

Scaling of feeding in marine calanoid copepods

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Abstract

We describe patterns of body size scaling of feeding by marine calanoid copepods based on a literature review. Maximum feeding rates of calanoid copepods, determined in the laboratory, were temperature independent and scaled in conformity to the three-quarters universal law followed by animals. Field feeding rates (log transformed) of marine calanoid copepods were dependent on food availability, temperature, and body size, and in combination, these three variables explained 81% of the variance. The scaling to body mass for field data, however, showed a much lower slope, indicating severe food limitation in the larger copepods. The direct effects of temperature in field feeding rates were difficult to ascertain because of the inherent association between body size, temperature, and trophic level in natural ecosystems.

The issue of body size as a scaling factor in ecology has raised debate for more than 150 yr (Schmidt-Nielsen 1984; Hoppeler and Weibel 2005). Growth and metabolic rates of living beings, their relative abundance, and many other biological and ecological variables seem to follow general scaling laws (Peters 1983), and examples for allometric scaling in biological systems can be found from the cell level to the ecosystem level (Marquet et al. 2005; West and Brown 2005). Although the question about the exact value of the power exponent was reopened in recent years, nowadays metabolic rates in many ectotherms and endotherms are widely accepted to follow a three-quarters power law (-0.25 if we consider weight-specific rates) (Peters 1983, West and Brown 2005). The reasons for such broad similarity, encompassing such a large range of physiologically and taxonomically different organisms, are still not clear (*see* Peters 1983; West and Brown 2005). The power exponent <1 indicates a size (weight) limitation in vital rates: larger animals have rates lower than expected for their size. For organisms with vascular systems, recent mechanistic theories have shown that the design properties of the vascular systems, optimized to the energy supply, could explain the three-quarters power scaling of metabolic rates (West and Brown 2005). However, for ectotherm organisms, we still lack experimentally supported theories to explain such allometric regularities.

The allometry of metabolic rates in marine zooplankton has been shown in studies by Vidal and Whitley (1982), Ikeda (1985), and Uye and Yashiro (1988), and specifically for copepods by the recent work of Ikeda et al. (2001). In

general, these studies showed that the weight exponent of the allometric equations were independent of temperature and close to a value of 0.7–0.8. It is important to notice that these metabolic rates were typically measured under starving conditions (filtered seawater). Therefore, the rates reported in these studies are closer to a basal metabolism than to the routine or active one. Regarding feeding, Peters and Downing (1984) developed a general empirical model for zooplankton feeding and discussed the issue of body size scaling in copepods. However, the feeding rates reported in their study were probably biased because they originated from old studies that viewed copepods as essentially herbivorous and omitted other food sources (*see* review by Calbet and Saiz 2005); not contemplating properly possible departures from the three-quarters law in the feeding of copepods under field conditions.

It is now time, in our opinion, to summarize the current knowledge on marine copepod feeding rates and to search for general patterns and limiting factors of an ecological relevance. Such an exercise can provide a view of where previous work has led to, and help to efficiently plan future research on copepod feeding. In this paper, we use the available literature to describe the scaling patterns of marine copepod feeding in relation with body size, and we explore the effect of temperature on feeding rates and the issue of food limitation of copepod feeding. Such ambitious objectives will be pursued, however, under the constraint of the literature data existing. We have reviewed the available literature on copepod ingestion rates in the field on natural autotrophic and heterotrophic prey, and we have restricted our analysis to body size, temperature, and food concentrations as major factors affecting copepod feeding. Other important variables (e.g., prey size, food quality) were reported in only a few papers, and therefore these data were omitted from our analysis. To study feeding limitation in the oceans, we compare the observed field rates with maximum copepod ingestion rates obtained in the laboratory with cultured prey. These laboratory maximum ingestion rates must be taken cautiously as a reference value because the cultured food offered in laboratory experiments may not have been necessarily the most suitable prey for that species of copepod. We had to restrict our analysis to the copepodite and adult stages of

Acknowledgments

We thank K.-G. Barthel, D. Bonet, C. Castellani, J. Dutz, S. Gasparini, A. Hirst, X. Irigoien, G. Kleppel, T. Kobari, M. Koski, J. Merrell, E. F. Møller, J. C. Nejtgaard, D. Stoecker, A. Tsuda, and J. Zeldis, who provided data and answered questions about their studies. We acknowledge the authors of all the papers used in this study, and thank the two anonymous reviewers for their helpful comments and corrections. This work was supported by projects PETROZOO (VEM2003-20037) and MICROROL (CTM2004-02575/MAR) from the Spanish Ministry of Education and Science.

calanoid copepods because suitable studies for the naupliar stages and for cyclopoid copepods provided so few data that it did not warrant proper statistical analysis; for the sake of the comparison, nevertheless, these data will be briefly introduced in the Discussion section.

