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The interrelationship of copepod fecundity and mortality

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Abstract

The fecundity of copepod species that carry attached eggs is commonly assessed by the egg ratio (eggs female^{-1}), whereas the fecundity of broadcast-spawning copepods is assessed by measures of daily per capita rates of egg production. Variability in these measures, when corrected for temperature and allometric relationships with body size of adult females, is often assumed to reflect variability in food supply in nature and to thus provide an index of food limitation of population growth and of secondary production. We show that the measured fecundity of both brooding and broadcast-spawning copepods is affected by the mortality rate of adult females. We recognize three reproductive stages of adult female copepods: prereproductive, reproductive, and postreproductive. Mortality affects realized fecundity by shifting the relative abundance levels in these stages. Changes in mortality rates can generate substantial temporal variations in measured fecundity, even for copepods that are unlimited by ambient food supply and reproduce at physiological maximum rates. To correct for the effects of mortality on realized fecundity, precise experimental determination of the reproductive schedule of adult females is needed, along with measures of mortality rates in nature.

Variability in the egg production rate (EPR) of planktonic copepods is an important demographic parameter in any quantitative description of population growth. EPRs are relatively easily measured in the field by incubating adult females in natural particle suspensions. Such measurements provide a useful instantaneous rate term derived from natural populations. Because the EPR can be proportional to rates of juvenile somatic growth, at least for broadcast-spawning copepods (Sabatini and Kiørboe 1994; McLaren and Leonard 1995), copepod EPRs have also been used as measures of secondary production (e.g. Mullin 1993; Kiørboe and Nielsen 1994). EPRs have been used as an index of food limitation for natural populations (e.g. Checkley 1980; Runge 1985*a*; Peterson and Kimmerer 1994) because such rates typically vary in proportion to prey concentrations until satiating food conditions are reached. In such applications, especially when EPR is used as a measure of food limitation, it is generally assumed that the dominant factor affecting EPR variability is variability in food supply.

In an earlier analysis we noted the potential influence of adult female mortality rates on estimates of fecundity (Ohman and Wood 1995). We herein explore the interrelationship between fecundity and mortality for two types of copepod life histories. One type is the egg-carrying life history, as typified by *Pseudocalanus*. The observation has been made that small, egg-brooding copepods show less variability in EPRs in nature than do broadcast-spawning species (Ohman 1985*b*; Sabatini and Kiørboe 1994). The extent to which the observed variability is attributable to mortality rates rather than to resource limitation effects is of considerable interest. The second life history considered is that of broadcast-spawning copepods, represented here by members of *Calanus*. For the Calanidae in particular, temporal and spatial variabilities in EPRs seem to be extensive, which is usually interpreted as evidence for food limitation on reproductive rates (Peterson 1988; Mullin 1993; Plourde and Runge 1993). In contrast to Huntley and Lopez's (1992) suggestion that copepod somatic growth does not appear to be limited by food supply, there is ample evidence that reproductive rates of broadcast-spawning copepods in nature are below temperature-dependent maximum rates and vary as a function of food concentration.

We illustrate the quantitative influence that variations in mortality of adult female copepods can have on measurements of fecundity for both brooders and broadcast spawners and explore the sensitivity of these influences to the reproductive schedule of adult females. We show how variations in mortality rates can confound simple interpretations of variations in egg production rates in nature. We also note aspects of the reproductive biology of copepods that need further research to improve estimates of the influence of mortality on empirical measures of fecundity.

Methods

The life history of an adult female, egg-carrying copepod ranges from the instant she molts from copepodid stage 5 (t_0) until her life ends. We represent this history in three stages, as first proposed by Corkett and McLaren (1978) based on their experimental work with *Pseudocalanus* (Corkett and McLaren 1969). In a population that

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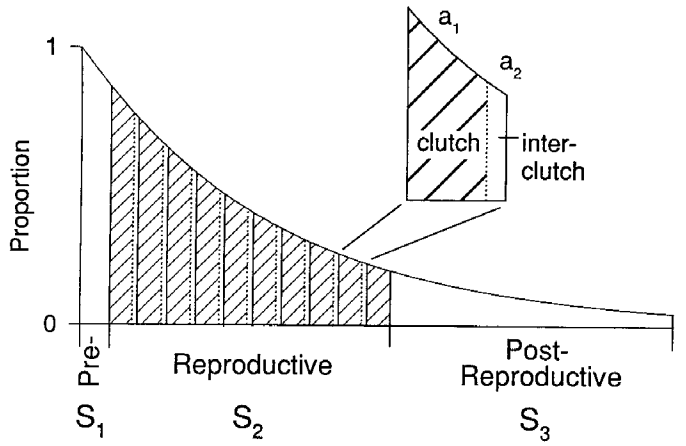

Fig. 1. Stage structure of adult females of a brooding (egg-carrying) copepod species. During shaded intervals, females bear attached eggs; during open intervals, they do not. a_1 indicates the embryonic duration and a_2 the interval between clutches.

