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The inevitability of mortality

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Studies of rates of ingestion, particle selection, metabolism, growth, moulting, and egg production have dominated the marine zooplankton literature for many decades. It is clear, however, that the historical emphasis on processes of growth, development, and fecundity is too limited: much more work is required on mortality in natural populations. In particular, stage-specific patterns of mortality, their variability over time and space, and analysis of the underlying causal agents – predators, parasites, starvation, senescence, and advective losses – are essential elements of any quantitative description of population growth. Examples given illustrate the sensitivity of different zooplankton behaviours, population dynamic processes, and interactions with other elements of marine ecosystems to the characteristics of the mortality function. Realized fecundity is shown to depend on adult female mortality rates. Application of a new method for estimating mortality rates for stage-structured populations to the copepod *Pseudocalanus newmani* illustrates that temporal variations in *per capita* mortality rates can be several times the magnitude of temporal variations in *per capita* fecundity. This emphasizes the need for quantitative assessments of the loss terms for natural populations.

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Key words: mortality rates, population dynamics, fecundity, behaviour, density-dependence, Copepoda, *Pseudocalanus newmani*.

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Introduction

A simple expression describing the time rate of change of a marine zooplankton population is:

$$\frac{dN}{dt} = (\text{birth} - \text{death} - \text{advection} + \text{diffusion} + \text{lateral migration})N \quad (1)$$

where N is abundance and each of the terms inside the parentheses is a *per capita* rate. In recent decades, studies have focused on the birth-rate term of this population dynamics equation, which implicitly includes the processes of ingestion, metabolic losses, somatic growth, and development that lead ultimately to reproductively mature females and release of viable offspring. Often this focus has occurred to the exclusion of other fundamental terms of population growth. Here we first develop the argument that the death-rate term is an especially important quantity for a variety of issues concerning natural zooplankton populations. Second, since zooplankton have yet to inherit the earth, death rate must more or less balance birth rate, and there is no

prior reason to suppose that death rates are any less variable than birth rates. Third, mortality rates remain poorly known. We do not address the remaining terms in Equation (1) because techniques are currently available in the oceanographic community for estimating advection, diffusion, and behavioural migration.

Part of the past emphasis on birth-rate processes in marine zooplankton studies can be traced to conceptual and part to methodological sources. The conceptual bias originates to some extent from the pervasiveness of Lindeman's (1942) trophic-dynamic concept as an appealing simplification of aquatic ecosystems. The emphasis upon energy transfer between successive trophic levels highlights production processes and transfer coefficients between levels, rather than the demography of component populations. The trophic-dynamic concept was also perceived as a useful tool in predicting fishery yields, though ultimately this approach met with little success (e.g. Lasker, 1988). More generally, the most widespread paradigm in marine planktonic ecosystem studies has been a "bottom up"

perspective, based on the assumption that variability of planktonic populations (or entire trophic levels) is governed principally from below by the availability of resources rather than from above by variability in predators, disease, or parasites. A third element of this conceptual bias is the intense interest, from an ecosystem perspective, in grazing processes: phytoplankton-grazer interactions have been the core of studies treating the processes controlling phytoplankton blooms and the importance of zooplankton as mediators of elemental vertical fluxes.

Methodological considerations have also contributed to an emphasis on processes contributing to birth rates. Many of the rate terms relevant to birth-rate estimates can be measured at sea or at shore-side laboratories. Short-term incubations can be carried out to obtain instantaneous measures of ingestion, particle selection, respiration, excretion, moulting, and egg production. Meaningful determinations can be made on a small, but representative, part of the population isolated within containers with a suspension of natural prey items collected *in situ*.

In contrast, mortality rates measured in isolated containers are unlikely to be at all representative of mortality rates in natural populations. For example, while it is often feasible to incubate a zooplankton with a broad spectrum of natural prey items, it is rarely possible to include a spectrum of predators that may range from heterotrophic dinoflagellates, small poecilostomatoid copepods, and scyphostome medusae to mobile planktivorous fish and mammals. In addition, mortality rates have numerous components in addition to predation, including starvation, parasitism, and senescence. It is difficult to know, *a priori*, which of these sources of mortality is the most important. For example, many investigators assume that parasitism is relatively insignificant for natural zooplankton popula-

tions, but this assumption itself rests on prior knowledge of the mortality rates and the mortality attributable to other causes. Sampling problems, including the need to obtain repeated unbiased population samples over time, have made mortality estimation difficult. The theoretical weakness of most models for mortality estimation (see Wood and Nisbet, 1991; Wood, 1994) has been a further hindrance.

We differentiate two types of mortality. The first is loss from a population through death, assuming that a large enough volume has been sampled that advective losses are relatively small. The second is loss from a geographic region or locality through physical transport or behavioural migration (e.g. Sinclair, 1988). We discuss the first source, though the technique proposed below could be used to resolve the second source if the advection-diffusion and behavioural migration terms were well enough defined.

