

# Temperature-dependent growth of *Thysanoessa macrura*: inter-annual and spatial variability around Elephant Island, Antarctica

Ryan M. Driscoll<sup>1,2,3,\*</sup>, Christian S. Reiss<sup>2</sup>, Brian T. Hentschel<sup>3,4</sup>

<sup>1</sup>Department of Ocean Sciences, University of California Santa Cruz, Santa Cruz, California 95064, USA

<sup>2</sup>Antarctic Ecosystem Research Division, NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, California 92037, USA

<sup>3</sup>Department of Biology, and <sup>4</sup>Coastal and Marine Institute, San Diego State University, San Diego, California 92182-4614, USA

**ABSTRACT:** Somatic growth of pelagic invertebrates is controlled by temperature and food, both of which vary in space and time. Species-specific growth rate responses to environmental variability may affect populations through changes in reproductive potential; therefore, measuring spatial and temporal variability in growth rates of highly abundant zooplankton is critical to predict the impact of climate change on pelagic ecosystems. Here, we used length frequencies from bi-annual surveys conducted 1 month apart to estimate growth rates of one the most abundant euphausiids in the Southern Ocean, *Thysanoessa macrura*. We analyzed summer data from 4 separate years (1995, 1998, 2001, and 2004) that varied widely in temperature and primary production. Stations within the surveys were grouped by water characteristics: warm, low salinity Antarctic Circumpolar Current (ACC) water, and cold, saline Bransfield Strait and Weddell Sea (MBW) water, to assess inter-annual and spatial variability in cohort growth. Mid-summer cohort growth rates of *T. macrura* varied between years and water masses, ranging from  $-0.037$  mm d<sup>-1</sup> in MBW water in 2004 to  $0.081$  mm d<sup>-1</sup> in ACC water in 1995. Growth rates were faster in ACC water than in MBW water during all years. Growth rates were strongly correlated with temperature ( $R^2 = 0.82$ ) but weakly correlated with copepod density ( $R^2 = 0.38$ ), and were not correlated with chl *a* concentration ( $R^2 = 0.11$ ). These results suggest that the growth rates of *T. macrura* may increase in regions exhibiting warming trends, such as the Antarctic Peninsula. This contrasts with published data on the growth rates of *Euphausia superba*, which is predicted to be impacted negatively by climate warming.

**KEY WORDS:** *Thysanoessa macrura* · Temperature-dependent growth · Antarctica

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

Somatic growth and reproductive potential of pelagic invertebrates is controlled by temperature and food (McLaren 1978, Runge 1980, Huntley & Boyd 1984) and can also vary following seasonal (Pinchuk & Hopcroft 2007) as well as event driven changes to the environment (e.g. upwelling-downwelling events [Shaw et al. 2010]). Species-specific physiological responses to environmental and climatic variability are expected to affect populations on a variety of spa-

tial and temporal scales (Helmuth et al. 2005). Ultimately this will cause some species to decline and others to increase in importance as they respond to changes in their environment. Measuring the spatio-temporal variability in the growth of highly abundant zooplankton like euphausiids can provide important insights into the likely impacts of climate change on pelagic ecosystems.

Growth rates have been estimated for a number of euphausiid species and related to seasonal environmental variability (Siegel 1987, 2000, Nicol 2000). In

the Gulf of Alaska, for example, the growth rates of *Thysanoessa spinifera*, *Thysanoessa inermis* and *Euphausia pacifica* in Autumn have been estimated to be  $0.02 \text{ mm d}^{-1}$ ,  $-0.025 \text{ mm d}^{-1}$ , and  $\sim 0.05 \text{ mm d}^{-1}$ , respectively (Pinchuk & Hopcroft 2007). In spring, growth rates of *T. spinifera* and *T. inermis* increased to  $0.091 \text{ mm d}^{-1}$  and  $0.123 \text{ mm d}^{-1}$ , respectively. In contrast to the 2 *Thysanoessa* species, growth rates of *E. pacifica* remained relatively constant ( $<0.07 \text{ mm d}^{-1}$ ) throughout the year (Pinchuk & Hopcroft 2007). These differences in growth rates are likely a response to seasonal variability in physical and biological factors affecting growth but also indicate there are significant species-specific adaptations to local environments. Such inter-specific differences in euphausiid growth rates have not been widely explored in the Southern Ocean, where euphausiids are central to the food web (Marr 1962, Atkinson et al. 2006).

Growth for the most well studied euphausiid in the Southern Ocean, *E. superba*, which is a key prey item in some regions, has a parabolic relationship to primary productivity and temperature (Atkinson et al. 2006). The Southern Ocean exhibits seasonal variability in sea surface temperature, sea ice extent and duration as well as seasonal productivity common to high latitude regions leading to a strong seasonal growth pattern (Buchholz 1991, Atkinson et al. 2006, Wiedenmann et al. 2008). Changes to the seasonal production in parts of the Southern Ocean are thought to be responsible for the reported decline in the abundance of *E. superba* (Atkinson et al. 2004) and recent modeling suggests considerable modification of the spawning and environmental habitat owing to climate change over the next 50 yr (Hill et al. 2013). Yet, considerably less research has been conducted on the potential response of other Southern Ocean euphausiids to climate change.

In addition to seasonal variability, the Southern Ocean also exhibits substantial spatial variability in environmental conditions due to the presence of the warm Antarctic Circumpolar Current (ACC) interacting with colder, more saline shelf seas and coastal bays (Amos 2001, Atkinson et al. 2009). In regions like the Antarctic Peninsula where islands, circulation patterns, and bathymetry can keep water masses separate over small distances, such conditions could also influence growth rates for animals that remain within them. Therefore, properly accounting for the regional variability in environmental properties would also be necessary for understanding variability affecting growth rate estimates and population responses to changing environments.

Of the abundant Southern Ocean euphausiids *Thysanoessa macrura* is numerically the most abundant in many areas of the pelagic environment and exhibits a number of life history traits that suggest it may respond differently to environmental change when compared to *E. superba*. For example, *T. macrura* has a broader spatial distribution (Siegel 1987, Haraldsson & Siegel 2014) and an earlier spawning season (Hagen & Kattner 1998, Haraldsson & Siegel 2014) than *E. superba*. *T. macrura* also has a more omnivorous diet (Farber-Lorda 1994), different lipid composition (Falk-Petersen et al. 1999), while its shorter life span (Siegel 1987, Haraldsson & Siegel 2014) suggests a higher intrinsic productivity. From these life history traits we can infer that *T. macrura* may have relatively greater plasticity compared to *E. superba* when confronted with a changing pelagic environment (Haraldsson & Siegel 2014). Parmesan (2006) and Ji et al. (2010) suggest that greater plasticity may provide organisms an advantage under predicted climate change scenarios. Given the potential decline in *E. superba* abundance and its key role in the ecosystem, the ubiquitous *T. macrura* may play an increasingly important role in the ecosystem if its population is not adversely affected by climate trends.