Notation

a_1	Duration of a single clutch (embryonic duration), d
a_2	Duration of the interclutch period, d
CS	Clutch size (number of eggs laid per reproductive female in one spawning event), N
EHR	Daily per capita egg hatching rate (egg brooders; for total female population), egg ♀$^{-1}$ d^{-1}
EPR	Daily per capita egg production rate (broadcast spawners; for total female population), eggs ♀$^{-1}$ d^{-1}
k_1	S_1/a_1
k_2	a_1/a_1
k_3	a_2/a_1
m	Instantaneous mortality rate, d^{-1}
q	Total number of clutches
R	Recruitment rate to adult female stage, N d^{-1}
S_1	Prereproductive stage, d
S_2	Reproductive stage, d
S_3	Postreproductive stage, d
S	$S_1 + S_2 + S_3$, d

is food-satiated, females do not produce a clutch immediately at t_0; instead, there is a brief period before males locate females, copulation and spermatophore placement have been accomplished, and oogenesis is complete. We designate this prereproductive period as the first stage, S_1 (*see Fig. 1* and list of notations). Next, we designate the protracted interval when the female is competent to release viable eggs as the reproductive period, S_2. During the reproductive period, iteroparous females produce several clutches. The duration of a single clutch is the embryonic development time (a_1; Fig. 1), which is a well-defined function of temperature (McLaren et al. 1989). For egg-carrying copepods there is usually a brief interclutch period (a_2) between hatching of one clutch and laying of the next. After the interval equal to $a_1 + a_2$, another clutch will be released until the maximum number of clutches (q) has been produced. S_2 is thus defined as $(q)a_1 + (q - 1)a_2$. In laboratory conditions, in the absence of predators, we designate a third stage, S_3, in which postreproductive females cannot synthesize viable eggs yet they remain otherwise physiologically viable (e.g. Corkett and McLaren 1978; Kiørboe and Sabatini 1994). We initially assumed that the duration of S_3 is equivalent to that of S_2, then later examined departures from this assumption.

The durations of S_1, S_2, and S_3 for members of egg-carrying *Pseudocalanus* under optimal food conditions are not known precisely and will vary among species. However, following Corkett and McLaren (1978) and Ohman (1985), we assumed that a female can produce 10 clutches, that the postreproductive period is equivalent in duration to the total reproductive period, that a_2 is one-fourth of a_1, and that S_1 is equal in duration to $a_1 + a_2$. This life history is illustrated in Fig. 1. The upper curved line in Fig. 1 illustrates a constant mortality rate (m). Later, when examining departures from this "standard" pattern, we express the durations of S_1, a_1, and a_2, which are in units of time (d), as a multiple of the embryonic duration (a_1). Hence, we define the scaled prereproductive period k_1 as S_1/a_1, the scaled embryonic duration k_2 as $a_1/a_1 = 1.00$, and the scaled interclutch duration k_3 as a_2/a_1.

The schematic life history of broadcast-spawning copepods differs in several respects. Broadcast spawners can produce successive clutches of eggs without first waiting for the previous clutch to hatch. Spawning seems to be a relatively brief event and is often nocturnally synchronized in some species of *Calanus* (e.g. Harding et al. 1951; Runge 1985*a*; Uye et al. 1990). Observations of spawning in natural populations (e.g. Runge 1987) suggest that at least some populations spawn once a day, in early morning. Initially, we considered the interval between spawnings (a_2) to be 24 hours for well-fed animals and to continue nightly until females have laid the maximum number of clutches (q). We also evaluated the effects of varying spawning intervals from 12 h to 4 d. The total duration of S_2 of broadcast-spawners is $q \times a_2$ in days.

When the recruitment rate (R, ind. d^{-1}) into the female stage and m are constant over time, we can express the total number of females (N_{tot}) at any time as

$$N_{tot} = R \int_0^S \exp(-mt)\, dt = \frac{R[1 - \exp(-mS)]}{m}. \quad (1)$$

S is the total lifespan of the females ($S_1 + S_2 + S_3$). We scale the recruitment rate so that $R = 1$. Equation 1 applies to both brooders and broadcast spawners. For the brooders, we can express the number carrying eggs (N_{a_1}) as

$$N_{a_1} = R \sum_{i=0}^{q-1} \int_0^{a_1} \exp\{-[S_1 + i(a_1 + a_2)]m\} \cdot \exp(-mt)\, dt = \frac{R[1 - \exp(-ma_1)]}{m} \cdot \sum_{i=0}^{q-1} \exp\{-(S_1 + i(a_1 + a_2)]m\}. \quad (2)$$

