Icebergs as Unique Lagrangian Ecosystems in Polar Seas

K.L. Smith Jr.,^{1,*} A.D. Sherman,¹ T.J. Shaw,² and J. Sprintall³

¹Monterey Bay Aquarium Research Institute, Moss Landing, California 95039; email: ksmith@mbari.org, alana@mbari.org

²Department of Chemistry and Biochemistry, University of South Carolina, Columbia, South Carolina 29208; email: shaw@mail.sc.edu

³Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093; email: jsprintall@ucsd.edu

Annu. Rev. Mar. Sci. 2013. 5:269-87

First published online as a Review in Advance on August 28, 2012

The Annual Review of Marine Science is online at marine.annualreviews.org

This article's doi: 10.1146/annurev-marine-121211-172317

Copyright © 2013 by Annual Reviews. All rights reserved

*Corresponding author

Keywords

pelagic community, carbon cycle, carbon export, Southern Ocean, Labrador Sea

Abstract

Global warming and its disproportionate impact on polar regions have led to increased iceberg populations. Southern Ocean studies in the northwest Weddell Sea have verified substantial delivery of terrestrial material accompanied by increased primary production and faunal abundance associated with free-drifting icebergs. It is hypothesized that input and utilization of macro- and micronutrients are promoted by conditions unique to freedrifting icebergs, leading to increased production, grazing, and export of organic carbon. In Arctic regions, increased freshwater input from meltwater acts to stratify and stabilize the upper water column. As has been observed in the Southern Ocean, Arctic-region icebergs should drive turbulent upwelling and reduce stratification, potentially leading to increased nitrate delivery to the local ecosystem. Increasing populations of icebergs in polar regions can potentially be important in mediating the drawdown and sequestration of CO_2 and can thus impact the oceanic carbon cycle.

INTRODUCTION

Rising global temperatures, especially in polar regions, lead to changes in nutrient availability and carbon export as a consequence of fronts, vertical stratification, meltwater input, and ice loss. In the Antarctic, free-drifting icebergs have been shown to increase carbon export via a combination of enhanced vertical mixing, increased micronutrient inputs, and efficient carbon export by the enhanced biological community (Smith et al. 2007, 2011; Shaw et al. 2011a; Stephenson et al. 2011). The extent to which these physical, chemical, and biological processes are enhanced by icebergs in northern latitudes and mediate carbon export is not known.

Icebergs are conspicuous features in the polar seascape; they have received considerable notoriety and have been tracked by the International Ice Patrol in Arctic regions ever since the sinking of the *Titanic* in 1912 (Int. Ice Patrol 2011). However, studies of these unique floating islands have been largely ignored until recently, with the unprecedented melting of glaciers and ice sheets in both the Antarctic and Arctic regions in response to the onset of global warming (Zwally et al. 2002, 2005; Rignot et al. 2011).

Icebergs range in size from smaller ice fragments—growlers (<5 m in largest dimension) and bergy bits (<15 m in largest dimension)—up to very large tabular icebergs that can exceed 300 km in length, with the majority of icebergs being from 60 to 2,200 m in length and from 150 to 550 m in thickness (Gladstone et al. 2001, Woodworth-Lynas et al. 2009). The size and shape of icebergs are related to the parent ice mass in both the Antarctic and Arctic (Dowdeswell et al. 1992, Dowdeswell & Bamber 2007). Icebergs fragment and become smaller with age owing to evaporation, melting, wave-induced erosion, and fracturing (Kristensen 1983, Scambos et al. 2005). Depending on the topography and seasonal pack ice distribution, icebergs can be divided into three general categories: (*a*) grounded icebergs, which are geographically stationary because they are in contact with the seafloor; (*b*) constrained icebergs, which are unrestrained. This review concentrates on the physical, chemical, and biological properties and processes associated with free-drifting icebergs in both the southern and northern polar regions.

SOUTHERN POLAR REGIONS (ANTARCTIC-GENERATED ICEBERGS)

In the Antarctic (Figure 1), regional warming around West Antarctica, including the Antarctic Peninsula (Vaughan et al. 2001, Thompson & Solomon 2002, Steig et al. 2009), has been correlated with retreating glaciers (De Angelis & Skvarca 2003, Cook et al. 2005), resulting in significant ice mass losses over the past several decades (Wingham et al. 2009). There have been increased occurrences of large icebergs (>18.5 km long) originating from ice shelves in the Ross, Bellingshausen, and Weddell Seas (Scambos et al. 2000, Long et al. 2002), attributed primarily to major calving events in the Ross and Weddell Seas (Ballantyne 2002, Stuart & Long 2011). Orheim (1988, as cited in Williams et al. 1999) estimated a population of \sim 200,000 icebergs in the Southern Ocean with maximum dimensions of tens of meters to tens of kilometers. Icebergs from many geographic sources become entrained in the counterclockwise Antarctic Coastal Current, which is often diverted by topographic features (Gladstone et al. 2001). East of the Antarctic Peninsula, the Antarctic Coastal Current combines with the offshore Antarctic Slope Front and Weddell Front, extending over the continental shelf and slope and creating a strong barotropic northward flow in the northwest Weddell Sea (Thompson & Heywood 2008) that entrains large numbers of icebergs from origin sites around Antarctica (Ballantyne 2002, Schodlok et al. 2006, Stuart & Long 2011). Of all large icebergs (>5 km in maximum dimension) detected by the SeaWinds satellite scatterometer around the Antarctic continent from 1999 to 2009, 90% passed through



Figure 1

The Antarctic continent, showing the general trajectories (*white arrows*) of icebergs moving counterclockwise. The majority reach the Weddell Sea and become entrained along the eastern side of the Antarctic Peninsula, an area known as the Antarctic Iceberg Alley (Stuart & Long 2011).

the Weddell and Scotia Seas (Stuart & Long 2011) (**Figure 1**). Smaller icebergs (in the range of <1 km in maximum dimension) can also be detected by altimeter waveform analysis (Tournadre et al. 2008). Drifter studies over a 43-year period have shown a decrease in travel time from the western tip of the Antarctic Peninsula across the South Scotia Ridge to South Georgia related to the positive trend in the Southern Annular Mode (Renner et al. 2012).

Many earlier Antarctic studies investigated the seasonal pack ice that serves as a habitat for complex communities of marine organisms. These organisms occupy habitats ranging from internal brine pockets in the ice matrix to external surfaces that extend meters below the air-water interface (Lizotte & Arrigo 1998, Gradinger 1999, Kang et al. 2001, Thomas & Dieckmann 2002). The edge of the seasonal pack ice is associated with increased primary production or blooms attributed in part to the release of primary producers entrapped during sea ice formation the previous season, and in part to the stability of the surrounding surface water created by the melting ice (Smith & Nelson 1986, Knox 1994). Pack ice may also serve as a source of iron during spring and summer melting, providing this nutrient that is required for primary production (Sedwick et al. 2000).

There is evidence that large icebergs influence surface primary production by preventing pack ice migration and restricting the area of open sea for phytoplankton growth (Arrigo et al. 2002, Arrigo & van Dijken 2003). It was hypothesized that freshwater from the melting ice of freedrifting icebergs could create an upwelling effect in the surrounding seawater; if the draft of an iceberg were sufficient to penetrate the nutricline and pycnocline, then nutrient-rich waters could be introduced at the surface to enrich phytoplankton growth (Neshyba 1977, Sancetta 1992). In high-latitude regions, upwelling of micronutrient iron is likely to promote overall productivity. Upwelling is also associated with diatom blooms, even in macronutrient-replete waters (Vernet et al. 2011). The differential motion of the upwelling water could force pack ice away from the iceberg, resulting in an area of open water immediately surrounding the iceberg and allowing the penetration of sunlight to primary producers (Jacobs et al. 1979).

