

Krill can shrink as an ecological adaptation to temporarily unfavourable environments

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Abstract

Because environments vary with both predictable patterns and with unpredictable but recurring events, ecologists have long been interested in the ecological adaptations that organisms use to survive periods in which the environment may be exceptionally harsh. In the north-east Pacific, one example of this is periodic warming episodes. Here, we demonstrate for the first time that krill (*Euphausia pacifica* Hansen), which is a centrally important species in coastal-upwelling systems, can survive periods of abnormally high temperatures by shrinkage between molts, even if food is plentiful. In addition, we demonstrate that there is a high amount of individual variation in growth rates of krill. Krill are centrally important within pelagic foodwebs both worldwide and within the north-east Pacific, thus we explore the potential ecological consequences of such shrinkage for both krill and their predators.

Keywords

Community structure, El Niño, krill, life history strategy, shrinkage

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INTRODUCTION

Krill (euphausiids) form a key trophic link between primary producers and higher level consumers in oceanic food webs worldwide. Indeed, most marine species (including humans) are only one or two trophic levels away from krill. That is, they are either prey of krill, predators of krill or predators of krill predators. *Euphausia pacifica* Hansen is widely distributed throughout the north-east Pacific and is often the dominant (both in terms of numerical abundance and biomass) krill species within both oceanic and coastal-upwelling ecosystems (Brinton 1962). Along the west coast of North America it can be found from Alaska to as far south as 25°N, where mean temperature in the top 250 m of the water column can be 15°C and maximum surface temperatures can exceed 20°C (Brinton 1976). Recruitment, growth and reproductive activity within populations of *E. pacifica* are known to correlate with seasonal patterns of primary productivity (Smiles & Percy 1971; Brinton 1976; Ross *et al.* 1982; Bollens *et al.* 1992; Tanasichuk 1998).

Because krill play a central role in pelagic food webs, their demography and life history can have important implications for community structure and function. Life history strategies are means that organisms use to achieve successful reproduction in uncertain environments. Consequently they must address components that may be relatively predictable on a variety of time scales as well as

those that are recurring but relatively unpredictable. There is widespread consensus among ecologists that populations respond to climactic events that may alter north-east Pacific marine ecosystems on interannual (i.e. El Niño) and interdecadal (i.e. regime shifts) time scales (Wooster 1983; Roemmich & McGowan 1995; Brodeur *et al.* 1996; McGowan *et al.* 1998). Such events affect temperature, salinity, and patterns of nutrient input and can have profound and extended impacts throughout food webs (Chelton *et al.* 1982; Barber & Chavez 1983; Roemmich & McGowan 1995; McGowan *et al.* 1998). Here we demonstrate that *E. pacifica* can shrink as a result of acclimation to acute interannual temperature increase associated with El Niño events. Shrinkage can provide a mechanism for dealing with unpredictable warming events and additionally may have important implications for both krill population dynamics and fishery/predator interactions.

METHODS

Experimental design

Euphausia pacifica individuals were collected in late June and early July 1997 from Monterey Bay, CA (36°48.06 N, 121°59.15 W) using BONGO nets fitted with 333 µm mesh. After capture, krill were maintained at ambient water temperature (approximately 14–15°C) in 20 litre plastic buckets (maximum density of eight individuals per

litre) and transported to the laboratory. One hundred juveniles (total body lengths ranging between 8 and 12 mm) were transferred individually into 2 litre plastic buckets filled with 1 litre of filtered (0.2 µm) seawater. Cultures were maintained at ambient ocean temperature and in constant darkness within a flowing seawater bath covered with a black plastic tent. Individuals were fed daily on a diet of the centric diatom *Thalassiosira weissflogii* at a concentration between 1.0 and 9.0×10^3 cells/ml (determined through three replicate counts with a haemocytometer). In order to compare food levels to *in situ* values, cell concentration counts were converted to Chlorophyll A (Chl A) values by using the standard value for Chl A/cell ratio of 5.56 picograms for *Thalassiosira weissflogii* (J. Goldman, personal communication). Using this approach, we calculated Chl A values of 9.8–93.2 µg Chl A/l within our experimental treatment, which is well above the average values reported for Spring/Summer blooms in Monterey Bay (5–6 µg Chl A/l–F. Chavez, personal communication). In addition, as *E. pacifica* has been shown to have an omnivorous diet (Ohman 1984; Dilling *et al.* 1998), cultures were supplemented every other day with newly hatched *Artemia* nauplii. Temperature, food (phytoplankton) concentration and individual mortality were recorded daily and containers were examined for the presence of molts. All molts were recovered for subsequent measurement and individuals were transferred to fresh containers with new phytoplankton and *Artemia*. Dead individuals were replaced for a period of 1 week after the start of the experiment from spare cultures maintained at identical conditions.

