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Towards a global model of in situ weight-specific growth in marine planktonic copepods

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Abstract The dependency of in situ weight-specific fecundity of adult females (as egg production) and growth of juveniles (as somatic production) upon individual body weight in marine planktonic copepods was examined. A compilation was made of results where wild-caught individuals were incubated in natural seawater (often pre-screened to remove large organisms), at near in situ temperatures, over short periods of the order of 24 h. The results demonstrate that for the adult broadcast-spawning group weight-specific fecundity rates are dependent upon body weight, but independent of temperature. We postulate this may be the result of global patterns in available phytoplankton. Weight-specific growth rates are dependent upon individual temperature and body weight in juvenile broadcast-spawners, with rates declining as body weight increases. Sac-spawners have growth/fecundity rates that are independent of body weight in adults, juveniles, and both combined, but which are temperature-dependent. Globally applicable equations are derived which may be used to predict growth and production of marine copepods using easily quantifiable parameters, namely size-distributed biomass and temperature. Some of the variability in growth which remained unaccounted for is the result of variations in food quantity and quality in the natural environment. Comparisons of the rates compiled here over the temperature range 10 to 20 °C with previously compiled food-saturated rates over the same temperature interval, revealed that in situ rates are typically sub-optimal. Adults appear to be more food-limited than juveniles, adult rates in situ being 32 and 40% of those

under food saturation in broadcasters and sac-spawners, respectively, while juvenile in situ rates are on average ~70% of those at food saturation in both broadcasters and sac-spawners.

Introduction

In order to appreciate the role of zooplankton in material flow and transformation in the sea, it is essential that their rates of growth and production can be determined, and the factors of control understood. Determining natural rates of growth in marine zooplankton is costly in time and effort, and a number of globally applicable models which allow prediction from a few easily measurable parameters such as temperature (Huntley and Lopez 1992) or temperature and body weight (Ikeda and Motoda 1978; Hirst and Shearer 1997) have been developed.

There has been much dispute over whether models of in situ weight-specific growth and fecundity need to be body-weight sensitive in copepods, but most recently Hirst and Shearer (1997) showed that juvenile weight-specific growth is body-weight dependent, while for adult female weight-specific fecundity this question was left unresolved. Kiørboe and Sabatini (1995) reported important differences between the growth rates of broadcast-spawners, i.e. those which shed eggs freely, and sac-spawners, i.e. those which carry their eggs externally on the body. The two spawning types were not distinguished by Hirst and Shearer, their aims being to compare the prediction abilities of previous global models and to produce a broadly applicable empirical equation without the need for separation of copepod taxa. These divisions were made in the present investigation, and the adult and juvenile distinction was also included. The principal aims of the present study were (1) to determine whether both weight-specific growth of adult females (fecundity) and juveniles (somatic) are body size and temperature-dependent in marine

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planktonic copepods; (2) to determine the differences between broadcast and sac-spawners; (3) to derive globally applicable equations for each of these groups (adults and juveniles, broadcasters and sac-spawners) that allow prediction of in situ growth of marine planktonic copepods.

Materials and methods

Data set

Data were taken from currently published literature on experimentally determined copepod growth. Studies included in this compilation were those where recently caught wild individuals were incubated at near in situ temperatures (i.e. within 5 °C of their environment), in natural seawater, but with possible pre-screening to remove larger predators and large organisms, over periods of typically around a day. If copepods were incubated for longer than a day, only studies where food was replaced daily were included. Studies where there was some form of adult female selection on the grounds of their reproductive readiness/maturity (e.g. Dam et al. 1994; Kosobokova 1994; Liang et al. 1994; Ashjian et al. 1995) were not included, as these give bias estimates of the total female population growth rate. Our selection criteria had the consequence that not only studies in which food was supplemented, but also those in which incubations were in filtered seawater were excluded (e.g. Plourde and Runge 1993; Bautista et al. 1994; Ohman and Runge 1994). Although large species may have similar growth rates in filtered and natural seawater over 24 h (e.g. Plourde and Runge 1993; Laabir et al. 1995), this is certainly not true in many smaller species (Dagg 1978; Guerrero et al. 1997; Saiz et al. 1997), and even at times in some large species (Armstrong et al. 1991). Investigations in which rates were described as being reduced because of too small a container size were also not included (e.g. Ianora and Buttino 1990). No selection took place on the grounds of the vertical location from which incubation water was taken, e.g. chlorophyll maxima, sea surface or several depths, etc. (see Saiz et al. 1997), only that it was from within close horizontal proximity and collected almost simultaneously to the copepods. The data compiled here were only derived from copepods collected within the epi-pelagic zone i.e. 0 to 200 m; deeper collections were excluded. The model results are therefore only meant for prediction over this depth range; this has other important implications (see "Discussion"). For a study to be included, weight-specific growth rates (d^{-1}), temperature of incubation (°C), and either measurements or approximations of the body weights of the growing individuals must have been retrievable from the paper, or communicated personally by an author. In some instances no weights were measured or assumed in the original study for adult females; in these cases absolute rates were extracted (e.g. eggs female $^{-1}$ d $^{-1}$), weight-specific rates were then derived using average egg and/or adult carbon weights for the species (from Kiørboe and Sabatini 1995). When weights were given as dry or ash-free dry weight, they were converted to carbon assuming this to be 40% of dry weight (Omori and Ikeda 1984; Parsons et al. 1984; Båmstedt 1986); ash-free dry weight was assumed to be 89% of dry weight (Båmstedt 1986). When weight-specific growth rates were derived using dry or nitrogen weights, we assumed these to be equal to carbon-specific rates. Although not every published account fulfilling the selection criteria may have been included here, those missing were not actively excluded, but simply missed in the literature trawl. The degree of averaging of growth and temperature measurements varies between studies. Rates were generally determined on tens of specimens, although at times < 10 individuals were examined, a point which has important implications (see "Discussion"). Some of the data represent averages from more than one location and/or time, however, the majority were derived from collections at a single location and time. All data were divided here on the basis of whether they represent adult fecundity or juvenile somatic growth, and into broadcasting or sac-spawning species. In the literature,