Nutrient enrichments have also been measured in association with free-drifting icebergs in the Southern Ocean. Nonbiogenic fixed nitrogen associated with icebergs was previously thought to provide a major nitrogen contribution to the Southern Ocean epipelagic zone (Parker et al. 1978); however, other investigations have shown only a minor contribution (Biggs 1978), with variation related to the origin of individual icebergs (Jacobs et al. 1979). Increased concentrations of iron and chlorophyll *a* accompanied by an increased abundance of nanoplankton were measured in the wake of a drifting iceberg in the southern Indian Ocean (de Baar et al. 1995). At higher trophic levels, the density of acoustically reflective targets, believed to be zooplankton and micronekton, was twice as high under a free-drifting iceberg as it was in surrounding open water in the Weddell Sea (Kaufmann et al. 1995). Juvenile icefish were observed within small caves in the walls of a large iceberg in the Ross Sea (Stone 2003). Top predators such as chinstrap penguins and Antarctic fur seals are known to associate with icebergs in the northwest Weddell Sea (Joiris 1991, Ribic et al. 1991). Communities of seabirds, including southern fulmars, Wilson's storm petrels, Antarctic petrels, and mottled petrels, have been associated with icebergs in the Ross Sea (Ainley et al. 1984).

The Southern Ocean is the largest of the high-nutrient, low-chlorophyll regions of the world oceans, and it is thought to play an important role in global carbon dynamics (Sarmiento & Orr 1991). The poor efficiency in preformed macronutrient utilization leads to the net loss of previously sequestered CO_2 from the Southern Ocean (Sigman et al. 2010). Hence, evaluating factors that may mediate carbon export, past and present, is essential to predicting carbon budgets. Phytoplankton in much of the Southern Ocean are limited by iron availability (de Baar et al. 1990, Martin et al. 1990, Boyd et al. 2000, Gervais et al. 2002, Coale et al. 2004), leading Martin (1990) to suggest that iron fertilization of the Southern Ocean may have contributed to the drawdown of atmospheric CO₂ during the Last Glacial Maximum. More recent analyses have questioned the importance of this mechanism (Rothlisberger et al. 2004, Kohfeld et al. 2005) but remain uncertain about the magnitude of terrestrial dust fluxes (Maher & Dennis 2001, Wolff et al. 2006). Aeolian dust inputs, well represented in Antarctic ice cores (Petit et al. 1999), have received the most attention, but icebergs could also serve as a significant source of iron to the Southern Ocean. High iron concentrations have been measured in floating ice of glacial origin (Martin et al. 1990), and there is evidence that iron concentrations are elevated in the wake and immediate vicinity of icebergs (Westerlund & Ohman 1991, de Baar et al. 1995, Löscher et al. 1997). Although these authors calculated the potential dissolved iron contribution from melting ice to be minor relative to the contributions of shelf transport and upwelling of deep waters, they did not consider the terrigenous particulate material contained within glacially derived icebergs. Depending on availability, the terrigenous particulate material could represent a much larger source of iron to the surrounding waters than the contributions calculated simply from the melting of ice (Raiswell et al. 2008).

The loss of approximately 150 Gt (1 Gt = 10^9 metric tons) of ice per year from all of Antarctica (Velicogna & Wahr 2006), in large part as collapsed ice shelves, begs for an evaluation of the contribution of detrital material as an iron source to the surface waters of the Southern Ocean. Aeolian dust was considered the primary natural iron source, but more recent studies indicate that upwelling, frontal activity, vertical diffusive mixing, shelf transport, and icebergs are more significant (Law et al. 2003, Blain et al. 2007, Dulaiova et al. 2009, Pollard et al. 2009, Shaw et al. 2011b). Terrigenous material contained within glacial icebergs may be a much larger source of iron to the surrounding waters than the contributions simply from ice melt (Lancelot et al. 2009, Raiswell 2011). Recent tracer studies using short-lived radium isotopes suggest that the delivery

of ice-rafted detrital material by icebergs to surface waters of the Weddell and Scotia Seas exceeds current dust input by several orders of magnitude and paleo dust estimates by at least a factor of 10 (Shaw et al. 2011b). Given the increasing abundance of these drifting islands of ice, natural iron enrichment from free-drifting icebergs could have a pronounced impact on the surrounding oceanic ecosystem.

Based on the scattered observations described above, a multidisciplinary study was undertaken in the northwest Weddell Sea to test the null hypothesis that free-drifting icebergs impart no significant chemical or biological characteristics to the surrounding water compared with waters some distance away. Two icebergs, 0.1 and 30.8 km² in aerial surface area, respectively, and the surrounding waters were sampled in austral spring using conventional oceanographic instruments such as CTD (conductivity, temperature, depth)/rosettes, trawls, and underway surface water monitoring. Significant enrichments of terrigenous material and chlorophyll and increased numbers of krill and seabirds were found surrounding each iceberg out to a radius of \sim 3.7 km (Smith et al. 2007). Further extrapolation of this area of enrichment to a population of icebergs derived from satellite images suggested that free-drifting icebergs could influence the pelagic ecosystem over a considerable area of the Southern Ocean. A subsequent study using satellite-derived ocean color and iceberg tracking also showed enhanced phytoplankton biomass several days after the passage of icebergs in the Weddell Sea (Schwarz & Schodlok 2009).

This first multidisciplinary study of icebergs demonstrated their influence on the surrounding pelagic ecosystems, including increased inputs of terrestrial material as well as increased abundance of phytoplankton, zooplankton, and micronekton (Smith et al. 2007). Nutrient enrichment related to these free-drifting icebergs should have a pronounced impact on the surrounding oceanic ecosystem, as artificial (Boyd et al. 2000, Coale et al. 2004) and natural (Blain et al. 2007, Pollard et al. 2009) enrichment studies have already shown in areas of the Southern Ocean. Given the higher abundance of pelagic consumers such as krill surrounding icebergs, iron fertilization by the melting of debris-laden ice should result in significantly higher carbon export, as exhibited in natural iron enrichment studies with established communities (Blain et al. 2007, Pollard et al. 2009) compared with the lower export indicated by short-term, artificial iron fertilization experiments (e.g., Coale et al. 2004). The community of consumers surrounding free-drifting icebergs and areas of natural iron upwelling ensure the rapid and efficient conversion and packaging of primary producers to particulate organic carbon as fecal material. Increased primary production and sedimentation associated with the expanding number of free-drifting icebergs have the potential to increase the drawdown and sequestration of CO₂ in the Southern Ocean, thus impacting the global carbon cycle in possibly significant proportions.

The finding that icebergs are hot spots of chemical and biological enrichment (Smith et al. 2007) fueled new interest in these floating islands. Free-drifting icebergs and their resident zooplankton communities contribute to a thriving system of efficient carbon and iron cycling with hypothesized enhanced sedimentation from this enriched surface layer, and the emergent picture of the iceberg zone of influence was one of altered properties and processes across all levels of the water column in what is termed the iceberg ecosystem. The next step was to quantify the impact of the interactions between the unique physical, chemical, and biological processes that could make icebergs foci of efficient carbon sequestration.

It became evident from these earlier studies that more sophisticated instrumentation would be necessary to further define the properties and processes involved in iceberg enrichment of the surrounding pelagic ecosystems and icebergs' potential to serve as sites of CO_2 drawdown and carbon export and final sequestration. One instrument developed in the study of free-drifting icebergs was the Lagrangian sediment trap (LST) (Sherman et al. 2011). The LST is essential for collecting sinking particulate matter surrounding individual icebergs, and these measurements have been used to estimate the export flux of carbon from these unique pelagic ecosystems at depths below the iceberg keels. The autonomous LST consists of a float containing a variable-buoyancy engine that enables the instrument to sink to a set depth beneath the iceberg, drift at that depth, and then resurface on preset time intervals. Four sediment-trap funnels and opening/closing sample cups are mounted on each LST to collect sinking particulate matter (Sherman et al. 2011).

Subsequent field studies using LSTs and other water-sampling devices were conducted in the northwest Weddell Sea along the Antarctic Iceberg Alley (**Figure 1**) in austral summer of 2009. The results from this fieldwork support the hypothesis that Antarctic icebergs serve as areas of local enrichment in particulate organic carbon export (Smith et al. 2011), as measured by LST sampling (Sherman et al. 2011) and proxy ²³⁴Th export from the surface waters (Shaw et al. 2011a). Fluxes of total mass and carbon were two to three times higher proximal to the icebergs than at a reference site 74 km away. Smith et al. (2011) found that sinking material was enriched in diatom frustules, crustacean and fish fecal pellets, detrital aggregates, and mineral grains; the bacterial production rates in this sinking material were over 400 times higher than in surrounding waters, providing evidence for the accumulation of labile organic matter. Enhanced carbon export was correlated with zones of altered physical, chemical, and biological factors.

