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Journal

Limnology and Oceanography, 41(1)

ISSN

0024-3590

Authors

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Publication Date

1996

DOI

10.4319/lo.1996.41.1.0126

Peer reviewed



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Source: *Limnology and Oceanography*, Vol. 41, No. 1, (Jan., 1996), pp. 126-135

Published by: American Society of Limnology and Oceanography

Stable URL: <http://www.jstor.org/stable/2838844>

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Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord

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Abstract

The population surface method for estimating mortality was modified to incorporate diapause of copepodid stage 5 and missing naupliar stages and applied to a 2-yr time series of the planktonic copepod *Pseudocalanus newmani* in a temperate fjord. The fitted model captures nearly all of the observed dynamics of the population and yields age-, stage-, and time-specific measures of mortality along with confidence limits. Average mortality rates for eggs and adult females were quite similar, as would be expected for species that carry eggs until hatching. Instantaneous mortality rates of adult males were on average 11–12 times higher than those for adult females. Average mortality rates were high for copepodid 1 (C1), declined in stages C2 through C4, and increased again at C5. This bimodal pattern of mortality with developmental stage probably results from changing susceptibility to different guilds of predators with ontogeny. Mortality rates for C5 and adult females were not significantly different between the overwintering period and the active growth season. Mortality rates of adult female *P. newmani* varied in a nonlinear manner with the abundance of predators as a result of predator avoidance behavior, underscoring the importance of zooplankton behavior in interpreting population dynamics.

Zooplankton populations in seasonal environments experience temporal variability in temperature, food availability, and sources and rates of predation and parasitic attack. The probability of mortality for members of such populations is thus likely to vary through time. Moreover, since predators typically remove selected size classes (e.g. Kerfoot and Sih 1987) and starvation can differentially affect animals of different sizes or life history stages (cf. Vidal 1980), the probability of mortality is likely also to vary with developmental stage. Hence, methods for estimating mortality should accommodate mortality that varies simultaneously over time and among stages. Yet most of the available methods for estimating mortality rates for stage-structured populations assume that mortality rates are either constant through time, uniform across stage, or both constant and uniform (see Manly 1989; Wood and Nisbet 1991). An exception is the matrix projection method of Caswell and Twombly (1989), which is applicable only when the time interval between population samples is shorter than the duration of the shortest developmental stage.

Cohort analysis has been applied to multivoltine populations in circumstances where a sequence of cohorts is clearly definable from field data (e.g. Landry 1978a), but in general, cohort analysis is most applicable to univoltine populations (e.g. those developing at high latitudes). Early methods for deriving stage durations and mortality rates from cohort analysis have been criticized because of the interdependence of these two quantities (Braner and Hairston 1989; Miller and Tande 1993), and remedies have been proposed (Aksnes and Hoisæter 1987). However, for multivoltine populations, clear recognition of a sequence of unambiguous discrete cohorts remains less the rule than the exception, highlighting the need for alternative mortality estimation procedures.

A further limitation of many procedures for estimating mortality is that they require prior specification of a model for population growth or the shape of the recruitment function to a given developmental stage. Often the validity of the underlying models is unknown. A preferred method for estimating mortality would make minimal prior assumptions about the form or existence of an underlying population growth model.

The population surface method of Wood (1994; also Wood and Nisbet 1991) presents an effective alternative. In studies with simulated data, this method has been shown to be robust to moderate levels of sampling error and to avoid the demographic instabilities common to some other methods (Wood 1994) as well as to generate both time- and stage-dependent mortalities with confidence limits. The principle behind the population surface method is that the population per unit age interval can be described as a smooth function of age and time. If we can infer this function from data, then it immediately

Acknowledgments

Supported by NSF OCE 90-19639 (M.D.O.) and by the NERC Center for Population Biology, Silwood Park, Ascot Berks, U.K. (S.N.W.).

We thank Dag Aksnes, three anonymous referees, and Michael Pace for comments on the manuscript. The computer programs used for this analysis are available as C programs or a compiled "Windows" program from S.N.W.

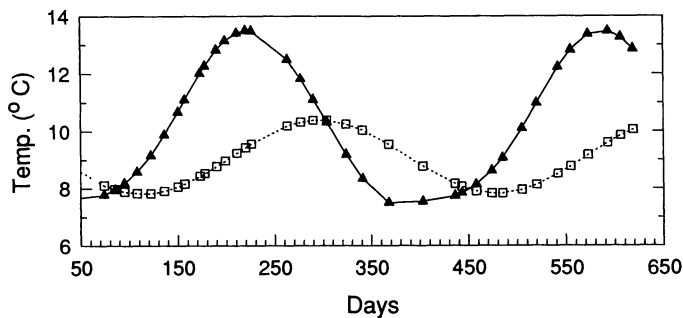


Fig. 1. Seasonal variation in temperature at the depth of the chlorophyll maximum layer (▲) and at 75 m (□) in Dabob Bay. Points illustrate Eq. 7 and 8 for the dates on which field samples were taken.

gives us death rates at any age and time. For adults, we assume that the population is a smooth function of time and that the dynamics of the adult population must be consistent with those of the juvenile population. The method involves representation of the unknown age structure and adult population functions by bicubic spline approximation, imposition of the biological facts that population size and death rates are nonnegative quantities, optimal choice of model complexity, and calculation of confidence intervals (*see* Wood 1994). After the continuous age structure of a population (i.e. its population surface) has been inferred, it is easy to convert back to stage-specific rates by integrating the population surface or the death rate surface it defines. The method does not require identification of discrete cohorts and is suitable for both continuously and episodically reproducing populations.