different workers have used different equations to estimate growth, and such differences can result in inter-comparison problems. We have standardised here such that adult weight-specific growth (g , d^{-1}) was assumed to be linear in form, as eggs are shed and not added to the body weight of the female:

$$g = W_e/W_a, \quad (1)$$

where W_e weight of eggs produced over 24 h, and W_a adult weight. Although the term used to define egg production is generally consistent in broadcast-spawners, it is not in sac-spawners; for example compare the definitions of Webber and Roff (1995b) and Nielsen and Sabatini (1996). Consequently, some slight variability between measurements may result from the lack of standardisation. Juvenile weight-specific growth (g , d^{-1}) was assumed to be exponential and of the form:

$$g = \ln[W_{t+1}/W_t], \quad (2)$$

where W_t weight at time zero, and W_{t+1} weight at time $t + 1$, i.e. after 1 d.

Although Hirst and Shearer (1997) previously included the data of Gerber and Gerber (1979) and Schnack et al. (1985), since growth was derived indirectly as missing components in physiological energy-matter budgets in these studies, they were excluded from the present investigation. Given our improved selection criteria of data, many of the errors associated with indirect estimates from physiological budgets (Huntley 1996) were not applicable to this set. Those errors associated with estimating growth from generation times (Kleppel et al. 1996), which may be directed at the previous global model of Huntley and Lopez (1992), are also inapplicable here. There are however, inherent problems in the methods included here: handling stress, copepod and food-patch destruction, altered migration habits for prey and predators, possible change in the light/dark cycle, reduced turbulence, altered con-specific and predator composition, and other 'bottle effects'. Although the weight-specific growth rates have been termed in situ in this study, they should therefore be regarded as approximations to this. All compiled results used here, including details of sources and calculations, are available on request as an appendix from A.G. Hirst.

The data set includes studies conducted at temperatures ranging from -2.3 to 29.0 °C, polar to tropical regions, highly eutrophic to oligotrophic waters, and estuarine to offshore waters. The number of species included was ~41, while individual body carbon weights covered almost five orders of magnitude (from 0.075 to 3620 µg C). A total of 952 measurements of growth with accompanying body weights and temperatures are incorporated, with this data being collected from over 50 studies. 743 measurements were made for adult females, 209 for juveniles, 793 for broadcast-spawners, 153 for sac-spawners and 6 for broadcast + sac-spawners (spawning type inseparable). No single study or species dominated the data set, although polar data and open-ocean data were least represented. Data for sac-spawners were more limited than those for broadcast-spawners, extending over a small range of temperatures and body weights (see Fig. 1). In this investigation, weight-specific growth values have been \log_{10} -transformed prior to regression analyses; this therefore demanded the exclusion of zero values, and 17 values are excluded.

Statistical analysis

Backwards stepwise-regression analyses were completed separately on adult broadcasters (AB), adult sac spawners (AS), juvenile broadcasters (JB), juveniles sac-spawners (JS), adult + juvenile broadcasters (AB + JB), adult + juvenile sac-spawners (AS + JS), and on the entire data set (AB + AS + JB + JS). The dependent variable was \log_{10} weight-specific growth (g , d^{-1}) and the independent variables were temperature (T , °C) and \log_{10} body weight (BW , µg C individual $^{-1}$), F-to-enter was set at 4.0, and F-to-remove at 3.9. In those cases where neither of the independent variables was removed, multiple linear regressions relating $\log_{10} g$ to both temperature and $\log_{10} BW$ were completed

Table 1 Statistical results of regression (multiple linear and least-squares linear) relating dependent variable weight-specific growth rate [$\log_{10} g$ (d^{-1})] to independent variables temperature (T , °C) and/or \log_{10} body weight (BW , μg C individual $^{-1}$). Multiple linear regression values given only in those cases where backwards-stepwise regression analysis demonstrated that both independent variables should be included (F -to-enter = 4.0 and F -to-remove = 3.9). For those data sets in which an independent variable did not statistically significantly add to prediction, results from linear regression using the remaining independent variable (*ind. var.*) are given (N number of data points)

Group	Backwards stepwise regression	Multiple linear regression			Linear regression			r^2	P	N		
		a	b	c	a	b	$ind. var.$					
		$\log_{10} g = a[T] + b[\log_{10} BW] + c$			$\log_{10} g = a + b[ind. var.]$							
Broadcast-spawners												
Adult	T removed	0.0111	-0.2917	-0.6447	0.538	(<0.001 ; 0.040)	-0.6516	-0.5244	$\log_{10} BW$	0.435	<0.001	(671)
Juvenile	both included	0.0087	-0.4902	-0.7568	0.490	(<0.001 ; <0.001)						(105)
Adult + juvenile	both included											(776)
Sac-spawners:												
Adult	$\log_{10} BW$ removed											(54)
Juvenile	$\log_{10} BW$ removed											(99)
Adult + juvenile	$\log_{10} BW$ removed											(153)
Broadcast + sac-spawners:												
Adult	both included	0.0133	-0.3569	-1.0475	0.361	(<0.001 ; <0.001)						(726)
Juvenile	both included	0.0370	-0.0795	-1.3840	0.347	(0.011; <0.001)						(209)
Adult + juvenile	both included	0.0208	-0.3221	-1.1408	0.435	(<0.001 ; <0.001)						(935)

(SigmaStat Package, Jandel Scientific). The coefficients a , b and c in the equation described by the form $\log_{10} g = a[T] + b[\log_{10} BW] + c$, are given in Table 1 together with R^2 values and significance levels. In those cases where one of the independent variables was found not to add significantly to the prediction, then a linear regression was completed relating $\log_{10} g$ to the remaining independent variable; these results are also given in Table 1.

