Review

of the Dissertation of Marina Varfolomeeva

Biotic interactions, structure, and long-term changes in marine benthic assemblages

submitted for the degree of Doctor of Philosophy in Biology at the Saint-Petersburg State University

The dissertation consists of 97 pages, including 3 figures, and 6 published articles.

The significance and status of the dissertation in the field

Dissertation describes a technically sound piece of scientific research in marine ecology. Applying various approaches, M. Varfolomeeva has studied different aspects of epibenthic communities' structure and functioning. The direct and reliable evidences of interspecific interactions in these communities are scarce yet, so the theme of the dissertation is highly actual. Marina Varfolomeeva and her co-authors have demonstrated that interactions between key foundation species (barnacles and ascidians) are rather complex, including settlement facilitation, competition for food, spatial interference and overgrowth, and population dynamics (recruitment, survival and growth). She has also demonstrated that the ontogenetic shifts in the sign of interactions create an important feedback loop for the patch dynamics of the system. Thus, these foundation species act as facilitation cascade. This result is new and interesting. Also, she has studied the long-term variability in community structure, and has demonstrated how the interplay of spatial and temporal scales results in the complex dynamics. All these findings are original and give us a new insight into the mechanisms underlying the complex dynamics of epibenthic communities.

The sufficiency and quality of the material

The material is sufficient, high-quality, and carefully examined.

As regarding to the "dynamical" part of the study, it is based on rather long-term observations reasonably sufficient for making the reliable conclusions (but see "Comments and shortcomings" below).

The adequacy of the methods used

Most of studies are methodologically perfect, based on testing several clearly formulated alternative hypotheses. A wide spectrum of methods has been applied, including long-term observations, field manipulative experiments, stable isotope analysis, etc. Methods of statistical

analysis are also adequate and correctly used, their results are correctly interpreted (but see "Comments and shortcomings" below).

The validity of results

The results are based on sufficient data that are carefully analyzed and interpreted, and can mainly be evaluated as valid. Statistical analysis has been performed appropriately and rigorously. The conclusions are drawn appropriately based on the data presented.

The logic of the dissertation's structure

The papers on that the dissertation is based differ in both methods applied and, partly, in objects studied. Nevertheless, the author makes the good efforts to bring all the pieces together into a whole picture. The dissertation includes the synopsis that briefly but comprehensively represents and summarizes all the findings and provides the general outlines of the whole study.

The knowledge and use of literature in the field

Most of the relevant literature are referenced and considered, and the own results are discussed in general context of this literature.

The project's contribution to the research area

To the best of my knowledge, this is the first complex study of facilitation cascade in epibenthic community.

The section concerning the stable isotope signatures and trophic interactions is also interesting. No significant shift of stable isotope signatures in the presence of a potential competitor shows that the effect of feeding interference between Modiolus and Styela rustica is weak (if present at all). The author suggests that these species do not compete for food. In addition, horse mussels showed an unexpectedly high difference in $\delta15N$ between the foot and adductor muscles. This is important methodological result, which should be taken in account in further food web studies based on stable isotope signatures. In general, this is a good piece of work, which makes a noticeable contribution to the ecology of marine epibenthic communities. The results have been published in journals with high impact factor. This fact corroborates the high level of the project.

The author's input into the achievement of the dissertation results

In all the publications presented, Marina Varfolomeeva had participated directly, taking part in concept formation, study design, field sampling, data analysis, and writing the manuscripts.

Language

The manuscript is written in standard English, good enough and rather understandable (at least for me who is not native English-speaker).

The comments and shortcomings of the manuscript

I have no serious criticism to this dissertation. However, some minor comments should be made.

- Introduction: Why "environmental heterogeneity" and "physical factors" are treated as separate forces (Page 3)?
- Soft-bottom macrofauna dynamics: I'm not sure about the applicability of nested ANOVA for the temporal data with possibly complex periodicity. For example, according to the analysis, the season adds relatively little to the total variability, as compared with interannual and spatial components. Visual inspection of your Fig. 2 (pages 36-37), however, shows the evident seasonal changes for many species (and this seems natural, indeed!). Could this discrepancy be the result of your analytical approach (nested ANOVA)? Why more conventional procedures have not been applied in addition, such as time series analysis with seasonal trend filtering or Fourier analysis?
- Stable isotope study: Why mussels-ascidians system was chosen for this study, while the barnacles-ascidians system is the main object for other studies?
- Barnacles-Ascidian long-term dynamics: What the treatment unit in your regression analysis was year (12 points) or plot (30 points)? In any case, were these numbers sufficient for reliable effect estimation in multiple regression analysis?

In addition, the $\delta 13C$ isotope ratios differ noticeably indicating not only quantitative (i.e. along food size spectra) but also qualitative differences in the diets. In particular, *Styela* shows more depleted 13C signature close to the values typical for suspended particulate organic matter (SPOM), while *Modiolus* was more 13C-enriched, indicating possibly higher role of microalgae or fresh phytodetritus in its diet. It conforms well to the differences in their efficiency to capture smallest particles. Unfortunately, this result is only mentioned in brief by the author but not discussed sufficiently.

- The text is somewhere repetitious. Some repetitions could be shortened by means of better structuring the dissertation ("from problem to problem", instead of "from paper to paper" exposition).
- Two spatial scales at Fig. 1 are shifted (e.g., 100 km2 equals 108 m2, not 1010).

All these comments concern the minor debatable particulars and are not a matter of principle. In general, I conclude that the dissertation represents a good job with many novel and interesting results. It certainly complies with the international standard for PhD dissertations in the corresponding field.

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Andrey I. Azovsky,

Dr. Sc., Professor

Dept. of Hydrobiology, Biological Faculty, M.V. Lomonosov Moscow State University