

REVIEW

Scaling of fecundity, growth and development in marine planktonic copepods

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ABSTRACT: We compiled information from the literature on female and egg sizes and maximum egg production, growth and developmental rates in marine planktonic copepods. While specific growth and developmental rates are invariant with body mass, weight-specific fecundity scales with female body mass^{-0.26} in both broadcast-spawning and egg-carrying copepods. Egg sizes increase with female size and, consequently, egg production rates (no. of eggs $\varphi^{-1} \text{ d}^{-1}$) are constant with size. Developmental rates were similar among egg-carrying and broadcast-spawning copepods, but the latter grow faster by 30 to 50% and have weight-specific fecundities that are 2.5 times and egg production rates that are 7.5 times those of the former. Nauplii develop faster (by a factor of 2) but grow slower (by 20 to 40%) than copepodites in both spawning types. The main demographic implications of these findings are (1) that mortality is independent of body mass *per se*, (2) that sac spawners suffer higher overall mortality rates than broadcast spawners and (3) nauplii suffer higher mortality than copepodids.

KEY WORDS: Copepods · Allometry · Fecundity · Growth · Development

INTRODUCTION

Vital rates (e.g. feeding, metabolism, growth) of both animals and plants typically scale nonlinearly with body mass and are often described by an allometric relation of the type:

$$V = aW^b, \quad (1)$$

or
$$v = aW^{b-1} \quad (2)$$

where V and v are the absolute and weight-specific vital rate in question, and a and b are constants. The exponent b is frequently close to 0.67, and $b - 1$ thus near -0.33 (Zeuthen 1953, Hemmingsen 1960, Banse 1982).

The present study was prompted by the following observations and considerations (Kiørboe & Sabatini 1994): weight-specific juvenile growth and development times in planktonic copepods appear to be inde-

pendent of body mass (i.e. $b = 1$) (Huntley & Lopez 1992), whereas the size of eggs scale with body mass raised to an exponent of ca 0.65 (Kiørboe & Sabatini 1994). If weight-specific female egg production scales with body mass the same way as juvenile growth, egg production in terms of no. of eggs $\varphi^{-1} \text{ d}^{-1}$ is bound to increase with body mass (proportional to ca $W^{1.0/0.65} = W^{0.35}$). This, in turn, implies that instantaneous mortality rates should increase with increasing body mass in copepods, because the eggs produced by 1 female should, on average, result in only 1 female surviving to the next generation — otherwise the population would either go extinct or the population size would increase infinitely. This is a counterintuitive and uncomfortable observation, and Kiørboe & Sabatini (1994) consequently called for a thorough examination of existing data on the scaling of fecundity, growth and developmental rates in copepods.

The purpose of this study is to review and report observations on fecundity, growth and development in planktonic copepods and to examine the demographic implications hereof.

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MATERIAL AND METHODS

We are looking for patterns that transcend species differences. We are aware that there are differences in specific growth and fecundity rates between species, but we expect that the species effect is secondary to body mass scaling effects when a sufficiently large range in body masses is considered, as has been shown for the vital rates of other (even more diverse) groups of organisms, be it plants (e.g. Nielsen & Sand-Jensen 1990) or animals (e.g. Fenchel 1974, Banse 1982). Yet, the nature of the data we are to report forced us to classify planktonic copepods into sac-spawning (egg-carrying) and broadcast-spawning (free) types. Kiørboe & Sabatini (1994) showed that fecundity rates and egg hatching times differ substantially between these 2 types, and that the difference recurs across taxonomic groups (e.g. calanoid and cyclopoid copepods). We therefore retain some degree of type-classification in the data we report here. Also, Oncaeatidae, although pelagic, are not really planktonic. Evidence is accumulating that these copepods occur mainly associated with large marine snow aggregates, and that their ecology and lifecycle strategy therefore differs radically from that of truly planktonic copepods (Paffenhöfer 1993, Dagg 1994). We therefore also separate this group out in our data presentation.

Our main data source is observations reported in the literature. We based our literature search mainly on the electronic version of Aquatic Sciences and Fisheries Abstract (1978 onwards). Below we describe how data were selected and transformed.

We compiled only information on marine pelagic copepods, and only average maximum (in contrast to absolute maximum) rates measured experimentally in the laboratory at temperatures ranging between 10 and 20°C and at saturating food concentrations were considered in this presentation.

The rates obtained at the experimental temperatures were converted to the rate at a temperature of 15°C by assuming a $Q_{10} = 3.0$ for growth, developmental and egg production rates. This value of Q_{10} was derived from the exponential temperature coefficient (0.111) obtained by Huntley & Lopez (1992) in their review of copepod growth versus temperature in the range -5 to 25°C. About the same Q_{10} value has been reported also for individual copepod species: *Eurytemora affinis*: 3.1 and *E. herdmani*: 3.0 in the range 2 to 23.5°C (Katona 1970); *Oithona nana*: 3.06 (Haq 1965); *Calanus glacialis*: 2.9 in the range 4 to 13.5°C (Hirche & Bohrer 1987); *O. similis*: 3.1 in the range 9 to 14°C (Sabatini & Kiørboe 1994, calculated from Eaton 1971). When rates were reported for several experimental temperatures in the same study we used only that rate measured closest to 15°C.

Whenever possible we avoided combining information from several studies, e.g. to calculate weight-specific egg production from the egg production rate measured in one study and female body weight of the same species measured in another. However, this was frequently necessary. In those cases we used averages of, for example, female body weight measured in all other available studies (Appendix 1).

We selected carbon and days as our common units. Body weights reported as dry wt or ash-free dry weight (AFDW) were converted to carbon assuming 0.4 $\mu\text{g C } \mu\text{g}^{-1}$ dry wt (Parsons et al. 1984) or 0.46 $\mu\text{g C } \mu\text{g}^{-1}$ AFDW (Paffenhöfer & Harris 1976). Egg carbon was estimated from egg size by assuming $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Kiørboe et al. 1985, Huntley & Lopez 1992) if not reported in the original paper. All temperature-corrected and carbon-converted raw data have been tabulated in Appendices 1 to 6.

Egg production rates (Appendix 2). In most cases egg production rates were reported as eggs $\varphi^{-1} \text{d}^{-1}$, in some cases also as weight-specific rates. When weight-specific rates were not available in the original report they were estimated from no. of eggs $\varphi^{-1} \text{d}^{-1}$ and reported (or calculated) egg and female carbon contents.

Developmental rates (Appendix 3) and development times (Appendix 4). Information about copepod development is available in the literature as total development time, as stage durations, or as cumulative development time of stages, from which stage durations can be estimated. Total development times have been reported somewhat differently in the various reports, i.e. as time from egg to C6 or time from N1 to C6. The way used to calculate the cumulative development times also differs among papers; thus, 'mean time of stage' yields estimates that are ca 10% faster than 'median development time' (Peterson & Painting 1990). In Appendices 3 & 4 we have specified the type of calculation. We did not attempt to correct for these variations, since it does not bias our results, but only introduces some noise. We estimated development rates by averaging the reciprocal of the single-stage durations reported in the original papers. Since 'isochronality' (sensu Landry 1983) is not a general 'rule' among copepods (Hart 1990), average developmental rates were calculated separately for nauplii (N1 to N6), copepodids (C1 to C6) and late copepodids (C4 or C5 to C6). When development rates of males and females were reported separately we used only the female rate.

