

# Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska

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**Abstract** The euphausiids *Thysanoessa inermis* (Kroyer 1846), *Thysanoessa spinifera* (Holmes 1900), and *Euphausia pacifica* (Hansen 1911) are key pelagic grazers and also important prey for many commercial fish species in the Gulf of Alaska (GOA). To understand the role of the euphausiids in material flows in this ecosystem their growth rates were examined using the instantaneous growth rate (IGR) technique on the northern GOA shelf from March through October in 2001–2004. The highest mean molting increments (over 5% of uropod length increase per molt) were observed during the phytoplankton bloom on the inner shelf in late spring for coastal *T. inermis*, and on the outer shelf in summer for *T. spinifera* and more oceanic *E. pacifica*, suggesting tight coupling with food availability. The molting rates were higher in summer and lower in spring, for all species and were strongly influenced by temperature. Mean inter-molt periods calculated from the molting rates, ranged from 11 days at 5°C to 6 days at 8°C, and were in agreement with those measured directly during long-term laboratory incubations. Growth rate estimates depended on euphausiid size, and were close to 0 in early spring, reaching maximum values in May (0.123 mm day<sup>-1</sup> or 0.023 day<sup>-1</sup> for *T. inermis*) and July (0.091 mm day<sup>-1</sup> or 0.031 day<sup>-1</sup> for

*T. spinifera*). The growth rates for *E. pacifica* remained below 0.07 mm day<sup>-1</sup> (0.016 day<sup>-1</sup>) throughout the season. The relationship between *T. inermis* weight specific growth rate (adjusted to 5°C) and ambient chlorophyll-*a* concentration fit a Michaelis–Menten curve ( $r^2 = 0.48$ ) with food saturated growth rate of 0.032 day<sup>-1</sup> with half saturation occurring at 1.65 mg chl-*a* m<sup>-3</sup>, but such relationships were not significant for *T. spinifera* or *E. pacifica*.

## Introduction

The euphausiids *Thysanoessa inermis*, *Thysanoessa spinifera*, and *Euphausia pacifica* occupy a key role in the northern Gulf of Alaska (GOA) ecosystem, both as pelagic grazers and a prey for many vertebrates. These species undergo extensive diel vertical migrations (e.g., Mauchline 1980) and are thought to feed on a variety of phyto- and microzooplankton, as well as suspended organic matter (Ponomareva 1966; Dilling et al. 1998; Nakagawa et al. 2001, 2004; Bargu et al. 2003). They are a major prey for many of the commercially harvested fishes in the GOA, including all species of salmon (e.g., Armstrong et al. 2005), pollock (e.g., Wilson et al. 2006), herring (e.g., Hart 1973), and sablefish (e.g., Sigler et al. 2001), as well as seabirds and baleen whales (Mauchline 1980). In order to appreciate the role of euphausiids in material flow and transformation in the ocean, it is essential that their rates of growth and production, and the factors controlling these rates are understood.

The growth of oceanic zooplankton, including euphausiids, is governed primarily by temperature and

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food (e.g., Huntley and Boyd 1984; Clarke and Peck 1991; Hirst et al. 2003). Both factors undergo substantial seasonal variability in high latitudes. Euphausiids may respond to changes in these factors in two ways: by altering the duration of the inter-molt period (IP), and by changing the growth increment (Buchholz 1991; Iguchi and Ikeda 1995). The IP is thought to be affected mainly by temperature (e.g., Kawaguchi et al. 2006; Tarling et al. 2006) and to a smaller degree by individual size (Fowler et al. 1971; Iguchi and Ikeda 1995). In contrast, the growth increment appears to be strongly influenced by quantity and quality of food (Iguchi and Ikeda 1995; Ross et al. 2000) and may become negative under unfavorable conditions leading to body shrinkage (Nicol et al. 1992; Marinovic and Mangel 1999).

Traditionally, growth rate measurements on *T. inermis*, *T. spinifera*, and *E. pacifica* in the North Pacific were estimated using the natural cohort technique (e.g., Smiles and Pearcy 1971; Smith 1991; Tanasichuk 1998a, b). The primary assumptions of this method are that the same population is observed over time, and that mortality of individuals is not size-dependent (Quetin et al. 2003). These assumptions are most likely violated on the northern GOA shelf due to the rugged topography, strong currents and abundant euphausiid predators of different size and hunting habits. An alternative incubation technique, allowing direct measurement of both molting frequency and growth increments, has been applied to *E. pacifica* (Iguchi and Ikeda 1995), however, the long periods of incubation required by this approach at low subarctic temperatures may introduce artifacts and errors to the rates being measured. In contrast, the instantaneous growth rate (IGR) incubation technique (Quetin and Ross 1991) permits measurement of both components of euphausiid growth in relation to environmental factors over relatively small temporal and spatial scales without assuming population constancy and size-independent mortality (Quetin et al. 2003). With the IGR method, experiments with freshly collected krill are likely to reflect the natural growth rate of individuals in the field (Nicol 2000; Ross et al. 2000). The IGR method has been applied to study various aspects of Antarctic krill growth (e.g., Nicol et al. 1992; Ross et al. 2000; Atkinson et al. 2006; Tarling et al. 2006), and was recently applied to euphausiid populations off the Oregon coast (Shaw et al. 2004).

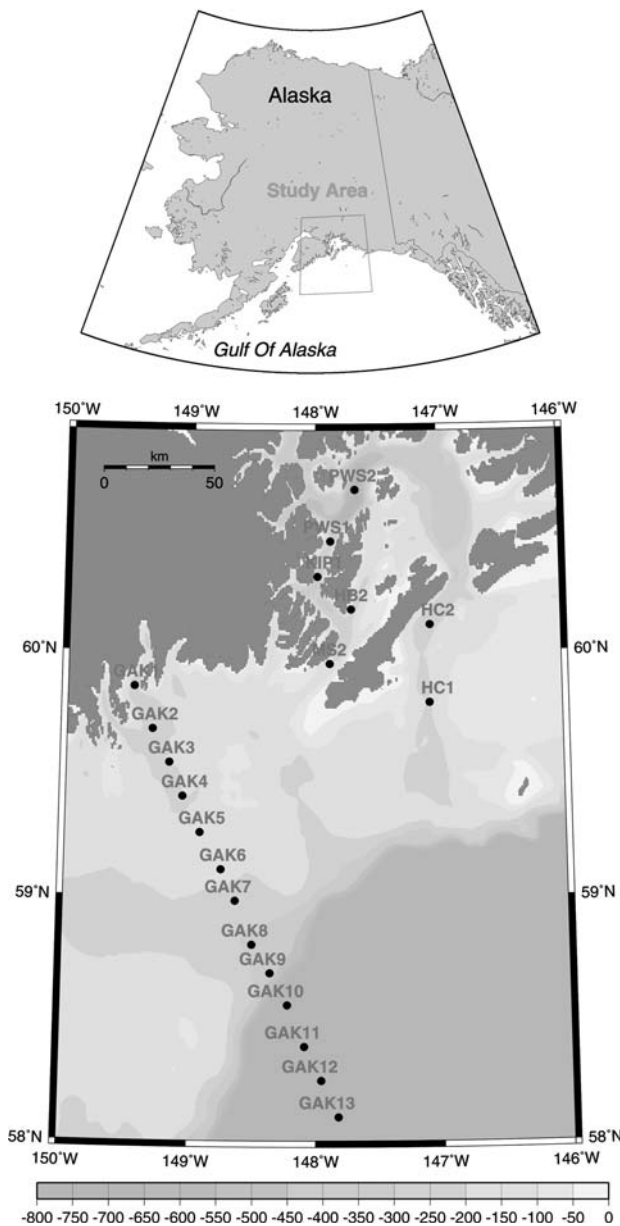
Despite the evident importance of euphausiids in the northern GOA shelf ecosystem, information on their growth rates within the temperature range of the GOA is absent. The US North Pacific GLOBEC Long-Term Observation Program (LTOP) in the northern

GOA seeks to address such deficiencies in our knowledge (Weingartner et al. 2002). In the present study, we document seasonal variability in growth rates of the major euphausiid species from the northern GOA measured with the IGR technique, examine factors controlling euphausiid growth throughout the productive season, and compare euphausiid growth rates with those of copepods in the context of the GOA food web.