Several methods have been used to estimate the growth rates of Antarctic euphausiids including laboratory rearing (Ikeda 1985), *in vivo* instantaneous growth rate estimation (IGR; Nicol 2000), inter-annual variability in length-at-age (Smiles & Pearcy 1971), and by measuring changes in length frequency within a season from repeated sampling over a summer (Nordhausen 1992, Nicol 2000, Shelton et al. 2013). Each approach has its own benefits and caveats. Laboratory rearing experiments and IGR experiments estimate the growth of individuals by measuring the increase in body length between molts and the interval of time between molts (Ikeda 1985, Nicol 2000). Laboratory rearing experiments can estimate growth over long temporal periods with more precise environmental control but less realistic conditions (Nicol 2000). IGR experiments measure growth by comparing the body length of pre- and post-molt animals within a few days of being captured (Quetin & Ross 1991, Nicol 2000). This technique makes the assumption that it measures growth under natural conditions (e.g. at sea) but only for the inter-molt period immediately prior to capture and can be confounded by effects of captivity after just a few days (Nicol 2000). The large number of samples required and the large effort makes it difficult to use on a continual basis. Repeated sampling uses the dif-

ference in modes or percentiles of length frequency distributions between consecutive surveys to infer average growth rates of a cohort over a range of temporal scales from days to years (Smiles & Pearcy 1971, Siegel 1987, Shelton et al. 2013, Haraldsson & Siegel 2014). There are challenges in assigning changes in length solely to growth, rather than size-based mortality (Siegel 1987) or advection from the sampling area (Shelton et al. 2013). However, an important advantage of repeated sampling is that it can be applied retroactively to archived samples, allowing for inter-annual comparison of growth rates with concurrent environmental data (Siegel 1987) if the growth is sufficient to measure between sampling periods.

The US Antarctic Marine Living Resources (AMLR) Program has collected zooplankton samples twice each austral summer since 1990 as part of an ecosystem study to support the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). Antarctic krill are the focus of that program; all other euphausiids, like *T. macrura*, are enumerated but not measured, staged, or sexed. These preserved samples provide a rich source of data that can be analyzed to address the biological consequences of climate change in this ecosystem. In this study, we analyzed a subset of archived samples collected during paired January and February cruises in 4 years to determine whether sufficient growth occurred between surveys to retrospectively estimate mid-summer cohort growth rates of *T. macrura* in waters around the West Antarctic Peninsula (WAP). We used 4 years with different water temperature, chl *a*, and copepod concentrations to maximize the probability of detecting changes in length. We estimated growth rates by comparing shifts in the modal lengths of length frequency distributions between Jan and Feb cruise legs. We grouped samples within water masses having similar properties (water zones, based on water temperature and salinity) and then related patterns of growth to the environmental (temperature) and biological (chl *a* concentration and copepod density) properties. In this manner we reduced the effects of advective losses and variability in size-based mortality because the same environments were

sampled in both months. We discuss the results in relation to the changing climatic conditions of the peninsula region.

## MATERIALS AND METHODS

### At-sea sample collection

Since 1988, the US AMLR has conducted an oceanographic and biological survey in the waters around the Antarctic Peninsula, surveying an area more than 124,000 km<sup>2</sup>. Sampling has concentrated around Elephant Island (EI) at the tip of the peninsula and part of the South Shetland Islands chain (Fig. 1). In general, the US AMLR Program survey has consisted of 2 cruise legs. The first leg begins in mid-January and a second leg repeats the survey grid several weeks later in February (Table 1). In a given year, each survey of the EI area lasts between 6 and 10 d, with 21, 28, 28, and 32 d intervals between the January and February cruise legs for

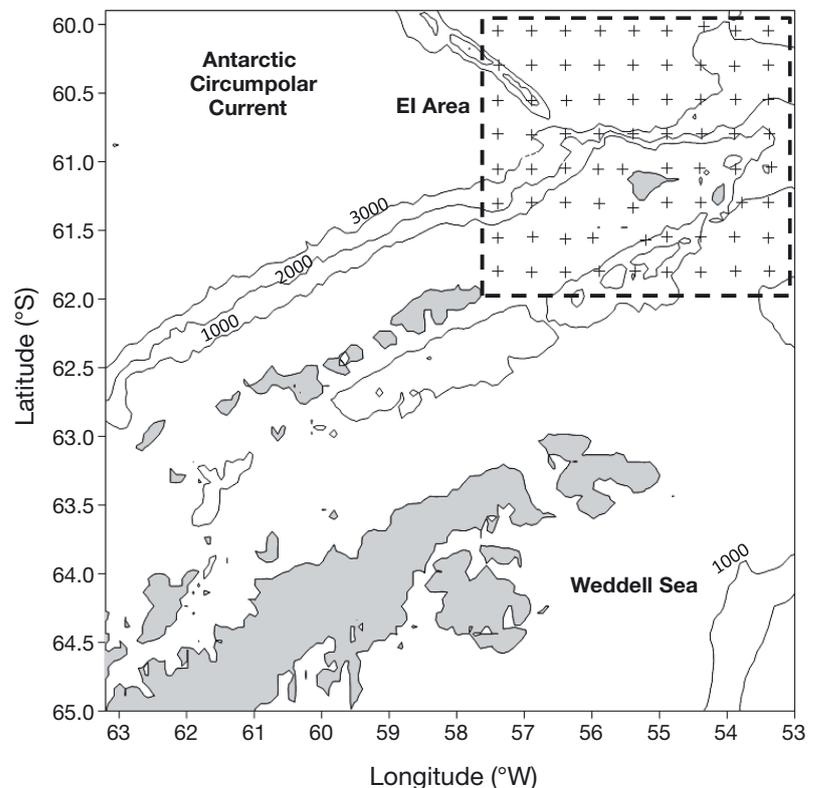


Fig. 1. Antarctic Peninsula region and Elephant Island (EI) showing the EI survey area (dashed box) and Antarctic Marine Living Resources (AMLR) stations (plus signs). The boundary between the Antarctic Circumpolar Current water zone and the Mixed Bransfield-Weddell water zone runs roughly diagonally (southwest to the northeast) through the EI area. Bathymetric contour lines in meters

Table 1. No. stations sampled and no. ind. measured in the Antarctic Circumpolar Current (ACC) water and Mixed Bransfield and Weddell Sea (MBW) water during each cruise leg in each year around Elephant Island. The number of stations analyzed for *Thysanoessa macrura* varies among years due to occasional degradation of samples and loss during storage

Year	Leg	Start date of cruise leg	Total no. ACC Stns/ subsamples	No. Ind. measured	Total no. MBW Stns/ subsamples	No. Ind. measured
1995	1	18 January	35/13	1268	26/9	1282
	2	15 February	36/8	390	28/16	2144
1998	1	16 January	33/22	1779	23/15	1115
	2	16 February	33/21	803	20/13	881
2001	1	17 January	27/13	865	25/13	781
	2	17 February	32/18	991	22/13	1300
2004	1	21 January	25/22	1512	16/13	1556
	2	24 February	21/14	1387	14/13	1570

1995, 1998, 2001 and 2004, respectively (Table 1). The EI area was sampled along predefined transects with fixed stations either 20 or 40 km apart. In general, 40–60 stations were sampled during each leg.

Zooplankton tows were conducted at each station using a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) with 505  $\mu\text{m}$  mesh, fished obliquely to either 170 m depth or 20 m above the bottom at stations <190 m deep. A General Oceanics Model 2030 flowmeter was used to determine the volume of water filtered during each tow. The collected samples were sorted aboard ship, and larval and post-larval *Thysanoessa macrura* were identified and enumerated. Copepods were enumerated for each tow and identified to species level when possible. Samples were then preserved in 5% buffered formalin and transported to Southwest Fisheries Science Center for storage (Lipsky 2004). *T. macrura* are known to be omnivorous, and we tested the hypothesis that growth would be related to zooplankton prey. For this study, all species were summed and the number of total copepods reported, as species identifications were not consistent between years. Therefore, we used total copepod abundance in each year (collected in the IKMT net tows) as an index of prey, but recognize that the actual prey preference by this euphausiid is unknown.

