Increasing temperature may shift availability of euphausiid prey in the Southern Ocean

Kate Richerson[1,2,5,*]**, Ryan Driscoll**[1,3]**, Marc Mangel**[1,4]

[1]**Center for Stock Assessment Research, Department of Applied Mathematics and Statistics,
University of California Santa Cruz, Santa Cruz, CA 95064, USA**
[2]**Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95064, USA**
[3]**Department of Ocean Sciences, University of California Santa Cruz, Santa Cruz, CA 95064, USA**
[4]**Theoretical Ecology Group, Department of Biology, University of Bergen, Bergen 9020, Norway**

[5]*Present address:* **School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA**

ABSTRACT: Climate change is predicted to affect Southern Ocean biota in complex ways. Euphausiids play a crucial role in the trophodynamics of the ecosystem, and their status under future environmental scenarios is the subject of much concern. *Thysanoessa macrura* is the most widely distributed, numerically abundant, and ubiquitous euphausiid south of the Polar Front and may be an underappreciated prey species. *T. macrura* is eurythermic and may be better able to tolerate warming ocean temperatures in comparison to the more stenothermic Antarctic krill *Euphausia superba*. We use temperature-dependent growth models and biomass per recruit to investigate how the availability of this euphausiid to predators may change under a range of temperature scenarios. We contrast this with the availability of *E. superba* and find that, under some ranges of temperature change, increasing *T. macrura* growth may be able to partially compensate for decreasing *E. superba* growth in terms of biomass available for predators. However, in spite of its considerable biomass, other aspects of this species, such as its size and habitat, may limit its potential to replace *E. superba* in the diet of many predators.

KEY WORDS: *Thysanoessa macrura* · *Euphausia superba* · Growth · Temperature · Climate change · Krill predators · Southern Ocean · Euphausiids · Modeling

INTRODUCTION

Climate change is expected to have profound impacts on the Southern Ocean ecosystem. Over the past decades, notable changes include a reduction in stratospheric ozone (reviewed by Thompson et al. 2011) and associated change in wind patterns (Marshall et al. 2006), with consequences for ocean circulation and sea ice dynamics (Stammerjohn et al. 2008). Ocean waters have been warming (Turner et al. 2009, Schmidtko et al. 2014) and freshening (Rintoul 2007, Hellmer et al. 2011), leading to weakened deep convection (de Lavergne et al. 2014). Sea ice has been declining in some areas (Parkinson & Cavalieri 2012), and the total sea ice extent is projected to decrease by a third over the twenty-first

century (Bracegirdle et al. 2008). The Southwest Atlantic region has experienced particularly rapid warming over the twentieth century, with sea surface temperatures (SSTs) increasing by ~1.3°C around the Antarctic Peninsula since the 1950s (Meredith & King 2005) and ~2.3°C near South Georgia since the 1920s (Whitehouse et al. 2008). These changes are expected to have far-reaching consequences for both marine and terrestrial habitats (Ducklow et al. 2013, Constable et al. 2014, Lee et al. 2017, Mintenbeck 2017) and have led to concerns over the future of the Antarctic krill *Euphausia superba* population (reviewed by Flores et al. 2012). *E. superba* is a major prey source for many species of fish, squid, seabirds, and marine mammals, forming a crucial link between primary production and higher tropic levels (Sme-

tacek & Nicol 2005). Antarctic krill recruitment is correlated with the extent and duration of winter sea ice, and the long-term decline in krill abundance in the Southwest Atlantic has been linked to changes in sea ice extent and duration (Siegel & Loeb 1995, Atkinson et al. 2004). In addition, changing ocean temperatures may affect the biomass and population structure of *E. superba* and consequently its availability to predators (Wiedenmann et al. 2008). Thus, the future of *E. superba* and its predators remains uncertain.

E. superba is widely considered the most important euphasiid in the Southern Ocean; however, there are 6 euphausiid species found south of the Polar Front that may also make important contributions to predator diets (Cuzin-Roudy et al. 2014). Of these, *Thysanoessa macrura* is the most abundant, common, and widespread, with a larger geographic range than *E. superba* and a population that outnumbers *E. superba* in many locations and seasons[1] (Nordhausen 1992, Dietrich et al. 2011, Marrari et al. 2011a, Mackey et al. 2012, Steinberg et al. 2015). We lack thorough studies of the population dynamics of *T. macrura*, but in at least some parts of the Antarctic Peninsula, its numbers appear to be increasing (Steinberg et al. 2015). Because it is the most ubiquitous Southern Ocean euphausiid, *T. macrura* forms a significant component of the diets of a number of predator species, including seabirds (Bocher et al. 2000, Connan et al. 2008), penguins (Deagle et al. 2007), fish (Williams 1985, Saunders et al. 2015), and whales (Nemoto & Nasu 1958). For some predators, *T. macrura* is an important alternate food source in years when *E. superba* is scarce (Kock et al. 1994). In addition, *T. macrura* is a relatively high-quality prey item, with higher lipid content and energy density than *E. superba* (Färber-Lorda et al. 2009, Ruck et al. 2014). In light of its abundance, energy content, and broad distribution, the importance of this species for the ecosystem may have been underestimated (Nordhausen 1992).

Though much remains unknown about the life history of *T. macrura*, it is clearly different than that of *E. superba*. In contrast to the large and long-lived *E. superba*, *T. macrua* reaches a smaller asymptotic size of 37.5 to 45 mm (Siegel 1987, Driscoll 2013, Haraldsson & Siegel 2014) and has a shorter lifespan of ~4 yr (Siegel 1987), a more carnivorous diet (Kattner et al.

