

Optimal development time in pelagic copepods

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ABSTRACT: According to life history theory, development times have evolved to an optimum solution of the trade-offs between rapid development and high fecundity: rapidly developing individuals have a higher chance of surviving to maturity than do slowly developing ones, but they mature at a smaller size and, thus, have lower fecundity. Here we develop a model to predict egg-to-adult times in marine pelagic marine copepods that maximizes fitness, quantified either as lifetime reproductive output or population growth rate. The model is tested against global data sets of development time as a function of temperature. The optimum development time increases when the enhancement of fecundity with delayed maturation increases, and it decreases with increasing juvenile mortality. Our predictions match the patterns in nature for broadcast spawners, for which most data are available, but appear to underpredict development times for sac-spawning copepods. The partial uncoupling of growth and development rates in copepods demonstrated in laboratory experiments, the substantial variation in age at maturity observed in copepod field populations, as well as the fair match of predicted and observed development times together suggest that development rates in marine pelagic copepods are tuned to the prevailing predation mortality. Observations in freshwater zooplankton suggest that life histories may be adapted to local conditions of growth and predation mortality. The striking lack of similar observations in marine zooplankton calls for work to explore the significance of environmental modulation of life histories of marine zooplankton. Possible future research avenues are proposed, including studies of the effects of seasonal environments, variable presence of predators and the effects of sexual selection on life histories of marine planktonic copepods.

KEY WORDS: Fitness · Net reproductive rate · Population growth rate · Fecundity · Mortality

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INTRODUCTION

Through the process of natural selection the behaviour and ecology of an organism have been tailored to maximize its fitness, that is, to maximize its offspring's contribution to future generations. Many aspects of organism biology are best understood in this perspective. This applies also to fundamental properties of the life history, such as development times (e.g. egg hatch times and egg-to-adult time). Among copepods and other ectotherms there are consistent patterns in development times that are related to organism size and temperature (Hirst & Kiørboe 2002, Hirst & López-Urrutia 2006). Both growth and development rates of an organism are related to its rate of food acquisition, but within the constraints posed by feeding and

growth rates, the duration of juvenile stages and developmental rates may vary substantially. At a given growth rate, the organism may mature early at a small size or it may mature later at a larger size. In copepods, maturation and development are closely related since a juvenile has to pass through all naupliar and copepodid stages before it matures; in most pelagic copepods, this implies 6 naupliar stages and 5 copepodid stages prior to maturation in the 6th copepodid stage. But even here, development may be fast or slow relative to the growth rate resulting in, respectively, small and large adults. Variable size at maturation in copepods is commonly observed for field populations in seasonal environments (Uye & Sano 1995, Hirst et al. 1999) and in the laboratory under varying food or temperature conditions (Ban 1994).

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According to classical life history theory (e.g. Stearns & Crandall 1981, Roff 1984, Kozłowski 1992), the optimum development rate represents the optimum solution to the trade-offs between high survival and high fecundity at maturation. Rapidly developing individuals mature fast and, hence, have a higher survival at time of maturation than do slowly developing individuals, but they mature at a smaller size and, therefore, have a lower potential fecundity than large adults. The optimum solution to this dilemma is the development rate that results in the largest offspring production, or the highest population growth rate, depending upon the measure of fitness.

Life history theory has been successful in predicting variations in age and size at maturation in a variety of organisms, including insects (Nylin & Gotthard 1998), fish and lizards (Charnov et al. 2001, Olsen et al. 2004), snails (Lafferty 1993) and cladocerans (Stibor 1992, Macháček 1993, Fiksen 1997). Life history theory has also been successful in predicting the duration of the pelagic larval phase in benthic invertebrates (e.g. Havenhand 1993, Miller 1993) as well as trends in egg hatching times in pelagic animals (Kjørboe & Sabatini 1994, Hirst & López-Urrueta 2006). Life history theory in conjunction with assumptions of evolutionary stable strategies has also been applied to copepods to predict natural mortality rates (Myers & Runge 1983). In this study we examine optimum development times in pelagic copepods by means of a simple life history model using 2 different fitness criteria. We compare the predicted optimum with actually observed development times for copepod field populations. Because mortality rates of copepod field populations depend on the ambient temperature (Hirst & Kjørboe 2002) we compare observations with predictions as a function of temperature. Development time may be adaptable on short time scales, but here we ignore differences in mortality pressure between environments and consider only trends that transcend any between-site and within-species variability except that predicted from temperature.