Here we apply the population surface method to a natural, unenclosed copepod population for the first time. We extend the method to accommodate diapause of copepodid stage 5 and to incorporate information on seasonal and stage-specific changes in vertical migration behavior that influence temperatures at which animals develop and therefore the durations of developmental stages. The method is also modified to allow for missing stages, which arose in this case because of the lack of data on abundance of nauplii.

The population data for the planktonic copepod *Pseudocalanus newmani* have been reported previously (Ohman 1985) with an attempt to extract mortality estimates (Ohman 1986). We re-examine these data now because of the availability of a new and robust method that permits estimation of time- and stage-dependent variations in mortality. In our analysis we test the hypothesis that mortality rates decline monotonically with developmental stage, as has been previously assumed (e.g. Miller and Tande 1993). We also examine the hypothesis that mortality rates of overwintering animals are appreciably lower than those of corresponding stages during the season of active population growth, as might be expected if diapause achieves a reduction in predation risk (Hairston 1987).

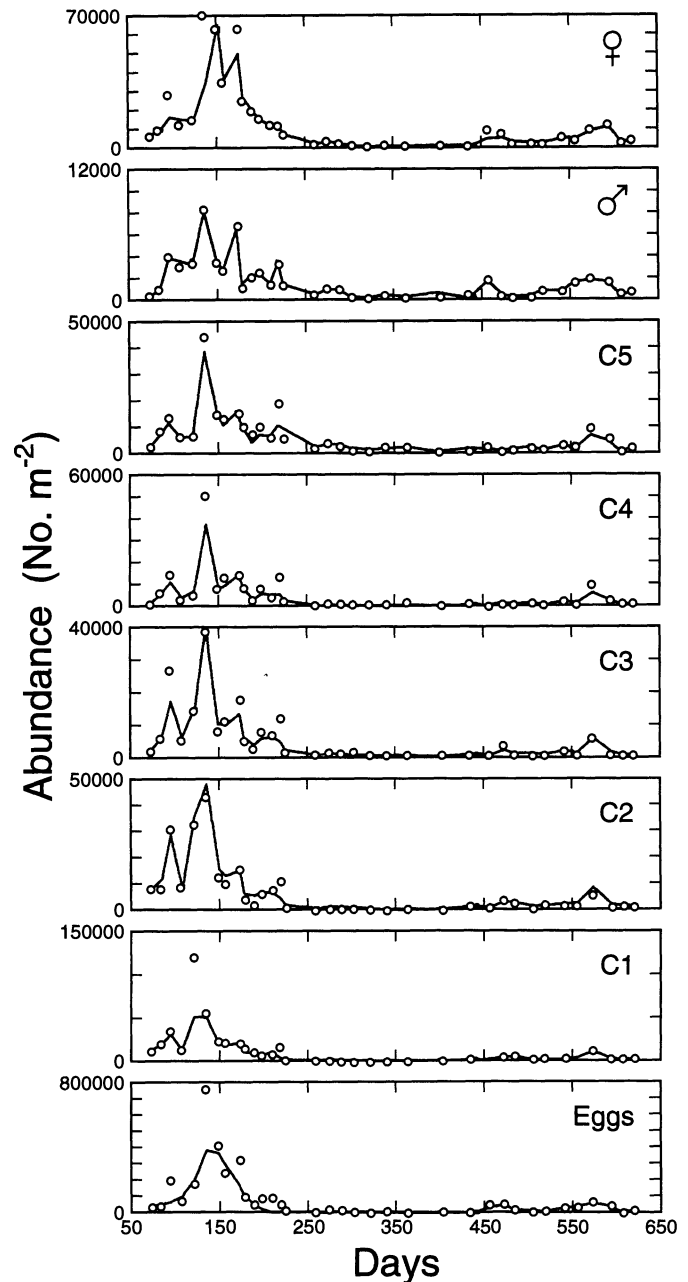


Fig. 2. Temporal variation in abundance of developmental stages of *Pseudocalanus newmani*. Points illustrate the mean values from population censuses, and lines indicate abundances from the fitted population surface.

Methods

The model—In order to estimate mortality rates, eggs, larvae, and juveniles to the end of C5 were represented with the McKendrick-von Foerster equation:

$$\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial a} + \mu \eta = 0. \quad (1)$$

η is the number of individuals of age a at time t , and μ is per capita death rate. The model η was represented with