1996, Hagen et al. 2001, Färber-Lorda & Mayzaud 2010), and an earlier spawning season in the late winter and early spring (Makarov 1979, Falk-Petersen et al. 2000). *E. superba* may spawn multiple times over a season (Cuzin-Roudy 2000), and this may also be possible for *T. macrura* (Nordhausen 1992). Because *T. macrura* is eurythermic, with the widest latitudinal range of all Southern Ocean euphausiids (thermal range −1.8 to 8°C, based on a review of the literature by Cuzin-Roudy et al. 2014), there is speculation that it may be less affected by warming ocean temperatures in comparison to the stenothermic *E. superba* (−1.8 to 5°C, Cuzin-Roudy et al. 2014, Siegel & Watkins 2016). This differential response to changing thermal conditions may affect the availability of euphausiids to predators in the future.

Over the 21st century, summer SSTs south of 60°S are projected to rise by 0.5°C to 1.25°C, while winter SSTs are predicted to change between −0.25°C and 0.1°C (Turner et al. 2009). Regardless of season, bottom waters on the shelf at 200 m are expected to rise by 0.5°C to 0.75°C in most areas, and bottom waters from the surface down to 4000 m along the continental margin are predicted to rise by 0.25 to 0.5°C (Turner et al. 2009). Because euphausiids are ectotherms, changes in the thermal habitat are likely to have important consequences for growth, maturation, and mortality (Pörtner 2010). In addition, Antarctic marine organisms are particularly sensitive to changes in temperature (Peck et al. 2010). Wiedenmann et al. (2008) found that increased ocean temperatures may have profound effects on the available biomass of *E. superba*. Here, we explore how changing temperatures may affect the growth and biomass of *T. macrura* and contrast the results to the possible fate of *E. superba*. In particular, we focus on the biomass per recruit of these 2 species expected to be available to predators under different temperature scenarios. Though many predators consume both *E. superba* and *T. macrura*, these 2 euphausiid species differ in terms of size, vertical distribution, patchiness, reproductive season, and other characteristics. Thus, changing relative availability of these prey species may affect predators through mechanisms other than biomass alone.

MATERIALS AND METHODS

Overview

To explore how changing temperatures may affect the availability of *Thysanoessa macrura* and *Euphau-*

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[1]Because *T. macrura* is difficult to distinguish from its congeners *Thysanoessa vicina* (found south of the Polar Front) and *Thysanoessa gregaria* (found north of the Polar front), some studies only report them at the genus level (e.g. Mackey et al. 2012)

sia superba to predators, we use biomass per recruit (BPR), which is the expected lifetime biomass of a recruit. Using BPR requires a (1) an estimate of natural mortality and (2) a temperature-dependent growth model (Wiedenmann et al. 2008). Because these have not been fully described for *T. macrura*, we begin with them.

Mortality and maturity

The theory of growth-maturity-longevity (GML; Beverton 1992) relates the optimal size/age at maturity, growth (in terms of the von Bertalanffy *k*), and natural mortality. According to the GML theory, the expected fecundity ϕ of an individual that matures at age *a* is

$$\phi(a) = e^{-Ma}cL(a)^b = e^{-Ma}c[L_\infty(1 - e^{-ka})]^b \quad (1)$$

where L_∞ is asymptotic length, *k* is the von Bertalanffy growth coefficient (see below for more details), *M* is natural mortality, and *c* and *b* are constants that characterize the relationship between length and fecundity (Mangel 2017). The optimal age at maturity $a^\star$ maximizes the right hand side of Eq. (1) and is (Beverton 1992, Mangel 2006)

$$a^\star = \frac{1}{k}\ln\left(1 + \frac{bk}{M}\right) \quad (2)$$

The length at the optimal age of maturity is

$$L(a^\star) = L_\infty\left(\frac{b}{b + M/k}\right) \quad (3)$$

If *M* is unknown, and $a^\star$, *b*, L_∞ and *k* are known, this can be rearranged to solve for *M*

$$M = kb\left(\frac{L_\infty - L(a^\star)}{L(a^\star)}\right) \quad (4)$$

We used empirical measurements of 2006 *T. macrura* specimens obtained during the United States Antarctic Marine Living Resources (US AMLR) Program cruise (August to September 2014) around the South Shetland and Elephant Islands to estimate $L(a^\star)$, assuming that it is equivalent to the length at which 50% of females are mature during the spawning season (R. Driscoll & K. Richerson unpubl. data). The length frequencies of juveniles and adults indicate near knife-edge maturity, with maturation occurring between 10 and 12 mm (measured as Standard Length 1; Mauchline 1980). Thus, we set $L(a^\star)$ = 11 mm. Fecundity scales linearly with length in *E. superba* (Nicol et al. 1995), so we assume the same in *T. macrura* takes a similar form and set *b* = 1. A range

Table 1. von Bertalanffy growth parameters for *Thysanoessa macrura* from the literature and estimated natural mortality from Eq. (4). *k*: von Bertalanffy growth coefficient; L_∞: asymptotic length; *M*: natural mortality

k (yr^{-1})	L_∞ (mm)	*M* (yr^{-1})	Source
0.521	40	1.37	Driscoll (2013)
0.266	45.2	0.83	Haraldsson & Siegel (2014)
0.432	37.5	1.04	Siegel (1987)

of von Bertalanffy growth parameters for *T. macrura* have been reported in the literature (Table 1), possibly due to variation in methodology, environmental conditions, and/or sampling season. We use these sets of parameters and Eq. (4) to generate a plausible range of natural mortality rates.