Methods

Field data collection—We searched the literature for copepod grazing rates in marine ecosystems on the Aquatic Sciences and Fisheries Abstract electronic database, and >400 selected references were examined. Although most copepods are in fact omnivorous and use a variety of prey types, traditionally, most studies have focused on (pigmented) phytoplankton; in the last 25 yr, ciliates and other heterotrophs have been considered as a suitable and relevant prey item for copepods. We consequently restricted our collection to field studies reporting data on copepod ingestion rates of both phytoplankton and heterotrophic prey (at least ciliates, a major heterotroph contributor to copepod diet; Calbet and Saiz 2005). Most data on grazing on phytoplankton come from cell counts, and often autotrophic and heterotrophic forms of nano-flagellates and dinoflagellates are not distinguished. Therefore, most studies considered here include feeding rates on those heterotrophic forms. In studies where heterotrophic prey were separately distinguished, their contribution to copepod diet was accounted for as well. Following the recommendations of Calbet and Saiz (2005), data on ciliates (both biomass and ingestion rates upon) were increased 30% to correct for preservation losses in cell numbers (unless already corrected in the original paper).

The copepod grazing rates were derived from incubations on natural seawater conducted over a daily cycle to avoid biased estimates of daily ration. We omitted from consideration copepod grazing rates on phytoplankton determined by the gut content method because of uncertainties with the pigment degradation to nonfluorescent forms in copepod guts (Conover et al. 1986; Penry and Frost 1991). In some cases, the authors were contacted to provide essential variables for our study, like copepod body mass, temperature, or initial prey biomass, not reported in the original paper.

The resulting field data set for calanoid copepods (90 data points, Table A1.1 in Web Appendix 1: http://www.aslo.org/lo/toc/vol_52/issue_2/0668a1.pdf) includes reports from oceanic and coastal waters, extending from polar to tropical regions. The present data set stems from the one used by Calbet and Saiz (2005), extended to incorporate further studies and to include heterotrophic prey other than ciliates in copepod diet. All data are expressed on a carbon basis because most of the included papers and data provided by the authors expressed results as carbon. In the few studies in which body mass data were not available, it was derived from the literature (see Table A1.1 in Web Appendix 1).

Laboratory data collection—We also surveyed the literature as explained above for maximum ingestion rates of copepods fed cultured food in the laboratory. Table

A1.2 in Web Appendix 1 lists the studies considered and the variables taken into account. Maximum ingestion rate data originate from feeding incubations, either functional response experiments or single-point experiments conducted at very high (satiating) conditions. Data from the gut content method were not considered (see above). This screening resulted in 27 suitable studies that provided maximum rates for 27 species of copepodite and adult stages of calanoid copepods (65 data points in total). The data sets were classified according to diet (herbivorous: algae; carnivorous: heterotrophic dinoflagellates, ciliates, metazoans); when different prey were used in the same work, only those that provided the highest rates were considered. All data are expressed on a carbon basis, following the procedures mentioned above.

Results

Copepod feeding rates in the field—Table 1 summarizes the ingestion rates of marine calanoid copepods compiled from the literature. Copepod daily rations are presented as a function of the trophic degree of the study site (estimated as sestonic carbon availability) and copepod body mass. The overall low daily rations reported demonstrate the degree to which copepod feeding in the oceans is food limited, especially in the more oligotrophic environments and for the larger-sized copepods. Figure 1 shows bivariate plots of calanoid copepodite ingestion rates as a function of food concentration, body size, and temperature. Ingestion rates are presented per capita to avoid spurious correlations of weight-specific rates with body size (mass). For all statistical analyses, the variables of ingestion rate, food concentration, and body size were logarithmically transformed to allow for nonlinear relationships between the variables; temperature was not transformed because the logarithm of a biological rate is usually regarded as being a linear function of temperature (Q_{10} concept). Regression analyses (Fig. 1) showed that all single factors considered had significant effects (Table 2), although the amount of variance explained by body weight and temperature was very low (<10% in both cases). Food availability, on the other hand, explained 52% of the variance in (log) ingestion rates.

In order to simultaneously take into account the effects of food concentration, body size, and temperature on calanoid feeding rates, a multiple regression model was built,

$$\log(I) = a + b \log(W) + c \log(C) + dT \quad (1)$$

where I is ingestion rate ($\mu\text{g C ind}^{-1} \text{d}^{-1}$), W is body weight ($\mu\text{g C ind}^{-1}$), C is food concentration ($\mu\text{g C L}^{-1}$), T is temperature ($^{\circ}\text{C}$), a is the intercept, and b , c , and d are the corresponding regression coefficients. A backwise step procedure showed that temperature had to be dropped from consideration ($F_{1,87} = 0.56$, $p > 0.4$); the other two variables were significant and explained 81% of the variance in (log) feeding rates (Table 2). This unexpected result (because temperature is considered one of the major factors driving biological activity) pointed out a possible

Table 1. Summary of the data set on field ingestion rates of calanoid copepods. Ingestion rates (as daily ration, % body C ingested d⁻¹) and temperature (°C) are given as a function of food availability in the study site (µg C L⁻¹) and body mass of copepods (small, <10 µg C ind⁻¹, corresponding to calanoid genera including *Acartia*, *Centropages*, *Paracalanus*, and *Temora*; medium, 10–200 µg C ind⁻¹, corresponding to *Calanus finamarchicus* and *Calanus helgolandicus*; large, >200 µg C ind⁻¹, corresponding to larger *Calanus* species, *Eucalanus* and *Neocalanus*). Median values and range (in parentheses) are given.