## Methods

The euphausiids *T. inermis* (Kroyer 1846), *T. spinifera* (Holmes 1900), and *E. pacifica* (Hansen 1911) were collected along the Seward Line and within Prince William Sound in the northern GOA during GLOBEC LTOP cruises in 2001–2004 (Fig. 1). Night-time euphausiid aggregations were located in the upper 50 m of the water column with an HTI acoustic system, then fished using a 1-m<sup>2</sup> MOCNESS equipped with black 100- $\mu$ m mesh nets and non-filtering cod-ends, towed at 0.25–0.5 m s<sup>-1</sup>. Collections were immediately diluted into a 20-l pail to facilitate sorting. Active, undamaged euphausiids were gently removed from the catch and placed individually in 750-ml tissue-culture flasks filled with seawater collected simultaneously at the site. The euphausiid species were not identified at the time of collection to minimize handling time, so most of the experiments contained individuals of more than one species (Table 1). Water samples for fluorometric estimation of chlorophyll-*a* concentration were collected at these stations by Niskin bottles and the chl-*a* concentration was averaged over the upper 50 m of the water column (D.A. Stockwell and T.E. Whitley, unpublished data). The euphausiids were maintained at near ambient mixed layer water temperature (5°C in March–May, 8–12°C in July–August, and 10°C in October) in darkness and were checked every 12–24 h for molts. If an individual molted, the exuviae and the individual were preserved in 5% formalin. At the end of each experiment, all remaining euphausiids were preserved.

To estimate the magnitude of possible negative growth (body shrinkage), several experiments lasting 10–20 days under restricted-food conditions were conducted in April–May (at 5°C) and July–August (at 8°C) of 2001 (Table 1). The euphausiids were placed in filtered seawater upon arrival at the lab (2–3 days after collection) with no food subsequently added and water changed once a week. The duration of experiments conducted in 2002–2004 was 48 h. Molting rates (MR, % population per day) were determined in each experiment only for species that totaled more than 30



**Fig. 1** Map of sampling locations in the northern Gulf of Alaska

individuals. IPs (days) were directly measured during the long-term experiments, and calculated for short-term incubations as the inverse of the observed MR.

All length measurements were made digitally to  $\pm 1 \mu\text{m}$  with an accuracy of  $\pm 5 \mu\text{m}$  (Roff and Hopcroft 1986). The lengths of exopodites of both uropods (mm) were measured on all molts ( $UL_m$ ) and preserved euphausiids ( $UL_p$ ), and then averaged. Sometimes, one of the uropods was damaged and therefore was not measured. In these cases, the measurements were based on a single molt and postmolt uropod pair. If

both uropods were damaged then the individual was used only for the MR calculations. Individual length-specific molting increment (MI) was computed as:

$$MI = \frac{UL_p - UL_m}{UL_m} \times 100 (\%).$$

Mean UL in experiments was 2.26 mm (range 1.11–2.99 mm, SD = 0.35,  $n = 451$ ) for *T. inermis*; 2.21 mm (range 0.77–3.57 mm, SD = 0.53,  $n = 227$ ) for *T. spinifera*; and 2.79 mm (range 1.2–3.7 mm, SD = 0.43,  $n = 281$ ) for *E. pacifica*.

The relationships between UL, carapace length (CL), and total length (TL) were estimated using linear regressions for euphausiids from the GOA collected in March of 1999 as outlined in Coyle and Pinchuk (2005). CL (mm) was measured from the tip of the rostrum to the posterior dorsal margin of the carapace. The TL (mm) was defined as distance from the tip of the rostrum to the distal end of the telson excluding spines. No correction was made for shrinkage of TL in formalin preserved samples. The TL range of specimens used to establish equations was 7.6–24.1 mm for *T. inermis*, 10.2–30.4 mm for *T. spinifera*, and 3.0–20.5 mm for *E. pacifica*:

$$\begin{aligned} CL &= 3.07UL - 1.11 (n = 239, r^2 = 0.88) \text{ for } T. inermis, \\ CL &= 2.56UL - 0.69 (n = 621, r^2 = 0.85) \text{ for } T. spinifera, \\ CL &= 1.48UL + 0.25 (n = 340, r^2 = 0.86) \text{ for } E. pacifica. \\ TL &= 2.46CL + 2.99 (n = 246, r^2 = 0.92) \text{ for } T. inermis, \\ TL &= 2.57CL + 2.76 (n = 224, r^2 = 0.88) \text{ for } T. spinifera, \\ TL &= 3.76CL + 0.87 (n = 266, r^2 = 0.94) \text{ for } E. pacifica. \end{aligned}$$

The relationships between CL and dry weight (DW, mg) were determined using log-transformed linear regressions. The euphausiids were collected from the study area in 1998–1999 (Coyle and Pinchuk 2005), frozen and transferred to the Seward Marine Center laboratory, where they were thawed, dried at 60°C and weighed to  $\pm 1 \mu\text{g}$  on a Cahn microbalance. The CL range of specimens used to establish equations was 3.0–10 mm for *T. inermis*, 1.9–12.0 mm for *T. spinifera* and 1.9–7.5 mm for *E. pacifica*:

$$\begin{aligned} \log DW &= 2.50 \log CL - 1.162 (n = 838, r^2 = 0.79) \text{ for } T. inermis, \\ \log DW &= 3.39 \log CL - 1.854 (n = 2,531, r^2 = 0.87) \text{ for } T. spinifera, \\ \log DW &= 3.03 \log CL - 1.161 (n = 945, r^2 = 0.89) \text{ for } E. pacifica. \end{aligned}$$

To facilitate better comparison with published data, these regressions were used to compute increases in length and weight between moltings as:

**Table 1** Summary of growth and molting rate experiments in the northern Gulf of Alaska showing the number of euphausiids incubated

Month	2001				2002				2003				2004					
	Station	TI	TS	EP	Station	TI	TS	EP	Station	TI	TS	EP	Station	TI	TS	EP		
March	PWS1 <sup>a</sup>	9	5	–	GAK6	128	15	2	GAK12	2	18	99						
					GAK3	58	20	3	GAK2	112	51	7						
					GAK1	129	48	3										
April	GAK13 <sup>a</sup>	5	2	74	GAK11	177	1	28	GAK4	132	34	4						
					GAK3	172	18	–	GAK6	189	17	–						
									GAK1	51	141	–						
May	GAK13 <sup>a</sup>				GAK1	81	43	1	GAK2	52	35	92	GAK1-2	24	72	74		
					GAK7	192	5	–										
July	GAK9 <sup>a</sup>	21	3	7	GAK7	1	180	5	GAK8	110	6	73						
					GAK7 <sup>a</sup>	17	4	20	GAK5	131	33	9						
August	GAK12 <sup>a</sup>	2	–	35	GAK11	–	158	25	PWS1	33	100	1						
					GAK9 <sup>a</sup>	4	19	9	GAK5	164	29	7	GAK4	34	58	64		
					GAK6 <sup>a</sup>	13	2	16					GAK3	2	19	153		
October					GAK2	19	44	83	GAK12	–	–	207	GAK4	–	54	128		
					GAK4	77	66	21					GAK11	–	29	111		
					GAK1	66	30	57					GAK6	3	–	192		

TI *Thysanoessa inermis*, TS *Thysanoessa spinifera*, EP *Euphausia pacifica*

<sup>a</sup> Long-term experiments lasting more than 48 h, only molted euphausiids included

$$G_L = \frac{TL_p - TL_m}{IP} \text{ (mm day}^{-1}\text{)}$$

and,

$$G_W = \frac{DW_p - DW_m}{IP} \text{ (mg day}^{-1}\text{)}$$

and weight-specific growth rates between moltings as:

$$g_w = \frac{\ln DW_p - \ln DW_m}{IP} \text{ (day}^{-1}\text{)}.$$

All data were uploaded into a MS ACCESS database and analyzed using standard STATISTICA and SigmaPlot 8.0 routines. Factorial ANOVA was run to test for inter-annual and seasonal differences in MI and MR of each species. To elucidate the relative importance of major factors controlling growth, backwards stepwise-regression analyses were done separately on each euphausiid species. The dependent variables were MI and MR, and the independent variables were daily mean temperature ( $T$ , °C) and chl-*a* concentration (Chl, mg m<sup>-3</sup>). Since euphausiids display an asymptotic growth pattern (e.g., Tanasichuk 1998a, b), their length-specific growth increments tend to decrease when individual size increases. While the proportion of CL to TL in euphausiids is known to change when mature, and often differs between males and females (e.g., Miller 1983; Timofeev 1996), TL is subject to severe shrinkage after preservation (e.g., Kulka and Corey 1982). Since we did not have an opportunity to freeze the individuals after the shipboard experiments,

rigid CL was chosen to provide a measure of individual size. Therefore, CL<sub>m</sub> was added as an independent variable when analyzing MI. Euphausiid size was not included when analyzing MR, since the estimates of MR were obtained for a population in an experiment, rather than derived from individual measurements. *p*-to-enter was set at 0.049 and *p*-to-remove at 0.05. Then multiple linear regressions relating MI and MR to the remaining variables were completed and standardized regression coefficients computed.