### Environmental data and primary production

Preceding each zooplankton tow, water column temperature, salinity and oxygen concentrations were collected at each station using a Seabird SBE 9/11 Conductivity, Temperature and Pressure (CTD). Each CTD cast was made to a depth of ~750 m, or

10 m from the bottom at stations <760 m deep. An attached rosette sampled water for chl *a* determination at 10 depths (5, 10, 15, 20, 30, 40, 50, 75, 100, and 200 m). Chl *a* concentration ( $\mu\text{g l}^{-1}$ ) was determined fluorometrically using the method of Holm-Hansen et al. (1965).

Temperature and salinity profiles obtained from each CTD cast were used to characterize the water mass properties at each station and to separate stations into 3 nominal water zones for this study, following the water zone classification of Amos (2001). In general, the EI area is dominated by 2 water zones whose border runs

roughly diagonally from the southwest to the northeast. The northern portion of the EI area is comprised of the Antarctic Circumpolar Current (ACC) surface water with relatively warm water (2 to 4°C), low salinity (<34 psu) and has both cold winter water (0°C, >100m) and upper circumpolar deepwater (2°C, >400 m) beneath it. The southern portion of the EI area is comprised of a mixture of Weddell Sea Shelf water characterized by colder (–0.5°C) and saltier (>34.1 psu) water and water from the Bransfield Strait, a coastal bay between the South Shetland Islands and the Antarctic Peninsula that has intermediate temperature (0–2°C) and salinity between 33.9–34.1 psu (Holm-Hansen et al. 1997). For this study, stations classified as either ACC water or warm intermediate water are grouped under the label ACC and stations classified as mixed Bransfield Strait and Weddell Sea water or cold intermediate mixed water are grouped under the label Mixed Bransfield-Weddell (MBW).

We calculated the upper mixed layer (UML) depth as the depth at which the density differed by 0.05  $\text{kg m}^{-3}$  from the mean density between 5 and 10 m (Hewes et al. 2009) for each station. We calculated the mean chl *a* concentrations for the UML as an index of primary production available to *T. macrura*. The average water temperature at 10 m depth for each zone and year was used as a representation of inter-annual variability in water temperature.

### Laboratory sampling

The total number of samples available for retrospective analysis from each survey varied due to at-sea sampling circumstances (weather, malfunctions

etc.) in each survey year, and to sample degradation and loss during storage (Table 1). For this study, we focused on removing and measuring *T. macrura* from archived samples collected in the EI area during 4 years that exhibit contrasting water temperature and chl *a* concentrations in the UML averaged over the whole area (Hewes et al. 2009) during the sampling period. The years 1995, 1998, 2001 and 2004 had average water temperatures of 1.7, 1.4, 1.6, and 1.1°C and average UML chl *a* concentrations of 1.3, 0.5, 0.6, and 0.7 mg m<sup>-3</sup>, respectively (see Fig. 2). In this manner, we selected years with the most environmental contrast in order to determine whether the changes in length frequency were measurable over the 1 mo interval between surveys.

### Determination of growth rate

*T. macrura* were removed from archived samples, their lengths were measured to construct length frequency distributions for each year, cruise leg and water type (ACC or MBW). The techniques for obtaining accurate length measurements are well established for *E. superba* (De la Mare 1994) and were easily adapted for *T. macrura*. We estimated length by measuring the distance from rostrum tip to telson tip, which is defined as a standard length for euphausiids (Mauchline 1980). All postlarvae (>10 mm) were measured to the nearest 0.5 mm under magnification using a stereo microscope (Leica SD6). Length frequency distributions for *T. macrura* derived from subsamples of all the tows were converted to length densities representing the abundance of animals in the survey area by using the total number of *T. macrura* in each tow and dividing by the volume of water sampled. Converting to length density requires accounting for the abundance of animals at each station and the statistical properties of the samples. This is especially critical if the number of zero tows represent a large fraction of the samples. Although *T. macrura* were patchy, the number of zero hauls was minimal. Despite the more log-normal distribution of abundances, we calculated statistics based on the Aitchison delta-distribution; this accounts for 2 properties of the data: the skewness of the distribution and the probability of tows containing 0 animals (Aitchison 1955, De la Mare 1994). We used CMIX software (Australian Antarctic Division, version 3.1.1), which incorporates the delta-distribution to account for both properties and to provide a robust estimate of the length density and an estimate of its variance for each length class (De la Mare 1994).

One of the major assumptions of estimating growth from repeated sampling is that the same population (length frequency, growth, etc.) is sampled during both sampling periods so that length differences can be attributed to growth and not to other processes. In an open environment, this assumption can be violated by advection of animals through the area between cruise legs, active migration into or out of the sampling space, as well as by differential mortality (Nicol 2000). Advection of animals out of the sampling areas is possible as the prevailing mean currents within the Antarctic Circumpolar Current are easterly, and can exceed 20 cm s<sup>-1</sup>. However, our approach aimed to reduce the effects of advection in 2 ways. Firstly, by surveying over a large area (48 231 km<sup>2</sup>) we reduced the potential for animals to be quickly advected through the sampling area. It is known that there are significant eddies and counter currents along the coast and these features can act to increase residence time within the area. Whilst there are no estimates of retention rate in the EI area, surface drifters released in this region during summer are often retained for many weeks north and east of the EI in the lee of the Shackleton Transverse Ridge, and in shelf waters around the South Shetland Islands (US AMLR Program: <https://swfsc.noaa.gov/aerd>). Secondly, by grouping stations within the survey area for each leg according to water mass properties, not by geographic location alone, we reduced the potential to bias length frequency distributions associated with shifts in the boundary between the 2 zones. By comparing data only among areas with similar temperature, salinity and production, we increased the probability that animals within water mass areas would have similar histories, and minimize mixing of animals with different histories between areas.

Size- or sex- specific differential mortality within the sampling space may also influence the estimation of growth from comparing length frequency distributions (Siegel 1987). However, there is little quantitative data on the sources of mortality for *T. macrura*. Its main predators are unknown, although it is occasionally found in the stomachs of fish (Kock et al. 2012), sea birds (Croxall et al. 1999) and mammals (Nemoto & Nasu 1958), all of which predate mainly on *E. superba* (Siegel 2000) in this region. We assume size-dependent mortality has a negligible effect in our analysis because *T. macrura* has a relatively small size range (10 to 27 mm) compared to species like *E. superba* (~10 to ~60 mm) so marine mammals and penguins are not directly targeting them. Other flying seabirds that may feed on *T. macrura* could

select for smaller individuals if there is an ontogenetic shift in the vertical distribution of *T. macrura* affecting their availability to predators, but there is little known about either for this species.

We used samples collected during the night and day to ensure that sufficient samples were analyzed to develop robust length frequency distributions. *A priori* we omitted a total of 28 twilight tows due to the possible confounding factor of differing vertical migration rates between larger and smaller individuals that has been suggested for other euphausiids (Nicol 2000). Pooling daytime and nighttime samples also includes some assumptions and potential biases; night-time abundance estimates can be larger than daytime estimates due to diel vertical migration and/or decreased avoidance of the IKMT during darkness. Furthermore, since nights are longer during February, the January survey leg has a lower proportion of night-time tows and, therefore, might be biased toward lower apparent abundances compared to February survey legs. Thus, prior to combining day and night samples, we verified that the proportions of length classes did not differ significantly between daytime and night-time tows ( $\chi^2 = 1105$ ,  $p = 0.245$ ) before estimating differences in length frequencies between legs.

## Data analysis

### Growth rates

In many invertebrate taxa, younger or smaller individuals often have faster growth rates than older or larger individuals, thus potentially skewing overall cohort growth rates (Vidal 1980). *T. macrura* are thought to live 3 yr or more, but age classes can be difficult to distinguish from length frequency data (Siegel 1987). To mitigate the effects of potential age- or size-specific growth rates on cohort growth rate, we analyzed the length frequency distributions by quartiles to provide an estimate of the growth rates of different sizes of *T. macrura*.

