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A vertical life table approach to zooplankton mortality estimation

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Abstract

Zooplankton mortality is commonly estimated from time series of abundances (horizontal life table approach) with the assumption that transport processes are of minor influence. This assumption is commonly violated in the marine environment. We provide equations appropriate for analysis of stage distributions in zooplankton samples at a single time (vertical life table approach) that, in certain circumstances, facilitate mortality estimation without requiring time series of abundances. A primary assumption is that daily recruitment to a particular stage should not be characterized by a strong upward or downward trend. To improve the accuracy of parameter estimates, however, knowledge about such trends may be taken into account. The accuracy and precision of mortality estimation were assessed with an individual-based simulation model. Results obtained from application of the vertical approach to the copepod *Pseudocalanus newmani* are comparable to those obtained independently by a horizontal method. We conclude that the vertical approach may provide mortality estimates under conditions in which horizontal techniques are inappropriate. In contrast to estimates obtained with horizontal techniques, vertical estimates represent snapshots of the population.

Traditionally, estimates of zooplankton mortality have been sought in order to gain knowledge about marine productivity and to quantify transfers between components of the foodweb. Recently, mortality (or rather mortality risk) has also drawn attention as an important process that influences behavior (Ohman and Wood 1995; Aksnes 1996). Neither food availability (as expressed in optimal foraging theory) nor transport processes can alone or together account for distribution and migration patterns in plankton. For example, mortality risk is a major factor that governs habitat choice and vertical migration behavior in zooplankton (Aksnes and Giske 1990; Ohman 1990; Loose and Dawidowicz 1994). In the rapidly developing literature on models of habitat profitability, habitat choice, and optimal behavior (Gilliam 1982; Houston et al. 1993; Tyler and Rose 1994), mortality risk represents a major explanatory variable. Along with models of mortality and mortality risk of the pelagic habitat (Aksnes and Giske 1993; Giske et al. 1994; Petersen and Gadomski 1994), there is an increasing need for empirical estimates of mortality.

Unfortunately, the pelagic environment presents challenges for mortality estimation. Wood (1994, p. 23) noted a fundamental problem in population dynamics studies: "There were two bears yesterday and there are three bears today. Does this mean that one has been born, or that 101 have been born and 100 have died?" For planktonic populations, a frequent answer to this question is that the two individuals observed yesterday have left and the three today have just arrived (due to advection). In this case, temporal changes in abundances are likely to contain little information about mortality unless the abundances are integrated over an area large enough to minimize the influence of advection. Despite transport processes, however, the distribution of developmental stages vs. absolute abundances at a given time may contain valuable information about mortality and recruitment processes. We call the use of such information the vertical life table approach, in contrast to the horizontal life table approach, which also uses information given by changes in abundance over time.

Given the implications of advection, Mullin and Brooks (1970) applied the vertical approach to calculate mortality coefficients from field samples of *Calanus pacificus*. The continuous breeding of *C. pacificus* facilitated the use of this approach. In a response to this work, Fager (1973) elaborated on the vertical approach and provided a method for calculating possible ranges of values of the estimated mortality coefficients. Many population dynamics techniques for stage-structured populations have subsequently been proposed (*see* Manly 1990 and Wood 1994). These techniques, however, focus on the horizontal approach. Here, we reconsider the vertical approach. We were motivated in part by the recognition in another study of the dependence of stage ratios on mortality rates (Ohman et al. 1996). We investigated the sensitivity of vertically derived mortality estimates to violations of the assumptions of the estimator as well as to sampling noise. In these sensitivity analyses, we used an individual-based simulation model (IBM, or i-configuration model according to the terminology suggested by Caswell and John 1992) to generate abundances. The main reason we chose this kind of simulation model is that stage duration and mortality risk are characteristics likely to vary in nature.

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Notation

t	Time (d)
i	Developmental stage index
q	The adult stage (or the adult combined with one or more preceding stages), having infinite duration
$q - 1$	A juvenile stage recruiting to the adult stage
Parametric values	
α_i	True duration of stage i (d)
β_i	Measure of trend in recruitment to stage i (d^{-1})
$\rho(t)$	True recruitment rate to a stage at day t (ind. d^{-1})
ρ_i	True recruitment rate to stage i (ind. d^{-1})
θ_i	True mortality rate of stage i (d^{-1})
θ	True mortality rate of the combined stage $i/(i + 1)$ (d^{-1})
ν_i	True number of individuals in stage i (ind.)
Estimates	
a_i	Estimate of α_i (d)
m	Estimate of θ (d^{-1})
n_i	Estimate of ν_i (ind.)
r_i	$= n_i/n_{i+1}$
Individual-based simulation model	
R	Uniform random number in the interval 0 . . . 1
$\alpha_{i,x}$	Juvenile stage duration of individual i recruited at day x (d)
$\rho(x)$	Juvenile recruitment at day x (ind.)
θ_r	Mortality risk [$\exp(-\theta)$ is daily survival probability] (d^{-1})
σ	Standard deviations of the distribution of α, ρ, or θ
S, J, A	Variables indicating individual survival having value 0 or 1 (*see text*)
$\nu_j(t)$	Number of individuals in the juvenile stage at day t (ind.)
$\nu_a(t)$	Number of individuals in the adult stage at day t (ind.)

Such parameterization is more straightforward in an i-configuration model than in traditional population models (*see* DeAngelis and Gross 1992), and this facilitated analyses on the sensitivity of the estimation technique to violations of assumptions about individual constancy. Finally, we compared results from the vertical approach to results obtained independently with a horizontal approach.