To quantify relationships between  $g_w$  and Chl alone, the individual values were averaged for each experiment, adjusted to 5°C using  $Q_{10}$  of 2.25 (Winberg 1983; Iguchi and Ikeda 1995), and then fit to a Michaelis-Menten uptake function curve expressed as:

$$g_w = \frac{g_{w_{\max}} \text{Chl}}{K_d + \text{Chl}},$$

where  $g_{w_{\max}}$  is the asymptotic  $g_w$ , and  $K_d$  is half-saturation constant. Since euphausiids may experience negative growth, the data were transformed by adding a positive factor of 0.004 before fitting and estimated values  $g_{w_{\max}}$  were converted back afterwards.

## Results

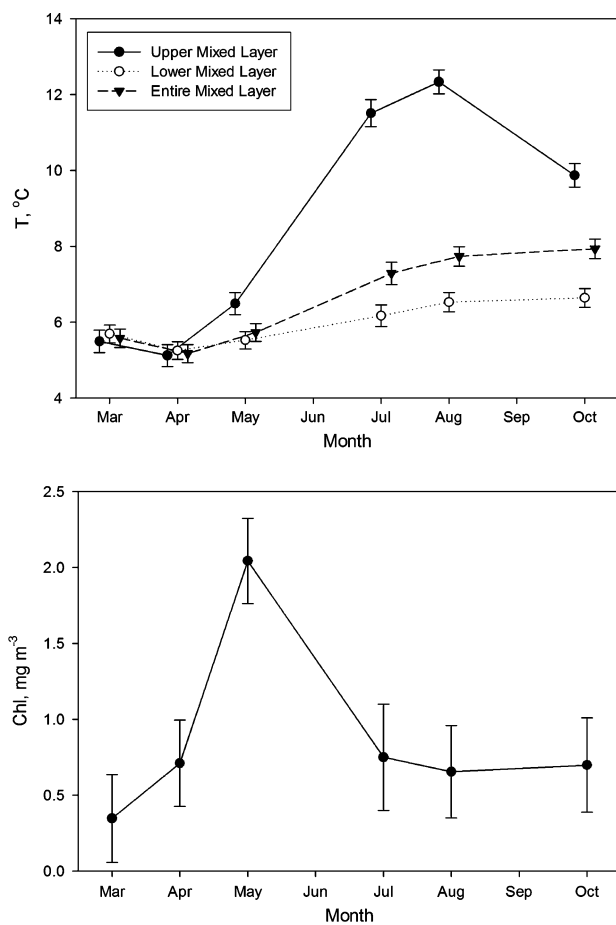
### Seasonal variability in environment

The mean temperature was ~5°C throughout the water column from March through May (Fig. 2a). The upper

layer (0–25 m) warmed to  $\sim 12^{\circ}\text{C}$  in July–August, then decreased to  $\sim 10^{\circ}\text{C}$  by October, while the layer below the thermocline remained cool (between 5 and  $6^{\circ}\text{C}$ ) throughout the year. The mean water column chl-*a* content was lowest ( $<0.5\text{ mg m}^{-3}$ ) in March gradually increasing through April with maximum ( $\sim 2\text{ mg m}^{-3}$ ) in May, indicating the development of the spring phytoplankton bloom (Fig. 2b). In summer and fall, chl-*a* content decreased to  $\sim 0.7\text{ mg m}^{-3}$ , and in December it was  $<0.5\text{ mg m}^{-3}$ .

### Seasonal variability in euphausiid growth

While there were no significant inter-annual differences in euphausiid length-growth, seasonal patterns affecting both MI and MR were distinctive for all three species, despite the large individual variability observed. The minimal MI values were observed in March, indicating close to zero growth or shrinkage

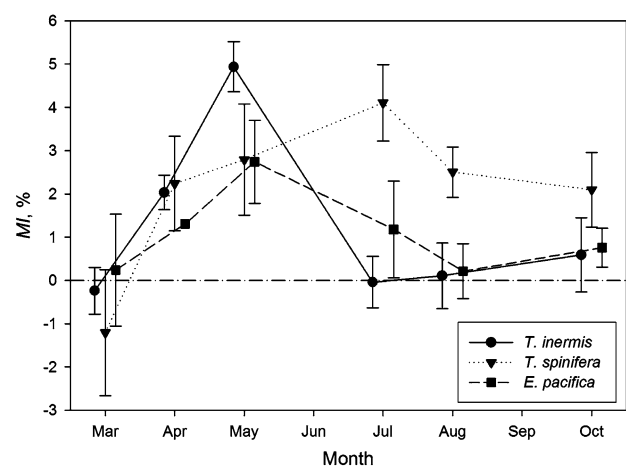


**Fig. 2** Seawater temperature above and below the thermocline, and through the entire mixed layer (0–100 m) (a); and chlorophyll-*a* concentrations (b), along the Seward line in the northern Gulf of Alaska in 2001–2003 (vertical bars are 95% CI)

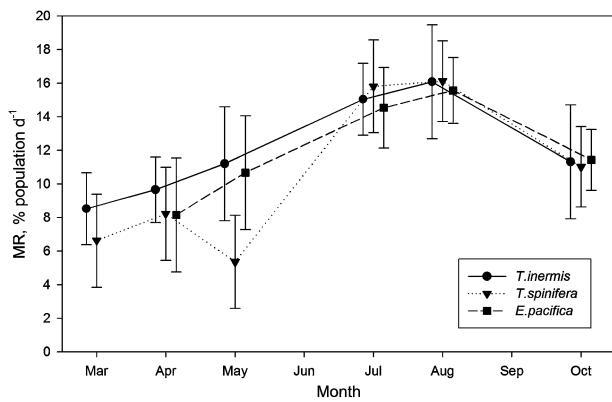
(Fig. 3). Growth intensified through the spring, peaking in May with  $\sim 5\%$  change in UL per molt for *T. inermis*. By mid-summer, the MI values decreased significantly for *T. inermis*, while remaining high for other species. In late summer, MI values of *T. inermis* were near 0%, with a slight increase during October. In contrast, *T. spinifera* had a less modulated MI of  $\sim 2\text{--}4\%$  change in UL from April through the end of production season. For *E. pacifica* the pattern was most similar to that of *T. inermis*, but it maintained a positive MI throughout the summer and fall. In contrast to MI, the highest mean MR (14–16% of population per day) were recorded in July–August for all species, while the lowest mean MR ( $\sim 6\text{--}10\%$  of population per day) were consistently observed in March through May (Fig. 4). In October, the mean MR was intermediate ( $\sim 10\%$  of population per day).

The major factors controlling the MI in the experiments were chl-*a* concentration (positive correlation) and body size (negative correlation), while the MR depended almost exclusively on water temperature (positive correlation) for all species (Table 2). Only *T. inermis* showed a weak negative correlation between the MI and temperature, and a positive correlation between the MR and chl-*a* content.