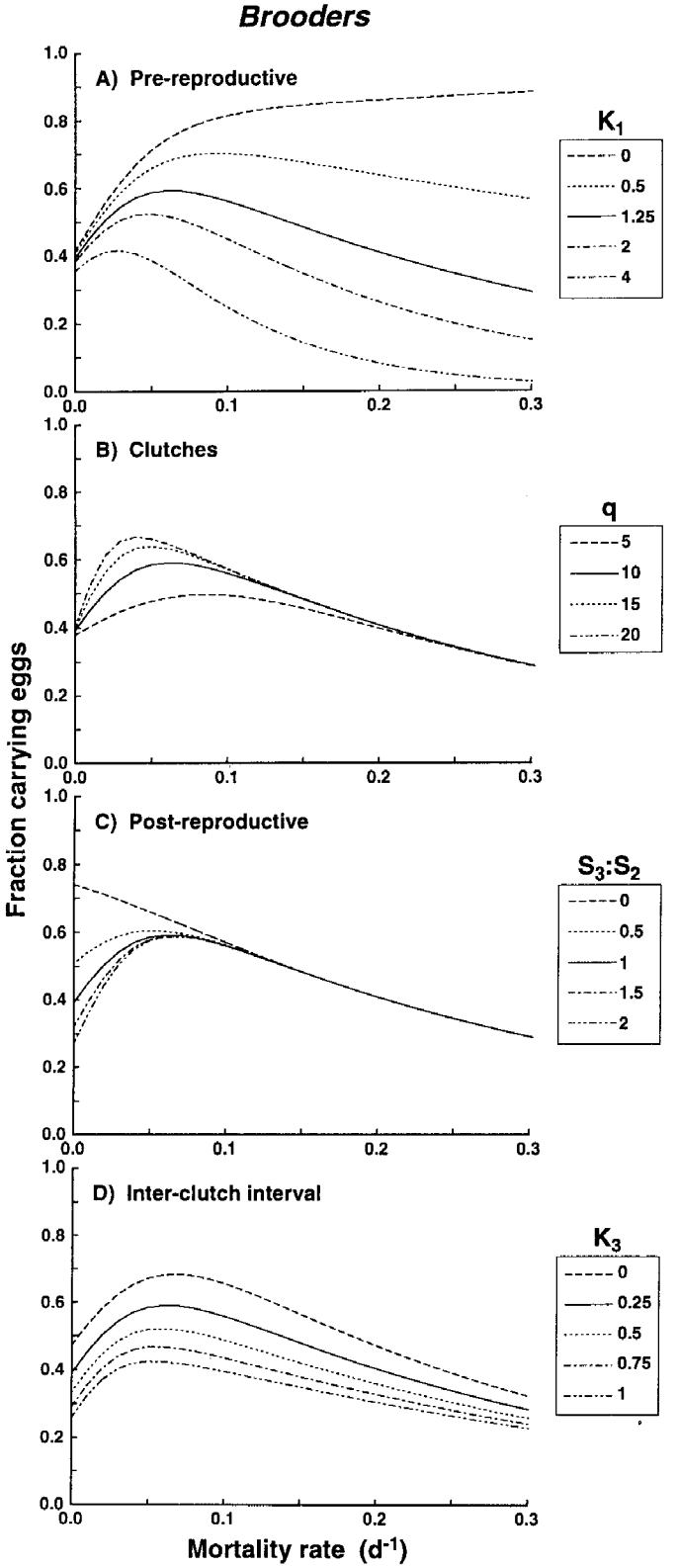

Fig. 2. Egg-brooding copepods. The sensitivity of the fraction of females carrying eggs to the mortality rate (abscissa) and to several reproductive characteristics is shown. A. Duration of the prereproductive period, measured as a fraction of the embryonic duration ($k_1 = S_1/a_1$). B. Number of clutches (q). C. Duration of the postreproductive period, measured as a fraction of the reproductive period (S_3/S_2). D. Duration of the interclutch interval, measured as a fraction of the embryonic duration ($k_3 = a_2/a_1$). Standard conditions are indicated by a solid line.

The first exponential term of the integrand in Eq. 2 expresses the survival rate up to the current clutch period. From Eq. 1 and 2, for the brooding life history, the fraction of females carrying eggs (N_{a1}/N_{tot}) can be expressed as a function of stage durations, number of clutches, and mortality.

In the case of the broadcast spawners, the number in the reproductive stage (N_{S_2}) is given by:

$$N_{S_2} = R \int_0^{S_2} \exp(-mS_1)\exp(-mt)\, dt$$

$$= R \exp(-mS_1)\left[\frac{1 - \exp(-mS_2)}{m}\right]. \quad (3)$$

From Eq. 1 and 3, the fraction of females in the reproductive stage is then given by N_{S_2}/N_{tot}, and the daily per capita EPR is found according to

$$\mathrm{EPR} = \left(\frac{N_{S_2}}{N_{tot}}\right)\left(\frac{\mathrm{CS}}{a_2}\right), \quad (4)$$

where the clutch size (CS) is the number of eggs laid per reproductive female in one spawning event.