The coupling of physical and chemical processes is evident in the form of micronutrient delivery to surface waters surrounding Antarctic icebergs. Processes leading to meltwater production have been identified and quantified, providing a basis for the additional coupling of the upwelled micronutrient input to biological processes that affect carbon export. Helly et al. (2011) found that at the surface, meltwater was detectable as far away as 19 km and persisted for at least 10 days, yet unexpectedly low particle and chlorophyll *a* concentrations were observed close to the iceberg; following iceberg passage, however, they observed elevated surface chlorophyll *a* concentrations in its wake for at least 10 days. This response by the phytoplankton community demonstrated the coupling of horizontal and vertical advection of iceberg meltwater to a sustained increase in phytoplankton production.

Stephenson et al. (2011) found that iceberg sidewall and basal melting below the surface contribute comparable amounts of meltwater to the water column via diffusive and turbulent upwelling processes, respectively. However, upwelling of basal meltwater mixtures appears to be localized and intermittent and may have contributed to the observed variability in micronutrient supply (Lin et al. 2011), microbes (Murray et al. 2011, Vernet et al. 2011), and zooplankton (Kaufmann et al. 2011) associated with icebergs. In contrast, thermohaline staircases consistent with sidewall melting by double-diffusive circulation cells were evident up to 18 km from an iceberg (Stephenson et al. 2011). This horizontal spreading of meltwater provides a means by which the seasonal thermocline can be enriched in nutrients from ice melt over a much larger area than that associated with turbulent upwelling. Shaw et al. (2011b) used the conservative tracer ex ²²⁴Ra to estimate inputs of the nonconservative chemical inventories of iron from terrestrial particles in proximity to icebergs. Radium is released from icebound terrestrial material when exposed to seawater, and the excess ²²⁴Ra inventory is proportional to the original material (and iron) input. Dissolved iron enrichments have been correlated with low-salinity surface water, and vertical gradients and enrichments of iron(II) and particulate iron down the iceberg face have indicated meltwater iron sources (Lin et al. 2011, Lin & Twining 2012).

Cefarelli et al. (2011) found that phytoplankton close to an iceberg were enriched in diatoms and impoverished in phototrophic flagellates, supporting the hypothesis that vertical meltwater movement and/or micronutrient iron input facilitates a community response (as diatom growth). In a study by Vernet et al. (2011), high variability resulted in no statistically significant increase in phytoplankton biomass or production within the euphotic zone in the vicinity of one iceberg, with the exception of an 11% increase in biomass 2 km away. An additional source of algal production was discovered in the form of extensive diatom communities, dominated by *Thalassioneis signyensis* (Ferrario et al. 2011) and associated ciliates and foraminifera, growing attached to small sand-grain-size rocks surrounding ablation pockets on the submerged flanks of free-drifting icebergs (Robison et al. 2011).

Kaufmann et al. (2011) found that the macrozooplankton and micronekton communities near free-drifting icebergs were dominated by Antarctic krill (*Euphausia superba*) and salps (*Salpa thomp-soni*), which constituted 60%–95% of the community biomass. During sampling in the summer and fall, mean biomass was significantly elevated within 1.85 km of the icebergs but then declined with increasing distance. This trend was not apparent in late-fall sampling with reduced ambient light conditions. Concentrations of photosynthetic pigments in the guts of *E. superba* and *S. thompsoni* tracked patterns in surface productivity (Kaufmann et al. 2011), suggesting that grazing could be an important process contributing to sedimentation near icebergs. When phytoplankton are abundant, food passes rapidly through the guts of krill, producing carbon- and nitrogen-rich pellets that sink through the water column at speeds from 27 to 1,218 m day⁻¹ (Atkinson et al. 2012).

The species composition of near-field zooplankton observed by Sherlock et al. (2011) with a remotely operated vehicle within 40 m of the ice surface did not change with distance from icebergs; however, the biomass was greater within 5 m of an iceberg than at distances farther away. The dominant species observed included juvenile nototheniid fishes, *S. thompsoni*, the medusae *Periphylla periphylla* and *Calycopsis borchgrevinki*, the ctenophores *Callianira antarctica* and *Beroe* spp., and the siphonophore *Diphyes antarctica*. Schools of the krill *E. superba* and *Thysanoessa macrura* were also observed.

Flying seabird abundance and distribution are also influenced by free-drifting icebergs. Ruhl et al. (2011) observed that the abundance of seabirds was two to six times greater within approximately 0.5 km of icebergs than it was at distances farther away. The most dominant species were the cape petrel (*Daption capense*), Antarctic fulmar (*Fulmarus glacialoides*), and Wilson's storm petrel (*Oceanites oceanicus*). The distribution of species was also altered around icebergs, especially for *D. capense*, which was most abundant in the immediate vicinity of the icebergs. In contrast to earlier studies (e.g., Joiris 1991, Ribic et al. 1991), there were only occasional sightings of penguins, seals, and whales around these tabular icebergs.

In summary, the above studies of large Antarctic tabular icebergs showed that physical, chemical, and biological processes are altered by the presence of an iceberg, in association with meltwater production and iron enrichment (**Figure 2**). The iceberg zone of influence extends tens of kilometers away, from the surface to at least 200 to 1,500 m depth, and lasts for several weeks. There was also enhanced carbon export associated with one iceberg. The iceberg ecosystem is enriched at higher trophic levels (such as zooplankton and birds) but not at lower trophic levels (including bacterioplankton and phytoplankton), suggesting top-down control of phytoplankton distribution by zooplankton aggregated around the icebergs. It is hypothesized that increased grazing is a major source of the sedimenting material collected in the LST samples. That icebergs are a major source of terrestrial material is clear, yet the fate and impact of the added iron and associated carbon biomass remain uncertain.

NORTHERN POLAR REGIONS (ARCTIC-GENERATED ICEBERGS)

In the Arctic, many glaciers associated with the Greenland ice sheet have had accelerated mass loss over the past 18 years, contributing to increased loss of ice along the margins (Pritchard et al. 2009, van den Broeke et al. 2009, Cazenave & Llovel 2010, Rignot et al. 2011) and a 46% increase in the number of icebergs between 1996 and 2005 (Woodworth-Lynas et al. 2009). A massive



Coupled physical, chemical, and biological processes observed in proximity to free-drifting icebergs in the northwest Weddell Sea.

iceberg, four times the size of Manhattan, calved from northwest Greenland in 2010 (Hood 2010) and one year later was still adrift, headed south along the Labrador coast (Int. Ice Patrol 2011). There has also been increased mass loss from glaciers between 2007 and 2009 in the Canadian Arctic Archipelago to the west of Greenland (Gardner et al. 2011).

The sub-Arctic Labrador Sea currently contains the largest population of free-drifting icebergs originating from the Arctic (Woodworth-Lynas et al. 2009). Most of these icebergs calved from the southeastern and western regions of Greenland, with smaller numbers originating from the tidewater glaciers of Ellesmere and Baffin Islands. Arctic icebergs tend to be smaller than Antarctic icebergs, with recent size measurements ranging from 50 to 1,200 m in length (Woodworth-Lynas et al. 2009). These icebergs follow a counterclockwise trajectory through Baffin Bay and then become entrained in the Labrador Current, which consists of cold, fresh Arctic water in the upper layer separated from the warmer, saltier, and more nutrient-rich mixed West Greenland Irminger Water below. This flow continues south into the Labrador Sea and forms a constrained trajectory along the continental margin known as the Arctic Iceberg Alley (**Figure 3**).