Two distinctive size groups were found in experimental populations for all three species, visually separated at 2.2 mm UL (16.9 mm TL) for *T. inermis*, 2.5 mm UL (17.4 mm TL) for *T. spinifera*, and 2.6 mm UL (16.3 mm TL) for *E. pacifica* (Fig. 5, insets). Therefore, mean growth rates were calculated per month separately for each size group to account for the effect of body size, revealing that smaller euphausiids



**Fig. 3** Mean length-specific molting increments (MI, % of uropod length) of *Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica* in the northern Gulf of Alaska in 2001–2004 (vertical bars are 95% CI, reference line drawn at 0 increment to denote negative/positive growth)



**Fig. 4** Mean molting rates (MR, % population per day) of *Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica* in the northern Gulf of Alaska in 2001–2004 (vertical bars are 95% CI)

grew faster both in terms of length increase (Fig. 5) and weight-specific rates (Table 3). Distinctive seasonal patterns of growth emerged for *Thysanoessa* species, similarly starting at 0 or negative growth of both size groups in March. In *T. inermis*, small individuals increased growth in April (0.044 mm day<sup>-1</sup> or 0.034 mg day<sup>-1</sup>), reached maximal growth in May during the spring bloom (0.123 mm day<sup>-1</sup> or 0.109 mg day<sup>-1</sup>), remained high in July and decreased (0.019 mm day<sup>-1</sup> or 0.013 mg day<sup>-1</sup>) in October (Fig. 5). Large euphausiids also maintained positive growth in April (0.023 mm day<sup>-1</sup> or 0.029 mg day<sup>-1</sup>), with maximum rates in May (0.102 mm day<sup>-1</sup> or 0.121 mg day<sup>-1</sup>), but showed negative or 0 growth from July through October (to -0.025 mm day<sup>-1</sup> or -0.028 mg day<sup>-1</sup>). While small *T. spinifera* also showed highest growth rates in May (0.091 mm day<sup>-1</sup>), they grew steadily throughout the season decreasing to

0.02–0.03 mm day<sup>-1</sup> only in October. The growth of large *T. spinifera* was constantly low (<0.02 mm day<sup>-1</sup>) through most of the season. In contrast, *E. pacifica* did not show any distinctive seasonal growth pattern, with growth rates for small individuals remaining constantly low (<0.07 mm day<sup>-1</sup>) from spring to fall, and large individuals growing slightly slower (Fig. 5).

After removing the temperature effect on growth through Q<sub>10</sub> standardization, the relationship between the mean  $g_w$  and ambient chl-*a* concentration fit to a Michaelis–Menten form best for *T. inermis* ( $r^2 = 0.48$ ) with food-saturated weight specific growth rate ( $g_{w,max}$ ) of  $0.032 \pm 0.008$  (SE,  $p < 0.001$ ) day<sup>-1</sup> and half saturation ( $K_d$ ) occurring at  $1.65 \pm 0.74$  ( $p = 0.03$ ) mg chl-*a* m<sup>-3</sup>. There were poor fits ( $r^2 < 0.1$ ) for *T. spinifera* and *E. pacifica* (Fig. 6), suggesting that other factors contribute substantially to variations in the  $g_w$  of these species. Inclusion of body weight in addition to the Michaelis–Menten relationship to chl-*a* did not substantially improve the model, likely because the weight ranges of euphausiids used in the experiments were not broad enough to resolve the differences in the weight specific growth rates.

#### The influence of starvation on euphausiid growth

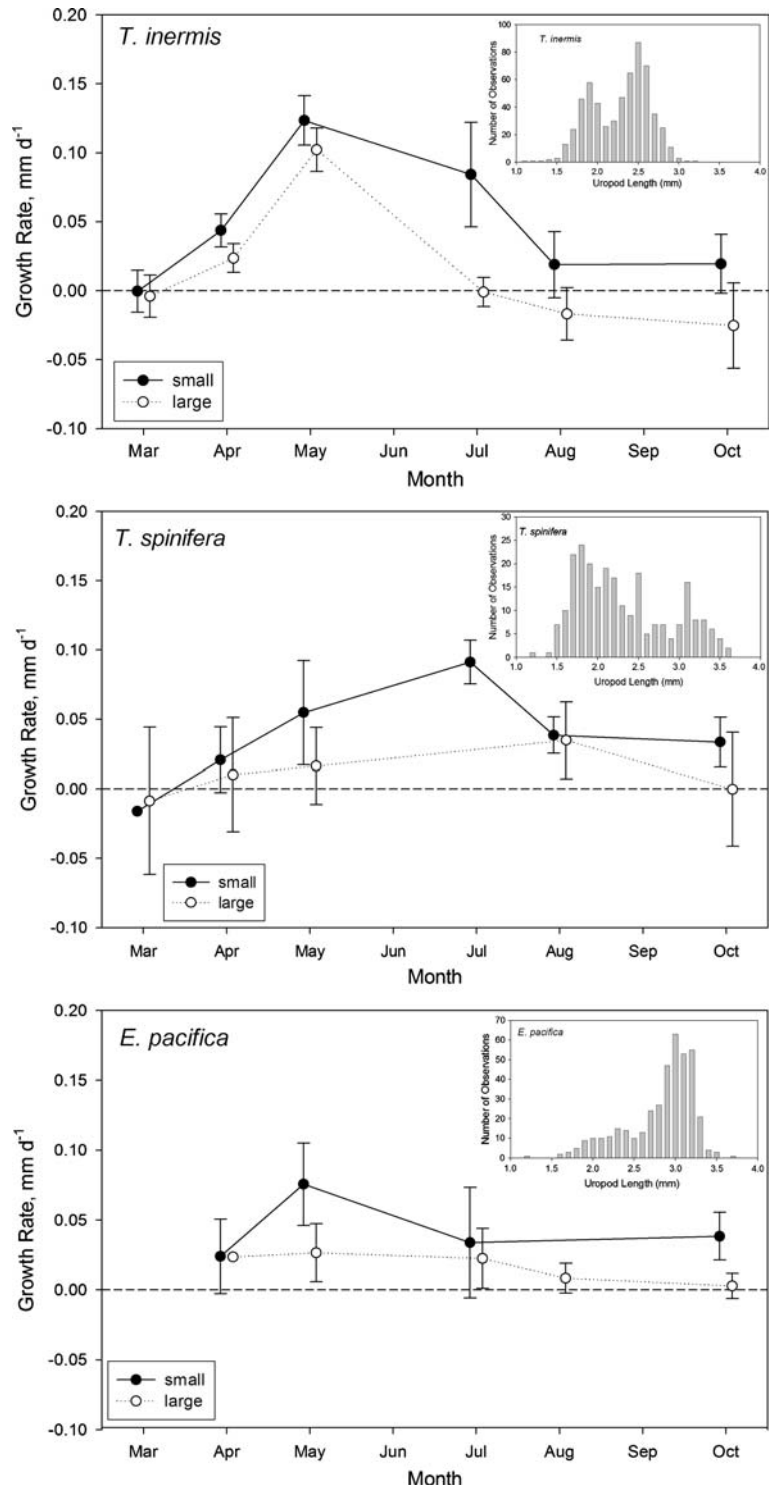
While individual euphausiid MI remained positive during the first 4 days following collection, shrinkage in length was subsequently observed for all species, reflecting the absence of food conditions (Fig. 7). Once turned negative after day 5, the MI appeared to remain constant averaging  $-3.07 \pm 0.33\%$  ( $n = 110$ ) for *T. inermis*,  $-3.22 \pm 1.05\%$  ( $n = 11$ ) for *T. spinifera*, and  $-4.37 \pm 0.27\%$  (SE,  $n = 166$ ) for *E. pacifica*, with minimal values of about -10% occurring in all species.

**Table 2** Relationships between dependent [molt increment (MI) and molting rate (MR)] and independent [temperature (*T*), chlorophyll-*a* concentration (*Chl*) and pre-molt carapace length (*CL*)] variables

Species	Backwards stepwise regression	Multiple linear regression			$r^2$	$p$ ( <i>T</i> ; <i>Chl</i> ; <i>CL</i> )	<i>n</i>
		MI					
		$\beta_T$	$\beta_{Chl}$	$\beta_{CL}$			
<i>T. inermis</i>	All included	-0.175	0.436	-0.236	0.31	<0.001; <0.001; <0.001	427
<i>T. spinifera</i>	<i>T</i> removed		0.255	-0.440	0.18	-; <0.001; <0.001	166
<i>E. pacifica</i>	<i>T</i> removed		0.196	-0.303	0.14	-; <0.001; <0.001	255
		MR					
		$\beta_T$	$\beta_{Chl}$				
<i>T. inermis</i>	All included	0.850	0.401	0.74	<0.001; 0.006	22	
<i>T. spinifera</i>	<i>Chl</i> removed	0.867		0.75	<0.001	20	
<i>E. pacifica</i>	<i>Chl</i> removed	0.625		0.39	0.002	22	

The coefficients  $\beta_T$ ,  $\beta_{Chl}$ , and  $\beta_{CL}$  correspond to *T*, *Chl*, and *CL*, respectively

**Fig. 5** Mean length growth rates ( $\text{mm day}^{-1}$ ) of two major size groups of euphausiids (based on length-frequency distributions) in the northern Gulf of Alaska with a reference line marking 0-growth



The IPs measured directly during the long-term incubations were significantly ( $p < 0.05$ ) different for selected temperatures and closely corresponded to our estimates derived from the shipboard experiments (Table 4). There were no substantial differences between consecutive IPs for all species at any given temperature (Table 4).