We also illustrate the potential effects of mortality on a field population by drawing on the case of *Pseudocalanus newmani* in Dabob Bay, a temperate fjord. We correct for the dependence of CS on female body size from temporal variations in median prosome length (PL, in mm; N = 8,834 ind. measured, 200–300 from each sampling date; Ohman 1985) and the expected CS from

$$\mathrm{CS} = 18.219(\mathrm{PL})^{2.298}. \quad (5)$$

Egg hatching rates were then calculated from CS/ED, where ED is the temperature-dependent embryonic duration (in d) described by the Bêlehrádek function (McLaren et al. 1989)

$$\mathrm{ED} = 1{,}572(11.30 + T)^{-2.05}. \quad (6)$$

Instantaneous mortality rates of adult female *P. newmani* were calculated by the population surface method of Wood (1994) as explained by Ohman and Wood (1995). Mortality rates are the smoothed running means of mortality estimates on the same dates and the same 2-yr period during which body size variations were measured.

Results

Egg-carrying copepods—We initially discuss the egg-carrying life history of females with uniform body size that reproduce under optimal food conditions. The slope of the upper line in Fig. 1 indicates the mortality rate of females. Varying this mortality rate changes the propor-

tion of females in each of the reproductive stages by shifting the relative areas for S_1, S_2, and S_3. This is indicated by the "standard conditions" (Fig. 2A, solid line), where the prereproductive period is 1.25 times the embryonic duration ($k_1 = 1.25$), the interclutch period is one-fourth the embryonic duration ($k_3 = 0.25$), 10 clutches are produced ($q = 10$), and the postreproductive period is equal in duration to the reproductive period ($S_3 = S_2$). Under optimal conditions, with no mortality until the end of S_3, the expected fraction of females carrying eggs is 39% (Fig. 2A, solid line), not 100% as is sometimes assumed. Although Eq. 1 and 2 are undefined at $m = 0$, the expected fraction carrying eggs under no mortality until the end of S_3 can be obtained from $q(a_1)S^{-1}$.

As the mortality rate increases from 0 to 0.3 d^{-1} (which corresponds to a finite rate of 0–26% d^{-1}), the fraction of females carrying eggs increases to a maximum because of the shrinking contribution of postreproductive females (Fig. 2A). However, further increases in the mortality rate cause the proportion of egg-carrying females to decline as the contribution of prereproductive females increases. The shape of this relationship varies with the duration of the prereproductive period (variable k_1 in Fig. 2A). With very long prereproductive periods ($k_1 = 4$), the maximum fraction of females carrying eggs occurs at lower mortality and declines to <5% of females at high mortalities. If there is no prereproductive period ($k_1 = 0$), this fraction increases monotonically to ~85% of females. Note that the fraction of females carrying eggs is less sensitive to k_1 at low mortality rates (<0.05 d^{-1}) than at high mortality rates.

Varying q affects the fraction of females carrying eggs (Fig. 2B). This effect is most pronounced at low-to-intermediate mortality rates. Clutch size has virtually no effect at high mortality rates because females are likely to survive only to produce the first few clutches. Varying the postreproductive period from 0 to 2 times the reproductive period (Fig. 2C) again affects the fraction of females carrying eggs only at low mortality rates. Given low mortality rates and longer postreproductive periods, fewer females will be found carrying clutches. Notably, when there is no postreproductive period, the fraction of females carrying eggs declines in a simple monotonic manner with mortality rate (Fig. 2C, upper line). This monotonic decline also holds if postreproductive females are present and can be differentiated from other females.

Varying the interclutch duration from 0 to 1 times the embryonic duration decreases the expected fraction of females carrying eggs at all mortality rates (Fig. 2D).

Broadcast-spawning copepods—For the life history of broadcast-spawning copepods, we used units of days rather than durations scaled relative to the embryonic period because successive spawning events in broadcast spawners are not constrained by egg development time as they are with brooders. We first considered a species with a prereproductive interval of 8 days, followed by the release of clutches of 50 eggs on each of 60 successive nights, followed by an equal postreproductive interval. We based these standard conditions on approximations to *Calanus finmarchicus* in the Gulf of St. Lawrence and northwest Atlantic waters (based on Runge 1985*b*; Hirche 1990; Plourde and Runge 1993). Although females can have ripe ova immediately at t_0 under some circumstances (Tande and Hopkins 1981), there is a finite prereproductive period before females are successfully inseminated. Based on evidence from Plourde and Runge (1993) that 1 week was required for *C. finmarchicus* oocytes to complete vitellogenesis, we assumed that $S_1 = 8$ d and then let S_1 decrease to 0.

As was the care for the life history of egg-carrying copepods, for the standard conditions there is an intermediate mortality rate that generates maximum EPRs (Fig. 3A, solid line), below which postreproductive females depress the expected EPR and above which prereproductive females depress EPR. Note that even while reproductive females release 50 eggs nightly, the per capita rate that includes all females is reduced to a maximum of ~32 for standard conditions and to virtually 0 for conditions of long prereproductive periods and high mortality rates. When there is no prereproductive period, EPR increases monotonically with mortality rate (Fig. 3A).