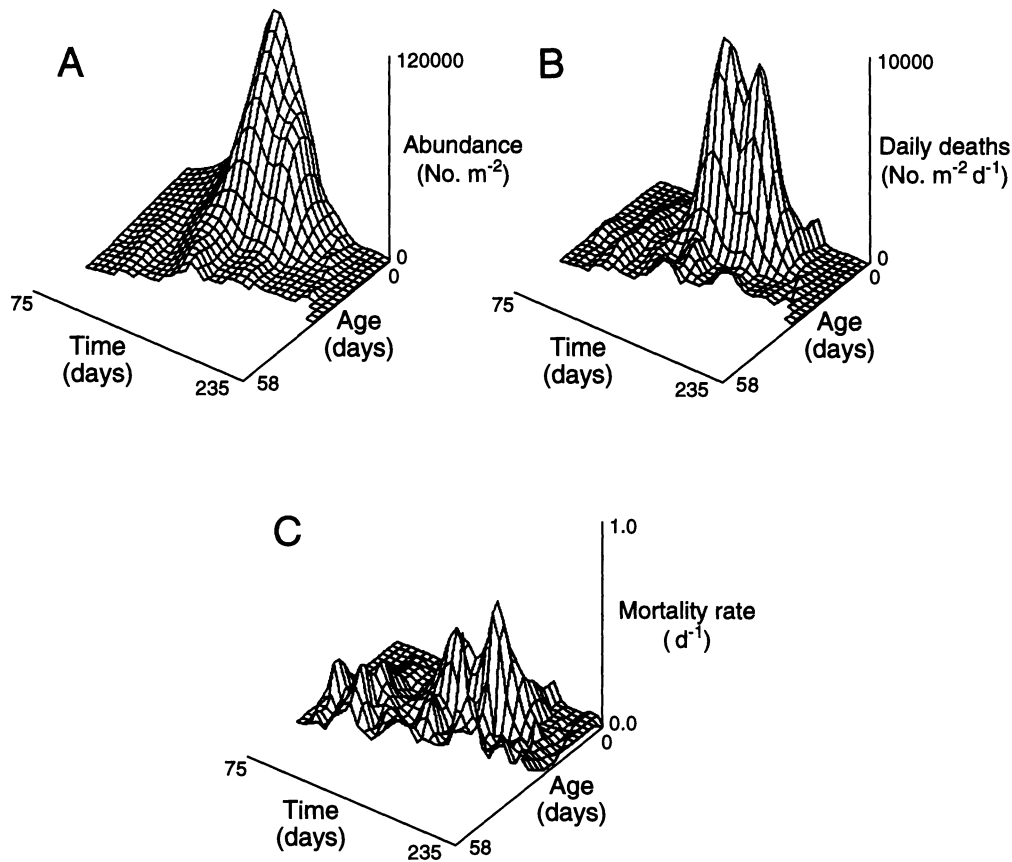


Fig. 3. Surfaces illustrating temporal and age-specific variations in abundance (A), numbers dying per day (B), and instantaneous mortality rate (C) of *Pseudocalanus newmani*, for preadult individuals in year 1. The independent variables are time (calendar date) and age of animals (days).

spline functions and inequality constraints, ensuring that positive death rates were imposed in the manner described by Wood (1994). Adults were modeled as

$$\frac{dN_A}{dt} = R(t) - \mu_A(t)N_A(t) \quad (2)$$

where

$$R(t) = \eta(\alpha_M, t) \left(1 - \frac{d\alpha_M}{dt} \right), \quad (3)$$

and α_M is the age at maturation from the final juvenile stage. $N_A(t)$ was represented with a spline function constrained to be positive and also constrained to ensure positive adult death rate. This latter condition can be imposed by requiring that

$$\eta(\alpha_M, t) \left(1 - \frac{d\alpha_M}{dt} \right) - \frac{dN_A}{dt} \geq 0 \quad (4)$$

at a finely spaced set of times. Note that this constraint affects both the juvenile and adult parts of the model. Representation of the model using spline functions allows the smoothness of the model to be controlled by minimizing a weighted sum of the wiggleness of the model and

its deviation from the population data. If high weight is given to the deviation of model from data, then a complex model fitting the data very closely will result. If wiggleness is given a high weight, then a smooth model which will not fit the data so closely will result, as described in detail by Wood (1994). Here variances were available from the data so that the complexity of the model could be chosen by minimizing the expected mean-square deviation of the model from the true underlying population dynamics (this minimizes equation 10 of Wood 1994). Thus, the method incorporates sampling error into the fit of the population surface. The standard deviation of abundance for each developmental stage was described as a function of abundance (n) from linear regressions of standard deviations of replicate counts against water-column abundance: for eggs $\sigma_e = 1,000 + 0.13n_e$; for copepodid stages $\sigma_c = 500 + 0.07n_c$; and for adults $\sigma_A = 840 + 0.07n_A$.

Since naupliar data were missing, these stages were treated as one stage containing zeros but given a weight of 1/5,000 of the lowest weight in the rest of the data. This ensures that the missing stages do not influence the fitted population surface. The estimates for the naupliar stages are therefore obtained from consistency with the egg and copepodid stages.

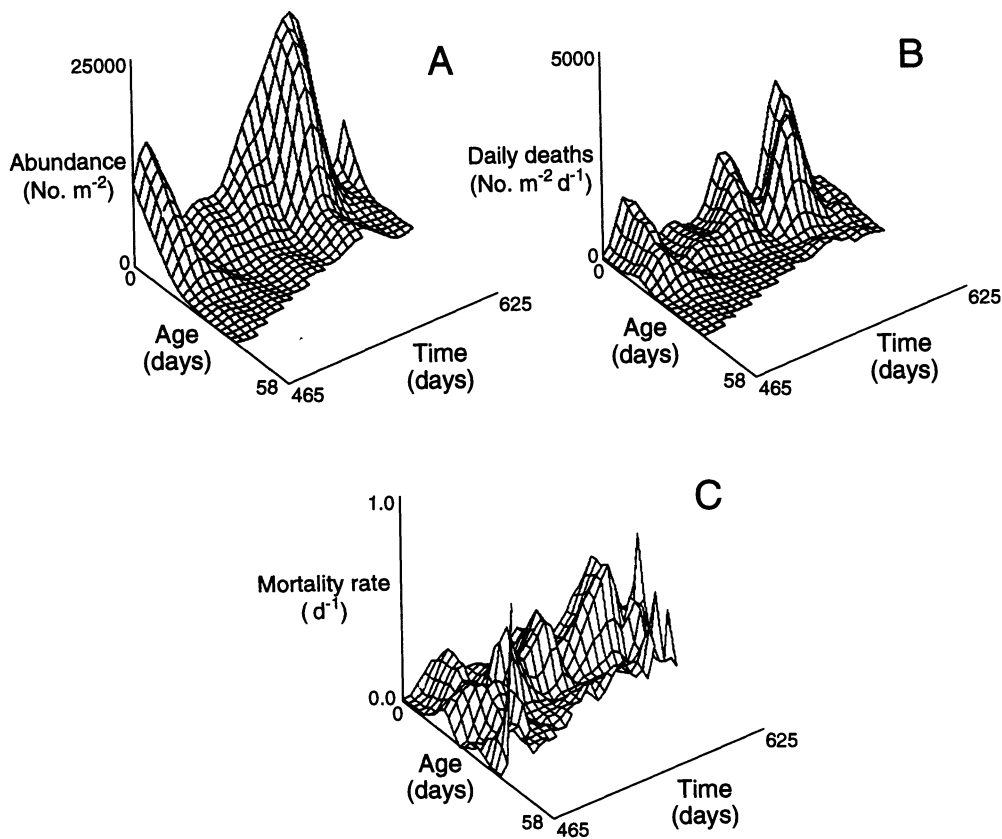


Fig. 4. As fig. 3, but in year 2.

