

A comparison of seasonal growth and development of the copepods *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska

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The juvenile growth rates and development times of subarctic Calanus marshallae and temperate/sub-tropical C. pacificus were investigated during nine cruises (May through October, 2001–04) in the northern Gulf of Alaska. The artificial cohort method based on a length-weight regression was used for growth estimates and the reciprocal of the molting rate for developmental time. The copepodite stage duration ranged from 3 to 16 days for C. marshallae (C1–C4) and 3–23 days for C. pacificus (C1–C5). Seasonally, copepodid growth rates increased from May to October, ranging between 0.055 and 0.291 day⁻¹ (mean ± SE: 0.176 ± 0.008 day⁻¹) for C. marshallae, while growth rates increased from August to October between 0.018 and 0.296 day⁻¹ (mean ± SE: 0.142 ± 0.016 day⁻¹) for C. pacificus. After standardization to 5°C (Q₁₀ of 2.7), growth rate averaged 0.118 ± 0.007 day⁻¹ and 0.075 ± 0.009 day⁻¹ for C. marshallae and C. pacificus, respectively. Calanus marshallae growth rate is satisfactorily described by a Michaelis–Menten model using chlorophyll-a concentration (r² = 0.33) after temperature correction, but the prediction improves with a composite nonlinear model combining body weight into the Michaelis–Menten function (r² = 0.55). Considering the limited range of data available for C. pacificus, the combination of the data for both species suggests that C. pacificus has a similar functional response to growth despite the differences in the geographic and temporal distributions with C. marshallae. Measured juvenile growth rates of the two Calanus species in this study were comparable to other calanoid species in the same area and showed reasonable agreement to Calanus growth models but less with global copepod growth models.

INTRODUCTION

Growth is among the key process rates determining the roles of copepods in the trophodynamics of marine ecosystems (Kjørboe, 1997). Thus, over the past few decades, the estimation of growth and reproductive rates of copepods has become a central aspect of marine plankton research (Runge and Roff, 2000). At present, our knowledge of juvenile copepod growth rates in the nature has been predominantly limited to tropical and temperate waters, as indicated by recent

synthesis (Hirst and Lampitt, 1998; Hirst and Bunker, 2003), and there is a conspicuous lack of data in subpolar and polar waters. Almost no vital rates exist for the common copepod species characteristic of the entire subarctic Pacific, except for natural cohort analysis (Vidal and Smith, 1986) and recent efforts in the northern coastal Gulf of Alaska (GAK) (Liu and Hopcroft, 2006a, b).

The species of genus *Calanus* are abundant members in the zooplankton community in most oceanic waters

(Brodsky, 1972; Bradford and Jillett, 1974). Across the subarctic Pacific, *Calanus marshallae* and *C. pacificus* are the two predominant sibling species, and both have multi-generational annual life cycles (Conover, 1988). Typically, *C. marshallae* is present in the neritic zooplankton assemblage from spring to winter over the northern GAK shelf, while *C. pacificus* occurs inshore mostly during the summer (Incze *et al.*, 1996; Coyle and Pinchuk, 2003, 2005). From late spring to early winter, these two species contribute important secondary production after the departure of larger-bodied *Neocalanus* species from the upper layer. To the north, *C. marshallae* is a key species in the Bering Sea (Napp *et al.*, 2002; Baier and Napp, 2003), accounting for up to 63% of the diet of juvenile walleye pollock during the summer (Grover, 1991). To the south, *C. pacificus* is considered a key species in the California Current system (e.g. Rebstock, 2001; Peterson and Keister, 2003).

Despite the prevalence of the two *Calanus* species in the subarctic Pacific, to date we have only a few direct measurements of their juvenile growth, all made with different approaches: *C. marshallae* stages C1–C3 using the natural cohort method in the southeastern Bering Sea (Vidal and Smith, 1986), C1–C5 using the molt-rate method off the Oregon coast (Peterson *et al.*, 2002), plus extensive laboratory rearing of *C. pacificus* (Vidal, 1980a, b; Landry 1983) and *C. marshallae* (Peterson, 1979, 1986). Notably, the studies on *C. marshallae* off Oregon do not encompass the temperature range this species typically occupies in subarctic waters. The objectives of this study are threefold: to fill the gap of juvenile growth rates of *C. marshallae* and *C. pacificus* in the northern GAK; explore the seasonal relationships between growth rate and food availability, temperature and body size; and to compare our measured rates with rates predicted by proposed global copepod growth models.

METHOD

Sample collections and experimental work were conducted during the U.S. GLOBEC program, Long-Term Observation Program in the Coastal GAK (see Weingartner *et al.*, 2002), in parallel with the results published for other species (Liu and Hopcroft, 2006a, b). There were six cruises per year from 2001 to 2003 in March, April, May, June/July, August and October. In 2004, only three cruises were conducted in March, May and July. Experimental work was set up at four GAK stations along the Seward line from inshore to just past the shelf break (i.e. GAK1, 4, 9, 13), plus one

station along the western Knight Island Passage of Prince William Sound (either KIP2 or PWS2) where the depth is 500–800 m (see Fig. 1 in Liu and Hopcroft 2006a, b). Temperature and ambient phytoplankton concentration, in terms of size-fractionated chlorophyll *a*, were determined in parallel at these stations (Stockwell and Whitlege, unpublished results; see Fig. 3 in Liu and Hopcroft, 2006b). Experimental methodology is identical to that employed for *Neocalanus flemingeri/plumchrus* and *Metridia pacifica* in this region, during the same period, by the same authors (see details in Liu and Hopcroft, 2006a, b). Essentially, it involved on board incubations, at *in situ* surface temperature, of copepodites with natural food in seawater collected in the upper 20 m and prescreened through 100 μm mesh. Food concentrations at the beginning and the end of experiments were measured as size-fractionated chlorophyll *a*.