The influence of the number of clutches produced (30–90, Fig. 3B) and the duration of the postreproductive period (0–120 d, Fig. 3C) are greatest at low mortality rates. Increasing the interclutch interval decreases the EPR with consistent effects across mortality rates (Fig. 3D).

Natural populations—We illustrate the magnitude of the mortality effect on the fecundity of a natural population of egg-carrying copepods by considering a temperate fjord population of *P. newmani*. We selected this example because of existing robust mortality estimates for females (Ohman and Wood 1996) and our knowledge of reproductive characteristics of the population in the same study site (Ohman 1985). Figure 4A shows temporal variations in average instantaneous mortality rates of adult female *P. newmani* over a 2-yr period, varying from near 0 in winter to 0.08 d^{-1} in the summer, when predator abundance is high. We used mortality rates from Fig. 4A in combination with the solutions presented in Fig. 2 to estimate the fraction of females actually carrying eggs on each date. For this purpose, we used the standard case where $k_1 = 1.25$, $k_3 = 0.25$, and $q = 10$. The expected fraction of *P. newmani* females carrying eggs ranges from 41 to 59% (Fig. 4B).

To also consider the influence of mortality on daily egg hatching rate (EHR) of *P. newmani*, we first examined seasonal variations of expected clutch size. Clutch size varies strongly with body size, which in turn changes with seasonal variations of temperature. Figure 4C illustrates the expected clutch size for reproductive females based on observed variations in median prosome length (0.725–0.980 mm during this 2-yr period; Ohman 1985) and on the assumption that each female produces the size-dependent clutch. Expected clutch size varies from 8.7 to 17.4 eggs $female^{-1}$. The expected EHR in Fig. 4D was then obtained from the expected clutch size divided by the embryonic duration, where temperature-dependent embryonic duration varies seasonally (temperature vari-

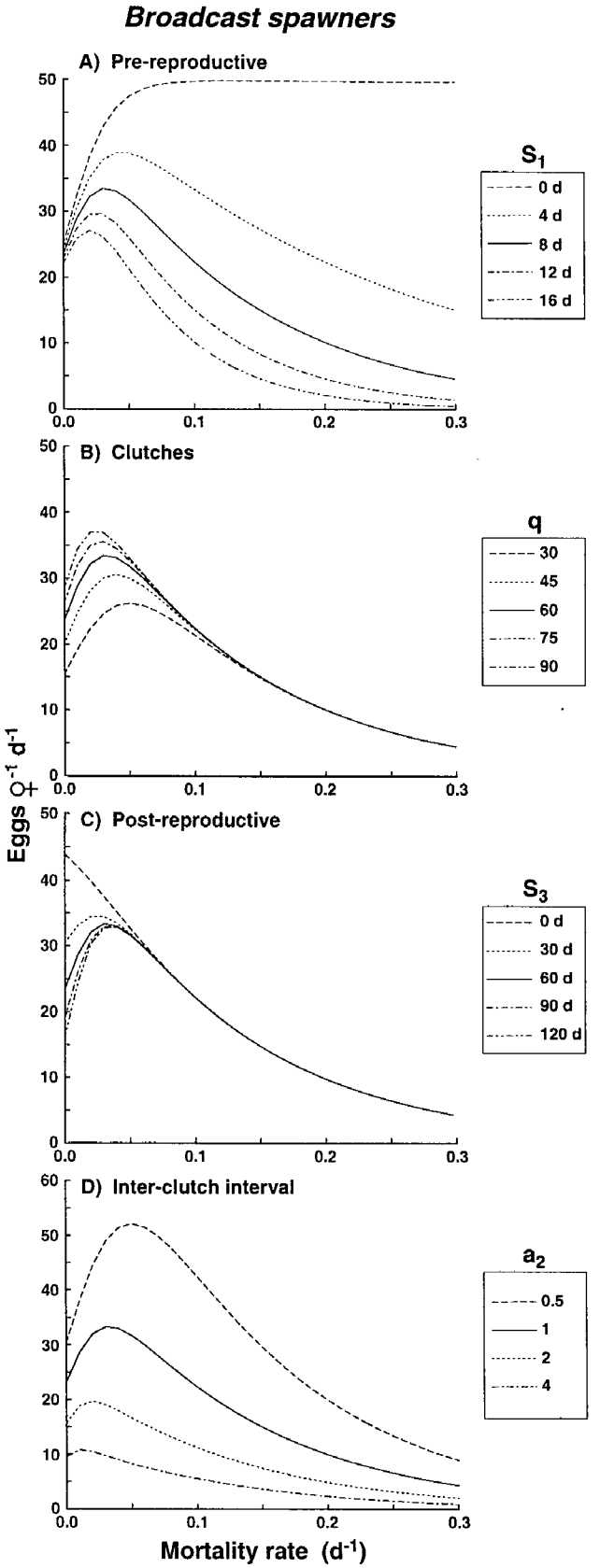

Fig. 3. Broadcast-spawning copepods. The sensitivity of the daily egg production rate to the mortality rate (abscissa) and to several reproductive characteristics is shown. A. Duration of the prereproductive period (S_1). B. Number of clutches (q). C. Duration of the postreproductive period (S_3). D. Interval between clutches (a_2). Standard conditions are indicated by a solid line. Clutch size = 50.

ation from Ohman 1985). These rates vary from 2.3 to 5.4 eggs female^{-1} d^{-1}.