Weight-specific growth rates (Appendices 5 & 6). Most of the reported weight-specific growth rates were estimated in the original papers from the slope of the regression of body weight versus time, or weight of the stages versus development time. With a few exceptions weight (carbon, dry wt or AFDW) was obtained

from length-weight relationships. We calculated weight-specific growth rates for nauplii (N1 to N6), copepodids (C1 to C6) and late copepodids (C4 or C5 to C6) separately by averaging the single-stage rates determined experimentally.

We also estimated weight-specific growth rates (g) indirectly from the approximate relationship

$$g = \ln(W_{\varphi}/W_{\text{egg}})/D, \quad (3)$$

where W_{φ} and W_{egg} are the carbon content of females and eggs, respectively and D is the development time (Appendix 6). This provides an independent set of growth rate estimates.

RESULTS

Egg size and egg hatching time

Data on egg sizes and egg hatching times in planktonic copepods have been reviewed by Kjørboe & Sabatini (1994) but here we complement the data they compiled. Egg sizes increase with female body mass in both egg-carrying and broadcast-spawning copepods, but the weight exponent differs significantly between the 2 groups, 0.93 and 0.62, respectively (Table 1, Fig. 1). For the egg-carrying copepods the weight exponent is not significantly different from 1.0, and egg

Table 1. Regression parameters and determination coefficients (r^2) for the relations shown in Figs. 1 to 7. n: number of observations. Significance levels are: * $p < 5\%$, ** $p < 1\%$, *** $p < 0.1\%$, ns: not significant

Dependent variable	Independent variable	Sac- (S) or broadcast (B) spawners	Intercept \pm SE	Slope \pm SE	n	r^2	p	Fig.
Log(Egg size), $\mu\text{g C}$	Log(φ size), $\mu\text{g C}$	S	-1.841 0.098	0.930 0.084	21	0.87	***	
		B	-1.859 0.100	0.621 0.057	41	0.75	***	
		B+S	-1.825 0.080	0.662 0.051	62	0.74	***	
Log(Fecundity), d^{-1}		S	-0.850 0.066	-0.260 0.058	10	0.72	***	2
		B	-0.474 0.079	-0.262 0.067	35	0.32	***	
Log(Egg prod. rate), no. of eggs $\varphi^{-1} \text{d}^{-1}$	Log(φ size), $\mu\text{g C}$	S	0.803 0.069	-0.128 0.060	10	0.36	ns	3
		B	1.386 0.080	0.141 0.069	35	0.11	ns	
Log(Development time), d	Log(φ size), $\mu\text{g C}$	B+S	1.383 0.030	-0.008 0.030	31	0.003	ns	4
Log(Development rate), stages h^{-1}	Log(φ size), $\mu\text{g C}$	B+S Nauplii	-1.558 0.082	0.071 0.061	22	0.06	ns	5a
		B+S Copepodids	-1.674 0.054	-0.066 0.043	26	0.09	ns	5b
		B+S C4/5 to Adult	-1.865 0.067	-0.061 0.048	23	0.07	ns	5c
		S Nauplii	-0.719 0.089	-0.032 0.114	4	0.04	ns	6a
Log(Growth rate), d^{-1}	Log(φ size), $\mu\text{g C}$	B Nauplii	-0.661 0.072	0.091 0.061	14	0.16	ns	6b
		S Copepodids	-0.637 0.087	0.052 0.087	6	0.05	ns	
		B Copepodids	-0.474 0.070	-0.008 0.054	16	0.001	ns	6c
		S C4/5 to Adult	-1.046 0.040	0.394 0.051	5	0.95	**	
		B C4/5 to Adult	-0.278 0.118	-0.249 0.081	11	0.51	*	
		S	-0.803 0.100	0.126 0.100	6	0.19	ns	7
Log(Growth rate = $\ln(W_{\varphi}/W_{\text{egg}})/D$), d^{-1}	Log(φ size), $\mu\text{g C}$	B	-0.584 0.058	-0.011 0.039	14	0.007	ns	

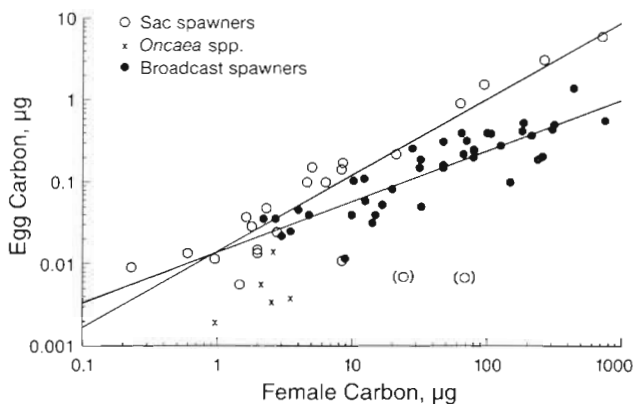


Fig. 1. Egg size as a function of female body mass in sac- and broadcast-spawning marine pelagic copepods. Observations in parentheses as well as for *Oncaea* sp. not included in regressions. Regression statistics are given in Table 1

size thus appears to be approximately proportional to female size in this group. Eggs of oncaeateid copepods are significantly smaller than eggs of other cyclopoid and calanoid copepods, but the range in female sizes was insufficient to calculate a regression.

Egg hatching times are independent of female size ($r^2 = 0.26$, $n = 11$ and $r^2 = 0.01$, $n = 17$ for sac- and broadcast spawners respectively) and of egg size ($r^2 = 0.45$, $n = 8$ and $r^2 = 0.11$, $n = 18$, respectively) but differ significantly between sac- and broadcast spawners ($\bar{x} = 3.88 \pm 2.32$ and 1.51 ± 0.59 d, respectively, at 15°C).

Weight-specific fecundity and egg production rate

Weight-specific fecundity rates decline with female body size and scale with body mass raised to an exponent of -0.26 for both sac- and broadcast spawners (i.e. $b = 0.74$; Fig. 2, Table 1). The intercepts, however, differ significantly ($p < 1\%$), and broadcast spawners have weight-specific fecundities that are on average ca 2.5 times the weight-specific fecundity of sac spawners.

Because weight-specific fecundity and weight-specific egg sizes in broadcast spawners scale with female body mass in almost the same way (exponents -0.26 and -0.38) it is not surprising that egg production in terms of no. of eggs $\text{♀}^{-1} \text{d}^{-1}$ is size independent (Fig. 3, Table 1). In sac spawners egg production decreases slightly with female size, but the decrease is not statistically significant. Thus, small and large copepods have similar daily egg production rates. However, broadcast spawners produce on average 7.5 times as many eggs as sac spawners, with overall average maximum egg production rates of 40 ± 23 and 5.3 ± 2.2 eggs $\text{♀}^{-1} \text{d}^{-1}$ at 15°C .

