AGU PUBLICATIONS

Geophysical Research Letters

RESEARCH LETTER

10.1002/2016GL070846

Under ice habitats for Antarctic krill larvae: Could less mean more under climate warming?

J. Melbourne-Thomas[1,2], S. P. Corney[2], R. Trebilco[2], K. M. Meiners[1,2], R. P. Stevens[2], S. Kawaguchi[1,2], M. D. Sumner[1,2], and A. J. Constable[1,2]

[1]Australian Antarctic Division, Department of the Environment, Kingston, Tasmania, Australia, [2]Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Hobart, Tasmania, Australia

Key Points:
- Outputs from a sea ice model are used to identify potential habitat for Antarctic krill larvae
- Model results indicate that the area of larval krill habitat may increase under climate change
- Processes affecting different krill life stages under future scenarios require further consideration

Supporting Information:
- Supporting Information S1

Correspondence to:
J. Melbourne-Thomas,
Jess.Melbourne-Thomas@aad.gov.au

Citation:
Melbourne-Thomas, J., S. P. Corney, R. Trebilco, K. M. Meiners, R. P. Stevens, S. Kawaguchi, M. D. Sumner, and A. J. Constable (2016), Under ice habitats for Antarctic krill larvae: Could less mean more under climate warming?, *Geophys. Res. Lett.*, *43*, 10,322–10,327, doi:10.1002/2016GL070846.

Received 22 DEC 2015
Accepted 30 SEP 2016
Accepted article online 4 OCT 2016
Published online 15 OCT 2016

Abstract Overwintering of larvae underneath Antarctic pack ice is a critical stage in the life cycle of Antarctic krill. However, there are no circumpolar assessments of available habitat for larval krill, making it difficult to evaluate how climate change may impact this life stage. We use outputs from a circumpolar sea ice model, together with a set of simple assumptions regarding key habitat features, to identify possible regions of larval krill habitat around Antarctica during winter. We assume that the location and suitability of habitat is determined by both food availability and three-dimensional complexity of the sea ice. A comparison of the combined area of these regions under current conditions with a warm climate scenario indicates that while total areal sea ice extent decreases, there is a consistently larger area of potential larval krill habitat under warm conditions. These findings suggest that decreases in sea ice extent may not necessarily be detrimental for krill populations.

1. Introduction

Antarctic krill, *Euphausia superba*, play a central role in Southern Ocean food webs and nutrient cycling [e.g., *Ratnarajah et al*., 2016] and are also an important commercial species on a global scale [*Nicol et al*., 2011]. The life cycle and winter survival of Antarctic krill is closely linked with sea ice [*Flores et al*., 2012; *Kawaguchi*, 2016; *Nicol*, 2006] (Figure 1). Unlike adults, krill larvae cannot survive long starvation periods [*Meyer and Oettl*, 2005], and they use algae on the underside of ice floes as an important component of their diets during winter and early spring when food in the water column is scarce [*Daly*, 2004; *Meyer*, 2011]. Larval krill may also use the underside of sea ice—which can have high three-dimensional complexity—as a protected platform for feeding (sheltered from under ice currents) and a spatial refuge from predation [*Meyer et al*., 2009]. The association of larval krill with sea ice habitat has been linked to krill recruitment success [*Quetin and Ross*, 2003; *Siegel and Loeb*, 1995] and population changes; in some areas of the Southern Ocean krill density in summer is positively correlated with latitudinal extent of the sea ice edge in the preceding winter [*Atkinson et al*., 2004].

Sea ice conditions in Antarctica are currently changing [*Parkinson and Cavalieri*, 2012] and understanding the effects of these changes on krill populations has important implications for Antarctic ecosystem function [*Constable et al*., 2014] as well as for fisheries [*Nicol et al*., 2011]. The distribution and within-season evolution of important features of the under ice habitat for larval krill (such as thickness and structural complexity, as described below) remains unclear, mostly due to the inaccessibility of these habitats. Nevertheless, a key question is whether larval krill habitat area is dependent on overall sea ice extent.