Growth

Method I: Quadratic growth curve

Since *T. macrura* is an ectotherm, its growth rate will be a peaked function of temperature, as in *E. superba* (Atkinson et al. 2006). Driscoll et al. (2015) measured *T. macrura* living in waters near the lower end of their broad thermal range (−1.8 to 8°C, Cuzin-Roudy et al. 2014), so that peak growth rates likely occur above of the range temperatures reported by Driscoll et al. (2015). Thus, we use a modified version of the growth model developed by Atkinson et al. (2006) for *E. superba* to estimate growth in *T. macrura* over a range of temperatures. Atkinson et al. (2006) modeled the daily growth rate (DGR; mm d^{-1}) of *E. superba* (DGR$_s$) as a function of length *L* (mm), chlorophyll *a* concentration (a proxy for food availability; mg m^{-3}) indicated as *F,* and temperature *T* (°C).

$$\text{DGR}_s(L,F,T) = a + bL + cL^2 + d\frac{F}{e + F} + fT + gT^2 \quad (5)$$

Because Driscoll et al. (2015) found that *T. macrura* growth was not correlated with either copepod or phytoplankton availability, we do not include food in the model for *T. macrura* growth (DGR$_M$) and use

$$\text{DGR}_m(L,F,T) = a + bL - cL^2 + fT - gT^2 \quad (6)$$

We assume that chlorophyll *a* varies across the growing season and use concentrations approximating those found in the Polar Front by Moore & Abbott (2002), which represent reasonable values for levels

found across much of the Southern Ocean (Moore & Abbott 2000). Specifically, we use concentrations of 0.21, 0.35, 0.6, 0.39, 0.3, 0.24, and 0.22 mg m^{-3} for October, November, December, January, February, March, and April, respectively.

Driscoll et al. (2015) found negative growth at temperatures <1°C, but Haraldsson & Siegel (2014) inferred positive growth rates in the Lazarev Sea, where temperatures are commonly <1°C even during summer (Lal 2008). In addition, the temperature range of *T. macrura* extends into waters well below 1°C (Cuzin-Roudy et al. 2014). Consequently, we explore 2 parameterizations of the growth curve: one where DGR is negative below 1°C (Model 1), and one where it is negative below 0°C (Model 2). We set maximum DGR to 0.12 mm d^{-1} (Driscoll et al. 2015) and assumed that DGR is maximized at $L = 9$ mm, drops to 0 at 7°C, and that *T. macrura* does not grow larger than 40 mm (Table 2). For details on how the coefficients were derived, see Supplement 1 at www.int-res.com/articles/suppl/m588p059_supp.pdf. In Fig. 1, we show the relationship between DGR and temperature at a variety of lengths and the growth rates found by Driscoll et al. (2015) for the 50th size percentile (15.79–18.3 mm in the Antarctic Circumpolar Current and 16.5–17.9 mm in the Weddell Sea).

We follow Wiedenmann et al. (2008) and assume minimal growth in May–September for both species. The extent to which *E. superba* alters its metabolism and feeding in the winter is debated; several studies (Torres et al. 1994, Atkinson et al. 2002, Meyer et al. 2010) suggest that it follows a 'compromise' winter strategy, with reduced metabolism and limited, opportunistic feeding. This may be driven by seasonal

Table 2. Coefficients for models predicting growth on the basis of temperature and length (*Thysanoessa macrura*) and temperature, length, and food (*Euphausia superba*; Atkinson et al. 2006). Model 1 assumes *T. macrura* is negative below 1°C, and model 2 assumes it is negative below 0°C

| Parameter | *T. macrura* | | *E. superba* |
	Model 1	Model 2	
a	−0.103	−0.0101	−0.066
b	0.00225	0.00225	0.002
c	−0.000125	−0.000125	−0.000061
d	–	–	0.385
e	–	–	0.328
f	0.107	0.0686	0.0078
g	−0.0133	−0.00980	−0.0101

changes in light, rather than by changes in food availability (Teschke et al. 2007, 2011). This results in little to no growth, or even shrinkage in the winter. While there are limited data on *T. macrura* overwintering strategies, there is some evidence of protein and lipid depletion in the winter (Torres et al. 1994), and their winter excretion rates are low compared to other omnivorous zooplankton (Huntley & Nordhausen 1995). In addition, Haraldsson & Siegel (2014) fit an oscillating von Bertalanaffy growth curve to *T. macrura* and conclude that there is evidence of reduced growth in the winter and accelerated growth in the summer. However, it appears that *T. macrura* growth is less affected by seasonality than that of *E. superba* (Siegel 1987, Haraldsson & Siegel 2014). Thus, we assume that *E. superba* growth is 0 in the non-growing season (May–September), while *T. macrura* growth is 10% of the rate calculated from Eq. (6).
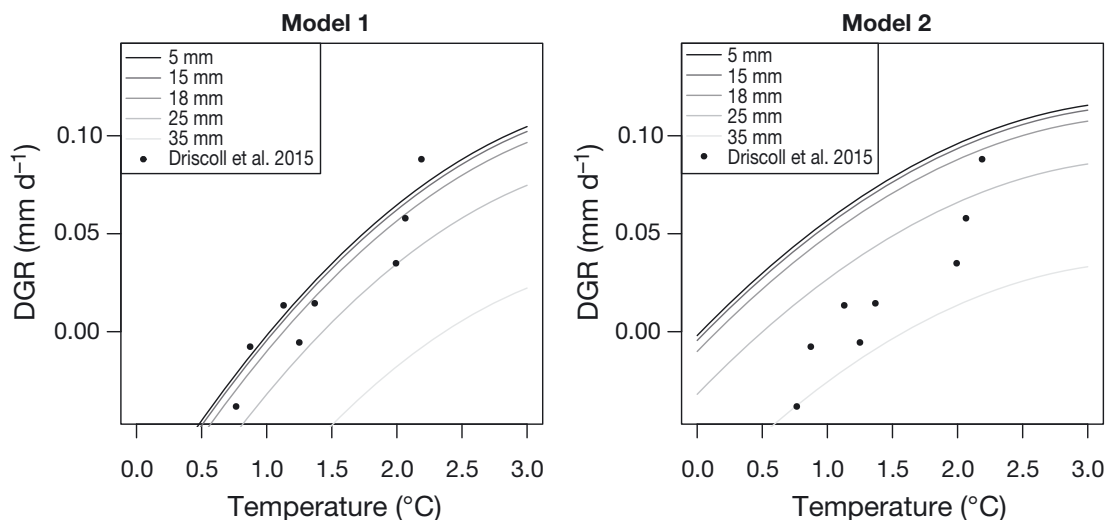