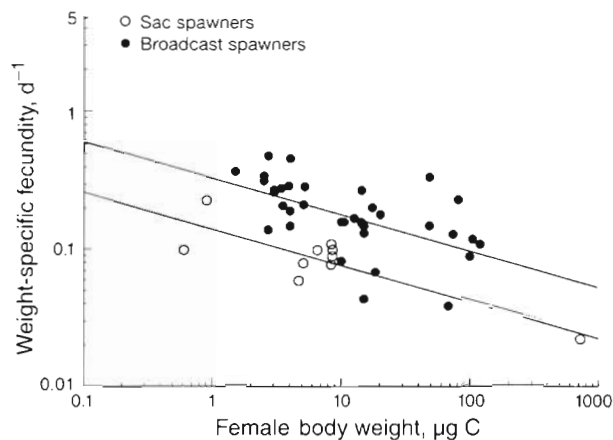


Fig. 2. Weight-specific fecundity ($\mu\text{g C } \mu\text{g}^{-1} \text{C d}^{-1}$) as a function of female body weight in sac- and broadcast-spawning marine pelagic copepods. Regression statistics are given in Table 1

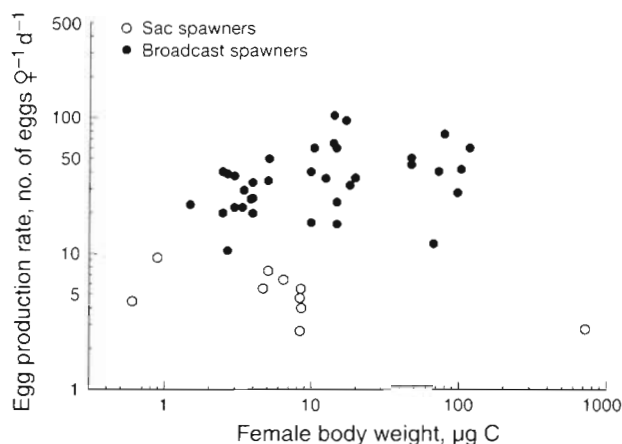


Fig. 3. Egg production rate as a function of female body mass in sac- and broadcast-spawning copepods

The 7.5-fold difference in the number of eggs produced per day and the 2.5-fold difference in weight-specific fecundity between broadcast- and sac spawners suggests that, on average, carried eggs are ca 3 times bigger than freely spawned eggs. This difference is most pronounced for the larger copepods, and less pronounced for the smaller ones (Fig. 1).

Development time and development rate

Development time, i.e. the time from egg to adult, is independent of female size (Fig. 4, Table 1), and also does not differ significantly between sac- and broadcast spawners ($p > 5\%$, t -test; Table 2).

Developmental rates calculated separately for nauplii, copepodids and late copepodid stages (C4 or

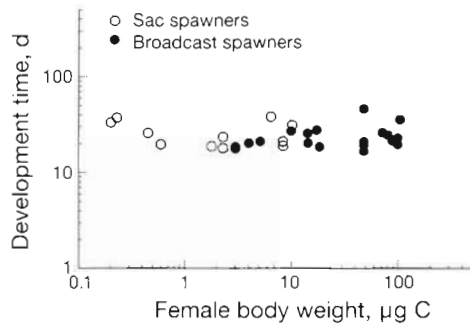


Fig. 4. Development time as a function of female body mass in sac- and broadcast-spawning copepods

C5 to adults) are all independent of female size and also do not differ significantly between sac- and broadcast-spawners (Fig. 5, Table 2). However, for both groups developmental rates slow down as development progresses, and are highest for nauplii and slowest for late copepodids (Table 2); these differences are statistically significant (ANOVA, $p < 0.1\%$).

Growth rate

Weight-specific growth rates determined experimentally are independent of female size, both in nauplii, copepodids and late copepodid stages (Fig. 6). Growth rates estimated indirectly as $\ln(W_f/W_{egg})/D$, where W_f , W_{egg} and D are weights of females and eggs and developmental times, respectively, are also independent of female size (Fig. 7, Table 1).

Average growth rates vary significantly and consistently between sac- and broadcast spawners, and between nauplii, copepodids and late copepodids (Table 3). Broadcast spawners grow 30 to 50% faster than sac spawners and copepodids grow ca 25% faster than nauplii and late copepodids in both spawning types. Thus, nauplii develop faster but grow slower than copepodids.

DISCUSSION

Allometry

The allometric scaling of copepod fecundity with female body mass ($b \approx 0.74$) for both sac- and broadcast spawners accords with our general expectation (e.g. Zeuthen 1953, Hemmingsen 1960, Fenchel 1974, Banse 1982). It is also consistent with the allometric scaling of feeding rates in marine calanoid copepods ($b = 0.37$

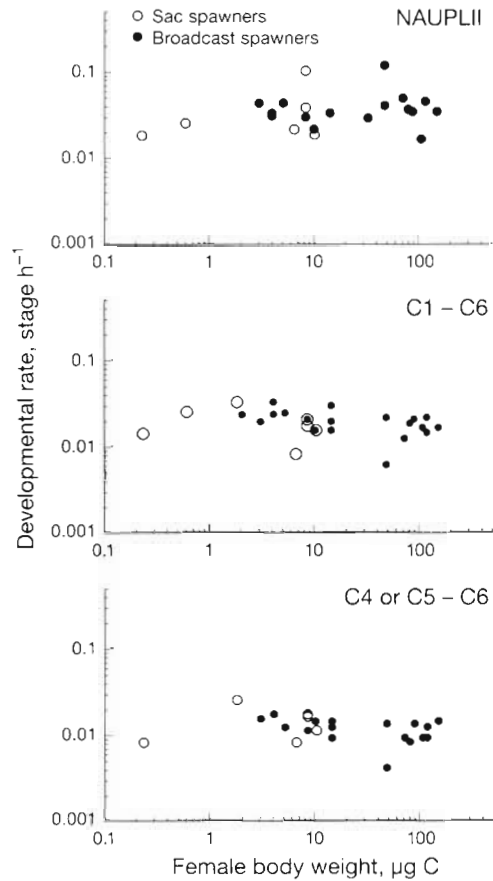


Fig. 5. Developmental rate as a function of female body weight in sac- and broadcast-spawning copepods; plotted separately for nauplii (egg or N1 to N6), copepodids (C1 to C6), and late copepodids (C4 or C5 to adult)

to 0.75) as demonstrated by the extensive ($n = 550$) laboratory data compiled by Peters & Downing (1984) and with the scaling of metabolic rates in aquatic crustaceans, including planktonic copepods ($b \approx 0.8$; e.g. Ivleva 1980, Vidal & Whitledge 1982). Given this background it is surprising that juvenile growth rate

Table 2. Total development time and developmental rate of nauplii, copepodids (C1 to C6) and late copepodids (C4/5 to C6) (average \pm SD) in sac spawners, broadcast spawners and in both groups considered together at 15°C. n: no. of observations

	Development time (d)	Developmental rate (stage h ⁻¹)		
		Nauplii	Copepodids	C4/C5 to Adults
Sac spawners	25.71 \pm 7.52 n = 12	0.036 \pm 0.032 n = 6	0.019 \pm 0.008 n = 7	0.014 \pm 0.007 n = 6
Broadcast spawners	23.82 \pm 7.14 n = 19	0.038 \pm 0.021 n = 16	0.019 \pm 0.006 n = 19	0.012 \pm 0.003 n = 17
Sac + broadcast	24.55 \pm 7.23 n = 31	0.038 \pm 0.024 n = 22	0.019 \pm 0.006 n = 26	0.012 \pm 0.004 n = 23