The experimental method for estimating growth rates in this case is the “artificial cohort” method (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Hopcroft and Roff, 1998; Hopcroft *et al.*, 1998), details of which have been previously presented (Liu and Hopcroft, 2006a, b). In brief, artificial cohorts were created by sequential passage through submerged screens (1300, 1000, 800, 600, 500, 400, 300, 200, 150 and 100 μm). Prior to incubation, each size-fraction was gently homogenized and evenly divided. One half was concentrated and preserved in 5% buffered seawater formalin as the time zero sample (T-0), and the other half equally divided among several of the 20 L carboys previously filled with prescreened seawater. After 5 days (in March, April and May, when water was coldest) or 4 days (in June/July, August and October, when water was

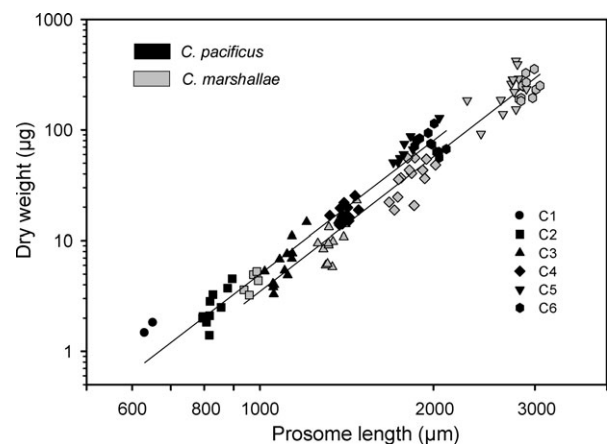
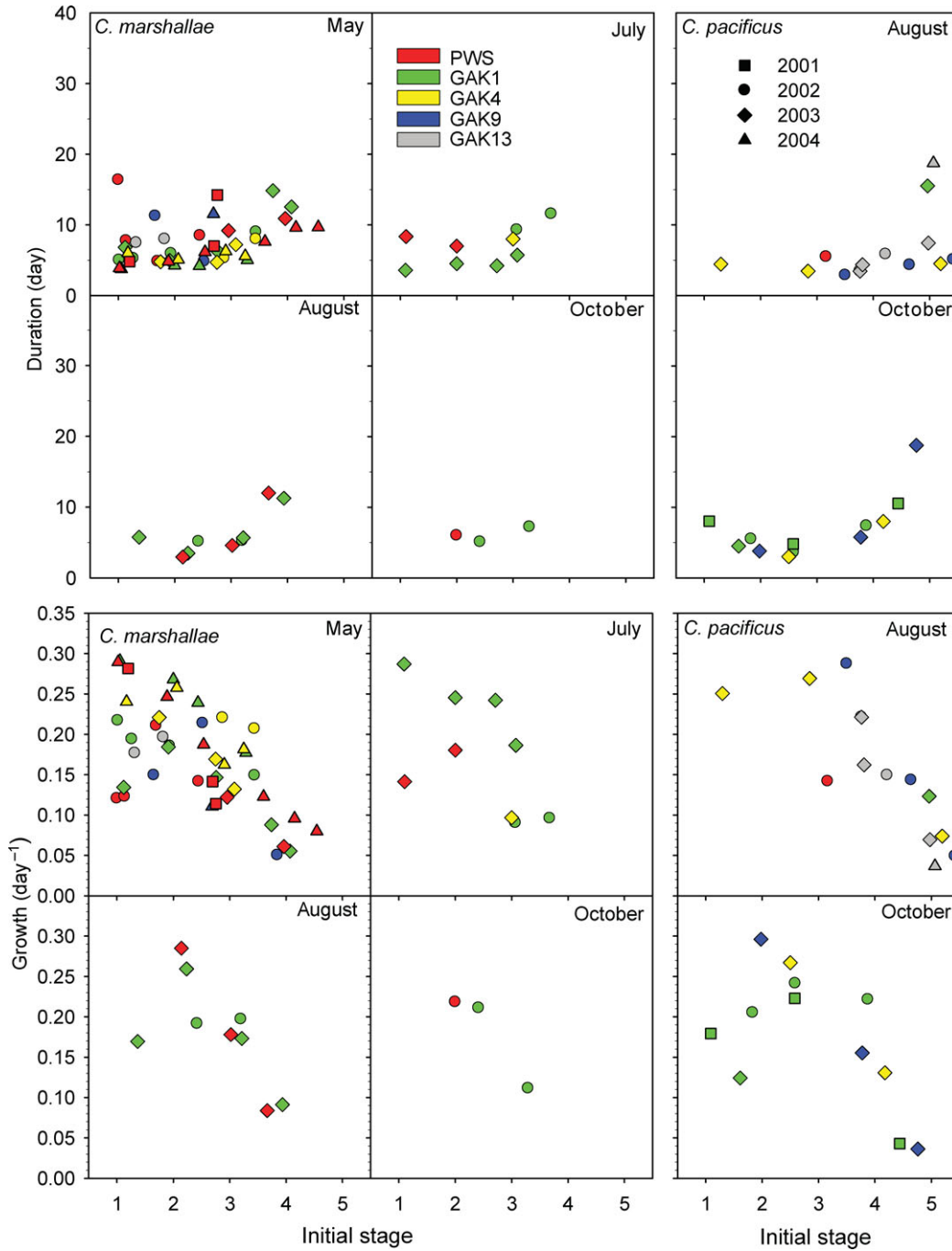


Fig. 1. Relationship between PL (μm) and DW (μg) for *C. marshallae* and *C. pacificus* stages C2–C6 in the northern Gulf of Alaska.



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Fig. 2. Stage durations (upper panels) and growth rates (lower panels) of *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–04. Stage is the average of the population at start of incubation.

warmer), the carboys were filtered through 45 μm sieves, copepods were pooled by the original size fractions and preserved immediately in 5% buffered seawater formalin as the final sample (T-5 or T-4).

Back at the laboratory, preserved samples were identified to species and stage based on the morphological

features given for copepodite stages of *C. marshallae* and *C. pacificus* (Frost, 1974; Peterson, 1979). Prosome lengths were measured with computer assistance (Roff and Hopcroft, 1986) and the progression of the cohorts was determined by changes in the stage and body size. Weights were predicted using the relationships between

