (Caffey 1985; Chapman 2002; Norén and Lindgarth 2005) or even at shorter time scales (Morrisey et al. 1992; Jarrett and Pechenik 1997; Lawrie and McQuaid 2001; De Biasi et al. 2003; Porri et al. 2006). Temporal variation may be asynchronous in different patches, and spatial pattern can be viewed as a mosaic of patches at different stages of succession (Watt 1947). Processes affecting larger spatial scales are slower, and their effect is often lagged (Wiens 1989; Zajac et al. 1998). Biotic interactions and seasonal factors are faster and affect spatial pattern at smaller scales (Zajac et al. 1998; **Fig. 1**).

Quality predictions of long-term dynamics of spatial pattern can be made only by increasing temporal and spatial scales of observation or taking into account several temporal and spatial scale simultaneously (Wiens 1989; **Fig. 2**). However, there are very few multi-scale and long-term studies that would explicitly take into account several spatial and temporal scales together (e.g., Caffey 1985; Chapman 2002; Porri et al. 2006), probably due to great labour and time expenditure. As a result, very little is known about long-term dynamics of spatial structure at different scales. Detection of scales where the

most variation occurs is crucial to understanding underlying mechanisms (Underwood and Chapman 1996) and factors affecting long-term dynamics.

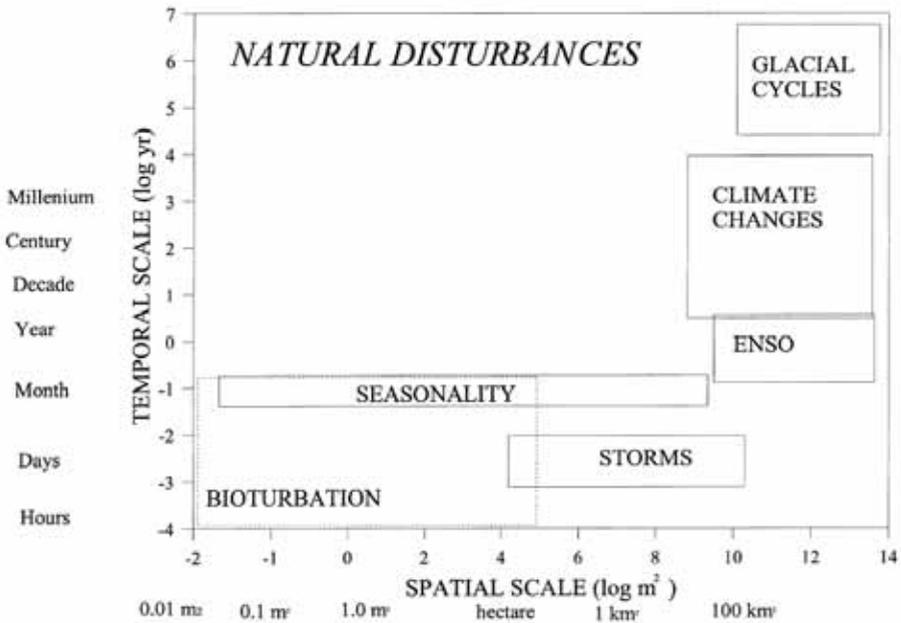


Fig. 1. Spatial and temporal scales of natural disturbances in soft-sediment habitats. Small-scale processes, including biotic interactions, happen over shorter time scales. Large-scale processes are slower and take longer time to develop. After Zajac et al. (1998; Fig. 1) with kind permission from Springer Science and Business Media.

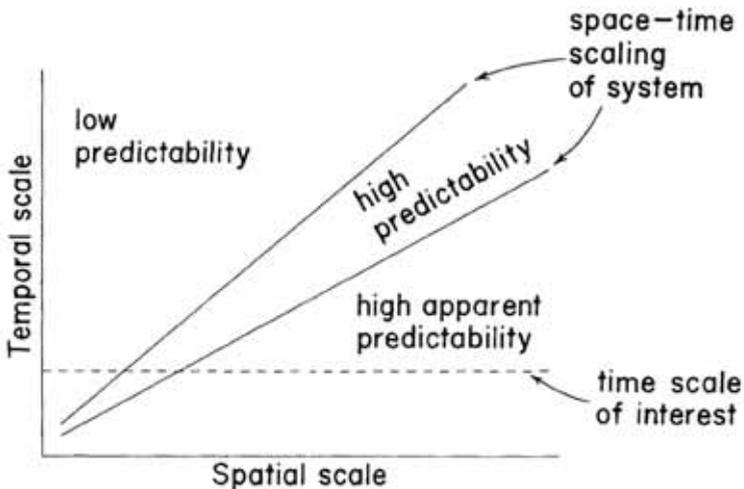


Fig. 2. Spatial and temporal scales of the systems are correlated. To predict spatial pattern correctly the study need to be conducted near the space-time scaling of the system. When appropriate scaling is unknown, multi-scale studies are a possible decision. After Wiens (1989; Fig. 3).