Data analysis

Intermolt period (IP) (the number of days between successive ecdyses) was determined for all surviving krill throughout the course of the experiment. Molt increment (MI) (the percentage increase in size between molts) was calculated by measuring the percentage increase of mean uropod lengths (UL) between successive molts. If one uropod was damaged, then only the undamaged uropod was used to calculate percentage growth. Uropod lengths (tip of exopod to base of coxa) were determined by photographing the abdominal portion of each ecdysis with a Pulnix digital camera mounted on a Wild dissecting scope and then measuring each resulting image to the nearest 0.01 mm utilizing NIH image analysis software. To verify the relationship between UL and total length (TL), we measured UL and TL for 69 individuals and conducted a linear regression. We found that $TL = 5.643UL - 0.054$ ($r = 0.969$; $P < 0.001$). Temperature, food concentration, daily mortality, IP and MI were compared for the beginning (day 1–14), middle (day 22–

35), and end (day 43–56) of the experiment. Mean values were initially tested for normality and homogeneity of variance and then the appropriate multiple comparison test was used to test for significant differences between the various periods of the experiment.

RESULTS

Mean temperatures differed significantly between the beginning (mean = 15.50°C) middle (mean = 16.46°C) and end (mean = 18.18°C) of the experiment (ANOVA; $F = 27.51$, $P < 0.001$) (Fig. 1A). Phytoplankton concentration remained high within culture vessels throughout the experiment with no significant differences during the beginning, middle and end (Kruskal–Wallis Test; $H = 12.4$, $P > 0.05$) (Fig. 1B). Daily mortality remained relatively constant at approximately 2%–3%, with no significant differences between the beginning, middle, and end of the experiment (ANOVA; $F = 2.54$, $P = 0.09$). IP remained relatively constant at 3–4 days throughout the experiment, though there was a slight, significant increase between the beginning (mean = 3.40 days) of the experiment and the middle (mean = 3.64) or end (mean = 3.54) of the experiment (Kruskal–Wallis Test; $H = 14.013$, $P < 0.001$). In contrast, mean MI decreased significantly with increasing temperature (Fig. 1D) (Kruskal–Wallis Test; $H = 9.428$, $P < 0.01$), with positive values (mean = 1.84%) recorded during the initial period when temperatures were lowest, and negative values (i.e. shrinkage) associated with the increasingly warmer temperatures during the middle (mean = –0.45%) and end periods (mean = –0.53%). We further examined this relationship by conducting a linear regression between temperature and mean MI (defined as the mean MI of all krill during one intermolt period) and found a negative and significant correlation ($R^2 = 0.572$, $P < 0.001$) (Fig. 2).

DISCUSSION

Like most species of krill, *E. pacifica* undergoes diurnal migrations, rising to the surface to feed at night and descending to depths as great as 500 m during the day; though in coastal regions, the bulk of euphausiid populations tends to remain above 250 m (Smiles & Percy 1971; Brinton 1976; Youngbluth 1976; Bollens *et al.* 1992; Tanasichuk 1998). As a consequence of such migrations, individuals in the field would be exposed to temperatures similar to those in our experiment for only part of each 24 h cycle. In addition, we provided individuals with continuous access to abundant food, which would not have been the case for natural populations during the concurrent period. Nevertheless, two striking conclusions can be drawn from these results.