Methods

Equations for analysis of stage structure—We initially assumed that the true (i.e. parametric) daily recruitment rate (ρ_i) to a stage i is constant over a period that corresponds to the true duration of the stage (α_i), that the duration of this stage is the same for all individuals, and that the mortality for the period α_i can be expressed by a single constant rate (θ_i). Then, the true number of individuals (ν_i) in stage i on day x may be expressed as (a list of notation is provided)

$$\nu_i = \rho_i \int_{x-\alpha_i}^{x} \exp[-\theta_i(x - t)]\, dt = \rho_i[1 - \exp(-\theta_i\alpha_i)]/\theta_i. \quad (1)$$

The definite integral represents the survivors from those recruited during the last α_i days. In the case of the adult stage (q), however, the stage duration can be considered infinite:

$$\nu_q = \rho_q \int_{-\infty}^{x} \exp[-\theta_q(x - t)]\, dt = \rho_q/\theta_q. \quad (2)$$

For two successive stages, the recruitment rate to the second stage ($i + 1$) is the product of the recruitment and the stage-specific survival of the first stage:

$$\rho_{i+1} = \rho_i \exp(-\theta_i\alpha_i). \quad (3)$$

Note that a particular stage i does not need to be synonymous with a morphological stage, such as a specific nauplius or copepodid stage, but that morphological stages may be combined in different ways. In making such combinations, one should be aware that a combination that includes the adult stage makes the stage infinite in duration (i.e. Eq. 3) and that recruitment to a combined stage equals recruitment to the youngest individual stage of the combined stage (i.e. recruitment to the combined copepodid stage 2+3+4 equals the recruitment to stage 2).

Estimation of mortality—We assume that the mortality rate of stage i and $i + 1$ (θ) can be considered equal for a period corresponding to the duration of two consecutive stages ($\alpha_i + \alpha_{i+1}$). Then, the number in stage $i + 1$ at day x can be expressed as

$$\nu_{i+1} = \rho_{i+1} \int_{x-\alpha_{i+1}}^{x} \exp[-\theta(x - t)]\, dt = \rho_{i+1}[1 - \exp(-\theta\alpha_{i+1})]/\theta. \quad (4)$$

By combining Eq. 1, 3, and 4 (and by setting $\theta_i = \theta$), the ratio of the numbers of individuals in two consecutive stages is expressed as a function of the mortality and the stage durations:

$$\nu_i/\nu_{i+1} = [\exp(\theta\alpha_i) - 1]/[1 - \exp(-\theta\alpha_{i+1})]. \quad (5)$$

In the case of the adult and the preceding stage, this reduces to

$$\nu_{q-1}/\nu_q = \exp(\theta\alpha_{q-1}) - 1. \quad (6)$$

Data requirements for mortality estimation—As is commonly assumed in analyses of zooplankton dynamics, stage durations should be known independently (a_i denotes an estimate of α_i). Furthermore, to apply Eq. 5 and 6 in mortality estimation, we need estimates of the ratio of the numbers of individuals in two consecutive stages ($r_i = n_i/n_{i+1}$). The abundance estimates (n_i) do not need to represent the true absolute abundance of a population (which is a requirement of horizontal methods). We assume, however, that two successive stages are sampled in an unbiased manner and are equally influenced

Table 1. The survival variable, $S_{i,x}(t)$ of the individual-based simulation model. Individual death or survival is invoked by $R_{i,x}(t)$, which is a random number with a uniform distribution between 0 and 1.

$S_{i,x}(t) = 1$ ind. i recruited at day x is alive at day t	if $(t = x)$ today is the birthday	or $[t > x$ the ind. was born	and $S_{i,x}(t-1) = 1$ the ind. was alive yesterday	and $R_{i,x}(t) \leq \exp(-\theta_r)]$ the ind. survived from yesterday until today
$S_{i,x}(t) = 0$ ind. i recruited at day x is not alive at day t	if $(t < x)$ the ind. has not been born	or $[S_{i,x}(t-1) = 0)$ the ind. has already died	or $R_{i,x}(t) > \exp(-\theta_r)]$ the ind. did not survive from yesterday until today	

by transport processes over the period corresponding to the duration of two stages.

With use of Eq. 5 and 6, a mortality estimate (m) is obtained:

$$[\exp(ma_i) - 1]/[1 - \exp(-ma_{i+1})] = r_i \quad \text{(two juvenile stages)} \tag{7a}$$

$$m = \ln(r_{q-1} + 1)/a_{q-1} \quad \text{(juvenile and adult stage).} \tag{7b}$$

Equation 7a corresponds to equation 3 of Mullin and Brooks (1970) and is solved iteratively. As demonstrated later, the final mortality estimate should be an average of several m estimates obtained by replicated sampling of the water body under study.

Individual-based simulation model—We formulated an i-configuration model that describes the abundances of juveniles and adults given the daily recruitment rate, the individual mortality risk, and the individual juvenile stage duration. A total of $\rho(x)$ juveniles recruit at day x (the time step of the model is 1 d). The survival of each individual is represented by $S_{i,x}(t)$, where a value of 1 means that the individual number i recruited at day x is alive at day t, and a value of 0 means that the individual is dead or unborn (Table 1). The duration of the juvenile stage is stored in $\alpha_{i,x}$, which gives the duration of individual number i recruited at day x. Hence, a live individual moves from the juvenile to adult stage when the age of the individual exceeds the individual stage duration.

The variables $J_{i,x}(t)$ and $A_{i,x}(t)$ denote whether a living individual is a juvenile or an adult:

$$J_{i,x}(t) = 1 \quad \text{if } [S_{i,x}(t) = 1 \text{ and } t - x \leq \alpha_{i,x}] \quad [\text{else } J_{i,x}(t) = 0] \tag{8}$$

$$A_{i,x}(t) = 1 \quad \text{if } [S_{i,x}(t) = 1 \text{ and } t - x > \alpha_{i,x}] \quad [\text{else } A_{i,x}(t) = 0]. \tag{9}$$

Hence, assuming that $\rho(x)$ juveniles are recruited at day x, the total number in the juvenile and adult stages at day t is calculated according to

$$\nu_j(t) = \sum_{x=1}^{t} \sum_{i=1}^{\rho(x)} J_{i,x}(t) \tag{10}$$

$$\nu_a(t) = \sum_{x=1}^{t} \sum_{i=1}^{\rho(x)} A_{i,x}(t). \tag{11}$$

Simulated mortality estimates were then obtained by application of Eq. 7b to the generated $\nu_j(t):\nu_a(t)$ ratios. To assess the errors arising from violations of the assumptions of this equation, we varied the daily number of recruits, the individual stage duration, the individual mortality risk, the daily mortality risk, and the mortality risk between stages according to a random normal frequency distribution. An increasing standard deviation was used to express increasing violations of the assumption of constancy. The accuracy and precision of a mortality estimate were assessed from the mean and standard deviation of 300 solutions to Eq. 7b (Fig. 1). Ideally, each of these 300 estimates would have been obtained from independent time series generated by the simulation model. Comparisons, however, indicated that the variance calculated on the basis of mortality estimates obtained within a time series corresponded to the variance obtained from independent time series. Note that the simulation analysis does not assess errors that arise from variability in mortality, stage duration, on recruitment correlated with time, but only errors that originate from random variability uncorrelated with time.

