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**Critical Literature Review**  
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***Climate change effects and the future for Antarctic krill***

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**Abstract**

Climate change effects are already being observed in some regions of the Southern Ocean, where reduced duration and extent of winter sea-ice, ocean warming and ocean acidification threaten the survival of Antarctic krill. This species is critical to the Antarctic ecosystem, where most marine mammal and bird species depend on it as a food source. Whilst there may be some positive effects from the impacts of climate change, their combined effect is likely to be negative and threaten the life cycle and distribution of krill.

Long term studies in the southwest Atlantic have linked decreased krill abundance with reduced coverage of winter sea-ice. The Southern Ocean is particularly vulnerable to ocean acidification, which is likely to disrupt the hatching success of krill larvae, and ocean warming may have implications for the range and distribution of krill populations. Recorded catch levels in the krill fishery have also seen recent increases, and fishing pressure coupled with climate change implications may place the future of Antarctic krill in jeopardy.

This review will examine current predicted climate change effects and their potential impacts on krill, and whether the combined pressures of increased fishing and a changing environment in the Southern Ocean are effectively managed within the current CCAMLR framework.

# Climate change effects and the future for Antarctic krill

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## Introduction

Some regions of Antarctica are already experiencing environmental transformation as a result of climate change, particularly loss of winter sea-ice, ocean warming and ocean acidification (Flores et al. 2012b, Kawaguchi and Nicol 2009). Antarctic krill (*Euphausia superba*) is a keystone species that is critical to Antarctic ecosystem function, being an important food source for most marine mammals and birds in the Southern Ocean. Whilst some impacts of climate change can have positive effects on population sizes, their combined effect is likely to be negative and threaten the life cycle and distribution of krill (Flores et al. 2012b, Pinones et al. 2013). The life-cycle stage that is likely to be most adversely affected is the winter survival of larval krill that feed on algae underneath the surface of sea-ice. Long term studies in the southwest Atlantic have shown an 80% decrease in krill abundance over the past 30 years, associated with reduced coverage of winter sea-ice (Meyer 2010). The Southern Ocean is particularly vulnerable to ocean acidification, which leads to increased levels of CO<sub>2</sub> in seawater. Research by Kawaguchi et al. (2013) has demonstrated that increased partial pressure of CO<sub>2</sub> disrupts the hatching success of krill larvae, and that this is exacerbated by the fact that krill eggs sink passively to depths in the ocean where the partial pressure of CO<sub>2</sub> is greater than that of the atmosphere.

Changes to the physical and chemical conditions in the Southern Ocean brought about by climate change could have catastrophic effects on krill abundance, with dire consequences for the entire ecosystem (Flores et al. 2012b, Kawaguchi et al. 2013, Trivelpiece et al. 2011). In recent years krill has also become an important resource for fisheries with recorded catch levels increasing yearly since the 2009/2010 season, potentially placing additional pressure on krill populations (Flores et al. 2012b). In a recent report, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) documented reported krill catches increasing from 156,289 tonnes in the 2011/12 season to 212,000 tonnes in the 2012/13 season, and notified total predicted catches for 2013/2014 season of 545,000 tonnes (CCAMLR 2013).

This review will examine current projections of major climate change effects and their potential impacts on krill, and the effectiveness of the ecosystem-based management approach practiced by CCAMLR in dealing with the combined pressures of increased krill fishing and a changing environment in the Southern Ocean.

## **Climate change effects and their impact on krill**

### *Changes in sea-ice*

Over the past decades, considerable regional variation in sea-ice extent has been recorded around Antarctica. According to Turner et al. (2009), average monthly sea-ice extent between 1979 and 2008 has been declining in the west Antarctic Peninsula region by almost 7% per decade, whereas other regions have seen increases in sea-ice extent over the past three decades. Combined with observations in the Ross Sea of close to a 5% per decade increase, Turner et al. (2009) predict an overall increase in sea-ice extent of around 1%. However, while much attention has been given to the areal extent of ice coverage, its thickness and duration may be of greater ecological importance (Flores et al. 2012b). Sea-ice duration in both the western Antarctic Peninsula region and southern Bellingshausen Sea has reduced by 85 days over the 1979 to 2004 period (Stammerjohn et al. 2008), which is consistent with increased temperatures and declining ice cover observed in these regions (Turner et al. 2009). In the Ross Sea, however, the duration of sea-ice has been lengthening over the 1979 to 2004 period by 23.1 days per decade (Stammerjohn et al. 2008). Worby et al. (2008) have produced average circumpolar ice thickness distributions for the period 1981 to 2005. This study showed that the western Weddell Sea (an area of high krill abundance and harvesting) has the highest annual mean ice thickness, and also the highest variability in ice thickness compared to other Antarctic sea-ice regions.