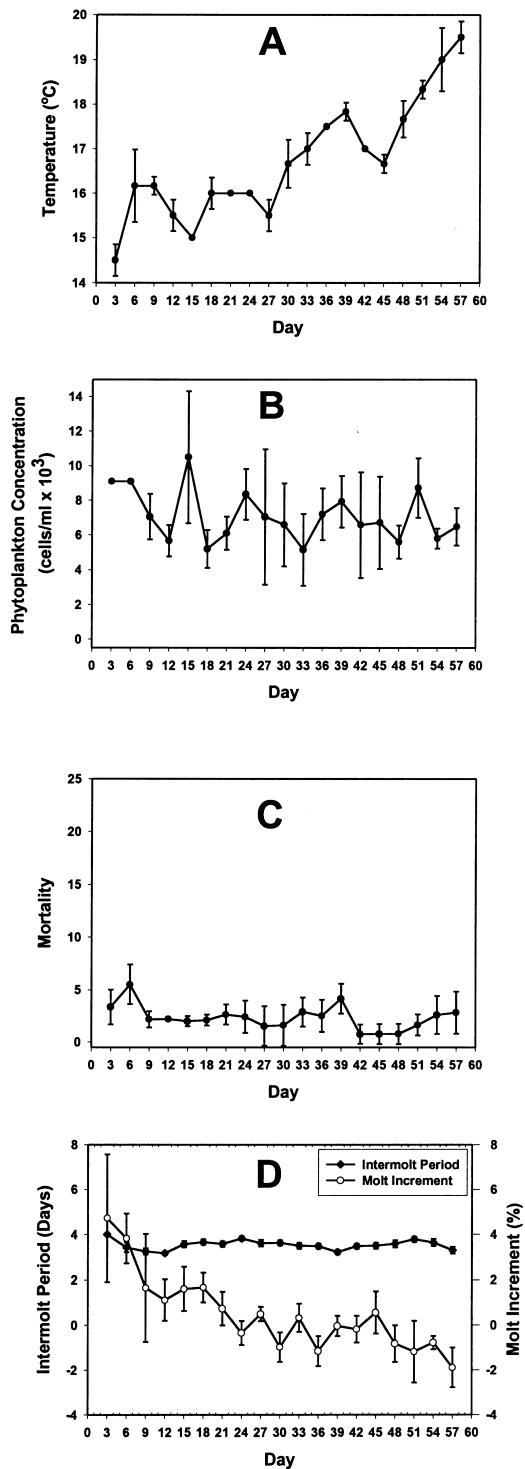


Figure 1 Results from a growth experiment on *E. pacifica* juveniles during July and August 1997. *Y*-values for all graphs represent discreet means (± 1 se) for data binned over 3 days. (A) Mean ambient ocean temperature. (B) Mean phytoplankton concentration in culture vessels. (C) Mean daily mortality rates for *E. pacifica*. (D) Mean intermolt period and molt increment for *E. pacifica* individuals.

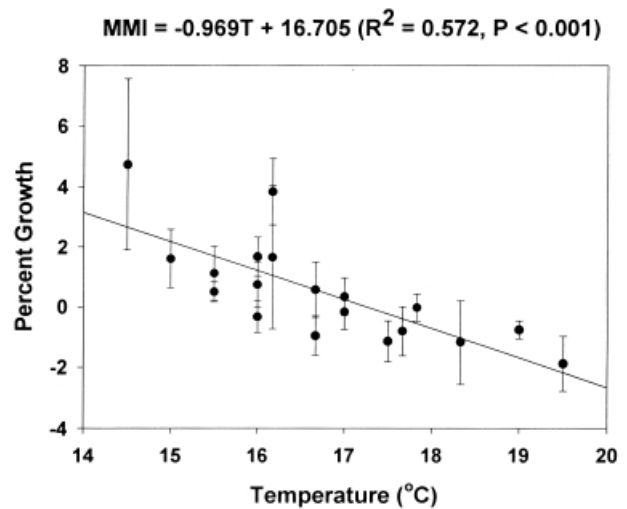


Figure 2 Regression plots (predicted, \pm se) for temperature and mean molt increment (MMI) (\pm se) for *E. pacifica* cultured in the laboratory; $MMI = -0.969T + 16.705$ ($R^2 = 0.572$, $P < 0.001$).