Characteristic	<50 µg C L ⁻¹			50–250 µg C L ⁻¹			>250 µg C L ⁻¹		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Daily ration	9.9 (1.1–49)	1.9 (0.59–3.1)	0.07 (0.04–0.61)	55 (2.2–263)	8.6 (2.6–81)	1.7 (0.03–11)	125 (35–265)	29 (0.84–59)	10 (9.3–11)
Temperature	20.2 (15.0–23.1)	6.2 (3.0–15.0)	3.5 (3.5–19.5)	15.0 (11.5–30.0)	11.5 (3.0–21.7)	3.2 (-1.7–9.5)	15.8 (12.0–29.5)	11.0 (-1.7–16.5)	2.1 (-1.7–2.1)
Sample size	9	8	7	18	8	10	14	13	3

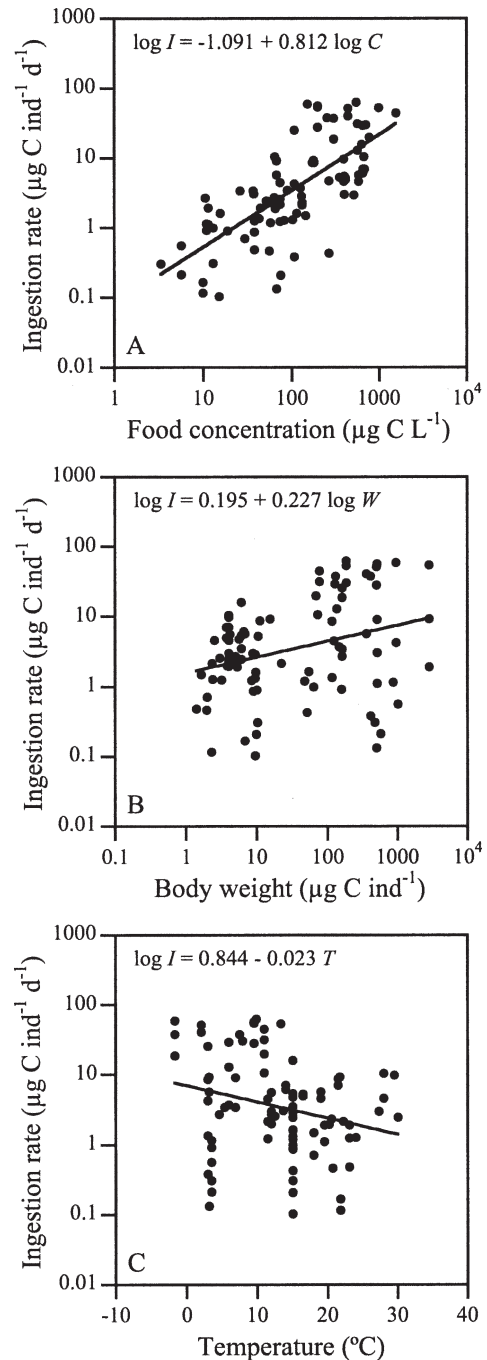


Fig. 1. Bivariate plots of ingestion rates of calanoid copepods (including adults) as a function of, respectively, (A) food concentration, (B) body weight, and (C) temperature. Linear regression equations fitted to the logarithmically transformed data are given and drawn in each panel. See Table 2 for further details.

flaw in our analysis. Linear correlation analysis between the predicting variables indicated that temperature and body size were inversely correlated ($r = -0.75$, $n = 90$, $p < 0.001$); all other possible pairwise combinations showed no significant correlation ($p > 0.05$). Very likely, the inverse correlation between temperature and body size, although

Table 2. Regression analysis of calanoid copepod ingestion rates (I , $\mu\text{g C ind}^{-1} \text{d}^{-1}$) from field studies. Summary of fit, F -test of ANOVA of the model, and parameter estimates are provided. C , food concentration, $\mu\text{g C L}^{-1}$; T , temperature, $^{\circ}\text{C}$; W , body mass, $\mu\text{g C ind}^{-1}$; W_{res} , residuals of the log W - T relationship; RMSE, root mean square error; MR, mean of response; 95% CI, 95% confidence interval. Standardized regression coefficients in multiple regression analyses are indicated as a' , b' , c' , and d' , respectively.