Fig. 1. Modeled daily growth rates (DGR) for *Thysanoessa macrura* across temperatures at a variety of sizes for the 2 quadratic models explored. Data points from Driscoll et al. (2015) show estimated daily growth rates for the 50th size percentile

Method II: von Bertalanffy growth

Eq. (1) to (3) are based on the von Bertalanffy model for size-at-age (vB; von Bertalanffy 1938)

$$L(a) = L_\infty(1 - e^{-ka}) \qquad (7)$$

To estimate the vB growth coefficient k at different temperatures, we use the results in Driscoll (2013) in combination with the Ford-Walford plot (Ford 1933, Walford 1946). We created Ford-Walford plots at a range of temperatures, using the mean size-at-age for Classes 1, 2, and 3 predicted by the relationships found by Driscoll (2013) and assuming that size in age Class 4 is 35 mm across all temperatures (consistent with the growth curve identified by Driscoll 2013). The relationship between k (yr^{-1}) and temperature T (°C) is then

$$k(T) = 0.123\,T + 0.294 \qquad (8)$$

In Supplement 2 at www.int-res.com/articles/suppl/m588p059_supp.pdf, we further discuss the linear temperature dependence. We set $L_\infty = 45.2$ mm (Haraldsson & Siegel 2014).

BPR

Computing BPR requires following size and survival of a cohort through time. If $N(a)$ is the number of individuals of age a and R is the initial size of the cohort, the dynamics are

$$N(a) = R \text{ for } a = 1 \qquad (9)$$
$$N(a) = N(a-1)e^{-M} \text{ for } a > 1$$

The number of individuals of age a in the cohort dying $N_D(a)$ is

$$N_D(a) = N(a)(1 - e^{-M}) \qquad (10)$$

For *E. superba*, we set $M = 0.91$ yr^{-1} (0.0025 d^{-1}, and 40% annual survival), an intermediate value from the range reported by Siegel & Nicol (2000). For *T. macrura*, we set $M = 1.08$ yr^{-1} (0.0030 d^{-1}, and 34% annual survival), using the mean of the 3 mortality rates estimated above.

If predation is the only source of mortality, the BPR available to predators of the cohort at age a is

$$\text{BPR}(a) = \frac{1}{R} N_D(a) \cdot \alpha L(a)^\beta \qquad (11)$$

Table 3. Parameters used in length–weight relationships for *Euphausia superba* and *Thysanoessa macrura*

Species	Length range (mm)	α	β	Source
E. superba	2–5	0.0470	2.121	Ikeda (1984)
	10–40	0.0072	3.021	Hofmann & Lascara (2000)
	40–60	0.0016	3.423	Hofmann & Lascara (2000)
T. macrura	8.87–16.92	0.00165	3.705	Färber-Lorda (1994)
	17.20–21.82	0.00013	4.564	Färber-Lorda (1994)

where α and β are scaling parameters that convert length to weight (see Table 3 for values). For *T. macrura*, we first used the same standard length as Färber-Lorda (1994), using the conversion relationship in Miller (1983).

Over the lifetime of a cohort, the total BPR is

$$\text{BPR}_{total} = \frac{1}{R} \sum_{a=1}^{a=a_{max}} N_D(a) \cdot \alpha L(a)^\beta \qquad (12)$$

where a_{max} is the maximum age. We set R = 1000 and use a timestep of 1 d, and we assume that the *T. macrura* cohort is born on 1 September, while the *E. superba* cohort is born on 1 February (Siegel 1987). We then explore BPR for each model at temperatures ranging from 0 to 3 C.