First, the data unequivocally demonstrate that *E. pacifica* individuals are capable of shrinkage between molts (i.e. a decrease in MI) in response to prolonged exposure to elevated temperatures (Fig. 1A, E). Shrinkage in krill has previously only been experimentally documented for Southern Ocean krill (*E. superba*) in response to poor feeding conditions (Ikeda & Dixon 1982; Quetin & Ross 1991; Nicol *et al.* 1992), though it has been proposed for a number of temperate species (Brinton 1976; Falk-Petersen 1984; Hosie & Ritz 1989; Dalpadado & Skjoldal 1996). It is well established that metabolic rate increases with temperature for this species (Small & Hebbard 1967; Iguchi & Ikeda 1995). However, in our experiment, despite access to excess food, individuals still shrank when temperatures increased. Ross (1980a, b) demonstrated that both weight specific production and growth efficiency were higher for *E. pacifica* individuals cultured at 12°C as opposed to 8°C. More recently Iguchi & Ikeda (1995) determined that the maximum growth efficiency for *E. pacifica* occurred at temperatures between 11 and 12°C. Our data suggests that at temperatures substantially higher than this ($> 16.5^\circ\text{C}$) individuals are incapable of offsetting their metabolic costs through feeding. This would follow if the maximum assimilation rate was physiologically constrained as has been suggested by several investigations on other species of temperate euphausiids (McClatchie 1986, 1988; McClatchie *et al.* 1991).

Second, though IP varied little with increasing temperature (Fig. 1D), there was considerable variation in individual MI at any given temperature (Figs 1D, 2). The lack of a temperature effect on IP could be accounted for if maximum molt frequency was physiologically constrained, as has been demonstrated in previous

laboratory investigations of this species (Small & Hebbard 1967; Fowler *et al.* 1971). In contrast, the variation in individual MI implies that growth rates may vary considerably between individuals exposed to similar conditions. MI in euphausiids may be affected by several factors including temperature (Small & Hebbard 1967; Fowler *et al.* 1971), size (Iguchi & Ikeda 1995; Labat & Cuzin-Roudy 1996), food (Smiles & Percy 1971; Ross *et al.* 1982; Falk-Petersen 1984; Dalpadado & Skjoldal 1996), and reproductive status (Brinton 1976; Bollens *et al.* 1992; Labat & Cuzin-Roudy 1996). These factors were controlled for in our experimental design as all individuals were of the same life history stage (juveniles < 12 mm) and maintained in identical culture conditions, thus the observed variation in growth rates was most likely due to individual genetic variability.

Size distributions of krill around the Antarctic (Siegel 1987; Nicol 1990) and North-east Pacific (Smiles & Percy 1971; Brinton 1976; Ross *et al.* 1982; Bollens *et al.* 1992; Tanasichuk 1998) are often bimodal. Our data suggest that unimodal size distributions could bifurcate into bimodal distributions as a consequence of individual variation in growth. Interestingly, samples of *E. pacifica* populations collected from Monterey Bay during periods corresponding to the beginning and end of our experiment contained size classes that shifted from a unimodal to a bimodal distribution (Fig. 3). While it is impossible to attribute this change solely to individual variation in growth, our results in the laboratory are consistent with this observation.

There is increasing evidence that interannual warming events have episodically occurred in the north-east Pacific for millennia (Zhang *et al.* 1997; Quinn *et al.* 1998), causing cycles of seasonal productivity in marine ecosystems to be subject to unpredictable disturbance. Growth mechanisms leading to bimodal distributions in salmonids have been hypothesized to be an adaptive response to an unpredictably fluctuating environment (Mangel 1994), thus shrinkage in krill may represent an effective strategy to deal with increasing temperatures and/or decreased productivity associated with acute and unpredictable interannual climactic events.