Little is known about Arctic icebergs and their impact on the surrounding pelagic ecosystem. A study of one Greenland iceberg intercepted in the Labrador Sea showed no appreciable alteration of chlorophyll content in the surrounding water (Shulenberger 1983) but hinted at mixing effects on nitrate concentrations. Fish were observed in small caves within the walls of a coastal iceberg off Greenland (Holmquist 1958). Many more recent studies in the Antarctic have suggested that icebergs play a significant role in changing the pelagic ecosystem [see Southern Polar Regions (Antarctic-Generated Icebergs), above]. Do icebergs in the Arctic also exhibit enrichment or



Figure 3

The Labrador Sea, showing the general trajectories (*white arrows*) of icebergs originating from Greenland and the Canadian Arctic Archipelago through Baffin Bay. This area is known as the Arctic Iceberg Alley. Image copyright © 2010 by Google (data SIO, NOAA, US Navy, NGA, GEBCO; image IBCAO, copyright © 2012 CNES/Spot Image; image copyright © 2012 TerraMetrics).

alteration processes of the pelagic ecosystem, ultimately leading to enhanced productivity and carbon export?

In the North Atlantic, productivity maxima (as blooms) tend to be associated with fronts and mesoscale eddies that promote the vertical exchange of macro- and micronutrients (Frajka-Williams et al. 2009, Yebra et al. 2009, Poulton et al. 2010, Bagniewski et al. 2011). However, freshwater input from increasing meltwater in the Arctic polar region acts to enhance stratification and stabilize the upper water column, thereby potentially reducing the nutrient upwelling. The change in the available nutrient supply appears to have been responsible for an ecosystem regime shift observed in the northwest Atlantic (e.g., Greene et al. 2008). In addition, the increased stability impedes the deep vertical convection of Labrador Sea Water (Lazier et al. 2002, Avsic et al. 2006, Yasheyaev 2007), reducing vertical exchange and ultimately providing a positive feedback to warming via reduced carbon sequestration. In contrast, warming-induced increases in iceberg injection have the opposite effect through enhanced carbon export in the Antarctic (Smith et al. 2007, 2011; Shaw et al. 2011a; Stephenson et al. 2011). The extent to which these or additional iceberg-related processes translate into enhanced ecosystem processes and carbon export in Arctic regions may therefore reflect a significant negative feedback to the warming-induced ice loss. Given the increasing abundance of free-drifting icebergs within the Labrador Sea, phenomena associated with them could have a pronounced impact on the surrounding oceanic ecosystem and the potential to increase CO_2 sequestration at a regionally significant level. The potential for intermediate-depth upwelling and increased carbon export efficiency leading to deepwater CO_2 storage is intriguing and warrants further investigation.

In the Labrador Sea, macronutrients (nitrate and silicate) become limiting in summer (Harrison & Li 2008) shifting the pelagic ecosystem from one that favors carbon export to one dominated by smaller size classes of phytoplankton and grazers. Long-term monitoring of this region suggests that the ecosystem shift may be more than seasonal, representing instead a long-term trend (Harrison & Li 2008). The possibility that iceberg zones of influence may be supporting or moderating this trend has not been considered, though conditions around Antarctic icebergs appear to support larger phytoplankton (see above). Primary production is typically limited by nitrogen supply in the coastal Arctic and western sub-Arctic Atlantic (Tremblay & Gagnon 2009) and would be expected to respond to the mixing and upwelling of nitrogen in proximity to an iceberg. Higher levels of primary production could lead to higher levels of extracellular enzyme activity associated with sinking aggregates in the Arctic (Kellogg et al. 2011).

In waters surrounding free-drifting icebergs, the presence of a mature community appears to generate enhanced carbon export [see Southern Polar Regions (Antarctic-Generated Icebergs), above]. For example, high consumer densities (Smith et al. 2007, Kaufmann et al. 2011) may enhance carbon flux in the vicinity of icebergs (Shaw et al. 2011a, Smith et al. 2011). The iceberg grazer community surrounding Antarctic icebergs appears to efficiently remove phytoplankton and activate carbon cycling and sedimentation out of the euphotic zone. In the Labrador Sea, iceberggenerated shifts may occur in the phytoplankton communities themselves, including aggregation processes that enhance carbon export (e.g., Kellogg et al. 2011), perhaps independently of grazers. The expected zooplankton grazers along the Arctic Iceberg Alley would be dominated by copepods, larvaceans, and euphausiids that can serve as prey for chaetognaths (Pepin et al. 2011).

Figure 4 depicts a possible scenario of coupled physical, chemical, and biological processes around a free-drifting iceberg in the Labrador Sea. In the Arctic, icebergs have the potential to mediate the availability of macronutrients through localized upwelling and stratification, as well as to provide a mature biological community. The impact of these processes has yet to be resolved in the Arctic region (hence the question marks in the figure).

COMPARISON OF ANTARCTIC AND ARCTIC ICEBERG ECOSYSTEMS

Physical Dynamics

Turbulent and diffusive mechanisms are responsible for subsurface melting around icebergs. Variations in the vertical and horizontal extent of the iceberg meltwater impact the redistribution of heat and freshwater and thereby affect the abundance and distribution of carbon, nutrients, and pelagic organisms. Melting of sidewall ice into a salinity gradient through a double-diffusive process leads to vertically stacked circulation cells manifested as thermohaline staircases (e.g., Huppert & Turner 1980, Jacobs et al. 1981). The horizontal spread of sidewall meltwater provides a means by which iceberg-generated micronutrient-enriched waters or upwelled macronutrients may extend over a large area (**Figure 2**). However, in the Weddell Sea, the depth, thickness, and number of thermohaline steps are quite variable throughout the water column and are dependent on the distance to and size of the iceberg (Stephenson et al. 2011). At the iceberg base, enhanced turbulent mixing upwells water from below the permanent thermocline into the near-surface layer (Gade 1979, Jacobs et al. 1996, Stephenson et al. 2011). The near-surface waters in the vicinity



Figure 4

Likely (as yet unstudied; *question marks*) physical and chemical processes and potential biological responses expected in the vicinity of free-drifting icebergs in the Labrador Sea.

of icebergs are typically cold and fresh (Helly et al. 2011), and so the upwelled mixtures appear as warm and salty anomalies (Wahlin et al. 2010, Stephenson et al. 2011). The turbulent mixing is associated with large injections of deeper macronutrient-rich water into the upper layer that stimulates primary production around Antarctic icebergs (Lin et al. 2011, Murray et al. 2011, Vernet et al. 2011) (**Figure 2**). Stimulation of the pelagic ecosystem by vertical mixing of basal meltwater from Arctic icebergs provides an intriguing mechanism for enhancing carbon export in the deep basin of the Labrador Sea (**Figure 4**), especially given an increasingly stable upper-ocean stratification associated with the recent warming-induced amplification of freshwater flux in Arctic seas.

Studies of Antarctic icebergs have clarified the need for a three-dimensional characterization of the physical, chemical, and biological properties to estimate and enable understanding of the impact of turbulence and diffusive processes on chemical inputs, biological production, and ultimately carbon export associated with icebergs. Chemical inputs and community response (as carbon export) were found to correlate with the distribution of meltwater as a function of depth and orientation to the icebergs (Shaw et al. 2011a, Stephenson et al. 2011). However, chemical inventories need to be reconciled with the intermittent and/or localized nature of the intense vertical turbulent mixing to verify the assumption that free-drifting icebergs are associated with a persistent iceberg zone of influence.

In the Antarctic, numerous studies have directly measured the microstructure turbulence and detected the presence of thermohaline steps and elevated mixing near glacier tongues (e.g., Stevens

et al. 2011) and along the ice shelves of the continental margin of the northwest Weddell Sea (e.g., Muench et al. 2002, Absy et al. 2008). The few direct microstructure measurements in the Arctic region suggest that although turbulent dissipation is generally weak in the interior (Rainville & Winsor 2008), the mixing rates are remarkably nonuniform and may still be important along the boundaries and in marginal seas (Sundfjord et al. 2007). In a recent study, Lenn et al. (2009) found that double-diffusive convection dominates the vertical mixing in the upper ocean of the Siberian sector of the Arctic Ocean. However, to our knowledge, there have been no published microstructure measurements directly associated with icebergs in either polar region, and so the relative roles of turbulent and diffusive mixing in the chemical inputs and biological productivity associated with icebergs remain very much an open question.