MATERIALS AND METHODS

Optimal development time. Fitness measures, R_0 and r : We seek the optimal development rate by using 2 alternative fitness measures, the net reproductive rate (R_0) and the Malthusian growth parameter (r) derived from life history theory. R_0 , or the number of offspring that an average female delivers to the next generation, is a commonly accepted fitness measure (e.g. Stearns 1992), and is also used in models of optimal development rates (Charnov et al. 2001). It is roughly equal to the ratio of reproductive rate to mor-

talidity rate and, thus, equivalent to the fitness measure used in optimal foraging theory, the rate of gain over the mortality rate (e.g. Gilliam & Fraser 1987, Houston & McNamara 1999). The alternative, but related, measure of fitness, r (Giske et al. 1993, Fiksen 1997) can also be used. The correct choice of fitness parameter depends on how density dependence acts on the population (Mylius & Diekmann 1995, de Valpine 2000). When density dependence is important, e.g. due to competition, R_0 is the appropriate fitness measure, while r applies when competition is unimportant and population regulation is density independent. Since it is unknown whether or not density dependence is important for the regulation of copepod populations, we apply both fitness measures.

The following is an extension of Kjørboe & Sabatini (1994) and is based on classical life history theory (e.g. Stearns 1992) adapted to pelagic copepods. The net reproductive rate is the lifetime egg production of an average female:

$$R_0 = \int_0^{\infty} I_x m_x dx \quad (1)$$

where I_x is the survival probability at age x and m_x is the expected age-specific fecundity (no. eggs female⁻¹ d⁻¹). Assuming that egg, juvenile and adult mortalities are constant (γ , μ and δ), and that the egg hatching time and juvenile development time to maturation are ρ and κ , respectively, we get:

$$I_x = e^{-\gamma x} \quad \text{for } x < \rho \quad (2a)$$

$$I_x = e^{-\gamma \rho} e^{-\mu(x-\rho)} \quad \text{for } \rho \leq x < \kappa \quad (2b)$$

$$I_x = e^{-\gamma \rho} e^{-\mu \kappa} e^{-\delta(x-\rho-\kappa)} = e^{(\delta-\gamma)\rho} e^{(\delta-\mu)\kappa} e^{-\delta x} \quad \text{for } x \geq \kappa \quad (2c)$$

Assume further that fecundity is zero until maturation and $m_x = m$ is constant for $x > (\kappa + \rho)$ then:

$$R_0 = e^{(\delta-\gamma)\rho} e^{(\delta-\mu)\kappa} m \int_{\kappa}^{\infty} e^{-\delta x} dx = e^{-\gamma \rho} \frac{m}{\delta} e^{-\mu \kappa} \quad (3)$$

The parameter r is now given by (assuming a 1:1 sex ratio):

$$r = \frac{\ln(R_0/2)}{T} \quad (4)$$

where T is the generation time:

$$T = \int_0^{\infty} x I_x m_x dx / \int_0^{\infty} I_x m_x dx = \int_{\kappa+\rho}^{\infty} x I_x m_x dx / \int_{\kappa+\rho}^{\infty} I_x m_x dx = \frac{1+\delta(\kappa+\rho)}{\delta} \quad (5)$$

Optimisation of fitness measures: Assume now that fecundity increases with developmental time raised to some power α :

$$m = f \kappa^\alpha \quad (6)$$

where f is a proportionality constant. Then:

$$R_0 = e^{-\gamma \rho} \frac{f \kappa^\alpha}{\delta} e^{-\mu \kappa} \quad (7)$$

The development time that yields the highest net reproductive rate can be found:

$$\frac{dR_0}{d\kappa} = 0 \Rightarrow \kappa = \frac{\alpha}{\mu} \quad (8)$$

which is to say that optimum development time varies inversely with juvenile mortality rate and is independent of fecundity as well as adult and egg mortality.