The small-scale variability is most intriguing as it is common and originates from different sources (Fraschetti et al. 2005). Small-scale variability is shaped not only by environmental heterogeneity or disturbance (Sousa 1984; Ysebaert and Herman 2002), but also by biotic interactions like facilitation (Bruno et al. 2003; Yakovis et al. 2004, 2005), competition (Connell 1961; Menge 1976), or effect of consumers (Paine 1974; Benedetti-Cecchi et al. 2000). Local demographic processes are other important drivers of variability (e.g., Whitlatch et al. 1998). Outcomes of biotic interactions are sometimes mediated by environmental heterogeneity and physical factors (e.g., Underwood 1980; Benedetti-Cecchi et al. 2000). Positive and negative biotic interactions often co-occur in one system, often even the sign of interaction depends on age of an organism (Flores-Martinez et al. 1994; Callaway and Walker 1997). All those processes superimpose producing the complex pattern of small-scale variability.

There is growing theoretical (Wootton 2001) and field (see Thrush et al. 1997 for marine and Wisz et al. 2012 for terrestrial habitats) evidence that small-scale processes can echo at larger scales. In benthic communities effects of biotic interactions are most prominent at small scale, probably because of relatively small size and low mobility of infauna. Biotic interactions are one of the keys to understanding small-scale dynamics as evidenced from the studies of disturbance (Fig. 3; Zajac et al. 1998) and may help to reveal mechanisms of changes or spatial structure development in a whole assemblage.

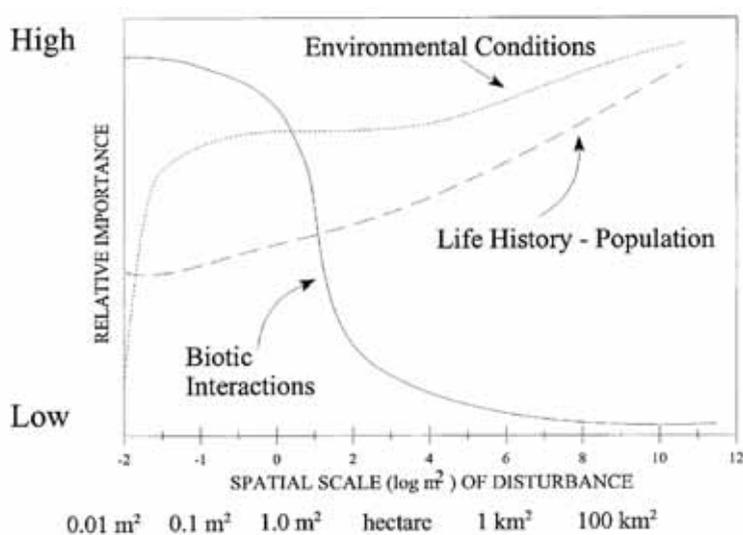


Fig. 3. Relative importance of factors controlling successional dynamics as predicted for disturbance at different scales. Effects of biotic interactions are most prominent at small scale, life history events control processes at meso- to large scales, while environmental factors influence multiple scales. After Zajac et al. (1998; Fig. 4) with kind permission from Springer Science and Business Media.

Foundation species create habitat for other species and structure numerous communities (Dayton 1972) like kelp forests, coral reefs, mussel beds, intertidal canopy-forming algae, mangroves, or terrestrial forests (Jones et al. 1997; Bruno and Bertness 2001; Stachowicz 2001). Foundation species can provide substrate where it is lacking

(Hacker and Madin 1991; Ellison and Farnsworth 1992), create habitats with complex architectural properties (Crooks and Khim 1999), provide refuges from disturbances (Woodin 1978), modify local conditions that may affect growth, mortality, feeding or recruitment of other species (Stephens and Bertness 1991; Leonard 1999; Volkenborn and Reise 2006). The strength of facilitation by foundation species depends on their age structure or density (Woodin 1978; Callaway and Walker 1997), environmental conditions (Norkko et al. 2006), and the scale of observations (Eklöf et al. 2011). Sometimes foundation species not only facilitate but also compete with each other and with others (Dayton 1975), and they may have indirect negative effects on some other species as well (Jones et al. 1997). Because of the links connecting foundation species to many others, demographic processes in their populations are important for the whole assemblage.