RESULTS

Comparison of growth trajectories across models

As temperature increases, size-at-age for *Thysanoessa macrura* increases up to 4°C (Model 1) or 3.5°C (Model 2) and declines thereafter. In contrast, vB size-at-age increases consistently with temperature. *Euphausia superba* size-at-age decreases at temperatures over ~0.5°C, as determined by the model of Atkinson et al. (2006) (Fig. 2). For *T. macrura*, the effects of temperature are more pronounced at lower temperatures in the quadratic models relative to the vB model, with large differences between size-at-age across relatively small differences in temperature. In contrast, near the peak growth temperature, differences are relatively small. The effect of seasonal differences in growth is more pronounced in the quadratic models, with faster growth in the summer and slower growth in the middle in comparison to the oscillating vB. Overall, the quadratic model shows a stronger effect of temperature on growth, with a greater range of size-at-age at most temperatures relative to the vB model.
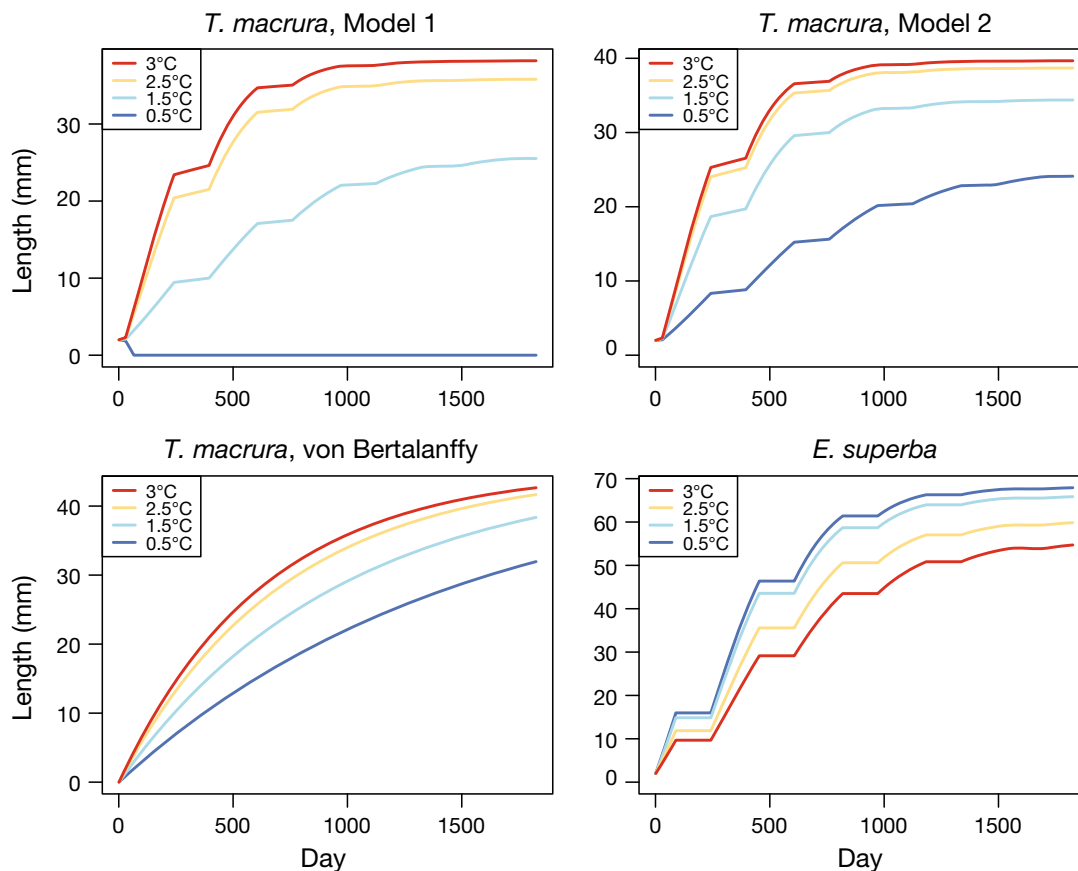
Fig. 2. Growth trajectories at different temperatures for the 3 different growth models explored for *Thysanoessa macrura* and compared with *Euphausia superba*, based on the model of Atkinson et al. (2006)

BPR

Temperature has a strong effect on BPR for all models. Between 0 and 1°C, *E. superba* BPR is at least an order of magnitude larger than that for *T. macrura* (Fig. 3). However, at 2°C, maximum daily *T. macrura* BPR (Model 1) begins to approach *E. superba* BPR, and by 3°C, both Model 1 and Model 2 *T. macrura* BPRs are generally greater than that of *E. superba*, while vB *T. macrura* BPR is similar to that of *E. superba.* The interplay of mortality and growth is apparent in the dips in BPR during winter, given that growth slows, but we assume that predation remains constant. *E. superba* BPR is maximized around age 2+ (the third summer after birth), while *T. macrura* BPR is maximized around age 1+ (the second summer after birth), suggesting the age class most available to predators may vary across these species.

Though total *T. macrura* BPR is greater than total *E. superba* BPR at higher temperatures, it does not approach the maximum total *E. superba* BPR at any temperature (Fig. 4a). At 3°C, total *T. macrura* BPR is

27.5 (vB) to 57.3% (Model 2) of maximum total *E. superba* BPR. However, the sum of total biomass available to predators (i.e. total *E. superba* BPR plus total *T. macrura* BPR) remains relatively high over a range of temperatures, even though *E. superba* biomass alone drops off rapidly (Fig. 4b). For example, for Model 2, combined total BPR is greater than or equal to *E. superba* BPR up to 1.9°C, while at this temperature, *E. superba* BPR alone is about two-thirds of its maximum. Thus, over this range, increasing *T. macrura* BPR can potentially compensate for decreasing *E. superba* BPR. Between 2 and 3°C, *T. macrura* begins to dominate the total available biomass (Fig. 4c), and at 3°C, *T. macrura* composes up to 72% of the total available biomass.