Chemical Inputs and Proxies

Similar physical processes that lead to an enriched ecosystem and carbon export in the vicinity of Antarctic icebergs should be important in waters surrounding Arctic icebergs. Chemical contributions to carbon export in the Southern Ocean mediate the efficiency of ambient macronutrient utilization through micronutrient input. In contrast, stratification and the availability of macronutrients partially mediate carbon export in the Labrador Sea. In the Weddell Sea, deficits in ²³⁴Th showed increased carbon export correlated with enhanced vertical mixing and biogenic particle concentrations downstream of Antarctic icebergs on spatial scales similar to those identified for physical processes (Shaw et al. 2011a). Enhanced carbon export likely reflects a combination of increased macro- and micronutrient inputs coupled with rapid biomass turnover and greater export efficiency in proximity to icebergs. Although micronutrient limitation is not likely to have a similar impact in the Arctic because of the large inputs of terrestrial material from rivers compared with the Antarctic, the same physical processes will impact macronutrient availability (**Figures 2** and **4**).

Biological Processes

Warming surface waters in the Antarctic are creating changes in the dominance of zooplankton species that in turn will impact grazing and ultimately carbon export (Bernard et al. 2012). It can be expected that these structural shifts in pelagic communities will also be reflected in the community dynamics surrounding free-drifting icebergs. As icebergs drift northward through the Antarctic Iceberg Alley and into the Scotia Sea (**Figure 1**), the upper-water-column temperatures will increase. Will there be a transition in the pelagic community associated with icebergs during their transit? Such community changes will certainly impact the ecosystem dynamics and ultimately the cycling of nutrients and carbon.

Similar changes would be expected with Arctic icebergs as they drift south in the Arctic Iceberg Alley through the western Labrador Sea (**Figure 3**). Increased freshening and stratification of surface waters due to freshwater export from the Arctic Ocean into the Labrador Sea and southward are creating a shift in the plankton community structure (Greene et al. 2008) that will impact the pelagic ecosystem associated with icebergs transiting through this area.

FUTURE STUDIES

Studies have shown that large Antarctic icebergs enhance local carbon export, yet no single mechanism has been identified that could account for the observed increase. A number of processes have been observed that may contribute to the net increase in carbon export around icebergs: increased productivity, iron fertilization, nutrient upwelling, and grazer-mediated export. Initial results suggest that productivity effects combined with enhanced carbon export efficiency result from a set of coupled physical, chemical, and biological processes that occur to produce a unique ecosystem. As such, the interactions between the biological components of the ecosystem and the physical and chemical environment need to be quantified to evaluate their contributions to carbon export on both local and regional scales.

One interesting connection that deserves further investigation is the potential importance of euphausiids in the processing of iceberg detrital material, specifically iron. In the Antarctic, krill feed on the seabed at depths from 200 to 2,000 m when pelagic food is sparse. When caught in surface waters of the Scotia Sea, these krill have been found to retain a significant amount of particulate iron in their stomachs (Schmidt et al. 2011). Acidic digestion of particulate iron by krill associated with icebergs could facilitate a labile source of this micronutrient to enhance phytoplankton growth.

Atmospheric winter warming around the Antarctic Peninsula has created a rise in ocean temperature as well as a decline in perennial and seasonal sea ice (Martinson et al. 2008, Stammerjohn et al. 2008). Off the western Antarctic Peninsula, the zooplankton community structure is shifting to increased grazing pressure by salps, which continue to expand their ranges to the south and thus impact carbon export (Bernard et al. 2012). This decline in krill abundance and increase in salp abundance have been reported over extensive areas of the Southern Ocean (Atkinson et al. 2004). Changes in zooplankton community structure could also alter the ecosystem dynamics associated with free-drifting icebergs in both polar regions.

New instrumentation such as autonomous underwater vehicles (e.g., Brierley et al. 2002, McPhail et al. 2009) can be equipped with a variety of sensors to detect changes in physical, chemical, and biological properties surrounding icebergs in both space and time. In addition, the LSTs discussed above are valuable in sampling the export flux of particulate matter from beneath and around icebergs (Sherman et al. 2011). In the past, the physical processes of turbulent mixing and diffusion associated with icebergs have been based on established techniques that infer the presence of these processes through temperature and salinity measurements. Ideally, direct measurements of the turbulent dissipation and property microstructure would provide a better comparison of the relative contributions of turbulent mixing and double-diffusive processes to the chemical inventories and pelagic communities associated with icebergs. More important, microstructure observations, when combined with the nutrient and chemical gradient measurements, would permit direct assessment of the vertical turbulent fluxes and upwelling of these inputs into the productive euphotic layer.

Critical questions remain concerning the overall importance of iceberg ecosystems in the drawdown of CO₂ through primary production and the ultimate export and sequestration of carbon to deeper waters. Studies to date have concentrated on the physical, chemical, and biological processes associated with individual Antarctic icebergs. However, it is important to expand these local studies to a regional scale (Smith et al. 2007), taking advantage of satellite tracking of icebergs. In addition, the unique feature that 90% of large Antarctic icebergs pass through the Antarctic Iceberg Alley in the northwest Weddell Sea (Stuart & Long 2011) (**Figure 1**) makes this an ideal location for this scaling effort. Similarly, the narrow boundary flow in the Labrador Current that forms the Arctic Iceberg Alley constrains the trajectories of free-drifting icebergs originating from the Arctic (**Figure 3**). An effort must also be made to include the greater number of smaller icebergs (<1 km in maximum dimension) using satellite-derived altimeter analysis (Tournadre et al 2008).

From the number and size of each iceberg detected through the polar Iceberg Alleys per unit of time, the export flux of nutrients and freshwater into the adjacent seas can be estimated. These relatively narrow areas could also be instrumented with bottom moorings. These moorings could be equipped to detect the overlying ice conditions and measure the sinking flux of particulate matter collected in sediment traps as an indication of carbon sequestration in these areas compared with a reference site experiencing little iceberg traffic. Such efforts will result in a better understanding of the impacts of increased iceberg production and enable the direct measurement of natural CO_2 drawdown and processes related to carbon exchanges in the pelagic zones, as has been suggested by recent studies of these systems in the Southern Ocean.

The emergent iceberg ecosystem is greater than the sum of its parts, and the results of a thorough study of this system will extend beyond iceberg impacts on carbon export to an understanding of carbon cycling in the Southern Ocean. Future climate change scenarios suggest the importance of the Southern Ocean in the global carbon cycle, including possible effects on carbon sequestration (Anisimov & Fitzharris 2007). It is envisioned that similar studies could be directed to the study of Arctic-region icebergs.

SUMMARY

Recent major calving events from the ice shelves in the Ross and Weddell Seas have led to a significant increase in the number of icebergs in the Southern Ocean. Similarly, major calving events from the Greenland ice cap glaciers and Canadian Arctic Archipelago glaciers have contributed to a substantial increase in the number of icebergs in the Arctic and sub-Arctic regions around Greenland and northern Canada. Recent research has shown that Antarctic free-drifting icebergs are hot spots of chemical and biological enrichment, with enhanced micronutrient iron concentrations that influence the surrounding pelagic ecosystem. In the Arctic and sub-Arctic, we expect iceberg-induced upwelling of nitrate to be the more likely stimulant to biological activity. Regardless of region-specific mechanisms, a resulting increase in productivity and sedimentation associated with icebergs can potentially stimulate carbon fixation and export, thus increasing CO_2 drawdown and sequestration. The increasing numbers of icebergs in both the Antarctic and Arctic regions can potentially be important but as yet ignored components in understanding the impact of global warming on the oceanic carbon cycle.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This contribution would not have been possible without the input of many of our iceberg project colleagues whose published research forms the basis of this review. Support for K.L.S. and A.D.S. was provided by the David and Lucile Packard Foundation and a grant from the National Science Foundation Office of Polar Programs (ANT-0636813). Support for T.J.S. was provided by a grant from the National Science Foundation Office of Polar Programs (ANT-0636813). Support for T.J.S. was provided by a grant from the National Science Foundation Office of Polar Programs (ANT-0636813). Support for T.J.S. was provided by a grant from the National Science Foundation Office of Polar Programs (ANT-0636319). Support for J.S. was provided by a grant from the National Science Foundation (ARRA OCE-08050350).