The following sources of error influence the mortality estimate obtained by the vertical approach: errors in the measured stage durations and in the observed stage composition, the number of individuals analyzed (i.e. counted), and violation of the assumptions underlying the estimators (i.e. recruitment to stage i varies over the period $x - \alpha_i - \alpha_{i+1} \ldots x$; individuals have different stage durations during this period; the mortality risk varies between individuals and(or) over time during the above period).

Application to a natural population—For application of the vertical method to a natural population, we used census information for the copepod *Pseudocalanus newmani* in Dabob Bay, a fjord environment in which the influence of advection is much reduced compared to oceans (Ohman 1986). We compared the results obtained with our vertical method with the results of the horizontal population surface method described by Ohman and Wood (1996). Water-column total abundances (mean No. ind. m^{-2}, copepodid stages 1–4 plus adults, based on replicated vertical hauls generally from 150 to 0 m with a 73-μm mesh net) over a 2-yr period were reported by Ohman (1985). We further restricted mortality estima-

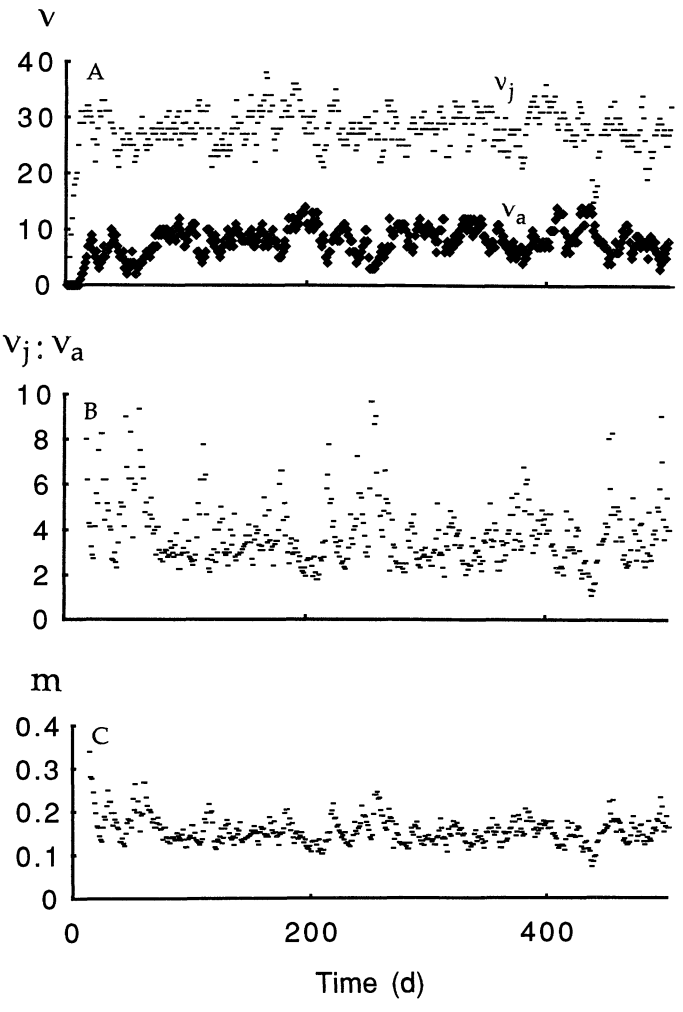

Fig. 1. A. Times series of juveniles (ν_j) and adults (ν_a) generated by the individual-based model given by Eq. 10 and 11. B. The ratio of $\nu_j : \nu_a$. C. Distribution of the mortality estimates obtained by Eq. 7b. Recruitment rate (ρ), juvenile stage duration (α), and true mortality risk (θ) were 5 ind. d^{-1}, 10 d, and 0.15 d^{-1}.

tion to the spring–summer interval, when recruitment rates and stage durations were well known and the probability of flushing events was much reduced.

Results

Because of the probabilistic nature of death represented in the individual-based model, we have an additional source of error in the mortality estimate that is not commonly assessed in studies of this kind. This error decreases with increased numbers of animals recruiting to the juvenile stage of the model. The recruitment rate is an indirect measure of the number analyzed (i.e. the individuals that are counted in the field sample). Hence, we term the error associated with the level of recruitment rate the inherent error associated with the number analyzed. This error should not be confused with sampling and subsampling errors, which also tend to decrease as more individuals are analyzed. As shown in Fig. 1A, a

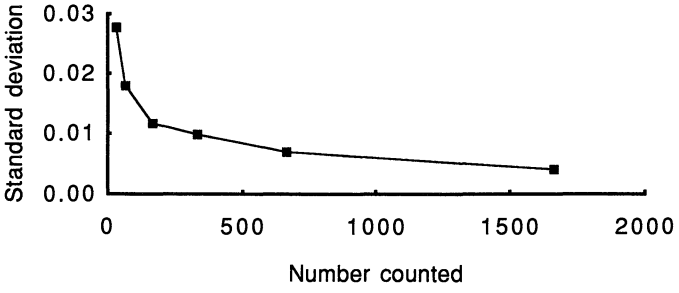

Fig. 2. Inherent error of the mortality estimate as a function of the number of individuals analyzed (*see text*). Results are from the individual-based simulation model (Eq. 10 and 11) and the mortality estimator (Eq. 7b). Stage duration (α = 10 d) and instantaneous mortality risk (θ_r = 0.15 d^{-1}) were kept constant. Points on the curve were obtained by using daily recruitment rates (ρ) of 5, 10, 25, 50, 100, and 250 ind.

recruitment rate of 5 ind. d^{-1} corresponds to numbers of individuals fluctuating around 26 and 7 in the juvenile and adult stage, respectively (when mortality and juvenile stage duration are 0.15 d^{-1} and 10 d). Hence, this gives an average number of 33 individuals in each simulated sample. In this case, the inherent error of the mortality estimate corresponds to a SD of 0.028. This SD drops to <0.01 when >300 animals are analyzed (Fig. 2). For our standard run, we assumed a recruitment rate of 25 ind. d^{-1}, a juvenile stage duration of 10 d, and a mortality risk of 0.15 d^{-1}. These parameters generated an average of 167 individuals in the juvenile and adult stage, and the inherent error corresponded to a SD of 0.0116.

