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Neil S. Banas

Robert G. Campbell

University of Rhode Island, rgcampbell@uri.edu

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Traits controlling body size in copepods: separating general constraints from species-specific strategies

Neil S. Banas^{1,*}, Robert G. Campbell²

¹Department of Mathematics and Statistics, University of Strathclyde, Glasgow G1 1XQ, UK

²Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02881, USA

ABSTRACT: A new synthesis of laboratory measurements of food-saturated development and growth across diverse copepod taxa was conducted in a theoretical framework that distinguishes general allometric constraints on copepod physiology from contingent strategies that correlate with size for other reasons. After temperature correction, the allometry of growth rate is inconsistent between the ontogeny of *Calanus* spp., where it follows the classic -0.3 power-law scaling, and a broader spectrum of adult size W_a (0.3 to $2000 \mu\text{g C}$, *Oithona* spp. to *Neocalanus* spp.), across which the classic scaling appears to represent only an upper limit. Over the full size spectrum, after temperature correction, a growth rate g_0 relative to the -0.3 power law correlates with adult size better than does relative (temperature-corrected) development rate u_0 ; in contrast, at a finer scale of diversity (among *Calanus* spp., or among large ($>50 \mu\text{g C}$) calanoids in general), u_0 is the better correlate with adult size and the effect of g_0 is insignificant. Across all these scales, the ratio of relative growth and development rates g_0/u_0 is a better predictor of adult size than g_0 or u_0 alone, consistent with a simple model of individual growth.

KEY WORDS: Copepods · Body size · Development rate · Growth rate · Zooplankton · Trait-based · Diversity

INTRODUCTION

Body size is often cited as a 'master trait' controlling or serving as a proxy for many aspects of functional diversity in phytoplankton, zooplankton, and other guilds (Litchman & Klausmeier 2008, Kiørboe & Hirst 2014). Allometric explanations have a long pedigree in biology (Bergmann 1847, Kleiber 1932, Brooks & Dodson 1965, Silvert & Platt 1978), and the past decade has seen a flourishing of size-based theory-building and data meta-analysis in plankton biology (Baird & Suthers 2007, Saiz & Calbet 2007, Banas 2011, Edwards et al. 2012, Ward et al. 2012, Wirtz 2012, Record et al. 2013, Andersen et al. 2015). Marine pelagic copepods have been the focus of much of this work, not only because of their abundance and trophic importance in the world ocean but also because their definite number of molts and

determinate growth make them good subjects for quantification of ontogenetic patterns in the lab (Forster et al. 2011). Numerous studies exist linking copepod vital rates (development, growth, ingestion, fecal pellet production, egg production) to size as well as temperature and prey (Kiørboe & Sabatini 1995, Hansen et al. 1994, Hirst & Kiørboe 2002, Bunker & Hirst 2004, Saiz & Calbet 2007, Kiørboe & Hirst 2014).

Still, basic ambiguities remain in how growth rate, development rate, and adult body size are linked across copepod taxa. One can imagine an animal becoming a large adult either by growing quickly or maturing slowly; which of these ontogenetic models is more appropriate? Is it fair to think of growth rate as controlling adult size in this ontogenetic sense, or should we rather think of growth (or metabolic processes in general) as being controlled by body

*Corresponding author: neil.banas@strath.ac.uk

size, according to a general scaling like the often-observed three-quarters or two-thirds power law? Likewise, what are the causal relationships behind the biogeography of copepod size, e.g. the fact that the dominant *Calanus* spp. show a clear decline in size from the Arctic to the subtropics? To what extent is the large size of high-latitude *Calanus* a necessary consequence of general laws, like the differential temperature-dependence of growth and development (Forster & Hirst 2012), and to what extent a strategy or adaptation to a particular, contingent combination of conditions (e.g. seasonality and prey and predator patterns; McLaren 1966, Falk-Petersen et al. 2009, Varpe 2012, Melle et al. 2014)?

These interpretive distinctions might appear rather abstract as long as one is working in a descriptive mode, but they have huge consequences for predictive models, which need to be anchored in a mechanistically correct understanding of which traits are plastic and which are not as well as of which correlations among traits or between traits and environments are 'laws' and which might prove transient. The purpose of this study is to revisit the experimental literature on growth, development, and size in copepods with these distinctions in mind, propose a simple model of copepod ontogeny that formally distinguishes between fundamental constraints and variable strategy choices, and then show how applying this model to existing laboratory rate data yields a self-consistent picture and new hypotheses. The endpoint of this analysis, as developed below, is the suggestion that the overall allometry of growth and development in copepods be decomposed into 3 distinct mechanisms: (1) size-dependent variation in specific growth rate during ontogeny (which follows the classic three-quarters power law in *Calanus* spp.); (2) variable regulation of development rate, relative to a temperature-dependent baseline, particularly in large calanoids; (3) variable regulation of growth rate, relative to a baseline dependent on both temperature and a general three-quarters scaling, particularly in cyclopoids like *Oithona* spp. and small calanoids like *Pseudocalanus* spp. This differentiation of mechanisms is a hypothesis in need of experimental confirmation.

DATA SOURCES

Rate data were drawn from 45 published experiments (Tables 1 & 2). We confined our review to laboratory studies that observed growth and/or development under food-saturated conditions over a large

fraction of the 13-stage development sequence. We made exceptions to this standard for *Neocalanus* and *Rhincalanus* spp., the largest taxa in the study, because rearing experiments with large, long-lived calanoids are especially difficult, and as a result, the high end of the size spectrum has not been well resolved in past reviews of this sort. Nine species of *Calanus*, along with *Neocalanus flemingeri/plumchrus*, *Neocalanus cristatus*, *Calanoides acutus*, and *Rhincalanus gigas*, constitute the 'large calanoid' category in our statistical analyses, with adult sizes 50–2000 $\mu\text{g C}$. These along with *Pseudocalanus* spp. and others in the 5–20 $\mu\text{g C}$ size range compose the calanoids as a whole. The data compilation also includes 5 non-calanoid species <5 $\mu\text{g C}$: 4 cyclopoids (3 *Oithona* spp. and *Oncaea mediterranea*) and the harpacticoid *Microsetella norvegica*. The dataset is available in Microsoft Excel format in the online Supplement at www.int-res.com/articles/suppl/m558p021_supp.xls.

Development rate is defined as the reciprocal of total development time from spawning to adulthood. For studies that observed only a portion of development, it was thus necessary to estimate what fraction of total development time the observed stages represented. This estimation was made using the assumption of equiproportionality (a single series of relative stage durations) within broad size ranges. We used results from Campbell et al. (2001) for species with adult size on the order of $\geq 100 \mu\text{g C}$ (*Calanus* spp. and *Neocalanus* spp.), results from Sabatini & Kiørboe (1994) for *Oithona* spp., and equal stage durations (isochronality) for *Pseudocalanus* spp., which approximates the results of Lee et al. (2003). A number of studies published Belěhrádek functions rather than raw development-time data (Table 1), and in these cases, we simply use the fit as if it were data, across the particular temperature range where it was defined. Because Belěhrádek fits have so many degrees of freedom, they generally match the source data quite closely. In studies in which neither tabular data nor a published fit were available, graphical data from figures were digitized using GraphClick software (www.arizona-software.ch/graphclick/) on high-resolution scans, a method which introduces only 0.5 to 1% additional error.