LITERATURE CITED

Absy JM, Schroder M, Muench R, Hellmer HH. 2008. Early summer thermohaline characteristics and mixing in the western Weddell Sea. Deep-Sea Res. II 55:1117–31

- Ainley DG, O'Connor EF, Boekelheide RJ. 1984. The marine ecology of birds in the Ross Sea, Antarctica. Ornithol. Monogr. 32, Am. Ornithol. Union, Washington, DC. 97 pp.
- Anisimov O, Fitzharris B. 2001. Polar regions (Arctic and Antarctic). In Climate Change 2001: Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change, ed. JJ McCarthy, OF Canziani, NA Leary, DJ Dokken, KS White, pp. 801–41. Cambridge: Cambridge Univ. Press
- Arrigo KR, van Dijken GL. 2003. Impact of iceberg C-19 on Ross Sea primary production. Geophys. Res. Lett. 30:1836
- Arrigo KR, van Dijken GL, Ainley DG, Fahnestock MA, Markus T. 2002. Ecological impact of a large Antarctic iceberg. *Geophys. Res. Lett.* 29:1104
- Atkinson A, Schmidt K, Fielding S, Kawaguchi S, Geissler PA. 2012. Variable food absorption by Antarctic krill: relationships between diet, egestion rate and the composition and sinking rates of their fecal pellets. *Deep-Sea Res. II* 59–60:147–58
- Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–3
- Avsic T, Karstensen J, Send U, Fischer J. 2006. Interannual variability of newly formed Labrador Sea Water from 1994 to 2005. *Geophys. Res. Lett.* 33:L21S02
- Bagniewski W, Fennel K, Perry MJ, D'Asaro EA. 2011. Optimizing models of the North Atlantic spring bloom using physical, chemical and bio-optical observations from a Lagrangian float. *Biogeosciences* 8:1291–307
- Ballantyne J. 2002. A multidecadal study of the number of Antarctic icebergs using scatterometer data. Brigham Young Univ. Rep., Feb. 27. http://www.scp.byu.edu/data/iceberg/IcebergReport.pdf
- Bernard KS, Steinberg DK, Schofield OME. 2012. Summertime grazing impact of the dominant macrozooplankton off the Western Antarctic Peninsula. *Deep-Sea Res. I* 62:111–22
- Biggs D. 1978. Non-biogenic fixed nitrogen in Antarctic surface waters. Nature 276:96-97
- Blain S, Queguiner B, Armand L, Belviso S, Bombled B, et al. 2007. Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature* 446:1070–71
- Boyd PW, Watson AJ, Law CS, Abraham ER, Trull T, et al. 2000. Mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* 407:695–701
- Brierley AS, Fernandes PG, Brandon MA, Armstrong F, Millard NW, et al. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. *Science* 295:1890–92
- Cazenave A, Llovel W. 2010. Contemporary sea level rise. Annu. Rev. Mar. Sci. 2:145-71
- Cefarelli A, Vernet M, Ferrario ME. 2011. Phytoplankton composition and abundance in relation to freefloating Antarctic icebergs. Deep-Sea Res. II 58:1436–50
- Coale KH, Johnson KS, Chavez FP, Buesseler KO, Barber RT, et al. 2004. Southern Ocean iron enrichment experiment: carbon cycling in high- and low-Si waters. *Science* 304:408–14
- Cook AJ, Fox AJ, Vaughan DG, Ferrigno JG. 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* 308:541–44
- De Angelis HD, Skvarca P. 2003. Glacier surge after ice shelf collapse. Science 299:1560-62
- de Baar HJW, Buma AGJ, Nolting RF, Cadée GC, Jacques G, Tréguer PJ. 1990. On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. *Mar. Ecol. Prog. Ser.* 65:105–22
- de Baar HJW, de Jong JTM, Bakker DCE, Löscher BM, Veth C, et al. 1995. Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373:412–15
- Dowdeswell JA, Bamber JL. 2007. Keel depths of modern Antarctic icebergs and implications for sea-floor scouring in the geological record. *Mar. Geol.* 243:120–31
- Dowdeswell JA, Whittington RJ, Hodgkins R. 1992. The sizes, frequencies, and freeboards of East Greenland icebergs observed using ship radar and sextant. J. Geophys. Res. 97:3515–28
- Dulaiova H, Ardelan MV, Henderson PB, Charette MA. 2009. Shelf-derived iron inputs drive biological productivity in the southern Drake Passage. *Glob. Biogeochem. Cycles* 23:GB4014
- Ferrario ME, Cefarelli AO, Robison BH, Vernet M. 2011. Thalassioneis signyensis (Bacillariophyceae) from northwest Weddell Sea icebergs, and emendation of the generic description. J. Phycol. 48:222–30
- Frajka-Williams E, Rhines PB, Eriksen CC. 2009. Physical controls and mesoscale variability in the Labrador Sea spring phytoplankton bloom observed by Seaglider. *Deep-Sea Res. I* 56:2144–61

- Gade HG. 1979. Melting of ice in sea water: a primitive model with application to the Antarctic ice shelf and icebergs. *J. Phys. Oceanogr.* 9:189–98
- Gardner AS, Moholdt G, Wouters B, Wolken GJ, Burgess DO, et al. 2011. Sharply increased mass loss from glaciers and ice caps in the Canadian Arctic archipelago. *Nature* 473:357–60
- Gervais F, Riebesell U, Gorbunov MY. 2002. Changes in primary productivity and chlorophyll *a* in response to iron fertilization in the Southern Polar Frontal Zone. *Limnol. Oceanogr.* 47:1324–35
- Gladstone RM, Bigg GR, Nicholls KW. 2001. Iceberg trajectory modeling and meltwater injection in the Southern Ocean. J. Geophys. Res. 106:19903–15
- Gradinger R. 1999. Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice. *Polar Biol.* 22:169–77
- Greene CH, Pershing AJ, Cronin TM, Ceci N. 2008. Arctic climate change and its impact on the ecology of the North Atlantic. *Ecology* 89:S24–38
- Harrison WG, Li WKW. 2008. Phytoplankton growth and regulation in the Labrador Sea: light and nutrient limitation. J. Northwest Atl. Fish. Sci. 39:71–82
- Helly JJ, Kaufmann RS, Stephenson GR, Vernet M. 2011. Cooling, dilution and mixing of ocean water by free-drifting icebergs in the Weddell Sea. *Deep-Sea Res. II* 58:1346–63
- Holmquist C. 1958. An observation on young specimens of Ammodytes dubius. Meddelelser Grønl. 159:1-14
- Hood M. 2010. Giant Greenland iceberg a climate "warning sign." AFP, Aug. 16. http://www.google. com/hostednews/afp/article/ALeqM5inGfVX69zbp-Gs4_y0FEdtLKMLeA
- Huppert HE, Turner JS. 1980. Ice blocks melting into a salinity gradient. J. Fluid Mech. 100:367-84
- Int. Ice Patrol. 2011. Report of the International Ice Patrol in the North Atlantic: 2010 season. Bull. 96, CG-188-65, Int. Ice Patrol, New London, CT. 58 pp.
- Jacobs SS, Gordon AL, Amos AF. 1979. Effect of glacial ice melting on the Antarctic surface water. Nature 277:469–71
- Jacobs SS, Helmer H, Jenkins A. 1996. Antarctic ice sheet melting in the southeast Pacific. Geophys. Res. Lett. 23:957–60
- Jacobs SS, Huppert HE, Holdsworth G, Drewry DJ. 1981. Thermohaline steps induced by melting of the Erebus Glacier tongue. J. Geophys. Res. 86:6547–55
- Joiris CR. 1991. Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. *Polar Biol.* 11:415–24
- Kang SH, Kang JS, Lee S, Chung KH, Kim D, Park MG. 2001. Antarctic phytoplankton assemblages in the marginal ice zone of the northwestern Weddell Sea. *J. Plankton Res.* 23:333–52
- Kaufmann RS, Robison BH, Reisenbichler KR, Sherlock RE, Osborn KJ. 2011. Composition and structure of macrozooplankton and micronekton communities in the vicinity of free-drifting Antarctic icebergs. *Deep-Sea Res. II* 58:1469–84
- Kaufmann RS, Smith KL, Baldwin RJ, Glatts RC, Robison BH, Reisenbichler KR. 1995. Effects of seasonal pack ice on the distribution of macrozooplankton and micronekton in the northwestern Weddell Sea. *Mar. Biol.* 124:387–97
- Kellogg CTE, Carpenter SD, Renfro AA, Sallon A, Michel C, et al. 2011. Evidence for microbial attenuation of particle flux in the Amundsen Gulf and Beaufort Sea: elevated hydrolytic enzyme activity on sinking aggregates. *Polar Biol.* 34:2007–23
- Knox GA. 1994. The Biology of the Southern Ocean. Cambridge: Cambridge Univ. Press. 444 pp.
- Kohfeld KE, Le Quere C, Harrison SP, Anderson RF. 2005. Role of marine biology in glacial-interglacial CO₂ cycles. *Science* 308:74–78
- Kristensen M. 1983. Iceberg calving and deterioration in Antarctica. Prog. Phys. Geogr. 7:313-28
- Lancelot C, de Montety A, Goosse H, Becquevort S, Schoemann V, et al. 2009. Spatial distribution of the iron supply to phytoplankton in the Southern Ocean: a model study. *Biogeosciences* 6:2861–78
- Law CS, Abraham ER, Watson AJ, Liddicoat MI. 2003. Vertical eddy diffusion and nutrient supply to the surface mixed layer of the Antarctic Circumpolar Current. J. Geophys. Res. 108:3272
- Lazier JRN, Hendry R, Clarke A, Yashayev L, Rhines P. 2002. Convection and restratification in the Labrador Sea, 1990–2000. Deep-Sea Res. I 49:1819–35
- Lenn YD, Wiles PJ, Torres-Valdes S, Abrahamsen EP, Rippeth TP, et al. 2009. Vertical mixing at intermediate depths in the Arctic boundary current. *Geophys. Res. Lett.* 36:L05601

