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REPLY COMMENT

Effects of social behavior on survival and growth of krill: important, but how relevant?

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Ritz (2002) raises the point that social behavior in krill may act both to save energy and to decrease predation risk (e.g. Hamner & Hamner 2000, Ritz 2000). The benefits of social aggregation have long been recognized by behavioral ecologists (e.g. Mangel & Clark 1988, Gibson et al. 1990, Ranta 1993, Parrish & Edelstein-Keshet 1999, van Baalen & Sabelis 1999, Clark & Mangel 2000, Giraldeau & Caraco 2000). However, as Ritz (2002) mentions, the social behavior of krill is not well studied. We agree that a greater understanding of krill social behavior within an evolutionary and ecological framework will improve our ability to understand krill dynamics. However, the exclusion of social aggregation from our model does not represent a weakness in our approach or alter any of our general conclusions. Indeed, Ritz suggests an obvious extension of our model that can only be examined when more is known about the costs and benefits of aggregation size in Antarctic krill. In almost any study, factors exist that are potentially important in general, but are not relevant to the questions addressed by the study.

As we explained in Alonzo & Mangel (2001), the motivation for our work was to present a general conceptual framework, in which we use what is known about Antarctic krill and natural selection, to help us understand the distribution and abundance of krill. We also wished to study which conditions would select for krill shrinkage and explain observed patterns of growth. Previous work by Ritz and colleagues (McGaffin et al. 2002) shows that he concurs that krill shrinkage occurs and warrants further study. We used the model to show that a negative energy budget may explain why krill shrink. However, we also showed that size-dependent predation risk could select for shrinkage between reproductive events, even in the presence of positive energy budgets. We suggested this as another hypothesis to explain the observation that krill shrink. We do not argue that shrinkage is the only anti-predator behavior adopted by krill, and we explicitly model vertical migration to escape predation. Whether swarming represents an energy-saving or anti-predator behavior in no way negates the conclusions in our paper. Even if krill group size is driven by predation risk (Mangel & Clark 1988), shrinking would still decrease size-dependent predation risk (Hill et al. 1996, Reid et al. 1996). There is no reason to believe swarming and shrinking are mutually exclusive responses to predation or that swarming reduces size-dependent predation risk.

Ritz (2002) also states that not enough is known about metabolic and filtration rates. Although questions remain, we know more about krill metabolic costs, growth rates, and feeding patterns than for most marine invertebrates. While metabolic rates may be different in swarms, our equations generate realistic growth patterns using the best information available. Only the qualitative functional form of metabolic and feeding rates affect our conclusions. Finally, if sufficient information is not available for these rates in general, then we cannot have sufficient information to model their effects as a function of swarm size.

We agree that the social behavior of krill is an important area of research. But we do not agree that a failure to include social aggregation in our model changes the basic framework we develop, or the conclusions of our research. Ritz (2002) touches a fundamental issue of modeling: when should one construct models? Should modeling be done only after all the data are collected? In that case, of course, one would merely simulate nature in the computer, and the model would do little to guide empirical work. The alternative is to conduct modeling and empirical work sequentially, so that empirical work motivates models and provides parameters for them, and models suggest observations that need to be conducted and identify gaps in our knowledge. When more is known regarding the costs and benefits of swarm size in Antarctic krill, we will be happy to examine this extension of our model.

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