Optimisation of the other fitness measure, r , is more complicated. From Eq. (4) we get:

$$R_0 = 2e^{rT} \Rightarrow \frac{\partial R_0}{\partial \kappa} = 2e^{rT} \left(T \frac{\partial r}{\partial \kappa} + r \frac{\partial T}{\partial \kappa} \right) = R_0 \left(T \frac{\partial r}{\partial \kappa} + r \frac{\partial T}{\partial \kappa} \right) \quad (9)$$

Rearranging yields:

$$\frac{\partial r}{\partial \kappa} = \frac{1}{T} \left(\frac{1}{R_0} \frac{\partial R_0}{\partial \kappa} - r \frac{\partial T}{\partial \kappa} \right) \quad (10)$$

which is zero when:

$$r = \frac{1}{R_0} \frac{\partial R_0}{\partial \kappa} / \frac{\partial T}{\partial \kappa} = \left(\frac{\alpha}{\kappa} - \mu \right) \quad (11)$$

Combining Eqs. (4), (7) & (11) yields:

$$\frac{\alpha}{\kappa} (\delta^{-1} + \kappa + \rho) - \mu (\delta^{-1} + \rho) = \alpha \ln(\kappa) + \ln \left(\frac{e^{-\gamma p f}}{2\delta} \right) \quad (12)$$

The solution to this expression in terms of κ yields the optimum development time using r as the fitness measure. Examination of this expression reveals that optimum development time decreases with increasing juvenile mortality as described previously, but also with decreasing egg and adult mortality. Finally, in this formulation, the magnitude of the fecundity rate affects the optimal development time, such that higher fecundity implies faster development. These results are consistent with intuition.

Parameterisation. To provide estimates of optimum development times as a function of temperature we need estimates of the scaling of fecundity with development time (to determine the α and f parameters), as well as egg, juvenile and adult mortalities (γ , μ , and δ) as functions of temperature. Here we describe the parameterisation of each of these terms. We restrict all our analyses to data collected for female copepods in the epipelagic realm (0 to 200 m) and exclude observations of overwintering populations.

Fecundity versus development time (α , f): To estimate α and f we first compiled data on fecundity rates across species. We included only laboratory data where adults were kept under high food conditions (reported as approximately food saturated). Egg production rates were compiled together with egg and adult masses and temperature of incubation. The data set includes data from ~39 species (including 152 data points in total). Egg production rates were first corrected to 15°C using Q_{10} values of 1.60 and 3.15 for

broadcast and sac spawners, respectively (Bunker & Hirst 2004). We plot these temperature corrected fecundity rates as a function of adult body weight in Fig. 1a. Next we estimated development times (κ) for the animals producing each of the measured fecundity values from their corresponding egg and adult female carbon masses (EW and CW, respectively, both in $\mu\text{g C}$) by assuming a constant specific growth rate \hat{g} from the equation:

$$\kappa = \ln \left(\frac{CW}{EW} \right) / \hat{g} \quad (13)$$

A \hat{g} of 0.25 d^{-1} for juveniles at 15°C was assumed (Hirst & Bunker 2003), but we note that the estimate of α is independent of the magnitude of \hat{g} . The key assumption here is that the growth rate is size independent,