Mass-specific growth rate (Table 2) is in general calculable from a time series of body weights, e.g. average weight of individuals at each life stage and the median time intervals between them. This rate varies over the course of an individual's ontogeny as well as across taxa. Hirst et al. (2014) recently showed that stage-specific rates are quite sensitive to

Table 1. Parameters for Beléhrádek functions reported in the literature, which predict development time D (in days) as a function of temperature T as $D = a(T - \alpha)^b$. Results are given for the duration of embryonic and naupliar development (a_{E-N6}) and for complete development through the end of the last pre-adult stage (a_{E-C5}). The temperature ranges over which a_{E-N6} and a_{E-C5} were originally defined are also given. Adult sizes marked with ~ are nominal or estimated from other studies, as opposed to measured directly. a_{E-N6} for the study of *Calanus hyperboreus* by Jung-Madsen et al. (2013) is extrapolated from observations through N5

Species	Source	Adult size ($\mu\text{g C}$)	$-b$	$-\alpha$	a_{E-N6}	Valid range ($^{\circ}\text{C}$)	a_{E-C5}	Valid range ($^{\circ}\text{C}$)
<i>Calanus hyperboreus</i>	Corkett et al. (1986)	~1600	2.05	14.4	15 107	2–10		
<i>C. hyperboreus</i>	Jung-Madsen et al. (2013)	~1600	2.05	12.7	~16 800	0–10		
<i>C. glacialis</i>	Corkett et al. (1986), McLaren et al. (1988)	~300	2.05	12.97	9892	2–10		
<i>C. glacialis</i>	Jung-Madsen & Nielsen (2015)	~300	2.05	15.7	12 510	0–10		
<i>C. finmarchicus</i>	Campbell et al. (2001)	180	2.05	9.11	5267	4–12	15 047	8–12
<i>C. finmarchicus</i>	Corkett et al. (1986)	~180	2.05	10.6	7110	2–10	18 168	10
<i>C. finmarchicus</i>	Jung-Madsen & Nielsen (2015)	~180	2.05	13.7	10 105	0–10		
<i>C. helgolandicus</i>	Cook et al. (2007)	~115	2.05	6.01	4490	8–15	12 337	8–15
<i>C. sinicus</i>	Uye (1988)	60	1.44	0.7	558	10–20	1258	10–20
<i>C. abdominalis</i>	Slater & Hopcroft (2004)	20	1.58	8.7	1695	5–16	3167	5–16
<i>Pseudocalanus acuspes</i>	McLaren et al. (1989)	~10	2.05	12.59	10 401	0–12	20 155	4–12
<i>P. minutus</i>	McLaren et al. (1989)	~10	2.05	13.9	10 525	2–8	25 745	8
<i>P. moultoni</i>	McLaren et al. (1989)	~10	2.05	12.03	10 332	2–8	20 126	8
<i>P. newmani</i>	McLaren et al. (1989)	~10	2.05	11.3	7474	2–8	14 393	6–8
<i>P. marinus</i>	Uye et al. (1983)	6	1.8	1	1756	10–25	3638	10–25
<i>Microsetella norvegica</i>	Uye et al. (2002)	0.9	0.75	7.9	1303	21–27.5	2501	21–27.5

the particular numerical scheme used to estimate them from weight and stage-duration time series, and where possible, we have used their revised estimates in place of originally published rates. A number of growth rates were drawn from the review by Kiørboe & Hirst (2014), although where not otherwise indicated, mean growth rates were estimated by new fits to the original weight and stage-duration time series. The ontogenetic model which serves as the basis for these fits is explained over the course of the following 2 sections.

DEVELOPMENT RATE, ACROSS SPECIES AND COMMUNITIES

Forster et al. (2011) found that food-saturated development rate in copepods increased with temperature according to—if one chooses this functional form, as that study did not—an exponential law with a Q_{10} of 3.0. The development-rate data in this study (Fig. 1) are consistent with that mean Q_{10} . Still, a global fit of this sort, whatever the functional form, necessarily glosses over a great deal of variation at the species or population level. For example, 3 *Calanus* spp., which co-occur in some Atlantic Arctic habitats, appear to have comparable sensitivity of development rate to temperature but markedly different absolute development rates at a given temper-

ature (red lines, Fig. 1), a pattern of variation orthogonal to the community-level trend. If a particular animal's development rate u at a particular temperature T varies according to the following:

$$u(T) = u_0 Q_d^{T/10^{\circ}\text{C}} \quad (1)$$

where Q_d is an exponential base appropriate for development, then we can ask whether the scaling constant u_0 itself shows patterns across taxa.

Before addressing that question, it is important to consider exactly how the temperature correction is to be done. Q_d values vary markedly across the individual studies reviewed here: Campbell et al. (2001) reports 3.4 for development of *C. finmarchicus*, and refitting the Beléhrádek functions in Table 1 gives values from 1.7 to 3.6. However, we postulate that single-species Q_{10} values may be less meaningful than they appear. Rearing experiments that measure development rate across a range of temperatures generally stop at the point where thermal stress limits the number of individuals surviving and molting. If these experiments were continued with good resolution across the range of thermal stress, the result would almost certainly be not monotonic (like Q_{10} or Beléhrádek curves) but would rather be asymmetric domes, rising and then falling off sharply. We found only one rearing experiment in the literature that quantified the decline in development rate past the peak at the thermal optimum: Klein Breteler et al.

Table 2. Relative development rate u_0 (see Eq. 1), relative growth rate g_0 (see Eq. 4), and ancillary data for all species included in this review. Adult sizes marked with ~ are nominal or based on other studies. For studies which give development series for multiple temperatures, only the highest-temperature treatment (or in the case of Klein-Breteler et al. [1995], the treatment in which the highest rate was recorded) is given. All data are from food-replete conditions, and all are from laboratory as opposed to field observations, with the exception of g_0 for *Neocalanus* spp. In some cases, u_0 was extrapolated from a subset of life stages (noted under 'Basis for u_0 ') under the assumption of equiproportionality, as discussed in the text. *Estimates based on observations of less than half of the development period