Body-weight dependence was also examined using a second approach. Firstly, the growth rates were divided on the basis of incubation temperature into four 10 °C temperature categories; > -10.0 to ≤ 0.0 , > 0.0 to ≤ 10.0 , > 10.0 to ≤ 20.0 and > 20.0 to ≤ 30.0 °C. Growth rates within each of these bands were then adjusted to the mid-temperature value, i.e. -5, 5, 15 and 25 °C, by applying a Q_{10} value of 3.0 (see Kiørboe and Sabatini 1995). The adjusted values are shown graphically in Fig. 1. When data availability allowed, least-squares regression-analysis (Type I) was completed on adult broadcast-spawners, juvenile broadcast-spawners, adult sac-spawning copepods and juvenile sac-spawning copepods, in each of the four temperature groups. Only when more than one species was included was a regression completed, as intra-specific patterns were not of interest. Regressions were also completed on adult and juvenile data combined for each of the spawning types, and on the entire data set. A summary of data in each temperature group, together with the results of the regression, the product-moment correlation coefficients, and significance levels are given in Table 2.

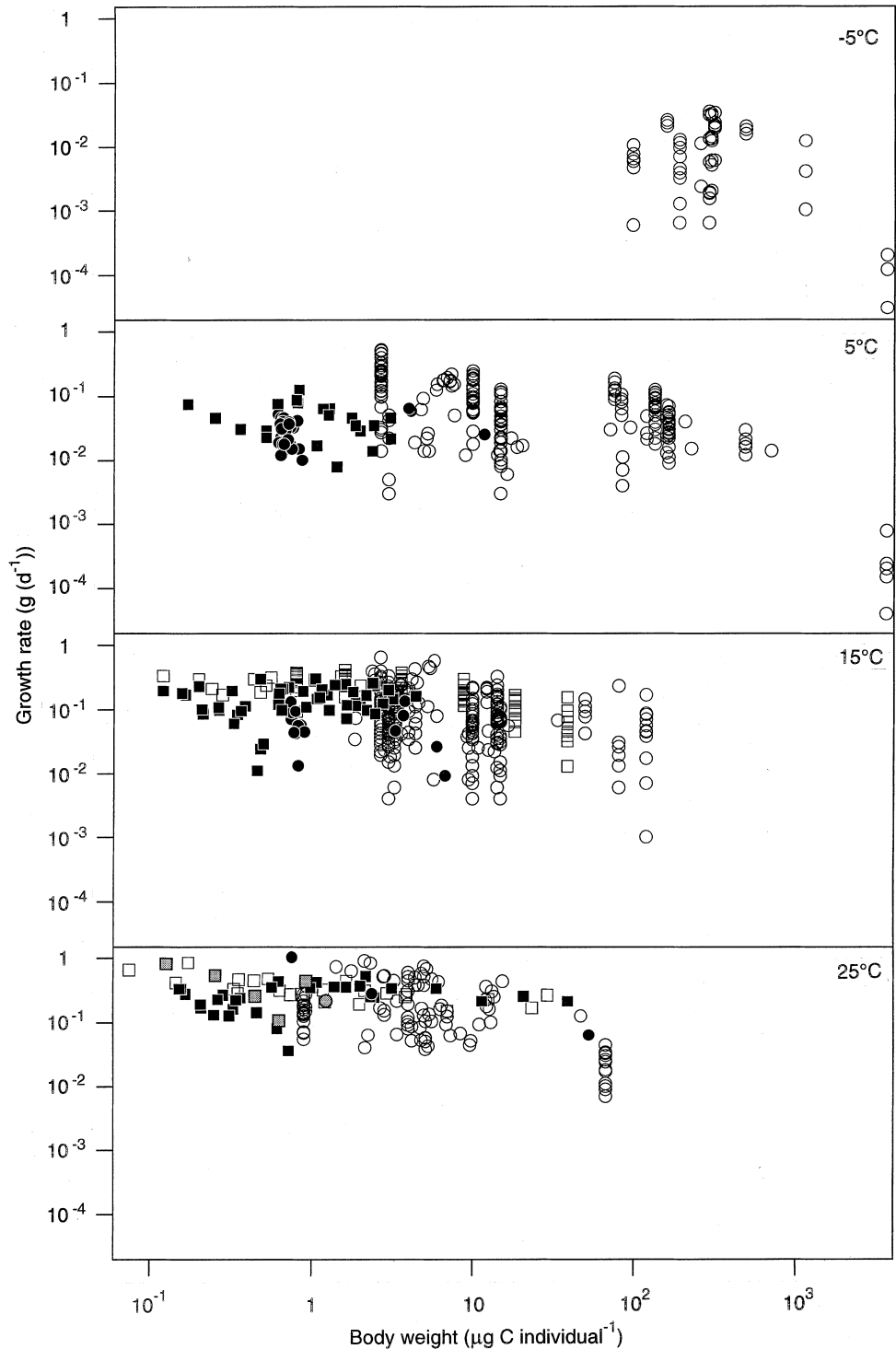
Results

Backwards stepwise-regression demonstrated that growth was not dependent on body weight in adult or juvenile sac-spawners, or for these two groups combined. Multiple linear regressions were therefore not completed, and instead linear regressions were used to describe the growth as a function of temperature (see Table 1). Backwards stepwise-regression showed that growth rates were dependent upon temperature and body weight for the entire data set (AB + AS + JB + JS), and also in juvenile broadcast-spawners.

For adult broadcast-spawners, the backwards stepwise-regression revealed that temperature did not add significantly to the prediction. We therefore examined further the apparent independence of temperature in this group by dividing the data into small body weight ranges, in order-of-magnitude steps (e.g. 0.5 to 1.5, 5 to 15 and 50 to 150 μg C individual $^{-1}$). Linear regressions were then completed on $\log_{10} g$ versus temperature for each of the delimited body weight groups. The data are shown in Fig. 2 and the statistical results in Table 3. The results from these three cases tested gave no evidence of a consistent and positive relationship between growth and temperature; in all cases there was no significant relationship ($P > 0.10$).