However, Fig. 4D remains uncorrected because it does not take into account the proportion of females in prereproductive, interclutch, or postreproductive periods. In Fig. 4E, we express the corrected expected EHR, now adjusted for the changing fraction of females carrying eggs (Fig. 4B) as influenced by measured mortality (Fig. 4A). For this population, the combined effect of variations in body size, temperature-dependent embryonic duration, and mortality rates causes the realized EHR to vary between 0.9 and 3.1 eggs female^{-1} d^{-1}. These rates are markedly lower than those found in Fig. 4D, which are uncorrected for mortality influences. Mortality-corrected EHRs show a greater range of variation (max/min = 3.4×) than do uncorrected rates (2.4×). Comparison of Fig. 4E with 4D shows the lower EHRs and increased range of variation that are expected for a natural population solely as a consequence of female mortality rates.

Figure 4F presents the observed EHR for a natural population of *P. newmani*. The temporal pattern of observed EHR is similar to the mortality-corrected pattern (Fig. 4E). The two patterns are correlated (Spearman's rank correlation $r_S = 0.513$, $P < 0.01$), although there is more variability in the observations. More importantly, the observed values of EHRs agree much better with mortality-corrected expectations (Fig. 4E) than with expected values, which do not account for the influence of mortality on female stage structure (Fig. 4D).

Discussion

For both the egg-carrying and broadcast-spawning copepod life histories considered here, there is a strong effect of adult female mortality rates on per capita fecundity. We did not consider the direct effects of mortality in removing eggs that would otherwise be potential recruits to a population (e.g. Peterson and Kimmerer 1994; Ianora et al. 1995); instead, we considered the indirect effects that mortality has through changing the stage structure of the adult females and shifting the relative abundance of reproductive females with respect to pre and postreproductive females. Edmondson (1960, 1993) noted the importance of female age structure when he applied his egg ratio method to rotifers and other egg-carrying zooplankton. He stated, "The egg ratio is changed by anything that changes the proportion of non-ovigerous animals to ovigerous animals" (Edmondson 1960, p. 67).

At high mortality rates, duration of the prereproductive period is the factor that most strongly influences fecundity of both the egg-carrying and broadcast-spawning life his-

tories of adult females. In contrast, at low mortality rates, duration of the postreproductive period and the number of clutches produced have a greater influence on fecundity. The interclutch interval has an effect that is largely independent of the mortality rate. These results indicate that in new experimental determinations of reproductive characteristics of female copepods, some a priori knowledge of mortality rates in nature would help to best allocate efforts to the most influential variables; otherwise, all aspects of the female reproductive schedule require attention. In the case of the *P. newmani* population that we considered, the mortality rates were usually relatively low, but the upper end of measured rates (0.08 d^{-1}) was sufficiently high that different assumptions about the duration of the prereproductive period would have significantly altered the expected fraction of females carrying eggs.

The sensitivity of fecundity to the duration of the prereproductive period (with high mortality rates) suggests that this period should be under strong selection pressures. The prereproductive period would be expected to be shortened to a physiological minimum. These pressures may account for precocious reproductive maturity in copepodid stage 5 females in some populations (Tande and Hopkins 1981). If further foreshortening is not physiologically possible, prereproductive females may remain in a part of the water column where mortality risk (due to predation) is considerably lower than that found at depths where spawning females occur. For members of the Calanidae, in which dormant copepodid stage V females occur at a depth and spawning females occur at the surface, it may be advantageous for newly molted females to remain at a depth until they are ready to spawn. This constraint may explain previous observations of bimodal vertical distributions of female copepods (e.g. Hirakawa 1991; Arashkevich et al. 1996; M. Ohman unpubl. data).

Even where three reproductive stages of females exist in a population, it may be possible to simplify the life history to only two stages. If postreproductive females were separated from prereproductive and reproductive females by morphological criteria (e.g. Razouls 1974; Smith 1990; Norrbin 1994) or perhaps by age-pigment analysis or other means of age assessment, postreproductive females could be excluded from calculation of EPRs. If only the S_1 and S_2 stages are considered, the functions in Figs. 2 and 3 decline monotonically. Experimental determination of the duration of the postreproductive period would then be unnecessary. Furthermore, in a two-stage life history, the stage ratio approach of Aksnes and Ohman (1996) could be used to estimate female mortality rates.