## Discussion

In this study, strong and distinct seasonal patterns were found in several of the metrics used to describe growth in euphausiids. Molt rate was most strongly governed by temperature, while growth increment was affected by food and body-size. Weight-specific growth was

**Table 3** Seasonal mean weight-specific growth rates ( $g_w$ , day<sup>-1</sup>) for two size groups of euphausiids in the northern Gulf of Alaska

Month	<i>Thysanoessa inermis</i>		<i>Thysanoessa spinifera</i>		<i>Euphausia pacifica</i>	
	Small $g_w \pm SE$ ( $n$ )	Large $g_w \pm SE$ ( $n$ )	Small $g_w \pm SE$ ( $n$ )	Large $g_w \pm SE$ ( $n$ )	Small $g_w \pm SE$ ( $n$ )	Large $g_w \pm SE$ ( $n$ )
March	0 ± 0.001 (37)	-0.001 ± 0.001 (37)	-0.004 ± N/A (1)	-0.001 ± 0.008 (3)		
April	0.009 ± 0.001 (61)	0.004 ± 0.001 (79)	0.005 ± 0.004 (15)	0.002 ± 0.006 (5)	0.006 ± 0.003 (11)	0.004 ± N/A (1)
May	0.023 ± 0.002 (27)	0.016 ± 0.001 (35)	0.014 ± 0.006 (6)	0.003 ± 0.004 (11)	0.016 ± 0.003 (9)	0.005 ± 0.002 (18)
July	0.022 ± 0.003 (6)	0 ± 0.001 (78)	0.031 ± 0.002 (34)		0.007 ± 0.004 (5)	0.004 ± 0.002 (17)
August	0.005 ± 0.002 (15)	-0.003 ± 0.002 (24)	0.012 ± 0.002 (49)	0.006 ± 0.004 (11)		0.001 ± 0.001 (69)
October	0.004 ± 0.002 (19)	-0.004 ± 0.003 (9)	0.011 ± 0.003 (26)	0 ± 0.006 (5)	0.009 ± 0.002 (27)	0.001 ± 0.001 (96)

SE Standard error,  $n$  Number of observations

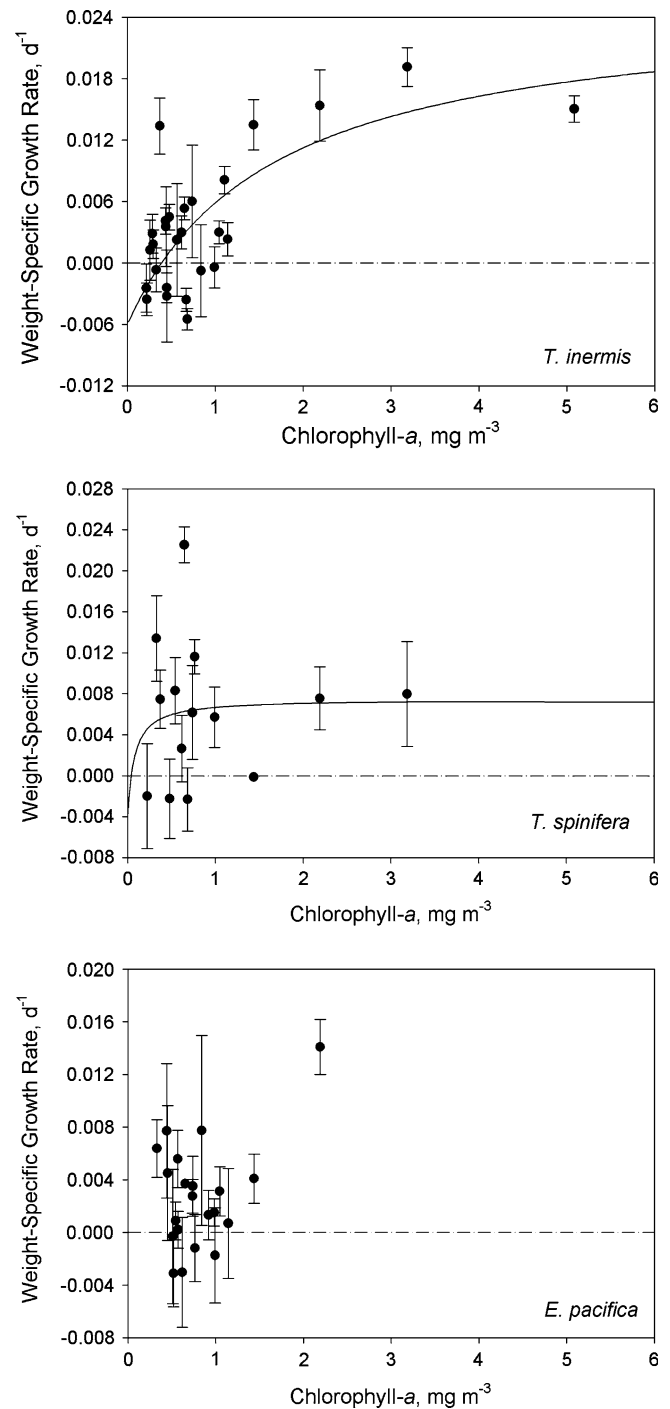
governed by all three. While the effect of temperature on the euphausiid MR and IP has long been recognized (e.g., Lasker 1966; Fowler et al. 1971; Sameoto 1976; Dalpadado and Ikeda 1989; Quetin et al. 1994), the effects of food and body size remain less studied. Consistent with our observations, growth increment appears to remain uninfluenced by temperature in euphausiids (Iguchi and Ikeda 1995) as well as other pelagic crustaceans such as mysids and amphipods (Gaudy and Guerin 1979; Ikeda 1990). However, Atkinson et al. (2006) showed a significant relationship between growth increment and temperature for Antarctic krill (*Euphausia superba*) with the former being maximal at 0.6°C. The IP of *E. pacifica* also tends to increase with increasing individual size (Fowler et al. 1971; Iguchi and Ikeda 1995). Extensive field studies on *E. superba* indicate that effects of food availability, size and other factors (such as synchrony of molting) are superimposed on the effect of temperature (Quetin et al. 1994). In contrast to initial observations on *E. pacifica* (Lasker 1966), it has now been shown that food-deprived conditions can significantly extend the IP of *E. superba* (Ikeda and Dixon 1982; Ikeda and Thomas 1987). Consistent with our observations, feeding studies on Antarctic krill revealed that their MI is also dependent both on food quantity and quality (Ross et al. 2000).

In the present study, the increase in the MI in May coincided with the increased content of chl-*a* in the water due to the spring phytoplankton bloom. In contrast, the MR increased later in the season when the summer stratification resulted in development of warm surface layer. The multiple regression analysis also confirmed that temperature is the major factor controlling molting, while growth increment is limited mainly by food availability. The only exception was *T. inermis*, which showed weak inter-dependence between MR and chl-*a*, and between MI and temperature. The higher summer temperatures may suppress growth of this cold-water species changing the balance of parameters in metabolic responses.

The strong functional relationship between weight-specific growth rates and ambient chl-*a* concentration in *T. inermis* indicates that the growth rate in this species is closely coupled with the availability of phytoplankton. In contrast, the lack of a similar relationship in *T. spinifera* and *E. pacifica* suggests that these species rely on prey items other than phytoplankton (see below). Interestingly, the egg production of *E. pacifica* was closely coupled with chl-*a* content (Pinchuk and Hopcroft 2006), which suggests that a phytoplankton diet might be of particular importance for *E. pacifica* reproduction. Recent studies indicate that sex and maturity can influence MI and MR (Atkinson et al. 2006; Tarling et al. 2006). We did not distinguish between males, females and juveniles nor determine maturity stage of euphausiids in our experiments, and this may account for some of the scatter in our data.