Fig. 1 and Table 2 summarise the copepod data included for each of the four 10 C° temperature bands, together with the results of the linear regression analysis. There were significant negative relationships (with P set at 0.05), with $\log_{10} g$ declining with increasing $\log_{10} BW$ for all broadcast-spawning sets of data, both for adults and juveniles, and both combined. For sac-spawners, the data did not show weight-dependence at any of the temperatures tested, either for adults, juveniles or

Fig. 1 Measured weight-specific growth of adult female (circles) and juvenile (squares) copepods as a function of spawning type (white broadcast; black sac; grey both). Data are divided into four temperature ranges, and adjusted to mid-temperature of each range (i.e. -5, 5, 15 and 25 °C using a Q₁₀ value of 3.0 (see Table 2 for statistical results))



adults + juveniles. These results are consistent with those from the backwards stepwise-regression.

Discussion

The results from this study agree broadly with those of an earlier empirical analysis, in which a data set dominated by juvenile broadcast-spawners showed decreasing

weight-specific growth with increasing body weight (Hirst and Shearer 1997). In the present paper we extend the analyses to consider differences between adults and juveniles and broadcasting and sac-spawners, using a much more extensive set of data. Weight-specific growth by sac spawners (adults, juveniles, and adults + juveniles) was independent of body weight, but increased with temperature. This is in contrast to broadcasting copepods (adults, juveniles and adults + juvenile) in

Table 2 Summary of linear (least-squares) regression analysis examining relationship between weight-specific growth rate and body weight (N number of data points)

T (°C)	Adult fecundity (A) or juvenile somatic growth (J), broadcast (B) or sac (S) spawners	(N)	No. species	Wt range ($\mu\text{g C individual}^{-1}$)	$\log_{10}[\text{g}]$ vs $\log_{10}[\text{BW}]$		r^2	P
					Intercept	Slope		
-5	AB	(71)	4	98–3620	-0.587	-0.715	0.139	<0.01
5	AB	(222)	~17	2.67–3620	-0.705	-0.424	0.309	<0.001
	AS	(33)	>3	0.618–11.8	-1.559	0.180	0.058	>0.05 ^{NS}
	AS + JS	(54)	>3	0.171–11.8	-1.507	-0.005	0.00003	>0.10 ^{NS}
	AB + AS + JS	(276)	>20	0.171–3620	-1.135	-0.184	0.097	<0.001
15	AB	(275)	~15	1.85–119.5	-0.970	-0.284	0.090	<0.001
	JB	(81)	5	0.12–38.8	-0.570	-0.339	0.551	<0.001
	AB + JB	(356)	~15	0.12–119.5	-0.822	-0.362	0.178	<0.001
	AS	(18)	>3	0.720–6.74	-1.250	-0.302	0.119	>0.10 ^{NS}
	JS	(48)	3	0.12–4.419	-0.876	0.125	0.034	>0.10 ^{NS}
	AS + JS	(66)	>5	0.12–6.74	-0.998	-0.069	0.082	>0.10 ^{NS}
	AB + AS + JB + JS	(422)	>20	0.12–119.5	-0.905	-0.284	0.149	<0.001
25	AB	(103)	11	0.90–67.7	-0.553	-0.500	0.339	<0.001
	JB	(24)	~5	0.075–29.394	-0.479	-0.193	0.548	<0.001
	AB + JB	(127)	~15	0.075–67.7	-0.555	-0.464	0.382	<0.001
	AS	(3)	3	0.760–53.120	-0.177	-0.617	0.952	>0.10 ^{NS}
	JS	(30)	3	0.153–39.179	-0.621	0.070	0.035	>0.10 ^{NS}
	AS + JS	(33)	4	0.153–53.120	-0.620	-0.015	0.001	>0.10 ^{NS}
	AB + AS + JB + JS	(166)	~20	0.075–67.7	-0.614	-0.367	0.319	<0.001

which weight-specific growth decreased with increasing body weight (see Tables 1 and 2). In all cases examined except adult broadcast-spawners, growth was temperature-dependent.

The fact that for adult broadcast-spawners there was no clear increase in weight-specific growth with temperature for given body weight ranges is rather unexpected. Comparisons made by Park and Landry (1993) using a much smaller data set, and without removing the effect of body weight, showed a similar result, however. On an intra-specific basis growth generally increases with temperature, and on an inter-specific basis it may also be expected to increase (see Clarke 1987); indeed, in the present study juvenile broadcast spawners and adult and juvenile sac-spawners, all demonstrated increasing weight-specific growth with temperature. Single species in some localities have natural growth rates that do not increase with increasing temperature, and in these cases food quantity or quality may be of overriding importance (e.g. McKinnon and Thorrold 1993). It has previously been suggested that growth in tropical and sub-tropical copepods may be reduced because food levels are lower than in temperate regions, with much of the phytoplankton dominated by pico- and nano-plankton which is largely unavailable to copepods (see Park and Landry 1993; Webber and Roff 1995a, b). Although the other groups (i.e. adult sac-spawners, and juvenile broadcast- and sac-spawners) demonstrated increasing growth with increasing temperature, they may have different dietary demands. Juvenile broadcast spawners may feed on small particles, while the sac-spawners included in the

data set here are commonly carnivorous or omnivorous, with the ability to feed raptorially (e.g. species of *Oithona*, *Oncaea*, *Euchaeta*). Although broadcasters may feed raptorially too, some are believed to feed entirely by mechanical filtration (Hansen et al. 1994), and their diet may be predominantly herbivorous. Important differences have previously been observed between the diets of sac-spawners such as species of *Oncaea*, *Corycaeus* and *Oithona* and the diets of calanoid copepods (Turner 1986). Sac-spawner growth in tropical regions may therefore be generally less influenced by the abundance of phytoplankton and more by the availability of suitable non-phytoplankton prey. The fact that studies in polar regions (and possibly temperate areas too) may be concentrated into periods with “better conditions” such as spring and summer (as in: Hirche and Bohrer 1987; Huntley and Escritor 1991; Tourangeau and Runge 1991; Lopez et al. 1993; Ward and Shreeve 1995) may lead to a bias towards higher growth rates being recorded. This would tend to lessen any relationship between increasing growth with increasing temperature. Diapausing individuals have also been actively excluded here, zero values are not included, and copepods generally diapause at depths outside those considered here.