Species	Source	Adult size ($\mu\text{g C}$)	Temperature ($^{\circ}\text{C}$)	u_0 (d^{-1})	Basis for u_0	g_0 (d^{-1})	Growth calculation notes
<i>N. cristatus</i>	Liu & Hopcroft (2005), Vidal & Smith (1986)	~2100	3	0.0038		0.157	Field obs.
<i>C. hyperboreus</i>	Corkett et al. (1986)	~1600	10	0.0054	see Table 1*		
<i>C. hyperboreus</i>	Jung-Madsen et al. (2013)	~1600	10	0.0042	see Table 1*		
<i>R. gigas</i>	Shreeve & Ward (1998)	1600	3	0.0028	C1–C3*	0.113	Via Hirst et al. (2014)
<i>C. acutus</i>	Shreeve & Ward (1998)	570	3	0.0108	C2–C4*		
<i>N. flemingeri/ plumchrus</i>	Liu & Hopcroft (2005)	~400	5	0.0046	N1–adult	0.120	Field obs.; their Fig. 6b
<i>C. glacialis</i>	Corkett et al. (1986), McLaren et al. (1988)	~300	10	0.0073	see Table 1*		
<i>C. glacialis</i>	Jung-Madsen & Nielsen (2015)	~300	10	0.0067	see Table 1*		
<i>C. acutus</i>	Atkinson (1998)	270	3	0.0080	E–C4*		
<i>C. finmarchicus</i>	Campbell et al. (2001)	180	12	0.0092	see Table 1	0.138	
<i>C. finmarchicus</i>	Corkett et al. (1986)	~180	10	0.0091	see Table 1		
<i>C. finmarchicus</i>	Jung-Madsen & Nielsen (2015)	~180	10	0.0068	see Table 1		
<i>C. glacialis</i>	Escribano & McLaren (1992)	160	3	0.0055	C4–adult*	0.137	Via Kiørboe & Hirst (2014)
<i>C. chilensis</i>	Escribano et al. (1997)	~150	18	0.0077	C3–adult*	0.100	Via Kiørboe & Hirst (2014)
<i>C. marshallae</i>	Peterson (1986)	120	10.1	0.0053		0.085	
<i>C. helgolandicus</i>	Cook et al. (2007)	~115	15	0.0080	see Table 1		
<i>C. helgolandicus</i>	Rey-Rassat et al. (2002)	115	15	0.0079		0.155	
<i>C. pacificus</i>	Landry (1983)	~100	15	0.0097			
<i>C. australis</i>	Peterson & Painting (1990)	100	19.5	0.0073			
<i>C. pacificus</i>	Vidal (1980)	100	15.5	0.0075	C2–adult*	0.156	
<i>C. sinicus</i>	Uye (1988)	60	20	0.0069	see Table 1	0.089	Hirst et al. (2014)
<i>C. carinatus</i>	Peterson & Painting (1990)	54	19.5	0.0098			
<i>C. abdominalis</i>	Slater & Hopcroft (2004)	20	16	0.0086	see Table 1	0.122	From 7°C data
<i>C. typicus</i>	Fryd & Haslund (1991)	11.25	17	0.0096		0.092	Via Kiørboe & Hirst (2014)
<i>P. acuspes</i>	McLaren et al. (1989)	~10	12	0.0094	see Table 1		
<i>P. minutus</i>	McLaren et al. (1989)	~10	8	0.0090	see Table 1		
<i>P. moulttoni</i>	McLaren et al. (1989)	~10	8	0.0096	see Table 1		
<i>P. newmani</i>	McLaren et al. (1989)	~10	8	0.0125	see Table 1		
<i>P. elongatus</i>	Klein Breteler et al. (1995)	~10	15	0.0100			
<i>Pseudocalanus</i> sp.	Landry (1983)	~10	15	0.0091			
<i>E. herdmani</i>	Escribano & McLaren (1992)	10	10	0.0073	C1–adult*	0.086	Via Kiørboe & Hirst (2014)
<i>T. longicornis</i>	Klein Breteler et al. (1982)	~8	15	0.0113		0.098	Hirst et al. (2014)
<i>C. hamatus</i>	Klein Breteler et al. (1982)	~8	15	0.0113		0.087	Hirst et al. (2014)
<i>P. newmani</i>	Lee et al. (2003)	7.9	15	0.0076	N1–adult	0.038	
<i>C. hamatus</i>	Fryd & Haslund (1991)	7.2	17	0.0088		0.070	Via Kiørboe & Hirst (2014)
<i>Pseudocalanus</i> sp.	Klein Breteler et al. (1982)	~7	15	0.0107		0.065	Hirst et al. (2014)
<i>P. marinus</i>	Uye et al. (1983)	6	25	0.0062	see Table 1	0.045	From 20°C data; via Hirst et al. (2014)
<i>Pseudocalanus</i> sp.	Vidal (1980)	5	15.5	0.0088	C2–adult*	0.064	
<i>A. tonsa</i>	Berggreen et al. (1988)	5	17	0.0124		0.060	Via Kiørboe & Hirst (2014)
<i>A. tonsa</i>	Klein Breteler et al. (1982)	~5	15	0.0107		0.085	Hirst et al. (2014)
<i>O. mediterranea</i>	Paffenhöfer (1993)	1.3	20	0.0038		0.027	Via Kiørboe & Hirst (2014)
<i>M. norvegica</i>	Uye et al. (2002)	0.9	27.5	0.0100	see Table 1	0.036	see their Fig. 11
<i>O. similis</i>	Sabatini & Kiørboe (1994)	0.6	15	0.0098		0.043	
<i>O. davisae</i>	Uchima (1985)	~0.3	20.5	0.0053			Via Sabatini & Kiørboe (1994)
<i>O. nana</i>	Haq (1965)	~0.3	20	0.0058			Via Sabatini & Kiørboe (1994)
<i>O. colcarva</i>	Lonsdale (1981a,b)	~0.3	15	0.0074			Via Sabatini & Kiørboe (1994)
<i>O. davisae</i>	Almeda et al. (2010)	~0.3	28	0.0057	N1–N6*	0.014	Via Kiørboe & Hirst (2014)

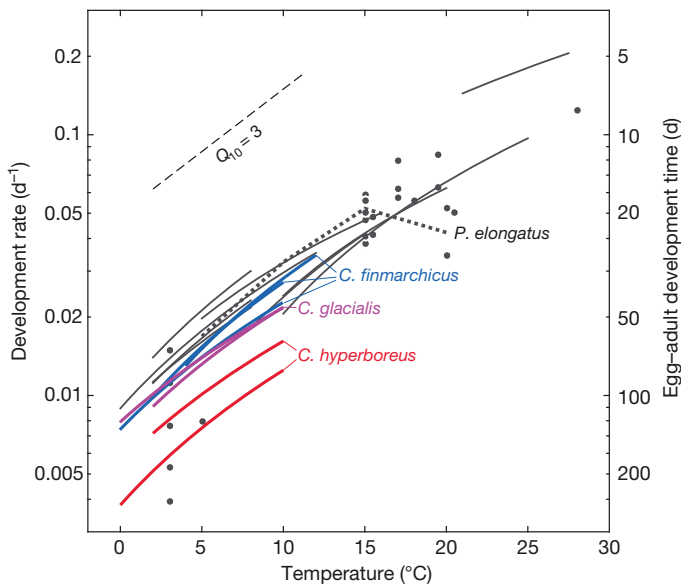


Fig. 1. Development rate u (the reciprocal of total development time) as a function of temperature T . Solid lines depict Belèhrádek functions reported in the literature (Table 1), with 3 large *Calanus* spp. highlighted (red, purple, blue). The dotted line shows results from Klein-Breteler et al. (1995) for *Pseudocalanus elongatus*, and dots indicate data from other experimental studies (Table 2). The dashed line indicates the slope corresponding to a Q_{10} of 3 (with arbitrary intercept)

(1995) (Fig. 1). A handful of studies have begun to resolve the falling side of the temperature response for ingestion rate (Møller et al. 2012, Alcaraz et al. 2014), but in the absence of clear empirical guidance, an ambiguity has grown up in the theoretical literature between expectations of monotonic, rising responses to temperature and dome-like, ‘thermal window’ responses (Pörtner 2002).