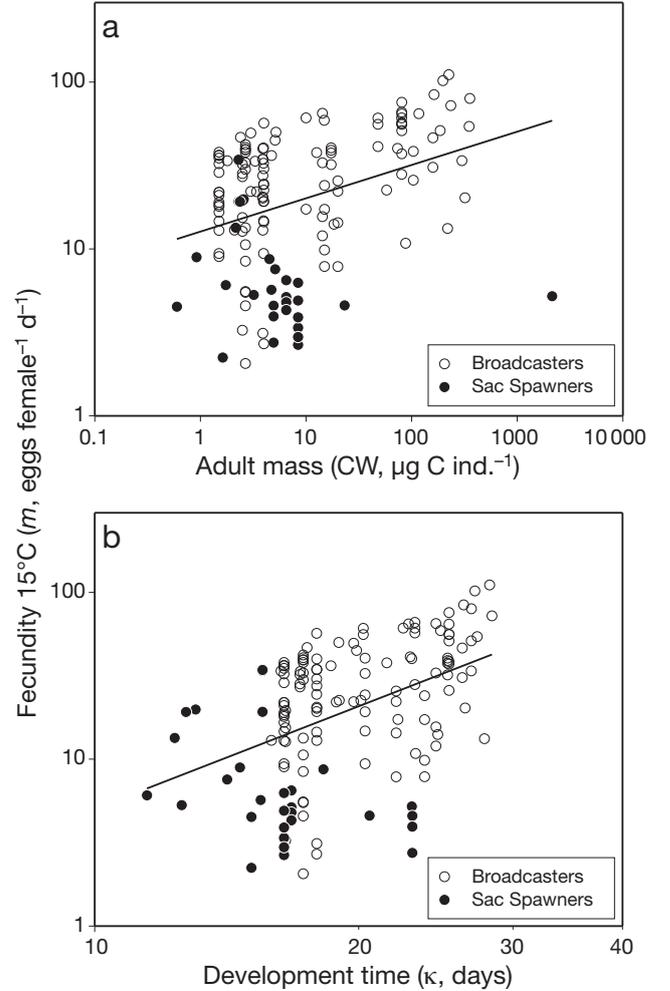


Fig. 1. (a) Food saturated egg production rate (m , no. eggs female⁻¹ d⁻¹) corrected to 15°C against adult mass (CW, $\mu\text{g C ind.}^{-1}$) [$\log_{10} m = 0.200 (\log_{10} CW) + 1.104$, $r^2 = 0.123$, $p < 0.001$]. (b) Food saturated egg production rate (m) corrected to 15°C against time taken to reach adulthood (κ , d) [$\log_{10} m = 2.039 (\log_{10} \kappa) - 1.336$, $r^2 = 0.191$, $p < 0.001$]. See 'Materials and methods' for details of determining development time

which is warranted by numerous observations for pelagic copepods (Huntley & Lopez 1992, Hirst & Bunker 2003).

When egg production is plotted as a function of development time estimated as previously detailed the slope provides an estimate of α ($\pm 95\%$ CI) as 2.04 (± 0.68) (Fig. 1b). The intercept of the regression in Fig. 1b (-1.336) gives the proportionality factor, f , at 15°C as $10^{(-1.336)} = 0.046$. To allow predictions of f across a range of temperatures we again applied the Q_{10} values of 1.60 and 3.15 for broadcast and sac spawners, respectively (Bunker & Hirst 2004), and used the following equation:

$$f_T = f_{15} Q_{10} e^{(T-15)/10} \quad (14)$$

Egg, juvenile and adult mortalities (γ , μ , and δ): We applied the relations between mortality and temperature determined for field populations of pelagic copepods by Hirst & Kiørboe (2002) and the equation for temperature dependent egg hatching times derived by Hirst & Bunker (2003). Separate equations were used for broadcast and sac spawning copepods (Table 1).

Observed development times. We compared our predictions of optimal development times as functions of temperature with the field observations of development times compiled by Hirst & Kiørboe (2002). This field data set includes 151 values from ~32 species taken within the growing season (i.e. excluding the overwintering period).