The differences between the scaling of growth with body mass in broadcast-spawners and sac-spawners found here and by others (e.g. Kjørboe and Sabatini 1995) may be the result of differences in the prey types taken, or because of other energetic considerations. Klekowski et al. (1977) showed that respiration rates scale against body size differently in herbivorous cope-

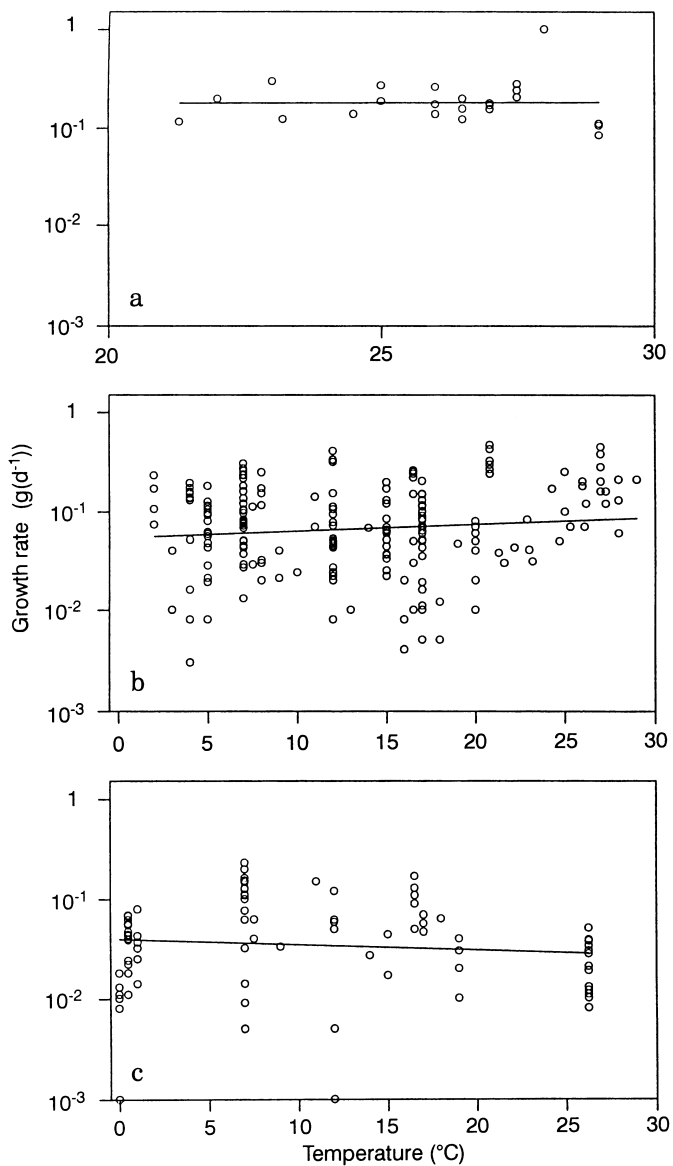


Fig. 2 Comparisons of \log_{10} weight-specific growth as a function of incubation temperature for adult broadcast-spawners in three body weight intervals: 0.5 to 1.5 $\mu\text{g C individual}^{-1}$ (a), 5 to 15 $\mu\text{g C individual}^{-1}$ (b), and 50 to 150 $\mu\text{g C individual}^{-1}$ (c). (see Table 3 for statistical results)

pods than in carnivorous copepods. Once again those defined in their study as herbivorous were predominantly broadcasters, while those classed as carnivores

were predominantly sac-spawners. Furthermore, two of the most common sac-carrying groups, namely Oithonidae and Oncaeidae, have daily rations which are lower than those for broadcast-spawning calanoids of a similar size (Paffenhöffer 1993).

The data compiled in the present study may be used to address the question as to whether weight-specific growth rates are generally food-saturated, as postulated by Huntley and Lopez (1992). Comparisons of the simulated in situ rates found here (at 15 °C) with the food-saturated rates compiled by Kiørboe and Sabatini (1995) (also at 15 °C, with the same temperature band and Q_{10} adjustment), can be made (Fig. 3). Under food-saturated conditions adult female weight-specific growth (fecundity) decreased with increasing body size both in broadcast-spawners and in sac-spawners, and although the slopes are parallel (with b values of -0.26), broadcasters' growth rates were 2.5 times those of sac-spawners (Kiørboe and Sabatini 1995). At 15 °C in situ growth rates were found to be weight-dependent in adult broadcast-spawners, with a slope of -0.28 ; this is similar to the slope for food saturation (Fig. 3a). For adult sac-spawners in situ, the slope is also similar at -0.30 (Fig. 3b), although in this instance the relationship for in situ growth is not significant ($P > 0.10$). This particular data set does only span an order of magnitude in body sizes and include only ~ 3 species. Food-saturated juvenile weight-specific growth rates are independent of weight for both broadcasters and sac-spawners. While in situ juvenile broadcasters show body-size dependence, the in situ rates in juvenile sac-spawners are body-size independent (see Fig. 3c, d;), however, the former set of data is largely dominated by a single species (*Calanus agulhensis*) and, if removed, the remaining points do not demonstrate a significant relationship ($P > 0.10$).