As yet there are no circumpolar assessments of the availability of larval krill habitat, making it difficult to estimate the effects of climate change on this life stage. Characteristics of sea ice environments that are likely to be important for krill larvae, such as thickness and three-dimensional complexity [*Frazer et al*., 2002; *Meiners et al*., 2012], are currently unavailable from remotely sensed data (although more products are available for the Arctic) [see *Kurtz and Markus*, 2012]. Instead, we use a moderately high resolution, circumpolar, standalone sea ice model to identify potential habitat regions for larval krill by assuming that the location and suitability of habitat is determined by both food availability and three-dimensional complexity of the sea ice. We then compare distribution maps generated from model output under current conditions with a warm climate scenario. Our study aims to use model output and biological knowledge to identify regions that may represent suitable habitat for overwintering krill larvae. This approach assists in identifying ecological processes that are not well understood but that may be critically important in determining future trajectories for this key Antarctic species.

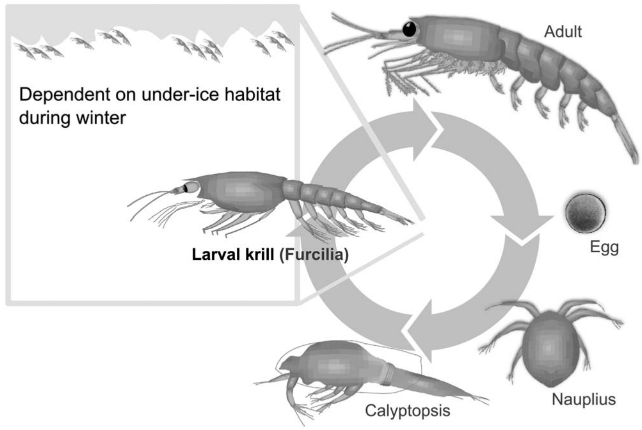

Figure 1. Simplified krill life cycle illustrating the importance of under ice habitats for larval krill.

2. Methods

2.1. Sea Ice Model

We used results from an 11 year (1998–2008) numerical simulation of Southern Ocean sea ice, conducted using the Los Alamos sea ice model (CICE4) [*Bailey et al*., 2010] configured in stand-alone mode on a quarter-degree grid, extending to 45°S (additional detail in Text S1 in the supporting information; full description in *Stevens* [2013]). A single-year warm climate scenario approximating conditions for 2100 was also undertaken. This two-degree warming scenario was constructed by perturbing the original forcing files with changes that are consistent with projections from the Intergovernmental Panel on Climate Change (IPCC)'s fourth assessment report (for a midrange scenario that assumes rapid economic growth before introduction of new and more efficient technologies midcentury).

The model is well constrained in its representation of the processes of sea ice formation and melt, and comparison with observed areal ice extent shows minimal deviations over the 1998–2003 period, particularly during winter [*Stevens*, 2013]. Sea ice thickness sensitivities in the CICE4 model are considered in detail in *Hunke* [2010, 2014]. The model configuration, evaluation process, sensitivity, and forcings for current and warm climates are detailed in *Stevens* [2013] and summarized in the supporting information (Text S1) [*Adams*, 2006; *Bailey et al*., 2010; *Bi and Marsland*, 2010; *Hunke*, 2010, 2014; *Meehl et al*., 2007].

2.2. Determining Larval Krill Habitat

We estimated potential larval krill habitat from model output for 3 months in winter/early spring (July, August, and September) when larvae use under ice habitats [*Meyer*, 2011; *Nicol*, 2006] and are likely to be grazing on ice algae (i.e., there is sufficient light for algal growth). Earlier months were not included because observational data indicate that larvae may be more omnivorous or carnivorous during this period [*Daly*, 2004; *Meyer*, 2011], although the reasons are unclear and likely region dependent.

Areas of suitable larval krill habitat were identified using two filters for food availability, with an overlay for habitat complexity used to indicate relative quality of suitable habitat, as described in Table 1. Food availability and habitat complexity are estimated at a quarter-degree scale and based on monthly means of each sea ice model variable. We assume that all habitat regions are equally accessible. Further details on habitat filters and overlays used to process sea ice model output are provided in the supporting information (Text S2) [*Bailey et al*., 2010; *Frouin and Pinker*, 1995; *Meiners et al*., 2012; *Morgan-Kiss et al*., 2006].

3. Results and Discussion

The area of modeled larval krill habitat increases from July to September (Figures 2 and 3). At a threshold of 0.45 W m^{-2} for shortwave radiation at the bottom of the ice, there are no areas of modeled habitat for larval krill in July under current conditions (which is consistent with larvae depending on zooplankton under the ice as their primary food source in midwinter [*Meyer*, 2011]). As an example, we illustrate where modeled regions occur at a lower threshold of 0.1 W m^{-2} for July (Figure 2); there are patches to the north of the Weddell Sea between 60°W and 0° and north of Prydz Bay in East Antarctica (around 70°E).

