

**Review**  
of the Dissertation of Marina Varfolomeeva  
submitted for the degree of Doctor of Philosophy in Biology  
at the Saint-Petersburg State University

The dissertation thesis by Marina Varfolomeeva consists of 97 pages and contains Introduction, Brief description of results, Discussion, Conclusion, 3 figures, reference list of 108 citations and 6 articles, published in international peer-reviewed journals (with tables and figures therein).

The dissertation deals with the problem of functioning of complex multispecies assemblages, their spatial and temporal heterogeneity and the role of biotic interactions in maintaining their structure. All these questions are among the major problems in community ecology both in terrestrial and aquatic realms.

The dissertation is based on several studies on typical intertidal and upper subtidal bottom communities in the White Sea. The authors applied a variety of approaches starting from observations through long-term monitoring of benthic assemblages (e.g., Varfolomeeva & Naumov, 2013; Yakovis et al., 2013), to manipulative field experiments to study the patterns of substrate colonization by different key species (Yakovis et al., 2007; Varfolomeeva et al., 2008). This experimental approach is very valuable and relatively rare in marine ecology research; the field experiments at the community level are complicated and difficult to perform, because they involve measuring biotic interactions between the members of the community as well as responses of these organisms to numerous geo-physico-chemical factors and processes in the ecosystem. In such studies the complexity of a system and quantity of possible combinations rises exponentially with the number of involved species. That is why while designing their experiments the authors limited the number of species under study to only 2-3 ones (foundation species or main competitors).

Long-term (> 10 years) regular observations on the seafloor assemblages especially those that consider different spatial and temporal heterogeneity are also rare and extremely important nowadays. Many experiments and observational studies lack the spatial and temporal heterogeneity within replicates that can vary functional response and allow the complementarity among species to be expressed as increased functional performance. Heterogeneity that occurs across a range of space and time scales is an important element of the functionality of ecosystems. One of the sections in the reviewed work (Varfolomeeva & Naumov, 2013) presents a rare case of study of the multi-scale temporal and spatial variability in intertidal communities. Basing on a 21-years-long monitoring (including seasonal data) the authors reveal the sources of variation in species abundance at several spatial and temporal scales, as well as the interactions between these types of variability. The obtained results are of general ecological importance, because they have direct methodological implications in sampling strategies and in the interpretation of synecological data. Among other things the results show the

strong dependence of recruitment patterns of foundation species on temperature variation (Yakovis et al., 2013). Therefore, these studies are timely due to a likelihood of climate change affecting the frequency of warmer and colder than normal summers and winters.

Besides studying the general patterns of multi-scale heterogeneity in bottom communities the author paid special attention to revealing the exact mechanisms and forces determining the outcome of the competition between the foundation species. Among them are ascidians, cirripedes, bivalve mollusks, which serve as ecosystem-engineers providing for associated species the environment with high complexity of habitat structure, enriched food supply and additional substrate. The key species interact with each other competing for space, food, etc, which results in successions and formation of a climax community (for review see Khalaman, 2013 and references therein). In the present dissertation the author came to a conclusion that interactions between foundation species can vary in strength and sign and can depend on age of the organisms, and 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. Besides a general ecological importance these results have a significant applied relevance. The detailed knowledge of mechanisms that underlie the formation of communities dominated by a single species is needed in different fields of aquaculture (Khalaman, 2001).

The material used in the study is sufficient and of high quality. Hundreds of samples during many years were collected by a big team of researchers, students and volunteers. In all cases the sampling schemes and experimental design were very well thought over and based on the aims of the study and on the most efficient and correct way of subsequent data processing.

The author took part in the research at most of the stages. The idea of the separate projects was suggested and developed by the author in 3 cases out of 6. In one case the author used the samples obtained by the other researchers during decades of observations (Varfolomeeva and Naumov, 2013), while in all other cases she personally took part in sampling and sample processing. The author of the dissertation is an expert in data analyses and statistics. She performed all data treatment in two projects and in one case did it together with her co-author. Ms. Varfolomeeva participated in writing of all her papers together with her co-authors. Taking all together I consider her personal direct input in designing the study, obtaining the results and delivering them to the international scientific community as high.

Six papers arising from the thesis are published in the high-rank international peer reviewed journals. This suggests that the obtained results are valid and of high quality. I think that these results make a significant contribution to the marine synecology. The study of spatial and temporal variation in intertidal assemblages revealed a highly significant interaction between spatial and temporal components, i.e., that spatial heterogeneity changed in time and the changes differed in direction

at different spatial scales. For example, it appeared that small-scale dynamics of spatial pattern could coexist with large-scale stability. Such studies that include both spatial and temporal variability at different scales are very rare in marine ecology. The importance of specific scales of variability to individual species depends on the traits of those species, such as size, mobility, food specificity, and the status of the species within the community. Therefore studies on the dominant species, the foundation species that determine the structure of the whole community are needed. This is the topic of 5 of 6 publications of the author, where the variety of biotic interactions from strong negative (competition), to neutral, to strong positive (facilitation) was recorded.

The dissertation is logically structured, written in a clear and strict academic style, it is easy to read and understand; I am not a native English speaker and I do not see any significant linguistic weaknesses.

Obviously, the author is perfectly aware of the international scientific literature on the topic. However unfortunately she does not know or ignores the extensive Russian literature on marine benthic ecology, spatial and temporal heterogeneity, successions and species interactions within the communities. Only 5 papers by Russian scientists (except 6 self-citations) are cited out of 108 references. Numerous Russian benthic ecologists worked earlier and are currently active at the Black Sea (e.g., E. Turpaeva, M. Dolgoplolskaya, V. Brayko, V. Grintsov), Pacific Russian seas (V. Oshurkov, A. Zviagintsev), and of course at the White Sea (V. Oshurkov, A. Azovskiy, V. Mokievskiy, T. Bek, A. Railkin, V. Khalaman). It looks strange that numerous works by e.g., Dr. Khalaman on the biotic interactions, temporal changes and succession in fouling communities in the White Sea dominated by the same or similar species as in the studied upper subtidal habitats are not mentioned (except the two minor publications).

As another drawback of the dissertation I would mention the lack of an overall review of the obtained results in a general context of a single story. It would be good to know how the author sees the whole picture emerging from the heterogeneous results of each specific project. The author also did not discuss or even mention to what extent the results (and conclusions) are geographically specific, can they be easily applied to other areas besides the White Sea, what local environmental/climatic conditions may limit the transfer of this knowledge to the ecosystems beyond the White Sea. These remarks however do not mar the generally positive impression of the reviewed dissertation.

Taking into account the above considerations I conclude that the dissertation by Marina Varfolomeeva complies with the international standards for PhD dissertations in the field of biology and ecology.

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