Often, communities are organised around several coexisting foundation species. Such species have been usually considered functionally similar (Bruno and Bertness 2001). In a very few cases coexisting foundation species were explicitly addressed separately. For example, cordgrass *Spartina alterniflora* can facilitate secondary foundation species—ribbed mussels *Geukensia demissa*—that in turn supports a diverse assemblage (Altieri et al. 2007). Interactions between coexisting foundation species that received recent attention include mostly unidirectional facilitation (Altieri et al. 2007; Gribben et al. 2009) or negative interactions that lead to exclusion at small scale (e.g., Van Wesenbeeck et al. 2007). However, potential effects of functionally different foundation species coexisting at small scale were rarely addressed.

It can be predicted that when foundation species coexist at smaller scales hierarchies of dependent (facilitated) species would form around each of them (Yakovis et al. 2008). The interplay of positive and negative interactions between coexisting foundation species would affect various aspects of their life like growth, mortality, diet and recruitment. This, in turn, may have consequences for long-term dynamics of the spatial pattern in the whole community.

Being interested in spatial pattern development, we studied the case of less structured soft-sediment habitats and more structured epibenthic ones on mixed sediments. We traced long-term dynamics of spatial structure in a soft-sediment intertidal community to assess relative importance of several temporal and spatial scales of variation in density and biomass of macrobenthic species, and to address persistence of pattern at different scales. We also explored the role of coexisting but functionally different foundation species in generating community structure: their effect on spatial distribution of dependent fauna, the possible interactions between foundation species resulting from overgrowth, and long-term recruitment variation.

2 BRIEF DESCRIPTION OF RESULTS

The results of this thesis were published in six papers listed below.

1. Varfolomeeva, M. A., Naumov, A. D., 2013. Long-term temporal and spatial variation of macrobenthos in the intertidal soft-bottom flats of two small bights (Chupa Inlet, Kandalaksha Bay, White Sea). *Hydrobiologia* 76, 175–189.
2. Yakovis, E. L., Artemieva, A. V., Shunatova, N. N., Varfolomeeva, M. A., 2008. Multiple foundation species shape benthic habitat islands. *Oecologia* 155, 785–795.
3. Yakovis, E. L., Artemieva, A. V., Fokin, M. V., Varfolomeeva, M. A., Shunatova, N. N., 2007. Effect of habitat architecture on mobile benthic macrofauna associated with patches of barnacles and ascidians. *Marine Ecology Progress Series* 348, 117–124.
4. Yakovis, E. L., Artemieva, A. V., Fokin, M. V., Varfolomeeva, M. A., Shunatova, N. N., 2013. Synchronous annual recruitment variation in barnacles and ascidians in the White Sea shallow subtidal 1999–2010. *Hydrobiologia* 706, 69–79.
5. Yakovis, E. L., Artemieva, A. V., Fokin, M. V., Varfolomeeva, M. A., 2012. Intraspecific variation in stable isotope signatures indicates no small-scale feeding interference between a horse mussel and ascidian. *Marine Ecology Progress Series* 467, 113–120.
6. Varfolomeeva, M. A., Artemieva, A. V., Shunatova, N. N., Yakovis, E. L., 2008. Growth and survival of barnacles in presence of co-dominating solitary ascidians: growth ring analysis. *Journal of Experimental Marine Biology and Ecology* 363, 42–47.

The processes operating at small spatial scales are important structuring forces in marine and terrestrial assemblages, yet their role in promoting community dynamics and long-term stability has not been sufficiently studied. Observations at several temporal scales are necessary to assess changes of spatial structure (Wiens 1989), however, the dynamics of spatial pattern is usually assessed using single time scale even in long-term multi-scale studies (e.g., Ysebaert and Herman 2002; Middelboe et al. 2003). Long-term observations (1987–2008) on density and biomass of main intertidal macrobenthic

species at two soft-sediment bights in Chupa Inlet (Kandalaksha Bay, the White Sea) revealed the importance of small-scale spatial pattern dynamics (Varfolomeeva and Naumov 2013). A hierarchical sampling design included two temporal (year, season within a year) and three spatial scales (bights—7 km, stations within a bight—10–100 m, and replicate samples—10s cm apart).

