

## Original Article

# The contribution of ice algae to the winter energy budget of juvenile Antarctic krill in years with contrasting sea ice conditions

Kim S. Bernard<sup>1\*</sup>, Lacey A. Gunther<sup>1</sup>, Sean H. Mahaffey <sup>1</sup>, Katelyn M. Qualls<sup>1</sup>, Monisha Sugla<sup>1</sup>, Benjamin T. Saenz<sup>2</sup>, Anthony M. Cossio<sup>3</sup>, Jennifer Walsh<sup>3</sup>, and Christian S. Reiss<sup>3</sup>

<sup>1</sup>College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, 104 CEOAS Admin Bldg., Corvallis, OR 97330, USA

<sup>2</sup>Resource Management Associates, 1756 Picasso Avenue, Suite G, Davis, CA 95618, USA

<sup>3</sup>National Oceanic and Atmospheric Administration, Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA

\*Corresponding author: tel: +1 541 737 9337; e-mail: [kbernard@coas.oregonstate.edu](mailto:kbernard@coas.oregonstate.edu)

Bernard, K. S., Gunther, L. A., Mahaffey, S. H., Qualls, K. M., Sugla, M., Saenz, B. T., Cossio, A. M., Walsh, J., and Reiss, C. S. The contribution of ice algae to the winter energy budget of juvenile Antarctic krill in years with contrasting sea ice conditions. – ICES Journal of Marine Science, 76: 206–216.

Received 5 January 2018; revised 2 July 2018; accepted 4 September 2018; advance access publication 18 October 2018.

Krill overwintering strategies vary with ontogeny and year; understanding this variability is essential to predicting how the species will respond to climate change in the future. Overwintering studies have focused on larval and adult krill, but we know little about how juvenile krill overwinter. The late winter diet of juvenile krill is important because it will determine their growth and development rates and consequently their reproductive potential the following spring. A diet rich in ice algae would promote growth and reproductive development. The Bransfield Strait (northern Antarctic Peninsula, AP) is an important overwintering ground for krill; it has been proposed this region offers a food-rich winter environment. We examined the contribution of ice algae to the energy budget of overwintering juvenile krill during 2 years with contrasting sea ice conditions. Grazing on ice algae contributed ~146% to their winter energy budget in 2015, even though ice concentrations were ≤50% and consisted of newly formed pancake ice. However, when sea ice advanced late in the Bransfield Strait (2016), ice algae contributed significantly less (~16%) to the winter energy budget of juvenile krill. Delayed sea ice advance may negatively affect growth and reproductive development of overwintering juvenile krill.

**Keywords:** Antarctic krill, Antarctic Peninsula, energy budget, euphausiids, grazing, ice algae, overwintering, sea ice

## Introduction

Antarctic krill, *Euphausia superba* (hereafter “krill”), serves as a key species in the Southern Ocean supporting vast numbers of predators, including whales, seals, seabirds, penguins, and fishes (Laws, 1977; Reid, 1995; Pakhomov *et al.*, 1996; Wienecke *et al.*, 2000; Murase *et al.*, 2002; Thiele *et al.*, 2004; Nicol *et al.*, 2008).

Winter is a critical, but under-studied, season for krill. The need to understand how krill are adapted for the Antarctic winter is underscored by the fact that this season is the most susceptible to the impacts of climate change (Flores *et al.*, 2012b).

There are ontogenetic differences in krill physiology that determine their strategies for overwintering, and understanding how

---

Bernard, K. S., Gunther, L. A., Mahaffey, S. H., Qualls, K. M., Sugla, M., Saenz, B. T., Cossio, A. M., Walsh, J., and Reiss, C. S. 2018. The contribution of ice algae to the winter energy budget of juvenile Antarctic krill in years with contrasting sea ice conditions. – ICES Journal of Marine Science.

each stage of the krill life cycle responds to variable winter conditions is crucial to interpreting krill population dynamics (Meyer and Teschke, 2016). The majority of research on krill overwintering has been conducted on larval krill and adults. Overwinter survival of larvae is one of the key factors contributing to the success of the krill population (Quetin and Ross, 2003). Larval krill must continue to feed throughout the winter, or they will not survive and recruit to the population the following spring (Meyer and Teschke, 2016; Ryabov *et al.*, 2017).

Adult krill suppress their metabolism (Meyer, 2012) and undergo a reproductive resting period during autumn and winter (Cuzin-Roudy, 2000; Ross and Quetin, 2000), in which mature females and males regress to their respective immature forms (Poleck and Denys, 1982). During this time, it has been suggested they survive on lipid reserves built up during the summer and autumn (Meyer and Teschke, 2016). Towards the end of winter, sexual development is re-initiated in preparation for the spring–summer reproductive season (Denys and McWhinnie, 1982; Poleck and Denys, 1982). However, winter conditions may determine the timing of adult reproductive development and spawning in the spring because sexual re-maturation is controlled largely by winter food availability (Kawaguchi *et al.*, 2007; Kawaguchi, 2016).

It is less certain precisely where juvenile krill, specifically Age Class 1 (AC1, 1-year old), fit on this spectrum, but it is likely they adopt a mix of both larval and adult overwintering strategies (Atkinson *et al.*, 2002). Understanding how AC1 krill overwinter is important because female krill become sexually mature as early as in their second year, i.e. Age Class 2 (AC2; Siegel and Loeb, 1994), and their diet as AC1 krill towards the end of winter and early spring may determine their growth rates (Schmidt *et al.*, 2014) and consequently their size and maturity at the onset of their second year. Since fecundity in krill increases allometrically with body size (Ross and Quetin, 1983; Cuzin-Roudy, 2000) larger AC2 females would produce more eggs in their first reproductive season.

Growth and development in krill exert a high demand for polyunsaturated fatty acids (PUFA) (Pond *et al.*, 2005), which krill obtain by feeding on diatoms (Schmidt *et al.*, 2014) or heterotrophic dinoflagellates (Tang and Taal, 2005; Schmidt *et al.*, 2006). Thus, a diet rich in diatoms and/or heterotrophic dinoflagellates would promote growth and development in juvenile krill and could be important towards the end of winter. Indeed, delayed development of juvenile krill has been observed in the winter pack-ice zone of the Lazarev Sea and has been attributed to a lack of PUFA and a diet dominated by copepods (Schmidt *et al.*, 2014).

### The Bransfield Strait, an important overwintering ground

The Bransfield Strait, at the northern AP, is considered to be an important overwintering ground for krill (Schmidt *et al.*, 2014). Reiss *et al.* (2017) found that krill biomass (determined from net catches) and density (determined from acoustic estimates) were an order of magnitude higher in the Bransfield Strait during winter than they were during summer, suggesting that krill actively move into the region to overwinter. Interestingly, this pattern occurred irrespective of the presence of sea ice in the region (Reiss *et al.*, 2017), and was an important region for juveniles and adults alike (Reiss, unpublished data).

Krill in the Bransfield Strait continue feeding throughout the winter (Huntley *et al.*, 1994; Schmidt *et al.*, 2014). The reasons for this are likely due to the elevated food supply in the Bransfield Strait compared to, for instance, the Lazarev Sea (Schmidt *et al.*, 2014). The Bransfield Strait has a relatively short sea ice season, and consequently, significant primary production will persist even into July (Arrigo *et al.*, 2008), potentially providing phytoplankton for grazing krill in the late autumn and early winter (Schmidt *et al.*, 2014). Although sea ice formation occurs later in this region than it does in other regions, like the Lazarev Sea, day length is comparatively long, due to the lower latitude. Therefore, ice algae biomass may still accumulate, providing overwintering krill with an alternate source of autotrophic food (Fritsen *et al.*, 2011).

Krill in the Bransfield Strait may also be feeding on detritus and heterotrophic prey during the winter. The majority of the Bransfield Strait is a shallow shelf (~100 to 300 m) and has a relatively high benthic biomass, even during the winter (Smith *et al.*, 2012). Krill from shelf regions along the northern AP have been recorded at the seafloor, and it is likely benthic detritus or benthic diatoms are additional food sources to those krill overwintering there (Schmidt *et al.*, 2011; Cleary *et al.*, 2016). In addition, although many Antarctic copepod species spend the winter at depth in diapause, there are several species that continue to feed in the upper ocean during autumn and winter, including *Metridia gerlachei* and *Calanus propinquus* (Ashjian *et al.*, 2008). Both species are known prey items for krill (Price *et al.*, 1988; Atkinson and Snjyder, 1997; Atkinson *et al.*, 1999; Meyer, 2012; Schmidt *et al.*, 2014).