Importance of mortality

Although it is self-evident from Equation (1) that mortality rates are an essential component of descriptions of population growth, a limited number of examples may help illustrate the sensitivity of many scientific issues in zooplankton ecology to the mortality rate term. Table 1 lists a few selected issues spanning zooplankton behavioural ecology, life history traits, population dynamics, and ecosystem dynamics where quantitative mortality estimates are needed. Each issue, whether resolving the adaptive significance of a behavioural trait, or the sensitivity of an ecosystem process to mortality rates, requires both qualitative and quantitative measures of population losses.

Among behavioural traits, diel vertical migration stands out as a topic where a large literature has accumulated but, until recent years, little quantitative work has addressed its adaptive significance. Figure 1 (see Ohman (1990) for details) illustrates that small changes in mortality rate, achieved through predator avoidance, markedly change the fitness of different zooplankton migration behaviours. Migration-induced reductions in mortality rate of between 10% (when copepodid III through adult female stages migrate) and 18% (when only adult females migrate), are enough to increase the fitness of migrant populations above the fitness of non-migrant populations. These small differences in mortality rate are easily achieved in nature (Ohman, 1990; see also Fig. 4 below). Aksnes and Giske (1990) showed that the importance of mortality risk for migrant zooplankton differs for species of different generation times. Assessments of the costs and benefits of zooplankton aggregation responses have long been debated (Ohman, 1988), but will remain only qualitative until *per capita* risk can be assessed for different behaviours. Evaluation of diapause as a predator

Table 1. Some representative issues requiring quantitative estimates of mortality rates.

Behavioural and life history traits
Diel vertical migration
Aggregation responses
Diapause
Brooding vs. broadcast spawning
Population dynamics
Relative importance of predation, starvation, parasitism, senescence
Impact of selective predators
Density-dependent vs. density-vague population control
Top down vs. bottom up population control
Interpretability of egg production rates
Ecosystem dynamics
Balanced vs. unbalanced production cycles
Nutrient limitation vs. grazing control of phytoplankton

Figure 1. Population growth advantage for a vertically migrating copepod as a function of the mortality reduction achieved through migration. At the zero line the rate of increase of a vertical migrant population (r_{migrant}) equals the rate of increase of a non-migrant population ($r_{\text{non-migrant}}$); above this line migratory *Pseudocalanus newmani* achieve an advantage. The family of curves illustrates the effects as predator avoidance begins at increasingly earlier developmental stages (from female to CIII). d_3 is the mortality rate of migratory stages. This analysis applies to the case where the temperature difference between upper and lower strata is 4°C and the ratio of mortality rates for early:late developmental stages is 2.0 (from Ohman, 1990).

avoidance mechanism (Hairston *et al.*, 1990) would benefit from comparisons of the absolute mortality risks to animals in resting and non-diapause habitats. In addition, the relative advantages of life-history traits, such as brooding or broadcasting eggs (Kiørboe and Sabatini, 1994), rests on accurate knowledge of egg mortality for both types of spawners.

Mortality rates are of course fundamental to any population dynamics problem (Table 1). Assessments of the role of selective predators in the differential removal of different stages or species remains an open issue for most marine populations, as does the relative importance of predation by non-visually feeding carnivorous zooplankton and sight-hunting planktivorous fish. Both of these topics have seen substantial investigation by freshwater zooplankton workers (Kerfoot and Sih, 1987). Resolution of theoretical issues, such as the existence of density-dependent or density-vague population control processes (Strong, 1986) require mortality rate measures. The relative importance of predation (top down) and resource limitation (bottom up) effects on natural zooplankton populations will not be resolved until mortality of natural populations has been quantified.

The importance of understanding not only egg production but egg mortality has been emphasized by recent studies illustrating remarkably high egg mortality for broadcast spawning copepods (e.g. Ianora and Poulet, 1993; Peterson and Kimmerer, 1994; Kiørboe and Sabatini, 1994). Variations in mortality rates can

Figure 2. Dependence of reproductive stage distributions on mortality rate, for adult female *Pseudocalanus newmani*. A. Instantaneous distribution of females of three different reproductive stages (pre-reproductive, reproductive, post-reproductive) under constant mortality. B. Cumulative distribution of females in the three reproductive stages as a function of mortality rate. C. Proportion of total females in the population carrying eggs, as a function of mortality rate per stage (where each stage lasts $1.25 \times$ the embryonic duration), for two cases: where the mortality rate of egg-bearing females is equal to that of non-ovigerous females ($1 \times$), and where the mortality rates of egg-bearing females is twice that of non-ovigerous females ($2 \times$). In (A) and (B) stippling indicates the reproductive portion of the population (modified from Ohman, 1985).