- The contribution of different scales in variation of density and biomass differed between the common macrobenthic species. Most species demonstrated higher abundance variation at the scale of station and smaller, several species, however, showed higher variation between the bights.
- The spatial pattern changed in time, often asynchronously between bights or stations, as evidenced by comparable magnitude of interactive and temporal variability for most species.
- The assemblages were more variable at small scales and more stable at larger scales: inter-annual changes were more frequent and strong between stations than bights; at the bight scale, seasonal variation was often higher than interannual one.

Small-scale spatial patterns are often shaped by biotic interactions. Foundation species generate particularly strong effects on dependent fauna (Dayton 1972; Bruno and Bertness 2001). Often a community develops around multiple coexisting habitat-forming species (Jones et al. 1997; Bruno and Bertness 2001; Stachowicz 2001). However, the effects of apparently different organisms are rarely assessed separately (Yakovis et al. 2008; Angelini et al. 2011). In the shallow subtidal zone in the White Sea, barnacles *Balanus crenatus*, sometimes overgrown by solitary ascidians (mainly *Styela* spp. and *Molgula* spp.), are often found in epibenthic patches on hard substrates scattered over muddy sediment. Barnacles form clusters (aggregations) on bivalve shells, small stones and conspecifics, while ascidian clumps develop on barnacles and their empty shells. Within the clusters, barnacle shells create a complex structure rich with sediment-filled cavities. The assemblages of mobile macrofauna associated with epibenthic patches differ in species composition and abundance from the surrounding unstructured sediment. 459 epibenthic patches were analysed to assess the effect of coexisting foundation species on sessile fauna (Yakovis et al. 2008).

- Different foundation species attracted specific sessile taxa.
- Higher number of foundation species in a patch enhanced species diversity. Barnacles dominated on the primary substrate. Together with ascidians and red algae, barnacles provided habitat for most sessile species (72% of individuals).
- The size structures of barnacles (live individuals and empty shells) and ascidians were interrelated, suggesting long-term patch dynamics from barnacle to ascidian dominance.
- The small-scale spatial patterns indicated that the patches formed by multiple foundation species were primarily structured by facilitation of dependent taxa, and facilitation and competition between different foundation species.

Foundation species affect dependent ones not only by their biological properties like biodeposition or sediment reworking (Norkko et al. 2006; Volkenborn and Reise 2006). Some foundation species, like kelp or seagrasses, also modify habitat creating biogenic structures as evidenced by experiments with artificial imitations (Lee et al. 2001; Norderhaug et al. 2002). We hypothesised that the clusters of barnacles *Balanus crenatus* would add to heterogeneity and complexity of otherwise almost unstructured sediment and tested this hypothesis in a manipulative experiment using artificial imitations of barnacle clusters exposed for 1 or 2 years (Yakovis et al. 2007a). The final composition of mobile fauna in such imitations was compared to natural aggregations and the surrounding unstructured sediment. Barnacles from the epibenthic patches affected mobile macrofauna partly due to complex cavity-loaded structure provided by their shells as evidenced by a field experiment.

- The assemblages in natural and artificial epibenthic patches were much more similar to each other than to unmanipulated bare sediment.
- The bivalves *Musculus discors* and polychaetes *Pholoe minuta* dominated numerically both in natural epibenthic patches and artificial epibenthic patches, whereas the polychaetes *Rhodine loveni* and *Apistobanchus tullbergi* dominated in unmanipulated bare sediment.

Recruitment of foundation species can potentially affect the whole assemblage (Bruno and Bertness 2001). Barnacles *Balanus crenatus* and ascidians are foundation species that form multispecies patches. They differ in timing of reproduction (Mileikovsky 1970; Khalaman 2001), duration of planktonic larval life (Herz 1933; Khalaman et al. 2008) and occupy mostly different substrates when adult (Yakovis et al. 2005, 2008; Yakovis 2007). We hypothesised that the recruitment pattern of these species would be differently affected by large-scale climatic factors and local conditions and tested this hypothesis using long term (1999–2010) observations (Yakovis et al. 2013). In contrast to our initial expectations recruitment of the both coexisting foundation species exhibiting alternative ecological strategies was similarly regulated by large-scale climatic factors, and not by local substrate availability or abundance of adults as indicated by the long-term study of natural epibenthic patches.

- Barnacle recruits were observed mainly on the surface of shells, stones, and conspecific adults. Ascidian recruits were found mostly on adult barnacles, indicating facilitation by *Balanus crenatus*.
- Annual recruitment rates of barnacles and ascidians were correlated. Warm autumns were followed by the increased recruitment in both species. Cold winters and summers were associated with recruitment decrease.
- Mean annual recruitment rates showed 26-fold variation for barnacles and 30-fold for ascidians.
- Recruitment of the both foundation species was not limited by hard substrate availability or abundance of adults.