Our knowledge of the winter diet specifically of juvenile krill is limited. However, several recent studies have shown that sea ice algae and ice-associated biota are important food sources for juvenile krill overwintering in the northern Weddell Sea (Kohlbach *et al.*, 2017; Schaafsma *et al.*, 2017) and in the waters off East Antarctica (Jia *et al.*, 2016). It is possible, therefore, that AC1 krill in the northern AP and, specifically the Bransfield Strait where they are primarily concentrated, might also be feeding on ice-associated prey.

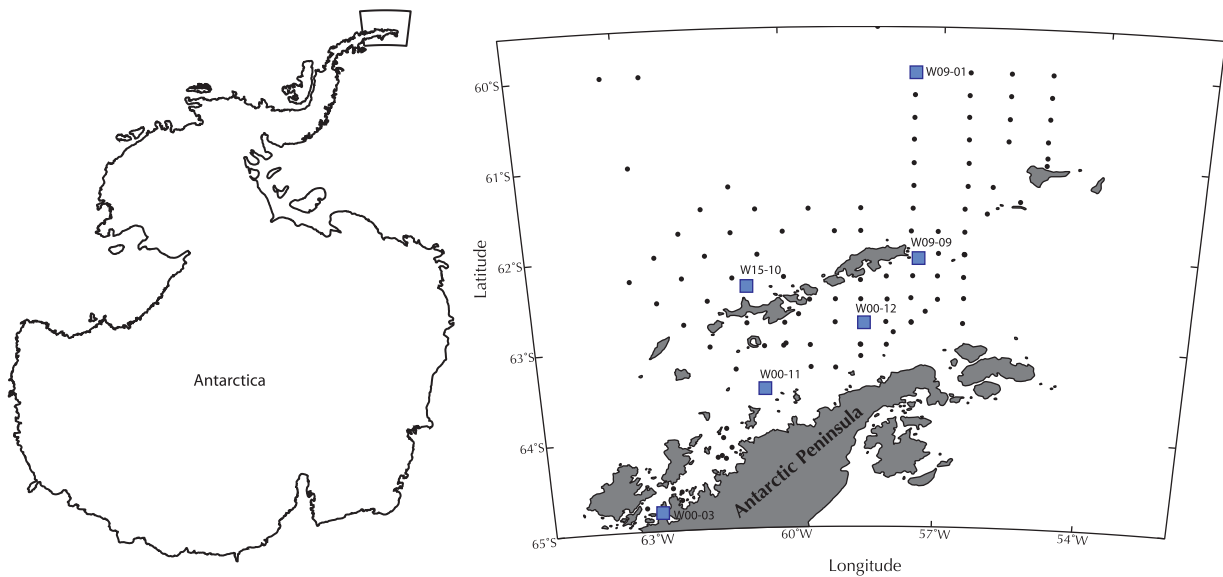
### Warming in the northern AP

Long-term warming at the northern AP (Vaughan *et al.*, 2003) has resulted in a decline in sea ice extent and duration (Stammerjohn *et al.*, 2008), and delayed pack ice formation has resulted in reduced sea ice algae biomass (Fritsen *et al.*, 2008; Smith *et al.*, 2008; Fritsen *et al.*, 2011; Lowe *et al.*, 2012). If ice-associated biota are also an important food source for AC1 krill overwintering in the northern AP, then the changes in sea ice duration and extent that have occurred in the region may have ramifications for the success of the krill population. Here, we focus specifically on the role of ice algae in the winter energy budget of AC1 krill in the northern AP, comparing them to AC2 and older (i.e. AC2+) krill for reference. We compare our findings between 2 years with contrasting sea ice conditions and, correspondingly, differing ice algae availability.

## Methods

### Study area

Our study was conducted in August 2015 and 2016, during the 4th and 5th US Antarctic Marine Living Resources (AMLR) Program's winter surveys on board the R.V.I.B. *Nathaniel B.*



**Figure 1.** Map of the Antarctic Peninsula showing station locations (filled circles) sampled during August 2015 and 2016 where krill were collected for grazing rate measurements. Stations marked with a square identify those where krill were collected for respiration rate experiments (station names are also provided for these).

Palmer to the northern sector of the Antarctic Peninsula (Figure 1).

### Sea ice and model-derived ice algae biomass and productivity

We used the Sea Ice Ecosystem State (SIESTA) model (Saenz and Arrigo, 2012, 2014) to estimate sea ice algal biomass and productivity in our study region for August 2015 and 2016 (see Supplementary Materials). We allowed the SIESTA simulation to spin up for approximately 1 year, with simulation beginning near the sea ice minimum in March 2014 and ending at the end of August 2016. Outputs of the SIESTA model include sea ice area, sea ice thickness, snow thickness, light limitation, and ice algae production ( $\text{g C m}^{-2} \text{ day}^{-1}$ ) and biomass ( $\text{g C m}^{-2}$ ) for the bottom 20 cm of the sea ice.

### Collection of krill

Krill were collected at each station using a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) with a  $2.54 \text{ m}^2$  mouth area and  $505 \mu\text{m}$  mesh net. Tows were conducted obliquely through the water column to a maximum depth of 170 m, or 10 m above the seafloor. Net depth was monitored in real time using a pressure sensor mounted to the bridle of the IKMT. A calibrated General Oceanics flow meter (model 2030R), mounted to the depressor frame at the front of the net, was used to measure the volume of seawater filtered during each tow. The IKMT catches were processed on board immediately following each tow.

### Length, dry mass, and elemental composition

A subset of 136 krill (from 12 stations) collected during the survey in 2016 was used for measurements of length (L, mm) and dry weight (DW, mg). Of this, 37 krill (from 4 stations) were used for additional measurements of carbon (C, mg) content (body carbon, or BC). We used Standard Length 1 (SL1) (Mauchline, 1980) for length measurements; krill were measured

from the anterior tip of the rostrum to the posterior tip of the uropods, excluding the terminal setae. Measured individuals were then placed in pre-weighed tin boats in an oven at  $60^\circ\text{C}$  for 48 h, after which tin boats and krill were re-weighed and krill DW was determined. Weight percent organic carbon contents were determined by high-temperature combustion in a Thermo Quest EA2500 Elemental Analyzer, following the procedure of Goñi et al. (2005).

An exponential model described the relationship between DW and L (Supplementary Table S2, Figure S1a). A linear regression model described the relationship between BC and DW (Supplementary Table S2, Figure S1b). L–DW and DW–BC regressions were used in subsequent analyses.

### Respiration rate experiments

Krill used for respiration rate experiments were collected at five stations occupied at the northern AP in August 2016 (Figure 1). Once on deck, the catch was quickly placed into buckets of seawater and healthy, actively swimming krill were selected for respiration rate experiments (see Supplementary Materials). At the end of each experiment, krill lengths and DW were determined as described above.

Individual respiration rates ( $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ ) were calculated as the product of the slope of the linear regression of oxygen concentration over time and experimental container volume in liters. We used an  $R^2$  value  $>0.9$  as our cut-off for subsequent analysis. In total, seven individual experimental samples were excluded on this basis. Individual respiration rates were also converted to DW-standardized respiration rates [ $\mu\text{l O}_2 (\text{mg DW}^{-1}) \text{ h}^{-1}$ ] for each krill. Linear regressions were used to model the relationship between krill DW and individual respiration rates.