We speculate that the confusion here is mainly a matter of scale, following the model that Eppley (1972) showed phytoplankton growth rate to follow, in which vital rates in individual species or populations show window-like responses to temperature, while the outer envelope of these individual responses rises according to a Q_{10} law (Fig. 2). Alcaraz et al. (2014) proposed that the thermal-window response they observed in *C. glacialis* ingestion might be a template for community-level patterns as well, but one can show that if a community in a given environment is assembled from populations at a range of points relative to their thermal optima, the community response will follow the same power law as the metacommunity upper bound, for a wide range of assumptions regarding the shape of the population-level temperature response curve.

This logic suggests that temperature correction should be applied differently depending on whether it

is in service of a population-level or community-level question. For population-level questions, a population-specific Q_d in Eq. (1) is of course most appropriate and most likely will give results that reflect the position and shape of the thermal window. However, to explore community-level patterns in the physiology of animals in near-optimal conditions, the most consistent approach is to retain only the *highest*-temperature treatment from each single-species study—this serves as an estimate of the peak of each thermal window—and use the community-level $Q_d = 3.0$ Forster et al. (2011) for all species. This method yields values for u_0 (Eq. 1) that indicate whether the optimal development rate of a species is high or low relative to the community. This is our primary interest in this study, and we will use u_0 to refer to a ‘relative development rate’ defined using the community-level Q_d in this way, as opposed to a rate temperature-corrected to 0°C for a specific population, $u|_{T=0^\circ\text{C}}$. In general, the distinction is not important to the results below, although it does make a difference to the interpretation of fine-scale differences between some species pairs (e.g. *C. finmarchicus* and *C. glacialis*: Fig. 1; Jung-Madsen & Nielsen 2015).

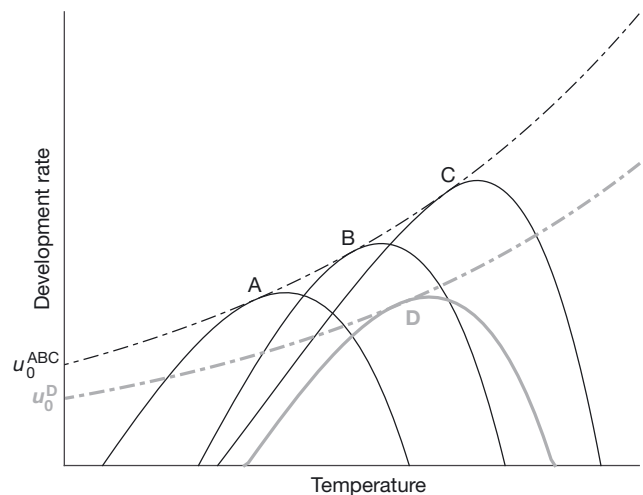


Fig. 2. Conceptual sketch of the relationship between development rate and temperature at the population and community levels, after the Eppley (1972) model of phytoplankton growth rate. Species A, B, and C differ in their thermal optima, but their maximum development rates obey a common exponential upper bound. The development rate of Species D falls below this upper bound even at its maximum; this difference between D and A, B, and C can be characterized by the intercept of the apparent exponential bound u_0 , also referred to in this study as relative development rate. One might define an apparent population-level exponential dependence (Q_{10}) by fitting a curve to the rising side of the thermal window for A, B, C, or D, but the result would not be a reliable estimate of the community-level exponential upper bound

Relative development rate u_0 varies from 0.0028 to 0.0125 d^{-1} across the full spectrum of diversity reviewed here (Fig. 3), corresponding to food-saturated development times of 80 to 360 d at 0°C or 15 to 70 d at 15°C. The variation within each of the best-represented individual genera (*Calanus*, *Pseudocalanus*, and *Oithona*) is comparable. Across the full size spectrum, u_0 is uncorrelated with adult size W_a , but they are in fact significantly correlated at finer scales: across all calanoids, across the large calanoids, and across *Calanus* in particular (Table 3). Slower development is associated with larger adult sizes, as in the set of 3 co-occurring *Calanus* spp. highlighted in Fig. 1.

One could imagine both causal and non-causal reasons for this correlation to occur. The most obvious causal explanation is that growth at a given rate, sustained over a longer number of days, necessarily would produce a larger final size. Non-causal explanations might well invoke the huge contrasts in life-history strategy across the calanoid size spectrum: all else being equal, one would expect rapid ontogenetic development to have a different significance to a continuously reproducing population of *Pseudocalanus* than to a population of *C. hyperboreus* with a strategy of extended diapause and a multi-year life cycle. To make further sense of the significance of variations in u_0 , we need to consider growth rate, development rate, and size together in a unified framework.

GROWTH RATE, ACROSS ONTOGENY AND DIVERSITY

The same questions regarding species- and community-level temperature response arise for growth rate g as for development rate u , and we have addressed the problem of temperature correction the same way, with a method that is most appropriate for community-scale questions: retaining only the maximum-rate treatment from each study (usually the highest-rate treatment) and applying a community-level exponential base of $Q_g = 2.5$ (Forster et al. 2011). The question then arises: can growth rate be corrected for size in an analogous way? Kiørboe & Hirst (2014) found that growth in pelagic heterotrophs, across many taxa and 14 orders of magnitude