DISCUSSION

The fate of *Euphausia superba* in a changing ocean has been the subject of much concern and speculation. Rising temperatures, acidification, and declin-
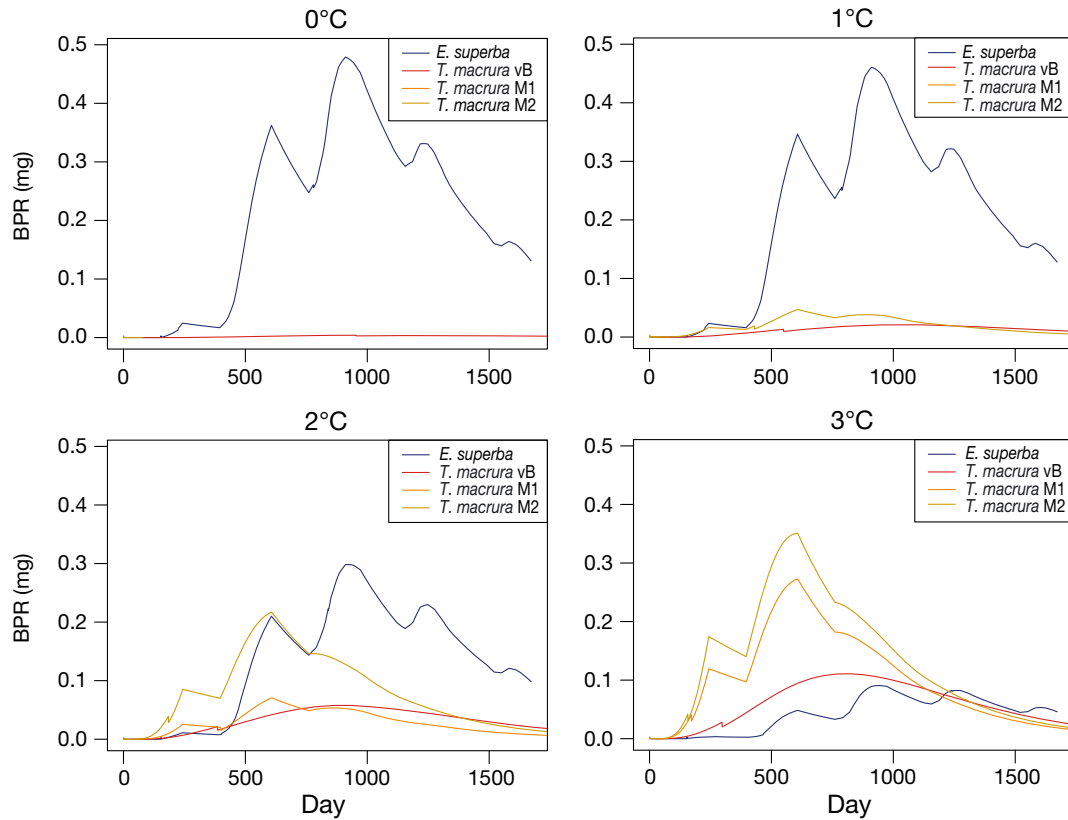
Fig. 3. Biomass per recruit (BPR, the expected lifetime biomass of a recruit) over time for *Thysanoessa macrura* calculated using 3 different growth models and *Euphausia superba*, using a version of the model from Atkinson et al. (2006), at 4 different temperatures. vB: von Bertalanffy; M1: Model 1; M2: Model 2

ing sea ice are all predicted to have negative effects on this species, likely leading to altered food sources, diminished growth potential, reduced habitat, and new competitors (Flores et al. 2012, Hill et al. 2013).

In contrast, little attention has been given to the potential effects of climate change on other euphasiids, such as *Thysanoessa macrura*. However, since it is relatively eurythermic species, *T. macrura* may be
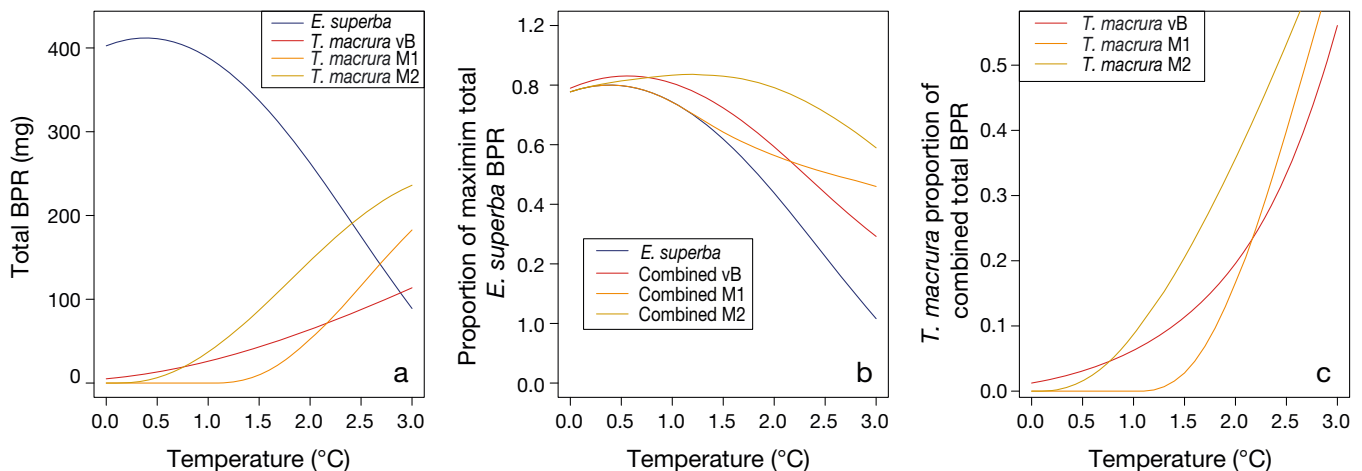

Fig. 4. (a) Total BPR for *Thysanoessa marcura* and *Euphausia superba* over a range of temperatures; (b) proportion of maximum total *E. superba* BPR for both species combined (*E. superba* BPR shown for reference); (c) *T. macrura* as proportion of total combined *E. superba* and *T. macrura* BPR. vB: von Bertalanffy; M1: Model 1; M2: Model 2