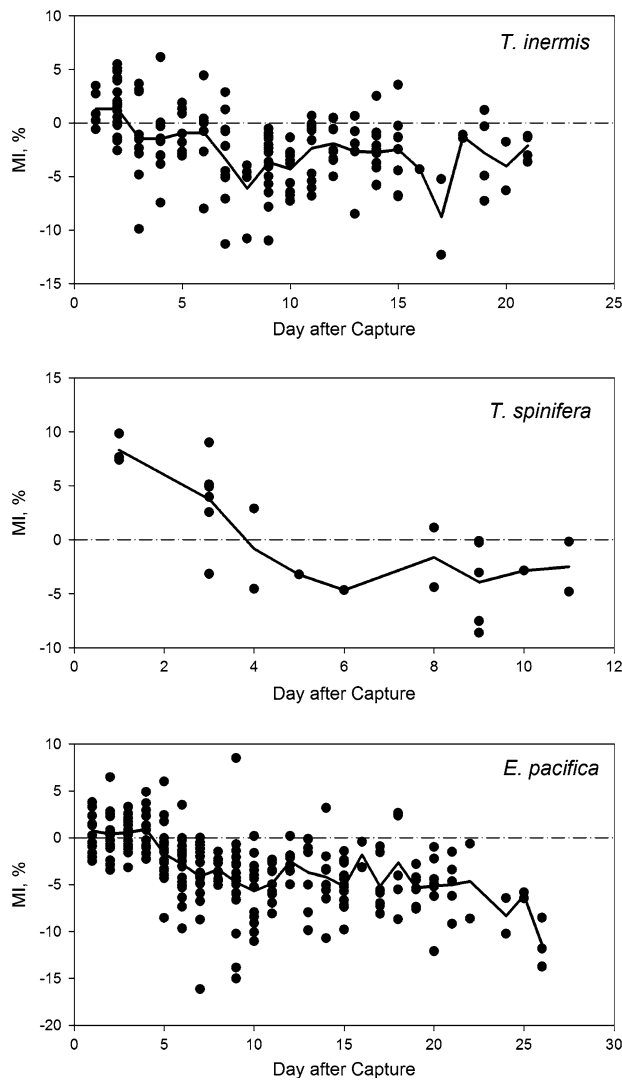
The mean weight-specific growth rates of *T. inermis* were highest (0.016–0.023 day<sup>-1</sup>) in the midst of the phytoplankton bloom in May, while later they decreased to -0.004 day<sup>-1</sup> for small individuals and to -0.004 for large individuals. Similarly, in the Bering Sea estimated *T. inermis* growth rates were highest in late April and May (0.045–0.06 day<sup>-1</sup>), decreasing to 0.01–0.013 day<sup>-1</sup> by June (Smith 1991). In the North Sea, adult *T. inermis* grew at 0.044 and 0.153 mg DW day<sup>-1</sup> before and after the bloom, respectively (Lindley and Williams 1980), which is comparable with our estimates of 0.028–0.034 mg DW day<sup>-1</sup> for April and 0.109–0.120 mg DW day<sup>-1</sup> in May. Negative growth of -0.0005 day<sup>-1</sup> for *T. inermis* in winter has been observed off Northern Norway, while the summer growth rates ranged between 0.012 and 0.007 day<sup>-1</sup> for different size groups (Hopkins et al. 1984). Our measurements also show negative (-0.001 day<sup>-1</sup>) or zero growth for *T. inermis* in March. These comparisons emphasize the importance of the spring bloom as a major source of energy for *T. inermis* growth, and suggest that the Bering Sea environment provides better conditions for *T. inermis* growth than more northern and southern parts of its range.

**Fig. 6** Functional relationships between ambient chlorophyll-*a* concentrations and weight-specific growth rate of euphausiids from the northern Gulf of Alaska approximated with Michaelis–Menten curve



The growth rates of *E. pacifica* also increased slightly during the bloom, but, unlike those of *T. inermis* and *T. spinifera*, did not change throughout the production season, suggesting that this species relies on food sources other than spring diatoms. The morphology of the *E. pacifica* feeding basket allows effective retention of particles  $>5 \mu\text{m}$  (Suh and Choi 1998), enabling them to consume smaller diatoms, dinoflagellates, and microzooplankton, which are usually

abundant throughout the summer in the North Pacific (Landry et al. 1993). Our estimates of small *E. pacifica* growth rates ( $0.02\text{--}0.08 \text{ mm day}^{-1}$ ) are close to those reported for specimens of similar size from Washington ( $0.05\text{--}0.08 \text{ mm day}^{-1}$ ) (Cooney 1971; Bollens et al. 1992), British Columbia ( $0.047\text{--}0.075 \text{ mm day}^{-1}$ ) (Hulsizer 1971; Heath 1977, cited after Bollens et al. 1992), and Northern Japan ( $0.056 \text{ mm day}^{-1}$ ) (Taki and Ogishima 1997). Not surprisingly, they are lower



**Fig. 7** Shrinkage of euphausiids under starvation as indicated by molt increment (*MI*), *solid line* is the running mean

than growth rates measured at the warmer, southernmost parts of *E. pacifica*'s range ( $0.07\text{--}0.09\text{ mm day}^{-1}$ ) off Southern California and Oregon (Smiles and Percy 1971; Brinton 1976).

Euphausiids can employ various mechanisms to survive in high latitudes during periods of low food availability in winter. They can rely on lipid reserves accumulated during spring and summer blooms, switch to suitable food, or cease feeding. The latter would result in shrinkage or reduction of metabolic rates. Our mean long-term food-deprivation MI estimates of  $\sim 3\%$  are similar to those reported for Antarctic krill (Nicol et al. 1992), and it appears that under experimental conditions both the North Pacific and Antarctic euphausiids can achieve a relatively constant shrinkage rate within a few days of food limitation. Our estimates of natural MI show zero or negative growth for all three species in March, suggesting shrinkage occurs November through February. However, the natural shrinkage was substantially less than that observed during food deprivation experiments. This implies that shrinkage and starvation do not reach critical levels and that euphausiids are able to find enough food or to store sufficient reserves to survive through the winter in the northern GOA. Long starvation tends to extend IP of *E. superba* and *Meganyctiphanes norvegica* (Ikeda and Dixon 1982; Buchholz 1985), but the effect does not necessarily become significant after the first sequential molts. The lack of a significant increase in IP in our long-term experiments suggests that their duration was not long enough (at the given temperature), or that the euphausiids were still using lipid reserves to maintain constant metabolic rates.

An important caveat in the interpretation of our results is that that length is an imperfect estimate of

**Table 4** Inter-molt periods (IP) calculated from IGR experiments and consecutive inter-molt periods (IP1 and IP2) measured during long-term incubations

Species	Temperature			
	5°C		7°C	8°C
	IP $\pm$ CI ( <i>n</i> )		IP $\pm$ CI ( <i>n</i> )	IP $\pm$ CI ( <i>n</i> )
From IGR experiments				
<i>T. inermis</i>	10.1 $\pm$ 1.4 (13)		8.8 $\pm$ 3.6 (2)	6.5 $\pm$ 1.9 (7)
<i>T. spinifera</i>	16.4 $\pm$ 1.7 (9)		9.5 $\pm$ 2.5 (4)	6.4 $\pm$ 1.9 (7)
<i>E. pacifica</i>	10.6 $\pm$ 2.3 (5)		9.0 $\pm$ 1.9 (7)	6.9 $\pm$ 1.6 (10)
Direct measurements	IP1 $\pm$ CI ( <i>n</i> )	IP2 $\pm$ CI ( <i>n</i> )	IP1 $\pm$ CI ( <i>n</i> )	IP2 $\pm$ CI ( <i>n</i> )
<i>T. inermis</i>	10.3 $\pm$ 0.9 (13)	11.6 $\pm$ 2.6 (5)	6.6 $\pm$ 0.3 (67)	7.0 $\pm$ 0.5 (29)
<i>T. spinifera</i>	10.1 $\pm$ 1.5 (7)	–	7.0 $\pm$ 1.1 (8)	7.5 (2)
<i>E. pacifica</i>	10.9 $\pm$ 0.5 (58)	11.1 $\pm$ 1.0 (9)	6.7 $\pm$ 0.3 (57)	8.2 $\pm$ 0.7 (13)