Regional variations in the extent and duration of sea-ice cover in Antarctica may have disguised the potentially more insidious problem of reduced sea-ice thickness. A recent study by DeLiberty et al. (2011) contradicts some existing models that show a co-variance between sea-ice thickness and extent, and demonstrates that ice thickness and ice extent respond distinctly differently to thermodynamic processes during the annual cycle. With the predicted continuation of climate and ocean warming (IPCC 2013), a more comprehensive understanding of sea-ice thickness versus areal extent is required to more accurately predict the response of sea-ice to climate change.

Antarctic krill (hereafter 'krill') are affiliated with sea-ice at each stage of their life cycle (Flores et al. 2012b, Siegel et al. 1990), and Atkinson et al. (2004) have demonstrated a strong positive correlation between krill abundance and winter sea-ice extent. Larval krill do not have the capacity to store food energy from autumn phytoplankton blooms and are therefore dependent on sea-ice biota as a food resource during winter (Meyer et al. 2009). This dependency becomes critical when the sea-ice duration changes because the timing of ice formation at specific latitudes determines the level of food abundance in the winter sea-ice (Quetin et al. 2007). Surfaces underneath sea-ice afford a protective, micro-habitat for larvae and floating, upturned ice 'rafts' can transport juvenile krill and protect them from predation (Meyer et al. 2009). Sea-ice transport plays a critical role in recruitment of krill from the Antarctic continental shelf to the South Georgia region (Fach et al. 2006) and declining sea-ice

may therefore affect downstream recruitment with specific consequences for larvae and juvenile stages.

Ice algae increase their productivity during spring and as sea-ice melts it releases algae and nutrients into the water which initiates intense blooms of phytoplankton around the margins of the ice zone (Flores et al. 2012a). Krill rely on these sea-ice triggered blooms for summer feeding and it is thought that this productivity process sustains large populations of top predators (Perissinotto et al. 1997). Climate and ocean warming in the Antarctic region is likely to reduce the total area of ice algae productivity and force a southward contraction of these grazing grounds which will further reduce algal productivity due to lower light availability (Flores et al. 2012b).

There is a complex relationship between sea-ice and the life cycle of krill. Reduced duration and extent combined with changes to the geographical range of this habitat is likely to have compounded negative effects on reproduction and survival, with ramifications for the entire Antarctic food web.

### *Warming of the Southern Ocean*

The Antarctic Circumpolar Current (ACC) is the largest ocean current on Earth and its waters have warmed at a more rapid pace than the entire global ocean (Flores et al. 2012b). Between the 1950's and the 1980s, mid-depth Southern Ocean temperatures have risen by 0.17°C and between 1951 and 1998 surface water temperatures on the western side of the Antarctic Peninsula increased more than 1°C (Gille 2002). Mean temperature in the top 100m of the water column at South Georgia has risen by 0.9 °C in January and 2.3 °C in August over the past 80 years (Whitehouse et al. 2008). Turner et al. (2009) report that summer sea-surface temperatures (SSTs) south of 60 ° are predicted to be between 0.5 °C and 1.25 °C warmer in 2100 than present conditions, and winter SSTs are likely to be between 1°C warmer or -0.25 °C cooler than present. This report also projects that waters to 4000m depth along the continental margin are expected to experience seasonally independent warming of ~0.25°C, and possibly up to or slightly over 0.5°C at 200 to 500m depth. However, the Southern Ocean is one of the regions where the largest discrepancies are found both among model types and between models and observations (Flores et al. 2012b).

Krill have adapted to the cool, stable temperatures that have been a feature of their habitat since the formation of the Drake Passage 39 to 35 million years ago (Flores et al. 2012b). The temperature difference between the coldest and warmest habitats in their range of distribution is only ~7°C, making it likely that temperature changes in the range of 1 to 2°C will significantly impact krill physiology, behaviour and distribution (Mackey et al. 2012). Being stenotherm crustaceans, krill are unlikely to tolerate temperature variations beyond the regular range of their habitat (Mackey et al. 2012),

particularly over the longer term (Atkinson et al. 2006). Conversely, increased water temperatures may be beneficial for adult krill in colder habitats due to increased metabolic rates and food availability (Atkinson et al. 2006), however it is possible that warmer surface temperatures may drive krill to deeper waters with foraging implications for air-breathing predators (Schmidt et al. 2011).