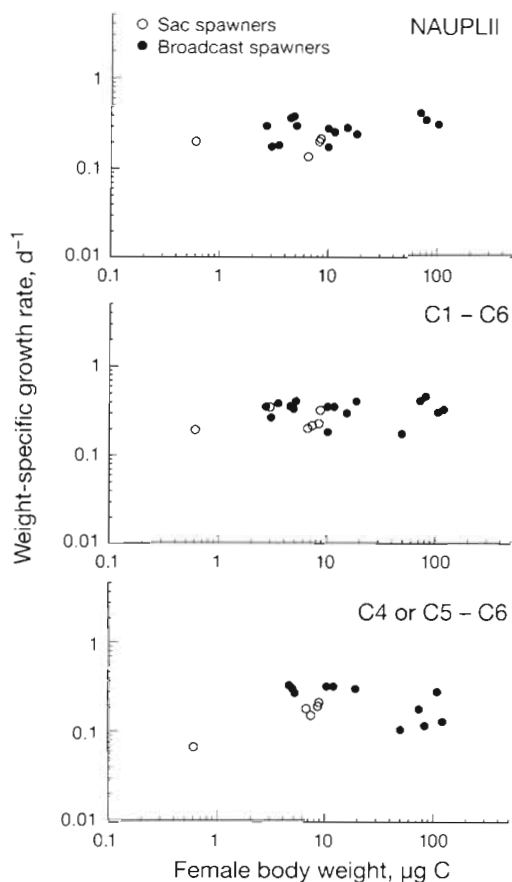


Fig. 6. Weight-specific growth rate ($\mu\text{g C } \mu\text{g}^{-1} \text{C d}^{-1}$) as a function of female body weight in sac- and broadcast-spawning copepods; plotted separately for nauplii, copepodids and late copepodids

appears to be directly proportional to body mass and specific growth rate, thus, independent of size (i.e. $b \approx 1$). Our data clearly demonstrate this, and the same result was reached by previous authors on less extensive data sets (Huntley & Lopez 1992). We have no suggestions as to the physiological basis of this discrep-

Table 3. Measured weight-specific growth rates of nauplii, copepodids (C1 to C6) and late copepodids (C4/5 to C6) and total growth rate estimated from egg and female carbon contents (W_{egg} and W_{f}) and developmental times (D) in sac spawners, broadcast spawners and in both groups considered together at 15°C. Average \pm SD is shown; n: no. of observations

	Measured growth rate (d^{-1})			$\ln(W_{\text{f}}/W_{\text{egg}})/D$
	Nauplii	Copepodids	Total	
Sac spawners	0.185 ± 0.035 n = 4	0.255 ± 0.066 n = 6	0.220	0.182 ± 0.038 n = 4
Broadcast spawners	0.282 ± 0.075 n = 14	0.339 ± 0.078 n = 16	0.311	0.254 ± 0.047 n = 12
Sac + broadcast	0.261 ± 0.079 n = 18	0.316 ± 0.083 n = 22	0.289	0.236 ± 0.054 n = 16

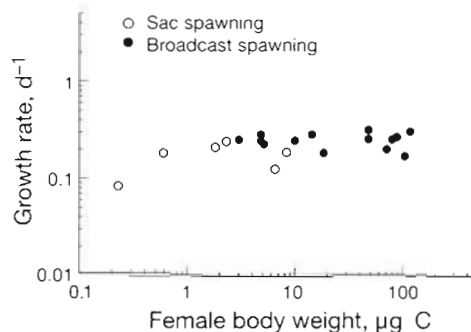


Fig. 7. Weight-specific growth rate ($\mu\text{g C } \mu\text{g}^{-1} \text{C d}^{-1}$) calculated from carbon contents of eggs (W_{egg}) and females (W_{f}) and developmental time [$\ln(W_{\text{f}}/W_{\text{egg}})/D$] as a function of female body weight in sac- and broadcast-spawning copepods

ancy between the mass dependency of juvenile and female growth rates.

Because of the approximate relation $g = \ln(W_{\text{f}}/W_{\text{egg}})/D$, it may at first appear inconsistent that both g and D are size independent in broadcast spawners while at the same time $W_{\text{f}}/W_{\text{egg}}$ depend on female size (scale with $W_{\text{f}}^{0.38}$). Replacing $W_{\text{f}}/W_{\text{egg}}$ with $aW_{\text{f}}^{0.38}$ in Eq. (3), where a is a constant, yields:

$$g = (\ln a + 0.38 \ln W_{\text{f}})/D = (\ln a)D + (0.38/D)\ln W_{\text{f}} \quad (4)$$

i.e. g is bound to increase with body mass if D is constant, as also noted by Frost (1980). However, at 15°C the slope of increase is only $0.38/D \approx 0.015$ (because $D \approx 25$ d; Table 2), and the relation, therefore, too weak to detect with noisy data. In fact, for broadcast spawners regressions of g vs $\ln W_{\text{f}}$ in both nauplii and copepodids yield slightly positive slopes that do not differ significantly from 0.015 (nor from 0). These observations and considerations suggest that weight-specific juvenile growth in copepods is independent of, or, if anything, increases slightly with body mass.

Demographic implications

Size dependency of copepod mortality rates

The egg production rate, mortality and developmental time of a population together describes its population dynamics. The net reproductive rate, R_0 , i.e. the number of offspring per female that survives until the next generation, is given by:

$$R_0 = \int l_x m_x dx \quad (5)$$

where x is the age, l_x is the age-specific

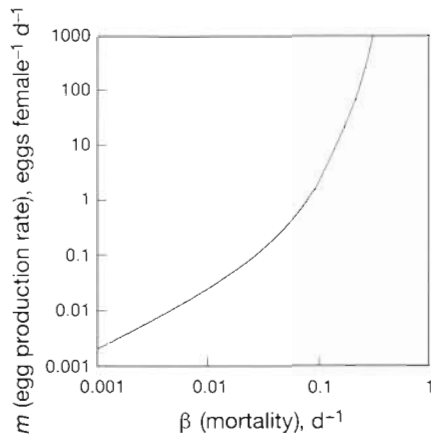


Fig. 8. Theoretical relationship between egg production rate and mortality rate for a hypothetical copepod population in steady state, assuming a 1:1 sex ratio and a developmental time of 25 d

survival and m_x the age-specific egg production rate. For simplicity and for the purpose of the following considerations we will initially assume that the mortality rate, β (d^{-1}), is age independent, and that the egg production rate is constant for $x \geq D$ and zero for $x < D$. It can then be shown that (Kjørboe & Sabatini 1994):

$$R_0 = (m/\beta)e^{-\beta D}, \quad (6)$$

where D is the developmental time. For the population to be maintained, R_0 should on average be equal to 2 (assuming a 1:1 sex-ratio); thus