RESULTS

Development times estimated using R_0 as a fitness measure provide predictions that are of a similar order of magnitude as that observed in broadcast spawning copepods, for which most data are available (Fig. 2a), but somewhat underpredict observed development times in sac spawning copepods (Fig. 2b). For the broadcasters, observed development times mainly scatter within the range of predicted development

times based on 95% CI of estimated α . Using r as the fitness measure generally yields estimates of development time that are lower than those based on R_0 and than those observed. Both types of fitness measure estimates suggest that optimal development time

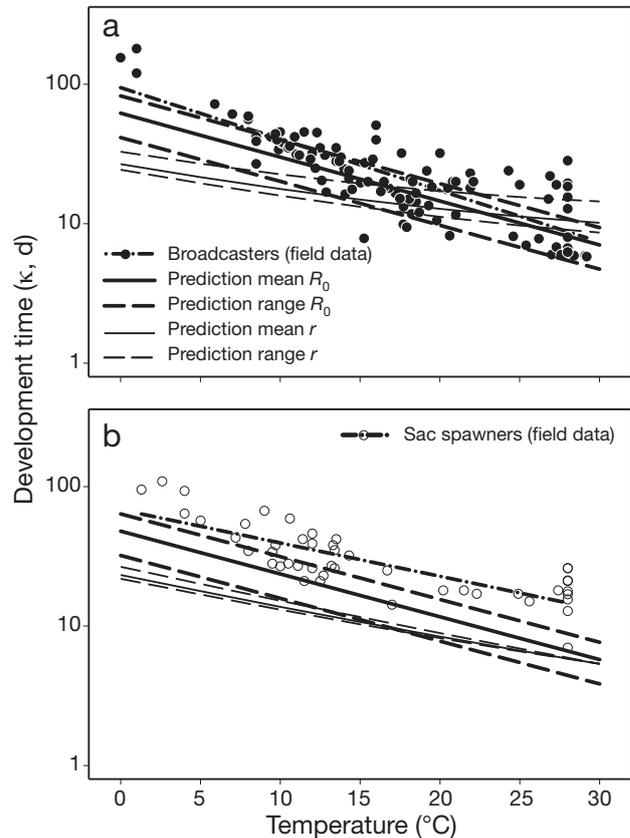


Fig. 2. Field measurements of development time of marine planktonic copepods versus temperature (data from Hirst & Kiørboe 2002) for (a) broadcast spawning and (b) sac spawning copepods. Regression through field data is given together with predictions from the optimal development time models (R_0 and r) when κ is 2.04. The range for the predicted development times are computed from the 95% CIs of the estimate of κ (95% CI ± 0.68)

Table 1. Parameters used to predict optimal development time as a function of temperature (T , $^\circ\text{C}$). Note that the equations for juvenile and adult mortality (μ , δ) are the same

	Broadcast spawners	Sac spawners	Source
α ($\pm 95\%$ CI)	2.04 (± 0.68)	2.04 (± 0.68)	This study (Fig. 1b)
Juvenile and adult mortality (μ , δ , d^{-1} , respectively) vs. temperature ($^\circ\text{C}$)	$\log_e \mu = 0.0725T - 3.415$	$\log_e \mu = 0.0707T - 3.157$	Hirst & Kiørboe (2002)
Egg mortality (γ , d^{-1}) vs. temperature ($^\circ\text{C}$)	$\log_e \gamma = 0.0725T - 1.112$	$\log_e \gamma = 0.0707T - 3.157$	Hirst & Kiørboe (2002)
Egg hatch time (ρ , d) vs. temperature ($^\circ\text{C}$)	$\rho = 1/[\exp(-1.822 + 0.0895T)]$	$\rho = 1/[\exp(-2.433 + 0.0877T)]$	Hirst & Bunker (2003)

would decline with temperature, as was observed. The scaling (slope) of the dependency is similar to that observed in the case of the R_0 -based estimates, while r -based estimates predict a weaker temperature dependency.

DISCUSSION

Life history theory in the present formulation predicts that the optimal development time depends on 4 things, viz. mortality rates (γ , μ , δ), egg stage duration (ρ), fecundity (f) and how much the reproductive output increases with a delay in maturation (α). The difference between the 2 fitness measures lies in whether fecundity and egg and adult mortalities, via their influence on generation time, have an effect on the optimum development time. Given the uncertainty in the estimate of α , predictions based on maximizing R_0 are consistent with the observed magnitudes and patterns in development times of field populations of pelagic copepods. It is unclear why estimates based on maximizing r yield such poor predictions, but it may have to do with the dependence of r on many parameters, each of which are estimated only within rather wide confidence limits.