The data—The stage structure of the *P. newmani* population in Dabob Bay, Washington, was determined from replicated vertical hauls from 150 to 0 m with a 73- μ m-mesh net over 2 yr (see Ohman 1986). Time series were available for egg, copepodid, and adult stages but not for nauplii. For the population surface method, stage durations estimated independently of stage abundance data are required. Temperature-dependent stage durations took into account seasonal diapause and changes in diel vertical migration behavior with both season and developmental stage (Ohman 1990). Temperatures for different developmental stages varied in the manner described by Ohman (1986) with some refinements. Nauplius 1 through copepodid 3 (C3) developed at a temperature approximated by that at the depth of the chlorophyll maximum layer ($T_{\text{Chl max}}$) both day and night. For C4 through adult females with attached eggs, the daytime temperature was $T_{\text{Chl max}}$, and the night temperature was also $T_{\text{Chl max}}$ from mid-September through mid-May. From mid-May through mid-September, when reverse diel vertical migration occurs, the night temperature for these migratory stages was the temperature at 75-m depth ($T_{75\text{m}}$).

Stage durations τ_i for each of seven subadult developmental stages ($i = \text{egg, pooled nauplii, C1, } \dots, \text{C5}$) were weighted for the proportion of a day spent at day (PD) and at night ($1 - PD$) temperatures from

$$\tau_i = (PD)(DT_{i,D}) + (1 - PD)DT_{i,N}. \quad (5)$$

The day development time ($DT_{i,D}$) and night development time ($DT_{i,N}$) for each stage (i) was obtained from the product of the appropriate stage-specific coefficient from table 1 of Ohman (1986) and the expression of Corkett and McLaren (1978) relating embryonic duration (ED) to temperature (T):

$$\text{ED} = 1,845(11.45 + T)^{-2.05}. \quad (6)$$

This procedure invokes the equiproportional rule, which McLaren et al. (1989) demonstrated to be appropriate for the genus *Pseudocalanus*. $T_{\text{Chl max}}$ as a function of day of the year (D) was obtained from

$$T_{\text{Chl max}} = 7.5 + 6.0X^{1.319} \exp[0.385(1 - X^{3.426})] \quad (7)$$

where $X = (365 - D)/143$. $T_{75\text{m}}$ as a function of D was described by

$$T_{75\text{m}} = 9.11 + 1.286 \cos\left(\frac{0.986D - 292.36}{57.3}\right) \quad (8)$$

(Fig. 1). The proportion of daylight hours (PD) as a function of D was obtained from

$$PD = \frac{8.37 + 7.68 \exp[-(X - 172)^2(11,327)^{-1}]}{24} \quad (9)$$

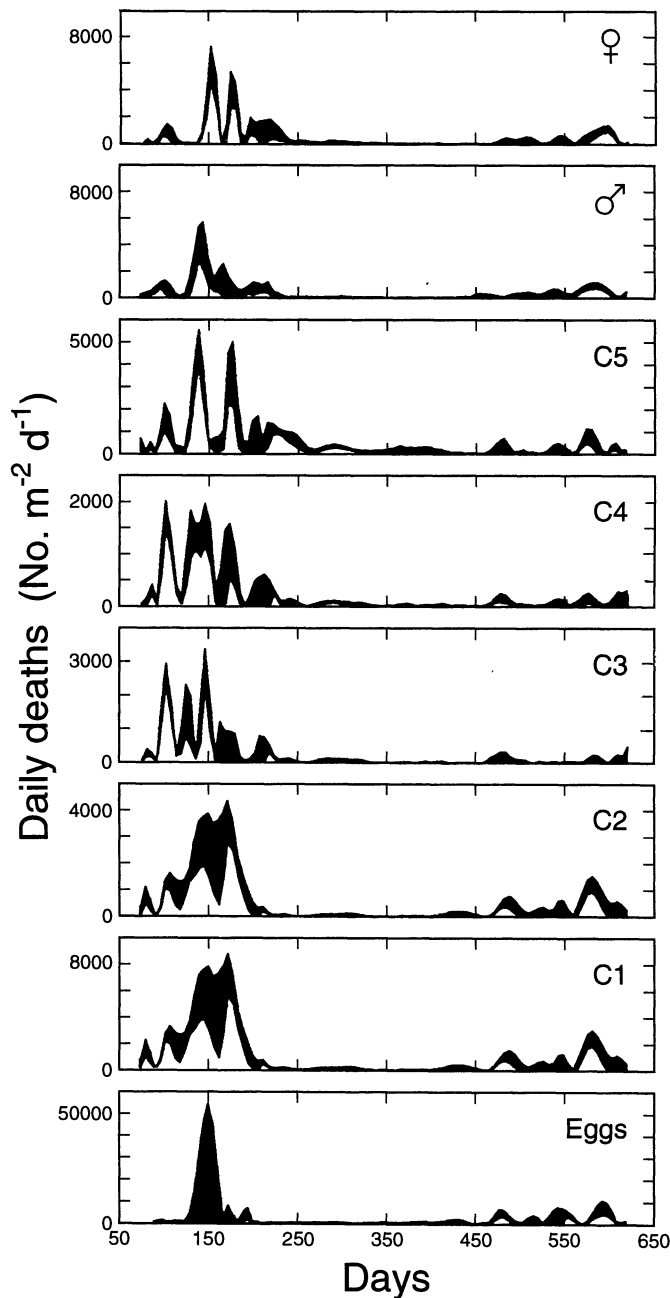


Fig. 5. Temporal variation in numbers of *Pseudocalanus newmani* dying per m^2 of sea surface per day by developmental stage. Dark bands illustrate 95% C.L.