$$m = 2\beta e^{\beta D}. \quad (7)$$

In this notation m is the realized egg production rate, not the maximum one. Fig. 8 is a graphical presentation of Eq. (7) for a hypothetical copepod population in steady state at 15°C and with a development time of 25 d. If we assume that the realized egg production rate, like the maximum one, is size independent, it follows that β , the mortality coefficient, is size independent. Although the fecundity of planktonic copepods is often considerably less than maximum in the field, likely due to food limitation (reviewed by Kjørboe 1991), there is no *a priori* reason to believe that the degree of food limitation should on average be different between small and large copepods. This is because the food size spectra of copepods can be described by log-normal distributions that have approximately equal variances (widths) between species (Berggreen et al. 1988). In the average pelagic environment the biomass of particulate matter appears to be approximately constant in equal, logarithmic size classes (Sheldon et al. 1972). Thus, even though small and large copepods feed on differently sized particles, the biomass of the food available to them is approximately the same in the average pelagic environment. It has

been suggested that the ingestion rate of small copepods saturates at lower food concentrations than that of larger copepods (e.g. Lam & Frost 1976). However, a recent extensive review has documented that the half-saturation constant of the functional response in ingestion rate to food concentration is size independent in copepods (P. J. Hansen, B. Hansen & P. K. Bjørnsen pers. comm.).

This analysis, thus, suggests that the mortality of planktonic copepods is invariable with adult size *per se*. More realistic and complex models, operating with age-/stage-dependent mortality rates, will not alter this conclusion materially. This conclusion is at variance with the pattern for aquatic organisms in general (Peterson & Wroblewski 1984) and pelagic invertebrates in particular (McGurk 1986); mortality rates typically scale with body mass^{-0.25}.

Mortality rates of sac- and broadcast spawners

Sac spawners develop at the same rate as broadcast spawners, but they have somewhat lower juvenile growth rates. This is basically a consequence of the eggs being relatively larger in sac spawners, and the weight increment from egg to adulthood consequently smaller. The similar developmental times and the very different egg production rates suggest that, overall, mortality rates are higher in broadcast than in sac spawners (cf. Eq. 5 and Fig. 8). Kjørboe & Sabatini (1994) considered the different demography and life-cycle strategies of sac- and broadcast spawners in detail and suggested that this difference in mortality was mainly due to an order of magnitude higher mortality rate of free than of carried eggs.

Age-/stage-dependent variation in mortality

The conclusion above, that copepod mortality rates do not vary with body mass, does not necessarily imply that mortality is age- or stage-independent. In fact, the patterns in growth and developmental rates may suggest that the mortality is elevated in the nauplii as compared to that in the copepodid stages.

Nauplii develop much faster than copepodids (by a factor of 2; Table 2), but they grow slower (by 20 to 40%; Table 3) both in sac- and in broadcast spawners. One possible and straightforward interpretation of this pattern is, that due to a lower swimming and escape capability, nauplii suffer a higher predation mortality risk than copepodids. It would, therefore, be adaptive to pass through the nauplii stages and develop motility/escape performance as quickly as possible in order to minimize cumulative pre-spawning mortality,

and this may be at the cost of a reduced somatic growth rate. Unfortunately, field data on nauplii and copepodid mortality rates are far too scarce to examine this interpretation.

Conclusions

Cross-taxonomic patterns in development, growth and fecundity rates in planktonic copepods suggest that (1) mortality rates are independent of body mass *per se*, (2) that nauplii experience higher mortality rates than copepodids, and (3) that broadcast spawners suffer from higher overall mortality rates than egg-carrying copepods, particularly in the egg stage. While the differences between egg-carrying- and broadcast-spawning copepods may relate to different life-cycle strategies (Kjørboe & Sabatini 1994), and the difference between nauplii and copepodids may reflect differences in predator escape capability, the apparent size independency of copepod mortality is at variance with the general pattern in aquatic invertebrates and remains unexplained.

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Appendix 1. Egg and female carbon weight of several species of copepods. Averages of all the available data for each species are also given. *Egg-carbon was calculated from volume and references thereby refer to the egg-diameter