### Individual ingestion rates

Individual ingestion rates (here we refer only to ingestion of autotrophs) were estimated for a total of 676 krill collected at 35

stations in 2015 and 31 stations in 2016. Ingestion rates were determined using the gut fluorescence technique (Båmstedt *et al.*, 2000), adapted as in Conover *et al.* (1986) and Durbin and Campbell (2007). Individual daily ingestion rates ( $I$ , ng Chl-*a* ind.<sup>-1</sup> day<sup>-1</sup>) were calculated as the product of instantaneous gut pigment content ( $G$ , ng Chl-*a* ind.<sup>-1</sup>) integrated over a 24-h period and gut evacuation rate ( $k$ , h<sup>-1</sup>). Background fluorescence, measured from animals starved for at least 24 h in 0.2 µm filtered seawater, was negligible. A detailed description of ingestion rate measurements is provided in the [Supplementary Materials](#).

Individual ingestion rates were standardized by DW [ $\mu\text{g Chl}$  (mg DW)<sup>-1</sup> day<sup>-1</sup>], and we converted daily individual ingestion rates to carbon equivalents [ $\mu\text{g C}$  (mg DW)<sup>-1</sup> day<sup>-1</sup>] using a C:Chl-*a* ratio of 50 (Vernet *et al.*, 2012).

### Daily ration

Individual krill for which gut pigments had been measured were first converted to DW (mg) by applying our L–DW regression equations ([Supplementary Table S2](#)). We then determined BC (mg) by applying our DW–BC regression equations ([Supplementary Table S2](#)). Daily rations (DR, %) were calculated as carbon consumed as a percent of BC.

### Contribution of algae to the winter energy budget of krill

We calculated the contribution of an algal diet to the energy budget for each krill that we measured ingestion rates on. First, we estimated individual daily respiration rates. Next, we estimated individual energy requirements from food by calculating total minimum energy requirements minus energy available from lipid and protein stores. Finally, we calculated the percent of energy required from food that was met by grazing. A detailed description of these steps is provided in the [Supplementary Materials](#).

### Statistical analysis

We grouped krill into two stage/size categories: 20–30 mm (AC1) and >30 mm (AC2+). Since we collected few krill at stations occupied during daylight hours we chose to only use samples collected during the night and twilight hours. All data were log-transformed prior to analysis to achieve normal distribution and homogeneity of variance. We used two-way ANOVAs to compare standardized ingestion rates, daily rations, and algal contribution to energy budget between stage/size (AC1 and AC2+) and year (2015 and 2016).

## Results

### Sea ice and model-derived ice algae productivity and biomass

Satellite-based estimates of sea ice concentrations for 2015 show that sea ice appeared in the study region in June, gradually increasing to its peak in early August ([Figure 2](#) and [Supplementary Figure S3](#)). In all months examined, however, sea ice concentrations were low in our study region ([Figure 2](#)), suggesting the presence of sparse pancake ice rather than well-developed pack ice. Although sea ice was present in the study region from June 2015, ice algae production and biomass remained low until late July–early August, when values increased rapidly to approximately 1.5 mg C m<sup>-2</sup> day<sup>-1</sup> and over 10 mg C m<sup>-2</sup> respectively, remaining

relatively stable in our study region throughout August ([Figure 3](#) and [Supplementary Figure S3](#)).

Satellite-based estimation of sea ice concentrations in 2016, on the other hand, showed that sea ice was largely absent from our study region during May through July ([Figure 2](#) and [Supplementary Figure S3](#)), only increasing above 5 000 km<sup>2</sup> at the end of August ([Supplementary Figure S3](#)). For much of August 2016, model-derived ice algae biomass for the bottom 20 cm remained below 5 mg C m<sup>-2</sup> but increased up to 11 mg C m<sup>-2</sup> on by the end of the month ([Figure 3](#) and [Supplementary Figure S3](#)). Model-derived ice algae production remained <1 mg C m<sup>-2</sup> day<sup>-1</sup> for most of August 2016 but increased rapidly towards the end of the month to >2 mg C m<sup>-2</sup> day<sup>-1</sup> ([Supplementary Figure S3](#)).

### Individual respiration rates

As would be expected, individual respiration rates increased with body size from 13.9 µl O<sub>2</sub> ind.<sup>-1</sup> h<sup>-1</sup> for an individual weighing 17.6 mg DW (~25 mm length) to 133.1 µl O<sub>2</sub> ind.<sup>-1</sup> h<sup>-1</sup> for an individual weighing 291.2 mg DW (~53 mm length) ([Figure 4](#)).

### Diel gut pigment, gut evacuation rates, and ingestion rates

Gut pigment content of both AC1 and AC2+ krill varied significantly over the diel cycle ( $p \ll 0.001$ , one-way ANOVA), with greatest values occurring at night between 21:00 and 09:00 ([Supplementary Figure S4](#)). Gut evacuation rates ( $k$ , h<sup>-1</sup>) varied from 0.2 h<sup>-1</sup> for AC2+ krill to 0.5 h<sup>-1</sup> for AC1 krill ([Supplementary Figure S5](#)). Mean mass-specific daily ingestion rates were low, ranging between <0.001 and 0.62 µg Chl (mg DW)<sup>-1</sup> day<sup>-1</sup> for AC1 krill and <0.001 and 0.08 µg Chl (mg DW)<sup>-1</sup> day<sup>-1</sup> for AC2+ krill. Mean daily mass-specific ingestion rates of AC1 krill were significantly higher than for AC2+ krill in both 2015 and 2016 during our surveys ([Figure 5a](#), [Table 1](#)). Highest mean daily ingestion rates were recorded in 2015 ([Figure 5a](#), [Table 1](#)).

### Daily rations

Mean daily rations ranged from 0.002 to 7.6% for AC1 krill, and <0.001 to 0.8% for AC2+ krill. Daily rations were significantly higher in 2015 than in 2016 for both AC1 and AC2+ krill ([Figure 5b](#), [Table 1](#)). In both years, daily rations were significantly higher for AC1 krill than for AC2+ krill ([Figure 5b](#), [Table 1](#)).

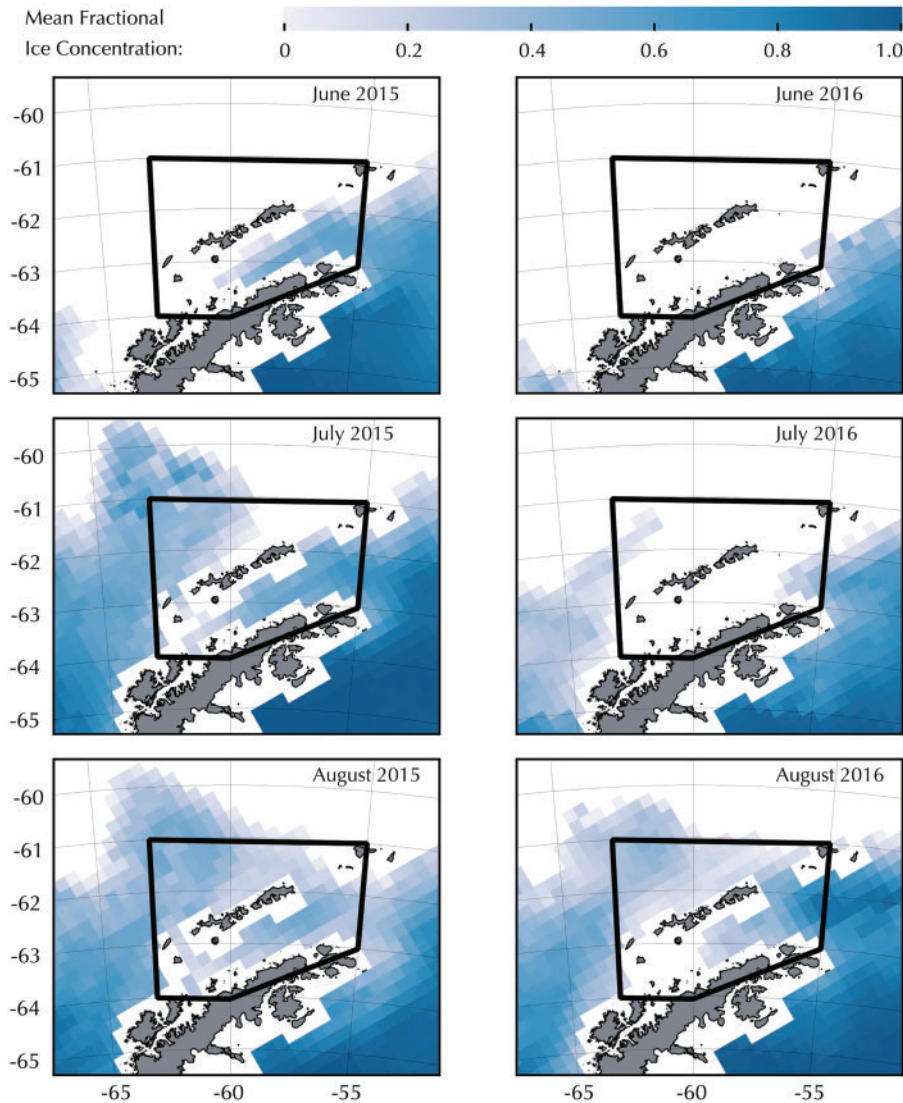
### Contribution of algae to the winter energy budget of krill