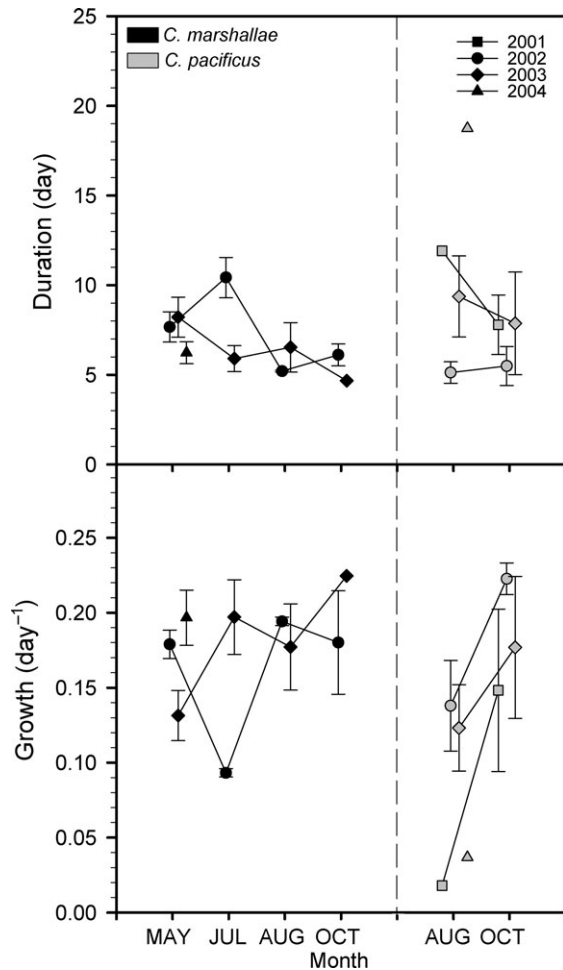


Fig. 3. Seasonal mean stage duration and growth rate of *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–04. Values plotted against initial stage and offset to improve interpretation. Error bars are standard errors.

prososome length (PL) and dry weight (DW) established in the northern Gulf of Alaska for *C. marshallae*: $\log DW = 4.034 \times \log PL - 11.561$ ($R^2 = 0.958$, $n = 57$, $P < 0.001$), and for *C. pacificus*: $\log DW = 4.001 \times \log PL - 11.304$ ($R^2 = 0.953$, $n = 62$, $P < 0.0001$), where PL is in μm , and DW is in μg (Fig. 1). Carbon weights were calculated assuming a constant carbon content per unit DW of 40% (Båmstedt, 1986), a simplification that is probably valid for the juvenile stages due to the lack of lipid accumulation. A minimum of 30 animals in both the initial and final of an experimental pair was required for data analysis, with 50–150 animals being more typical of experiments employed for analysis. In general, initial cohorts consisted predominately of a single stage, with lesser contributions from an adjoining stage, and occasionally lesser contributions from two adjoining stages. Clear cases of contamination (i.e. an

individual displaced two stages from the other individuals) were removed prior to analysis.

Development time was calculated as the reciprocal of the molting rate (MR) observed in each cohort. This approach is valid when age within stage is uniform and corrections have been proposed when this is not valid (Hirst *et al.*, 2005). However, because we frequently lacked concurrent site and experiment-specific molt rates for adjoining cohort “stages” and since our experiments typically contained a mixture of multiple stages, corrections could not be made. The growth rate (day^{-1}) within a given cohort over the incubation time t (days) was computed from the equation $g = (\ln W_t - \ln W_0)t^{-1}$, where W_0 and W_t are the mean DW of artificial cohorts at the start and the end of incubation period t (days) (Runge and Roff, 2000). Some bias and “noise” will exist in our estimates because we have used weight predicted from length to weight analysis rather than direct measurements (Kimmerer *et al.*, in press). The impacts may be greatest for later stages where development time is longer relative to preceding stages (and the incubation duration), and where both “structural” growth and lipid accumulation occur concurrently, and variably, in *Calanus* species (e.g. Campbell *et al.*, 2001; Rey-Rassat *et al.*, 2002).

Multiple linear regression analysis was used to explore the functional relationship of growth rate with copepodite stage, incubation temperature, chlorophyll-*a* concentration (both within our experiments and present in the upper 30 m) and body weight using the SAS system (Version 9). The best-fitted model was determined based on the r^2 and Mallows C_p criterion for model selection (Neter *et al.*, 1996). A composite non-linear model incorporating the body size with the traditional Michaelis–Menten relationship was developed using a combination of SAS (Version 8) and R (Version 1.8.1) statistical software (Liu and Hopcroft, 2006b), with equivalent r^2 calculated from appropriate model sum of squares (Anderson-Sprecher, 1994). For other, regression analyses and figure preparation Sigmaplot (Version 9) were used. When necessary, growth rates and stage durations were normalized to 5°C to facilitate comparison to other species in this region, and to 10°C to facilitate comparison to other studies, using a Q_{10} of 2.70 for food-saturated broadcast-spawning copepods (Hirst and Bunker, 2003), which is similar to a previous field estimate of 2.78 (Kleppel *et al.*, 1996). We chose their (Hirst and Bunker, 2003) food-saturated rate because we believe their derivation of the Q_{10} from field data is confounded by an abundance of data closer to food-saturation at colder temperatures, and predominately food-limited data at warmer temperatures, resulting in an underestimation of the operational Q_{10} .

RESULTS

Growth rate and development time of *C. marshallae* and *C. pacificus*

The occurrences of *C. marshallae* and *C. pacificus* tend to be seasonal in this study as indicated by the presence of sufficient animals for our rate determinations (Fig. 2). For both species, the estimated growth rate and stage duration were variable between stations and years but shared a similar pattern, that is, growth rate decreases with the increase of copepodite stage (Fig. 2). Visually, the mean monthly stage duration of *C. marshallae* tended to decline, while the growth rate increased through May to October (Fig. 3; Table I). However, these monthly mean differences were not significant except for the estimated stage durations in July of 2002, and in May of 2004 (Fig. 3). The overall mean stage duration and growth rates of *C. marshallae* were 7.0 ± 0.4 days and $0.176 \pm 0.008 \text{ day}^{-1}$, respectively. Similar to *C. marshallae*, the stage duration of *C. pacificus* copepodites appeared to be shorter, while growth rate tend to be faster, from August to October (Fig. 3, Table I). The overall mean stage duration and growth rates of *C. pacificus* were 7.8 ± 0.9 days and $0.142 \pm 0.016 \text{ day}^{-1}$, respectively.

After standardization to 5°C , stage duration and growth rate exhibited a similar tendency for both *C. marshallae* and *C. pacificus*, with stage duration increasing slightly with development stage. Growth rate noticeably slowed with the increase of developmental stages, although for *C. pacificus* this pattern was more variable compared to *C. marshallae* (Fig. 4, Table II). The mean 5°C standardized stage duration for all observations of *C. marshallae* was 11 days and growth rate was $0.118 \pm 0.007 \text{ day}^{-1}$.