The validity of the predicted development times, of course, depends on how well the parameters are determined and whether all sources of variability have been considered. Generally, the data bases available for estimating parameters are much larger for broadcast spawning than for sac spawning copepods (see references in Table 1) and, hence, the parameters are probably better determined. Accordingly, predictions are better for broadcast spawning copepods than for those that carry egg sacs. There are sources of variation that have not been considered. For example, variation in egg size may lead to variation in both fecundity and the survival of the juveniles, both of which may affect optimal development time. The R_0 -based estimate depends on only 2 parameters in a simple and straightforward manner (Eq. 8), while r -based estimates depend on many parameters in a convoluted way (Eq. 12). A sensitivity analysis reveals that r -based estimates of optimum development time are rather insensitive to fecundity (as f) and post-hatch mortalities (μ , δ) but quite sensitive to egg stage duration (ρ) and egg mortality (γ). Thus, estimates of optimum development time vary by <25% if the former parameters are varied by a factor of 2, while they vary by >60% if the latter parameters are varied by a factor of 2. Egg stage duration (ρ) is well constrained by observations, but estimates of egg mortality (γ) for field populations of copepods vary by orders of magnitude and are, thus, poorly determined (Hirst & Kiørboe 2002). An increase in egg

mortality by a factor of 2 leads to a ca. 65% increase in estimated juvenile development time, and this is all that it takes to bring the observations within the confidence limits (for α) of the prediction. A better fit of R_0 -based estimates to observations, therefore, cannot be taken as evidence that copepod field populations are under density dependent regulations.

Using either fitness measure, our optimal life history model implies that development rate is independent of the juvenile growth rate. That is, whether juvenile growth is fast or slow, juveniles should go through development at the same temperature-dependent optimum rate. Of course, there will be energetic constraints that limit the validity of this prediction; for example, development cannot proceed indefinitely if the organism does not feed and grow. The extreme example of such a situation is the overwintering populations of copepods that reside at depth during winter. In these copepods growth as well as development during winter is negligible and the timing of maturation, ascent and egg production is governed instead by the seasonality of the environment (e.g. Varpe et al. 2007). However, observations in constant laboratory environments do suggest that developmental rates in pelagic copepods are rather insensitive to variations in growth rate over a rather large range of growth rates (Vidal 1980a,b, Berggreen et al. 1988, Ban 1994). As a result, the body mass of adults depend on the food concentration at which the juveniles have been growing, such that well-fed juveniles result in large adults (rather than in early maturation). Similarly, copepod juvenile growth rate is typically less dependent on temperature than are development rates, yielding smaller adults at higher temperatures and vice versa. The widespread observation that adult sizes of individuals in the field vary with, for example, food availability and temperature in copepods (Dam & Peterson 1991, Uye & Sano 1995, Hirst et al. 1999) and many other organisms (Berrigan & Charnov 1994, Sibly & Atkinson 1994, Atkinson & Sibly 1997) is evidence that development rates are partly uncoupled from growth rates and, therefore, governed by other factors as well. The consistency we find between variation in the observed and predicted (by optimising for R_0) developmental rates leads us to conclude that development rates in pelagic copepods are tuned to the prevailing (predation) mortality rate to optimise their fitness, and that the order of magnitude of development times can be predicted from simple life history considerations.

The quality of the available data do not warrant a more detailed analysis of optimal development times in copepods, but there are several interesting and potentially fruitful questions about the adaptability and evolution of optimal development rates that may help define future research avenues. For example, life