Overall, algal contribution to the energy budget of all krill surveyed was significantly higher in 2015 than in 2016 ([Figure 5c](#), [Table 1](#)). In 2015, grazing on algae contributed an average of 146% to the minimum required energy intake for AC1 krill (range: 3.6–1 067%; [Figure 5c](#), [Table 1](#)). This was significantly more than the mean (mean = 12%) measured for AC2+ krill the same year (range: 0.3–131%). In 2016, feeding on algae contributed a mean of only 16% to the energy budget of AC1 krill (range: 0.4–42%), and significantly less (mean = 1%; range: 0.1–3.2%) to AC2+ krill ([Figure 5c](#), [Table 1](#)).

## Discussion

Antarctic krill is an abundant and successful Southern Ocean species that plays an important role linking lower trophic levels to





**Figure 2.** Mean satellite-derived fractional ice concentration for June–August 2015 (left panel) and 2016 (right panel). The black box represents our study area.

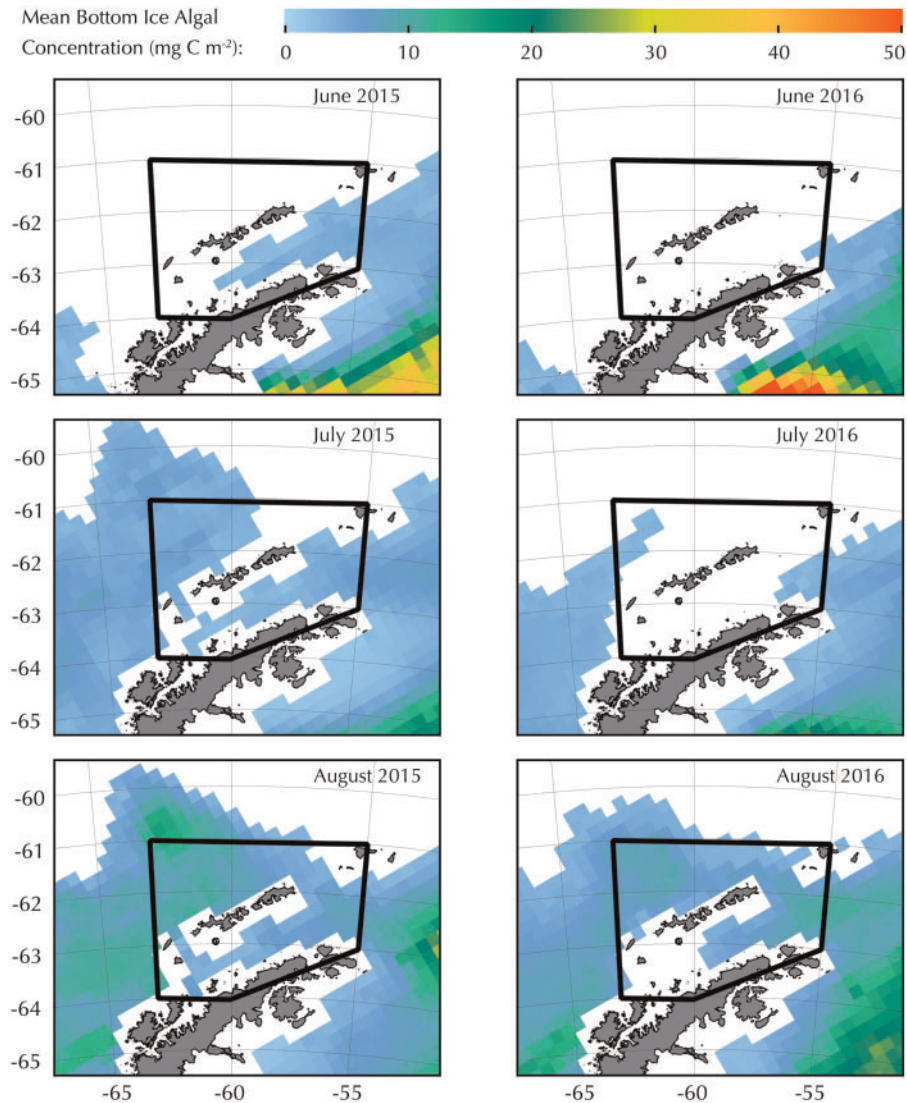
top predators. The success of krill can be attributed in part to their flexible nature, particularly with respect to the variety of strategies used to survive the typically food-poor winter. Krill occupy a wide range of habitat types around Antarctica, requiring specialized approaches to overwintering. While certain regions are considered to be more favourable to overwintering than others, the reasons for this are not yet fully understood. Our study, conducted at the northern AP, explores the contribution of ice algae to the winter energy budget of AC1 krill during 2 years with contrasting sea ice conditions.

### Sea ice and model-derived ice algae production and biomass

By late May 2015, sea ice had begun to appear in our study area. By mid-June 2015, sea ice area had increased to  $\sim 15\,000\text{ km}^2$ , continuing to increase to a maximum of  $\sim 50\,000\text{ km}^2$  in early August 2015. In contrast, sea ice was largely absent from our

study area in June 2016, with ice moving in and out of the region during July and early August. By mid–late August 2016, sea ice area increased rapidly to  $>25\,000\text{ km}^2$ , mostly because of advection from the Powell Basin and Weddell Sea to the east of the AP. Although sea ice conditions appear to be more favourable in 2015 than those in 2016, sea ice extent was relatively low, compared to previous years (Reiss *et al.*, 2017). Furthermore, sea ice concentrations in the Bransfield Strait (where the majority of krill were collected) never exceeded 50% in August in either year. This suggests that the majority of sea ice in our study region consisted of newly formed pancake ice, rather than well-developed pack ice. This concurs with visual observations of sea ice made during our surveys.

Model-derived winter ice algae biomass and productivity varied between 2015 and 2016. The earlier formation of sea ice in 2015 is likely responsible for the establishment of a more productive ice algae community, although biomass remained low until early August when increased day length promoted growth of the



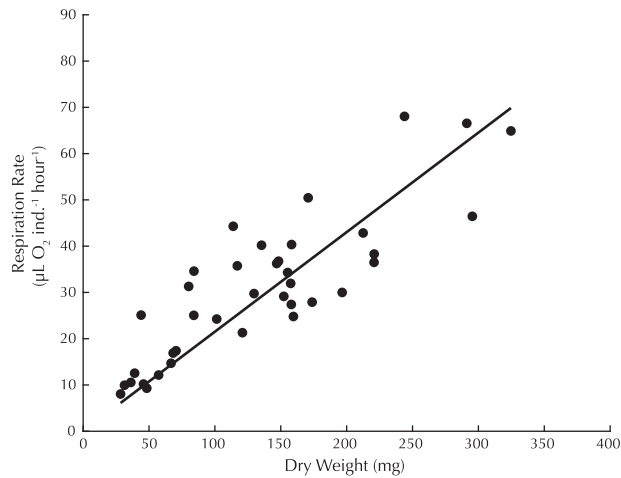
**Figure 3.** Mean model-derived ice algae concentration ( $\text{mg C m}^{-2}$ ) in the bottom 20 cm of the sea ice for June–August of 2015 (left panel) and 2016 (right panel). The black box represents our study area.

algae. In contrast, ice algae productivity and biomass remained low throughout the winter of 2016 in response to delayed sea ice formation. By mid-August 2016, ice algae biomass and productivity increased rapidly when sea ice with high algal biomass moved into the area from the Weddell Sea.