a) $\log(I) = a + b \log(C)$
 $R^2 = 0.52$, RMSE = 0.487, MR = 0.544, $F_{1,88} = 93.62$, $p < 0.001$
 $a = -1.091$ (95% CI, -1.442 to -0.740), $t = -6.18$, $\text{df} = 88$, $p < 0.001$
 $b = 0.812$ (95% CI, 0.645 to 0.978), $t = 9.68$, $\text{df} = 88$, $p < 0.001$

b) $\log(I) = a + b \log(W)$
 $R^2 = 0.09$, RMSE = 0.666, MR = 0.544, $F_{1,88} = 9.02$, $p < 0.004$
 $a = 0.195$ (95% CI, -0.075 to 0.465), $t = 1.44$, $\text{df} = 88$, $p > 0.1$
 $b = 0.227$ (95% CI, 0.077 to 0.377), $t = 3.00$, $\text{df} = 88$, $p < 0.004$

c) $\log(I) = a + b T$
 $R^2 = 0.06$, RMSE = 0.677, MR = 0.544, $F_{1,88} = 6.11$, $p < 0.016$
 $a = 0.844$ (95% CI, 0.564 to 1.123), $t = 6.00$, $\text{df} = 88$, $p < 0.001$
 $b = -0.023$ (95% CI, -0.042 to -0.005), $t = -2.47$, $\text{df} = 88$, $p < 0.016$

d) $\log(I) = a + b \log(W) + c \log(C)$
 $R^2_{\text{adj}} = 0.81$,* RMSE = 0.296, MR = 0.582, $F_{2,84} = 182.02$, $p < 0.001$
 $a = -1.751$ (95% CI, -2.003 to -1.500), $t = -13.86$, $\text{df} = 84$, $p < 0.001$, $a' = 0$
 $b = 0.355$ (95% CI, 0.287 to 0.423), $t = 10.31$, $\text{df} = 84$, $p < 0.001$, $b' = 0.492$
 $c = 0.893$ (95% CI, 0.790 to 0.996), $t = 17.31$, $\text{df} = 84$, $p < 0.001$, $c' = 0.826$

e) $\log(I) = a + b W_{\text{res}} + c \log(C) + d T$
 $R^2_{\text{adj}} = 0.81$,† RMSE = 0.297, MR = 0.582, $F_{3,83} = 120.80$, $p < 0.001$
 $a = -0.820$ (95% CI, -1.061 to -0.578), $t = -6.76$, $\text{df} = 83$, $p < 0.001$, $a' = 0$
 $b = 0.382$ (95% CI, 0.280 to 0.485), $t = 7.40$, $\text{df} = 83$, $p < 0.001$, $b' = 0.356$
 $c = 0.897$ (95% CI, 0.794 to 1.001), $t = 17.23$, $\text{df} = 83$, $p < 0.001$, $c' = 0.830$
 $d = -0.031$ (95% CI, -0.039 to -0.022), $t = -7.27$, $\text{df} = 83$, $p < 0.001$, $d' = -0.345$

* Three outlier data points were not used in this analysis. The inclusion of these values did not modify significantly the regression coefficient estimates, but R^2_{adj} decreased to 0.67 and RMSE increased to 0.397.

† Three outlier data points, which extended away >1.5 times the interquartile range for W_{res} , were not used in this analysis. The inclusion of these values did not significantly modify the regression coefficient estimates, but R^2_{adj} decreased to 0.67 and RMSE increased to 0.398.

not high enough to explain collinearity effects (Zar 1999), suggested a masking effect between both variables.

In an attempt at skipping over this masking effect, and as temperature should be the factor body mass depends on, and not vice versa, we derived a new body mass variable free of temperature effects by taking the residuals of the linear regression analysis between log body mass and temperature ($R^2 = 0.56$, root mean square error = 0.624, mean of response = 1.539, $F_{1,88} = 111.77$, $p < 0.001$). These residuals (W_{res}), already log transformed, were used instead of body mass in the following multiple regression model:

$$\log(I) = a + b W_{\text{res}} + c \log(C) + d T \quad (2)$$

The new fitted model (Table 2) was significant but explained the same amount of variance (81%) than the previous model without temperature. The slope of the log $I_{\text{max}} - W_{\text{res}}$ relationship was 0.382 and was significantly different from 0.75 ($t = -7.077$, $\text{df} = 83$, $p < 0.001$).

The contribution of each independent variable on driving copepod ingestion rates was assessed by fitting the model with standardized variables (Zar 1999). The analysis showed that the contribution of food concentration to the model was higher (standardized regression coefficient $c' = 0.830$) than that of the other two predicting

variables (standardized regression coefficients $b' = 0.356$ and $d' = -0.345$, Table 2).