Interactions between coexisting foundation species are an important process that can drive small-scale dynamics (Van Wesenbeeck et al. 2007). Our results suggest that interactions between foundation species can vary in strength and sign and can depend on age of the organisms.

Spatially close individuals of large suspension-feeders may compete for food. We studied a case that provided no evidence of feeding interference between co-dominating horse mussels *Modiolus modiolus* and ascidians *Styela rustica* that frequently co-occur in mixed and single-species clumps on hard substrates (Yakovis et al. 2012). We compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios within the tissue of each species in presence and absence of a potential competitor to avoid consequences of tissue- and species-specific isotope fractionation rates (Dalerum and Angerbjörn 2005).

- The stable isotope ratios differed between species (*Modiolus modiolus* and *Styela rustica*) and sites (8.1 km apart).
- The two muscular tissues of *M. modiolus* substantially differed in stable isotope ratios: -21.582 ± 0.048 ($\delta^{13}\text{C}$) and 6.551 ± 0.063 ($\delta^{15}\text{N}$) in foot muscle versus -20.970 ± 0.063 ($\delta^{13}\text{C}$) and 7.806 ± 0.074 ($\delta^{15}\text{N}$) in adductor muscle.
- In either species, the stable isotope ratios did not differ in presence and absence of a potential competitor. In combination with interspecific differences, this indicated absence of interference competition for food.

Another case we studied indicated negative consequences of overgrowth by ascidians on barnacles *Balanus crenatus* co-occurring in the epibenthic patches. We compared age-based annual vertical growth increments and dead:live ratios of barnacles from natural patches dominated by ascidians or barnacles.

- Regardless of the biomass of conspecific neighbours barnacles grew slower in ascidian- than in barnacle-dominated patches.
- Dead:live ratios of barnacles aged 1+...2+ and 4+...9+ were higher in ascidian-dominated patches.
- Estimated mortality risk, calculated as a ratio of remaining empty shells' counts in ascidian- vs. barnacle-dominated patches, increased with age of barnacles from around 1:1 to 5.6 times greater in the 9+ age group.

Our results show that the ontogenetic shift from facilitation to negative interactions between foundation species may create an important feedback loop for dynamics of the small-scale spatial pattern and may be one of the factors promoting succession. Juvenile ascidians occupy habitat only after the establishment of adult barnacles. Growing up, they apparently contribute to decline of the latter. We suggest that long-term coexistence of foundation species at large scale may originate from asynchronous dynamics at smaller scale of the patches.

3 DISCUSSION

3.1 Long-term dynamics of spatial structure

In many marine communities small-scale spatial variation of species abundance is common and sometimes even considered as a basic property of spatial pattern (reviewed by Fraschetti et al 2005). In our study, the density and biomass of most species varied at small spatial scale (10–100m) while several species showed large-scale heterogeneity (7km), but only for a few of them it was higher than small-scale one. Our results confirm that small-scale spatial variability is high in soft-sediment macrobenthos (Varfolomeeva and Naumov 2013). At larger scales, spatial patterns may appear less variable because of averaging of local heterogeneity (Wiens 1989), and low large-scale spatial replication leading to loss of statistical power (Debinsky and Holt 2000). The latter explanation seems unlikely, because in the present survey significant large-scale variability was detected for 8 of 18 studied species, indicating the strength of the effect. Lack of data on environmental variables at small-scale did not allow us to separate the role of environmental heterogeneity, physical factors, and biotic interactions in generating the spatial pattern. Further studies can overcome these limitations by combining results of several long-term surveys over a broad spatial extent with environmental measurements and climatic data.

Dynamics of spatial structure can be reliably studied only when several spatial and temporal scales are taken into account (Wiens 1989). We found evidence that small-scale dynamics of spatial pattern can coexist with large-scale stability: inter-annual changes were more frequent and strong between stations than bights; at the bight scale, seasonal variation was often higher than interannual one. Landscape ecology predicts that small-scale processes flow faster than large-scale ones (Wiens 1989; Zajac et al. 1998), so it is possible that our study was not long enough to detect long-term temporal variation at the large spatial scale. We find this explanation unlikely because of the known similar cases where instability at smaller scales produces quasi-stability at higher scales. For instance, long-term stability may result from asynchronous successions in a patchy environment, like it happens in wind-generated gaps on mussel beds (Paine and Levin

1981), or gaps from falling trees in forests (Watt 1947; Bormann and Likens 1979). It happens even when fine-scale patches do not have distinct borders like in mountain grasslands (Herben et al. 1993). There, the small-scale changes seem unidirectional and their effect levels off, while external large-scale processes can induce directional changes. These examples support the concept that communities may be organised like metacommunities that consist of changing sub-units (local communities) populated by interacting organisms and linked by dispersal (Leibold et al. 2004).