While the model-derived mean ice algae biomass and productivity in our study area were several orders of magnitude lower than ice algae are capable of achieving in sea ice (Arrigo, 2017), it does represent a concentrated food source relative to the water column. Furthermore, there is reason to suspect that the model estimations may be biased towards producing low values. The passive microwave sea ice detection algorithms used to generate sea ice concentrations that are then used by the SIESTA model to predict ice algae biomass and productivity are less reliable at low ice concentrations, and warmer temperatures (Comiso and Steffen, 2001). Furthermore, the relatively low spatial resolution ( $25 \text{ km}^2$ ) of the passive microwave sea ice grid causes a large fraction of the study area to be masked from analysis due to the proximity of land (i.e. coastline and islands).

### Grazing on ice algae by AC1 krill

Grazing on autotrophic material was an important part of the diet of AC1 krill, but not for AC2+ individuals. The gut fluorescence technique does not differentiate between phytoplankton and ice algae; however, we reason, below, that grazing by AC1 krill during both years was primarily on ice algae. Using daily rations of AC1 krill and the regression equation presented by Atkinson *et al.* (2002) for the relationship between daily ration and food concentration, we back-calculated the potential food concentrations on which AC1 krill would have been feeding in both years. We predict that for daily rations of AC1 krill observed in 2015, potential autotrophic food concentrations would have been extremely high,  $\sim 395 \text{ mg C m}^{-3}$ . This is two orders of magnitude more than the average available phytoplankton biomass recorded during our 2015 survey ( $5.0 \text{ mg C m}^{-3}$ ; see Supplementary Table S7). Even for the extremely low daily rations recorded in August 2016, predicted food concentrations ( $45 \text{ mg C m}^{-3}$ ) were an order of magnitude higher than the



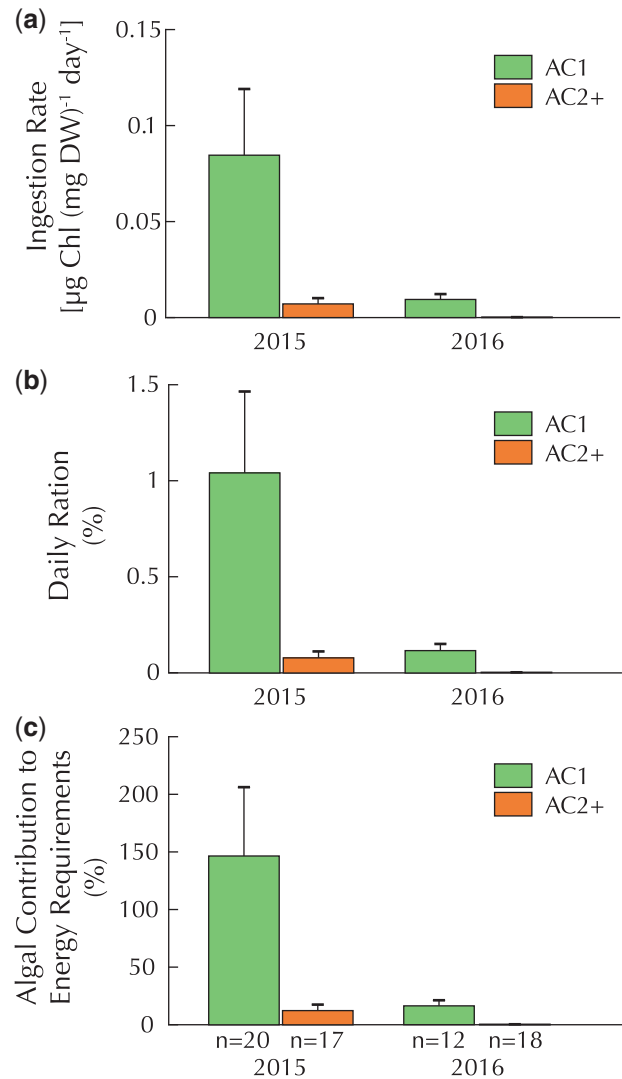
**Figure 4.** Winter respiration rates ( $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ ) of krill by individual dry weight (mg). Respiration rates measured along the northern AP in August 2016. Regression equation:  $y = 0.215 * x$ .  $R^2 = 0.6738$ .

available phytoplankton standing stock ( $3.6 \text{ mg C m}^{-3}$ ; see Supplementary Table S7).

Although model-derived ice algae concentrations were relatively low in both years compared to other regions (Arrigo, 2017), concentrations were greater than the available phytoplankton in the water column (Supplementary Table S7). In August 2015, theoretical ice algae biomass in the Bransfield Strait, where krill were mostly concentrated, was approximately  $5 \text{ mg C m}^{-2}$  (determined for the bottom 20 cm of the sea ice). These concentrations are the equivalent of  $\sim 25 \text{ mg C m}^{-3}$  in seawater. Considering that the majority of bottom ice algae is in the bottom 5 cm of the sea ice, these values could rise to the equivalent of  $100 \text{ mg C m}^{-3}$ . While this is only a third of the predicted food concentrations based on daily rations, this value is averaged over  $25 \text{ km}^2$  and, since 50% or less of that area would have been covered by ice, it is likely that at the scale of the ice floe the concentrations of ice algae would have been at least double what the SIESTA model estimated. Furthermore, as mentioned above, our ice algae values are likely underestimated due to constraints with satellite data. Despite lower ice algae biomass in 2016, by the end of August ice algae biomass in the Bransfield Strait had also reached  $\sim 5 \text{ mg C m}^{-2}$ , the equivalent of  $25 \text{ mg C m}^{-3}$  (or  $100 \text{ mg C m}^{-3}$  at the upper extreme).

Thus, we propose that, like juvenile krill in the Weddell Sea (Kohlbach et al., 2017; Schaafsma et al., 2017), AC1 krill in the Bransfield Strait were grazing on ice algae during our study. In a corresponding study conducted over a longer time frame (2012–2016), analysis of bulk stable isotopic ratios of  $\delta^{15}\text{N}$  suggest that postlarval krill were primarily carnivorous, except for in August 2012 (a winter with good sea ice conditions) when average  $\delta^{15}\text{N}$  were significantly lower, suggesting herbivory (Walsh and Reiss, submitted). Since the majority of krill in August 2012 were  $\leq 30 \text{ mm}$  in length, i.e. AC1 krill dominated the population in 2012 (Walsh and Reiss, submitted), these findings support our hypothesis that AC1 krill are primarily herbivorous, at least during winters with good sea ice conditions.

However, we emphasize that our results do not imply grazing on ice algae throughout the winter. Walsh and Reiss (submitted) also examined fatty acid ratios of 16:1( $n=7$ )/18:4( $n=3$ ) in krill over



**Figure 5.** Variability in mean (a) daily ingestion rates [ $\mu\text{g Chl (mg DW)}^{-1} \text{ day}^{-1}$ ], (b) daily rations (% of body carbon consumed as algae), and (c) algal contribution to energy requirements (% of energy requirements met from grazing), for AC1 and AC2+ krill in 2015 and 2016.

**Table 1.** Results of two-way ANOVAs for comparisons of mean ingestion rate (IR), daily ration (DR), and algal contribution to energy budget (ACEB) between stage (AC1 and AC2+), year (2015 and 2016), and stage  $\times$  year.

	IR		DR		ACEB	
	F	p	F	p	F	p
Stage (DF=2)	59.72	$\ll 0.0001$	64.49	$\ll 0.0001$	19.23	$\ll 0.0001$
Year (DF=1)	34.1	$\ll 0.0001$	34	$\ll 0.0001$	20.9	$\ll 0.0001$
Stage $\times$ year (DF=2)	0.06	0.8002	0.08	0.7787	0.02	0.9007

Degrees of freedom (DF) are shown in parenthesis for each category, F is the ANOVA F-statistic, p is the probability.

a consecutive 5-year period as an index of diatom consumption (Schmidt et al., 2006) and found that although values for larval and postlarval krill varied among years, they were consistently



low and never exceeded a value of 5. According to Schmidt *et al.* (2006), the ratio of 16:1(*n*-7)/18:4(*n*-3) in krill fed a monoculture diet of diatoms for 3 weeks is >5, indicating that the ratios observed by Walsh and Reiss (submitted) were representative of a non-diatom-dominated diet. Because lipid accumulation provides a longer-term dietary history than gut fluorescence, these results suggest that grazing on ice algae was not consistent throughout the winter, but rather became more important in late winter as day length rapidly increased and primary productivity, although still low, was rising.