- Lin H, Rauschenberg S, Hexel CR, Shaw TJ, Twining BS. 2011. Free-drifting icebergs as sources of iron to the Weddell Sea. Deep-Sea Res. II 58:1392–406
- Lin H, Twining BS. 2012. Chemical speciation of iron in Antarctic waters surrounding free-drifting icebergs. Mar. Chem. 128–29:81–91
- Lizotte MP, Arrigo KR, eds. 1998. Antarctic Sea Ice: Biological Processes, Interactions and Variability. Antarct. Res. Ser. Vol. 73. Washington, DC: Am. Geophys. Union. 198 pp.
- Long DG, Ballantyne J, Bertoia C. 2002. Is the number of icebergs around Antarctica increasing? *Eos Trans. AGU* 42:469–74
- Löscher BM, de Baar HJW, de Jong JTM, Veth C, Dehairs F. 1997. The distribution of Fe in the Antarctic Circumpolar Current. Deep-Sea Res. II 44:143–87
- Maher BA, Dennis PF. 2001. Evidence against dust-mediated control of glacial-interglacial changes in atmospheric CO₂. Nature 411:176–80
- Martin JH. 1990. Glacial-interglacial CO2 change: the iron hypothesis. Paleoceanography 5:1-13
- Martin JH, Gordon RM, Fitzwater SE. 1990. Iron in Antarctic waters. Nature 345:156-58
- Martinson DG, Stammerjohn SE, Ianuzzi RA, Smith RC, Vernet M. 2008. Western Antarctic Peninsula physical oceanography and spatio-temporal variability. *Deep-Sea Res. II* 55:1964–87
- McPhail SD, Furlong ME, Pebody M, Perrett JR, Stevenson P, et al. 2009. Exploring beneath the PIG Ice Shelf with the Autosub3 AUV. In Oceans 2009 IEEE Bremen: Balancing Technology with Future Needs. Piscataway, NJ: Inst. Electr. Electron. Eng. 6 pp. http://eprints.soton.ac.uk/66414
- Muench RD, Padman L, Howard SL, Fahrbach E. 2002. Upper ocean diapycnal mixing in the northwest Weddell Sea. *Deep-Sea Res. II* 49:4843–61
- Murray AE, Peng V, Tyler C, Wagh P. 2011. Marine bacterioplankton biomass, activity and community structure in the vicinity of Antarctic icebergs. *Deep-Sea Res. II* 58:1407–21
- Neshyba S. 1977. Upwelling by icebergs. Nature 267:507-8
- Orheim O. 1988. Antarctic icebergs-production, distribution and disintegration. Ann. Glaciol. 11:205 (Abstr.)
- Parker BC, Zeller EJ, Heiskell LE, Thompson WJ. 1978. Nonbiogenic fixed nitrogen in Antarctica and some ecological implications. *Nature* 271:651–52
- Pepin P, Colbourne E, Maillet G. 2011. Seasonal patterns in zooplankton community structure on the Newfoundland and Labrador shelf. Prog. Oceanogr. 91:273–85
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–36
- Pollard RT, Salter I, Sanders RJ, Lucas MI, Moore CM, et al. 2009. Southern Ocean deep-water carbon export enhanced by natural iron fertilization. *Nature* 457:577–81
- Poulton AJ, Charalampopoulou A, Young JR, Tarran GA, Lucas MI, Quartly GD. 2010. Coccolithophore dynamics in non-bloom conditions during late summer in the central Iceland Basin (July–August 2007). *Limnol. Oceanogr.* 55:1601–13
- Pritchard HD, Arthern RJ, Vaughan DG, Edwards LA. 2009. Extensive dynamic thinning on the margins of the Greenland and Antarctic ice sheets. *Nature* 461:971–75
- Rainville L, Winsor P. 2008. Mixing across the Arctic Ocean: microstructure observations during the Beringia 2005 Expedition. *Geophys. Res. Lett.* 35:L08606
- Raiswell R. 2011. Iceberg-hosted nanoparticulate Fe in the Southern Ocean: mineralogy, origin, dissolution kinetics and source of bioavailable Fe. *Deep-Sea Res. II* 58:1364–75
- Raiswell R, Benning LG, Tranter M, Tulaczyk MS. 2008. Bioavailable iron in the Southern Ocean: the significance of the iceberg conveyor belt. *Geochem. Trans.* 9:7
- Renner AHH, Thorpe SE, Heywood KJ, Murphy EJ, Watkins JL, Meredith MP. 2012. Advective pathways near the tip of the Antarctic Peninsula: trends, variability and ecosystem implications. *Deep-Sea Res. I* 63:91–123
- Ribic CA, Ainley DG, Fraser WR. 1991. Habitat selection by marine mammals in the marginal ice zone. Antarct. Sci. 3:181–86
- Rignot E, Velicogna I, van den Broeke MR, Monaghan A, Lenaerts JTM. 2011. Acceleration of the contribution of the Greenland and Antarctic ice sheets to sea level rise. *Geophys. Res. Lett.* 38:L05503
- Robison BH, Vernet M, Smith KL. 2011. Algal communities attached to free-drifting Antarctic icebergs. Deep-Sea Res. II 58:1451–56