able to tolerate warming better than *E. superba.* We found that for some ranges of temperature increases, increased growth by *T. macrura* may be able to partially compensate for declining *E. superba* biomass on a per-recruit scale. That said, it is important to note that this increased *T. macrura* biomass may not provide the same net energy gain for many predators, even if the biomass is equivalent or greater to that of *E. superba.* For example, humpback *Megaptera novaeangliae* and fin whales *Balaenoptera physalus* exhibit horizontal niche partitioning, with the former foraging in areas dominated by *E. superba* and the latter in areas dominated by *T. macrura* (Herr et al. 2016), so that changing availability of *E. superba* and *T. macrura* would affect these predators differently. In comparison to *E. superba*, *T. macrura* is smaller (Siegel 1987), less aggregated (Daly & Macaulay 1988), and often distributed deeper in the water column than *E. superba* (Marrari et al. 2011b, but see Kawaguchi et al. 2011, Schmidt et al. 2011). These differences are relevant to predators, particularly air-breathing predators, as prey characteristics such as depth, patchiness, and density are known to affect foraging behavior (e.g. Alonzo et al. 2003, Santora et al. 2009, Benoit-Bird et al. 2013). Deeper and less-aggregated prey patches are likely to increase search and dive costs for some predators, and smaller prey may result in smaller energetic gain relative to handling costs. Thus, *T. macrura* biomass may not always be energetically equivalent to equal *E. superba* biomass from the perspective of a predator. However, for some predators, different eupahusiid species may be relatively exchangeable. For example, for macaroni penguins *Eudyptes chrysolophus*, fledging mass is related to the total proportion of euphausiids (including *Thysanoessa* spp., *E. superba*, and *E. frigida*) in their diet, not to the contributions from individual species (Waluda et al. 2012). For euphausiid predators that forage where *T. macrura* is abundant (e.g. mesopelagic fishes; Saunders et al. 2015) and/ or that appear to specialize on *T. macrura* (e.g. fin whales), increasing abundances of this species may be beneficial.

It is also important to consider the potential effects of movement, spatial connectivity, and heterogeneity over the lifetime of Antarctic euphausiids when interpreting the results of this study. Ocean currents structure the Southern Ocean, and their generally eastward flow may transport euphausiids thousands of kilometers over their lifetimes (Thorpe et al. 2007). This means that krill may experience widely variable temperatures, mortality risks, and other environmental conditions over their lifetime, and thus, the euphasiid biomass available to predators at any one location may be influenced by conditions in distant areas. For example, the large aggregations of *E. superba* at South Georgia likely originate from other areas, particularly the Antarctic Peninsula region (Atkinson et al. 2001). In addition, *E. superba* is an adept swimmer and is known to migrate in response to environmental cues, with important consequences for spatial location, growth, survival, and reproduction (Richerson et al. 2015). Though little is known about the swimming behavior of *T. macrura,* its relatively large size suggests it is likely also be capable of directed movement. Such behavioral responses may modulate the effects of temperature on growth and risk of predation mortality.

Although we only focused on temperature in this model, other components of the Southern Ocean habitat are being altered by climate change. Food availability is an important predictor of *E. superba* growth, and Hill et al. (2013) note that a 50% change in primary production could have a greater effect on growth than temperature. However, the impact of climate change on primary production in the Southern Ocean remains unclear. Boyce et al. (2010) found significant reductions in phytoplankton in the Southern Ocean over the past century, and Montes-Hugo et al. (2009) reported a 12% decline in phytoplankton near the western Antarctic Peninsula (WAP) over the past 30 yr. In contrast, Moreau et al. (2015) argue that climate change is increasing primary production near the WAP, and Whitehouse et al. (2008) suggest that warming around South Georgia is likely to increase phytoplankton growth in that region. Thus, though altered primary production is likely to influence euphausiid growth, the direction and magnitude of that change remains unclear and will likely vary across space and time. Because *T. macrura* is more omnivorous, its growth may be less directly affected by changes in phytoplankton relative to *E. superba.* However, the zooplankton species consumed by *T. macrura* are themselves likely to be influenced by changes in primary productivity, with consequences for this species and other zooplankton consumers. While experiments suggest that increasing temperatures may lead to decreased feeding opportunities for copepods (Sommer & Lengfellner 2008), the consequences for Southern Ocean zooplankton species and their predators remains unknown.

This study focuses on growth and does not account for the potential effects of climate change on the recruitment success and population dynamics of *E. superba* and *T. macrura.* The recruitment and abundance of *E. superba* is positively correlated with the

extent and duration of sea ice the previous winter (Siegel & Loeb 1995, Atkinson et al. 2004), potentially due to its positive effects on ice algae in the winter and spring phytoplankton blooms (Nicol 2006). Models suggest that projected changes in sea ice, temperature, and chlorophyll *a* will reduce krill spawning habitat over the next century. Variation in ice due to El Niño Southern Oscillation cycles may alter spring bloom conditions, influencing *E. superba* reproduction and recruitment (Siegel & Loeb 1995, Quetin & Ross 2001). Because *T. macrura* spawns in the winter, its reproductive cycle appears to be less dependent on the spring bloom. Thus, changes in sea ice and phytoplankton phenology may have a smaller effect on recruitment in comparison to *E. superba*. Both *T. macrura* and *E. superba* abundances are correlated with measures of El Niño Southern Oscillation near the north Antarctic Peninsula; however, their responses differ in some respects (Loeb & Santora 2015). Thus, future changes in climate and ice conditions are likely to affect both species, but their population responses may differ. In addition, *E. superba* is likely to be negatively affected by acidification, with egg development inhibited by decreasing pH (Kawaguchi et al. 2013), while the impact of acidification on *T. macrura* is unknown.

E. superba and *T. macrura* co-occur over much of their habitat, so that interspecific interactions between them may influence the dynamics of these 2 populations. As an omnivore, *T. macrura* has the potential to be both a competitor with, and predator on, *E. superba,* particularly the egg and larval stages. Changing conditions may shift the balance between these species and interact with other environmentally driven changes in complex ways. This may also be true for other species that may interact with euphausiids. For instance, salps *Salpa thompsoni*, which are another important grazer in the Southern Ocean, may see greater overlaps and increased competition with *E. superba* under future ocean conditions (Pakhomov et al. 2002). Like other effects of climate change, these potential interspecific interactions are likely to be spatially variable and multifaceted.

