

COMMENT

Natural mortality, fecundity and development time in marine planktonic copepods — implications of behaviour

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E-mail: dag.aksnes@ifm.uib.no*Kjørboe T, Sabatini M (1995) Scaling of fecundity, growth and development in marine planktonic copepods. Mar Ecol Prog Ser 120:285–298*

In an extensive review Kjørboe & Sabatini (1995) concluded that cross-taxonomic patterns in development, growth, and fecundity rates in planktonic copepods suggest that mortality rates are independent of body mass per se. The authors also conclude that this finding is at variance with the pattern for aquatic organisms in general (Peterson & Wroblewski 1984) and pelagic invertebrates in particular (McGurk 1986); mortality rates typically scale with (body mass)^{-0.25}.

The first part of Kjørboe & Sabatini's argument is based on empirical evidence indicating that juvenile development time and daily egg production rate are independent of body size. The second part assumes that, in order for a population to be of constant size in the long run, 2 individuals (1 male and 1 female) must survive each generation (generation time is here assumed to be approximated adequately by juvenile development time). Using the definition of reproductive output (R_0) this criterion was expressed (Kjørboe & Sabatini 1995):

$$R_0 = 2 = (m/\beta) e^{-\beta D} \quad (1)$$

Hence, because daily egg production (m) and juvenile development time (D) is independent of size, mortality (β) should also be independent of size.

I agree that there is no reason that body size per se should influence the death process, although predation risk is known to be associated with a number of factors related to body size. Some of these factors, such as visibility, tend to increase predation risk as size increases, while others, such as escape capabilities, tend to decrease predation risk as size increases. Such am-

biguous effects suggest that a true mechanistic understanding of predation risk and mortality can hardly be obtained unless the predation process of a particular prey-predator system is carefully analysed. Ambiguous size-related effects are likely to introduce variability in mortality at size in any simple mathematical function that intends to describe mortality rate versus body weight for a large group of species. My interpretation of the analyses of Peterson & Wroblewski (1984) and McGurk (1986) is that this variability is the most striking result. Their reviews demonstrate that the mortality rate frequently spans 2 to 3 orders of magnitude for a given body size.

I disagree, however, with the approach leading to Kjørboe & Sabatini's suggestion that mortality rate should be independent of body size. Their review of fecundity, growth and development in copepods primarily includes studies where food is abundant and predation and certain kinds of behaviour are eliminated (i.e. laboratory rearings). Hence, the conclusion that development times and egg production rates are independent of body size is valid for an environment rich in food and without natural mortality, but not necessarily for the natural marine environment. This is also expressed in the assumption made by Kjørboe & Sabatini (p. 291): 'If we assume that the realised egg production rate, like the maximum one, is size independent, it follows that β , the mortality coefficient, is size independent.' (Although not explicitly stated, they also assume that the realised generation time, like the minimal one, is size independent.) Generally, these assumptions are not likely to be true.

Behaviour influences fitness through mortality risk and life history traits such as fecundity and time of maturation. For the planktonic copepod, the predation pressure is often most intense where food is abundant and temperature is highest (i.e. surface water). Due to the strong impact of mortality risk on fitness, sole maximisation of feeding and growth is often likely to be a poor evolutionary adaptation for the planktonic copepod, except for in a predator-free environment (such as the laboratory). In the marine pelagic environment, higher fitness may be obtained by vertical migrations (Ohman et al. 1983, Aksnes & Giske 1990, Ohman 1990). Accordingly, many dominant zooplankton species (such as several *Calanus* species) have evolved this behaviour. Besides the reduction in predation pressure, vertical migration exposes the zooplankton to alterations in temperature (affecting realised develop-

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ment times) and to alterations in food intake (affecting realised fecundity). In an environment where food (for example phytoplankton) and high temperatures are located in the surface layer, migration to deeper cooler habitats devoid of food is likely to increase development time and reduce daily birth rate. To be an evolutionarily stable solution, however, this cost should be outweighed by the benefit of reduced mortality risk.