Although krill are expected to be affected both positively and negatively by ocean warming, depending on regional effects on food webs, it is likely that rising water temperatures will produce increasingly negative consequences (particularly at early developmental stages) and result in a southward shift in krill distribution (Flores et al. 2012b).

### *Ocean acidification*

Absorption of atmospheric CO<sub>2</sub> by the world's oceans results in chemical changes that reduce the pH level, the concentration of carbonate ions and the availability of minerals important for the growth, reproduction and survival of a variety of marine life, in a process termed ocean acidification (Garrard et al. 2012). Since the industrial revolution current atmospheric CO<sub>2</sub> levels have caused a decline of about 0.1 pH units (a 30% increase in acidity), and under a "business as usual" emissions scenario this level is projected to drop by an average 0.5 units (to about pH 7.8) by the year 2100 (IGBP, IOC, SCOR 2013). It is commonly accepted that unremitting anthropogenic CO<sub>2</sub> emissions will impact marine species and ecosystems, however comprehensive research into the mechanisms, range of sensitivities and evolutionary ramifications is only just beginning (Dupont & Portner 2013). The majority of research has focussed on the effects of ocean acidification (OA) on calcareous marine organisms such as corals and pteropods (Kawaguchi et al. 2011), however it has become clear that the impacts of OA extend much further than just calcifying species and can affect a range of biological processes that are critical to the survival of a broad range of organisms (Dupont & Portner 2013).

The effects of OA in the Southern Ocean are expected to be particularly acute given that CO<sub>2</sub> and CaCO<sub>3</sub> are more soluble in cold water, and due to regional upwelling of colder, deep sea water (Kawaguchi et al. 2011). Recent evidence from *in situ* time series studies shows that OA is already increasing in large regions of the Southern Ocean (Midorikawa et al. 2012). Considerable differences in regional concentration of CO<sub>2</sub> are likely to occur, with some of the largest projected increases forecast for areas of high krill population density (Flores et al. 2012b).

Little is known about the physiological effects of OA on krill, however recent experiments on the effects of elevated partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>) on captive krill larvae (Kawaguchi et al. 2011, 2013) has provided some indication of their sensitivity to ocean CO<sub>2</sub> levels. Model-based projections of CO<sub>2</sub> concentrations in the Southern Ocean measured in  $\mu\text{atm}$  (1  $\mu\text{atm}$  = 1 ppm in air) indicate that

PCO<sub>2</sub> of surface water may reach 584 µatm in the Scotia Sea and 870 µatm in the Weddell Sea by 2100 (Kawaguchi et al. 2011). These levels may be in excess of 1000 µatm by 2100, potentially reaching 1400 µatm in the Weddell Sea region at krill depths of 300-500m (Kawaguchi et al. 2011). Normal larvae development was observed under a pCO<sub>2</sub> range of up to 1000 µatm, however at 2000 µatm their development was almost totally subdued. Krill eggs may be particularly vulnerable to increased CO<sub>2</sub> levels as they sink passively to hatch at depths of 700-1000m where pCO<sub>2</sub> is already at a greater level than the atmosphere (Kawaguchi et al. 2013). Whilst krill appear to have some ability to cope with increased pCO<sub>2</sub> due to natural exposure through vertical migration (Kawaguchi et al. 2011), exposure to elevated pCO<sub>2</sub> levels has been shown to disrupt embryonic development and increase metabolic costs in post-larval krill (Kawaguchi et al. 2013).

Further challenges to the survival of krill (and other organisms) may be presented by the effects of OA on phytoplankton which is their major food source (Haberman et al. 2003). The effects of OA on phytoplankton have been extensively researched with results indicating that changes in carbonate chemistry of seawater can impact growth, photosynthesis and nitrogen fixation (Morton et al. 2009). Although it seems logical to assume that photosynthesising organisms would benefit from increased carbon concentration in seawater, their varied strategies for carbon utilisation mean that some taxa may respond less positively and have increased energetic costs to manage the changed chemical environment (Harley et al. 2012). Photosynthetic organisms (including phytoplankton) also require a range of metals for growth and survival, and decreased pH can alter their bioavailability or toxicity in the marine environment (Garrard et al. 2012). The variation in species response to OA is also likely to lead to changes in community composition, with significant impacts on the function of the marine food web (Garrard et al. 2012).