For *C. pacificus*, the changes in standardized stage duration and growth rate were similar to *C. marshallae*, i.e. the standardized growth rate tends to slow with increasing stage and development time became slightly lengthened. The overall mean 5°C standardized stage

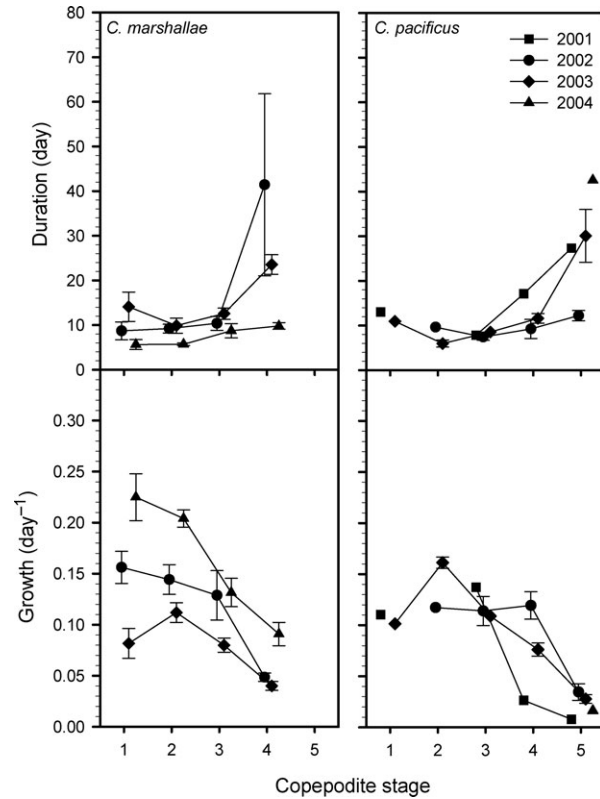


Fig. 4. Mean stage duration and growth rate both corrected to 5°C for *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska 2001–04. Values plotted against initial stage and offset to improve interpretation. Error bars are standard errors.

duration for *C. pacificus* was 15 days and growth rate was $0.075 \pm 0.009 \text{ day}^{-1}$.

Analysis of growth rate factors

For both species, temperature was not a simple regression explanatory variable of growth rate but growth rate was better predicted by body size after Q_{10} standardization of temperature for both *C. marshallae* ($r^2 = 0.19$, $P < 0.0001$) and *C. pacificus* ($r^2 = 0.67$, $P < 0.0001$;

*Table I: Comparison of growth rate (day^{-1}) and development times (days, in parenthesis) based on all seasonal observations for *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska*

Species	T ($^\circ\text{C}$)	Growth rate and developmental time				
		May	July	August	October	Average
<i>Calanus marshallae</i>	5.0–15	0.171 ± 0.009 (7.4 \pm 0.5)	0.174 ± 0.024 (6.9 \pm 0.9)	0.181 ± 0.022 (6.2 \pm 1.0)	0.191 ± 0.027 (5.7 \pm 0.6)	0.176 ± 0.008 (7.0 \pm 0.4)
<i>Calanus pacificus</i>	10.0–15.0			0.119 ± 0.020 (8.2 \pm 1.3)	0.182 ± 0.026 (7.2 \pm 1.3)	0.142 ± 0.016 (7.8 \pm 1.0)

Mean \pm standard error values; T = temperature.

Table II: Comparison of temperature-corrected growth rates (day^{-1}) and development times (days, in parenthesis) for *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska

Species	T (°C)	Growth rate and developmental time					Average
		C1	C2	C3	C4	C5	
<i>Calanus marshallae</i>	5.0	0.156 ± 0.019 (9.4 ± 1.5)	0.145 ± 0.011 (8.7 ± 0.8)	0.109 ± 0.009 (11.0 ± 0.8)	0.058 ± 0.009 (18.7 ± 2.5)		0.119 ± 0.007 (11.0 ± 0.7)
<i>Calanus pacificus</i>	5.0	0.106 ± 0.004 (12.0 ± 1.0)	0.147 ± 0.015 (7.2 ± 1.3)	0.118 ± 0.009 (7.7 ± 0.4)	0.088 ± 0.014 (11.4 ± 1.4)	0.027 ± 0.004 (22.0 ± 3.4)	0.075 ± 0.009 (15.0 ± 1.9)

Mean ± standard error.

Fig. 5). For *C. marshallae*, the best fitted multiple regression model included temperature, chlorophyll *a*, body size and stage as significant explanatory variables ($r^2 = 0.594$, $P < 0.0001$) (Table III). However, the attempt to fit a similar model for *C. pacificus* was unsuccessful, likely due to the limited range of temperature and chlorophyll *a* present in the *C. pacificus* observations.

After standardization to 5°C (Q_{10} of 2.7), the growth rates of *C. marshallae* were significantly related to chlorophyll *a* in the form of a Michaelis–Menten relationship (Fig. 5, Table III). Chlorophyll-*a* concentration exhibited the same explanatory power in the fitted Michaelis–Menten model for the standardized growth rates at 5 and 10°C with $r^2 = 0.337$ and $P < 0.0001$ (Table III) and saturated growth rates (G_{max}) of 0.223 day^{-1} at 5°C, and 0.366 day^{-1} at 10°C.

A composite nonlinear model incorporating body size with the Michaelis–Menten relationship accounts for up to 54.6% of the variance in the standardized growth rate at 5 and 10°C ($P < 0.0001$). Moreover, within this model body size was negatively related to growth rate across chlorophyll-*a* concentrations. Interestingly, the estimated saturated growth rate (G_{max})

in the composite model was slightly faster than its counterpart in the Michaelis–Menten relationship even under a relatively low half-saturated food concentration (K_{chl}) (Table III).

To work around the problem of limited temperature and chlorophyll range in the *C. pacificus* data, we combined data from both species and re-ran simple Michaelis–Menten and composite nonlinear models. We found the parameterization and variability explained in both models were similar to that for *C. marshallae* alone, indicating that the two species have the same functional responses, because otherwise parameters would change and explained variability would decline (Fig. 5, Tables III and IV).