Recruitment (ρ)—We now consider the case where recruitment fluctuates according to a random normal distribution with a mean of 25 ind. d^{-1} and SD (σ) increases from 0 to 12 ind. d^{-1} (Fig. 1A), which corresponds to a coefficient of variation (C.V.) of 0–0.5. The accuracy of the mortality estimate was not influenced by this variability in recruitment because no bias was observed in the mortality estimate. The precision, however, was slightly influenced as the SD increased from 0.0116 to 0.0200 from 0 to highest variability (σ = 12 ind.). Thus, the mortality estimate seems rather robust to recruitment fluctuations that can be considered random.

Stage duration (α)—The impact of individual variability in stage durations on mortality estimates is seldom analyzed since aggregated models do not commonly account for such variability (however, *see* Caswell 1989). Our simulations demonstrate that variability in stage duration causes underestimation of mortality. At the highest variability level (σ = 6 d), the bias corresponds to 25% of the true mortality (Fig. 1B). This bias develops as relatively more individuals experience a short stage duration while variability in duration increases. The shorter average duration occurs because mortality risk acts for shorter periods for those with short stage duration vs. those with a long duration. Consequently, a higher proportion of short-stage individuals will reach adult stage, which leads to underestimation of mortality. Surprisingly,

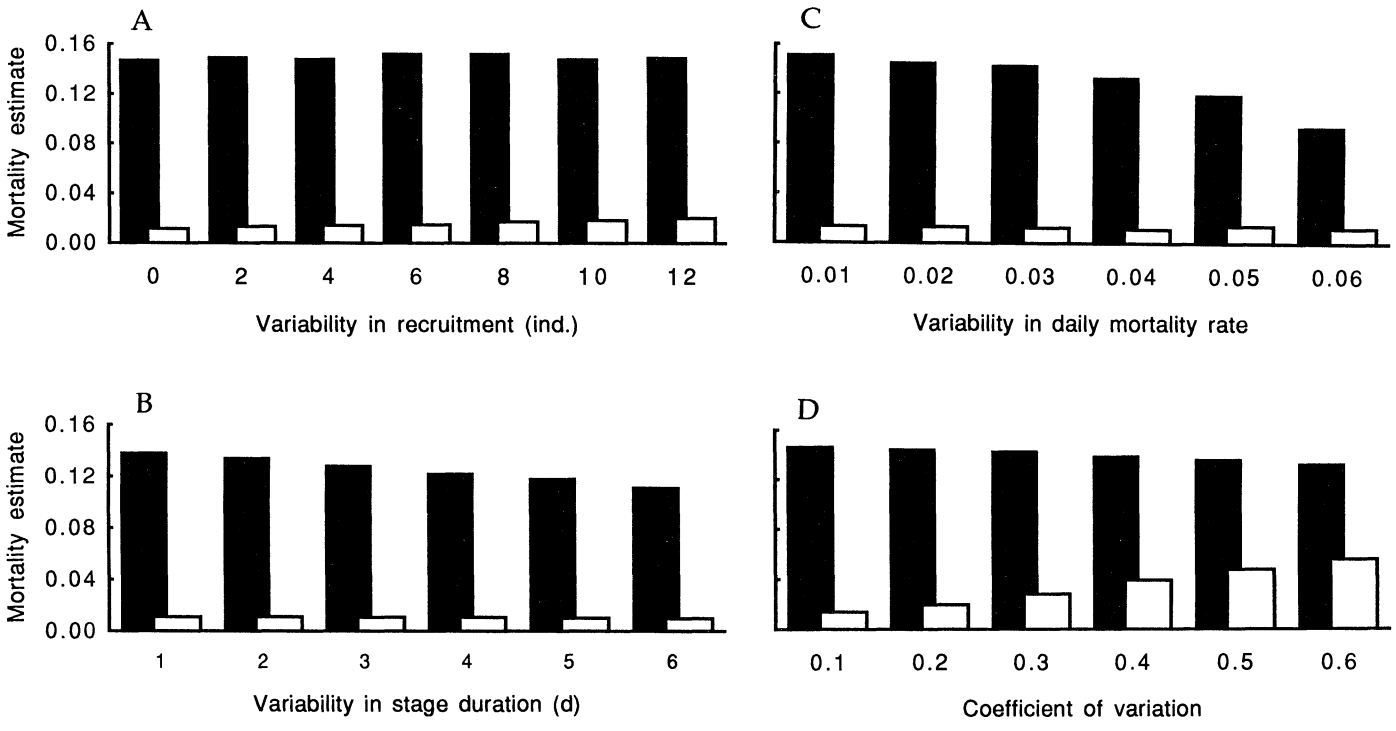

Fig. 3. Sensitivity of the mortality estimate (mean—■; standard deviation—□) to different levels of noise in recruitment (A), stage duration (B), daily mortality rate (C), and sampling (D). Results are from the individual-based simulation model (Eq. 10 and 11) and the mortality estimator (Eq. 7b). Parameter values in simulations included mean daily juvenile recruitment (ρ = 25 ind.), mean juvenile stage duration (α = 10 d), and mean instantaneous mortality risk (θ_r = 0.15 d^{-1}). No noise was applied in the first run (variability level 0 in A), and the SD in this run represents the inherent error due to the actual number analyzed (*see text*). Noise levels are given as the SD of the normal frequency distribution except for the noise level of r_i, which is given as the C.V.

however, precision of the mortality estimate is largely unaffected by variable stage duration (precision improves slightly with increased variability in stage duration).