where $X = D$ for $D < 355$ and $X = D - 365$ for $D \geq 355$. (Note that the numerator in Eq. 9 is a correction of equation 2 reported by Ohman 1986.) Diapause was treated by letting the upper age boundary of C5s increase by 1 d per day from late summer through winter. The sex ratio was assumed to be 1 : 1 for all preadult stages.

The uniformity of per capita death rate (pcdr) across developmental stages was tested for each year separately (excluding diapause). We tested H_0 (the average pcdr was

the same in all juvenile stages) against H_A (the average pcdr was different in some stages). The test statistic used was the mean absolute deviation of stage-specific average death rate from the mean average pcdr. The distributions of the test statistics were generated by Monte Carlo simulation assuming multivariate normality for the mean pcdr. The covariance matrix for the pcdrs is obtained by linear approximation given the covariance matrices for total death rate and the population surface that are produced by this method (Wood 1994). By the central limit theorem, we expect the mean death rate and population estimates to be approximately normal in distribution. The random numbers used in the Monte Carlo test were generated with the routines given by Press et al. (1988). Random vectors with the appropriate multivariate normal distribution were then obtained by standard transformation methods. One million samples were generated to obtain each significance level.

Results

A fundamental step in applying the method of Wood (1994) is accurate representation of the observed population stage structure over time by the fitted model η . The fitted model (Fig. 2, lines) recovered most of the observed dynamics (Fig. 2, points) of the sampled population of *P. newmani* despite the absence of data for naupliar stages. Transient peaks in abundance of eggs and copepodid 1 in year 1 were not well reproduced, although for other times and developmental stages, the correspondence was quite satisfactory and within the limits of sampling error measured in this population. Note that Figs. 3 and 4 express the results in terms of age—a continuous variable—while Figs. 2, 5, and 6 express the results for discrete developmental stages.

The fitted population surface for years 1 and 2 (Figs. 3A, 4A) reveals 4–5 successive generations of *P. newmani* in the active growth season of both years, shown as ridges moving from upper right to lower left in Fig. 3A and from upper left to lower right in Fig. 4A. Note that these are not distinct cohorts of animals of identical age but partially overlapping generations of individuals with a distribution of birthdates centered around a common time period. The surfaces describing absolute numbers of daily deaths (Figs. 3B, 4B), derived from the population surfaces in panels A and solutions to Eq. 1, reveal that for most generations the highest number of deaths occurs in the first 14–18 d of life.

Surfaces of instantaneous per capita mortality rate (Figs. 3C, 4C) are derived from the quotient of the daily deaths for each age class and the estimated population size from the population surface. Instantaneous mortality rates illustrate that the probability of death is initially quite low (for eggs), increases to a maximum between days 4 and 18 of life, then generally declines. The time interval of highest mortality usually corresponds to the naupliar and C1 stages, depending on the time of year and corresponding temperature-dependent rates of development. For most generations a secondary increase in mortality rate

occurs with further increases in age. However, early in year 1 there was no pronounced peak in mortality rates of young individuals preceding the peak mortality of 30–40-d-old animals.

Mortality rates can be expressed as a function of stage rather than age by incorporating known temporal changes in stage durations from Eq. 5 to 9. Accordingly, time series of absolute numbers of daily deaths (Fig. 5) illustrate that peak losses of each developmental stage generally show a strong seasonal pattern with maxima in spring–summer, as might be expected from the time series of abundance in Fig. 2. However, peak numbers of deaths sometimes follow the maxima in stage abundance (cf. C1–C4 in Figs. 5 and 2).

Instantaneous mortality rates (Fig. 6) vary among stages, through time, and between years. Note that the scale of the ordinate for females in Fig. 6 is a fourth as large as that for earlier developmental stages and four times greater for males. The heavy lines represent running means, which serve to average short-term fluctuations in mortality rates associated with sampling error and to illustrate temporal trends. The high apparent mortality rate of C5 and adult males between days 400 and 425 seems to be an artifact of a long sampling interval during winter when the probability of flushing of fjord waters was relatively high. Adult female and egg mortality rates are averaged in Fig. 6 as the best estimator of the combined mortality. C1, adult males, and females-eggs all have intervals of elevated mortality in the spring–summer season of active population growth. However, C2–C5 stages show relatively constant mortality rates throughout the 2-yr study (again, except for the probable flushing event in winter).

Instantaneous mortality rates averaged over the two seasons of active population growth illustrate a recurrent bimodal pattern of mortality (Fig. 7). The two life-history intervals of highest mortality are the nauplii-C1 and C5 stages, with an interval of low mortality from copepodid stages C2 to C4. The hypothesis of no difference of mortality rates among juvenile stages was rejected for both year 1 ($P = 0.003$; see methods) and year 2 ($P = 0.012$). Average mortality rates for adult females were appreciably lower than for C5s and similar to average mortality rates for eggs estimated independently. Average mortality rates for adult females were 0.047 d^{-1} in year 1 and 0.045 d^{-1} in year 2. Corresponding average mortality rates for adult males were 11–12 times higher— 0.570 and 0.490 d^{-1} . The extremely high uncertainty of male mortality rates is attributable to the low abundance of males and the consequent unreliability of the estimates (Wood 1994). The variability in mean mortality rates was greatest in stages C1–C2 and C5. In comparisons between years, the results suggest that year 1 was characterized by lower mortality rates for younger developmental stages and higher mortality rates for older developmental stages, although these differences are not statistically significant ($P > 0.05$, Fig. 7).