DISCUSSION

Growth and development of *C. marshallae* and *C. pacificus*

Calanus marshallae and *C. pacificus* are the two common species whose distributions overlap across the northern

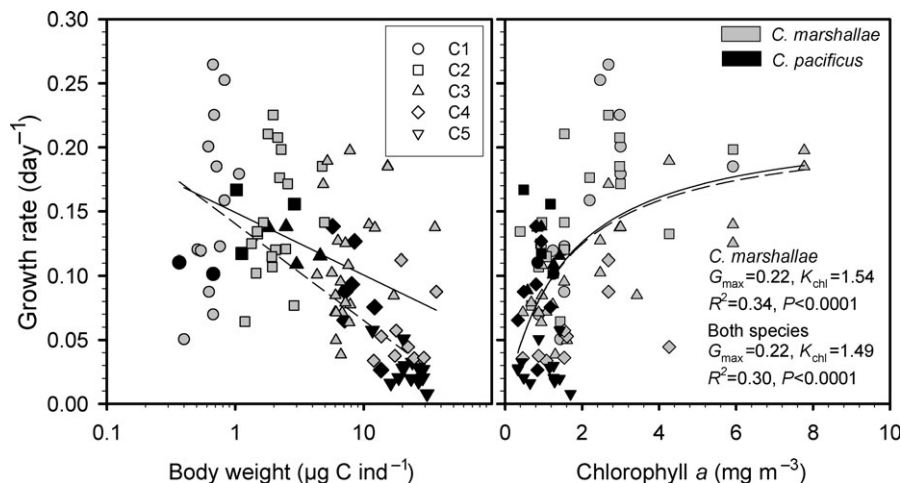


Fig. 5. Relationship between temperature-corrected growth rates and body size, chlorophyll *a* for *C. marshallae* and *C. pacificus* in the northern Gulf of Alaska.

Table III: Relationship for *C. marshallae* between growth rate (g , day^{-1}), initial stage (Stg), temperature (T , $^{\circ}\text{C}$), total chlorophyll a concentration (Chl, mg m^{-3}) and body weight (BW, $\mu\text{g C ind}^{-1}$) in the northern Gulf of Alaska

Function	Equation	n	$T(^{\circ}\text{C})$	Coefficients (p)					$r^2(p)$
				a_1	a_2	a_3	a_4	a_5	
Multiple regression	$\text{Log } g = a_1 + a_2T + a_3\text{Chl} + a_4\log \text{BW} + a_5\text{Stg}$	67	5.0–15.0	-0.3659 (0.0114)	0.0228 (0.0038)	0.0345 (0.0085)	0.4224 (0.0226)	-0.3891 (0.0003)	0.594 (<0.0001)
Michaelis–Menten	$g = \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	67	5		g_{\max} 0.223 (<0.0001)		K_{chl} 1.538 (0.0049)		0.337 (<0.0001)
Michaelis–Menten	$g = \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	67	10		g_{\max} 0.366 (<0.0001)		K_{chl} 1.534 (0.0049)		0.337 (<0.0001)
Composite nonlinear	$g = a*\log \text{BW} + \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	67	5		a -0.0476 (<0.0001)	g_{\max} 0.2405 (<0.0001)	K_{chl} 1.0723 (<0.0001)		0.546 (<0.0001)
Composite nonlinear	$g = a*\log \text{BW} + \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	67	10		a -0.0782 (<0.0001)	g_{\max} 0.3952 (<0.0001)	K_{chl} 1.0723 (<0.0001)		0.546 (<0.0001)

The saturated growth rate (G_{\max} , day^{-1}) and half saturated food concentration (K_{chl} , mg m^{-3}) are calculated after Q_{10} standardization to both 5°C and 10°C .

Table IV: Functional relationships for combined *C. marshallae* and *C. pacificus* between growth rate (g , day^{-1}), total chlorophyll a concentration (Chl, mg m^{-3}), and body weight (BW, $\mu\text{g C ind}^{-1}$) in the northern Gulf of Alaska

Function	Equation	n	$T(^{\circ}\text{C})$	Coefficients (p)			$r^2(p)$
				g_{\max}	K_{chl}	a	
Michaelis–Menten	$g = \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	97	5	g_{\max} 0.2182 (<0.0001)	K_{chl} 1.5563 (0.0049)		0.3038 (<0.0001)
Michaelis–Menten	$g = \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	97	10	g_{\max} 0.3585 (<0.0001)	K_{chl} 1.5563 (0.0049)		0.3038 (<0.0001)
Composite nonlinear	$g = a*\log \text{BW} + \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	97	5	a -0.0529 (<0.0001)	g_{\max} 0.2169 (<0.0001)	K_{chl} 0.7101 (<0.0001)	0.554 (<0.0001)
Composite nonlinear	$g = a*\log \text{BW} + \text{Chl}[g_{\max}]/(\text{Chl} + K_{\text{chl}})$ (C1–C4)	97	10	a -0.087 (<0.0001)	g_{\max} 0.3563 (<0.0001)	K_{chl} 0.7101 (<0.0001)	0.554 (<0.0001)

The saturated growth rate (G_{\max} , day^{-1}) and half saturated food concentration (K_{chl} , mg m^{-3}) are calculated after Q_{10} standardization to both 5°C and 10°C .

Gulf of Alaska, particularly in summer. This paper is the first attempt to examine the growth and development of these two important copepod species, and to explore the underlying relationship between growth rate and other factors based on a multiple-year field approach. Understanding the differential response of these species to environmental variables will provide insight on how long-term climate shifts might affect their abundance and productivity in the Gulf of Alaska and adjoining regions.

Based on this study, it initially seemed that *C. marshallae* grew and developed faster than *C. pacificus* with or without seasonal thermal influences. However, the similar functional responses of growth rate for both species in two different model analyses indicates that the observed discrepancy in growth rate was an artifact of the different space, time and hence environmental conditions in the data sets (i.e. not intra-species differences). Generally, *C. marshallae* are herbivorous copepods (Peterson, 1986; Vidal and Smith, 1986), and predominantly occur in the late spring and early summer during the bloom in the Gulf of Alaska (Coyle and Pinchuk, 2003, 2005). During this time, the chlorophyll-*a* concentration and water temperature are favorable for newly recruited young, as well as old, copepodites to grow and develop close to their maximum rate (Figs 2 and 3). In terms of the food conditions, it is important to note that chlorophyll *a* is not always an accurate measure of food availability; but here chlorophyll *a* as a proper food indicator for *C. marshallae* has been shown to be significant, particularly if body size is considered (Tables III and IV).