Mortality risk (θ_r)—Random variability in the individual mortality risk did not affect either the accuracy or the precision of the mortality estimate (not plotted in Fig. 3). On the other hand, varying the day-to-day mortality risk (common to all individuals) led to inaccuracies. The effect was comparable to that of variable stage durations. Underestimation increased with increased levels of variability (Fig. 3C).

When the individual mortality risk differed between the juvenile and adult stage, the estimated mortality approximated the arithmetic average of the two parametric mortalities (Table 2). However, this is a biased estimate of the true average mortality of the two stages, which is equal to the weighted average (reflecting the abundance levels of the two stages) of the two stage-specific mortalities (*see Table 2*). Predators are size selective, and unequal mortality in adjoining life stages is likely in nature. Variable stage-specific mortality does represent a source of bias in the vertical approach, but the estimate will always be intermediate to the two stage-specific mortalities (i.e. when no other sources of variability is acting). As indicated in the analysis by Fager (1973), however, one should not derive stage-specific mortalities from estimates given for combined stages.

Stage composition (r_i)—As expected, the mortality estimate is sensitive to Gaussian noise in the juvenile : adult ratio (Fig. 3D). Increased noise level results in mortality underestimation and rapidly decreasing precision. The runs in which all sources of variability are included simultaneously (Table 3) indicate that the precision is most

Table 2. Estimates of mortality (m) when individual mortality risk (θ_r) is different for the juvenile and adult stages. Means and standard deviations of the mortality estimate distribution were based on 300 $\nu_j : \nu_a$ observations generated by the individual-based simulation model (Eq. 10 and 11). Daily recruitment (ρ) and juvenile stage duration (a) were 25 ind. d^{-1} and 10 d. The true mortality rate of the combined stage is equal to the weighted average $(\theta_j\nu_j + \theta_a\nu_a)/(\nu_j + \nu_a)$ [which is equal to $\rho/(\nu_j + \nu_a)$], where ν_j and ν_a represent the mean numbers of individuals in the two stages at steady state (i.e. mortality balances recruitment).

True mortality			Arith-metic avg	Estimates	
Juvenile (θ_j)	Adult (θ_a)	Combined stage		Mean	SD
0.15	0.15	0.150	0.15	0.148	0.0116
0.17	0.13	0.161	0.15	0.148	0.0122
0.19	0.11	0.171	0.15	0.146	0.0149
0.21	0.09	0.181	0.15	0.141	0.0122
0.13	0.17	0.139	0.15	0.151	0.0116
0.11	0.19	0.128	0.15	0.152	0.0106
0.09	0.21	0.117	0.15	0.149	0.0106

Table 3. Sensitivity of the mortality estimate (N = 300) to combined noice (σ) due to variability in recruitment (ρ), stage duration (α), mortality (θ), and sampling. Results are from the individual-based simulation model (Eq. 10 and 11) and the mortality estimator given by Eq. 7b. Parameter values used in the simulations included mean daily juvenile recruitment (ρ = 25 ind.), mean juvenile stage duration (α = 10 d), and mean instantaneous mortality risk (θ_r = 0.15 d^{-1}). Noise levels are given as the SD of the normal frequency distribution (σ) except for the noise level of r_i (the juvenile : adult ratio), which is given as the C.V. θ_r and θ_r' denote individual and daily mortality risk, respectively.

Level of random normal variability						
		σ-θ		C.V.	Estimates of mortality	
σ-ρ	σ-α	θ_r	θ_r'	of r_i	Mean	SD
2	1	0.01	0.01	0.1	0.139	0.0155
4	2	0.02	0.02	0.2	0.134	0.0209
6	3	0.03	0.03	0.3	0.121	0.0275
8	4	0.04	0.04	0.4	0.108	0.0360
10	5	0.05	0.05	0.5	0.092	0.0389
12	6	0.06	0.06	0.6	0.069	0.0364

affected by noise in r_i (i.e. the ratio between abundances of two consecutive stages). Although the precision is better in these combined runs than in the r noise runs (Fig. 3D), the bias is magnified.

Trends in recruitment—A temporal trend in recruitment to stage i over the period $\alpha_i + \alpha_{i+1}$ (for the juvenile/adult case a reasonable approximation for the duration of the adult stage is θ^{-1}), such as occurs with rapid passage of a cohort, is an important factor to consider in estimations. Rather than assessing the bias associated with trends in recruitment rate by simulation, we derived an analytical expression for this bias. This expression may be used for estimation purposes when trends in recruitment are known. We replace the constant recruitment rate ρ_i in Eq. 1 with the expression $\rho(t) = \rho(0)\exp(\beta t)$, where $\rho(0)$ is the recruitment rate at $t = 0$ and β is a measure of steepness of an exponential temporal trend in the recruitment rate. The number of the juvenile stage at time x is then given by

$$\nu_{q-1} = \rho(0) \int_{x-\alpha_{q-1}}^{x} \exp(\beta t)\exp[-\theta(x - t)]\, dt$$
$$= \rho(0)\exp(\beta x)\{1 - \exp[-\alpha_{q-1}(\beta + \theta)]\}/(\beta + \theta), \quad (12)$$

and the number of the adult stage at time x is given by the survivors of those recruited to the juvenile stage in the period before $x - \alpha_{q-1}$:

$$\nu_q = \exp(-\theta\alpha_{q-1})\rho(0) \cdot \int_{-\infty}^{x-\alpha_{q-1}} \exp(\beta t)\exp[-\theta(x - \alpha_{q-1} - t)]\, dt$$
$$= \rho(0)\exp(\beta x)\exp[-\alpha_{q-1}(\beta + \theta)]/(\beta + \theta). \quad (13)$$

Fortunately, combination of Eq. 12 and 13 reduces to

$$\nu_{q-1}/\nu_q = \exp[(\beta + \theta)\alpha_{q-1}] - 1. \quad (14)$$

This expression differs from Eq. 6 in that the trend in recruitment parameter adds to the mortality parameter. Hence, application of Eq. 7b leads to mortality overestimation when the trend is upward (positive β_{q-1}) and to underestimation with a downward trend (negative β_{q-1}). Equation 14 rather than Eq. 6 should be used to interpret estimates obtained with Eq. 7b when a persistent exponential trend in recruitment is known to occur. For the juvenile/juvenile case, the equation that includes trend in recruitment becomes slightly more complicated:

$$\nu_i/\nu_{i+1} = \exp(-\beta_i\alpha_i)\{\exp[(\beta_i + \theta)\alpha_i] - 1\} \div \{1 - \exp[-(\beta_i + \theta)\alpha_{i+1}]\}, \quad (15)$$

where β_i is a measure of the trend in recruitment to stage i. This equation corresponds to Eq. 5.