Temperatures for IGR experiments are estimated daily mean temperatures computed with respect to approximate time euphausiids spent above and below thermocline during 24-h day

*n* Number of observations

growth in terms of mass. The IGR technique as employed here only considers somatic increase in length, and length increase for females may be curtailed when resources are shifted into ovary development and egg production, or into lipid deposition rather than structural tissue as the autumn approaches, resulting in increased weight without increasing length. Our observations of the lack of positive growth in *T. inermis* in winter, intensive growth during the spring bloom, and its consequent decrease, reflect these ontogenetic changes. Cold water *T. inermis* are known to be herbivorous and heavily dependent on spring and summer phytoplankton blooms for accumulating wax esters (up to 50% of its DW) and achieving quick somatic growth (Falk-Petersen et al. 1981, 2000), while during winter only minor food intake occurs, and the lipid stores are mobilized to sustain metabolism and to fuel the single reproductive effort the following spring (Falk-Petersen et al. 2000; Pinchuk and Hopcroft 2006). *E. pacifica* is capable of producing multiple broods (average 102 eggs per brood) every 8 days throughout summer in the northern GOA (Pinchuk and Hopcroft 2006). Assuming egg DW of 3.3 µg (Iguchi and Ikeda 1994), this would require an additional investment of 0.042 mg DW day<sup>-1</sup> not accounted for in IGR estimates. Both these possibilities may have hampered our ability to fully understand the factors affecting somatic growth in all three species in terms of length increment and the predicted weight-specific growth.

Given our new appreciation of euphausiid rates in the GOA, it is instructive to consider their potential importance in comparison to the calanoid copepods that generally dominate this ecosystem both by abundance and biomass (Coyle and Pinchuk 2003). The temperature-adjusted weight-specific growth rates of euphausiids are considerably lower than those of the dominant copepods from the northern GOA (Table 5). This may lead to a hasty conclusion that euphausiids have limited impact on phytoplankton compared to copepods. However, euphausiids on average use ~66–75% of their assimilated carbon in respiration (Lasker 1966; Ross 1982), while copepods respire ~50% (Vidal 1980), a difference likely reflecting the more active swimming behavior of euphausiids. Furthermore, the weight-specific assimilation of *Calanus pacificus* at 12°C ranges between 29 and 66% per day (Vidal 1980), while that of *E. pacifica* is only 5–7% per day (Lasker 1966; Iguchi and Ikeda 1999). This is not surprising, since the assimilation rate must be equal to the sum of rates of anabolic and catabolic processes, and, therefore, the weight-specific rate of assimilation typically decreases with increasing body size (Vidal 1980). Since

**Table 5** Weight-specific growth rates (standardized to 5°C) of euphausiids and copepods from the northern Gulf of Alaska

Species	$g_w$	Source
Euphausiids		
<i>Thysanoessa inermis</i>	0.003	This study
<i>Thysanoessa spinifera</i>	0.007	This study
<i>Euphausia pacifica</i>	0.0025	This study
Copepods		
<i>Centropages abdominalis</i>	0.08	Slater and Hopcroft (2005)
<i>Neocalanus flemingeri/plumchrus</i>	0.105	Liu and Hopcroft (2006a)
<i>Metridia pacifica</i>	0.083	Liu and Hopcroft (2006b)
<i>Calanus marshallae</i>	0.118	H. Liu and R. R. Hopcroft (unpublished data)
<i>Calanus pacificus</i>	0.074	H. Liu and R. R. Hopcroft (unpublished data)

the DW of *C. pacificus* is generally tenfold less than that of *E. pacifica*, it thus appears that, on balance, the weight-specific feeding demands of euphausiids are similar to those of copepods.

On the GOA shelf, copepod biomass is usually 6–35 times that of euphausiids during the spring bloom, becoming almost evenly balanced in late summer and fall (Coyle and Pinchuk 2003). At the same time, euphausiids can form short-lived dense aggregations (Endo et al. 1985; Hanamura et al. 1989) ultimately dominating other zooplankton taxa. Because of such enormous seasonal and spatial disproportions in their distributions, mesoscale advection processes and predation likely determine the relative biomass, and hence importance, of these two groups in the zooplankton community at a given place and time.

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## References

- Armstrong JL, Boldt JL, Cross AD, Moss JH, Davis ND, Myers KW, Walker RV, Beauchamp DA, Halderson LJ (2005) Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. Deep-Sea Res II 52:247–265

- Atkinson A, Shreeve RS, Hirst AG, Rothery P, Tarling GA, Pond DW, Korb RE, Murphy EJ, Watkins JL (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnol Oceanogr* 51:973–987
- Bargu S, Marinovic B, Mansergh S, Silver MW (2003) Feeding responses of krill to the toxin-producing diatom *Pseudo-nitzschia*. *J Exp Mar Biol Ecol* 284:87–104
- Bollens SM, Frost BW, Lin TS (1992) Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fjord. *Mar Biol* 114:219–228
- Brinton E (1976) Population biology of *Euphausia pacifica* off southern California. *Fish Bull* 74:733–762
- Buchholz F (1985) Moulting and growth in euphausiids. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, Heidelberg, pp 339–345
- Buchholz F (1991) Moulting cycle and growth of Antarctic krill *Euphausia superba* in the laboratory. *Mar Ecol Prog Ser* 69:217–229
- Clarke A, Peck LS (1991) The physiology of polar marine zooplankton. *Polar Res* 10:355–369
- Cooney RT (1971) Zooplankton and micronekton associated with a diffuse sound-scattering layer in Puget Sound, Washington. PhD Thesis, University of Washington, Seattle, WA
- Coyle KO, Pinchuk AI (2003) Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fish Oceanogr* 12:327–338
- Coyle KO, Pinchuk AI (2005) Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep-Sea Res II* 52:217–245
- Dalpadado P, Ikeda T (1989) Some observations on moulting, growth and maturation of krill (*Thysanoessa inermis*) from the Barents Sea. *J Plankton Res* 11:133–139
- Dilling L, Wilson J, Steinberg D, Alldredge A (1998) Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus marshallae* on marine snow. *Mar Ecol Prog Ser* 170:189–201
- Endo Y, Hanamura Y, Taniguchi A (1985) In situ observations on the surface swarm of *Euphausia pacifica* in Sendai Bay in early spring with special reference to their biological characteristics. *La mer* 23:135–140
- Falk-Petersen S, Gatten RR, Hopkins CCE, Sargent JR (1981) Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: seasonal changes in the lipid class composition of *Meganctiphanes norvegica* (M. Sars), *Thysanoessa raschii* (M. Sars) and *Thysanoessa inermis* (Krøyer). *J Exp Mar Biol Ecol* 54:204–209
- Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can J Fish Aquat Sci* 57(Suppl 3):178–191
- Fowler SW, Small LF, Keckes S (1971) Effects of temperature and size on molting of euphausiid crustaceans. *Mar Biol* 11:45–51
- Gaudy R, Guerin J-P (1979) Comparative ecophysiology of the mysids *Hemimysis speluncola* Ledoyer (cave dwelling) and *Leptomysis lingvura* G. O. Sars (non-cave dwelling). Effect of temperature on growth and breeding. *J Exp Mar Biol Ecol* 38:101–119
- Hanamura Y, Kotori M, Hamaoka S (1989) Daytime surface swarms of the euphausiid *Thysanoessa inermis* off the west coast of Hokkaido, northern Japan. *Mar Biol* 102:369–376
- Hart JL (1973) Pacific fishes of Canada. *Fish Res Board Can Bull* 180:1–740
- Heath WA (1977) The ecology and harvesting of euphausiids in the Strait of Georgia. PhD Thesis, University of British Columbia, Vancouver, BC
- Hirst AG, Roff JC, Lampitt RS (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Adv Mar Biol* 44:1–142
- Hopkins CCE, Tande KS, Grovnik S, Sargent JR (1984) Ecological investigation of the zooplankton community of Balsfjorden, northern Norway: an analysis of growth and overwintering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus), *Thysanoessa inermis* (Krøyer) and *T. raschii* (M.Sars). *J Exp Mar Biol Ecol* 82:77–99
- Hulsizer E (1971) A study of the reproductive cycle of *Euphausia pacifica* at two stations in Puget Sound, 1968–1969. MS Thesis, University of Washington, Seattle, WA
- Huntley M, Boyd C (1984) Food-limited growth of marine zooplankton. *Am Nat* 124:455–478
- Iguchi N, Ikeda T (1994) Experimental study on brood size, egg hatchability and early development of a euphausiid *Euphausia pacifica* from Toyama Bay, southern Japan Sea. *Bull Jpn Sea Natl Fish Res Inst* 44:49–57
- Iguchi N, Ikeda T (1995) Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the southern Japan Sea, as influenced by temperature. *J Plankton Res* 17:1757–1769
- Iguchi N, Ikeda T (1999) Production, metabolism and P:B ration of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. *Plankton Biol Ecol* 46:68–74
- Ikeda T (1990) A growth model for a hyperiid amphipod *Themisto japonica* (Bovallius) in the Japan Sea, based on its intermoult period and moult increment. *J Oceanogr Soc Jpn* 46:261–272
- Ikeda T, Dixon P (1982) Observations on moulting in Antarctic krill (*Euphausia superba* Dana). *Aust J Mar Freshw Res* 33:71–76
- Ikeda T, Thomas PG (1987) Moulting interval and growth of juvenile Antarctic krill (*Euphausia superba*) fed different concentrations of the diatom *Phaeodactylum tricorutum* in the laboratory. *Polar Biol* 7:339–343
- Kawaguchi S, Candy SG, King R, Naganobu M, Nicol S (2006) Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. *Mar Ecol Prog Ser* 306:1–15
- Kulka DW, Corey S (1982) Length and weight relationships of euphausiids and caloric values of *Meganctiphanes norvegica* (M. Sars) in the Bay of Fundy. *J Crust Biol* 2:239–247
- Landry MR, Monger BC, Selph KE (1993) Time-dependency of microzooplankton grazing and phytoplankton growth in the Subarctic Pacific. *Prog Oceanogr* 32:205–222
- Lasker R (1966) Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. *J Fish Res Board Can* 23:1291–1317
- Lindley JA, Williams R (1980) Plankton of the Fladen Ground during FLEX 76. II. Population dynamics and production of *Thysanoessa inermis* (Crustacea: Euphausiacea). *Mar Biol* 57:79–86
- Liu H, Hopcroft RR (2006a) Growth and development of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska: validation of the artificial cohort method in cold waters. *J Plankton Res* 28:87–101
- Liu H, Hopcroft RR (2006b) Growth and development of *Metridia pacifica* (Copepoda: Calanoida) in the northern Gulf of Alaska. *J Plankton Res* 28:769–781