The length density distributions derived using the CMIX algorithm were converted to cumulative distributions and the estimated mean lengths at the 25th, 50th, and 75th percentiles were used as estimates of size during each survey leg. Two sources of potential bias are noted. First, given the skewed length distributions, the extreme tails of the distributions included only a few individuals larger than 27 mm. Because individuals of these sizes were not consistently collected between cruise legs, there were insufficient

numbers of individuals collected to calculate growth rates for this largest size class. So these largest animals (generally <10 individuals per cruise leg) were excluded from the analysis prior to calculating proportions. Second, it is possible that the smallest individuals might escape through the 505  $\mu\text{m}$  mesh of the net which may skew the 25th percentile as the animals grow between surveys. However, we believe that this source of bias is small as the IKMT routinely captures euphausiid larvae around 1 mm in length suggesting the net is still efficient at the smallest size classes of *T. macrura* (~10 mm) found in this study. The difference in the length between each of the 3 quartiles between the January and February surveys was calculated to obtain the growth (mm) between legs. Since the number of days between legs varied between years, (mean = 25 d, range = 21–32 d), growth was divided by the number of days between the mid-points of the January and February surveys in each year to standardize growth rates to  $\text{mm d}^{-1}$  for each quartile. In order to estimate variability in the measurement of growth, we calculated the length frequency distribution 5 times for each year and zone using a leave-one-out resampling scheme with replacement for each length frequency distribution we calculated. We then calculated the differences in length at each length class (25th, 50th and 75th percentile) to provide an estimate of the variability associated with sampling.

### Statistical analysis

We used ANOVA to test for differences in temperature, chlorophyll and copepod density between years and water zones. We used an inverse-variance weighted ordinary least squares (OLS) regression to examine the relationship between the mean daily growth and environmental predictors: temperature, chl *a* concentrations and total copepod abundance.

## RESULTS

### Environmental variables

Water temperature at 10 m exhibited significant inter-annual variability (ANOVA;  $F_{3, 209} = 12.58$ ,  $p < 0.001$ ) and variability associated with water zones ( $F_{1, 208} = 132.69$ ,  $p < 0.001$ ) (Fig. 2A). There was no significant interaction between the main effects of year and water zone ( $F_{3, 208} = 0.151$ ,  $p = 0.151$ ). For ACC water, the average UML water temperature

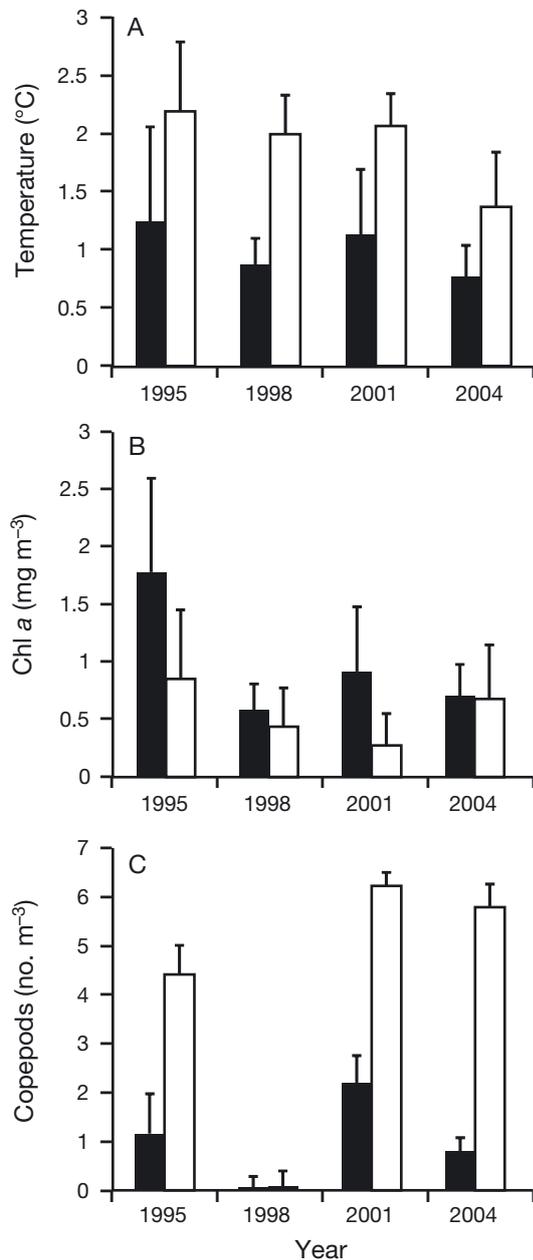


Fig. 2. (A) Mean temperature ( $^{\circ}\text{C}$ ) at 10 m, (B) mean upper mixed layer chl *a* concentration ( $\text{mg m}^{-3}$ ), and (C) mean copepod density ( $\text{n m}^{-3}$ ) in each year for Antarctic Circumpolar Current (ACC) stations (white) and Mixed Bransfield-Weddell (MBW) stations (black). Error bars = SD

was warmest in 1995 ( $2.2 \pm 0.57^{\circ}\text{C}$ , mean  $\pm$  SD) and coldest in 2004 ( $1.4 \pm 0.3^{\circ}\text{C}$ ). The ACC temperatures for 1998 and 2001 were intermediate between these 2 extremes (Fig. 2A). The same inter-annual pattern in temperature was found for MBW water stations, but the warmest MBW water of the 4 years, 1995 ( $1.25 \pm 0.48^{\circ}\text{C}$ ), was still significantly colder than the

coldest ACC water of the 4 years (2004) (*t*-test;  $t_{51} = -6.24$ ,  $p < 0.001$ ) (Fig. 2A).

Mean UML chl *a* concentration was greater in MBW water than in ACC water in each year, but the magnitude of this difference varied (Fig. 2B). UML chl *a* concentrations also varied significantly among years (ANOVA;  $F_{3,456} = 84.53$ ,  $p < 0.001$ ) and between water masses ( $F_{1,456} = 47.74$ ,  $p < 0.001$ ), with a significant interaction ( $F_{3,456} = 14.24$ ,  $p < 0.001$ ) (Fig. 2B). The highest mean chl *a* concentration was observed in 1995 both in the ACC water ( $0.85 \text{ mg m}^{-3}$ ) and in the MBW water ( $1.78 \text{ mg m}^{-3}$ ). The mean chl *a* concentration was low in both 2001 and 1998, where lowest chl *a* concentrations in the ACC were observed in 2001 ( $0.27 \pm 0.27 \text{ mg m}^{-3}$ ) and in 1998 in the MBW ( $0.58 \pm 0.22 \text{ mg m}^{-3}$ ).

The abundance of copepods also varied among years and water masses (Fig. 2C). The mean copepod density varied significantly among years (ANOVA;  $F_{3,341} = 6.68$ ,  $p < 0.001$ ) and prey concentrations were higher in the ACC than in the MBW each year ( $F_{1,341} = 17.792$ ,  $p < 0.001$ ); like water temperature, no significant interaction between water zone and year was found ( $F_{3,341} = 2.250$ ,  $p = 0.082$ ) (Fig. 2C). The highest density of copepods occurred in 2001, both in the ACC ( $6.23 \pm 11.41 \text{ n m}^{-3}$ ) and the MBW ( $2.2 \pm 4.52 \text{ n m}^{-3}$ ). The lowest density of copepods occurred in 1998 in both the ACC ( $0.06 \pm 0.06 \text{ n m}^{-3}$ ) and the MBW ( $0.06 \pm 0.11 \text{ n m}^{-3}$ ), both years of low chl *a* concentration.