Maximum feeding rates in the laboratory—Maximum feeding rates of calanoid copepods (I_{max} , in $\mu\text{g C ind}^{-1} \text{d}^{-1}$) as a function of body mass and diet are presented in Fig. 2A. Two extreme data points (corresponding to adults of *Euchaeta* spp.; away >1.5 times the interquartile range) were excluded because of their excessive influence on the regression. Rates under herbivorous and carnivorous diet clearly overlapped, and because ANCOVA showed no significant differences of the respective regression fits either in slope ($F_{1,59} = 0.092$, $p > 0.05$) or in intercept ($F_{1,59} = 0.735$, $p > 0.05$), all data were pooled to ensure a larger sample size for the following statistical analyses.

Simple regression analysis of log I_{max} on, respectively, log W and T (Fig. 2 and Table 3) showed no significant effects of temperature on maximum ingestion rates, whereas log body mass explained 70% of the variance in log-transformed maximum feeding rates of calanoid copepods. The slope of the log $I_{\text{max}} - \log W$ relationship was 0.703 and was not significantly different from 0.75 ($t = -0.810$, $\text{df} = 61$, $p > 0.05$).

We further explored the concurrent effects of body size and temperature on calanoid copepod maximum ingestion rates by multiple regression analysis. Contrary to what

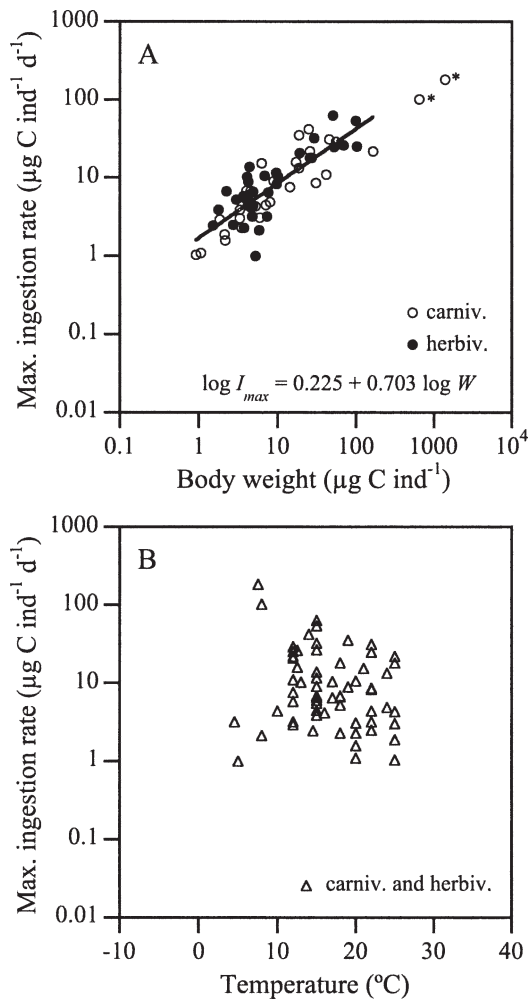


Fig. 2. Maximum feeding rates of calanoid copepods determined in the laboratory under satiating conditions as a function of (A) body weight and (B) temperature. Linear regression equation fitted to the logarithmically transformed data is given and drawn only in (A), because in (B) it was not statistically significant. Asterisks highlight extreme data points, extending away >1.5 times the interquartile range, not used in the statistical fits. carniv., carnivorous diet; herbiv., herbivorous diet. In (B), carnivorous and herbivorous data have been pooled. See Table 3 for further details.

happened to the field data, in the maximum ingestion data set temperature and log body mass were not correlated ($r = -0.15$, $n = 63$, $p > 0.1$), and therefore both variables were directly tested in the model. The multiple regression model tested was

$$\log(I_{\max}) = a + b \log(W) + cT \quad (3)$$

which was identical to Eq. 1 except for the lack of food concentration as independent variable (because here we are dealing with maximum rates). The least-square fit of the data to this model, however, confirmed that temperature had no significant effect ($F_{1,60} = 0.934$, $p > 0.1$).

Table 3. Regression analysis of maximum ingestion rates of calanoid copepods determined in the laboratory. I_{\max} , maximum ingestion rate, $\mu\text{g C ind}^{-1} \text{d}^{-1}$; W , body mass, $\mu\text{g C ind}^{-1}$; T , temperature, $^{\circ}\text{C}$; RMSE, root mean square error; MR, mean of response; 95% CI, 95% confidence interval.

$$\text{a) } \log(I_{\max}) = a + b \log(W)$$

$$R^2 = 0.70, * \text{ RMSE} = 0.242, \text{ MR} = 0.877, F_{1,61} = 145.52, p < 0.001$$

$$a = 0.225 \text{ (95\% CI, 0.101 to 0.349)}, t = 3.62, \text{ df} = 61, p < 0.001$$

$$b = 0.703 \text{ (95\% CI, 0.586 to 0.819)}, t = 12.06, \text{ df} = 61, p < 0.001$$

$$\text{b) } \log(I_{\max}) = a + b T$$

$$R^2 = 0.04, \text{ RMSE} = 0.482, \text{ MR} = 0.916, F_{1,63} = 2.38, p > 0.1$$

$$a = 1.218 \text{ (95\% CI, 0.809 to 1.626)}, t = 5.96, \text{ df} = 63, p < 0.001$$

$$b = -0.018 \text{ (95\% CI, -0.042 to 0.005)}, t = -1.54, \text{ df} = 63, p > 0.1$$

* Two outlier data points, which extended away >1.5 times the interquartile range, were not used in this analysis. See Fig. 2A.