Species	W_{egg} ($\mu\text{g C}$)	Source	$W_{\text{♀}}$ ($\mu\text{g C}$)	Source	Av. W_{egg} ($\mu\text{g C}$)	Av. $W_{\text{♀}}$ ($\mu\text{g C}$)
Sac spawners						
<i>Pseudocalanus elongatus</i>	0.140*	Frost (1989)	8.5	Paffenhöfer & Harris (1976)	0.140	8.4
			8.3	Klein Breteler et al. (1982)		
<i>Pseudocalanus sp.</i>			6.4	Vidal (1980a)		
<i>Pseudocalanus moultoni</i>	0.150*	Frost (1989)	5.1	Sigrun Jonasdottir pers. comm.	0.150	5.1
<i>Pseudocalanus newmani</i>	0.100*	Frost (1989)	4.7	Sigrun Jonasdottir pers. comm.	0.100	4.7
<i>Pseudocalanus minutus</i>	0.170*	Frost (1989)	8.6	Dagg (1977)	0.170	8.6
<i>Pseudodiaptomus hessei</i>			10.2	Jerling & Wooldridge (1991)		
<i>Pseudodiaptomus marinus</i>	0.100	Uye et al. (1983)	6.5	Uye et al. (1983)	0.100	6.5
<i>Euchaeta norvegica</i>	6.000	Hopkins (1977)	722.0	Hopkins (1977)	6.000	722.0
<i>Eurytemora affinis</i>	0.043*	Hirche (1992)	2.3	Hirche (1992)	0.048	2.30
	0.052	Heinle & Flemer (1975)				
<i>Eurytemora herdmani</i>	0.029	McLaren & Corkett (1981)	1.4	McLaren & Corkett (1981)	0.029	1.78
			2.9	Escribano & McLaren (1992)		
			1.0	Escribano & McLaren (1992)		
<i>Oithona colcarva</i>			0.5	Lonsdale (1981)		
<i>Oithona davisae</i>	0.009*	Uchima (1979)	0.2	Hiromi et al. (1988)	0.009	0.23
<i>Oithona nana</i>			0.2	Lampitt & Gamble (1982)		0.20
<i>Oithona plumifera</i>	0.038*	Own unpubl. obs.	1.6	G.-A. Paffenhöfer pers. comm.	0.038	1.63
<i>Oithona sumilis</i>	0.014*	Sabatini & Kjørboe (1994)	0.6	Sabatini & Kjørboe (1994)	0.014	0.60
<i>Oncaea mediterranea</i>	0.014*	Böttger-Schnack et al. (1989)	2.6	G.-A. Paffenhöfer pers. comm.	0.014	2.60
Broadcast spawners						
<i>Acartia clausi</i>	0.030*	Corkett & McLaren (1970)	2.5	Landry (1978)	0.036	2.67
			1.5	Uye (1981)		
			4.8	Klein Breteler et al. (1982)		
<i>Acartia clausi hudsonica</i>	0.041	Sekiguchi et al. (1980)	2.5	Sekiguchi et al. (1980)		
<i>Acartia clausi</i> = <i>A. omori</i>			2.0	Landry (1983)		
<i>Acartia grani</i>	0.030*	Vilela (1972)				
<i>Acartia tonsa</i>	0.046	Kjørboe et al. (1985a)	3.3	Kjørboe et al. (1985a)	0.046	3.98
			3.4	Ambler (1986)		
			4.0	Landry (1983)		
			5.2	Dagg (1977)		
<i>Acartia steuern</i>			3.9	Uye (1981)		
<i>Calanoides carinatus</i>	0.300*	Hirche (1980)	48.0	Peterson & Painting (1990)	0.310	48.00
	0.320	Borcher & Hutchings (1986)				
<i>Calanus australis</i>	0.240	Attwood & Peterson (1989)	73.6	Attwood & Peterson (1989)	0.240	80.80
			88.0	Peterson & Painting (1990)		
<i>Calanus finmarchicus</i>	0.400	Hirche (1990)	101.0	Hirche (1990)	0.400	119.5
			137.3	Smith (1990)		
<i>Calanus glacialis</i>	0.440	Hirche (1989)	307.3	Hirche (1989)	0.440	258.00
			209.0	Smith (1990)		
<i>Calanus helgolandicus</i>	0.320*	McLaren (1965)	71.1	Paffenhöfer (1976)	0.320	71.10
<i>Calanus hyperboreus</i>	0.560	Conover (1967)	757.0	Smith (1990)		
<i>Calanus marshallae</i>	0.188	Vidal & Smith (1986)	239.6	Vidal & Smith (1986)	0.188	171.80
			104.0	Peterson (1988)		
<i>Calanus pacificus</i>	0.250	Frost (1980)	80.4	Runge (1984)	0.250	80.40
			117.0	Vidal (1980a)		
<i>Calanus propinquus</i>	0.370	Kosobokova (1992)	215.0	After Huntley & Lopez (1992)	0.370	215.00
<i>Calanus sinicus</i>	0.200	Uye (1988)	80.0	Uye (1988)	0.200	80.00
<i>Centropages typicus</i>	0.031*	Dagg (1977)	14.9	Dagg (1977)	0.032	14.28
	0.027*	Davis & Alatalo (1992)	10.5	Davis & Alatalo (1992)		
	0.037	Fryd et al. (1991)	14.4	M. Fryd pers. comm.		
			17.3	Smith & Lane (1985)		
<i>Centropages hamatus</i>	0.040*	Klein Breteler (1982)	10.0	Klein Breteler et al. (1982)	0.040	10.00
<i>Eucalanus bungii</i>	0.204	Vidal & Smith (1986)	258.0	Vidal & Smith (1986)	0.204	258.00
<i>Labidocera trispinosa</i>	0.050	After Huntley & Lopez (1992)	33.0	Landry (1983)	0.050	33.00
<i>Labidocera euchaeta</i>	0.160*	Shaojing et al. (1989)	48.0	Senje & Song (1990b)	0.160	48.00
<i>Metridia pacifica</i>	0.100	Vidal & Smith (1986)	51.6	Vidal & Smith (1986)	0.100	51.60
<i>Paracalanus parvus</i>	0.022	Checkley (1980)	3.0	Checkley (1980), Landry (1983)	0.022	3.00
<i>Paracalanus sp.</i>			3.5	Uye & Shibuno (1992)		
<i>Temora longicornis</i>	0.040	Frost (1980)	18.4	Harns & Paffenhöfer (1976)	0.040	14.95
			11.5	Klein Breteler et al. (1982)		
<i>Temora stylifera</i>	0.059	Abou Debs & Nival (1983)	12.6	Abou Debs & Nival (1983)	0.059	12.60
<i>Tortanus discaudatus</i>	0.082*	McLaren (1966)	20.0	Lawrence & Sastry (1985)	0.082	20.00
<i>Sinocalanus tenellus</i>	0.036	Kimoto et al. (1986b)	5.1	Kimoto et al. (1986a)	0.036	5.10
<i>Undinula vulgaris</i>	0.220	Park & Landry (1993)	67.7	Park & Landry (1993)	0.220	67.70

Appendix 2. Maximum egg production rates and weight-specific fecundities converted to 15°C by assuming a $Q_{10} = 3.0$. Female carbon contents also shown

Species	Egg production rate 15°C (no. of eggs φ^{-1} d $^{-1}$)	Weight-specific fecundity 15°C (d $^{-1}$)	Source	W_{φ} (μ g C)
Sac spawners				
<i>Euchaeta norvegica</i>	2.77	0.023	Hopkins (1977)	722.0
<i>Euterpina acutifrons</i>	9.35	0.230	Zurlini et al. (1978)	0.9
<i>Oithona similis</i>	4.50	0.100	Sabatini & Kjørboe (1994)	0.6
<i>Pseudocalanus elongatus</i>	4.75	0.078	Corkett & Zillioux (1975)	8.4
<i>Pseudocalanus elongatus</i>	5.53	0.090	Paffenhöfer & Harris (1976)	8.5
<i>Pseudocalanus elongatus</i>	2.70	0.110	Frost (1985)	8.4
<i>Pseudocalanus minutus</i>	4.00	0.100	Dagg (1977)	8.6
<i>Pseudocalanus moultoni</i>	7.51	0.080	Jonasdottir (1989)	5.1
<i>Pseudocalanus newmani</i>	5.56	0.060	Jonasdottir (1989)	4.7
<i>Pseudodiaptomus marinus</i>	6.48	0.100	Uye et al. (1983)	6.5
Broadcast spawners				
<i>Acartia californiensis</i>	19.91	0.149	Trujillo Ortiz (1990)	4.0
<i>Acartia clausi</i>	40.41	0.346	Landry (1978)	2.5
<i>Acartia clausi</i>	10.60	0.140	Iwasaki et al. (1977)	2.7
<i>Acartia clausi</i>	23.09	0.375	Uye (1981)	1.5
<i>Acartia clausi</i> = <i>A. omori</i>	38.91	0.486	Ayukai (1988)	2.7
<i>Acartia steueri</i>	25.40	0.294	Uye (1981)	3.9
<i>Acartia tonsa</i>	50.00	0.290	Dagg (1977)	5.2
<i>Acartia tonsa</i>	22.00	0.280	Ambler (1986)	3.4
<i>Acartia tonsa</i>	25.58	0.192	Corkett & Zillioux (1975)	4.0
<i>Acartia tonsa</i>	33.52	0.467	Kjørboe et al. (1985b)	4.0
<i>Acartia clausi hudsonica</i>	20.00	0.320	Sekiguchi et al. (1980)	2.5
<i>Calanoides carianatus</i>	50.35	0.340	Borchers & Hutchings (1986)	48.0
<i>Calanus australis</i>	40.00	0.130	Attwood & Peterson (1989)	73.6
<i>Calanus marshallae</i>	41.57	0.120	Peterson (1988)	104.0
<i>Calanus pacificus</i>	28.00	0.090	Razouls et al. (1991)	98.7
<i>Calanus pacificus</i>	75.08	0.233	Runge (1984)	80.4
<i>Centropages hamatus</i>	17.00	0.083	Tiselius et al. (1987)	10.0
<i>Centropages hamatus</i>	40.00	0.160	Fryd et al. (1991)	10.0
<i>Centropages typicus</i>	60.00	0.149	Dagg (1977)	14.9
<i>Centropages typicus</i>	103.55	0.272	Fryd et al. (1991)	14.4
<i>Centropages typicus</i>	94.92	0.203	Smith & Lane (1985)	17.3
<i>Centropages typicus</i>	60.00	0.160	Nival et al. (1990), Davis & Alatalo (1992)	10.5
<i>Centropages typicus</i>	65.00	0.159	Tiselius et al. (1987)	14.3
<i>Labidocera euchaeta</i>	45.00	0.150	Seinje & Song (1989)	48.0
<i>Paracalanus parvus</i>	37.40	0.274	Checkley (1980)	3.0
<i>Paracalanus parvus</i>	22.00	0.264	Tiselius et al. (1987)	3.0
<i>Paracalanus</i> sp.	29.40	0.210	Uye & Shibuno (1992)	3.5
<i>Sinocalanus tenellus</i>	34.64	0.214	Kimoto et al. (1986b)	5.1
<i>Temora longicornis</i>	16.56	0.044	Corkett & Zillioux (1975)	15.0
<i>Temora longicornis</i>	24.00	0.133	Tiselius et al. (1987)	15.0
<i>Temora longicornis</i>	31.85	0.069	Harris & Paffenhöfer (1976)	18.4
<i>Temora styleferæ</i>	35.84	0.170	Abou Debs & Nival (1983)	12.6
<i>Tortanus discaudatus</i>	36.12	0.181	Lawrence & Sastry (1985)	20.0
<i>Undinula vulgaris</i>	11.84	0.039	Park & Landry (1993)	67.7