At smaller spatial scales, biotic interactions and demographic processes can be important factors shaping spatial structure, and potentially affecting the whole assemblage (Zajac et al. 1998). Detailed study of these processes may help us to better understand small-scale pattern dynamics.

3.2 Role of multiple coexisting foundation species in small-scale pattern generation.

Aggregations of several coexisting foundation species are potentially powerful agents shaping spatial patterns at small scales. Distribution of sessile organisms in the epibenthic patches of barnacles and ascidians indicated positive effect (facilitation) for many dependent species (Yakovis et al. 2008). Most sessile species resided on the surfaces of either foundation species, which supported specific assemblages of dependent taxa. Number of functionally different foundation species increased associated biodiversity (Yakovis et al. 2008) probably because of amplified habitat heterogeneity (Blanchard and Bourget 1999; Davies et al. 2005) and increased number of possible niches (MacArthur and MacArthur 1961).

At least some effects of barnacles as facilitators were determined by their mere presence, which sometimes is referred to as an autogenic habitat engineering (Jones et al. 1994, 1997). Field experiment evidenced that epibenthic patches of barnacles attracted mobile fauna similar to habitat mimics (Yakovis et al. 2007a). Many foundation species attract the dependent fauna because of their physical structure that increases structural complexity or heterogeneity. Manipulations with artificial units mimicking natural biogenic structures had shown that habitat architecture is an important factor in beds of mussels *Musculista senhousia* (Crooks and Khim 1999) or *Mytilus edulis* (Khaitov et al. 2007), in forests of *Laminaria hyperborea* (Christie et al. 2007), or in mangroves (Nagelkerken et al., 2010). Thus, the effect of a foundation species may be at least partly attributed to higher structural complexity of their aggregations, and not only to their properties as living organisms.

Our findings are consistent with widely recognised structuring role of facilitation (Bruno and Bertness 2001). The patches of barnacles and ascidians can be viewed as a hierarchy of facilitation cascades (Altieri et al. 2007; Angelini et al. 2011) acting at small spatial scale. Principal foundation species facilitate each other: barnacles harbour ascidians, and both are overgrown by red algae. Each of the coexisting foundation species in turn provides a substrate for a specific assemblage.

Thus, we suggest that coexisting foundation species strongly (positively and/or negatively) interact, each facilitating a number of dependent ones. Outcomes of such interactions would affect an entire community.

3.3 Recruitment variation of two foundation species with differing life histories

Spatial distribution of sessile benthic organisms is determined not only by post-recruitment processes like adult mortality from predation, competition or unfavourable conditions, but also by the pattern of recruitment. We checked whether the factors governing recruitment success would be different in coexisting foundation species: ascidians *Styela* spp. and barnacles *Balanus crenatus* (Yakovis et al. 2013). Ascidians and barnacles differ not only in their functional properties as foundation species (Yakovis et al. 2008) or taxonomic position, but also their larvae have different dispersal abilities, season of recruitment, while adults occupy different microhabitats within a community. In the White Sea, larvae of *Balanus crenatus* appear in plankton in July–August (Mileikovsky 1970); nauplii spend there 2–3 weeks (e.g. Herz 1933); adults occupy primary substrates (empty shells of *Serripes groenlandicus* and small stones) and shells of conspecifics. The co-dominant ascidian *Styela rustica* spawns in mid-September (Khalaman 2001); its tadpoles live only 1–2 days until settlement (Khalaman et al. 2008); adult ascidians overgrow adult barnacles and their empty shells (Yakovis et al. 2005, 2008; Yakovis 2007). Despite all those differences, large-scale climatic factors determined recruitment success for both species. Analysis of long-term recruitment patterns (1999–2010) indicated that spatial distribution of both ascidian and barnacle recruits was not affected by available free space (Yakovis et al. 2013), yet, for adults competition for space remains a potentially important structuring process. High interannual variation of recruitment was probably mediated by local conditions and interactions after recruitment.