- Marinovic B, Mangel M (1999) Krill can shrink as an ecological adaptation to temporarily unfavourable environments. *Ecol Lett* 2:338–343
- Mauchline J (1980) The biology of mysids and euphausiids. *Adv Mar Biol* 18. Academic Press, London:1–680
- Miller DG (1983) Variation in body length measurement of *Euphausia superba* Dana. *Polar Biol* 2:17–20
- Nakagawa Y, Endo Y, Taki K (2001) Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan. *Plankton Biol Ecol* 48:68–77
- Nakagawa Y, Ota T, Endo Y, Taki K, Sugisaki H (2004) Importance of ciliates as prey of the euphausiid *Euphausia pacifica* in the NW North Pacific. *Mar Ecol Prog Ser* 271:261–266
- Nicol S (2000) Understanding krill growth and aging: the contribution of experimental studies. *Can J Fish Aquat Sci* 57(Suppl 3):168–177
- Nicol S, Stolp M, Cochran T, Geijsel P, Marshall J (1992) Growth and shrinkage of Antarctic krill *Euphausia superba* from the Indian Ocean sector of the Southern Ocean during summer. *Mar Ecol Prog Ser* 89:175–181
- Pinchuk AI, Hopcroft RR (2006) Egg production and early development of *Thysanoessa inermis* and *Euphausia pacifica* (Crustacea: Euphausiacea) in the northern Gulf of Alaska. *J Exp Mar Biol Ecol* 332:206–215
- Ponomareva LA (1966) The euphausiids of the North Pacific, their distribution, ecology, and mass species. Israel Program for Scientific Translations, Jerusalem
- Quetin LB, Ross RM, Frazer TK, Amsler MO, Wyatt-Evens C, Oakes SA (2003) Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula. *Mar Biol* 143:833–843
- Quetin LB, Ross RM, Clarke A (1994) Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: El-Sayed S (ed) *Southern Ocean ecology: the BIOMASS perspective*. Cambridge University Press, Cambridge, pp 165–184
- Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. *Am Zool* 31:49–63
- Roff JC, Hopcroft RR (1986) High precision microcomputer based measuring system for ecological research. *Can J Fish Aquat Sci* 43:2044–2048
- Ross RM (1982) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at 8 and 12 C throughout the life span. *Mar Biol* 68:15–23
- Ross RM, Quetin LB, Baker KS, Vernet M, Smith RC (2000) Growth limitation in young *Euphausia superba* under field conditions. *Limnol Oceanogr* 45:31–43
- Sameoto DD (1976) Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. *J Fish Res Board Can* 33:2568–2576
- Shaw CT, Feinberg LR, Peterson WT (2004) Moulting and growth rates of two species of euphausiids off the Oregon coast: seasonal, spatial and life stage differences. In: *Abstract Book, ASLO/TOS Ocean Research 2004 Conference*, Honolulu, HI, 15–20 February 2004, p143
- Sigler MF, Rutecki TL, Courtney DL, Karinen JF, Yang M-S (2001) Young of the year sablefish abundance, growth, and diet in the Gulf of Alaska. *Alaska Fish Res Bull* 8:57–70
- Slater LM, Hopcroft RR (2005) Development, growth, and egg production of *Centropages abdominalis* in the subarctic Pacific. *J Plankton Res* 27:71–78
- Smiles MC, Pearcy WG (1971) Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *Fish Bull* 69:79–86
- Smith SL (1991) Growth, development and distribution of the euphausiids *Thysanoessa raschii* (M. Sars) and *Thysanoessa inermis* (Kroyer) in the southeastern Bering Sea. In: Sakshaug E, Hopkins CCE, Oritsland NA (eds) *Proceeding of the pro mare symposium on polar marine ecology*, Trondheim, 12–16 May 1990. *Polar Res* 10:461–478
- Suh H-L, Choi S-D (1998) Comparative morphology of the feeding basket of five species of *Euphausia* (Crustacea, Euphausiacea) in the western North Pacific, with some ecological considerations. *Hydrobiologia* 385:107–112
- Taki K, Ogishima T (1997) Distribution of some developmental stages and growth of *Euphausia pacifica* Hansen in the northwestern Pacific on the basis of Norpac Net Samples. *Bull Tohoku Nat Fish Res Inst* 59:95–117
- Tanasichuk RW (1998a) Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar Ecol Prog Ser* 173:163–180
- Tanasichuk RW (1998b) Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar Ecol Prog Ser* 173:181–195
- Tarling GA, Shreeve RS, Hirst AG, Atkinson A, Pond DW, Murphy EJ, Watkins JL (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. *Limnol Oceanogr* 51:959–972
- Timofeev SF (1996) Ontogenetic ecology of euphausiid crustaceans (Crustacea, Euphausiacea) of the northern seas (in Russian). Nauka, St. Petersburg
- Vidal J (1980) Physioecology of zooplankton. IV. Effects of phytoplankton concentration, temperature, and body size on the net production efficiency of *Calanus pacificus*. *Mar Biol* 56:203–211
- Weingartner TJ, Coyle KO, Finney B, Hopcroft RR, Whitledge TE, Brodeur R, Dagg M, Farley E, Haidvogel D, Haldorson L, Hermann A, Hinckley S, Napp J, Stabeno P, Kline T, Lee C, Lessard E, Royer T, Strom S (2002) The Northeast Pacific GLOBEC program: coastal Gulf of Alaska. *Oceanography* 15:48–63
- Wilson MT, Jump CM, Duffy-Anderson JT (2006) Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. *Mar Ecol Prog Ser* 317:245–258
- Winberg GG (1983) The Vant-Hoff's coefficient and the Arrhenius equation in biology. *Zh (in Russian). Obshei Biologii* 44:3–42