The degree of food limitation over 10 to 20 °C in nature may be assessed from these comparisons. For adult broadcast-spawners although the slopes for food-saturated and in situ rates are similar, the intercepts differ substantially (-0.474 and -0.970 , respectively). Thus, for an individual weighing 1 $\mu\text{g C}$, the predicted food-saturated growth rate is 0.336 d^{-1} , while in situ it is 0.107 d^{-1} . The same comparison for sac-spawning adults gives values of 0.141 and 0.056 d^{-1} at food saturation and in situ, respectively. In adult sac-spawners, the in situ rate is therefore 40% of the maximal rate, while for adult broadcast spawners it is 32%. In juvenile broadcasters, the mean rates under food saturation is

Table 3 Least-squares linear-regression results of \log_{10} weight-specific growth (g d^{-1}) as a function of temperature (T , °C) in adult broadcast-spawners, together with correlation coefficients and significance levels weight (N number of data points)

Body wt range ($\mu\text{g C individual}^{-1}$)	(N)	No. species	T range (°C)	$\log_{10}[\text{g}]$ vs T		r^2	P
				Intercept	Slope		
0.5–1.5	(23)	3	21.3–29	–0.766	+0.001	0.0001	> 0.10 ^{NS}
5–15	(216)	11	3–29	–1.265	+0.007	0.012	> 0.10 ^{NS}
50–150	(102)	6	0.0–26.25	–1.402	–0.005	0.013	> 0.10 ^{NS}

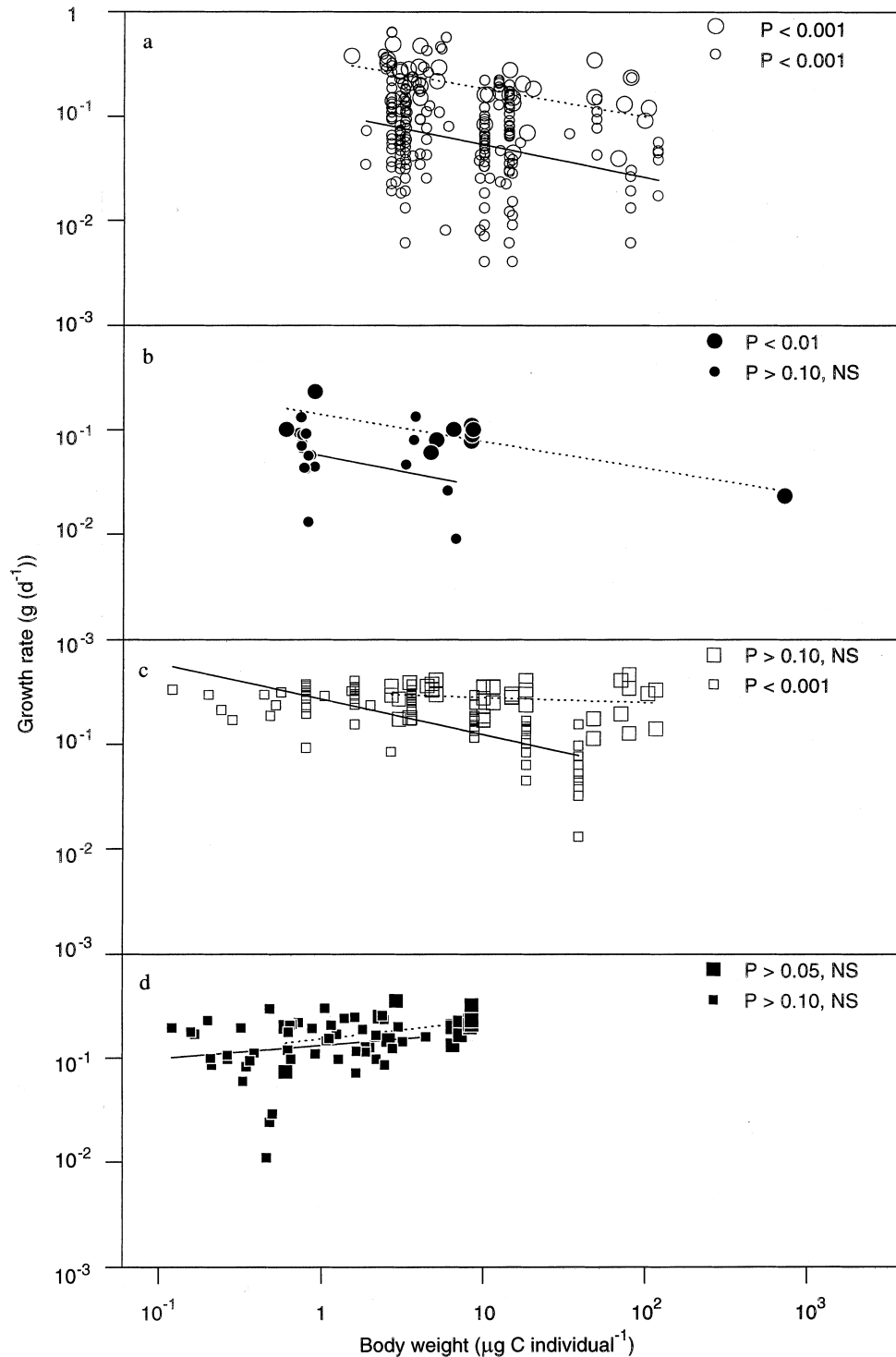


Fig. 3 Comparisons of food-saturated rates of copepod weight-specific growth (*large symbols; dotted lines* regressions), compiled by Kjørboe and Sabatini (1995), with in situ rates compiled here (*small symbols; continuous lines* regressions). Significance for each regression is given on graphs. **a** Adult broadcast-spawners; **b** adult sac-spawners; **c** juvenile broadcast-spawners; **d** juvenile sac-spawners. Both data sets adjusted to 15 °C using same methodology (although food-saturated juvenile weight-specific growth rates are regressed against adult body weight rather than the weight of the individuals for which growth was determined)