For *C. pacificus*, most of the younger copepodites occur in the winter or early spring, while later stages occur in the summer in this region (Incze *et al.*, 1997). In this study, the majority of data for this species was collected from the later copepodite stages during the summer and fall. Under warm temperatures and low food conditions (measured as chlorophyll *a*), the growth and development of later stages are possibly sub-optimal due to food-limitation (Vidal, 1980a, b). Recent studies show that late stage and adult *C. pacificus* feed on a mixture of microzooplankton (e.g. *Protoperdinium* spp., *Gyrodinium* species) at periods when there is low abundance of phytoplankton prey (Pierson *et al.*, 2005; Leising *et al.*, 2005). Such omnivorous feeding, in conjunction with a limited chlorophyll-*a* range, could contribute to the lack of a chlorophyll-*a* relationship in our study.

So far, several extensive studies on growth and development of *C. marshallae* have been made off the Oregon coast using laboratory approaches (Peterson, 1986, 1988; Peterson *et al.*, 2002) and in the southeastern Bering Sea (Vidal and Smith, 1986) using field approaches. Typically, our temperature-corrected growth

rate and development time were consistent with these previous results (Table V). This is surprising, because the persistent coastal downwelling in the northern Gulf of Alaska (Weingartner *et al.*, 2002), should frequently lead to sub-optimal feeding conditions for *C. marshallae* compared to the food-rich regions in the southeastern Bering Sea and off the Oregon coast upwelling zone. In this study, most data on growth and development of *C. marshallae* were collected from the early copepodites (C1–C4), during the spring bloom with abundant food, and this no doubt contributes to the similarity between rates in the Gulf of Alaska and Oregon. However, when temperature differences are considered, conditions in the Bering Sea appear even more optimal.

Several dominant copepod species coexist in the northern Gulf of Alaska. Our estimated growth rates for *C. marshallae* and *C. pacificus* are reasonably comparable with those of other calanoid copepods concurrently estimated in this region (Table VI). The relatively high-standardized growth rate of 0.119 day⁻¹ for *C. marshallae* is similar to the 0.107 day⁻¹ of *Neocalanus flemingeri/plumchrus* at 5°C (Liu and Hopcroft, 2006a), mainly because both species principally occur in the spring with similar rich food and favorable temperature conditions. Meanwhile, the growth rate 0.075 day⁻¹ for *C. pacificus* is closer to the 0.083 day⁻¹ for *Metridia pacifica* (Liu and Hopcroft, 2006b) which is based on year-round observations. Both appear to be lower than the laboratory determined rate of 0.141 day⁻¹ for the coastal species *Centropages abdominalis* (Slater and Hopcroft, 2005).

Relationship between growth and temperature, food condition and body size

Copepod growth is strongly influenced by temperature (e.g. Vidal, 1980; Huntley and Lopez, 1992), chlorophyll *a* (e.g. Vidal, 1980; Kimmerer and McKinnon, 1987) and body size (e.g. Vidal, 1980), with growth rates synergistically affected by the combination of these determinants (Hirst and Lampitt, 1998; Hopcroft *et al.*, 1998; Richardson and Verheye, 1998; Hirst and Bunker, 2003; Bunker and Hirst, 2004; Liu and Hopcroft, 2006a, b). This synergistic effect was clear from our statistical analysis, with temperature, chlorophyll *a*, body size and development stages together accounting for about 60% of the variability in the growth rate for *C. marshallae* (Table III).

Generally, rates of copepod growth tend to be negatively related to body size (Hirst and Lampitt, 1998; Hopcroft *et al.*, 1998; Hirst and Bunker, 2003); however, thermal variation can make this size-dependent relationship unclear (Vidal, 1980; Hopcroft *et al.*, 1998).

Table V: Comparison of growth rates (day^{-1}) and development times (days, in parenthesis) for *C. marshallae* in the subarctic Pacific and Oregon coast

Location	T (°C)	Growth rate and developmental time							Source
		C1	C2	C3	C4	C5	SEP	Average	
Gulf of Alaska	10	0.257 ± 0.031 (5.7 ± 0.9)	0.238 ± 0.017 (5.3 ± 0.5)	0.179 ± 0.016 (6.7 ± 0.5)	0.094 ± 0.014 (11.4 ± 1.5)		0.10 ^a	0.195 ± 0.012 (6.7 ± 0.4)	This study
Southeastern Bering Sea	0.5–6.0	0.15 (6.5)	0.15 (6.5)	0.14 (8)			0.06	0.147 (7)	Vidal and Smith (1986)
Oregon coast	11.8	0.19 (3.8)	0.19 (3.8)	0.20 (3.7)	0.14 (5.3)	0.12 (5.9)	0.05	0.14 (4.7)	Peterson <i>et al.</i> , (2002)
Oregon coast	10	0.176 (4.3)	0.176 (4.6)	0.176 (6.8)	0.176 (6.2)	0.024 (20.9)		0.146 (8.56)	Peterson (1986)

Daily specific egg production (SEP, day^{-1}) of females included for comparison. (Mean ± Standard error).

^aHopcroft, unpublished results.

Although *Calanus* temperature-corrected growth rate declined with increasing stage (Fig. 4), when stage was also included as a parameter statistical analysis suggested a positive relationship between growth rate and body size and a negative relationship to stage (Table III). The interactive influence between temperature, chlorophyll *a* and body size on copepod growth rate has been demonstrated in the laboratory (Vidal, 1980). In the field, a positive correlation between the temperature-corrected growth rate and body size within each stage has only recently been demonstrated for *Neocalanus flemingeri/plumchrus* in this study region under optimal food conditions during the spring bloom (Liu and Hopcroft, 2006a). This kind of positive relationship is also suggested visually for *C. marshallae* and *C. pacificus* here; however, none of them are significant (Fig. 5). Unlike *Neocalanus flemingeri/plumchrus*, the lack of a pure single stage assemblage in each experiment for *C. marshallae* blurs such patterns.