Modeled larval krill habitat is very patchy in August compared to September when isolated patches coalesce into a circumpolar distribution of available habitat (Figure 2). The limited habitat availability in August may impose a strong constraint on krill larvae survival. The subsequent distribution of larval krill at the end of winter would then be an outcome of this initial constraint combined with the movement of sea ice through suitable habitat regions in September.

Table 1. Summary of the Process Used for Identifying the Location of Potential Krill Habitat From Sea Ice Model Output[a]

	Summary	Biological Justification
Filter #1	Critical sea ice thickness indicating the presence of bottom algal communities	A circumpolar analysis of historical sea ice core data [*Meiners et al*., 2012] found that bottom ice algal communities generally occur in association with ice between 0.5 m and 1 m thick (due to favorable brine salinities, nutrient availability, temperature conditions and irradiance). We used this thickness range as our first filter.
Filter #2	Critical monthly mean radiation indicating a threshold for light-limited algal growth	We assume that bottom algal communities will only be available to larval krill if there is sufficient light for algal growth (determined by latitude, time of year, and transmission through ice and snow). Shortwave radiation at the bottom of the ice is calculated directly by CICE4. We assume that the compensation point for sea ice algal growth during winter is 1 μmol photons $m^{-2}s^{-1}$ [*Morgan-Kiss et al*., 2006], equating to 0.45 W m^{-2} (assuming that the photosynthetically active component of the total flux is 0.48) [*Frouin and Pinker*, 1995]. Regions were only considered suitable when shortwave radiation at the bottom of the ice was higher than this value.
Overlay	Color gradient for the area defined by the two filters: ridging rate indicating habitat complexity	CICE4 calculates the ice-area ridging rate (in units of % day^{-1}) as the area of each grid cell that is ridged per day. We assume that under ice habitat complexity will be high when ridging rate is high and that ridged areas will provide more crevices and therefore be preferable for larval krill.

[a]Further details are provided in the supporting information (Text S2).

Here we model possible larval krill habitat at a circumpolar scale based on a set of realistic hypotheses regarding the primary environmental attributes important for overwintering larval krill. Local factors will influence the fine-scale distributions of habitat, and not all suitable habitat will be occupied by larval krill (e.g., because under ice larval transport pathways mean that particular habitat areas are not occupied). Thus, comparing fine-scale predictions from this study with sparse, local-scale observations of larval krill underneath sea ice is very difficult. Nevertheless, the regions of larval krill habitat identified here do broadly correspond with documented larval and adult krill distributions at a circumpolar scale in other seasons, giving confidence in the results of our approach. Observations in *Discovery Reports* from the 1960s [*Marr*, 1962, Figure 146] show concentrations of krill observed between April and November extending from the tip of the Antarctic Peninsula to the east at the north of the Weddell and Lazarev Seas between 60°W and 30°E and also to the north of Prydz Bay. Modeled habitat is also consistent with observations of under ice concentrations of krill near to the ice edge in the Weddell Sea, between 60°W and 0° [*Brierley et al*., 2002].

Modeled sea ice extent is consistent with remotely sensed observations for the 1998–2008 period (Figure 3, indicating the generally high skill of these model results) and is lower in the warm climate scenario than under current conditions for July, August, and September, consistent with projections for future change in Antarctic sea ice from the IPCC's fifth assessment report (midrange scenario) [*Collins et al*., 2013]. The change in area for predicted larval krill habitat between the current and warm scenarios is opposite to that for areal sea ice extent; there is a greater area of habitat available to larval krill under the warm climate in all months (Figure 3), hence implying that habitat area for larval krill may not be dependent on overall sea ice extent. The most notable difference in the general location of modeled larval krill habitat between the current and warm climate is a contraction of habitat southward under the two-degree warming scenario (Figure 2). This is associated with the presence of thinner ice (i.e., in the 0.5–1 m thickness range) farther south but, critically, sufficiently far north for light to be available for algal growth. Ridging area rate within suitable habitat increases under the two-degree warming scenario (Figure 3) suggesting the potential for more spatially complex habitat under a warmer climate.