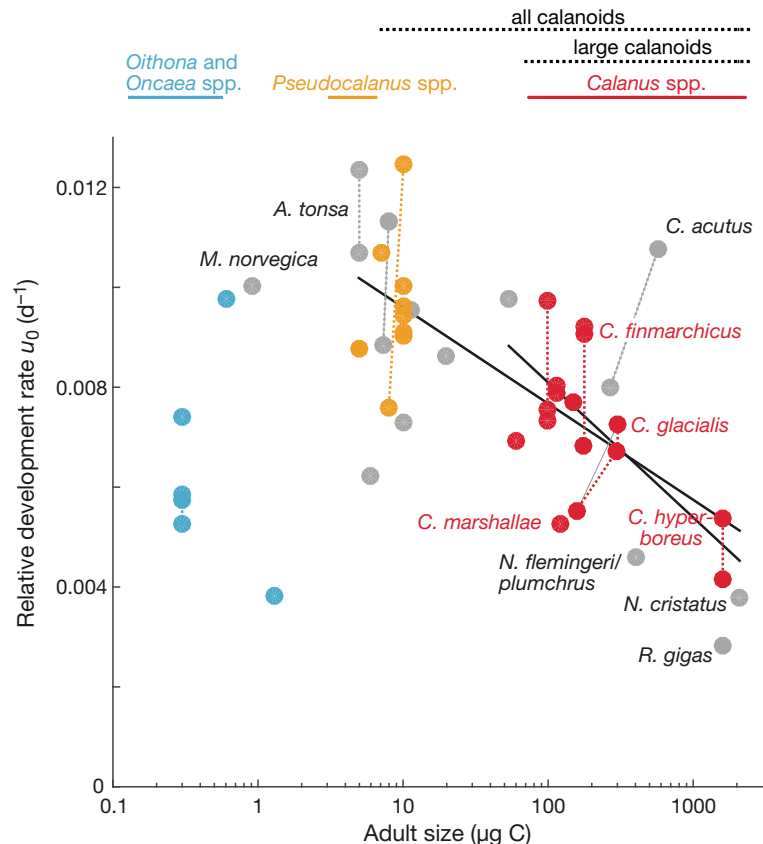


Fig. 3. Relative development rate u_0 , corrected to 0°C with a Q_{10} of 3, versus adult size W_a . Cyclopoids are shown in blue, *Pseudocalanus* spp. in yellow, and *Calanus* spp. in red, with other species (all calanoids except for the harpactacoid *M. norvegica*) in gray. Significant regression lines ($p < 0.05$) between u_0 and W_a are shown for calanoids $> 50 \mu\text{g C}$ and all calanoids (see Table 3). Dotted lines connect multiple estimates for the same species by different studies

Table 3. Pearson's r^2 between log body size $\ln W_a$ and various rate metrics, for 4 subsets of the species reviewed here. Only significant ($p < 0.05$) correlations are shown. Sample sizes range 16–47 for relative development rate u_0 and 7–26 for metrics involving relative growth rate g_0

	u_0	g_0	g_0/u_0	$\ln(g_0/u_0)$
<i>Calanus</i> spp.	0.32			
Large calanoids ($> 50 \mu\text{g C}$)	0.38		0.86	0.78
All calanoids ($> 5 \mu\text{g C}$)	0.47	0.55	0.86	0.88
All species		0.70	0.81	0.90

in body carbon, follows an allometric power law with exponent close to 0.7. That research is only the latest in a series of studies going back to Kleiber (1932) that have proposed the same. Accordingly, we might decompose interspecific variation in growth rate into a part that follows this general allometric law and a part that does not. This can be written as follows:

$$\bar{g} = g_0 Q_g^{T/10^\circ\text{C}} \bar{W}^{\theta-1} \quad (2)$$

where \bar{g} and \bar{W} are the mean specific growth rate and size over the course of an individual's ontogeny, $\theta = 0.7$, and g_0 is a relative growth rate that represents whether an individual's growth should be thought of as fast or slow once the most fundamental biophysical patterns (both temperature dependence and size dependence) have been accounted for. Note that in our discussion, as in the wider literature, this growth law is sometimes described in terms of the scaling of specific rates like \bar{g} (i.e. $\theta - 1 \approx -0.3$ in our notation) and sometimes in terms of the scaling of absolute mass fluxes (θ itself).

Comparing trajectories of growth rate vs. size $g(W)$ across species in our dataset (Fig. 4, Table 4) shows 2 things. First, there does indeed appear to be systematic variation in g_0 across the copepod size spectrum. A line fit across *Oithona*, *Pseudocalanus*, and *Calanus* does not have a slope corresponding to $\theta \approx 0.7$, which in Fig. 4 is exemplified by the allometric law for copepod ingestion rate found by Saiz & Calbet (2007) (dashed line), whose intercept has been converted to growth rate assuming a growth efficiency (ratio of ingestion to growth) of 0.3 and temperature-corrected down from an assumed average

of 10°C . This discrepancy between *Oithona* and *Pseudocalanus* rates and the presumed general trend has been noted before (Paffenhöfer 1993, Liu & Hopcroft 2008). Second, it also is evident that the allometric slope that applies over an individual's ontogeny is not necessarily the same as that which describes interspecific differences (Glazier 2005, 2006). After temperature correction, the ontogenetic $g(W)$ curves for *Calanus* spp. (red lines: Fig. 4) appear consistent with the adjusted Saiz & Calbet (2007) curve in both slope ($\theta = 0.7$) and intercept. Other species, however, show exponential growth ($\theta = 1$), and indeed Hirst & Forster (2013), in a separate review, found that an exponential-growth model ($\theta = 1$) best fit the ontogeny of copepod species overall.

In general, one could describe ontogenetic change in body size W with the following relation:

$$\frac{dW}{dt} = \begin{cases} 0 & , \text{egg - non-feeding stages} \\ g_0, Q_g^{T/10^\circ\text{C}} W^{\theta_i} & , \text{first feeding stage - adult} \end{cases} \quad (3)$$

such that

$$g = g_0, Q_g^{T/10^\circ\text{C}} W^{\theta_i-1} \quad (4)$$

over most of an individual's development. (Properly speaking, during the non-feeding stages $dW/dt < 0$ for total carbon and $dW/dt = 0$ for nitrogen or struc-