Application—Although the vertical approach is meant to apply when several samples are obtained at one time, it may also be applied for data obtained over time. Application of Eq. 7a and b on all 25 time points for the population of *P. newmani* in Dabob Bay provided the instantaneous mortality estimates 0.17, 0.02, 0.02, 0.10 and 0.04 d^{-1} for the stage pairs C1/C2, C2/C3, C3/C4, C4/C5, and C5/adult females (Table 4). In Table 4, we also provide stage-specific estimates obtained by Ohman and Wood (1996) with use of the horizontal technique of Wood (1994). Although the two sets of estimates cannot be compared directly (due to the stage combinations of the vertical approach), they indicate similar trends in the mortality pattern. Confidence intervals of the Ohman and Wood (1996) estimates, however, are generally smaller. In Fig. 4, we made the two sets of estimates more comparable by converting the Ohman and Wood estimates into combined-stage mortalities (Fig. 4). The two sets of estimates gave a significant ($P < 0.05$) Spearman's rank correlation coefficient of 0.71. The vertical approach gave one negative (−0.01) estimate for the stage C2/C3 (Fig. 4). Negative estimates are likely to occur with the vertical method when mortality is low and the variability in the stage composition from one sample to another is high. A possible way to avoid negative mortality estimates is to define individual negative point estimates equal to 0 before averaging. When we did this, the C2/C3 mortality estimate for the first year increased from −0.01 to 0.06 d^{-1}, which agrees with the horizontal method. Although this procedure may seem reasonable, we do not recommend it because systematic exclusion of negative point estimates leads to bias in the final mortality estimate. Negative mortality estimates, however, indicate violations of assumptions of the model (when precision of the estimate is high) or may simply express high sampling variability (when precision is low). In general, caution should be exercised in interpreting mortality estimates when either high variances or negative means are computed.

To analyze the role of likely variance sources, we initialized the individual-based model with stage-specific mortality estimates provided by Ohman and Wood (1996)

Table 4. Estimates of average daily instantaneous mortality for *Pseudocalanus newmani*. Combined stages use the vertical approach (Eq. 7b, $n = 25$). Estimates for individual stages and years are those of Ohman and Wood (1996); 95% confidence intervals are indicated.

	Copepodid stages					
	1/2	2/3	3/4	4/5	5/6–female	
Both years		0.17±0.06	0.02±0.06	0.02±0.10	0.10±0.06	0.04±0.02
	1	2	3	4	5	6–female
1st yr	0.12±0.03	0.06±0.02	0.06±0.02	0.08±0.02	0.13±0.07	0.05±0.01
2nd yr	0.17±0.08	0.08±0.06	0.04±0.05	0.04±0.04	0.08±0.08	0.04±0.02

and observed sources of variability for C5 and adult females (Table 5). We arrived at a simulated mortality estimate of 0.054 d^{-1} with a SD of 0.022 d^{-1}, while the corresponding vertical estimates obtained from the real data were 0.044 and 0.033 d^{-1}. The simulation indicated that the variance of the stage C5/adult female mortality estimate was dominated by the high recruitment variability (~85% of the variance was due to this source). The rather low noise level in the stage C5/adult female ratio (C.V. = 0.18) contributed to only 10% of the variance, while the remaining 5% was due to the inherent error of the number analyzed (on average, >100 ind. of the two stages were counted). The simulated combined mortality estimate (0.054) was skewed toward the true adult mortality (0.05). The true combined mortality (0.060), however, was also skewed toward the adult mortality, and the bias of the vertical method was not serious in this case.

Discussion

Various techniques have been suggested to extract demographic estimates from stage-structured populations of crustacean zooplankton and insects (*see* Manly 1990; Caswell 1989; Wood 1994). Wood (1994) found that an estimation technique based on the McKendrick–von Foerster equation gave more accurate estimates than three alternative methods, which included cohort analysis (e.g. Comita 1972; Rigler and Cooley 1974; Hairston and Twombly 1985; Aksnes and Høisæter 1987), the projection matrix method (Caswell and Twombly 1989; Twombly 1994), and the systems identification method (Parslow et al. 1979 and similar approaches applied in Matthews et al. 1978; Aksnes and Magnesen 1983). Although results from such comparisons should be interpreted with care because methods are sensitive to violation of different assumptions, the population surface method of Wood (1994) is promising. This method requires accurate estimates of stage abundances for a series of times as well as estimates of the durations of those stages. We have also assumed that the stage durations are known from independent measurements. Bias associated with measurement errors may be assessed from Eq. 5–7. In the case of a juvenile and adult stage, the bias in the mortality estimate is proportional to the factor a_{q-1}/α_{q-1}. This bias should be considered an important source of error common to all methods relying on "known" stage durations (Miller and Tande 1993).

Although robustness of Wood's (1994) method to moderate Gaussian noise in the abundance estimates has been demonstrated, the performance of horizontal methods decreases rapidly as the time series become biased by advection or other sources of horizontal patchiness. In their analyses of plankton catch variability, Winsor and Clarke (1940) found a tendency for the numbers of different plankton groups in any haul to be high or low together. Because stage composition is generally considered less variable than absolute abundance, field investigators frequently represent stage frequency data as time series of percentage stage composition rather than abundances. Recent evidence for spatial constancy in stage distribution is given by Solow and Steele (1995), who observed that, in contrast to biomass, stage structure of *Calanus finmarchicus* in the North Sea was essentially independent of location.