Globally, a significant Michaelis–Menten relationship exists between chlorophyll *a* and copepod growth rate after removing the temperature effect (Hirst and Bunker, 2003). This general pattern was also followed by *C. marshallae* in this study, with 33.7% explained variance in growth rate (Table III); however, the synergistic effect between chlorophyll *a* and body size still confounds the relationship with growth. Based on this evidence, a composite nonlinear model combining body weight into the traditional Michaelis–Menten function was first developed for *Metridia pacificus* (Liu and Hopcroft, 2006b). Fitting this model greatly enhanced the explainable variance in the growth rate by over 20% for *C. marshallae*, demonstrating that the composite

Table VI: Standardized growth rate (day^{-1}) of *C. marshallae* and *C. pacificus* to 5°C using Q_{10} (2.7) compared with other dominant species in the northern Gulf of Alaska

Species	Growth rate	SEP	Source
<i>Calanus marshallae</i>	0.119 ± 0.007		Present study
<i>Calanus pacificus</i>	0.075 ± 0.009		Present study
<i>Metridia pacifica</i>	0.083 ± 0.005		Liu and Hopcroft (2006b)
<i>Metridia pacifica</i>		0.10	Hopcroft <i>et al.</i> (2005)
<i>Metridia okhotensis</i>		0.11	Hopcroft <i>et al.</i> (2005)
<i>Neocalanus flemingeri/plumchrus</i>	0.107 ± 0.005		Liu and Hopcroft (2006a)
<i>Centropages abdominalis</i>	0.141 ^a		Slater and Hopcroft (2005)

Daily specific egg production (SEP, day^{-1}) of females included for comparison. (Mean ± Standard error).

^aGrowth rate corrected from original 6.9°C to 5.0°C ($Q_{10} = 2.7$)

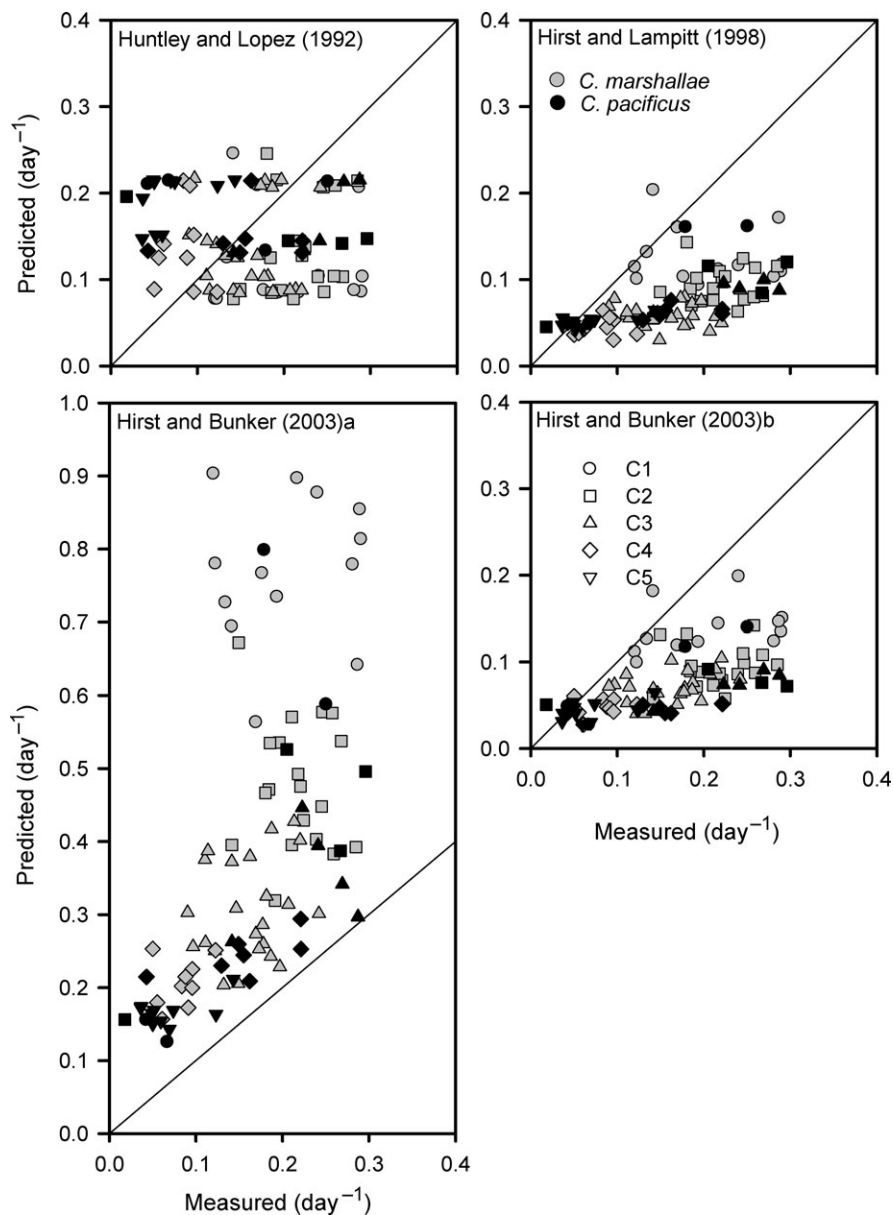


Fig. 6. Comparisons of the measured growth rates for *C. marshallae* and *C. pacificus*, and copepod growth rates predicted from the models of Huntley and Lopez (1992), Hirst and Lampitt (1998), and Hirst and Bunker (2003). Hirst and Lampitt (1998) equation for all data equation (adults and juveniles of both broadcast and sac-spawners); Hirst and Bunker (2003); a: for juveniles broadcasters; b: for all data combined.

nonlinear model provides a higher degree of prediction than its prototype (Table III). Similar use of the composite nonlinear model only resulted in a 7% increase for *Metridia pacifica* (Liu and Hopcroft, 2006b) and insignificant improvement (~1%) for *Neocalanus flemingeri/plumchrus* in the same study area. The wide range of chlorophyll *a* concentration experienced by *C. marshallae* accentuated the interaction between food concentration and body size on growth rate that has been demonstrated previously (e.g. Vidal, 1980; Hopcroft *et al.*, 1998).

