

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 consists of 97 pages, of which the general presentation of the material (Introduction, Brief Description of Results, Discussion) occupies 17, the list of references, 11, and the rest are 6 bound scientific articles co-authored by the defender of the thesis. These articles, published in the leading international scientific journals (Marine Ecology Progress Series, Oecologia, Experimental Marine Biology and Ecology, Hydrobiologia), have undergone rigorous peer review by experts in the relevant fields of marine biology. This fact alone is an indication of the high quality of these papers and, thus, of the materials and conclusions presented in the dissertation. Ms. Varfolomeeva is the first author of two of these papers and the co-author of the concept presented in three of them; she took part in the collection, processing and analysis of the material and participated in the writing in case of all these papers. Thus her input into the achievement of the dissertation results seems significant.

The introduction of the dissertation contains literature review on the research topic. The author demonstrates a good knowledge of the special literature as well as the general range of problems. The same is true of the discussion, which involves the literature not only on the marine benthic communities but even on terrestrial ones. This shows the erudition of the author. At the same time, I cannot help noticing that the general part of the dissertation makes no mention of the study area (it is literally not even mentioned). This should have been done, as the White Sea is rather unusual from the point of view of ocean science, and the reader should be given at least a general idea about it.

Further in the dissertation the author treats the material in the order of the published papers. As a result, the discussion looks like a collection of abstracts. I find this unfortunate, because the logical axis, which should be present in any dissertation, becomes rather vague. The author tried to arrange the papers into a logical sequence but, in my opinion, failed to do so. This is hardly possible anyway, as any paper is, by definition, a complete research which can stand on its own. It would have been only for the better if the author, abandoning a paper-by-paper presentation of material, had interpreted the whole bulk of the accumulated material and presented it within the framework of a general logical approach, citing the papers when necessary.

As a result of a certain heterogeneity of the material, the dissertation clearly splits into two parts. Its basis (5 papers) is made up by the detailed and diverse research, including field experiments, on model systems of fouling species. The main attention is paid to the competition of potential founders in the process of colonization of unsettled substrate. The first of the papers (Varfolomeeva & Naumov, 2013) falls out of this context, being devoted to the analysis of long-term changes in the silty-sandy intertidal zone in two close bights of the White Sea. I would like to emphasize that both parts of the dissertation are relevant and make an important contribution into marine biology.

The most interesting part for me personally is the analysis of the long-term time series, which close to my own field of research. This work (Varfolomeeva & Naumov, 2013) is in many respects unique, being based on the 21-year-long seasonal monitoring of intertidal benthic communities. In the world literature this is a singular example of materials obtained in the intertidal zone of a seasonally freezing sea and in the study area lying almost at the Polar Circle. Moreover, hardly a dozen publications in the marine biological literature deal with the analysis of such a long time series. The conclusion that the spatial pattern in the studied benthic assemblages is more variable at small temporal and spatial scales

and more stable at the larger scales is entirely justified (Varfolomeeva & Naumov, 2013). It fits well into the growing body of evidence about the importance of local factors in determining the community structure. It concerns not only the benthic communities but many others, including the host-parasite assemblages. I congratulate the authors on this work.

All its scientific importance notwithstanding, this paper, as noted above, stands somewhat apart from the problems of the other papers included into the dissertation. The author says that this paper demonstrates the importance of small-scale spatial events in macrobenthic communities and thus offers a transition to the discussion of interactions in the fouling assemblages presented in the other papers. However, I find this transition rather poorly justified, as in the former case we deal with the intertidal communities of benthos and the second, with the subtidal fouling communities, which exist under entirely different environmental parameters.

The second, and the major, part of the dissertation, devoted to the analysis of interactions in the fouling assemblages, has obviously been made according to a general plan. This part abounds in original methodological approaches (such as original design of the field experiments with artificial substrates and the use of stable isotopes). The soundness of the methodological basis leaves no doubts about the validity of the obtained data, which are extremely interesting. I will not repeat them here, as they are clearly presented in the dissertation itself. In my opinion, the most important of them are those testifying that the ontogenetic shift from facilitation to negative interactions between foundation species may be one of the factors promoting succession. For the first time, the feedback loop in the dynamics of these processes was revealed — juvenile ascidians occupy a habitat only after the establishment of adult barnacles. Growing up, these ascidians depress barnacles. Ascidians overgrown barnacles, in this way not only altering their growth and mortality but also affecting the dependent species. Noteworthy, this

kind of succession was shown in natural as well as in experimentally reproduced epibenthic patches. Of considerable interest are the data obtained with the use of stable isotopes (Yakovis et al. 2012, concept: E.L. Yakovis and M. Varfolomeeva). The absence of feeding interference between coexisting ascidians and horse mussels was convincingly shown. This may indicate that the interactions between foundation species not necessarily are strong.

Reading this absorbing section of the dissertation, I was surprised not to find any comparisons with the results obtained V.V. Khalaman, whose long-term research dealt with a similar topic (succession of fouling species, interspecies competition etc) in the same region (the White Sea). The dissertation contains but three references to Khalaman's works. Khalaman worked in a different part of the White Sea (the Kandalaksha Bay) and on different substrates (suspended artificial substrates) of the foulers, which would have made the comparison all the more interesting.

Some results of the studies made in the Kandalaksha Bay differ from those presented in the dissertation. First of all, the discrepancies concern the role of climate in the population dynamics of species in fouling communities. Khalaman & Naumov (2009) showed that in the fouling communities (on the suspended artificial substrates in subtidal zone) the long-term dynamics of population density was correlated with the average water temperature in the summer only for two polychaete species. In the opinion of Khalaman & Naumov (2009), cyclic fluctuations of the density of polychaete populations inhabiting the fouling communities can by some biological mechanisms regulate the densities of populations, including "predator-prey" interactions. On the contrary, it was shown in the paper by Yakovis et al. (2013, M.A. Varfolomeeva took part in sampling and measurements and writing the manuscript) that the recruitment success (one of the processes determining the dynamics of populations) of *Balanus*

crenatus and *Styela rustica* is determined by large-scale climatic factors. This discrepancy calls for a discussion.

To sum up, the materials presented in the PhD Thesis of Ms. Varfolomeeva are undoubtedly significant for the fields of marine biology dealing with the analysis of long-term changes in the composition of benthic communities and the interactions between species in them. Quantity and quality of the data are up to the standards. The thesis is well-written (as far as I can judge, not being a native speaker) and reads easily. My comments are mostly recommendations and/or invitations to discussion. On the whole, the dissertation, represented by several independent papers, has been performed at a high level of methodological approaches, the analysis of the obtained results and the validity of conclusions. It complies with the international standard for PhD dissertations in the field of marine biology and ecology.

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15.06.2013