Notably, close correspondence of recruitment patterns in ascidians and barnacles was probably due to different mechanisms as a consequence of different season of reproduction: mild autumns and colder winters can positively affect reproduction of adult barnacles and survival of juvenile ascidians. Mild autumns provide better feeding conditions for suspension feeders because longer ice-free periods boost phytoplankton growth (Arrigo et al. 2008). Cold winters can ensure better survival lowering metabolism levels (Honkoop and Beukema 1997) or suppress recruitment of predators (Beukema et al. 1998).

Close link between recruitment regulation of the foundation species may be governed by large-scale processes in spite of different life histories and microhabitat use. However, our study was carried out only at one location, and location-specific effects on recruitment may confound wider generalisations (Myers 1998). Further research including more sites is needed to separate site-specific effects on recruitment from climatic factors and biotic interactions.

3.4 Interactions between coexisting foundation species

We studied the interactions between coexisting foundation species on two different pairs of species. We introduced a method to assess feeding interference between large suspension feeders comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios in presence and absence of potential competitor and tested it on a case of ascidians living on horse mussels (Yakovis et al. 2012). We also addressed possible effects of overgrowth by ascidians on growth and risk of mortality of barnacles (Varfolomeeva et al. 2008).

3.4.1 Feeding interference in horse mussels and ascidians

Feeding interference is a potentially important process for sessile suspension feeders (Pullen and LaBarbera 1991; Okamura 1984, 1985, 1988), however it has been rarely addressed directly for large organisms perhaps because of difficulties in using direct counts of consumed tagged particles.

Nitrogen and carbon stable isotope ratios are often used to trace the sources of organic matter and to assess diets of animals (reviewed by Boecklen et al. 2011). The interpretation of isotope ratios is obscured by isotope fractionation rates, which depend on the metabolic rate of a species or a tissue (Dalerum and Angerbjörn 2005). Presence and absence of potential competitor affects the diet of an organism (Hanson and Leggett 1986; Haken and Batzli 1996). We assumed if such feeding interference is substantially strong and long-lasting, one may detect the consequent shift in stable isotope ratios. The comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios in presence and absence of a potential competitor can be made within the same tissue of a given species, helping to avoid consequences of tissue- and species-specific isotope fractionation rates. Different isotope signatures in presence and absence of a potential competitor would evidence interspecific feeding interference. We tested this approach on horse mussels *Modiolus modiolus* and ascidians *Styela rustica*—large suspension feeders with potentially overlapping feeding spectra (Stuart and Klumpp 1984; Lesser et al. 1992; Defossez and Hawkins 1997; Armsworthy et al. 2001; Petersen 2007; Jiang et al. 2008) often found in mixed and single-species clumps on small hard substrates scattered over muddy bottom.

Similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios in the tissues in presence and absence of a potential competitor, combined with interspecific differences in isotope signatures, indicated no evidence of feeding interference between coexisting ascidians and horse mussels (Yakovis et al. 2012).

Ascidians and horse mussels may use different particle fractions. Similar mechanism of resource partitioning was observed in a rope culture of *Mytilus edulis* coexisting with solitary ascidians *Ciona intestinalis* and suspension feeding gastropods *Crepidula fornicata* (Lesser et al. 1992). Then, the effect of feeding interference could be weak because of high food availability and no small-scale variation in its supply. In this case, the method's resolution may be too low to detect a small shift in isotopic ratios. We did

not measure food availability during collection of samples, however, we suggest that a subtle effect, even if detected, could be biologically insignificant.

We believe that the method of comparing stable isotope ratios in presence and absence of potential competitor may be a promising tool to investigate feeding interactions in nature. The method should be further tested on a case where strong effect is expected. Other methods may be used to check reliability: diatom-based gut content analysis of food size spectra in the animals sampled in the field (like in Tamberg et al. 2013), or in a laboratory experiment feeding with calibrated latex granules (like in Berry and Schleyer 1983) or natural seston and suspended particles (like in Armsworthy et al. 2001).

We found no sign of feeding interference between ascidians growing on horse mussels, however, there may be other interactions between these species. Overgrowth binds the species with interactions of varying strength (Wahl 2008). It provides a camouflage from predators (Wahl and Hay 1995) or, conversely, facilitates prey handling (Enderlein et al. 2003); often epibionts on the mollusk shells reduce growth and reproduction of basibiont (Dittman and Robles 1991; Wahl 1996; Buschbaum and Reise 1999). Our results suggest that interactions between foundation species not necessarily are strong. The strength of interaction is possibly context-specific, being mediated by local conditions in a similar fashion as facilitation effect is mediated by properties of foundation species (Heck and Wetstone 1977; Woodin 1978; Callaway and Walker 1997).