Larger animals (both within and between species) tend to migrate more than smaller animals. Whether larger animals simply have better swimming capabilities or have more motivation to carry out migrations (larger copepods such as *Calanus hyperboreus* and *C. finmarchicus* may be more easily seen and preferred by a predator such as herring, than the smaller *Paracalanus parvus*) is not important here. The sequence: 'large size — more time spent in deep water — reduced mortality (due to lower predation pressure), reduced birth rate (due to lower food intake), and increased development time (due to lower temperature)', however, suggests a correlation, not only between mortality and body size (negative), but also between realised birth rate and body size (negative), as well as between realised development time and body size (positive). I am not advocating that such relationships between vital rates and body weight, apply for the planktonic copepods as a group, or that it is productive to look for such single-factor relationships. Decreasing natural mortality with increasing body weight, however, need not be at variance with the size independent (maximal) birth rates and (minimal) development times that Kiørboe & Sabatini review.

In a fjord locality of western Norway, Aksnes & Magnesen (1983, 1988) found relatively high mortality rates ($>0.1 \text{ d}^{-1}$) for *Paracalanus parvus* as well as for the early copepodites of the larger *Calanus finmarchicus* (which corresponds with the prediction that mortality rate should be independent of size). For *C. finmarchicus* copepodid stage V, however, the mortality rate dropped significantly (below $<0.01 \text{ d}^{-1}$). This drop in mortality was probably related to the fact that this development stage spent more time away from the dangerous surface layer (*P. parvus* did not migrate and was always located in the surface water). The reduction in the mortality of *C. finmarchicus*, however, was associated with a penalty: The generation time of *C. finmarchicus* was 1 yr compared to about 2 wk for *P. parvus*. In a nearby fjord locality, Matthews et al. (1978) described a situation which was similar, but in which *C. finmarchicus* had more than 1 generation per year and a much higher average mortality rate than the yearly generation described by Aksnes & Magnesen (1983). The larger copepod, *C. hyperboreus*, however, had a yearly generation and an average mortality rate $<0.01 \text{ d}^{-1}$. Again, this low mortality rate was prob-

ably related to a deep average habitat location. These studies suggest that behaviour has a decisive influence on vital rates in a trade-off situation including depth dependent predation risk, temperature and food availability (Aksnes & Giske 1990). As suggested by the Kiørboe & Sabatini prediction, it is a possibility that a hypothetical situation, in which *C. hyperboreus*, *C. finmarchicus* and *P. parvus* all preferred the same habitat, would result in same fecundity, development time, and mortality rate. This situation, however, is rather unlikely.

Complementary to direct measurements, I believe that the most productive way to learn about copepod mortality rate and risk is through mechanistic modelling of the factors affecting mortality. Unlike maximal fecundity and minimal development time, mortality is a genuine *in situ* parameter, and traditional laboratory rearings do not address this variable. Mortality risk is closely related to behaviour such as vertical migration, and the behavioural dimension should be taken into account as a forcing factor for natural mortality rates as well as for natural birth rates and development times. Therefore, balancing mortality rate against fecundities and development times by means of an evolutionary criterion, valid under certain laboratory conditions (i.e. Eq. 1), is not likely to serve as a good predictor for natural mortality.

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LITERATURE CITED

- Aksnes DL, Giske J (1990) Habitat profitability in pelagic environments. *Mar Ecol Prog Ser* 64:209–215
- Aksnes DL, Magnesen T (1983) Distribution, development, and production of *Calanus finmarchicus* in Lindåspollene, western Norway, 1979. *Sarsia* 68:195–208
- Aksnes DL, Magnesen T (1988) A population dynamics approach to the estimation of production of four copepods in Lindåspollene, western Norway. *Mar Ecol Prog Ser* 45: 57–68
- Kiørboe T, Sabatini M (1995) Scaling of fecundity, growth and development in marine planktonic copepods. *Mar Ecol Prog Ser* 120:285–298
- Matthews JBL, Hestad L, Bakke JLW (1978) Ecological studies in Korsfjorden, Western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* 1971–1974. *Oceanol Acta* 1:274–284
- McGurk MD (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar Ecol Prog Ser* 34:227–242
- Ohman MD (1990) The demographic benefits of diel vertical migration by zooplankton. *Ecol Monogr* 60:257–281
- Ohman MD, Frost BW, Cohen EB (1983) Reverse diel vertical migration: an escape from invertebrate predators. *Science* 220:1404–1407
- Peterson I, Wroblewski JS (1984) Mortality rates of fishes in pelagic ecosystems. *Can J Fish Aquat Sci* 11:1117–1120