### **Krill fishery management**

Reported catches in the Antarctic krill fishery have been increasing over the past few years with catches rising from 156,289 tonnes in the 2011/12 season to 212,000 tonnes in the 2012/13 season, and notified total predicted catches for 2013/2014 season at 545,000 tonnes (CCAMLR 2013). Although these catch levels fall well below current estimates of total krill biomass in the Southern Ocean region, there is lingering concern over the sustainability of the fishery given that the current harvest increase is following a period of krill population decline in the southwest Atlantic sector (Flores et al. 2012b). Miller (2014) notes that decreases in krill abundance may be equally attributable to sea-ice decline or restoration of predator populations, highlighting the potential difficulties in understanding ecosystem dynamics and the ramifications for sustainable fisheries management.

CCAMLR applies the generalised yield model (GYM) to large statistical management areas in order to set precautionary catch limits over a 20 year period (Flores et al. 2012b). The model is based on an estimate of pre-exploitation krill biomass, and other parameters incorporated into the model such as recruitment, growth and mortality are all factors that are likely to be affected by climate change. The model does not currently take into account climate change impacts or inter-annual variability of krill biomass, however a review of assumptions around krill dynamics may form part of a new feedback management strategy currently under consideration (CCAMLR 2013). The feedback management system requires continuous adjustment of management measures as more information becomes available on regional or global changes (Flores et al. 2012b).

The ability of CCAMLRs stewardship measures to keep pace with the growing krill fishery is uncertain. Developments in catch efficiency, rapid diversification of krill products and an increase in the number of krill fishing countries suggest that the fishery is poised for great expansion in the short to medium term (Miller 2014). In an effort to distinguish changes due to environmental variability from those induced by fisheries, CCAMLR instituted the CCAMLR Ecosystem Monitoring Program (CEMP) in 1989. The aim of the program was to engage fishing vessels in scientific surveys and the collection of data on key krill predators, however a lack of standardised data has left CEMP unable to determine differences in the impacts of fishing versus environmental change (Flores et al. 2012b). The proposed feedback management system will not be viable without a more efficient evolution of CEMP, and future management of the krill fishery will need to take advantage of this largely under-utilised information source (Kawaguchi and Nicol 2009) to enhance its ability to counter the impacts of increased fishing pressure and environmental uncertainty with regard to climate change. Another important management measure to boost the resilience of krill populations to the effects of a changing climate and over-harvesting is the designation of marine protected areas (MPAs) to facilitate biodiversity conservation (Miller 2014). CCAMLR began the process of designing a representative network of MPAs, however only one MPA (in the South Orkney Islands) has been created so far, and agreement has not yet been reached over the proposal for a second MPA in the Ross Sea region (CCAMLR 2013).



## **Conclusion**

The multiple effects of climate change have the potential to have a profound effect on the structure and function of the Antarctic ecosystem. The scientific literature points to impacts at multiple levels - sea-ice decline, temperature increases and ocean acidification, with synergistic effects likely to negatively affect the abundance and distribution of krill. While there has been some progress in better understanding the multiple effects of climate change on the life history and ecology of krill, it is also apparent that key knowledge gaps remain in understanding the complex physiology, biology and ecology of krill. Urgent and ongoing research is critical to determining the ability of krill to either adapt to environmental change or shift their range to more tolerable habitats. New research and improved use of existing knowledge will be essential for CCAMLR to continue to develop adaptive management that incorporates the effects of climate change on krill and the Antarctic ecosystem. Recent research demonstrates that changes to ecosystems, krill distribution and recruitment are already occurring which could signal that management procedures may not achieve their goals within an effective time frame. Research priorities and management actions should be identified now to ensure the conservation of this key species and the ecosystems it supports.