Discussion

Body size scaling of feeding rates in marine calanoid copepods—Maximum feeding rates of calanoid copepods obtained in the laboratory, under cultured food, were well related to their body mass in spite of the fact that these data were not necessarily the maximum rates that could be displayed by an individual (i.e., it is possible that a better and more suitable prey could have been offered). Feeding on carnivorous and herbivorous diets did not significantly affect the power exponent, despite the likely differences in copepod foraging tactics and feeding mechanisms, and expected nutritional and stoichiometric differences between herbivorous and carnivorous prey. This similarity between the maximum ingestion rates of carnivores and herbivores appears in endotherms as well (Peters 1983).

Similar to basal metabolic rates (e.g., respiration, excretion), feeding rates of calanoid copepods under satiating conditions seemed to conform to the general trend of three-quarters scaling to body mass (Peters 1983; Hansen et al. 1997). It must be noticed, however, that the slope obtained (0.703) was not significantly different either from a slope of two-thirds ($t = 0.626$, $\text{df} = 61$, $p > 0.05$), which would be linked to surface/volume relationships. Given the uncertainty of the slope estimates it is impossible to distinguish between these scaling rules. Our slope estimate is also likely biased by the range of body sizes in our data set, because the information in the upper and lower range of values has a strong influence on the exact value of the slope. For instance, if we add to our data set the few available data on laboratory maximum ingestion rates of calanoid nauplii (Table A1.3 in Web Appendix 1), nauplii feeding rates seem to fit well with the pattern for the copepodite and adult stages (Fig. 3A; $\log I_{\max}$ – $\log W$ relationship on pooled data: $R^2 = 0.79$, root mean square error = 0.234, mean of response = 0.757, $F_{1,72} = 275.39$, $p < 0.001$) and the slope of the $\log I_{\max}$ – $\log W$ relationship gets closer to the 0.75 value ($b = 0.743$, 95% CI: 0.654–0.832, $t = 16.59$, $\text{df} = 72$, $p < 0.001$). Additional data on larger copepods, if they exist, would certainly have an influence in the slope as well.

Despite the scarcity of data on naupliar feeding rates, the good agreement in body mass scaling between naupliar and