0.292 d⁻¹ and the in situ mean is 0.200 d⁻¹, i.e. 68% of the food-saturated value. For sac-spawning juveniles, the mean food-saturated growth rate is 0.210 d⁻¹, while the mean in situ rate is 0.149 d⁻¹, i.e. 71% of the food-saturated rate (comparison of in situ and food-saturated data for each spawning type by unpaired *t*-tests revealed significant differences in both cases: *P* < 0.005). These results suggest that adult female growth is more food-limited than juvenile growth in nature. Our findings

contradict the views of Huntley and Lopez (1992) that growth of copepods in nature proceeds at maximal rates, and the suggestion of Huntley and Boyd (1984) that zooplankton in coastal regions are not often food-limited. However, we cannot ignore the fact that some of the difference between the food-saturated (from Kiørboe and Sabatini 1995) and in situ rates for adult females (compiled herein) may arise in part from factors other than food availability, including male shortage (fertilisation limitation), reproductive readiness and age for adult females. There is however growing evidence that natural populations are often food-limited; food concentration and growth are often significantly and positively correlated, and there is direct experimental work in which supplements to natural food have resulted in increased growth of wild-caught individuals (e.g. Durbin et al. 1983, 1992; Kimmerer and McKinnon 1987; Guerrero et al. 1997).

Significant proportions of single stage-classes of marine copepods may not be actively growing at times (Uye and Sano 1995), and variation between individuals at a single location and time may be dramatic (Hay 1995). The method adopted here, using rates which are generally averaged for many individuals will reduce this variability. It is a common aim in zooplankton studies to determine growth and production of single species or communities (within spatially defined areas), and not to assess the variation between individuals of the same size/stage. As such, although some of the variability between individuals of the same species has been excluded, our method should lead to better prediction over the typical scales of interest.

The empirically-derived equations do not predict zero or negative growth, although many copepods certainly do occupy non-growing stages/phases in the natural environment (during diapause, and as non-feeding stages). The data compiled here were derived from copepods collected exclusively within the epi-pelagic zone, i.e. 0 to 200 m, and should not be extrapolated beyond this depth limit. Meso-pelagic crustaceans have much lower rates of respiration and excretion than epi-pelagic organisms of the same body size at the same temperatures (Ikeda 1988); their growth rates are also likely to differ. Given that the equations should only be applied over 0 to 200 m, organisms outside the epi-pelagic zone will be excluded. Many coastal and estuarine species diapause as eggs that are deposited in the sediment (Grice and Marcus 1981), while offshore species commonly diapause at depth greater than 200 to 500 m (see Longhurst and Williams 1992); prediction errors associated with these zero and negative growth rates may therefore be largely excluded, although not entirely eliminated (see results of Smith 1990; Hay et al. 1991). The equations derived here should be applied in such a way as to be sensitive to life-history. Some of the scatter in the relationships described here will result from the diapausing state of individuals and the proportion of non-growing individuals in a population.

Adult male growth as spermatophore production has not been included in the data set here. The only measurements, of which we are aware, that attempt to approximate in situ growth of adult males, are those completed by Escaravage and Soetaert (1993) on *Eurytemora affinis*. Adult males may make up a large fraction of the total copepod biomass, but many workers have simply excluded them from estimate of total production by assuming that they do not grow (e.g. Uye 1982; Roff et al. 1988; Chisholm and Roff 1990; Webber and Roff 1995b; Liang and Uye 1996; Liang et al. 1996). Others have assumed that they represent a fixed proportion of adult or juvenile female weight-specific growth (e.g. 50% of juvenile: Landry 1978). Escaravage and Soetaert (1993) found, over a range of temperatures, that adult male growth was ~30 to 95% of the rate of adult female growth (fecundity), and 40 to 60% of juvenile (somatic) growth. We recommend that until more data is available the general empirical equations derived here be applied directly to adults regardless of their sex, allowing rapid and low-effort estimation. This will lead to some inherent inaccuracy because some adults have reduced mouth parts and possibly do not feed, and these will have reduced or negative growth rates. In families such as the Aetideidae and Euchaetidae, all males appear to have atrophied mouth parts, whilst in other families such as the Calanidae, Eucalanidae, Clausocalanidae, Calocalanidae, Paracalanidae and Scolecithrichidae, only some genera or some species of some genera have atrophied mouth parts in males (G. Boxshall, Natural History Museum, London, personal communication).

Fecundity products are commonly assumed to be adequate indicators of the total growth achieved by adult female copepods (as eggs), and a similar assumption may be made with regard to adult males (as spermatophores). There is evidence that adult females may have body weights which are not in steady-state (Durbin and Durbin 1992; Durbin et al. 1992; Thompson et al. 1994), and polar species with large lipid reserves may show particularly strong uncoupling (Smith 1990; Hirche and Kattner 1993); this should be considered before the equations developed here are used to predict in these extreme environments. Further experimental work is required to confirm the assumption of "steady state" of adult body weights in nature. Neither *Neocalanus cristatus* nor *N. plumchrus* feed as adult females (Beklemishev 1954). Egg production does not equate to growth in these species. Given these groups are not present at depths < 200 m (see Heinrich 1962; Ohman 1987) they are therefore excluded when applying the model to the epi-pelagic realm. A source of error associated with many growth measurements is that for juveniles exuvae production is often not included. Exuvae production has been estimated at 8.4% of copepodite ash-free dry wt production (Chisholm and Roff 1990), although given the values derived by Vidal (1980: see his Table 3), in some species exuvae production may be as high as 12% of carbon production. We have made

no corrections to allow for underestimation of growth when this has been omitted by individual investigators.