## References

- 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*, vol. 432, pp. 100-103.
- Atkinson, A, Shreeve RS, and Hirst AG 2006. 'Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food temperature, body length, sex and maturity stage', *American Society of Limnology and Oceanography*, vol. 51, no. 2, pp. 973-987.
- CCAMLR 2013, *Preliminary report of the thirty-second meeting of the Scientific Committee*, CCAMLR, Hobart.
- Cicerone, R 2004, 'The ocean in a high-CO<sub>2</sub> world', *Oceanography*, vol. 17, no. 3, pp. 72-78.
- DeLiberty, TL, Geiger, CA, Ackley, SF, Worby, AP and Van Woert, ML 2011, 'Estimating the annual cycle of sea-ice thickness and volume in the Ross Sea', *Deep Sea research Part II: Topical Studies in Oceanography*, vol. 58, no. 9-10, pp. 1250-1260.
- Dupont, S and Portner H 2013, 'A snapshot of ocean acidification research', *Marine Biology*, vol. 16, pp. 1765-1771.
- Fach, BA, Hoffmann, EE and Murphy EJ 2006, 'Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part II: krill growth and survival', *Deep Sea Research I*, vol. 53, pp. 1011-1043.
- Flores, H, van Franeker JA, Siegel, V, Haraldsson, M, Strass, V, Meesters, EH, Bathmann, U and Wolff, JW 2012a, 'The association of Antarctic krill *Euphausia superba* with the under-ice habitat', *PLoS One*, vol. 7, no. 2, e31775.
- Flores, H, Atkinson, A and Kawaguchi, S 2012b, 'Impact of climate change on Antarctic krill', *Marine Ecology Progress Series*, vol. 458, pp. 1-19.
- Garrard, S, Hunter, RC, Frommel, AY, Lane, AC, Phillips, JC, Cooper, R, Dineshran, R, Cardini, U, McCoy, SJ, Arnberg, M, Rodrigues Alves, BG, Annanne, S, de Orte, MR, Kumar, A, Aguirre-Martinez, GV, Maneja, RH, Basalloe, MD, Ape, F, Torstensson, A, Bjoerk, MM 2012, 'Biological impacts of ocean acidification: a postgraduate perspective on research priorities', *Marine Biology*, DOI 10.1007/s00227-012-2033-3.
- Gille, ST 2002, 'Warming of the Southern Ocean since the 1950s', *Science*, vol. 295, pp. 1275-1277.
- Haberman, L, Ross, RR and Quetin, LB 2003, 'Diet of the Antarctic krill (*Euphausia superba* Dana): II. Selective grazing in mixed phytoplankton assemblages', *Journal of Experimental Marine Biology and Ecology*, vol. 283, pp. 97-113.
- Harley, CDG, Anderson, KM, Demes, KW, Jorve, JP, Kordas, RL, and Coyle, TA 2012, 'Effects of climate change on global seaweed communities', *Journal of Phycology*, vol. 48, pp. 1064-1078.
- IGBP, IOC, SCOR 2013, 'Ocean acidification summary for policymakers – third symposium on the ocean in a high-CO<sub>2</sub> world', *International Geosphere-biosphere Programme*, Stockholm, Sweden.

IPCC 2013, *Climate change 2013, the physical science basis: summary for policymakers*, retrieved 5 December 2013, [http://www.climatechange2013.org/images/uploads/WGI\\_AR5\\_SPM\\_brochure.pdf](http://www.climatechange2013.org/images/uploads/WGI_AR5_SPM_brochure.pdf)

Kawaguchi, S, Ishida, A, King, R, Raymond, B, Waller, N, Constable, A, Nicol, S and Ishimatsu, A 2013, 'Risk maps for Antarctic krill under projected Southern Ocean acidification', *Nature Climate Change*, vol. 3, no. 9, pp. 843-847.

Kawaguchi, S, Kurihara, H, King, R, Hale, L, Berlie, T, Robinson, JP, Ishida, A, Wakita, M, Virtue, P, Nicol, S and Ishimatsu, A 2011, 'Will krill fare well under Southern Ocean acidification?', *Biology Letters*, vol. 7, pp. 288-291.

Kawaguchi, S and Nicol S 2009, 'Direct effects of climate change on the Antarctic krill fishery', *Fisheries Management and Ecology*, vol. 16, pp. 424-427.

Mackey, A, Atkinson, A, Hill, S, Ward, P, Cunningham, N, Johnston, NM and Murphy EJ 2012, 'Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea: historical distributions; relationships with food; and implications for ocean warming', *Deep Sea Research II*, vo. 59-60, pp. 130-146.