The timing of sea ice formation has been described as an important determinant of sea ice algal biomass in the well-studied Palmer LTER (Long Term Ecological Research) region of the West Antarctic Peninsula [*Fritsen*

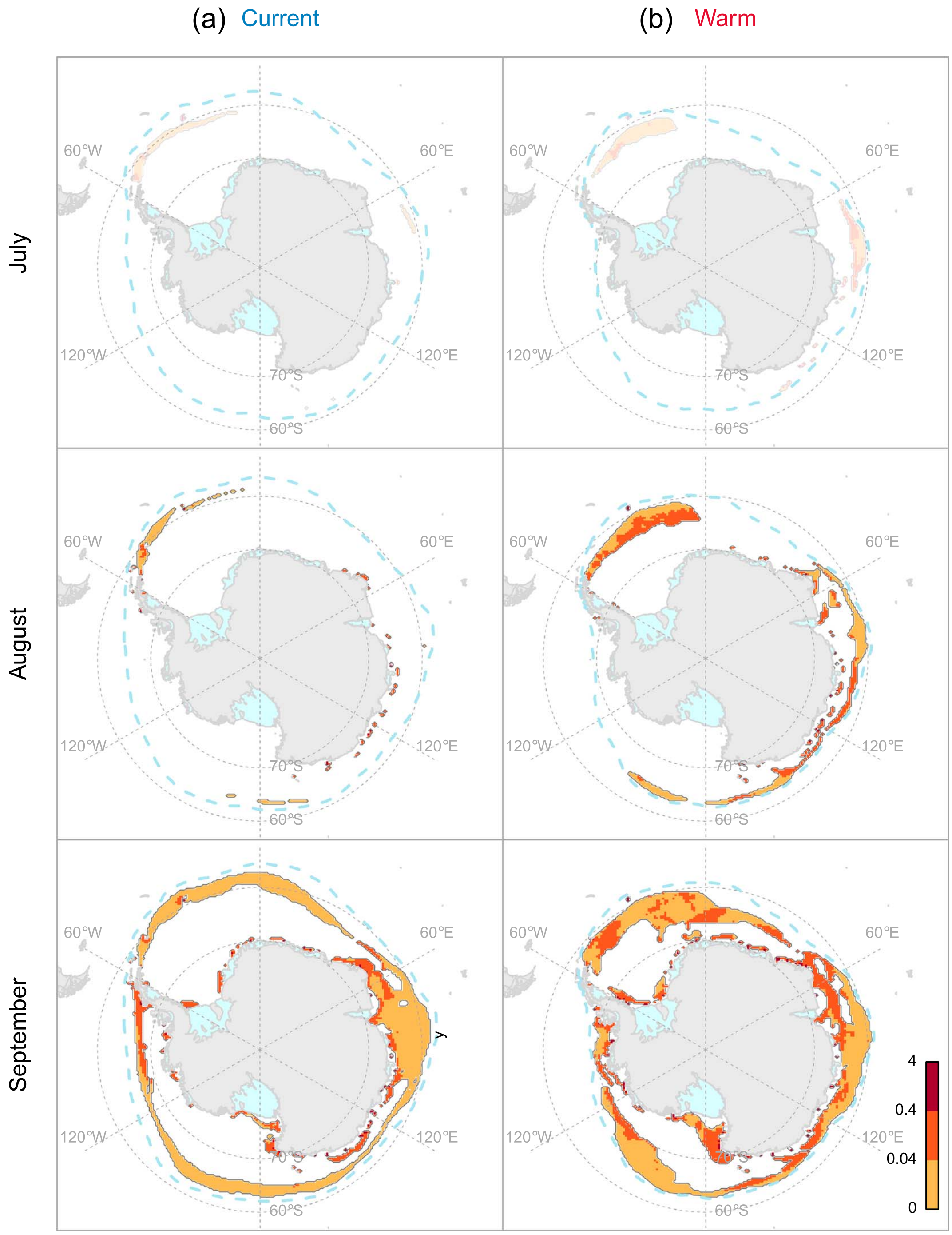

Figure 2. The location of modeled under ice habitat for larval krill under (a) current conditions (1998–2008) and (b) a warm climate scenario (2100) for each of (top row) July (lighter regions are for a 0.1 W m^{-2} threshold), (middle row) August, and (bottom row) September. Results are shown for 11 year means for each month. Blue dashed lines indicate the 15% ice concentration contour. Color scaling indicates ridging rate (in % day^{-1}).