### Length frequencies and growth rates

Length frequency distributions of *Thysanoessa macrura* were right skewed in all years and in both water masses (Fig. 3). The length frequency distribution at each percentile was consistently  $\sim 1 \text{ mm}$  smaller in the ACC water than in MBW water for all percentiles in each January cruise leg (Table 2, Fig. 3). The length frequency distribution for each percentile in January was similar among 1995, 2001 and 2004 for both the ACC water and the MBW water, but was on average  $1 \text{ mm}$  smaller in each water zone in 1998.

Growth was measureable in all years using repeated sampling, but growth varied among years and between water zones (Fig. 4). Average growth rate over all years, zones and percentiles was  $0.022 \text{ mm d}^{-1}$  and ranged from  $-0.046$  (75th percentile in 2004) to  $0.088 \text{ mm d}^{-1}$  (50th percentile in 1995). Mean growth rate averaged across all percentiles and years in ACC water ( $0.0383 \text{ mm d}^{-1}$ )

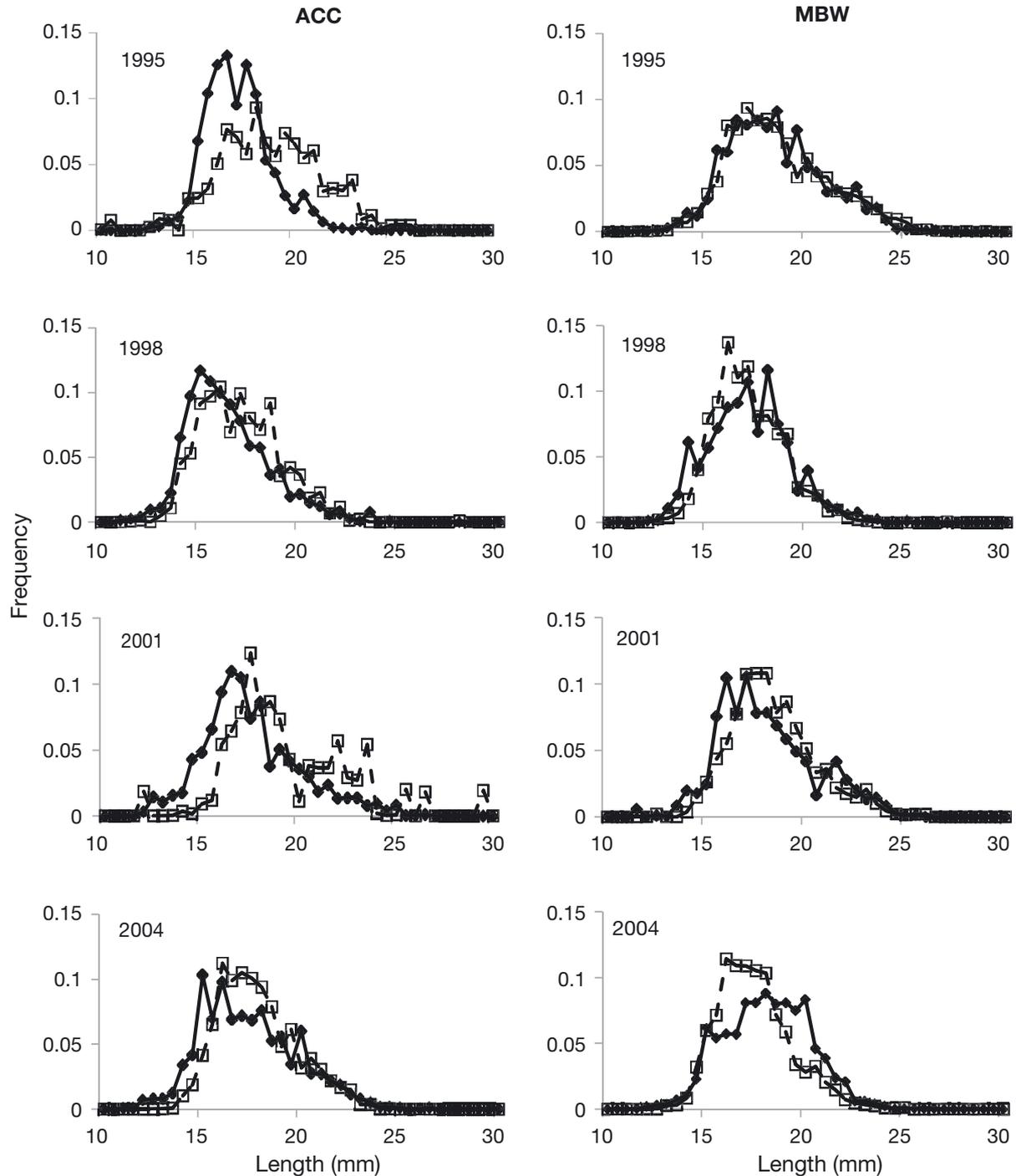


Fig. 3. Length frequencies of *Thysanoessa macrura* for the January (◆, —) and February (□, ---) cruise legs in each year for the Antarctic Circumpolar Current (ACC, left panels) and Mixed Bransfield-Weddell (MBW, right panels) stations

was significantly greater than in MBW water ( $-0.0069 \text{ mm d}^{-1}$ ) ( $t$ -test;  $t_3 = 4.94$ ,  $p < 0.016$ ). Negative growth rates were found in 1995, 1998 and 2004 in MBW water (Fig. 4). Averaged across years, growth rates increased from the 25th percentile to the 75th percentile in ACC water, but decreased

from the 25th percentile to the 75th percentile in MBW water. For almost every percentile in every year, growth in ACC water was greater than the maximum growth measured in MBW water, with the exception of calculations based on the 50th and 75th percentiles in 2004 (Fig. 4).

Table 2. Mean length (mm) for the 25th, 50th and 75th percentiles of *Thysanoessa macrura* in Antarctic Circumpolar Current (ACC) water and Mixed Bransfield and Weddell Sea (MBW) water around Elephant Island during the January and February cruise leg each year

	1995		1998		2001		2004	
	January	February	January	February	January	February	January	February
<b>ACC</b>								
<b>25th</b>	15.63	16.61	14.65	15.22	15.66	17.03	15.25	16.01
<b>50th</b>	16.62	18.33	15.79	16.61	16.86	18.31	16.83	17.24
<b>75th</b>	17.75	20.28	17.33	18.12	18.73	21.22	18.76	18.75
<b>MBW</b>								
<b>25th</b>	16.39	16.49	15.38	15.53	15.96	16.62	16.24	15.82
<b>50th</b>	17.92	17.91	16.75	16.55	17.37	17.78	17.83	16.96
<b>75th</b>	19.68	19.92	18.08	17.88	19.24	19.28	19.40	18.22

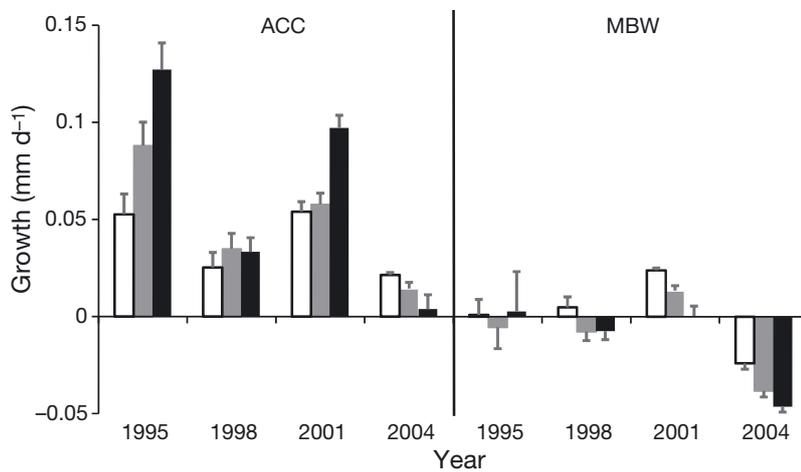


Fig. 4. Daily growth rates ( $\text{mm d}^{-1}$ ) for the 25th percentile (black bars), 50th percentile (grey bars) and 75th percentile (white bars) of *Thysanoessa macrura* in each year for the Antarctic Circumpolar Current (ACC) and Mixed Bransfield-Weddell (MBW) stations. Error bars = SD

