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COMMENT

Comment on Alonzo & Mangel (2001) Survival strategies and growth of krill: avoiding predators in space and time

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Alonzo & Mangel (2001) use a modelling approach to elucidate factors affecting distribution and feeding behaviour of Antarctic krill in different habitats. Occupation of these habitats by krill results in differential survival, predation risk, food availability and metabolic costs. I strongly agree with some of Alonzo & Mangel's main conclusions, e.g. that patterns of predation risk may be the key to understanding krill distribution. Also that krill should behave in a way that maximises survival. But I do not agree that 'size and temperature effects on metabolic costs, filtration rates' etc. are all well studied. Also I do not agree that it is necessary to postulate shrinkage, i.e. loss of body mass, as a strategy in response to predation pressure. One critically important factor in the life of krill has been neglected by most authors and also by Alonzo & Mangel: social aggregation. The fact that krill spend nearly all of their lives in schools affects every facet of their behaviour, and experimental work on other social species has shown that schooling enhances survival, food capture success and reproduction, while minimising metabolic costs.

Krill individuals do not need to shrink in response to increased predation pressure. They have other options: one is to adjust the size of the school. Ritz (1994) reviewed this in *Euphausia superba*. Daly & Macaulay (1991) were the first to suggest seasonal variation in predation intensity in combination with food availability as proximate factors influencing whether krill disperse or form schools. They proposed that aggregation in winter was a response to increased predation pressure despite low food abundance. In the face of abundant food, e.g. in summer, but also high predation pressure, krill would be expected to form large schools. In support of this, Bergstrom et al. (1990) described more or less orientated groups of krill, i.e. groups showing gregarious behaviour ('miniswarms'), forming in spring among decaying sea ice in the Weddell Sea. Ichii (1990) found large, high density schools at the pack ice edge in early summer. Sprong & Schalk (1992), working in the northern Weddell Sea, described krill migrating northwards in spring-summer with schools growing in size with distance away from the ice edge. The concept of school size responding seasonally to availability of food and predation pressure is well established for fish (e.g. Blaxter & Hunter 1982).

Experiments conducted by Ritz (1997) showed that mysids in different-sized swarms experienced very different success in capturing food. Moreover, when faced with a predatory threat, those in larger swarms continued to feed successfully, whereas the feeding success of those in smaller swarms was impaired. Where food capture success of Antarctic krill has been measured in situ (stomach fluorescence and faecal egestion, e.g. Pakhomov et al. 1997) and compared to results from laboratory studies (e.g. Quetin et al. 1994), the field results show a 3-fold increase, which I suggest is because the field krill had fed within a school (Ritz 2000); krill in laboratory experiments are invariably solitary or form small non-schooling groups.

Recent work on mysid swarms suggest that aggregation provides substantial energy savings and that all previous measurements of oxygen consumption made on isolated individuals are likely to be much too high (Ritz 2000). For example, Ritz et al. (2001) showed that mysids in a swarm expended 3 times less energy per unit weight than those in uncohesive small groups. I argue that any calculation of metabolic costs of krill must take account of savings derived from social aggregation. I agree with Verity & Smetacek (1996) that Antarctic krill are conspicuously successful because they have occupied a largely empty niche in the Southern Ocean; a niche filled in other oceans by schooling clupeid fishes.

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LITERATURE CITED

Alonzo SH, Mangel M (2001) Survival strategies and growth of krill: avoiding predators in space and time. Mar Ecol Prog Ser 209:203–217

Bergstrom BL, Hempel GG, Marschall HP, North A, Siegel V, Stromberg JO (1990) Spring distribution, size composition and behaviour of krill *Euphausia superba* in the western Weddell Sea. Polar Rec 26:85–89

Blaxter JHS, Hunter JR (1982) The biology of clupeid fishes. Adv Mar Biol 20:1–223

Daly KL, Macaulay MC (1991) Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the antarctic marginal ice zone. Mar Ecol Prog Ser 79:37–66

Ichii T (1990) Distribution of Antarctic krill concentrations exploited by Japanese krill trawlers and Minke whales. NIPR Symp Polar Biol 3:36–56

Pakhomov EA, Perissinotto R, Froneman PW, Miller DGM (1997) Energetics and feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. J Plankton Res 19:399–423

Quetin LB, Ross RM, Clarke A (1994) Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: El-Sayed SZ (ed) Southern Ocean ecology. Cambridge University Press, Cambridge, p 165–184

Ritz DA (1994) Social aggregation in aquatic crustaceans. Adv Mar Biol 30:155–216

Ritz DA (1997) Costs and benefits as a function of group size: experiments on a swarming mysid, *Paramesopodopsis rufa* Fenton. In: Parrish JK, Hamner WM (eds) Animal groups in three dimensions: how species aggregate. Cambridge University Press, Cambridge

Ritz DA (2000) Is social aggregation in aquatic crustaceans a strategy to conserve energy? Can J Fish Aquat Sci 57: 59–67

Ritz DA, Foster EG, Swadling KM (2001) Benefits of swarming: mysids in larger swarms save energy. J Mar Biol Assoc UK 81:543–544

Sprong I, Schalk PH (1992) Acoustic observations on krill spring-summer migration and patchiness in the northern Weddell Sea. Polar Biol 12:261–268

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130:277–293

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