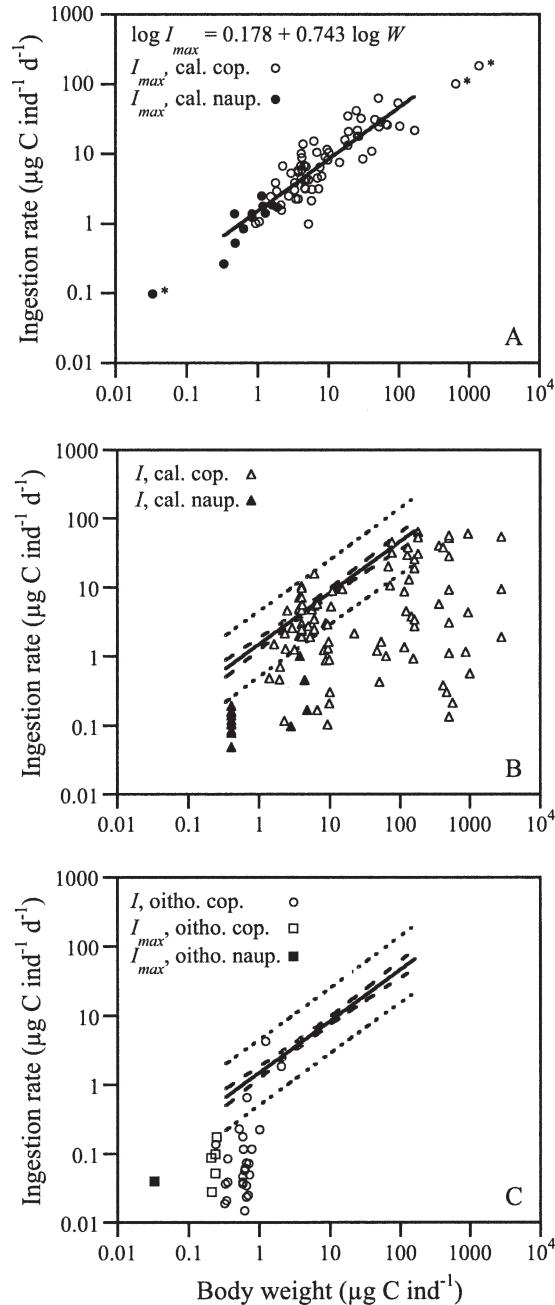


Fig. 3. (A) Maximum laboratory-determined feeding rates as a function of body weight for copepodite (including adult), and for naupliar stages of marine calanoid copepods. Linear regression equation is fitted to pooled log-transformed nauplii and copepodite data. Asterisks highlight extreme data points, extending away >1.5 times the interquartile range, not used in the statistical fits. (B) Field feeding rates as a function of body weight for copepodite (including adult), and for naupliar stages of marine calanoid copepods. For illustrative purposes, the linear fit corresponding to the equation shown in (A) (i.e., maximum rates of calanoids) and the corresponding 95% confidence (dashed line) and prediction (dotted line) intervals are also drawn. (C) Feeding rates as a function of body weight of copepods from the genus *Oithona*. Lines are as in (B). cal., calanoid; oitho., *Oithona*; cop., copepodite and adult stages; naup., naupliar stages; I , field ingestion rates; I_{max} , maximum ingestion rates determined under satiating conditions in the laboratory. See text for further details.

copepodite (including adults) stages is noticeable and quite unexpected because nauplii have less complex feeding appendages than the copepodite stages, and one might have expected lower maximum rates for nauplii. One may argue, hypothetically, that nauplii could compensate such lower morphological complexity through comparatively better physiological performance. This similarity also suggests that this common feeding scaling pattern in marine calanoid copepods holds not only among species but also through development.

The issue of food limitation—Food limitation of copepod feeding is prevalent in most of the oceans. Daily rations reported for marine copepods in the oceans are overall low, especially in oligotrophic environments (Table 1). This is further confirmed when field data for calanoid copepodites (including adults) is compared with the maximum ingestion rates obtained in the laboratory (Fig. 3B): most data from field studies fall well below maximum copepod feeding rates. We have also included in this plot the available field data for feeding rates of calanoid nauplii (Table A1.4 in Web Appendix 1). Field feeding rates of nauplii appear to be also much lower than maximum rates in the laboratory, indicating strong limitation, although this interpretation should be taken cautiously because of few studies available. Another aspect to point out from the comparison (Fig. 3B) is that the upper bound of the distribution of field copepod feeding rates overlaps with the confidence and prediction intervals for the maximum feeding rates reported in the laboratory, indicating that even if rarely copepod feeding rates can reach satiation in nature.

The approximate three-quarters body mass scaling law for the feeding of calanoid copepods appears to be an upper bound to their maximum ingestion rates, which are rarely achieved in nature. The main factor responsible for restraining field feeding rates of copepods, with respect to their maximum potential rates, is food availability, as the multiple regression analysis showed. This limitation reflects the change in slope for the ingestion-body weight relationship for field data (0.382, Table 2) when compared with the maximum laboratory rates, breaking the conformity to the general three-quarters scaling law. This reduction in slope reveals that food limitation is more frequent in the largest organisms, which is consistent with previous observations that growth rates of juveniles are less food-limited than those of adults (e.g., Kimmerer and McKinnon 1987; Peterson et al. 1991).

Food limitation does not necessarily imply starvation for large copepods because the low daily rations observed could possibly be compensated in the short term by the catabolism of lipid reserves, typical of large copepods from medium and high latitudes (Mauchline 1998). In addition, some of the very low copepod daily rations reported in nature raise the question how copepods can survive in the oceans and whether we are missing something in the whole picture. We cannot rule out the possibility that feeding incubations may sometimes underestimate actual feeding rates of copepods. Confounding effects mediated by trophic cascades (Nejstgaard et al. 2001), inappropriate quantification of carnivorous and detritivorous feeding, the

inadequate contemplation of prey patchiness (Mullin and Brooks 1976), and other inherent problems with bottle incubations, could lead to an underestimation of actual copepod daily rations in the field and exaggerate the apparent degree of food limitation. Nevertheless, recent analyses on global patterns of copepod growth in the oceans (e.g., Hopcroft and Roff 1998; Hirst and Bunker 2003) also confirm the issue of food limitation in marine copepods.

The issue of temperature dependence—Body size and temperature are considered the two most important variables affecting almost all biological times and rates. For poikilotherms like copepods one would expect metabolic rates to be higher at increasing temperature because of the biochemical kinetics dependence on temperature (Arrhenius rate law). Previous reports on zooplankton metabolic rates (e.g., respiration and excretion; Vidal and Whitledge 1982; Wen and Peters 1994; Ikeda et al. 2001), development, and growth rates (Hirst and Shearer 1997; Hirst and Lampitt 1998) have reported such significant effects of temperature.