Mid-summer growth rates of *T. macrura* were positively related to water temperature at each of the 3 quartiles: the 25th (inverse-variance weighted OLS;  $R^2 = 0.50$ ,  $p = 0.005$ ), 50th ( $R^2 = 0.82$ ,  $p = 0.002$ ), and 75th ( $R^2 = 0.86$ ,  $p < 0.001$ ) (Fig. 5A). The relationship between temperature and growth ( $y = 0.0664x - 0.0739$ ) translates to a growth rate of  $0.027 \text{ mm d}^{-1}$  per  $0.5^\circ\text{C}$  increase over the temperature range of this study. The coldest year in the study (2004) exhibited the slowest growth rates in both the ACC and MBW water zones at the 25th, 50th and 75th percentiles. The warmest year in the study (1995), had the fastest growth rates in the 50th ( $0.088 \text{ mm d}^{-1}$ ) and 75th percentiles ( $0.127 \text{ mm d}^{-1}$ ) in the ACC, and followed by the second warmest year (2001) where 50th and 75th percentiles =  $0.058 \text{ mm}$  and  $0.097 \text{ mm d}^{-1}$ , respectively.

No relationship was found between UML average chl *a* concentration and *T. macrura* growth across all

percentiles: 25th ( $R^2 = 0.12$ ,  $p = 0.386$ ), 50th ( $R^2 = 0.117$ ,  $p = 0.405$ ), and 75th ( $R^2 = 0.229$ ,  $p = 0.231$ ) (Fig. 5B). In 1995, the fastest growth rates in both the MBW and ACC water zones was observed in the 50th and 75th percentiles; this year was also the warmest and had the greatest concentration of chl *a*.

Copepod densities were higher in the ACC than in MBW water, with the exception of 1998 in which they were similar and very low in both. No relationship was found between copepod density and *T. macrura* growth in the 25th ( $R^2 = 0.162$ ,  $p = 0.324$ ), 50th ( $R^2 = 0.382$ ,  $p = 0.102$ ) or 75th percentile ( $R^2 = 0.446$ ,  $p = 0.070$ ) (Fig 5C).

## DISCUSSION

We used historical samples to provide the first estimates of the variability of growth rates of *T. macrura* in relation to temperature, chl *a* concentration, and prey availability. We found that shifts in length frequency of *Thysanoessa macrura* between months are large enough to be used to examine the variability of growth rates in relation to both environmental forcing and spatial structure (temperature and salinity) of water masses.

The growth rates reported here are similar to those in other studies using a variety of techniques. For example, Nordhausen (1992) also used repeated sampling to estimate growth and found that *T. macrura* grew 2.3 mm between mid-December and the end of March, increasing from 14.6 mm to 16.9 mm (a growth rate of  $\sim 0.028 \text{ mm d}^{-1}$ ). Our study expands on

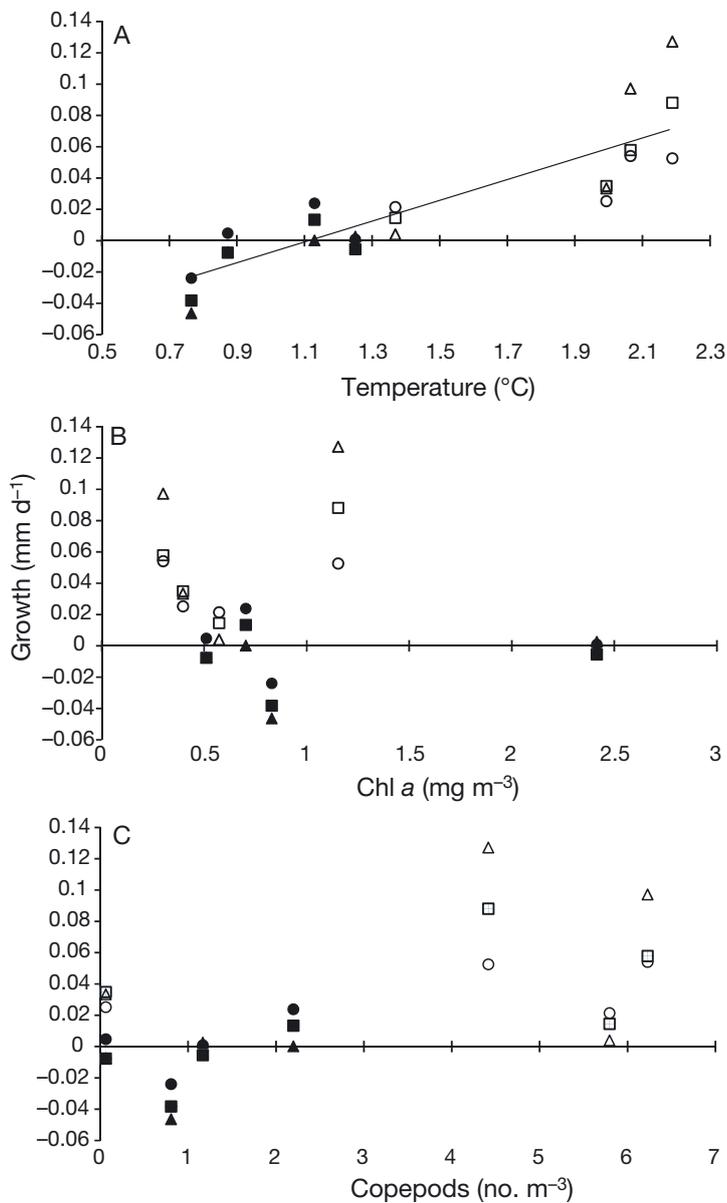


Fig. 5. Daily growth rates ( $\text{mm d}^{-1}$ ) of the 25th (●, ○), 50th (■, □) and 75th (▲, △) percentiles in Mixed Bransfield-Weddell (MBW) water (filled symbols) and Antarctic Circumpolar Current (ACC) water (open symbols) relative to (A) temperature ( $^{\circ}\text{C}$ ), (B) chl *a* concentration ( $\text{mg m}^{-3}$ ), and (C) copepod density ( $\text{no. m}^{-3}$ ). Inverse-variance weighted linear regression line for the 50th percentile is shown for temperature ( $y = 0.0573x - 0.0641$ ,  $r^2 = 0.85$ ). Linear regression lines for the 25th and 75th percentiles were similar, therefore omitted for clarity. Regressions were non-significant for both chl *a* concentration and growth, and copepod density and growth

these results because we were able to document these growth rates over a much shorter sampling interval, and over multiple years and across water zones. Haraldsson & Siegel (2014) estimated the size at age from length frequencies in nonconsecutive years and concluded that *T. macrura* grow from about

11.1 mm to 18–19.5 mm from Year 1 to Year 2, or  $\sim 0.019\text{--}0.023 \text{ mm d}^{-1}$  when averaged over a whole year. This is similar to the growth rates estimated during this study if one assumes growth slows during winter months. The growth rates from our samples collected in ACC water were also comparable to the summer growth rates of the congeneric taxa, *Thysanoessa spinifera* and *Thysanoessa inermis* ( $0.091 \text{ mm d}^{-1}$  and  $0.102 \text{ mm d}^{-1}$ , respectively) in the Bering Sea, a northern high latitude, cold, productive sea (Pinchuk & Hopcroft 2007). In addition, retrospective growth rates determined from preserved samples collected in MBW water were similar to autumn growth rates found for *T. spinifera* ( $-0.025 \text{ mm d}^{-1}$ ) and *T. inermis* ( $0.05 \text{ mm d}^{-1}$ ) (Pinchuk & Hopcroft 2007).