et al., 2010] and is hypothesized to influence krill recruitment in this region [*Quetin et al*., 2007]. Changes to the timing of sea ice advance in winter under a warm climate scenario are not considered here. Further factors that are beyond the scope of our study include spatial patterns of nutrient supply for ice algae and the condition of krill larvae at the start of winter. Our analysis is intended as an initial step to inform more complex habitat models for larval krill, and our approach has considered those processes that are

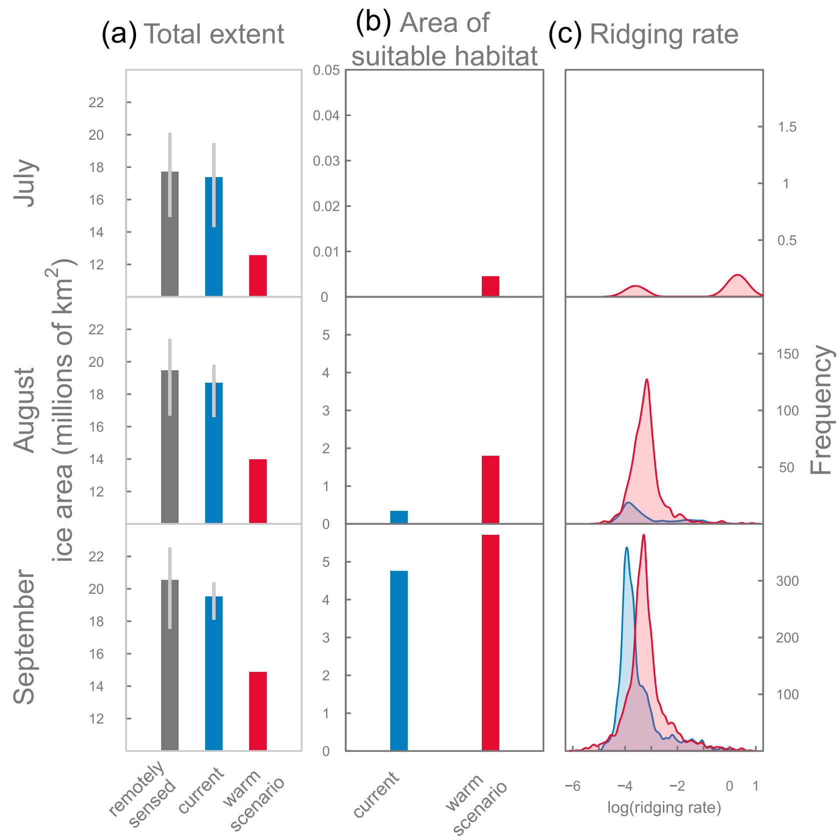

Figure 3. Comparison of (a) areal sea ice extent and (b) modeled larval krill habitat area and the distribution of (c) ridging rate values for current conditions (1998–2008; blue) and a warm climate scenario (2100; red). Remotely sensed sea ice extent for 1998–2008 [*Cavalieri et al*., 1996, updated yearly] is shown in grey in Figure 3a for comparison. Figures 3a and 3b show mean values (± standard error for remotely sensed and current sea ice extent; areas are calculated using mean states for each pixel, so errors are not additive for habitat area). Note differences in axes between panels (months) for Figures 3a and 3b.

documented at regional scales and for which we have some numerical estimates on which to base threshold suitability values.

The potential effects of climate change on populations of Antarctic krill have been explored with respect to the sensitivity of krill to ocean acidification at a circumpolar scale [*Kawaguchi et al*., 2013] and to changes in temperature and chlorophyll for the Weddell quadrant [*Hill et al*., 2013]. Our results indicate that climate change effects on different life stages of krill may not be consistently positive or negative in direction; the complexity of interactions over the lifetime of krill may yield unexpected population level outcomes. We suggest that further studies of climate change impacts for other life cycle stages would provide a clearer picture of potential futures for Antarctic krill populations. Further, models are needed to link these ecologies with future scenarios from global climate models (GCMs) in order to assess the consequences for krill populations as a whole. The variables used in our study—and that are likely to be important determinants of under ice habitats—were not required outputs for these models in the IPCC's latest assessment (Coupled Model Intercomparison Project Phase 5 (CMIP5)). There is a critical need to identify good proxies for krill habitat that could be derived from GCMs and therefore used to model changes in these habitats.