history theory and the simple models developed here predict that developmental times may vary among environments, particularly such that copepods should develop faster in environments with a high predation pressure. The present analysis has only considered patterns that transcend such variability, but decreased development times in high risk environments have been demonstrated both in fish (Reznick et al. 1990) and in several species of invertebrates (e.g. Lafferty 1993), including planktonic freshwater cladocerans (Dodson & Havel 1988, Stibor 1992, Macháček 1993). In some cases such differences in development rate have been due to phenotypic plasticity and a direct response to the presence of predators, e.g. mediated by chemical cues, such as has been shown for freshwater cladocerans (Dodson & Havel 1988, Stibor 1992, Macháček 1993). In other cases such differences have been genetically fixed in populations living in different environments. There are many examples from freshwater zooplankton that their morphology, behaviour, and life history traits (including development rates and clutch size) may change in short timescales in response to the presence of predators (cf. references above) and a similarly striking lack of evidence of such phenomena exists in marine zooplankton (with the exception of a few studies that demonstrate predator-induced changes in diel vertical migration, e.g. Bollens et al. 1992, 1994, Frost & Bollens 1992). Whether this is due to a lack of published studies or to a fundamental difference between the 2 environments is not clear. However, comparisons of life history traits (size at maturation, development times) between copepod populations living in environments with contrasting predation pressure or manipulation of mortality rates in experimental populations may help us understand how copepods are adapted to different marine environments.

One implicit assumption in the above considerations has been that the environment is invariable in time. However, many environments occupied by copepods are strongly seasonal, and the length of the productive season may constrain development times (e.g. Abrams et al. 1996, Varpe et al. 2007). Development time may have to be short enough that the offspring can reproduce within the productive seasonal window or reach a particular developmental stage suitable for overwintering. Thus, *Calanus* spp., for example, that live in Arctic environments where the season is very short may have faster development rates than expected from the above temperature dependent prediction. Similarly, cohorts produced late in the season may mature faster than those produced early, also when corrected for temperature differences. The concentration of planktonic predators may also change during the season in a predictable manner, which may similarly lead to season dependent optimal development times.

These are all predictions that in principle are testable, but which in practice may be difficult to test from sampling field populations due to simultaneous variability in several conditions (food, temperature, length of remaining season, predators). A combination of field collections and laboratory experiments may, therefore, be necessary.

An additionally implicit assumption is that growth and survival are independent. In reality, there are trade-offs between growth and survival that arise in 2 ways. First, energy allocation to growth may occur at the expense of maintaining the organism (turning over proteins and repairing DNA), and vice versa. That is, few organisms grow at the rate which is physiologically and energetically possible, and this applies also to copepods (Kiørboe et al. 1985). This is why it is possible to increase the growth rates of fish, for example, by using growth hormones (Fauconneau 1985, Matty & Lone 1985). Second, growth requires feeding and feeding is risky; in copepods feeding typically implies food searching motility with the implication of elevated risk of meeting a predator (e.g. Titelman & Kiørboe 2003a,b, Visser 2007). Together this implies that survival and growth are interdependent and both related to availability of food. Optimization models ideally need to consider such interdependencies. The general prediction that size at maturity decreases with increasing mortality is robust to the inclusion of growth and survival trade-offs, but the response in development times may depend on the functional relations between survival, growth and developmental rate (Abrams & Rowe 1996). These relations need to be explored theoretically and experimentally for planktonic copepods. Such an extension might also help improve predictions based on r as a fitness measure.

Finally, we have assumed that males and females have similar life histories, but in fact they can be different. First, the optimum trade-off between maturation size and breeding capacity may be different among the genders, since gamete production may depend differently on adult size in males and females. Second, adult mortalities are typically much higher in males than in females and gender specific differences in mortalities may be different between species as judged from variable but typically female-biased adult sex ratios in field populations (Kiørboe 2006, 2007). Gender specific differences in adult mortality may lead to sexually dimorphic life histories (Crowley 2000). Finally, mate competition in males may favour early male maturation in the race for females, consistent with the observation that males of marine pelagic copepods typically mature earlier and at a smaller size than females (e.g. Berggreen et al. 1988, Ban 1994).

In conclusion, the present study has demonstrated that development rates in marine pelagic copepods are

largely consistent with simple formulations of life history theory. However, more detailed theoretical and experimental studies of the effects of seasonal environments, variable presence of predators and the effects of sexual selection may provide deeper insights into the variable, but overall similar, life histories of marine planktonic copepods.

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