Using archived data we showed that growth rate is strongly related to water temperature. Growth often follows a logistic relationship with temperature in which there are physiological temperature thresholds, above and below which individuals cannot grow (Atkinson et al. 2006). We found a positive linear relationship between growth rate and temperature over the range of temperatures observed in our study. Our results were derived from analysis of samples collected near the lower range of the thermal environment inhabited by *T. macrura* and this may explain the linear temperature response (Nordhausen 1992). *T. macrura* exhibits a broad latitudinal distribution that extends from the high Antarctic to north of the polar front. The northern habitat is several degrees warmer than the waters around the Antarctic Peninsula. The summer temperature of MBW water on the other hand was close to the coldest temperatures that *T. macrura* experiences (the coldest is winter water in the Weddell or Ross Seas). Our estimates of growth were negative at temperatures  $< 1^{\circ}\text{C}$ . There are several possible explanations for this; firstly, the low temperatures in the MBW are near the minimum required for growth in *T. macrura*, so in this case we are not estimating growth but simply characterizing variability. However, Haraldsson & Siegel (2014) were able to estimate positive growth rates for *T. macrura* in the Lazarev Sea ( $60\text{--}70^{\circ}\text{S}$ ,  $\sim 1$  to  $-1.5^{\circ}\text{C}$ ), based on size-at-age data, indicating that *T. macrura* can grow in that region. The negative growth rates that were estimated for the MBW may also reflect limitations of the repeated sampling technique. For example, the difficulty in measuring growth in the MBW suggests

slower growth than in the ACC. And, if growth is very slow then more sampling would be required to resolve the smaller size difference between sampling periods under these circumstances. By grouping stations by water mass, we attempted to capture geographic shifts in water mass properties and increase the homogeneity of each group. Doing so decreased the number of samples lowering the overall ability to resolve small changes in the length frequencies between legs. We likely did not sample from the same swarms between legs but, by sampling with respect to the homogeneous oceanographic properties we likely sampled individuals from the same environmental conditions. Our approach attempted to reduce important and large sources of variability, but other unaccounted for sources of variability could exist and could affect our estimates of growth within the lower temperature water zones. It is still possible that individuals could have been advected into or out of the sampling space affecting the observed February length frequency; however, if the impact was large, the water properties would have also changed substantially. Thus, while there could be some small added variability from mixing or horizontal movement, our results still indicate that *T. macrura* grow slower in the colder water found in the Bransfield Strait where cold Weddell Sea Shelf waters mix.

Growth rates of *T. macrura* varied from  $-0.027$  mm  $d^{-1}$  to  $0.081$  mm  $d^{-1}$  for the 50th percentile. We expected the 25th percentile, which includes the smallest individuals, to be the fastest growing component of the population and the 75th percentile, which includes the largest individuals, to be the slowest growing component of the population. Instead, we found that individuals in the 25th percentile had the slowest overall growth rate and the individuals in the 75th percentile exhibited the most variability, including the fastest ( $0.127$  mm  $d^{-1}$ ) and the slowest ( $-0.04$  mm  $d^{-1}$ ) growth rates measured. It is possible that some years had inadequate sampling to resolve growth for individuals at the tails of the length distribution where abundance was low (i.e. the 25th and 75th percentiles). Haraldsson & Siegel (2014) found evidence of a seasonal vertical migration of *T. macrura* to deeper water that varied by length and sex. They also estimated different growth trajectories for males and females based on their size at age analysis. Together these 2 factors could impact our ability to estimate growth for the entire population if this seasonal ontogenetic migration occurs in our sampling area. We recommend that future studies better resolve size-dependent differences in growth rate and consider the sexes separately.

We have no ability to infer the spatio-temporal importance of size-dependent predation that might influence the growth rates estimated during this study. It is possible that growth rates are artificially high within the ACC relative to the MBW if such predation occurs. If so, then we have overestimated the growth rates in that area. Yet, without information regarding species-specific size-selective predation on *T. macrura*, it is impossible to ascertain the magnitude of such mortality on growth rates.

We found no relationship between growth rates and chl *a* concentration or with an index of prey availability, similarly to the findings of Nordhausen (1992). However, given that *T. macrura* is omnivorous and is thought to prey heavily on zooplankton, it is surprising that there was no correlation with copepod concentration (Vidal 1980). This could be due to the fact that we used a broad measure of potential prey availability in this correlation. Given that the prey preference of *T. macrura* is unknown, our use of total copepods might mask relationships related to its preference for individual copepod species. Unfortunately, copepods were not consistently identified to species level throughout the study period. Similarly, it is possible the naupliar or copepodid stages are preferred prey items, and the lack of enumeration of these stages could undermine our ability to find strong relationships. In addition, zooplankton prey respond to their environment independently of interactions with *T. macrura*, and it is possible that other factors could be influencing their dynamics as well. For example, the abundance of copepods was extremely low in 1998, and this could further confound any relationships with growth if both temperature and prey were responsible for growth of *T. macrura*.

Our findings contrast with the other abundant and better studied Antarctic euphausiid *E. superba*, which has strong relationships with both chl *a* concentration and sea surface temperature (Atkinson et al. 2006, Wiedenmann et al. 2008, Shelton et al. 2013). The difference between these species has important implications for the relative success of *T. macrura* versus *E. superba* as the region continues to warm (Anisimov et al. 2007) and the pelagic ecosystem changes (Montes-Hugo et al. 2009). Recent modelling studies have predicted that some areas of the Southern Ocean may become less favorable for Antarctic krill under predicted changes in temperature, but may benefit in areas where primary production increases (Hill et al. 2013). In those climate simulations, suitable krill habitat will decline significantly, potentially opening up large areas of the pelagic environment to more opportunistic and flexible species such as *T. macrura*.

Using repeated sampling allowed us to resolve significant differences in *T. macrura* growth rates in different water masses across a spatial scale of 10's of km. Nicol (2000) noted the lack of understanding of the relationship between *E. superba* growth rates and water masses, and suggested that this information would be critical to understanding its ecology, as well as the ecology of other euphausiids. In this study, we used *in situ* measurements of water properties to partition our sampling space allowing for finer resolution of both inter-annual and spatial variations in growth rate and their potential drivers: water temperature, primary production, and prey abundance. Using geographical variation in environmental conditions to represent different combinations of physical and biological drivers of growth, we may be able to gain a better understanding of how aspects of climate change, like trends in water temperature, primary production and trophic shifts may affect growth and population dynamics of this relatively less studied species. Given the possible vertical separation of the species suggested by Haraldsson & Siegel (2014), it may be beneficial to group samples by their respective environments both in horizontal and vertical space.