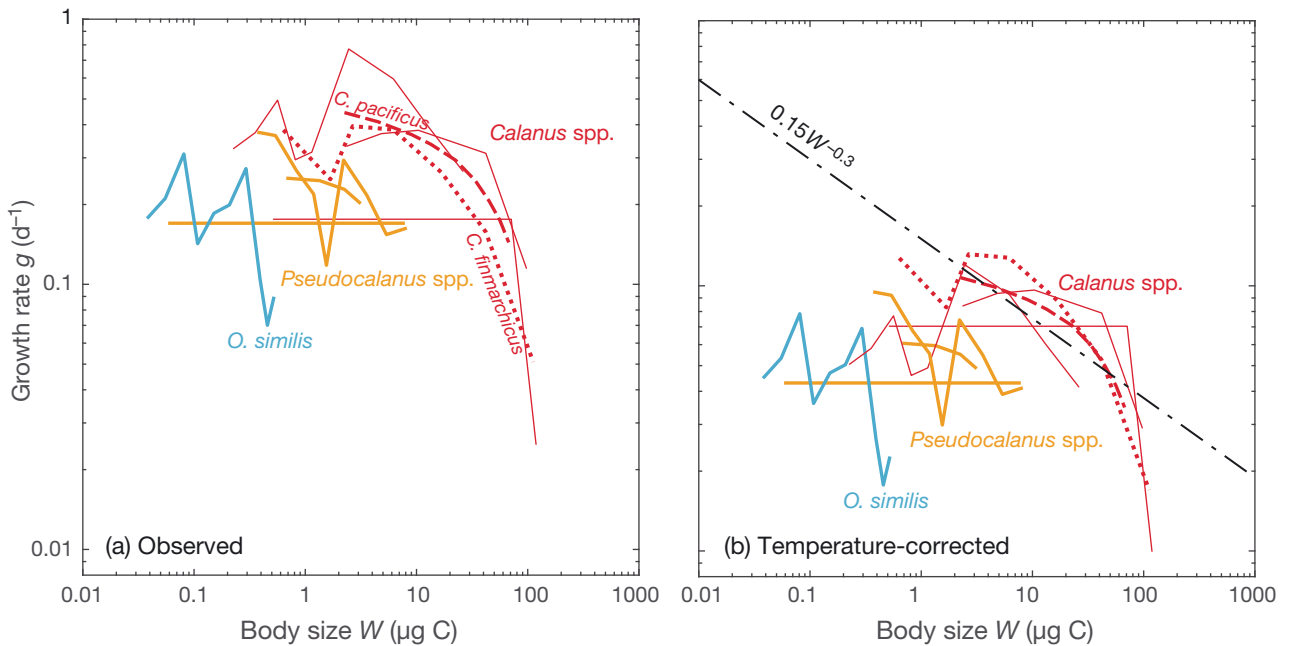


Fig. 4. Specific growth rate g as a function of body size W over the course of development in 9 species (*Oithona similis* in blue, *Pseudocalanus* spp. in yellow, *Calanus* spp. in red). *C. finmarchicus* (Campbell et al. 2001) is given by a dotted red line, and *C. pacificus* (Vidal 1980) by a dashed red line. Growth rates in (a) are at varying experimental temperatures (Table 2) and in (b) have been corrected to 0°C using a Q_{10} of 2.5. Horizontal lines represent exponential fits by Lee et al. (2003) and Peterson (1986) rather than raw stage data. The dash-dot black line in (b) shows the allometric fit by Saiz & Calbet (2007) to measured ingestion rates across a variety of copepod species, converted to temperature-corrected growth rate using an assumed growth efficiency of 30% and an ambient temperature of 10°C . Slopes of log-log regressions to the data in (b) are shown in Table 4

Table 4. Allometric exponent θ for growth rate, over the ontogeny of a number of species: see Eq. (3) and Fig. 4. Uncertainty bounds are given for all except Lee et al. (2003) and Peterson (1986) because these estimates of θ are based on published fits to $g(W)$ rather than individual measurements

Species	Source	Adult size	θ	95 % CI
<i>C. finmarchicus</i>	Campbell et al. (2001)	180	0.67	± 0.3
<i>C. marshallae</i>	Peterson (1986)	120	~ 0.8	
<i>C. helgolandicus</i>	Rey-Rassat et al. (2002)	115	0.75	± 0.4
<i>C. pacificus</i>	Vidal (1980)	100	0.68	± 0.1
<i>C. sinicus</i>	Uye (1988)	60	1.0	± 0.2
<i>P. elongatus</i>	Klein-Breteler et al. (1982)	10	0.74	± 0.2
<i>P. newmani</i>	Lee et al. (2003)	7.9	~ 1	
<i>Pseudocalanus</i> sp.	Vidal (1980)	5	0.87	± 0.2
<i>O. similis</i>	Sabatini & Kiørboe (1994)	0.6	0.68	± 0.3

tural biomass, but this issue has been ignored for simplicity.) Here, g_{0i} and θ_i are individual or species-specific traits, and averaging Eq. (4) over egg–adult development would allow one to define the relationship between these traits and the value of g_0 in Eq. (2). However, because our dataset does not resolve variation in θ_i with much precision, and the recent literature on this topic (Glazier 2006, Hirst & Forster 2013) does not suggest a hypothesis consistent with Table 4, in what follows we will make the greatly simplifying assumption that $\theta_i = \theta = 0.7$ and $g_{0i} = g_0$: that is, that the ontogenetic and the most general interspecific scalings are the same. Because g_0 is still allowed to vary, this assumption still leaves room for a different scaling at an intermediate scale of diversity. Indeed, Kiørboe & Hirst (2014) found that although $\theta = 0.7$ proved a good descriptor across pelagic heterotrophs as a whole, variation across the copepods or across the calanoid copepods was flatter, similar to the *Oithona*–*Calanus* pattern in Fig. 4 noted above.

With $\theta_i = \theta$ and $g_{0i} = g_0$, integrating Eq. (3) yields the following relation:

$$\frac{1}{1-\theta} W^{1-\theta} \Big|_{\text{egg-adult}} = g_0 Q_g^{T/10^\circ\text{C}} f_f \frac{1}{u} \quad (5)$$

where u is, as before, the reciprocal of the total egg–adult development time, and f_f is the fraction of that time spent in feeding stages. Combining this with Eq. (1) gives the following:

$$W_a^{1-\theta} - W_e^{1-\theta} = (1-\theta) f_f \left(\frac{Q_g}{Q_d} \right)^{T/10^\circ\text{C}} \frac{g_0}{u_0} \quad (6)$$

where W_e is egg weight. If we assume $W_e \ll W_a$, this becomes a convenient, approximate formula for adult size:

$$W_a \approx \left[(1-\theta) f_f \left(\frac{Q_g}{Q_d} \right)^{T/10^\circ\text{C}} \frac{g_0}{u_0} \right]^{\frac{1}{1-\theta}} \quad (7)$$

This model assumes food-saturated conditions, although one could straightforwardly incorporate models of the functional responses of growth and development under food limitation (cf. Eq. 12 in Record et al. 2013).

Eq. (7) allows a number of patterns to co-occur on different scales. First, it assumes that an individual's growth is size-dependent, following a general scaling sensu Kleiber (1932). Second, it incorporates the Forster & Hirst (2012) view of the 'temperature-size rule' (Atkinson 1994) in which all else being equal, within one species, individuals reared at higher temperatures have smaller adult

sizes because of the difference in Q_{10} values for growth and development. Finally, it allows u_0 and g_0 to vary freely among taxa and predicts that adult size is a sensitive function of the ratio of these traits, rather than depending on either one alone.

We showed above that u_0 is correlated with adult size among calanoids but not more broadly (Fig. 3). Calculating g_0 from Eq. (4) shows a complementary pattern (Table 2, Fig. 5), in which g_0 is correlated with adult size across the size spectrum as a whole but not across the $>50 \mu\text{g C}$ portion of the size spectrum or *Calanus* spp. (Table 3). Across all these scales of diversity, the ratio g_0/u_0 is significantly correlated with adult size and better correlated with adult size than u_0 or g_0 alone.

Eq. (7) in fact predicts a very specific relationship between $\ln(g_0/u_0)$ and $\ln W_a$, in which both the slope and intercept of the power law are controlled by (but different from) the allometric exponent θ . Assuming $\theta = 0.7$, $f_f = 0.85$ (as in *C. finmarchicus*; Campbell et al. 2001), and $T = 15^\circ\text{C}$ (the mean experimental temperature in our dataset; Table 2) gives a theoretical prediction that matches observations almost exactly in its slope (0.29 vs. $1 - \theta = 0.3$), although the intercept is biased by 11%. Note that the exponent relating W_a to g_0/u_0 in Eq. (7) is so high ($(1 - \theta)^{-1} \approx 3.3$) that only $\pm 10\%$ uncertainty in g_0 and u_0 individually yields 4-fold uncertainty in the predicted W_a . Thus, no matter how good or poor the statistics, applying Eq. (7) in practice will always involve an element of ad-hoc fitting.