also have more subtle consequences for population dynamics studies. Figure 2 illustrates that even for a food-satiated copepod reproducing at physiological maximum rates, considerable temporal variations in fecundity occur as a consequence of temporal variation in mortality of adult females. The proportion of egg-bearing female *Pseudocalanus newmani* in the population at any instant can vary from 32 to 59% of all females present, solely as a consequence of changing mortality rates of females (Fig. 2C, $1 \times$ curve). If egg-carrying *Pseudocalanus* females have a higher mortality risk than females that are not carrying eggs (e.g. twice the mortality rate, Fig. 2C, $2 \times$ curve), the proportion carrying eggs would be lower still, varying from 8 to

41% of females present. Hence, interpretations of the causes of variations in fecundity of natural zooplankton populations also require knowledge of variations in mortality rate.

At the level of ecosystem dynamics, sensible predation closure terms on the zooplankton are needed to properly model phytoplankton bloom dynamics, vertical fluxes, and the seasonality of plankton production cycles. For example, Steele and Henderson (1992) illustrated that qualitatively different plankton production cycles could be generated merely by varying the shape of the function describing predation on zooplankton from density-independent to different forms of density-dependence. Such changes may be sufficient to generate the major differences between the balanced sub-arctic Pacific ecosystem and the unbalanced North Atlantic ecosystem. Fasham's (1993) model of seasonal bloom dynamics and elemental fluxes in the sub-tropical and sub-arctic North Atlantic was markedly improved when he introduced a zooplankton loss rate that varied with zooplankton biomass, thus reinforcing the need for an understanding of zooplankton mortality for sensible modelling of ecosystem processes.

In the following sections we illustrate an application of a new method for estimating mortality (Wood, 1994) and contrast temporal variation in mortality rates with those of egg production rates for *P. newmani*.

Materials and methods

Egg production and mortality rates were compared for a population of the copepod *P. newmani* Frost residing in Dabob Bay, a fjord within Puget Sound. Adult female *P. newmani* carry attached eggs. Eggs, copepodids, and adults (but not nauplii) were counted over a 2-year interval as described previously (Ohman, 1985). Embryonic and post-embryonic stage durations were estimated as a function of time and temperature, taking account of seasonally variable temperatures at the depth of the chlorophyll maximum layer (Ohman, 1985) and seasonal and stage-specific variations in reverse diel vertical migration behaviour (Ohman, 1990). Daily egg hatching rate was obtained from the egg ratio (total eggs per total adult female *P. newmani*) divided by the embryonic duration. The temperature-dependent embryonic duration varied over time and was weighted for the portion of a day females spent at near-surface temperatures and at sub-surface temperature (see Ohman, 1990).

Time- and stage-dependent mortality rates were estimated by the method of Wood (1994) which, briefly, solves the McKendrick-von Foerster equation by describing the population per unit age interval as a smooth function of age and time for pre-adults. For adults the population is a smooth function of time and must be consistent with the dynamics of the juveniles.

The functions describing population surfaces are fitted to the observed population data using spline functions that are constrained to give positive death rates and smooth transitions in mortality between successive stages. The smoothing parameter was chosen by minimization of Equation (10) of Wood (1994) based on a variance model approximating the original population data. The missing nauplii were treated as one stage containing zeros with a weight of 1/5000 of the lowest weight of the remaining data. Confidence limits for *per capita* death rates were estimated as described in Wood (1994), where variance of population estimates is known.

Results

Analysis of average mortality rates in two successive years shows a recurrent pattern of mortality varying by developmental stage (Fig. 3). There are two life-history intervals of highest average mortality rates: naupliar stages through copepodid I and copepodid V. Between these occurs a stanza of relatively low mortality rates from copepodid stages CII–CIV. The large 95% confidence limits suggest that few of these differences are statistically significant, though the recurring pattern

Figure 3. Variation in mortality rate with developmental stage for *Pseudocalanus newmani* ($\bar{x} \pm 95\%$ bands) for the active growing season (Julian day 75–235) in two successive years (● = Year 1; ▲ = Year 2). Mortality rates and confidence limits established by a modification of the method of Wood (1994). Adult male and female mortality rates are shown on different scales, with 95% CL. Male mortality rates shown in parentheses. Nauplii were not enumerated but a mortality estimate for stages NI–NVI combined was obtained as indicated in the text.

between years suggests that the stage-specific trends are real. The average mortality rates of eggs and adult females are similar, as would be expected for an egg-brooding species. Mortality rates of adult females are considerably lower than those of CVs, especially in Year 1, which is consistent with the more strongly developed reverse migration response, and thus predator avoidance capability, of adult females (Ohman, 1990). Instantaneous mortality rates of adult males were on average 11–12 times those of adult females and highly variable because of the small population sizes of males which gives less stable parameter estimates (Wood, 1994).