The Antarctic Peninsula region is predicted to continue to exhibit dramatic changes in its climate, including increased sea surface temperature (Anisimov et al. 2007) and decreases in winter sea ice extent and duration (Stammerjohn et al. 2008). Coupled with these physical changes, primary production, phytoplankton community structure and water column biogeochemical process are likely to continue to change potentially opening up habitat for other species (Hewes et al. 2009, Montes-Hugo et al. 2009, Loeb and Santora 2012). Stenothermic organisms whose energy demands are tightly coupled to the spring bloom, such as *E. superba*, are likely to be directly impacted by climate change (Atkinson et al. 2004). Omnivorous species that have a relatively broad latitudinal distribution, such as *T. macrura* (Nordhausen 1992, Haraldsson & Siegel 2014), will likely have more complex responses to climate change. Although our data suggest that *T. macrura* will maintain or increase its growth rate over the predicted temperature increases, it is unclear what the population level response of *T. macrura* will be given the variability in ecosystems around Antarctica. Predicting the response of *T. macrura* and other taxa under different scenarios of climate change will require additional data on this and other poorly studied species' basic life history parameters, including differences in growth by sex, size at age and spawning regime.

**Acknowledgements.** This work represents part of a Master of Science thesis by the senior author. RMD thanks NOAA and SDSU for the financial support for the completion of this work. The authors thank the US AMLR Program, the crew and scientists, especially the zooplankton technicians, for their hard work collecting the years of quality data needed for this study. A special thanks to Dr. Valerie Loeb for her guidance and work in the field and to Rachel Pound for all her hours in the lab.

#### LITERATURE CITED

- Aitchison J (1955) On the distribution of a positive random variable having a discrete probability mass as the origin. *J Am Stat Assoc* 50:901–908
- Amos AF (2001) A decade of oceanographic variability in summertime near Elephant Island, Antarctica. *J Geophys Res* 106:401–423
- Anisimov OA, Vaughan DG, Callaghan TV, Furgal C and others (2007) Polar regions (Arctic and Antarctic). In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, p 653–685
- Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Atkinson A, Shreeve S, Hirst A, Rothery P, and others (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
- Atkinson A, Siegel V, Pakhomov EA, Jessopp MJ, Loeb V (2009) A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep-Sea Res I* 56:727–740
- Buchholz F (1991) Moulting cycle and growth of Antarctic krill *Euphausia superba* in the laboratory. *Mar Ecol Prog Ser* 69:217–229
- Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177: 115–131
- De la Mare W (1994) Estimating krill recruitment and its variability. *CCAMLR Science* 1:55–69
- Falk-Petersen S, Sargent JR, Lonne OJ, Timofeev S (1999) Functional biodiversity of lipids in Antarctic zooplankton: *Calanoides acutus*, *Calanus propinquus*, *Thysanoessa macrura* and *Euphausia crystallorophias*. *Polar Biol* 21:37–47
- Färber-Lorda J (1994) Length-weight relationships and coefficient of condition of *Euphausia superba* and *Thysanoessa macrura* (Crustacea: Euphausiacea) in southwest Indian Ocean during summer. *Mar Biol* 118:645–650
- Hagen W, Kattner W (1998) Lipid metabolism of the Antarctic Euphausiids *Thysanoessa macrura* and its ecological implications. *Limnol Oceanogr* 43:1894–1901
- Haraldsson M, Siegel V (2014) Seasonal distribution and life history of *Thysanoessa macrura* (Euphausiacea, Crustacea) in high latitude waters of the Lazarev Sea, Antarctica. *Mar Ecol Prog Ser* 495:105–118
- Helmuth B, Kingsolver JG, Carrington E (2005) Biophysics, physiological ecology, and climate change: Does mecha-

- nism matter? *Annu Rev Physiol* 67:177–201
- Hewes CD, Reiss CS, Holm-Hansen O (2009) A quantitative analysis of sources for summertime phytoplankton variability over 18 years in the South Shetland Islands (Antarctica) region. *Deep-Sea Res I* 56:1230–1241
  - Hill SL, Phillips T, Atkinson A (2013) Potential climate change effects on the habitats of Antarctic Krill in the Weddell quadrant of the Southern Ocean. *PLoS ONE* 8: e722246
  - Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. *ICES J Mar Sci* 30:3–15
  - Holm-Hansen O, Hewes CD, Villafañe VE, Helbling EW, Silva N, Amos T (1997) Distribution of phytoplankton in relation to different water masses in the area around Elephant Island, Antarctica. *Polar Biol* 18:145–153
  - Huntley M, Boyd C (1984) Food-limited growth of marine zooplankton. *Am Nat* 124:455–478
  - Ikeda T (1985) Life history of Antarctic krill *Euphausia superba*: A new look from an experimental approach. *Bull Mar Sci* 37:599–608
  - Ji R, Edwards M, Mackas DL, Runge JA, Thomas AC (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J Plankton Res* 32:1355–1368
  - Kock KH, Barrera-Oro E, Belchier M, Collins MA and others (2012) The role of fish as predators of Krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. *CCAMLR Science* 19:115–169
  - Lipsky JD (ed) (2004) AMLR 2003/2004 Field Season Report. NOAA Tech Memo NOAA-TM-NMFS-SWFSC-367. p 53–116
  - Loeb VJ, Santora JA (2012) Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: growth rates and interannual variations in reproductive activity (1993–2009). *Prog Oceanogr* 96:93–107
  - Marr JWS (1962) The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discov Rep* 32: 33–464
  - Mauchline J (1980) Measurement of body length of *Euphausia superba*. Dana. *BIOMASS Handbook* ser 11
  - McLaren IA (1978) Generation lengths of some temperate marine copepods—estimation, prediction, and implications. *J Fish Res Board Can* 35:1330–1342
  - Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. *Science* 323:1470–1473
  - Nemoto T, Nasu K (1958) *Thysanoessa macrura* as a food of baleen whales in the Antarctic. *Scientific Reports of the Whales Research Institute* 13:193–199
  - Nicol S (2000) Understanding krill growth and aging: the contribution of experimental studies. *Can J Fish Aquat Sci* 57:168–177
  - Nordhausen W (1992) Distribution and growth of larval and adult *Thysanoessa macrura* (Euphausiacea) in the Bransfield Strait Region, Antarctica. *Mar Ecol Prog Ser* 83: 185–196
  - Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637–639
  - Pinchuk AI, Hopcroft RR (2007) Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from northern Gulf of Alaska. *Mar Biol* 151:257–269
  - Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. *Am Zool* 31:49–63
  - Runge J (1980) Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnol Oceanogr* 25: 134–145
  - Shaw CT, Peterson WT, Feinberg LR (2010) Growth of *Euphausia pacifica* in the upwelling zone off the Oregon Coast. *Deep-Sea Res II* 57:584–593
  - Shelton AO, Kinzey D, Reiss C, Munch S, Watters G, Mangel M (2013) Among-year variation in growth of Antarctic krill *Euphausia superba* based on length-frequency data. *Mar Ecol Prog Ser* 481:53–67
  - Siegel VS (1987) Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Mar Biol* 96:483–495
  - Siegel VS (2000) Krill (Euphausiacea) life history and aspects of population dynamics. *Can J Fish Aquat Sci* 57: 130–150
  - Smiles M, Pearcy W (1971) Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *Fish Bull* 69: 79–86
  - Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *J Geophys Res Oceans* 113, C03S90, doi:10.1029/2007JC004269
  - Vidal J (1980) Physioecology of zooplankton. 1. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 56:111–134
  - Wiedenmann J, Cresswell K, Mangel M (2008) Temperature-dependent growth of Antarctic krill: predictions for a changing climate from a cohort model. *Mar Ecol Prog Ser* 358:191–202

Editorial responsibility: Edward Durbin,  
Narragansett, Rhode Island, USA

Submitted: June 25, 2013; Accepted: March 19, 2015  
Proofs received from author(s): May 29, 2015