One potential circularity in these results is that size enters the calculation of g_0 according to Eq. (2), and so we need to ask whether the observed correlations between size and g_0 and g_0/u_0 are simply reflecting this hidden dependence back to us. To rule out this possibility, we note that Eq. (7) can be rewritten as follows:

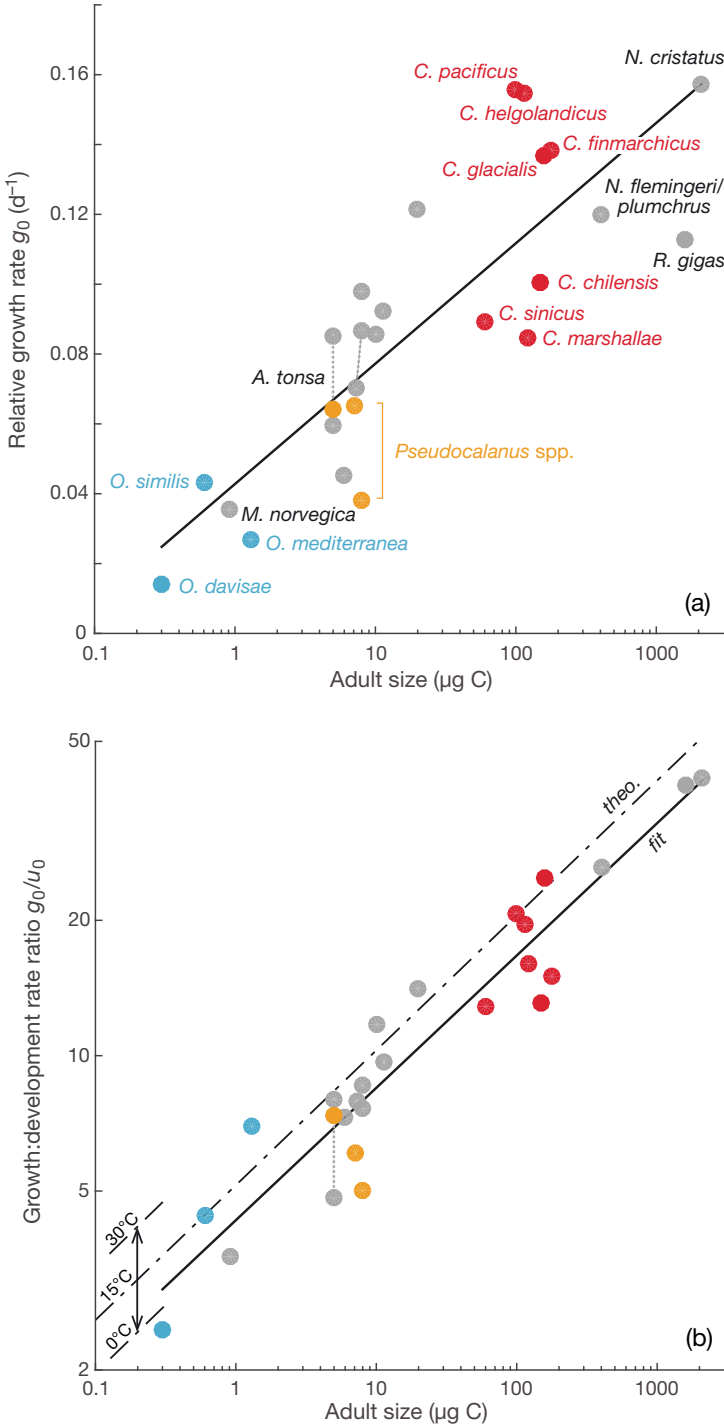


Fig. 5. (a) Relative growth rate g_0 as defined by Eq. (4) vs. adult body size W_a . The cyclopoids *Oithona* and *Oncaea* spp. are in blue, *Pseudocalanus* spp. in yellow, *Calanus* spp. in red, and other species in gray, as in Fig. 3. The solid line gives an empirical regression across all species. (b) As in (a) but for the ratio of relative rates g_0/u_0 . A theoretical (theo.) prediction according to Eq. (7) at $T = 15^\circ\text{C}$ is given by the dash-dot line; the variation in the intercept of the predicted relationship corresponding to temperature variation 0 to 30°C is also indicated

$$(1-\theta)f_f\left(\frac{Q_g}{Q_d}\right)^{T/10^\circ\text{C}} = \left(\frac{g_0}{u_0}\right)^{-1} \quad (8)$$

where g_a is relative growth rate scaled to adult size $g_0 W_a^{\theta-1}$ (which might be interpreted biologically as potential egg production rate, if upon maturation egg production replaces growth in an otherwise similar metabolic energy balance, as modelers often assume). As predicted by Eq. (8), in our dataset, g_a and u_0 are significantly correlated ($r^2 = 0.62$), their ratio is not significantly correlated with W_a , and their ratio is in fact quantitatively consistent with Eq. (8): 0.24 ± 0.06 vs. a prediction of 0.19.

Another potential concern is the fact that we have approximated W_e out of the solution between Eqs. (6) & (7), whereas other studies and other growth models (e.g. Huntley & Lopez 1992) have considered W_e to be fundamental to adult size variation. The post-hoc justification for this simplification comes from a sensitivity calculation based on Eq. (7) and the empirical power-law relationship between egg and adult size for broadcast spawners determined by Kjørboe & Sabatini (1995). Combining these and calculating the following ratio:

$$g_0 \frac{\partial W_a}{\partial g_0} \left(W_e \frac{\partial W_a}{\partial W_e} \right)^{-1} \quad (9)$$

yields the result that it takes a change in egg size of 50–110% (depending on W_a) to have the same effect on W_a as a 10% change in g_0 .

EVOLUTIONARY RECIPES FOR A COPEPOD SIZE SPECTRUM

On one level, the analysis above gives the impression of a metacommunity of marine copepods that has filled a broad trait space (relative development rate \times relative growth rate; Fig. 6). The growth model Eq. (7) implies that a given size class of copepods might comprise a spectrum of combinations of growth and development rates, and indeed, among e.g. *Calanus* spp., we can find examples of slower-growing/slower-developing and faster-growing/faster-developing species that have comparable adult sizes. Still, some amount of variation of this sort is statistically inevitable in an empirical study, and the uncertainties in our reconstruction of u_0 and g_0 are large. If one is inclined to look for an idealization of diversity patterns in this trait