It may seem strange that temperature did not seem to have a major effect on copepod feeding rates, and when significant (field data) the effect was contrary to that expected (Fig. 1C). A first plausible explanation for the puzzling effects of temperature might be that our data set did not cover a range of temperature wide enough to overcome masking effects due to data variability. However, this is not the case and the temperature ranges in our data sets (laboratory: 4.5–25°C; field: –1.7–30°C) are similar to those of Ikeda et al. (2001), and other studies where a relationship between metabolism and temperature has been found. There are other reasons, however, to conclude that our observation is not anecdotal or artifactual. In fact other studies have also reported the metabolic dependence on temperature to be not always tight or evident in natural populations of poikilotherms. For instance, the broad empirical analysis of marine and freshwater zooplankton feeding rates by Peters and Downing (1984) also showed no significant relationship (except for freshwater cladocerans, $Q_{10} = 1.86$) between feeding and temperature (2°C to 27°C interval). Further, the review by Robinson et al. (1983) showed that in contrast to endotherms, the scaling effect of temperature on metabolic rates of poikilotherms is significant but smaller than expected ($Q_{10} = 1.4$ – 1.7), and this could be explained by physiological adaptation (e.g., enzyme kinetic properties) to habitat temperature. According to Peters (1983), the steeper responses to temperature commonly reported ($Q_{10} > 2$) may represent acute responses to rapid changes in temperature without a chance for adaptation, or experimental artifacts. Temperature seems to explain a significant but small amount of the residual variance in metabolic rates remaining after regression on size alone (Peters 1983; Wen and Peters 1994). In addition, recent attempts at explaining why organisms grow larger at lower temperatures (while growth rates increase as temperature increases) based on a reinterpretation of von Bertalanffy's classic theory of growth (Atkinson and Sibly 1997), suggest that feeding rates would show

a lower dependence on temperature than do respiration or excretion rates.

In field studies, direct effects of temperature (i.e., the enhancement of vital rates) are masked by indirect effects such as changes in development time and adult size. In addition, other indirect effects are inherent to the characteristics of natural ecosystems: lower temperatures occur at higher latitude waters, inhabited by larger copepods provided with higher food availability, whereas warmer tropical waters are typically oligotrophic and dominated by small copepods. In our case, the first multiple regression model fitted to field feeding rates (Eq. 1, Table 2) indicated that temperature had no significant effects on copepod feeding rates. Contrarily, the second model (Eq. 2, Table 2), which used the residuals of the log W versus T relationship, showed a significant effect of temperature. One must notice, however, that in both cases the R^2 and the mean square error of the models were the same. The inclusion of temperature did not explain additional residual variance but simply changed the allocation of the explained variance. This is a consequence of the fact that the variable *temperature* used in our analysis does not only represent the effect of temperature on metabolism (direct effects) but also concurrent variations in body size of copepods and habitat features. For this reason, feeding rates and temperature appeared negatively related (Fig. 1): higher temperatures in our data set corresponded to smaller copepods, which had lower per capita ingestion rates.

In conclusion, the disagreement about temperature dependence in the literature could be a consequence of the intertwined effects of temperature and body size on metabolism, mediated by the inverse relationship of temperature with body size (e.g., McLaren 1965; Klein Breteler and González 1988; Atkinson and Sibly 1997) and development times (Gillooly et al. 2002), as well as to the effect of concurrent features characteristic of natural ecosystems.

Limitations and perspectives in copepod feeding studies—At present, data on feeding rates of marine copepods are still scarce and are mostly limited to coastal or shelf waters, mainly in the Northern Hemisphere, and to the later stages of calanoid copepods. Studies of copepod feeding in tropical and subtropical waters, which constitute the largest area of the oceans, remain uncommon. This restricted coverage is obviously reflected in our database and sets limits to any attempt to depict global copepod feeding patterns in the oceans. This lack of data also extends to the number of studied species and their representativeness in the marine copepod world. We found suitable field data for only 17 calanoid species; our analysis is missing many other major calanoid species as a result of the lack of knowledge on their feeding. This deficiency is more evident if we expand our analysis to other major components of the planktonic copepod realm such as the Cyclopoida and the Poecilostomatoidea. The shortage of information on the feeding of these groups is of concern and did not allow a thorough analysis. The only feeding data we have found regarding the genus *Oithona* (shown for illustrative

purposes in Fig. 3C and in Tables A1.5 and A1.6 in Web Appendix 1) fell in the lower range of values for calanoids and seem to be in agreement with the lower metabolic rates attributed to marine cyclopoids (Paffenhöfer 1993; Castellani et al. 2005).

Finally, there might be ecophysiological evolutionary adaptations to optimize copepod feeding in the natural environment that have not been addressed here because of the small database presently available. As remarked previously, colder and richer seas are typically inhabited by larger copepods, whereas the warmer oligotrophic parts of the oceans are dominated by small copepods. Certainly, the inclusion of life-history trait differences between the copepod species used and their habitat characteristics would provide further insight into our knowledge of copepod feeding.

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Received: 25 January 2006

Accepted: 25 September 2006

Amended: 18 October 2006