Comparison with global models

The results in this study compliment two recent studies to test the global models of copepod growth rate in the high latitudes waters of the northern Gulf of Alaska (Liu and Hopcroft, 2006a, b). All of the previous multi-species global models display variable degrees of difference between predicted and estimated growth rate for the two *Calanus* species in this study area (Figs 6 and 7; Table VII), similar to the findings for two other dominant copepod species in this area, e.g. *Neocalanus*

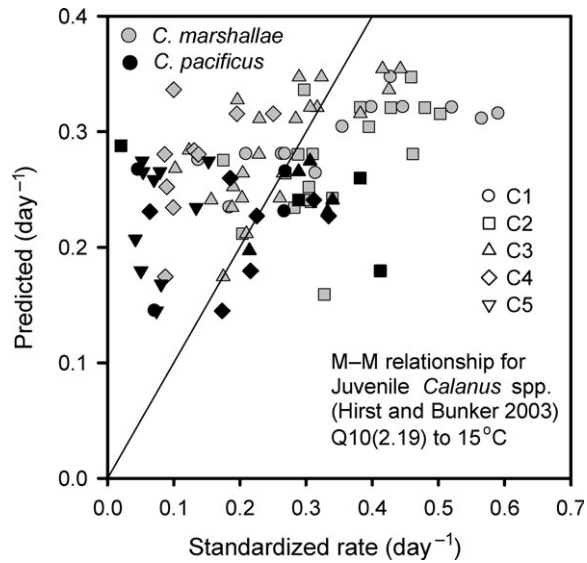


Fig. 7. Comparisons of the temperature-corrected growth rates for *C. marshallae* and *C. pacificus* with the rates predicted from the Michaelis–Menten relationship given for juvenile *Calanus* spp. by Hirst and Bunker (2003).

flemingeri/plumchrus and *Metridia pacifica*. Detailed discussions on comparing models of Huntley and Lopez (1992), Hirst and Lampitt (1998) and Hirst and Bunker (2003) can be found in our previous studies (Liu and Hopcroft, 2006a, b) and are not repeated here.

Although some of the limitations of the general broadcast models (Hirst and Bunker, 2003) might be attributed to the wide mixture of species within them, one would expect such modeling approaches to be more successful if restricted to a single species or genus. The two Michaelis–Menten relationships developed specifically for *Calanus* spp. (Hirst and Bunker, 2003), provide the opportunity for additional comparisons. After correcting our data with the same Q_{10} values employed in their study, we find reasonable agreement with their juvenile *Calanus* spp. relationship (Fig. 7). Notably, their model for *Calanus* juveniles predicts a much narrower range of growth rates, and a tendency to overestimate at low growth rate and underestimate when rates are high. A further analysis of growth rates at each developmental stage suggests that the global model for juvenile *Calanus* spp. at 15°C can match reasonably well with our measured rates for both *Calanus* species, but a large discrepancy occurs for later copepodite stages (Table VII). Overall, this suggests reasonable consistency in functional response across the genus. If this is true, temperature tolerance/preference may play a primary role in determining the spatial and temporal distribution of *Calanus* species, as has been suggested for other congeners generally (e.g. Halsband-Lenk *et al.*, 2002).

Table VII: Comparison of growth rates predicted by global models with measured rates for *C. marshallae* ($n = 67$) and *C. pacificus* ($n = 30$) in the northern Gulf of Alaska

Model	T (°C)	Copepodite Stage				
		C1	C2	C3	C4	C5
<i>Calanus marshallae</i>						
Huntley and Lopez (1992)	5.0–15.0	59%, 30–170%	63%, 35–136%	84%, 40–224%	165%, 70–256%	270%, 110–1010%
Hirst and Lampitt (1998)	5.0–15.0	61%, 37–144%	42%, 26–79%	37%, 19–80%	54%, 30–76%	69%, 32–210%
Hirst and Bunker (2003)a	5.0–15.0	380%, 220–750	212%, 138–288%	190%, 116–340%	249%, 189–500%	312%, 210–630
Hirst and Bunker (2003)b	5.0–15.0	68%, 44–128%	41%, 26–73%	44%, 28–80%	58%, 42–120%	67%, 46–181%
Hirst and Bunker (2003)c	15.0	82%, 53–200%	79%, 49–157%	112%, 79–262%	210%, 126–336%	274%, 193–1040%
<i>Calanus pacificus</i>						
Huntley and Lopez (1992)	10.0–15.0	81%, 74–85%	56%, 50–71%	72%, 60–92%	96%, 59–310%	310%, 150–1090%
Hirst and Lampitt (1998)	10.0–15.0	75%, 64–90%	42%, 32–56%	37%, 30–44%	40%, 27–117%	80%, 43–252%
Hirst and Bunker (2003)a	10.0–15.0	332%, 2.34–4.45%	183%, 1.45–2.56%	157%, 1.14–5.0%	157%, 1.33–8.67%	257%, 1.33–8.67%
Hirst and Bunker (2003)b	10.0–15.0	60%, 56–65%	31%, 24–45%	30%, 23–96%	30%, 23–96%	68%, 36–282%
Hirst and Bunker (2003)c	15.0	93%, 86–99%	63%, 44–83%	82%, 69–92%	100%, 68–360%	320%, 175–1410%

Values in terms of the percentage of predicted versus measured rates with their ranges. In Hirst and Bunker (2003), a: for juvenile broadcasters; b: for all data; c: Michaelis–Menten relationship for juvenile *Calanus* spp. at 15°C.

Inevitably, all models have limitations and some discrepancy between measured and predicted values will occur for any single species at a specific region. Recent critical examination of the mathematical underpinning of copepod growth rate methodologies (Hirst *et al.*, 2005; Kimmerer *et al.*, in press) suggests a wide range of biases may be pervasive in much of the existing literature, including those detectable in this study. The techniques employed here rely on MRs, and thus can be subject to biases if there is an uneven age of individuals within a stage or when there are large differences in development time between adjoining stages (Miller and Tande, 1993; Hirst *et al.*, 2005). The artificial cohort approach tends to be less biased than the traditional molt rate method, but because it does not directly measure weight increase, severe biases (generally overestimation) can still occur. The magnitude of these biases is dependent on sample size, stage, growth increment, efficiency of cohort creation, incubation time and stage duration (Kimmerer *et al.*, in press). These biases contribute to both errors and noise in data, and the resultant statistical relationships, that further hamper our ability to define both species-specific and “global” patterns. Direct weighing of animals in experiments of appropriate duration may be the only way to avoid such biases, but this approach unfortunately results in the sacrifice of the experimental samples.

An important contribution of this study, together with our two recent studies, is to remind us that we still need direct measurement of copepod growth rates, especially for ecosystems and species currently lacking this kind of information. Copepod growth rates are a fundamental parameter for further analysis of the flows of energy and matter through marine ecosystems. Significant errors in estimating secondary production arising from the use of biased growth data and/or inappropriate models, could have large consequences in quantifying the linkage of copepods to both higher and lower trophic levels, and how this might be altered by short-term and long-term climate change.

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