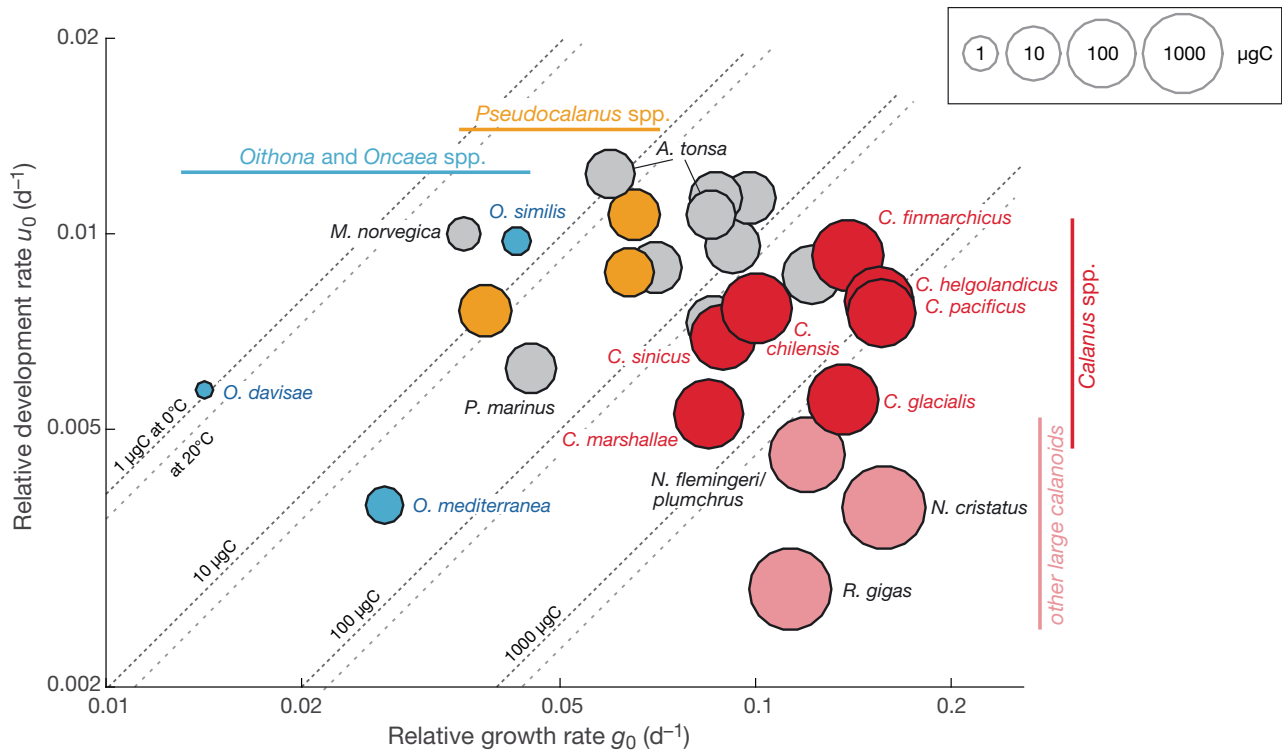


Fig. 6. Results from Figs. 3 & 5 replotted in a u_0 vs. g_0 (relative development vs. relative growth rate) trait space. Circle size indicates adult carbon weight W_a . Gray lines give theoretical contours of W_a based on Eq. (7), at 0°C (dashed) and 20°C (dotted). Color coding of taxa is as in previous figures

space, the regressions summarized above (Table 3) suggest a hypothesis: Evolution produces large copepods by reducing development rate and produces small copepods by reducing growth rate.

This hypothesis is appealing because it suggests (hazy) maximum rates for development and growth, general constraints beneath which many lower-energy strategies are possible. *C. finmarchicus* appears to be an example of an organism near the upper limit for both growth and development, for its size and for the temperatures in which it is found. Its foraging and reproductive strategies can be taken as the high-risk/high-reward end-member of a spectrum that extends down to small, ambush-feeding, sac-spawning organisms like *Oithona* spp. that trade energy gain and fecundity for reduced mortality (Kjørboe & Hirst 2014). At the opposite end of the size spectrum, the largest, high-latitude calanoid species such as *C. hyperboreus* and *Neocalanus flemingeri/plumchrus* also take low-energy strategies compared with *C. finmarchicus*, surviving short, unpredictable seasons of prey availability through adaptations like multi-year life cycles and high starvation tolerance (Conover 1988, Falk-Petersen et al. 2009, Sainmont et al. 2014). These examples hint at the variety of ways in which copepod diversity might be generated,

across the entire size spectrum, by adjusting one or another process relative to a metabolically determined maximum.

Still, without further experimental elaboration, this hypothesis is only an evolutionary ‘just so’ story. Much empirical work remains to be done testing the division we have proposed between general allometric/metabolic scalings and species-level traits (u_0 , g_0) that regulate growth and development relative to these scalings. More experiments along the lines of Møller et al. (2012) and Alcaraz et al. (2014) that carefully resolve both the rising and falling side of the response of zooplankton vital rates to temperature would confirm or reject the conceptual model depicted in Fig. 2, particularly if these experiments resolved an intermediate scale of diversity, e.g. for far-flung populations of a cosmopolitan species like *C. finmarchicus* that have adapted to contrasting temperature regimes. Beyond this, we need to better understand what mechanisms underlie u_0 and g_0 , which can be thought of most generally as the deviation of particular species (or individuals) from global scaling laws. Most crucially, is g_0 fundamentally a behavioral trait like ambush vs. cruise feeding (Kjørboe 2011) or a metabolic one? It is also possible that other traits we did not address in this review, such as rela-

tive egg size or responses to food limitation, deserve a more central place in the theory of adult-size diversity than we have given them here. A more mechanistic theory might need to elaborate the scheme used here by distinguishing naupliar from copepodid development because differences between congeners often appear only at late stages. Likewise, a more mechanistic theory would treat development not just as the passage of time, as in the theory above, but rather as an energetic investment that competes with growth during each individual life stage. Some distance down this chain of investigations, one can imagine isolating the genetic correlates of g_0 and u_0 sufficiently well to determine their actual phylogeny.

CONCLUSION

Most reviews of allometric or temperature-dependent patterns in the plankton have focused on best fits and central tendencies. Here, we have attempted to push one step further, taking the general scalings more-or-less as given (Q_d , Q_g , and θ , checked for consistency with our dataset but based on more general reviews) and instead focusing on interpretation of the residuals around these general scalings (u_0 , g_0). The ontogenetic relationship among growth, development, and size (Eq. 3) generated testable predictions (Eqs. 7 & 8) that we used as further consistency checks on our decomposition of measured rates (u , g) into general scalings and species-specific traits (u_0 , g_0).

The results suggest that while body size might act as a control on growth rate during ontogeny, and while it might set an overall ceiling on growth rate (there appear to be no copepods with a g_0 twice that of *C. finmarchicus*, for example), in general it is more apt to think of growth rate as a free, contingent strategy that controls adult size, rather than being controlled by it allometrically. Furthermore, it appears that adult size is regulated by growth-rate variations on one scale of copepod diversity and by development-rate variations on another, finer scale.

Many questions remain regarding what pressures and tradeoffs guide a population through the growth/development/size trait space in evolutionary time, either in the sense of historical phylogeny or future adaptation to the anthropocene. What the analysis above makes clear is the need for an approach that places life history and behavior—context without which variations in growth and development cannot be understood as strategies—on a level with fundamental metabolic considerations.

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