3.4.2 Overgrowth in barnacles and ascidians

Structure observed in the patches of barnacles and ascidians suggests that they are shaped by negative effects of overgrowth. In the ascidian-dominated patches barnacles grew slower and the proportion of their empty shells was higher than in the barnacle-dominated patches, so the hypothesis about negative interactions between ascidians and barnacles could not be rejected (Varfolomeeva et al. 2008). The results suggest alternative explanations: for instance, ascidians may flourish in the patches where barnacles decline because of other processes. Although casual relationships should be further established experimentally, following observations favour the retained hypothesis about negative interactions.

At the sites we studied adult ascidians reside mainly on barnacles (Yakovis et al. 2008), juveniles were also found on conspecifics (Yakovis et al. 2013). 10% of barnacles with orifice larger than 3 mm have an ascidian on their opercular plates, 21% of ascidians were found inside the orifice (Yakovis et al. 2008), and often they completely blocked it. We commonly observed ascidians growing on opercular plates of empty shells of dead barnacles. When the multi-tier ascidian clump builds up the overall effect can likely become unbearable for overgrown barnacles. Apart from complete blocking, negative effect on feeding can arise from other causes: ascidians harboured red algae and together they could screen barnacles from currents (Barnes 1955; Leonard 2000).

Different traits of foundation species often mediate their effects. It was shown for size, age, and density of plants (Callaway and Walker 1997) or tube-building polychaetes

(Woodin 1978), architectural complexity in seagrass beds (Heck and Wetstone 1977). Overgrowth by ascidians can alter growth and mortality of barnacles and thus may affect the dependent species.

Field observations suggest that the studied epibenthic patches shift from barnacle to ascidian dominance (Yakovis et al. 2005). The earlier stages of succession were experimentally reproduced on initially bare *Serripes groenlandicus* shells exposed for several years (Yakovis et al. 2005; Yakovis et al. 2007b). On initial stages of succession barnacles probably facilitate ascidians, as indicated by microhabitat distribution of adult ascidians in natural and experimentally reproduced epibenthic patches (Yakovis et al. 2007b; Yakovis et al. 2008). Later, as ascidians grow, the sign of interaction may change, as evidenced by our results.

The general theory about relative importance of various interactions along environmental stress gradients predicts that in the habitats with low stress, like subtidal zone, importance of competition would be low, relative to predation and protection from other negative factors provided by association with foundation species (associational defences; Bruno and Bertness 2001). However, this theory does not account for ontogenetic shifts of the sign of interactions. Successions where one species facilitates juveniles and then competes with adults are common (Flores-Martinez et al. 1994; Callaway and Walker 1997). Recently, demography was recognised as an important modifier of the interactions between foundation species along with environmental stress (Angelini et al. 2011). Our results suggest that the ontogenetic shift of the sign of interactions between foundation species may create an important feedback loop for the system's dynamics and may be one of the factors promoting succession at small-scales. Further research is needed to compare relative importance of associational defences, predation and competition for foundation species at different life stages.

Local communities in individual patches of barnacles and ascidians together make up a meta-community at larger spatial scale (Leibold et al. 2004). New unoccupied substrates like stones and empty bivalve shells are always present in the habitat and regularly colonised, thus, all the successional stages of the local communities regularly emerge in the system (Yakovis et al. 2013). We suggest, that long-term coexistence of foundation species at the metacommunity scale is maintained by asynchronous dynamics at smaller scale of the local communities like it happens in other cases (Watt 1947; Bormann and Likens, 1979; Paine and Levin, 1981; Herben et al. 1993).

Conclusion

In the soft-sediment assemblages studied, the highest spatial variation for most species was at small scale, which also was associated with most temporal changes.

As biotic interactions commonly shape small-scale spatial patterns, we focused on the communities assembled around foundation species, where biotic interactions are particularly strong.

The case of co-dominating barnacles and ascidians indicated that multiple coexisting foundation species boosted biodiversity, each providing habitat for specific dependent taxa. Some of their effects were related not to their biogenic properties but to increased habitat complexity.

Although foundation species studied had different life histories, their recruitment was similarly controlled by large-scale climatic processes.

Coexisting foundation species studied are engaged in interactions of varying strength and sign with each other. Since they create multiple superimposed facilitation cascades for dependent fauna, these interactions shape the entire community.

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