Our analysis of the natural population of *P. newmani* illustrates that measured rates of mortality combined with temperature influences on body size (hence, clutch size) and embryonic duration can generate substantial seasonal changes in EHRs—here, from 0.9 to 3.1 eggs female^{-1} d^{-1}. The observed range of EHRs in this population (0.3–3.2 eggs female^{-1} d^{-1}) corresponds relatively well with the upper limit, although the lower limit was below what was expected. This difference could be caused by inappropriate parameters (e.g. temporally varying values of k_1, k_3, etc., which are here assumed constant and equal to the standard case), by intervals of food limitation, or by departures from steady-state recruitment. Other evidence suggests that although there were a few periods of food limitation that depressed birth rate in this species, growth and reproduction were continuous and had food-satiated conditions for extended periods (Ohman 1985). Therefore, much, though not all, of the observed variation

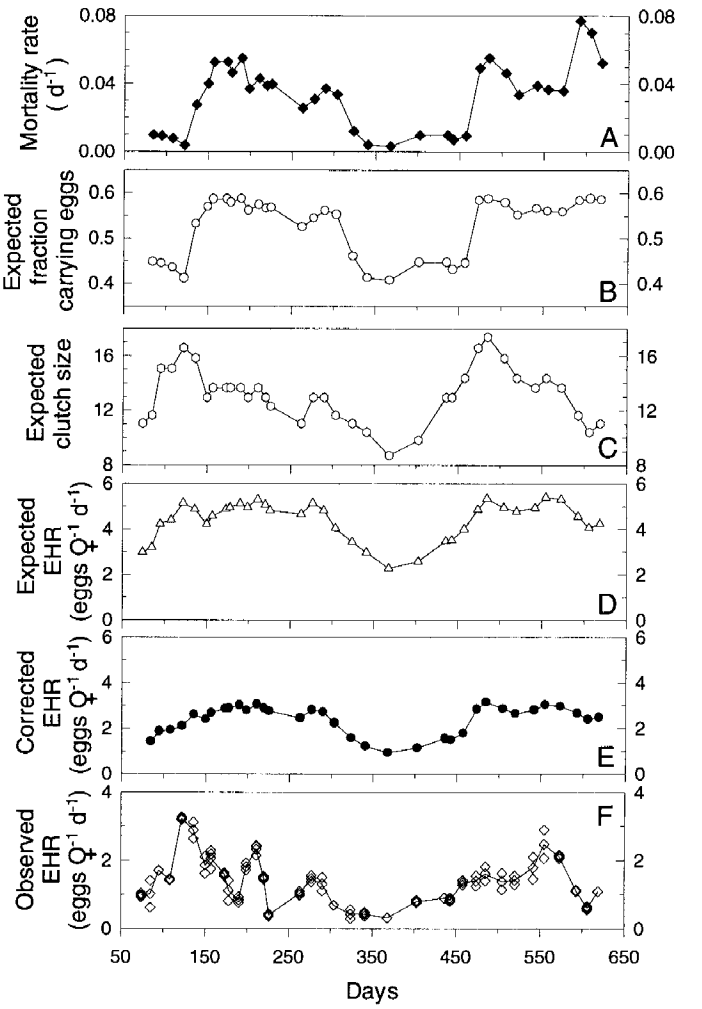

Fig. 4. Effects of mortality on fecundity of the egg-brooding copepod *Pseudocalanus newmani*. A. Observed instantaneous mortality rates for adult female *P. newmani* from Ohman and Wood (1995). B. Effects of mortality rates from preceding panel on the expected fraction of egg-carrying females (from the standard case in Fig. 2). C. Seasonal variations in expected clutch size from measured changes in prosome length in the field (Ohman 1985) and the relationship CS = $18.219(PL)^{2.298}$. D. Expected variations in egg-hatching rate, based on clutch size in the preceding panel, divided by seasonal variations in embryonic duration from observed temperature variations. E. Corrected egg hatching rate, from the product of panels B and D, thus taking account of seasonal changes in mortality rate, body size, and temperature-dependent embryonic duration. F. Observed in situ variations in egg hatching rate (from Ohman and Wood 1995).

in fecundity in this study site can be explained by variation in mortality, without reference to food limitation.