Acknowledgments
This study was supported by the Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystem Cooperative Research Centre and through the Australian Antarctic Science Program (projects 4343 and 4347). Model output supporting the conclusions in this paper is available via the Australian Antarctic Data Centre (doi:10.4225/15/57EB552A7A58C).

References

Adams, N. (2006), *Continued Developments in Numerical Weather Prediction and Weather Forecasting in Support of the Australian Antarctic Program*, The Antarctic Meteorological Observation, Modelling, and Forecasting Workshop, Boulder, Colo., 13–15 June.

Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery (2004), Long-term decline in krill stock and increase in salps within the Southern Ocean, *Nature*, *432*(7013), 100–103, doi:10.1038/nature0299.

Bailey, D., M. Holland, E. Hunke, B. Lipscomb, B. Briegleb, C. Bitz, and J. Schramm (2010), *Community Ice CodE (CICE) User's Guide Version 4.0*, Natl. Cent. for Atmos. Res., Boulder, Colo.

Bi, D., and S. Marsland (2010), *Australian Climate Ocean Model (auscom) Users Guide*, The Centre for Australian Weather and Climate Research, Melbourne, Australia.

Brierley, A. S., P. G. Fernandes, M. A. Brandon, F. Armstrong, N. W. Millard, S. D. McPhail, P. Stevenson, M. Pebody, J. Perrett, and M. Squires (2002), Antarctic krill under sea ice: Elevated abundance in a narrow band just south of ice edge, *Science*, *295*(5561), 1890–1892.

Cavalieri, D., C. Parkinson, P. Gloersen, and H. Zwally (1996 (updated yearly)), *Sea Ice Concentrations From Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data. 1998–2008*, NASA Natl. Snow and Ice Data Cent. Distributed Active Archive Center, Boulder, Colo.

Collins, M., et al. (2013), Long-term Climate Change: Projections, Commitments and Irreversibility, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. Stocker et al., Cambridge Univ. Press, Cambridge, U. K., and New York.

Constable, A. J., et al. (2014), Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota, *Global Change Biol.*, *20*(10), 3004–3025, doi:10.1111/gcb.12623.

Daly, K. L. (2004), Overwintering growth and development of larval *Euphausia superba*: An interannual comparison under varying environmental conditions west of the Antarctic Peninsula, *Deep Sea Res., Part II*, *51*(17–19), 2139–2168, doi:10.1016/j.dsr2.2004.07.010.

Flores, H., J.-A. van Franeker, V. Siegel, M. Haraldsson, V. Strass, E. H. Meesters, U. Bathmann, and W. J. Wolff (2012), The association of Antarctic krill *Euphausia superba* with the under-ice habitat, *PLoS One*, *7*(2), e31775, doi:10.1371/journal.pone.0031775.t004.

Frazer, T. K., L. B. Quetin, and R. M. Ross (2002), Abundance, sizes and developmental stages of larval krill, Euphausia superba, during winter in ice-covered seas west of the Antarctic Peninsula, *J. Plankton Res.*, *24*(10), 1067–1077.

Fritsen, C. H., J. C. Memmott, R. M. Ross, L. B. Quetin, M. Vernet, and E. D. Wirthlin (2010), The timing of sea ice formation and exposure to photosynthetically active radiation along the Western Antarctic Peninsula, *Polar Biol.*, *34*(5), 683–692, doi:10.1007/s00300-010-0924-7.

Frouin, R., and R. T. Pinker (1995), Estimating photosynthetically active radiation (PAR) at the earth's surface from satellite observations, *Remote Sens. Environ.*, *51*(1), 98–107, doi:10.1016/0034-4257(94)00068-X.

Hill, S. L., T. Phillips, and A. Atkinson (2013), Potential climate change effects on the habitat of Antarctic krill in the Weddell quadrant of the Southern Ocean, *PLoS One*, *8*(8), e72246, doi:10.1371/journal.pone.0072246.s005.

Hunke, E. C. (2010), Thickness sensitivities in the CICE sea ice model, *Ocean Modell.*, *34*, 137–149, doi:10.1016/j.ocemod.2010.05.004.