Benthic phytodetritus has also been proposed as an important food source for overwintering krill in this region (Schmidt *et al.*, 2014; Cleary *et al.*, 2016) and it is possible that the algal pigments we measured could have come from that food source. However, during our study, highest algal ingestion rates for either AC1 or AC2+ krill occurred at night, coinciding with the period of time when krill were in the surface waters, as observed using acoustic backscatter (Figure 6). We suggest, therefore, that although benthic phytodetritus is an important food source for krill, this is not likely contributing to the algal pigment measured in krill samples collected during our study.

### The implications of a late-winter ice algae diet for AC1 krill

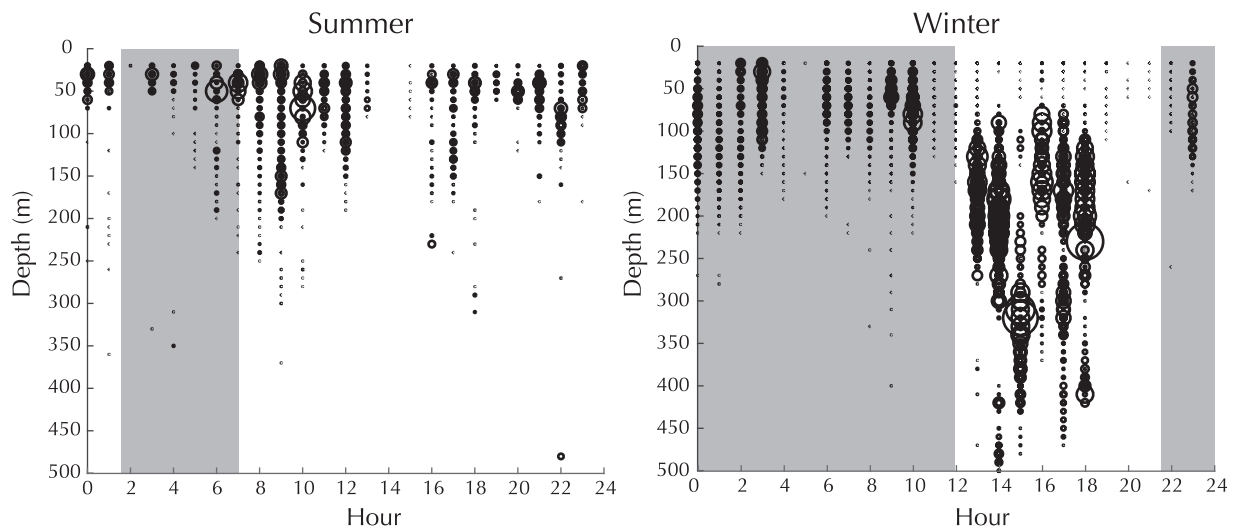
Although winter ingestion rates were low compared to those measured in summer (Bernard *et al.*, 2012), grazing on ice algae contributed a mean of nearly 150% to the winter energy budget of AC1 krill in 2015, exceeding the minimum energy demand. Excess energy consumed from ice algae could presumably be directed towards growth and development in AC1 individuals. However, in 2016, this value was significantly lower (~16%), likely reflecting the variable sea ice conditions and ice algae production and biomass between the 2 years. We did not measure feeding rates on other prey items, and it is likely that AC1 krill were feeding on alternative food sources during both years, but especially in August 2016. However, there are differences in the nutritional quality of food sources, and since food quality plays a major role in determining the physiology of juvenile krill, a diet

of ice algae may have important consequences for overwintering AC1 krill with implications for their reproductive potential.

Several field studies have examined the effects of food nutritional quality on krill growth rates and lipid storage, using analysis of local phytoplankton communities (Ross *et al.*, 2000; Atkinson *et al.*, 2006), or fatty acid markers and stable isotope compositions to infer diet history (Pond *et al.*, 2005; Schmidt *et al.*, 2006). Small krill feeding primarily on diatoms have higher proportions of PUFA, while those with a carnivorous diet have a greater proportion of storage lipids (triacylglycerols, TAG) (Hagen *et al.*, 2007; Schmidt *et al.*, 2014). Since growth and development in krill exerts a high demand for PUFA (Pond *et al.*, 2005), a diet of diatoms would promote growth of young krill (Ross *et al.*, 2000; Pond *et al.*, 2005; Atkinson *et al.*, 2006), while a diet dominated by copepods would result in greater accumulation of storage lipids and delayed development (Schmidt *et al.*, 2014).

Because age at maturity and age at first spawning in female krill at the AP occurs in their second year (i.e. AC2) (Siegel, 2000), late winter growth in AC1 females is important. Larger AC1 females entering spring as AC2 females will produce more eggs in their first reproductive year than smaller individuals (Ross and Quetin, 1983; Cuzin-Roudy, 2000). While feeding on spring pelagic phytoplankton blooms is necessary for oocyte maturation in female krill (Schmidt *et al.*, 2012), we suggest that feeding on ice algae in the late winter is important for maximizing size at first spawning.

Finally, regional differences in late-winter diet and food quality might also explain the observed differences in age at maturity and age at first spawning between the AP (AC2) and the Antarctic Indian Ocean (AC3) (Siegel, 2000). It is well-known that adult krill undergo a reproductive resting period during autumn and winter (Cuzin-Roudy, 2000; Ross and Quetin, 2000), in which mature females and males regress to their respective immature forms (Poleck and Denys, 1982). Towards the end of winter, sexual development is re-initiated in preparation for the spring-summer reproductive season (Denys and McWhinnie, 1982; Poleck and Denys, 1982). Experiments in the laboratory setting have shown that the availability of food during winter will



**Figure 6.** Bubble plot of the vertical distribution of acoustic energy attributed to krill during the summer of 2007 (left panel) and winter of 2016 (right panel) showing the magnitude of the daily vertical migration. Grey areas represent nighttime. Acoustic data were treated as described in Reiss *et al.* (2017).



determine the degree of sexual regression in adult krill and, consequently, the timing of sexual re-maturation (Kawaguchi *et al.*, 2007; Kawaguchi, 2016). Although these studies did not examine the role of food in sexual maturation of AC1 females specifically, it is plausible that the nutritional quality of the late winter diet may determine the age at maturity and age at first spawning. An understanding of the degree of life history plasticity and the mechanisms that govern life history traits, such as age at first spawning, is necessary for predicting how krill might respond to climate change (Suryan *et al.*, 2009).

## Conclusion

It has been suggested that changes in the timing of sea ice formation and a decrease in sea ice extent and availability of well-developed over-rafted pack ice may negatively impact krill populations (Kawaguchi and Satake, 1994; Loeb *et al.*, 1997; Atkinson *et al.*, 2004; Flores *et al.*, 2012a; Meyer, 2012; Ross *et al.*, 2014; Meyer *et al.*, 2017). However, the Bransfield Strait is a dynamic region and sea ice formation, extent and concentration vary substantially between years (Reiss *et al.*, 2017). The sea ice season is relatively short compared to other regions; consequently, much of the sea ice present is newly formed pancake ice, in which accumulated ice algae have limited time to develop into the substantial biomass observed in other sea ice environments (Arrigo, 2017). Furthermore, well-developed, heavily rafted pack ice is scarce in the Bransfield Strait.

Despite this, the Bransfield Strait remains an important overwintering region for krill (Reiss *et al.*, 2017). Our findings show that grazing on ice algae by overwintering AC1 krill can be sufficient to meet and exceed their minimum energy demands even when sea ice concentrations are relatively low and dominated by newly formed pancake ice as opposed to well-developed, over-rafted pack ice. The excess energy they consume from ice algae can go directly into growth and reproductive development and may explain the regional differences in age at maturity and age at first spawning.