Some of the variability in growth demonstrated in the present study at any given temperature and body size will arise from variation in the quantity and quality of available food, and also feeding history. The concentration of interfering particles such as a suspended sediment may also play a role in growth in coastal areas (Burkill and Kendall 1982; Irigoien and Castel 1995). In many of the studies from which data were utilised here, growth was found in the original study to be significantly (and positively) correlated with some descriptor of food abundance (e.g. Durbin et al. 1983; Kimmerer 1984; Peterson et al. 1991; Uye et al. 1992; McKinnon and Thorrold 1993; McKinnon 1996). Future work on global growth prediction should pursue this topic further, and improved prediction accuracy may come from considering food quantity and quality. Once food can be taken account of, we should be able to predict more accurately the variability in growth we know occurs. Carnivory, omnivory, detritivory, quality of food, prey selection and the feeding mechanisms used by copepods will make this task more difficult than simply considering chlorophyll *a* or particulate concentrations.

Given the scatter in weight-specific growth at a particular temperature and body size (Fig. 1), the equations derived can not be expected to give highly accurate prediction of growth and production under all circumstances. In Fig. 4 each measured value is compared against the prediction obtained using the overall equation which describes the entire data set (given in Eq. 3). Although the predicted values are of course not independent of the measured values, ~95% of the predicted

values are between 5 times and 0.2 times those measured, i.e. measured to predicted ratios of 5:1 and 1:5, respectively. We know of no generally available global model for predicting biomass of copepods or mesozooplankton. Biomass values established from a single point in time and from filtering less than several hundred cubic metres, are often extrapolated over days to months, and to encompass areas of hundreds of metres to tens of kilometres. The variability of copepod biomass over days to months and on the horizontal scale of 1 to 10 km may both be of the order 100-fold, while on the vertical scale of 10 to 100 m it may be of the order 1000-fold (Huntley and Lopez 1992). Investigations of copepod production commonly apply measured growth rates to biomass values determined with 200 μm -mesh nets, yet very large proportions of copepod biomass may pass through such nets. Although the results of our work demonstrate that growth in marine copepods is much more variable than suggested by the global model of Huntley and Lopez, biomass is still the component of the production equation that is least predictable and on which more effort needs now be focused.

Prediction using the equations presented here may be criticised for their accuracy; however, most studies where growth is measured directly only examine ~1 to 5 species in adult female and/or a few juvenile stages. In attempting to predict total copepod production, much inter-species and inter-stage extrapolation is completed in many studies of copepod production. It is obvious that typical methods of measuring growth are generally not practicable for measuring growth in entire copepod communities and at high resolution over wide areas. Our equations may present a credible alternative to the practical problems of growth determination.

The equations derived in this study allow rapid, inexpensive estimates of growth, with a need to only determine size distributed biomass and/or temperature. We suggested that the choice of relationship from Table 1, in estimations of growth and production, should depend on the availability of information, e.g. division of adults, juveniles, broadcast- and sac-spawning groups. Non-growing stages and eggs should be excluded if possible. The overall general relationship describing the entire set of data is given by:

$$\log_{10} g = 0.0208[T] - 0.3221[\log_{10} BW] - 1.1408 \quad (3)$$

This multiple linear regression has an R^2 of 0.435 and describes weight-specific growth (g) as a function of temperature (T) and body weight (BW). It should be noted that the data used to derive this empirical relationship is largely dominated by adult females and broadcast-spawning species.

Many weight-specific functions such as respiration (Ikeda 1970, 1974; Uye and Yashiro 1988) and clearance (Huntley and Boyd 1984) are broadly independent of taxonomic category. Furthermore, other zooplankton groups have weight-specific growth rates which are positively related to temperature and negatively related to body size (Båmstedt and Skjoldal 1980; Hopcroft and

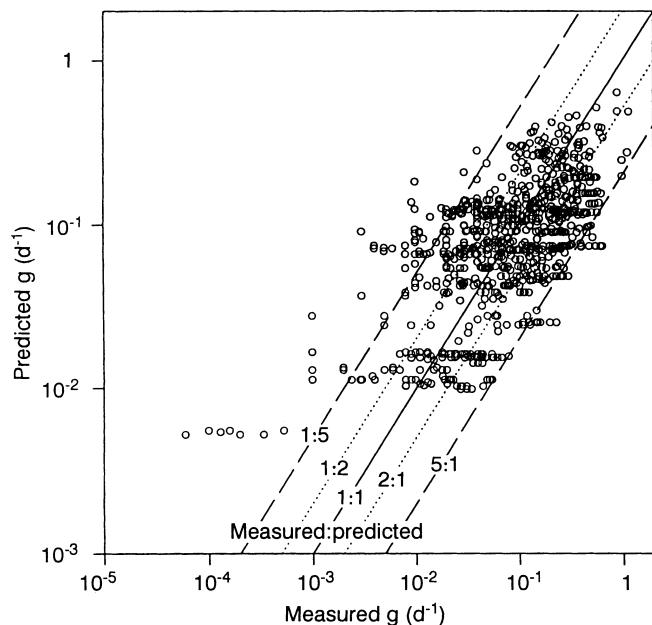


Fig. 4 Predicted weight-specific growth rates versus measured values. Various ratios of predicted to measured values are shown for visual demonstration of scatter

Roff 1995). Future work should explore the possibility that the global equations for growth produced herein may predict closely the growth of marine zooplanktonic groups such as crustaceans. Our approach is only a first step towards synthesising global patterns in marine planktonic copepod growth, and highlights the need for further collection of growth data. The measurements compiled are dominated by neritic collections, yet such areas make up only a small fraction of the total world ocean, whilst data for all groups except adult broadcast-spawners is completely absent below 3.0 °C, and sparse below 10 °C. Only when there is more extensive data on growth, and associated parameters such as food availability will it be possible to comprehensively understand the global patterns.

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