Covariation among stage abundances likely results from common advective influence. Abundance estimates of individual stages are not obtained independently; instead, they originate from the same sample and sampling procedure, and this also likely promotes covariation (e.g. due to common influence of gear performance, clogging, subsampling). Covariation among the estimates of ν_i and ν_{i+1} will decrease variance of the r_i estimate and thereby variance of the mortality estimate obtained with the vertical

Table 5. Expected distribution of the combined mortality estimates for *Pseudocalanus newmani* C5 and adult females. The individual-based model was initialized according to knowledge about the number of individuals counted, the observed variability in abundances of C4 (which was used as an indication of the variability in recruitment to C5), mortalities for C5 and C6 as estimated by Ohman and Wood (1996), and the observed C.V. of r_5 noise level.

Parameter	Mean	SD
Recruitment	8 ind. d^{-1}	16 ind. d^{-1}
Stage duration C5	4 d	
Mortality risk C5	0.10 d^{-1}	
Mortality risk adult female	0.05 d^{-1}	
True combined mortality	0.06 d^{-1}	
Noise level, r_5 estimates	0.18	
Mortality estimate distribution	0.054 d^{-1}	0.022 ind. d^{-1}

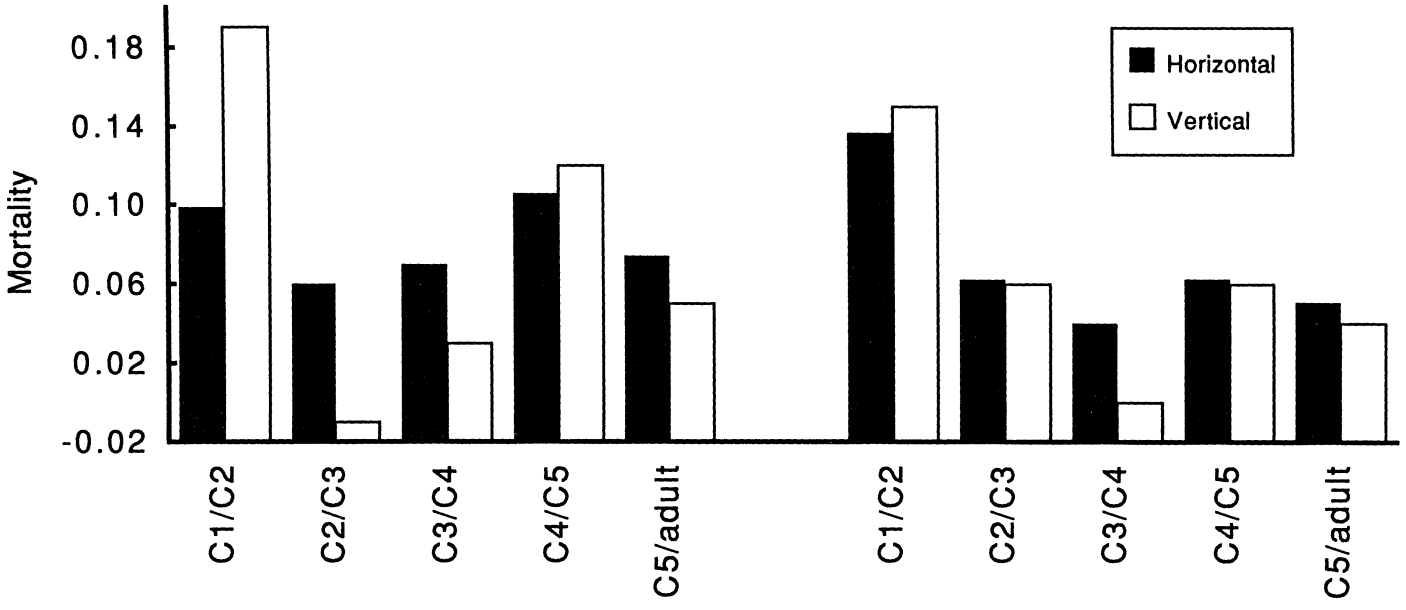

Fig. 4. Comparisons of the mortality estimates (d^{-1}) for *Pseudocalanus newmani* obtained by the vertical (Eq. 7) and horizontal (Ohman and Wood 1996) approaches. Estimates for the first and second year are given by the left and right part of the figure, respectively. Estimates from the horizontal approach were originally given for individual stages (*see Table 4*). Estimates for combined stages were obtained from weighted averages (according to the abundance levels of the two stages) of the stage-specific estimates.

approach. For the horizontal techniques, it is necessary that the absolute abundances are unbiased estimates of population density, governed only by recruitment and mortality. For such conditions, covariation among stage abundances is likely to magnify errors. With the vertical approach, different samples do not need to represent a constant fraction of the spatial volume occupied by a homogeneous population. As pointed out by Miller and Tande (1993), however, the requirement of constant (or known) sampling efficiency of the different stages should be emphasized. If this requirement is not met, bias will occur in any method.

Our results indicate that moderate random Gaussian variability in the true recruitment, stage duration, and mortality risk is not critical for mortality estimation by the vertical method. The main drawback of the vertical approach is sensitivity to trends in recruitment, which makes this approach most applicable to populations with continuous breeding characterized by overlapping generations. Equations 14 and 15, however, are valuable for analysis of situations with a known positive or negative trend in recruitment. Note that although horizontal methods allow for changes in recruitment and mortality, the recruitment and mortality functions between the sampling points are also constrained in these methods, and the impact of such constraints increases with increasing sampling intervals.

The vertical approach should ideally be applied to data obtained at one time rather than to data collected over an extended period. Additional sources of variability are likely to influence time series data, and this is probably reflected by the relatively large confidence intervals from the vertical approach when it was applied to the *P. newmani* data (Table 4). In the oceanic single-time situation, we think that the influence of the different variance components is likely to shift so that the component due to r noise will become more important than recruitment variability. Both variance components, however, are efficiently dealt with by taking several replicate samples. A C.V. of 60% in the r estimates generated a SD of 0.0556 (Fig. 3D). Hence, if this noise is the dominant source of variability, 10 replicate samples will provide an expected 95% confidence interval of $\sim \pm 0.04$ d^{-1} when true juvenile stage duration is 10 d and the mortality is 0.15 d^{-1}.

