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

The dissertation consists of 97 pages, including a 29 page synthesis section and 6 published articles, two of which are primary authorships for the candidate. The candidate is listed as fourth author on the remaining 4 articles, although her contributions appear to be significant, primarily sampling and writing. Articles are quite well-written, but in the 'synthesis' section the language is not as well controlled. The use (or lack of use) of articles (a, the) in Russian is nearly opposite that in English, and this home-language bias is apparent in the published papers, but primarily in the synthesis. Furthermore, text is choppy and paragraphs are not well linked in the synthesis. This is to be expected due to differing levels of review.

All six articles are published in international journals of high standing and are closely related in topic and study area. This makes a very nice package and, together, represent a substantial contribution to the field Arctic benthic ecology, and benthic community ecology in general. There are disappointingly few studies investigating factors contributing to community structure in high-latitude benthos, and this work combines a strong theoretical base with a strong sampling design and elegant statistical analyses. The work proceeds in a logical progression and the candidate and her co-workers should be proud of their accomplishments thus far. I eagerly await the follow-up studies that are surely on their way.

Six published papers and two first-authorships are definitely sufficient for a PhD degree in most universities I have experience with. As with most good work in ecology, the results raise more questions than the data themselves answer. This leaves room for continued studies, but also for discussion with the candidate regarding alternative hypotheses, occasional contradictory or unexpected results, and, most importantly, how the results can be best synthesized to obtain a more holistic picture of how these communities are structured and how they function in time and space.

In this review I will focus, somewhat disproportionately, on these points. This is not meant to dismiss the many highlights of the excellent work, or cast the work in a negative light. I hope that my impressions of the high quality of the published work will be apparent in my comments nonetheless.

As mentioned above, the articles present a well-designed series of studies that address the main questions regarding how communities are structured in shallow White Sea habitats, and what some consequences may be of structuring mechanisms and outcomes. An unusually broad combination of data sets and techniques, ranging from long-term surveys, focused sampling on different spatial scales, aging of barnacles, and stable isotope analysis, is employed. Each method is well-suited to address the main question(s) of each paper. Adequate levels of replication are exercised. Furthermore data are analyzed using statistically powerful techniques, and implications are largely constrained to appropriate scales (e.g. results are not applied to the entire Arctic system).

In addition, each article is firmly based in ecological theory, and relevant publications are cited. Introductions are particularly strong in this sense in paper 1, 2, 3 and 6. Furthermore, theoretical and empirical contexts are retained through the discussion when own results are brought up. Linking

relevant literature and context with thesis results is strong in the articles, but could have been better exhibited in the 'synthesis' portion of the thesis. Clearly the candidate is aware of the context since she helped write (or was primary author on) the included papers, but most topics get only a few sentences and are not well integrated with each other or to the results. Some of this is likely a consequence of the articles being peer-reviewed at least once, whereas this is probably the first outside review the synthesis receives.

This criticism can be extended to the synthesis in general. Admittedly, I am not exactly sure what is asked for at St. Petersburg State University, but I would have expected a stronger attempt at synthesizing the results of the papers. The three figures included in Introduction to this section need more explanation than provided. Even the Discussion section of the synthesis is structured as six separate sections, suggesting little effort to do such a synthesis. This, I believe, is important for a doctoral candidate to show evidence of: pulling together the individual studies into a more holistic picture of how the system operates. A figure that tries to do this would have been helpful.

I see the overarching question asked by this thesis to be (approximately): What determines whether a substrate is colonized by a barnacle or ascidian; and what may affect survival of the two species differentially? This lends itself well to a cartoon-type figure indicating community development in time and space, or a table where theory on facilitation, interference, patch dynamics, succession, etc. are indicated and evidence for each is noted. Of course, this could also be done in text alone. The synthesis falls short of integrating the results in this way.

Another issue I have that applies to both the articles and the synthesis is the hesitancy to make potentially controversial interpretations. Potential explanations for observed patterns are given but mostly in list form and without a more critical evaluation. Specific hypothesis-testing may have helped this. Papers 3 and 5, and to some extent the synthesis itself, do a better job of making bolder statements or predictions considering mechanisms or consequences. I understand that it is difficult to get some interpretations past reviewers, but I think authors should do more than leave it to the reader to decide what explanations seem most plausible.

I must here applaud the candidate for her efforts to point out the significant finding of the changing nature of species interactions during succession. This is quite synthetic and perhaps the strongest element of the synthesis section. While it is not completely novel, I believe that the thesis contains some of the best evidence for such a process on such a scale as addressed here.

There are several points of contention I have with interpretation found in the published articles that are either conclusions I disagree with or topics that could/should be considered. In papers 1 and 2, colonizing taxa that are not foundation species are considered as a whole, but it may be worthwhile to better investigate whether some subset of taxa respond differently that others in terms of colonization patterns and the mechanisms dictating them. This could help differentiate among taxa that just need colonizing space and others where interactions may be more biotically-driven. It is not surprising that essentially adding hard substrate to a muddy-bottom system increases biodiversity of epifauna, but what about infauna? Here is a missing element and one that is potentially important for infaunal community patterns and dynamics as well.

Are *Rhodine, Musculus,* and *Apistobranchus* really mobile macrofauna (paper 3)? Does that imply colonization by movement from one to another habitat (and not settlement of larvae)? I am not sure

of the distinction you are making as it seems that you are only really talking about 'fauna that we find in these patches,' and not motile vs. sessile.

In paper 4, are you really addressing questions of spreading potential given that your field work is confined to a small area within a relatively protected shallow sea? This also has some bearing on the enigmatic result of the system NOT being space limited, which may be in some conflict with the results of the other papers. This is something that I would have liked to have seen resolved in the synthesis. In addition, I am not convinced that air temperature is the best parameter to link with subtidal-community organization processes. Is there no water temperature measurement available?

On the basis of the above-mentioned criteria, I find the dissertation of sufficiently high quality to be acceptable as partial fulfillment of the requirements set out by St. Petersburg State University for the degree of Doctor of Philosophy. I congratulate the candidate on a well-constructed thesis and a valuable contribution to the field.

17 June 2013

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