In addition to the congruence of overall trends between years, there are interesting between-year differences that correspond to what is known about temporal variation in the abundance of predators. For example, in Year 1 mortality rates of younger stages (egg–CII) were somewhat lower than in Year 2, which agrees with the markedly lower abundance of carnivorous zooplankton in the winter–spring early growth season of Year 1 (Ohman, 1986, 1990). Conversely, the somewhat higher mortality rates of CIII–CV in Year 1 correspond with the much higher abundance of carnivorous zooplankton in the summer period of Year 1 compared with Year 2. The relatively high mortality rates of CI and CV, together with the large variance in these rates, suggest that these may be particularly sensitive stages that bear closer investigation in efforts to understand temporal variations in population abundance.

Temporal variations of egg hatching rates and mortality rates (of adult females and eggs) over a 2-year period are compared in Figure 4. Note that both panels in Figure 4 are scaled such that the maximum of the ordinate is at least 20 times the minimum observed value. In the case of egg hatching rates, significant variability occurs between dates, but the overall range of variation of mean values is 0.32–3.23 eggs female⁻¹ d⁻¹, or 10-fold, throughout the duration of the study (Fig. 2A). In contrast, average instantaneous mortality rates show an overall range of 0.0000–0.1390 d⁻¹ (Fig. 2B). If the measured values of mortality are smoothed with a running mean to reduce the influence of outliers, the resulting range of mean values in the time series is 0.0003–0.0778 d⁻¹. This represents 260-fold variation, even in the smoothed mortality rates. Thus the amplitude of variability of mortality rates over time is several times the amplitude of variability of egg hatching rates. Indeed, part of the variability in egg hatching rate (Fig. 4A) is itself caused by variations in mortality rates of adult female copepods (Fig. 3).

Discussion

The historical emphasis on assimilation, growth, and fecundity, referred to above collectively as the birth-rate

Figure 4. *Pseudocalanus newmani*. Temporal variation in (A) egg hatching rate (shaded region indicates range of observations) and (B) instantaneous mortality rate of females and eggs in two successive years (shaded region indicates 95% confidence limits of estimates; white-outlined line indicates 7-point running mean). Note that both panels are scaled with at least a 20-fold difference between the minimum and maximum observations.

term of the population dynamics equation, is clearly too limited for studies of population growth of natural populations. For the copepod species analysed here, the magnitude of temporal variability in *per capita* egg mortality rates is substantially greater than the magnitude of temporal variability in egg production rates. Furthermore, realized egg production rates depend on female mortality rates. These results imply that equal, if not greater, attention be given to the mortality term in future studies.

Previous comparisons of the relative importance of variations in birth and mortality rates have analysed copepod species that broadcast-spawn (free) eggs into the water column. Broadcast-spawning copepods generally show a much greater range in daily egg production rates than brooders (Ohman, 1985; cf. Ianora and Buttino, 1990; Mullin, 1993), but appear also to experience much higher egg mortality (Kiørboe and Sabatini, 1994). Ianora and Buttino (1990) inferred that seasonal fluctuations of *Centropages typicus* and *Acartia clausi* in the Gulf of Naples were affected more by variations in survivorship of early developmental stages than by variations in *per capita* fecundity. Mullin (1991), however, arrived at a different conclusion in a comparison of *Calanus pacificus* and *Rhincalanus nasutus* in the

Southern California Bight. He utilized the strength of correlations in abundance between successive developmental stages as an index of variations in mortality and natality and inferred that variations in *per capita* egg production for these two species were considerably greater than variations in mortality rate. Mullin noted the likely contrasts between these taxa and brooding copepod species and called for a comparative analysis with a species that carries its eggs (as in the present study). Our methods differ from previous authors, however, in that we have directly measured variability in *per capita* egg production at the same time as estimating variability in *per capita* mortality of eggs. Even without taking account of variability in survivorship of post-embryonic developmental stages, we conclude that temporal variations in mortality are much greater than variations in fecundity. Incorporation of post-embryonic survivorship (shown above in Figure 3 to have different levels of variation for different developmental stages) would further accentuate the importance of mortality in relation to fecundity as a dominant factor governing fluctuations of natural populations.

Mortality, or a specific causal agent of mortality, such as predators, starvation, parasites, disease or advection, is frequently invoked in a qualitative way as an explanation of behavioural traits or observed rates of population change. However, quantitative mortality assessments to test such assertions are rare because of sampling difficulties and problems with many existing models. The present analytical method for mortality estimation is robust (Wood, 1994) and may prove useful for a variety of natural populations. Future efforts to understand behaviour, population dynamics, and ecosystem dynamics will inevitably falter in the absence of attention to mortality.

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