Equations 1–7 and 12–15 are complementary to the more sophisticated horizontal techniques. When reliable time series are available, the information given by fluctuating abundances clearly should be used with the stage composition information. When abundance estimates are unreliable, however, it may be best to consider only the stage composition. The essence of the vertical approach is that mortality gives rise to fewer older individuals (i.e. of later developmental stages). On the basis of the simulations and the *P. newmani* application, the approach is potentially useful, with some precautions, for the analysis of a wide range of plankton data. The vertical approach should be considered when time series methods are likely to be unreliable (i.e. transport processes influence total abundances), when different development stages are equally influenced by advection, when there is no strong cohort structure over time (i.e. continuous reproduction), and when several r_t estimates are available so that a measure of precision is obtained. Finally, simulation by the simple individual-based model, as given by Eq. 8–11 and Table 1, may provide efficient guidance to sampling designs.

References

AKSNES, D. L. 1996. Natural mortality, fecundity and development time in marine planktonic copepods—Implications of behaviour. Mar. Ecol. Prog. Ser. **131:** 315–316.

———, AND J. GISKE. 1990. Habitat profitability in pelagic environments. Mar. Ecol. Prog. Ser. **64:** 209–215.

———, AND ———. 1993. A theoretical model of visual aquatic predation. Ecol. Model. **67:** 233–250.

———, AND T. HØISÆTER. 1987. Obtaining life table data from stage-frequency distributional statistics. Limnol. Oceanogr. **32:** 514–517.

———, AND T. MAGNESEN. 1983. Distribution, development, and production of *Calanus finmarchicus* in Lindåspollene, western Norway, 1979. Sarsia **68:** 195–208.

———, AND A. M. JOHN. 1992. From the individual to the population in demographic models, p. 36–61. *In* D. L. DeAngelis and L. J. Gross [eds.], Individual-based models and approaches in ecology: Populations, communities and ecosystems. Chapman & Hall.

———, AND S. TWOMBLY. 1989. Estimation of stage-specific demographic parameters for zooplankton populations: Methods based on stage-classified matrix projection models. Lecture Notes Stat. **55:** 93–107.

COMITA, G. W. 1972. The seasonal zooplankton cycles, production and transformations of energy in Severson Lake, Minnesota. Arch. Hydrobiol. **70:** 14–66.

DEANGELIS, D. L., AND L. J. GROSS. 1992. Individual-based models and approaches in ecology: Populations, communities and ecosystems. Chapman & Hall.

FAGER, E. W. 1973. Estimation of mortality coefficients from field samples of zooplankton. Limnol. Oceanogr. **18:** 297–301.

GILLIAM, J. F. 1982. Habitat use and competitive bottlenecks in size-structured populations. Ph.D. thesis, Michigan State Univ. 107 p.

GISKE, J., D. L. AKSNES, AND Ø. FIKSEN. 1994. Visual predators, environmental variables and zooplankton mortality risk. Vie Milieu **44:** 1–9.

HAIRSTON, N. G., AND S. TWOMBLY. 1985. Obtaining life table data from cohort analysis: A critique of current methods. Limnol. Oceanogr. **30:** 886–893.

HOUSTON, A. I., J. M. MCNAMARA, AND J. M. HUTCHINSON. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Phil. Trans. R. Soc. Lond. Ser. B **341:** 375–397.

LOOSE, C. L., AND P. DAWIDOWICZ. 1994. Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. Ecology **75:** 2255–2263.

MANLY, B. F. J. 1990. Stage-structured populations: Sampling, analysis and simulation. Chapman and Hall.

MATTHEWS, J. B. L., L. HESTAD, AND J. L. W. BAKKE. 1978. Ecological studies in Korsfjorden, Western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* 1971–1974. Oceanol. Acta **1:** 274–284.

MILLER, C. B., AND K. S. TANDE. 1993. Stage duration estimation for *Calanus* populations, a modelling study. Mar. Ecol. Prog. Ser. **102:** 15–34.

MULLIN, M. M., AND E. R. BROOKS. 1970. Production of the planktonic copepod *Calanus helgolandicus*. Bull. Scripps Inst. Oceanogr. **17:** 89–103.

OHMAN, M. D. 1985. Resource-satiated population growth of the copepod *Pseudocalanus* sp. Ergeb. Limnol. **21:** 15–32.

———. 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. J. Plankton Res. **8:** 673–713.

———. 1990. The demographic benefits of diel vertical migration by zooplankton. Ecol. Monogr. **60:** 257–281.

———, D. L. AKSNES, AND J. A. RUNGE. 1996. The interrelation of copepod fecundity and mortality. **41:** 1470–1477.

———, AND S. N. WOOD. 1995. The inevitability of mortality. ICES J. Mar. Sci. **52:** 517–522.

———, AND ———. 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. Limnol. Oceanogr. **41:** 126–135.

PARSLOW, J., N. C. SONNTAG, AND J. B. L. MATTHEWS. 1979. Technique of systems identification applied to estimating copepod population parameters. J. Plankton Res. **1:** 137–151.

PETERSEN, J. H., AND D. M. GADOMSKI. 1994. Light-mediated predation by northern squawfish on juvenile chinook salmon. J. Fish. Biol. **45:** 227–242.

RIGLER, F. H., AND J. M. COOLEY. 1974. The use of field data to derive population statistics of multivoltine copepods. Limnol. Oceanogr. **19:** 636–655.

SOLOW, A. R. AND J. H. STEELE. 1995. Scales of plankton patchiness: Biomass versus demography. J. Plankton Res. **17:** 1669–1677.

TYLER, J. A., AND K. A. ROSE. 1994. Individual variability and spatial heterogenity in fish population models. Rev. Fish Biol. Fish. **4:** 91–123.

TWOMBLY, S. 1994. Comparative demography and population dynamics of two coexisting copepods in a Venezuelan floodpain lake. Limnol. Oceanogr. **39:** 234–247.

WINSOR, C. P., AND G. L. CLARKE. 1940. A statistical study of variation in the catch of plankton nets. J. Mar. Res. **3:** 1–34.

WOOD, S. N. 1994. Obtaining birth and mortality patterns from structured population trajectories. Ecol. Monogr. **64:** 23–44.

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