In the case of the life history of broadcast-spawning *Calanus*, where egg production is likely to be food limited for extended periods (e.g. Runge 1985*a,b*; Mullin 1993), variations in mortality may interact with food limitation to confound simple interpretations of the causes of variations in EPRs. Increased mortality rates will act on the EPR in the same direction as does increased food limitation. For example, food limitation would be expected to increase the prereproductive period, reduce clutch size, and perhaps shorten the reproductive period, all of which would decrease the measured population EPRs. However, higher mortality rates will also decrease EPRs, thereby confounding simple interpretation of measured rates. The magnitude of mortality-induced variations in fecundity of the broadcast spawner *C. finmarchicus* can be roughly estimated from the data of Plourde and Runge (1993). In their study in the lower estuary of the Gulf of St. Lawrence, the measured per capita EPR varied from 28 to 79 eggs female^{-1} d^{-1}, or a factor of 2.8 during the late June to mid-August period, when regular recruitment seemed to be taking place. (The upper limit exceeds the values found in Fig. 3 because we set maximum clutch size at 50, and body size-dependent clutch size variations were not considered.) The overall range of measured EPRs in the Gulf of St. Lawrence indicates that a 3-fold variation in EPR could be accounted for by variation in mortality rates alone (Fig. 3).

The fraction of prereproductive *C. finmarchicus* (reproductive stages 1–through 3, as assessed by Plourde and Runge 1993 from maturity of oocytes) varied between 5 and 35% of all females during the summer period. Apparently, no postreproductive females occurred (i.e. all remaining *C. finmarchicus* females were reproductive, as assigned by Plourde and Runge to their stages 4–7). From Eq. 1 and 3 (and assuming that $S_1 = 8$ d, $a_2 = 1$ d, $q = 60$, and $S_3 = 0$; *see Fig. 3*) we can calculate that mortality rates between 0 and 0.05 d^{-1} would generate variation in the percentage of prereproductive females from 12 to 34%. That a lower percentage was observed probably reflects a departure from the assumption of continuous recruitment or from our assumed stage structure. Mortality rates reported for *C. finmarchicus* in different locales far exceed the range of 0.00–0.05 d^{-1} (e.g. Matthews et al. 1978; Aksnes and Magnesen 1983) and are likely to be easily met (or exceeded) in the Gulf of St. Lawrence. Although we do not claim that all of the observed variation in *C. finmarchicus* EPRs in this region is caused by variations in mortality rates, we point out that the effect of mortality rates is potentially significant.

We have assumed that the probability of mortality is equal for all females. This may not be the case if, for example, sight-hunting predators attack egg-carrying individuals preferentially over females without eggs (Bollens and Frost 1991). In this situation, variations in mortality rate would have an even larger influence in shifting the observed stage structure of females away from egg-bearing females (cf. Ohman and Wood 1995). Total EPRs would be depressed further still.

Another limitation of this analysis is that it applies only to intervals during which a population approximates continuous recruitment. Where a strongly pulsed cohort occurs, the stage structure shifts too rapidly to be accurately described by Fig. 1. Mortality will still influence observed fecundity, but in a quantitatively different manner than that described here. Lower fecundity rates than those shown in Figs. 2 and 3 would be expected during the arrival of a cohort of females, most of which are initially prereproductive, whereas higher fecundity rates would be expected if females in a cohort attain reproductive maturity synchronously.

For the egg-carrying life history, the fraction of females carrying eggs can occasionally be measured directly from field samples but will be difficult to quantify if nets or pumps cause such females to lose eggs. When eggs are not lost, the property measured is the fraction of females with attached eggs. This property differs from the fraction of reproductive females estimated by morphological examination (as usually applied to broadcast spawners; e.g. Batchelder 1986; Runge 1987) because animals in the interclutch period are scored as reproductive by the morphological technique, whereas interclutch animals are not included in a direct count of egg-bearing animals. Thus, for the 0 mortality case illustrated in the standard curve in Fig. 2, and assuming unbiased sampling, 39% of females are visibly carrying eggs (stage a_1) while 48% of females are in the reproductively active stage of the population (stage S_2). The two quantities need to be carefully distinguished.

We conclude that field estimates of the fraction of brooding females carrying eggs, of the per capita EPR of broadcast spawners, or of derivative measures of fecundity are strongly influenced by the mortality rate found in nature. The quantitative effect of mortality on fecundity is determined by several characteristics of the reproductive schedule of adult females, each of which requires considerable experimental attention, even for copepod species that have historically been well studied. Important factors to study include the duration of the prereproductive period, the interclutch interval, the total number of clutches, and the duration of the postreproductive period. Changes in clutch size with body size and age, as well as the influence of environmental properties (e.g. temperature and food) on each of these quantities, also need further study. Additionally, reliable methods are needed to differentiate postreproductive from prereproductive females and from those in the interclutch state. Robust measures of mortality are urgently needed (e.g. Wood 1994). Under these circumstances, accurate interpretations can be made of the processes that cause variability in copepod egg production in nature.

It has not escaped our notice that the specific relationship we have identified between variations in mortality and variations in fecundity immediately suggests an inverse method for mortality estimation. Where the reproductive parameters (S_1, S_2, S_3, a_1, a_2, and q) are well known and copepods experience protracted intervals of food-satiated reproduction, the dependent and independent variables in Figs. 2 and 3 can be reversed. Accord-

ingly, measured fecundity could be used as a direct estimator of the mortality rate of adult female copepods.

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