The predators of adult female *P. newmani* have been well characterized at this locality, comprising primarily the carnivorous copepod *Euchaeta elongata* and a chaetognath, *Sagitta elegans* (Ohman 1986, 1990). Compar-

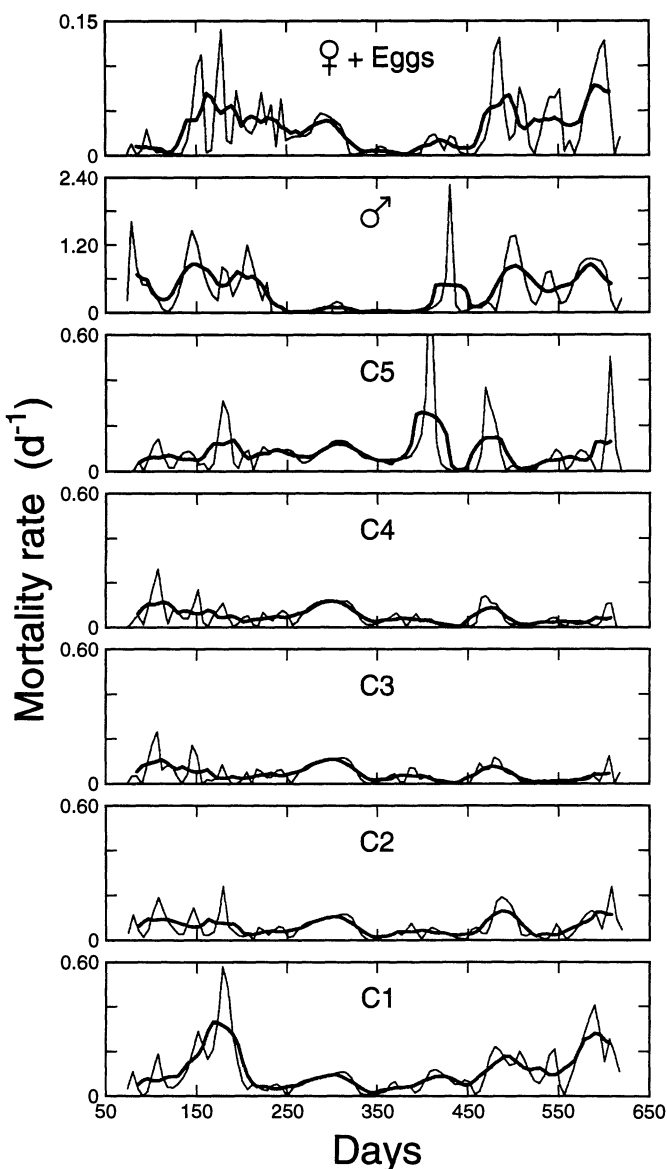


Fig. 6. Temporal variation in instantaneous mortality rate (d^{-1}) of *Pseudocalanus newmani* by developmental stage. Light lines illustrate average mortality estimates; heavy lines illustrate 7-point running means. Note difference in scale for adult males and females.

isons between predator abundances and instantaneous mortality rates of adult female *P. newmani* were made on those dates during the 2-yr study for which measures of both were available. *Pseudocalanus* female mortality initially increases with predator abundance and then saturates at still higher abundances (Fig. 8). The line in Fig. 8 describes a robust locally weighted smoothing fit (LOWESS; Cleveland 1979). There was no evidence of density dependence of mortality rates of adult female *P. newmani* (i.e. values of pcdr were uncorrelated with abundance of adult female *Pseudocalanus* ($r^2 = 0.036$, $P > 0.20$) or with all *Pseudocalanus* copepodids and adults combined ($r^2 = 0.002$, $P > 0.20$; relations not illustrated).

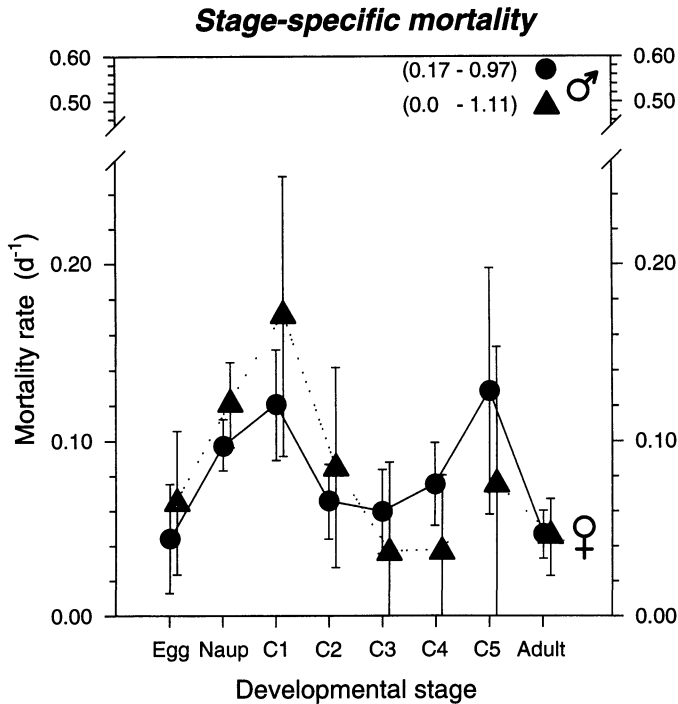


Fig. 7. Stage-specific variations in instantaneous mortality rates (d^{-1} ; $\bar{x} \pm 95\%$ confidence band for \bar{x}), averaged through the season of active population growth for year 1 (●) and year 2 (▲). Note that adult male mortality rates are shown on a different scale, with 95% confidence bands in parentheses.