CONCLUSIONS

Climate change is expected to have complex effects on Antarctic euphausiids and their predators. Our results suggest that the available biomass of eurythermic *Thysanoessa macrura* may increase as the available biomass of stenothermic *Euphausia*

superba declines. However, both species may be affected by changing primary productivity, ocean acidification, and other ecosystem changes. More work remains to be done in quantifying the life history and population dynamics of *T. macrura*, the most common and widespread euphausiid in the Southern Ocean, and identifying its future in a changing ocean.

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Increasing temperature may shift availability of euphausiid prey in the Southern Ocean

Kate Richerson*, Ryan Driscoll, Marc Mangel

*Corresponding author: katericherson@gmail.com

Supplement 1: Derivation of coefficients for *Thysanoessa macrura* quadratic growth model

In the growth model of Atkinson et al. (2006), growth of *E. superba* is a quadratic function of length and temperature. We use a similar structure for the growth of *T. macrura*. In deriving coefficients for the temperature- and length-dependent *T. macrura* growth model, we make the following assumptions:

1) Maximum possible growth rate is DGR_{max}=0.12 mm day^{-1}. This is the maximum growth rate observed by Driscoll et al. (2015).

2) L_{inf}=40 mm, the asymptotic size for *T. macrura* proposed by Driscoll (2013).

3) The maximum temperature at which growth is possible (ie DGR is positive) is T_{crit}=7 °C, near the maximum temperature in the range of *T. macrura*. Thus, the temperature T_{max} where growth rate is maximized for a given size is 4 °C (model 1) or 3.5°C (model 2).

4) For a given temperature, peak growth occurs at L_{max}=9 mm, or approximately 25% of maximum size. We chose this value because *E. superba* growth is likewise maximized around 25% of maximum size according to Eqn. 5.

Recall that a quadratic equation can be written in the form

$$y = j(x - h)^2 + k \qquad \text{(S1.1)}$$

where (h,k) is the vertex. If the intercept $(n,0)$ is known, we can solve for j as

$$j = \frac{-k}{(p - n)^2} \qquad \text{(S1.2)}$$

and rearrange the quadratic into the form

$$y = jx^2 - 2jhx + jh^2 + k \qquad \text{(S1.3)}$$

To solve for the parameters in Eqn. 6, I set $T=T_{max}$, so that Eqn. 6 becomes

$$DGR(L,T_{max}) = cL^2 + bL + a' \qquad \text{(S1.4)}$$

where the unknown constant $a' = gT_{max}^2 + fT_{max} + a$. This can also be represented in vertex form as

$$DGR(L, T_{max}) = j\left(L - L_{max}\right)^2 + DGR_{max} \qquad \text{(S1.5)}$$

Using the intercept $\left(L_{inf}, 0\right)$ we see that

$$DGR(L, T_{max}) = jL^2 - 2jL_{max}L + jL_{max}^2 + DGR_{max} \qquad \text{(S1.6)}$$

where from Eqn. S3 we have $j = -\dfrac{DGR_{max}}{\left(L_{inf} - L_{max}\right)^2}$.

Thus, for the growth equation

$$DGR_m(L, F, T) = a + bL - cL^2 + fT - gT^2 \qquad \text{(S1.7)}$$

we can see that $c = j$ and $b = -2jL_{max}$.

Setting $L = L_{max}$ we can solve for g and f analogously using the vertex (T_{max}, DGR_{max}) and the intercept $(T_{crit}, 0)$. We find that $g = -\dfrac{DGR_{max}}{\left(T_{crit} - T_{max}\right)^2}$ and $f = \dfrac{2DGR_{max}T_{max}}{\left(T_{crit} - T_{max}\right)^2}$. Once b, c, f, and g are known, it is then simple to solve for a, as

$$a = DGR_{max} - cL_{max}^2 - bL_{max} - gT_{max}^2 - fT_{max}.$$

Supplement 2: The Metabolic Theory of Ecology

According to the Metabolic Theory of Ecology (MTE), metabolic rates depend on both organism size and temperature (Brown et al. 2004). Because metabolic reactions proceed faster at elevated temperatures, the relationship between temperature and metabolic rate is characterized by the Boltzmann factor $e^{\frac{-E_a}{k_B T}}$, where E_a is the mean activation energy of metabolism, k_B is the Boltzmann constant, and T is absolute temperature. According to the von Bertalanffy growth equation, k is a parameter describing catabolic processes. Thus, according to the MTE k may vary with ocean temperature T_C (in °C) as

$$k = k_0 \exp\left(\frac{-E_a}{k_B\left(273 + T_C\right)}\right)$$
(S2.1)

where k_0 is a constant. This can be rearranged into

$$k = k_0 \exp\left(\frac{-E_a}{k_B} \cdot \frac{1}{273} \cdot \frac{1}{1 + \dfrac{T_C}{273}}\right)$$
(S2.2)

Using the Taylor approximation $\dfrac{1}{1+x} \approx 1 - x$ (when x small), this then becomes

$$k \approx k_0 \exp\left(\frac{-E_a}{k_B}\left(1 - \frac{T_C}{273}\right)\right)$$
(S2.3)

and can be rearranged as

$$k \approx k_0 \exp\left(\frac{-E_a}{273 k_B}\right)\left(1 + \left(\frac{E_a}{273^2 k_B} T_C\right)\right)$$
(S2.4)

With these assumptions, k is a linear function of temperature in the same form as Eqn. 8.