Hunke, E. C. (2014), Sea ice volume and age: Sensitivity to physical parameterizations and thickness resolution in the CICE sea ice model, *Ocean Modell.*, *82*, 45–59, doi:10.1016/j.ocemod.2014.08.001.

Kawaguchi, S. (2016), Reproduction and Larval Development in Antarctic Krill (*Euphausia superba*), in *Biology and Ecology of Antarctic Krill*, Advances in Polar Ecology, edited by V. Siegel, Springer, Switzerland, doi:10.1007/978-3-319-29279-3_6.

Kawaguchi, S., A. Ishida, R. King, B. Raymond, N. Waller, A. Constable, S. Nicol, M. Wakita, and A. Ishimatsu (2013), Risk maps for Antarctic krill under projected Southern Ocean acidification, *Nat. Clim. Change*, *3*(7), 1–5, doi:10.1038/nclimate1937.

Kurtz, N. T., and T. Markus (2012), Satellite observations of Antarctic sea ice thickness and volume, *J. Geophys. Res.*, *117*, C08025, doi:10.1029/2012JC008141.

Marr, J. (1962), The natural history and geography of the Antarctic krill (*Euphausia superba* Dana), *Discovery Rep.*, *32*, 33–464.

Meehl, G., et al. (2007), Global Climate Projections, in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., Cambridge Univ. Press, Cambridge, U. K., and New York.

Meiners, K. M., et al. (2012), Chlorophyll a in Antarctic sea ice from historical ice core data, *Geophys. Res. Lett.*, *39*, L21602, doi:10.1029/2012GL053478.

Meyer, B. (2011), The overwintering of Antarctic krill, *Euphausia superba*, from an ecophysiological perspective, *Polar Biol.*, *35*(1), 15–37, doi:10.1007/s00300-011-1120-0.

Meyer, B., and B. Oettl (2005), Effects of short-term starvation on composition and metabolism of larval Antarctic krill *Euphausia superba*, *Mar. Ecol. Prog. Ser.*, *292*, 263–270.

Meyer, B., V. Fuentes, C. Guerra, K. Schmidt, A. Atkinson, S. Spahic, B. Cisewski, U. Freier, A. Olariaga, and U. Bathmann (2009), Physiology, growth, and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica, *Limnol. Oceanogr.*, *54*(5), 1595–1614.

Morgan-Kiss, R. M., J. C. Priscu, T. Pocock, L. Gudynaite-Savitch, and N. P. Huner (2006), Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments, *Microbiol. Mol. Biol. Rev.*, *70*(1), 222–252, doi:10.1128/MMBR.70.1.222-252.2006.

Nicol, S. (2006), Krill, currents, and sea ice: *Euphausia superba* and its changing environment, *BioScience*, *56*(2), 111–120, doi:10.1641/0006-3568.

Nicol, S., J. Foster, and S. Kawaguchi (2011), The fishery for Antarctic krill—Recent developments, *Fish Fish.*, *13*(1), 30–40, doi:10.1111/j.1467-2979.2011.00406.x.

Parkinson, C. L., and D. J. Cavalieri (2012), Antarctic sea ice variability and trends, 1979–2010, *Cryosphere*, *6*(4), 871–880, doi:10.5194/tc-6-871-2012.

Quetin, L., and R. Ross (2003), Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region, *Mar. Ecol. Prog. Ser.*, *259*, 185–200.

Quetin, L., R. Ross, C. H. Fritsen, and M. Vernet (2007), Ecological responses of Antarctic krill to environmental variability: Can we predict the future? *Antarct. Sci.*, *19*(02), 253, doi:10.1017/S0954102007000363.

Ratnarajah, L., J. Melbourne-Thomas, M. P. Marzloff, D. Lannuzel, K. M. Meiners, F. Chever, S. Nicol, and A. R. Bowie (2016), A preliminary model of iron fertilisation by baleen whales and Antarctic krill in the Southern Ocean: Sensitivity of primary productivity estimates to parameter uncertainty, *Ecol. Modell.*, *320*(C), 203–212, doi:10.1016/j.ecolmodel.2015.10.007.

Siegel, V., and V. Loeb (1995), Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability, *Mar. Ecol. Prog. Ser.*, *123*, 45–56.

Stevens, R. (2013), A numerical investigation into Southern Ocean sea ice using CICE version 4.0, PhD thesis, 122 pp., Univ. of Tasmania. [Available at http://eprints.utas.edu.au/17585/.]