The ecological consequences of krill shrinkage during warming events such as El Niños are likely profound within North-east Pacific pelagic ecosystems. During such events, temperatures in the top 50–100 m of the water column increase as much as 10°C, thermocline depth lowers, and nutrient input into the euphotic zone decreases, resulting in a drastic reduction in primary production (Chelton *et al.* 1982; Roemmich & McGowan 1995; McGowan *et al.* 1998). Daytime distributions of *E. pacifica* within Monterey Bay are known to vary seasonally in response to both light and temperature (Barham 1957);

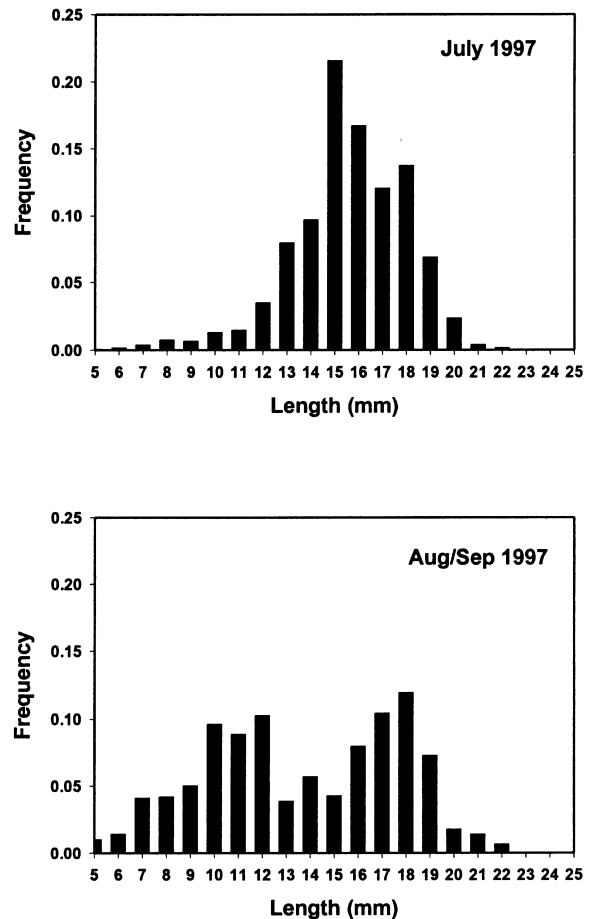


Figure 3 Size class distributions (total length) of a natural population of *E. pacifica* in Monterey Bay, CA during periods corresponding to the beginning (A) and end (B) of our laboratory experiment on krill growth. Marinovic (unpublished data).

however, our data suggest that if surface waters are about 16.5°C or higher, there is no net gain from feeding (Fig. 2) even if food is abundant, though this would most likely not be the case. Under this circumstance, we predict that migration of krill would be greatly suppressed resulting in few or no individuals in the surface waters (0–50 m) during periods of darkness and reduced numbers in the top 100–200 meters of the water column altogether. This would drastically diminish the availability of krill to surface or shallow water predators such as seabirds (Ainley *et al.* 1996; Veit *et al.* 1997) and roqual whales (Schoenherr 1991; Croll *et al.* 1998). Suppression of daily migration would further disadvantage krill, as competitors for food [e.g. salps, which are typically associated with warmer water communities in the north-east Pacific (McGowan *et al.* 1998)] would benefit from relatively unrestricted access to what limited food resources were available, as has been implicated for *E. superba* in the

Southern Ocean (Loeb *et al.* 1997). Furthermore, regardless of whether increased mortality within krill populations resulted from such events, shrinkage would cause total biomass to decrease, thus reducing the amount available to all krill predators. There is compelling evidence to suggest that zooplankton (and in particular krill) abundance in the top 200 m of the California Current has decreased dramatically in response to both acute (Chelton *et al.* 1982; Roemmich & McGowan 1995; McGowan *et al.* 1998) and longer term (Wooster 1983; Brodeur *et al.* 1996) climactic events, and furthermore that such declines have negatively impacted populations of krill predators (Smith 1985; Ainley *et al.* 1996; Veit *et al.* 1997).

In summary we have shown that krill can survive periods of high metabolic cost, induced by elevated ocean temperatures, by shrinking between molts even though food is abundant and IP is essentially constant. Furthermore shrinkage associated with elevated ocean temperatures and its corresponding behavioural responses almost certainly have profound consequences for both krill and their predators.

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