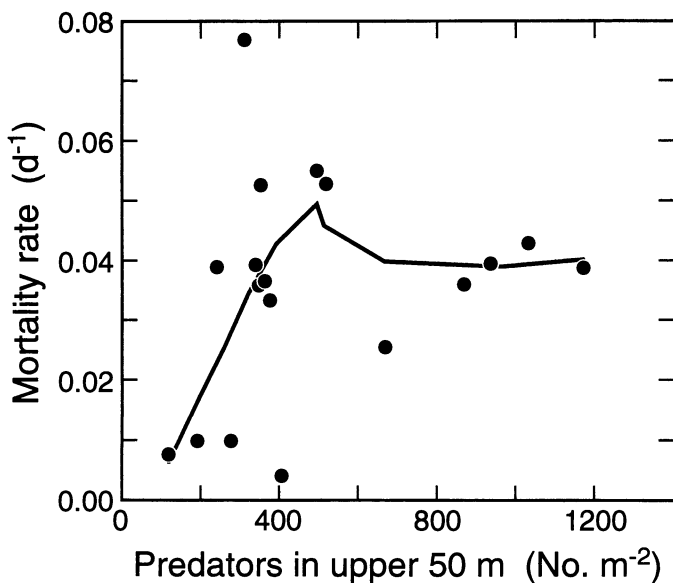


Fig. 8. Relationship between the instantaneous mortality rate of *Pseudocalanus newmani* adult females and the abundance of their primary predators (*Euchaeta elongata* and *Sagitta elegans*) in the upper 50 m at night. Average mortality rates from the running means in the top panel of Fig. 6. Line illustrates a nonparametric LOWESS fit.

Table 1. Mortality rates of *Pseudocalanus newmani* during active growing seasons and in the autumn–winter interval between. Values are the mean mortality rate $\pm 95\%$ confidence band for \bar{x} .

	Instantaneous mortality rate (d^{-1})	
	C5	Adult female
Growth season (year 1)	0.128 \pm 0.070	0.047 \pm 0.014
Overwintering	0.071 \pm 0.032	0.021 \pm 0.049
Growth season (year 2)	0.075 \pm 0.077	0.045 \pm 0.022

Mortality rates in autumn–winter are compared with those in spring–summer in Table 1 for *P. newmani* C5 and adult females—the two developmental stages found most commonly in winter. Summary statistics for other stages are not presented because, as noted above, the reliability of such estimates declines when abundances are low. Estimates during winter flushing were not included in the summary in Table 1. Although there seemed to be a winter dip in mean female mortality rates, it was not statistically significant ($P > 0.05$). Mortality rates for C5s and adult females were not significantly different in autumn–winter from rates in the active growing seasons.

Discussion

It is commonly assumed that instantaneous mortality rates decrease monotonically with successive developmental stages or increasing body size (e.g. Cushing 1974; Parslow et al. 1979; Peterson and Wroblewski 1984; Miller and Tande 1993), despite evidence to the contrary (e.g. Twombly 1994 and references therein). In our study we did not observe a monotonic trend, but rather a bimodal pattern of stage-specific mortality rates in two successive years. Although there were broad confidence limits associated with these averaged rates, the statistically significant dip in mortality rates in the young copepodid stages (C2–C4) in both years indicates that the pattern is reproducible and real. Efforts to describe mortality solely as a function of body size (Peterson and Wroblewski 1984) or body size with a covariate such as patchiness (McGurk 1987) do not account for this trend, which points to the limitations of broad size-related regressions for demographic studies.

High mortality of C1s (and inferred high rates of naupliar mortality) probably arises as a consequence of consumption by the abundant suspension-feeding zooplankton in this study site (especially *Euphausia pacifica*, *Metricaria pacifica*, *Calanus pacificus*, and perhaps *Oithona similis*). Decreased mortality of intermediate copepodid stages in comparison with C1 and nauplii is likely a consequence of improved ability to evade these suspension-feeders. This kind of size and stage specificity in prey evasion behavior has been documented for copepod developmental stages attacked by the copepod *Labidocera*

trispinosa (Landry 1978b). The subsequent increase in mortality rates of C5s arises from increased susceptibility of late developmental stages of *Pseudocalanus* to attack by carnivorous zooplankton, especially the predatory *E. elongata* (cf. Yen 1985; Greene and Landry 1985) and *S. elegans* (Ohman 1986). Hence, the life-history stanza between C2 and C4, where mortality rates are lower and relatively constant over time, seems to be a phase of reduced susceptibility to two different guilds of predators.

The decrease in mortality rate of adult female *P. newmani* in comparison with C5s arises as a consequence of differences in behavior between the two stages. While adult females avoid nocturnally feeding carnivorous zooplankton through reverse diel vertical migrations at times of high predator abundance, only some C5s do so (Ohman 1990). The onset of predator avoidance behavior by adult females at times of high predator abundance also accounts for the asymptotic relationship between female mortality rate and predators (Fig. 8). The migration behavior of adult females markedly modifies the mortality pattern that would be predicted on the basis of laboratory feeding experiments alone.

It should be borne in mind that our rates of naupliar mortality are arrived at indirectly. These rates are constrained to be consistent with the population surface fitted to the stages actually measured. Also, "naupliar" mortality represents a pooled estimate for a sequence of stages within which there is likely to be considerable stage-to-stage variability. We interpret these estimates with caution and merely point out that the pattern of elevated mortality for nauplii is concordant with a number of other studies of marine copepods, including another species of *Pseudocalanus* (Hay et al. 1988), and that the magnitudes of the inferred mortality rates are comparable to the mortality rates estimated for C1s.