However, during a lower sea ice year in which the waters in the Bransfield Strait were largely ice-free, we observed that grazing on ice algae by AC1 krill contributed substantially less to their minimum energy demands, and we assume that in these conditions AC1 krill supplement their diet with heterotrophic prey, possibly protozoans. As the northern AP continues to warm, we anticipate more frequent ice-free conditions in the Bransfield Strait. How this might affect the growth and development of AC1 krill, and ultimately influence their age at maturity and first spawning, remains unclear.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

## Acknowledgements

We are grateful to the logistics support group at Antarctic Support Contractors, and the Captain, officers, and crew of the R.V.I.B. Nathaniel B. Palmer, for their invaluable assistance at sea. We thank the team of students, technicians, and scientists who assisted in data collection at sea. Special thanks go to Kim Dietrich and Ryan Driscoll for overseeing and coordinating zooplankton collection. We are grateful to Dr. Jefferson Hinke, Dr. Douglas Krause, and Dr. George Watters, who provided useful feedback on an earlier version of the manuscript.

## Funding

This work was conducted in collaboration with the NOAA Antarctic Marine Living Resources Program and was funded in part through a donation from the G. Unger Vetlesen Foundation.

## References

- Arrigo, K. R., van Dijken, G. L., and Bushinsky, S. 2008. Primary production in the Southern Ocean, 1997–2006. *Journal of Geophysical Research*, 113: C08004.
- Arrigo, K. R. 2017. Sea ice as a habitat for primary producers. *In* Sea Ice. Ed. by D. N. Thomas. John Wiley & Sons, Ltd, New Jersey, USA.
- Ashjian, C. J., Davis, C. S., Gallager, S. M., Wiebe, P. H., and Lawson, G. L. 2008. Distribution of larval krill and zooplankton in association with hydrography in Marguerite Bay, Antarctic Peninsula, in austral fall and winter 2001 described using the Video Plankton Recorder. *Deep-Sea Research II*, 55: 455–471.
- Atkinson, A., and Snýder, R. 1997. Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. *Marine Ecology Progress Series*, 160: 63–76.
- Atkinson, A., Ward, P., Hill, A., Brierley, A. S., and Cripps, G. C. 1999. Krill-copepod interactions at South Georgia, Antarctica, II. *Euphausia superba* as a major control on copepod abundance. *Marine Ecology Progress Series*, 176: 63–79.
- Atkinson, A., Meyer, B., Stübing, D., Hagen, W., Schmidt, K., and Bathmann, U. V. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter—II. Juveniles and adults. *Limnology and Oceanography*, 47: 953–966.
- Atkinson, A., Siegel, V., Pakhomov, E., and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, 432: 100–103.
- Atkinson, A., Shreeve, R. S., Hirst, A. G., Rothery, P., Tarling, G. A., Pond, D. W., Korb, R. E. *et al.* 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography*, 51: 973–987.
- Båmstedt, U., Gifford, D. J., Irigoien, X., Atkinson, A., and Roman, M. 2000. Feeding. *In* ICES Zooplankton Methodology Manual, pp. 297–399. Ed. by R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley. Academic Press, London.
- Bernard, K. S., Steinberg, D. K., and Schofield, O. M. E. 2012. Summertime grazing impact of the dominant macrozooplankton off the Western Antarctic Peninsula. *Deep-Sea Research I*, 62: 111–122.
- Cleary, A. C., Durbin, E. G., Casas, M. C., and Zhou, M. 2016. Winter distribution and size structure of Antarctic krill *Euphausia superba* populations in-shore along the West Antarctic Peninsula. *Marine Ecology Progress Series*, 552: 115–129.
- Comiso, J. C., and Steffen, K. 2001. Studies of Antarctic sea ice concentrations from satellite data and their applications. *Journal of Geophysical Research*, 106: 31361–31385.
- Conover, R. T., Durvasula, R., Roy, S., and Wang, R. 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. *Limnology and Oceanography*, 31: 878–887.
- Cuzin-Roudy, J. 2000. Seasonal reproduction, multiple spawning, and fecundity in northern krill, *Meganctiphanes norvegica*, and Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquaculture Sciences*, 57: 6–15.
- Denys, C. J., and McWhinnie, M. A. 1982. Fecundity and ovarian cycles of the Antarctic krill *Euphausia superba* (Crustacea, Euphausiacea). *Canadian Journal of Zoology*, 60: 2414–2423.
- Durbin, E. G., and Campbell, R. G. 2007. Reassessment of the gut pigment method for estimating *in situ* zooplankton ingestion. *Marine Ecology Progress Series*, 331: 305–307.

- Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B. A., Milinevsky, G., Nicol, S., Reiss, C. *et al.* 2012a. Impact of climate change on Antarctic krill. *Marine Ecology Progress Series*, 458: 1–19.
- Flores, H., van Franeker, J. A., Siegel, V., Haraldsson, M., Strass, V., Meesters, E. H., Bathmann, U. *et al.* 2012b. The association of Antarctic krill *Euphausia superba* with the under-ice habitat. *PLoS One*, 7: e31775.
- Fritsen, C. H., Memmott, J., and Stewart, F. J. 2008. Inter-annual sea-ice dynamics and micro-algal biomass in winter pack ice of Marguerite Bay, Antarctica. *Deep-Sea Research II*, 55: 2059–2067.
- Fritsen, C. H., Memmott, J. C., Ross, R. M., Quetin, L. B., Vernet, M., and Wirthlin, E. D. 2011. The timing of sea ice formation and exposure to photosynthetically active radiation along the Western Antarctic Peninsula. *Polar Biology*, 34: 683–692.
- Goñi, M. A., Cathey, M. W., Kim, Y. H., and Voulgaris, G. 2005. Fluxes and sources of suspended organic matter in an estuarine turbidity maximum region during low discharge conditions. *Estuarine, Coastal and Shelf Science*, 63: 683–700.
- Hagen, W., Yoshida, T., Virtue, P., Kawaguchi, S., Swadling, K. M., Nicol, S., and Nichols, P. D. 2007. Effects of a carnivorous diet on the lipids, fatty acids and condition of Antarctic krill, *Euphausia superba*. *Antarctic Science*, 19: 183–188.
- Huntley, M. E., Nordhausen, W., and Lopez, M. D. G. 1994. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. *Marine Ecology Progress Series*, 107: 23–40.
- Jia, Z., Swadling, K. M., Meiners, K., Kawaguchi, S., and Virtue, P. 2016. The zooplankton food web under East Antarctic pack ice—a stable isotope study. *Deep-Sea Research II*, 131: 189–202.
- Kawaguchi, S., and Satake, M. 1994. Relationship between recruitment of the Antarctic krill and the degree of ice cover near the South Shetland Islands. *Fisheries Science*, 60: 123–124.
- Kawaguchi, S., Yoshida, T., Finley, L., Cramp, P., and Nicol, S. 2007. The krill maturity cycle: a conceptual model of the seasonal cycle in Antarctic krill. *Polar Biology*, 30: 689–698.
- Kawaguchi, S. 2016. Reproduction and larval development in Antarctic krill (*Euphausia superba*). In *Biology and Ecology of Antarctic Krill*, pp. 225–246. Ed. by V. Siegel. Springer, Switzerland.
- Kohlbach, D., Lange, B. A., Schaafsma, F. L., David, C., Vortkamp, M., Graeve, M., van Franeker, J. A. *et al.* 2017. Ice algae-produced carbon is critical for overwintering of Antarctic krill *Euphausia superba*. *Frontiers in Marine Science*, 4: 310.
- Laws, R. M. 1977. Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society B*, 279: 81–96.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., and Trivelpiece, S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387: 897–900.
- Lowe, A. T., Ross, R. M., Quetin, L. B., Vernet, M., and Fritsen, C. H. 2012. Simulating larval Antarctic krill growth and condition factor during fall and winter in response to environmental variability. *Marine Ecology Progress Series*, 452: 27–43.
- Mauchline, J. 1980. Measurement of Body Length of *Euphausia Superba* Dana. Commonwealth Scientific and Industrial Research Organisation, Australia, 9 pp.
- Meyer, B. 2012. The overwintering of Antarctic krill, *Euphausia superba*, from an ecophysiological perspective. *Polar Biology*, 35: 15–37.
- Meyer, B., and Teschke, M. 2016. Physiology of *Euphausia superba*. In *Biology and Ecology and Antarctic Krill*, pp. 145–174. Ed. by V. Siegel. Springer, Switzerland.
- Meyer, B., Freier, U., Grimm, V., Groeneveld, J., Hunt, B. P. V., Kerwath, S., King, R. *et al.* 2017. The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. *Nature Ecology & Evolution*, 1: 1853–1861.
- Murase, H., Matsuoka, K., Ichii, T., and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E–145°W). *Polar Biology*, 25: 135–145.
- Nicol, S., Clarke, J., Romaine, S. J., Kawaguchi, S., Williams, G., and Hosie, G. W. 2008. Krill (*Euphausia superba*) abundance and Adélie penguin (*Pygoscelis adeliae*) breeding performance in the waters off the Béchervaise Island colony, East Antarctica in 2 years with contrasting ecological conditions. *Deep-Sea Research II*, 55: 540–557.
- Pakhomov, E. A., Perissinotto, R., and McQuaid, C. D. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology Progress Series*, 134: 1–14.
- Poleck, T. P., and Denys, C. J. 1982. Effect of temperature on the molting, growth and maturation of the Antarctic krill *Euphausia superba* (Crustacea: Euphausiacea) under laboratory conditions. *Marine Biology*, 70: 255–265.
- Pond, D. W., Atkinson, A., Shreeve, R. S., Tarling, G., and Ward, P. 2005. Diatom fatty acid biomarkers indicate recent growth rates in Antarctic krill. *Limnology and Oceanography*, 50: 732–736.
- Price, H. J., Boyd, K. R., and Boyd, C. M. 1988. Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Marine Biology*, 97: 67–77.
- Quetin, L. B., and Ross, R. M. 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. *Marine Ecology Progress Series*, 259: 185–200.
- Reid, K. 1995. The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarctic Science*, 7: 241–249.
- Reiss, C. S., Cossio, A., Santora, J. A., Dietrich, K. S., Murray, A., Mitchell, B. G., Walsh, J. *et al.* 2017. Overwinter habitat selection by Antarctic krill under varying sea-ice conditions: implications for top predators and fishery management. *Marine Ecology Progress Series*, 568: 1–16.
- Ross, R. M., and Quetin, L. B. 1983. Spawning frequency and fecundity of the Antarctic krill *Euphausia superba*. *Marine Biology*, 77: 201–205.
- Ross, R. M., and Quetin, L. B. 2000. Reproduction in Euphausiacea. In *Krill Biology, Ecology and Fisheries*, pp. 150–181. Ed. by I. Everson. Blackwell, Cambridge.
- Ross, R. M., Quetin, L. B., Baker, K. S., Vernet, M., and Smith, R. C. 2000. Growth limitation in young *Euphausia superba* under field conditions. *Limnology and Oceanography*, 45: 31–43.
- Ross, R. M., Quetin, L. B., Newberger, T., Shaw, C. T., Jones, J. L., Oakes, S. A., and Moore, K. J. 2014. Trends, cycles, interannual variability for three pelagic species west of the Antarctic Peninsula 1993–2008. *Marine Ecology Progress Series*, 515: 11–32.
- Ryabov, A. B., de Roos, A. M., Meyer, B., Kawaguchi, K., and Blasius, B. 2017. Competition-induced starvation drives large-scale population cycles in Antarctic krill. *Nature Ecology & Evolution*, 1: 0177.
- Saenz, B. T., and Arrigo, K. R. 2012. Simulation of a sea ice ecosystem using a hybrid model for slush layer desalination. *Journal of Geophysical Research*, 117: C05007.
- Saenz, B. T., and Arrigo, K. R. 2014. Annual primary production in Antarctic sea ice during 2005–2006 from a sea ice state estimate. *Journal of Geophysical Research*, 119: 3645–3678.
- Schaafsma, F. L., Kohlbach, D., David, C., Lange, B. A., Graeve, M., Flores, H., and van Franeker, J. A. 2017. Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill, *Euphausia superba*, in ice-covered waters. *Marine Ecology Progress Series*, 580: 101–115.
- Schmidt, K., Atkinson, A., Petzke, K.-J., Voss, M., and Pond, D. W. 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: complementary insights from stomach content, fatty acids, and stable isotopes. *Limnology and Oceanography*, 51: 2409–2427.

- Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M. C. M., Pond, D. W., Tarling, G. A. *et al.* 2011. Seabed foraging by Antarctic krill: implications for stock assessment, benthic-pelagic coupling, and the vertical transfer of iron. *Limnology and Oceanography*, 56: 1411–1428.
- Schmidt, K., Atkinson, A., Venables, H. J., and Pond, D. W. 2012. Early spawning of Antarctic krill in the Scotia Sea is fuelled by “superfluous” feeding on non-ice associated phytoplankton blooms. *Deep-Sea Research II*, 59–60: 159–172.
- Schmidt, K., Atkinson, A., Pond, D. W., and Ireland, L. C. 2014. Feeding and overwintering of Antarctic krill across its major habitats: the role of sea ice cover, water depth, and phytoplankton abundance. *Limnology and Oceanography*, 59: 17–36.
- Siegel, V., and Loeb, V. 1994. Length and age at maturity of Antarctic krill. *Antarctic Science*, 6: 479–482.
- Siegel, V. 2000. Krill (Euphausiacea) life history and aspects of population dynamics. *Canadian Journal of Fisheries and Aquaculture Sciences*, 57: 130–150.
- Smith, R. C., Martinson, D. G., Stammerjohn, S. E., Iannuzzi, R. A., and Ireson, K. 2008. Bellingshausen and western Antarctic Peninsula region: pigment biomass and sea-ice spatial/temporal distributions and interannual variability. *Deep-Sea Research II*, 55: 1949–1963.
- Smith, C. R., DeMaster, D. J., Thomas, C. J., Sršen, P., Grange, L., Evrard, V., and DeLeo, F. 2012. Pelagic-benthic coupling, food banks, and climate change on the West Antarctic Peninsula Shelf. *Oceanography*, 25: 188–201.
- Stammerjohn, S. E., Martinson, D., Smith, R. C., and Iannuzzi, R. A. 2008. Sea ice in the western Antarctic Peninsula region: spatio-temporal variability from ecological and climate change perspectives. *Deep-Sea Research II*, 55: 2041–2058.
- Suryan, R. M., Saba, V. S., Wallace, B. P., Hatch, S. A., Frederiksen, M., and Wanless, S. 2009. Environmental forcing on life history strategies: evidence for multi-trophic level responses at ocean basin scales. *Progress in Oceanography*, 81: 214–222.
- Tang, K. W., and Taal, M. 2005. Trophic modification of food quality by heterotrophic protists: species-specific effects on copepod egg production and egg hatching. *Journal of Experimental Marine Biology and Ecology*, 318: 85–98.
- Thiele, D., Chester, E. T., Moore, S. E., Širovic, A., Hildebrand, J. A., and Friedlaender, A. S. 2004. Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep-Sea Research II*, 51: 2311–2325.
- Vaughan, D. G., Mashall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C. *et al.* 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climate Change*, 60: 243–274.
- Vernet, M., Kozłowski, W. A., Yarmey, L. R., Lowe, A. T., Ross, R. M., Quetin, L. B., and Fritsen, C. H. 2012. Primary production throughout austral fall, during a time of decreasing daylength in the western Antarctic Peninsula. *Marine Ecology Progress Series*, 452: 45–61.
- Walsh, J., Reiss, C., and Watters, G. Submitted to PNAS. Plasticity in Antarctic krill (*Euphausia superba*) decouples overwinter survival from sea-ice conditions.
- Wienecke, B. C., Lawless, R., Rodary, D., Bost, C.-A., Thomson, R., Pauly, T., Robertson, G. *et al.* 2000. Adélie penguin foraging behaviour and krill abundance along the Wilkes and Adélie land coasts, Antarctica. *Deep-Sea Research II*, 47: 2573–2587.

Handling editor: David Fields