Meyer, B, Fuentes, V, Guerra, C, Schmidt, K, Atkinson, A, Spahic, S, Cisewski, B, Freier, U, Olariaga, A and Bathmann U 2009, 'Physiology, growth and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica', *Limnology and Oceanography*, vol. 54, no. 5, pp. 1595-1614.

Meyer, B 2010, 'Antarctic krill, *Euphausia superba*, a model organism to understand the impact of global warming on the marine Antarctic ecosystem', *Polarforschung*, vol. 80, no. 1, pp. 17-22.

Midorikawa, T, Inoue, HY, Ishii, M, Sasano, D, Kosugi, N, Hashida, G, Nakaoka, S and Suzuki, T 2012, 'Decreasing pH trend estimated from 35-year time series of carbonate parameters in the Pacific sector of the Southern Ocean in summer', *Deep-Sea Research I*, vol. 61, pp. 131-139.

Miller, DGM 2014 'Antarctic marine living resources: The future is not what it used to be', in T. Tin, D. Liggett, P. Maher and M. Lamers (eds), *Antarctic futures*, Springer, Dordrecht, chapter 3.

Morton, SR, Hoegh-Guldberg, O, Lindenmayer, DB, Harriss Olson, M, Hughes, L, McCulloch, MT, McIntyre, S, Nix, HA, Prober, SM, Saunders, DA, Andersen, AN, Burgman, MA, Lefroy, EC, Lonsdale, WM, Lowe, I, McMichael, AH, Parlson, JS, Steffen, W, Williams, JE and Woinarski, JCZ 2009, 'The big ecological questions inhibiting effective environmental management in Australia', *Austral Ecology*, vol. 34, pp. 1-9.

Perissinotto, R, Pakhomov EA, McQuaid CD and Froneman PW 1997, 'In situ grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic polar front and the marginal ice zone', *Marine Ecology Progress Series*, vol. 160, pp. 77-91.

- Pinones, A, Hofmann, EE, Daly, KL, Dinniman, MS and Klinck, JM 2013, 'Modelling environmental controls on the transport and fate of early life stages of Antarctic krill (*Euphausia superba*) on the western Antarctic Peninsula continental shelf', *Deep-Sea Research I*, vol. 82, pp. 17-31.
- Quetin, LB, Ross, RM, Fritsen, CH and Vernet, M 2007, 'Ecological responses of Antarctic krill to environmental variability: can we predict the future?', *Antarctic Science*, vo. 19, pp. 253-266.
- Schmidt, K, Atkinson, A, Steigenberger, S, Fielding, S, Lindsay, MCM, Pond, D, Tarling, GA, Klevjer, TA, Allen, CS, Nicol, S and Achterberg, EP 2011, 'Seabed foraging by Antarctic krill: implications for stock assessment, benthic-pelagic coupling, and the vertical transfer of iron', *American Society of Limnology and Oceanography*, vol. 56, pp. 1411-1428.
- Siegel V, Bergstrom b, Stromberg JO and Schalk PH 1990, 'Distribution, size frequencies and maturity stages of krill *Euphausia superba*, in relation to sea-ice in the northern Weddell Sea', *Polar Biology*, vol. 10, pp. 549-557.
- Stammerjohn, SE, Martinson DG, Smith RC, Yuan, X and 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', *Journal of Geophysical Research*, vol. 113, CS03S90 doi:10.1029/2007JC004269.
- Trivelpiece, WZ, Hinke, JT, Miller, AK, Reiss, CS, Trivelpiece, SG and Watters, GM 2011, 'variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica', *Proceedings of the National Academy of Sciences*, vol. 108, no. 18, pp. 7625-7628.
- Turner, J, Bindshadler, R, Convey, P, di Prisco, G, Fahrbach, E, Gutt, J, Hodgson, DA, Mayewski, PA and Summerhayes, CP (eds) 2009, *Antarctic climate change and the environment*, SCAR, Cambridge.
- Whitehouse, MJ, Meredith, MP, Rothery P, Atkinson, A, Ward, P and Korb RE 2008, 'Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20<sup>th</sup> century: forcings, characteristics and implications for lower trophic levels', *Deep Sea Research I*, vol. 55, pp. 1218-1228.
- Worby, AP, Geiger CA, Paget MJ, Van Woert, ML, Ackley, SF and DeLiberty TL 2008, 'Thickness distribution of Antarctic sea ice', *Journal of Geophysical Research*, vol. 113, C05S92 doi:10.1029/2007JC004254.