Somewhat surprisingly, the mortality rates of overwintering C5s and of females in autumn–winter were not significantly lower than mortality rates in the spring–summer growth season. This pattern contrasts with the much reduced mortality of C5 *Calanus finmarchicus* overwintering in Lindåspollene, Norway (Aksnes and Magnesen 1983) and also with the assumptions made by Miller and Tande (1993) for overwintering *C. finmarchicus*. Clearly there is still appreciable risk for *P. newmani* C5 overwintering at depth, probably due to an abundant assemblage of co-occurring carnivorous zooplankton. What remains unknown (and perhaps unknowable), however, is whether the mortality rate for those individuals would have been higher still had they remained in the surface layer throughout winter (cf. Hairston 1987).

Previous efforts to estimate time-dependent mortality of *P. newmani* from these data (Ohman 1986) addressed only adults and used the questionable assumption (Parslow et al. 1979) of a uniform age distribution within a stage. The average survivorship curves from that study (Ohman 1986), while suggesting a bimodal pattern of survivorship, assumed equivalence of C4 and C5 mortality rates, which is shown here to be an inappropriate assumption. Thus, C5 mortality was underestimated and

adult mortality overestimated—just the sort of demographic instability about which Wood (1994) warned.

The method of translation between stage and age in the population surface method assumes that animals at the same state of development are of the same age (thus leading to a range of ages within each life-history stage). Departures from this assumption occur when successive cohorts that are spaced closely in time (or animals within one cohort) develop at markedly different rates. We saw no evidence for substantial departures from this assumption in our study.

The population surface method requires a priori knowledge of durations of each developmental stage. We were fortunate to have extensive information on the temperature regime experienced by different developmental stages over time and evidence from previous research that temperature was the dominant variable affecting development times in situ (Ohman 1985). In general, considerable effort is required to understand the vertical distribution of a population in relation to the thermal structure of the water column, as slight differences in depth in a thermally stratified water column will alter the stage durations. For example, a 1°C difference in temperature generates a difference of ~10% in stage duration for the present population. From the sensitivity analysis conducted by Wood and Nisbet (1991), the patterns of mortality determined from the population surface method would not be altered significantly by variations in stage duration of this magnitude, although larger errors would clearly alter mortality rate estimates and potentially alter inferred mortality patterns. The primary source of error associated with the mortality estimates is sampling error rather than errors in model fit. Thus we arrive at the familiar recommendation that extensive spatial sampling be conducted as the best way to estimate the true population means, variances, and mortality rates.

Since the confidence limits for mortality rate estimates generated by the population surface method incorporate both model uncertainty (i.e. bias) and sampling precision, they are not strictly comparable to confidence limits from estimation procedures that include sampling error alone. Although model uncertainty with the population surface method may often be small relative to sampling error, it is nonetheless present. Both sources of error should be included in rigorous assessments of the uncertainty of mortality rate estimates arising from any estimation procedure.

Comparative reviews of mortality estimation methods are given elsewhere (Manly 1989; Caswell 1989; Wood and Nisbet 1991; Wood 1994). Wood (1994) assessed the robustness of the population surface method and found that both the reconstructed population and the death rate surfaces were relatively insensitive to normally distributed errors of 20 and 40% of the population mean. (The average C.V. of mean abundance in the present study was 21%.) In Wood's analysis, introduction of a Poisson error distribution slightly increased the error in the death rate surface but not in the population surface. He also used simulated population data to compare the performance

of the population surface method with three other methods of mortality estimation: cohort analysis, the population projection matrix method of Caswell and Twombly (1989), and systems identification (Parslow et al. 1979). With the dynamics as simulated, the population surface method generated markedly more accurate parameter estimates than either cohort analysis or the population projection matrix method and somewhat better estimates than the systems identification technique. Tests of estimation procedures on simulated data remain a powerful means of assessing method accuracy and precision, although comparison with actual mortality measured in enclosures is also possible (Brett et al. 1992). Unlike systems identification, the population surface method does not require prior specification of the functional form of birth and death rate variation over time nor does it suffer from the demographic instabilities to which systems identification is prone (Wood and Nisbet 1991). The population surface method is, however, sensitive to low population abundances; it requires independent estimates of stage duration and, at present, does not accommodate distributions of durations within a developmental stage.

Few processes in natural zooplankton populations can be interpreted sensibly in the absence of knowledge of rates, or at least patterns, of mortality. Apart from their obvious importance to population dynamical studies, mortality rates also influence processes that historically have been evaluated in isolation. Even rates of egg production—a measure often used to infer food limitation—are influenced by the mortality rate experienced by females. This influence on fecundity occurs because under high mortality the age structure of adult females becomes strongly skewed, allowing prereproductive females to become a relatively large fraction of all females present (Ohman et al. in press). Under such conditions, temporal variations in mortality rates of females will appear as variability in reproductive output of the population. Mortality rates of eggs can be high and variable over time (e.g. Ianora and Poulet 1993). Also, as noted earlier, estimates of stage duration obtained from a temporal progression of developmental stages are influenced by differential mortality between successive stages (Miller and Tande 1993). Apart from such issues in population dynamics, the understanding of the adaptive significance of such behavioral traits as diel vertical migration or aggregation responses depends on knowledge of the risks associated with different behavioral options (e.g. Ohman and Wood 1995). Thus, the population surface method of Wood provides an apparently robust estimation procedure with many potential applications.

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Submitted: 28 November 1994

Accepted: 8 August 1995

Amended: 26 September 1995