Appendix 3. Development times converted to 15°C by assuming a $Q_{10} = 3.0$. The somewhat variable definitions of developmental times among studies have been indicated. Carbon content of females also shown

Species	Dev. time 15°C, d	Defined as	Source	W_f ($\mu\text{g C}$)
Sac spawners				
<i>Eurytemora affinis</i>	18.10	Hatching to adult	Heinle & Flemer (1975)	2.3
<i>Eurytemora affinis</i>	23.55	Egg to ovigerous fem.	Katona (1970)	2.3
<i>Eurytemora herdmani</i>	19.00	Egg to ovigerous fem	Katona (1970)	1.8
<i>Oithona colcarva</i>	26.00	Hatching to adult	Lonsdale (1981)	0.45
<i>Oithona davisae</i>	37.26	Hatching to adult	Uchima (1979)	0.23
<i>Oithona nana</i>	33.45	Hatching to egg-laying	Haq (1965)	0.2
<i>Oithona similis</i>	19.70	Egg to adult	Sabatini & Kjørboe (1994)	0.6
<i>Pseudocalanus elongatus</i>	21.00	Egg to adult	Landry (1983)	8.4
<i>Pseudocalanus elongatus</i>	21.36	Hatching to adult	Thompson (1982)	8.4
<i>Pseudocalanus elongatus</i>	19.07	Hatching to adult	Paffenhöfer & Harris (1976)	8.4
<i>Pseudodiapto hessei</i>	31.24	Egg to adult	Jerlings & Wooldridge (1991)	10.24
<i>Pseudodiaptomus marinus</i>	38.73	Egg to adult	Uye et al. (1983)	6.5
<i>Oncaea mediterranea</i>	51.06	Hatching to adult	Paffenhöfer (1993)	2.6
Broadcast spawners				
<i>Acartia tonsa</i>	20.30	Egg to adult	Landry (1983)	4
<i>Calanoides carinatus</i>	19.37	Egg to adult	Peterson & Painting (1990)	48
<i>Calanoides carinatus</i>	21.00	Egg to adult	Hirche (1980)	48
<i>Calanoides carinatus</i>	16.85	Egg to adult	Borchers & Hutchings (1986)	48
<i>Calanus helgolandicus</i>	26.20	Hatching to adult	Thompson (1982)	71.1
<i>Calanus australis</i>	21.48	Egg to adult	Peterson & Painting (1990)	88
<i>Calanus marshallae</i>	36.00	Egg to adult	Peterson (1986)	104
<i>Calanus pacificus</i>	19.80	Egg to adult	Landry (1983)	98.7
<i>Calanus pacificus</i>	23.00	Egg to adult	Mullin & Brooks (1970)	98.7
<i>Calanus sinicus</i>	24.70	Egg to adult	Uye (1988)	80
<i>Centropages hamatus</i>	27.36	Egg to adult	Fryd et al. (1991)	10
<i>Centropages typicus</i>	20.31	Egg to adult	Fryd et al. (1991)	14.4
<i>Centropages typicus</i>	25.82	Egg to adult	Carlotti & Nival (1992)	14.3
<i>Centropages typicus</i>	27.83	Egg to adult	Smith & Lane (1985)	17.32
<i>Labidocera euchaeta</i>	46.39	Egg to adult	Senjie & Song (1990a)	48
<i>Paracalanus parvus</i>	18.60	Egg to adult	Landry (1983)	3
<i>Paracalanus parvus</i>	17.80	Hatching to adult	Davis (1984)	3
<i>Sinocalanus tenellus</i>	21.20	Egg to adult	Kimoto et al. (1986a)	5.12
<i>Temora longicornis</i>	18.61	Hatching to adult	Harris & Paffenhöfer (1976)	18.4

Appendix 4. Developmental rates of nauplii, copepodids and late copepodids (C4 or C5 to C6) converted to 15°C by assuming a $Q_{10} = 3.0$. Developmental rates were calculated as the inverse of the stage duration; stage durations were calculated either from median development time (50% fractile of cohort) (MDT), mean time of stages (MTS), or from mean duration for isolated individuals (MDI). *Species with both C4 and C5 of longer duration than younger stages

Species	Developmental rate 15°C (stage h ⁻¹)			Method	Source	W_f ($\mu\text{g C}$)
	Nauplii	Copepodids	C4/C5 to C6			
Sac spawners						
<i>Eurytemora herdmani</i>		0.032	0.025	MTS	Escribano & McLaren (1992)	1.8
<i>Oithona davisae</i>	0.018	0.014	0.008	MTS	Uchima (1979)	0.2
<i>Oithona similis</i>	0.025	0.025		MDI	Sabatini & Kjørboe (1994)	0.6
<i>Pseudocalanus elongatus</i>	0.099	0.017	0.016	MDI	Thompson (1982)	8.4
<i>Pseudocalanus sp.</i>	0.037	0.020	0.017	MDT	Landry (1983)	8.4
<i>Pseudodiaptomus hessei</i>	0.018	0.015	0.011	MDI	Jerling & Wooldridge (1991)	10.2
<i>Pseudodiaptomus marinus</i>	0.021	0.008	0.008	MTS	Uye & Onbé (1975)	6.5
Broadcast spawners						
<i>Acartia tonsa</i>	0.032	0.032		MDT	Berggreen et al. (1988)	4.8
<i>Acartia tonsa</i>	0.030	0.023	0.017	MDT	Landry (1983)	4.0
<i>Acartia clausi</i>		0.023		MDT	Landry (1983)	2.0
<i>Calanoides carinatus</i> *	0.039	0.021	0.013	MDT	Peterson & Painting (1990)	48.0
<i>Calanus australis</i>	0.033	0.020	0.013	MDT	Peterson & Painting (1990)	88.0
<i>Calanus pacificus</i> *	0.043	0.021	0.012	MDT	Landry (1983)	117.0
<i>Calanus pacificus</i> *		0.014	0.009	MDT	Vidal (1980b)	117.0
<i>Calanus marshallae</i>	0.016	0.016	0.009	MDT	Peterson (1986)	106.0
<i>Calanus helgolandicus</i> *	0.047	0.012	0.009	MTS	Thompson (1982)	71.1
<i>Calanus sinicus</i>	0.035	0.018	0.008	MDT	Uye (1988)	80.0
<i>Sinocalanus tenellus</i>	0.042	0.024	0.012	MDT	Kimoto et al. (1986a)	5.1
<i>Rnincalanus nasutus</i> *	0.033	0.016	0.014	MDT	Landry (1983)	150.0
<i>Centropages hamatus</i>	0.021	0.015	0.014	MDT	Fryd et al. (1991)	10.0
<i>Centropages typicus</i> *	0.032	0.019	0.014	MDT	Fryd et al. (1991)	14.3
<i>Centropages typicus</i>		0.015	0.012	MDI	Carlotti & Nival (1992)	14.3
<i>Centropages typicus</i> *		0.029	0.009	MDT	Smith & Lane (1985)	14.3
<i>Labidocera trispinosa</i>	0.028			MDT	Landry (1983)	33.0
<i>Labidocera euchaeta</i> *	0.113	0.006	0.004	MTS	Senjie & Song (1990a)	48.0
<i>Paracalanus parvus</i>	0.042	0.019	0.015	MDT	Landry (1983)	3.0
<i>Temora longicornis</i> *	0.029	0.020	0.011	MDT	Klein Breteler & Gonzalez (1986)	8.4

Appendix 5. Weight-specific growth rates of nauplii, copepodids and/or for the entire development, converted to 15°C by assuming a $Q_{10} = 3.0$. Female carbon contents also shown

Species	Growth rate 15°C (d ⁻¹)			Source	W _♀ (µg C)
	Nauplii	Copepodids	All C4 or C5 to C6		
Sac spawners					
<i>Eurytemora herdmani</i>		0.354		Escribano & McLaren (1992)	2.9
<i>Eurytemora affinis</i>			0.250	Heinle & Flemer (1975)	2.3
<i>Pseudodiaptomus marinus</i>	0.133	0.205		Uye et al. (1983)	6.5
<i>Pseudocalanus</i> sp.		0.220		Vidal (1980b)	7.2
<i>Pseudocalanus elongatus</i>	0.198	0.230		Klein Breteler et al. (1982)	8.3
<i>Pseudocalanus elongatus</i>	0.211	0.324		Paffenhöfer & Harris (1976)	8.5
<i>Oithona similis</i>			0.200	Sabatini & Kjørboe (1994)	0.6
<i>Oncaea mediterranea</i>		0.150		Paffenhöfer (1993)	2.6
Broadcast spawners					
<i>Acartia clausi</i>	0.378	0.336		Klein Breteler et al. (1982)	4.8
<i>Acartia clausi</i> (<i>A. omori</i>)	0.294	0.358		Uye (1988)	2.7
<i>Acartia tonsa</i>			0.361	Berggreen et al. (1988)	4.5
<i>Calanus helgolandicus</i>	0.410	0.410		Paffenhöfer (1976)	71.1
<i>Calanus marshallae</i>			0.305	Peterson (1986)	104.0
<i>Calanus pacificus</i>		0.329		Vidal (1980b)	117.0
<i>Calanus sinicus</i>	0.341	0.462		Uye (1988)	80.0
<i>Centropages hamatus</i>	0.170	0.186	0.172	Fryd et al. (1991)	10.0
<i>Centropages hamatus</i>	0.275	0.356		Klein Breteler et al. (1982)	10.0
<i>Centropages typicus</i>	0.282	0.302	0.279	Fryd et al. (1991)	15.0
<i>Labidocera euchaeta</i>		0.176		Senjie & Song (1990b)	48.0
<i>Paracalanus parvus</i>	0.173	0.271		Uye (1988)	3.0
<i>Paracalanus</i> sp.	0.180	0.390		Uye (1991), Uye & Shibuno (1992)	3.5
<i>Sinocalanus tenellus</i>	0.296	0.413		Kimoto et al. (1986a)	5.1
<i>Temora longicornis</i>	0.237	0.408		Harris & Paffenhöfer (1976)	18.4
<i>Temora longicornis</i>	0.250	0.356		Klein Breteler et al. (1982)	11.5

Appendix 6. Growth rates (g) estimated from egg and female carbon contents (W_{egg} and $W_{\text{♀}}$, respectively) and development times (D) converted to 15°C, as $g = \ln(W_{\text{♀}}/W_{\text{egg}}) / D$

Species	W _♀ (µg C)	W _{egg} (µg C)	Dev. time 15°C (d)	Source	Growth rate (d ⁻¹)
Sac spawners					
<i>Eurytemora affinis</i>	2.3	0.043	18.10	Heinle & Flemer (1975)	0.250
<i>Eurytemora herdmani</i>	1.8	0.029	19.00	Katona (1970)	0.217
<i>Oithona davisae</i>	0.2	0.009	37.26	Uchima (1979)	0.087
<i>Oithona similis</i>	0.6	0.014	19.70	Sabatini & Kjørboe (1994)	0.191
<i>Pseudocalanus elongatus</i>	8.3	0.143	21.00	Landry (1983), Thompson (1982)	0.193
<i>Pseudodiaptomus marinus</i>	6.5	0.047	38.50	Uye et al. (1983)	0.128
Broadcast spawners					
<i>Acartia clausi</i>	4.8	0.025	18.00	Klein Breteler et al. (1982)	0.292
<i>Acartia tonsa</i>	4.8	0.030	20.30	Landry (1983)	0.250
<i>Calanoides carinatus</i>	44.0	0.300	19.37	Peterson & Painting (1990)	0.262
<i>Calanus australis</i>	88.0	0.240	21.48	Peterson & Painting (1990)	0.273
<i>Calanus marshallae</i>	104.0	0.188	36.00	Peterson (1986)	0.175
<i>Calanus pacificus</i>	117.0	0.250	19.80	Landry (1983)	0.311
<i>Calanus sinicus</i>	80.0	0.200	23.00	Uye (1988)	0.260
<i>Calanus</i> sp. ^a	71.1	0.320	26.20	Thompson (1982)	0.206
<i>Centropages hamatus</i>	10.0	0.040	21.82	Fryd et al. (1991)	0.253
<i>Centropages typicus</i>	14.3	0.037	20.31	Fryd et al. (1991)	0.293
<i>Labidocera euchaeta</i>	48.0	0.160	46.39	Senjie & Song (1990a)	0.325
<i>Paracalanus parvus</i>	3.0	0.030	17.80	Landry (1983)	0.259
<i>Sinocalanus tenellus</i>	5.1	0.036	21.20	Kimoto et al. (1986b)	0.234
<i>Temora longicornis</i>	18.4	0.040	32.50	Harris & Paffenhöfer (1976)	0.189

^a Corkett et al. (1986) considered *Calanus* sp. from Thompson (1982) to be *C. helgolandicus*

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