- Rothlisberger R, Bigler M, Wolff EW, Joos F, Monnin E, et al. 2004. Ice core evidence for the extent of past atmospheric CO₂ change due to iron fertilization. *Geophys. Res. Lett.* 31:L16207
- Ruhl HA, Ellena JA, Wilson RC, Helly JJ. 2011. Seabird aggregation around free-drifting icebergs in the northwest Weddell Sea and Scotia Seas. Deep-Sea Res. II 58:1497–506
- Sancetta C. 1992. Primary production in the glacial North Atlantic and North Pacific Oceans. *Nature* 360:249–51
- Sarmiento JL, Orr JC. 1991. Three-dimensional simulations of the impact of Southern Ocean nutrient depletion on atmospheric CO₂ and ocean chemistry. *Limnol. Oceanogr.* 36:1928–50
- Scambos TA, Hulbe C, Fahnestock M, Bohlander J. 2000. The link between climate warming and break-up of ice shelves in the Antarctic Peninsula. J. Glaciol. 46:516–30
- Scambos TA, Sergienko O, Sargent A, MacAyeal D, Fastook J. 2005. ICESat profiles of tabular iceberg margins and iceberg breakup at low latitudes. *Geophys. Res. Lett.* 32:L23S09
- Schmidt K, Atkinson A, Steigenberger S, Fielding S, Lindsay MCM, et al. 2011. Seabed foraging by Antarctic krill: implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnol. Oceanogr.* 56:1411–28
- Schodlok MP, Hellmer HH, Rohardt G, Fahrbach GE. 2006. Weddell Sea iceberg drift: five years of observations. J. Geophys. Res. 111:C06018
- Schwarz JN, Schodlok MP. 2009. Impact of drifting icebergs on surface phytoplankton biomass in the Southern Ocean: ocean colour remote sensing and in situ iceberg tracking. *Deep-Sea Res. I* 56:1727–41
- Sedwick PN, Ditukkio GR, Mackey DJ. 2000. Iron and manganese in the Ross Sea, Antarctica: seasonal iron limitation in Antarctic shelf waters. J. Geophys. Res. 105:11321–36
- Shaw TJ, Hexel CR, Smith KL, Sherman AD, Dudgeon R, et al. 2011a. ²³⁴Th-based carbon export around free-drifting icebergs in the Southern Ocean. *Deep-Sea Res. II* 58:1384–91
- Shaw TJ, Raiswell RW, Hexel CR, Vu HP, Moore WS, et al. 2011b. Input, composition and potential impact of terrigenous material from free-drifting icebergs in the Weddell Sea. Deep-Sea Res. II 58:1376–83
- Sherlock RE, Reisenbichler KR, Bush SL, Osborn KJ, Robison BH. 2011. Near-field zooplankton, ice-face biota, and proximal hydrography of free-drifting Antarctic icebergs. *Deep-Sea Res. II* 58:1457–68
- Sherman AD, Hobson BW, McGill PR, Davis R, McClune M, Smith KL. 2011. Lagrangian sediment traps for sampling at discrete depths beneath free-drifting icebergs. *Deep-Sea Res. II* 58:1327–35
- Shulenberger E. 1983. Water-column studies near a melting Arctic iceberg. Polar Biol. 2:149-58
- Sigman DM, Hain MP, Haug GH. 2010. The polar ocean and glacial cycles in atmospheric CO₂ concentration. *Nature* 466:47–55
- Smith KL, Robison BH, Helly JJ, Kaufmann RS, Ruhl HA, et al. 2007. Free-drifting icebergs: hot spots of chemical and biological enrichment in the Weddell Sea. Science 317:478–82
- Smith KL, Sherman AD, Shaw TJ, Murray AE, Vernet M, Cefarelli AO. 2011. Carbon export associated with free-drifting icebergs in the Southern Ocean. Deep-Sea Res. II 58:1485–96
- Smith WO, Nelson DM. 1986. The importance of ice edge phytoplankton production in the Southern Ocean. BioScience 36:251–57
- Stammerjohn SE, Martinson DG, Smith RC, Ianuzzi RA. 2008. Sea ice in the western Antarctic Peninsula region: spatio-temporal variability from ecological and climate change perspectives. *Deep-Sea Res. II* 55:2041–58
- Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT. 2009. Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* 457:459–63
- Stephenson GR, Sprintall J, Gille ST, Vernet M, Helly JJ, Kaufmann RS. 2011. Subsurface melting of a free-floating Antarctic Iceberg. Deep-Sea Res. II 58:1336–45
- Stevens CL, Stewart CL, Robinson NJ, Williams MJM, Haskell TG. 2011. Flow and mixing near a glacier tongue: a pilot study. Ocean Sci. 7:293–304
- Stone GS. 2003. Ice Island. Boston: N. Eng. Aquar. Press. 75 pp.
- Stuart KM, Long DG. 2011. Tracking large tabular icebergs using the SeaWinds Ku-band microwave scatterometer. *Deep-Sea Res. II* 58:1285–300
- Sundfjord A, Fer Y, Kasajima Y, Svendsen H. 2007. Observations of turbulent mixing and hydrography in the marginal ice zone of the Barents Sea. J. Geophys. Res. 112:C05008

Thomas DN, Dieckmann GS. 2002. Antarctic sea ice-a habitat for extremophiles. Science 295:641-44

- Thompson AF, Heywood KJ. 2008. Frontal structure and transport in the northwestern Weddell Sea. *Deep-Sea Res. I* 55:1229–51
- Thompson DWJ, Solomon S. 2002. Interpretation of recent southern hemisphere climate change. *Science* 296:895–99
- Tournadre J, Whitmer K, Girard-Ardhuin F. 2008. Iceberg detection in open water by altimeter waveform analysis. *J. Geophys. Res.* 113:CO8040
- Tremblay J-E, Gagnon J. 2009. The effects of irradiance and nutrient supply on the productivity of Arctic waters: a perspective on climate change. In *Influence of Climate Change on the Changing Arctic and Sub-Arctic Conditions*, ed. JCJ Nihoul, AG Kostianoy, pp. 73–93. Dordrecht: Springer
- van den Broeke M, Bamber J, Ettema J, Rignot E, Schrama E, et al. 2009. Partitioning recent Greenland mass loss. *Science* 326:984–86
- Vaughan DG, Marshall GJ, Connolley WM, King JC, Mulvaney R. 2001. Devil in the detail. *Science* 293:1777–79
- Velicogna I, Wahr J. 2006. Measurements of time-variable gravity show mass loss in Antarctica. Science 311:1754–56
- Vernet M, Sines K, Chakos D, Cefarelli AO, Ekern L. 2011. Impacts on phytoplankton dynamics by freedrifting icebergs in the NW Weddell Sea. Deep-Sea Res. II 58:1422–35
- Wahlin AK, Yuan X, Bjork G, Nohr C. 2010. Inflow of warm Circumpolar Deep Water in the central Amundsen Shelf. J. Phys. Oceanogr. 40:1427–34
- Westerlund S, Öhman P. 1991. Iron in the water column of the Weddell Sea. Mar. Chem. 35:199-217
- Williams RN, Rees WG, Young NW. 1999. A technique for the identification and analysis of icebergs in synthetic aperture radar images of Antarctica. Int. J. Remote Sens. 20:3183–99
- Wingham DJ, Wallis DW, Shephard A. 2009. Spatial and temporal evolution of the Pine Island Glacier thinning, 1995–2006. Geophys. Res. Lett. 36:L17501
- Wolff EW, Fischer H, Fundel F, Ruth U, Twarloh B, et al. 2006. Southern Ocean sea-ice extent, productivity and iron flux over the past eight glacial cycles. *Science* 440:491–96
- Woodworth-Lynas CMT, Dowdeswell EK, Dowdeswell JA. 2009. Decadal variations in iceberg climate, Greenland and Ellesmere Island: a pilot study. *Final Rep. 09–01*, Petra Int., Geol. Surv. Can. (Atl.), Mississauga, Can. 33 pp.
- Yasheyaev I. 2007. Hydrographic changes in the Labrador Sea, 1960-2005. Prog. Oceanogr. 73:247-76
- Yebra L, Harris RP, Head EJH, Yashayaev I, Harris LR, Hirst AG. 2009. Mesoscale physical variability affects zooplankton production in the Labrador Sea. *Deep-Sea Res. I* 56:703–15
- Zwally HJ, Comiso JC, Parkinson CL, Cavalieri DJ, Gloersen P. 2002. Variability of Antarctic sea ice 1979– 1998. J. Geophys. Res. 107:3041
- Zwally HJ, Giovinetto MB, Li J, Cornejo HG, Beckley MA, et al. 2005. Mass changes of the Greenland and Antarctic ice sheets and shelves and contributions to sea-level rise: 1992–2002. J. Glaciol. 51:509–27

Annual Review of Marine Science

Volume 5, 2013

Contents

Reflections About Chance in My Career, and on the Top-Down Regulated World <i>Karl Banse</i>
Causes for Contemporary Regional Sea Level Changes Detlef Stammer, Anny Cazenave, Rui M. Ponte, and Mark E. Tamisiea
Gravity Flows Associated with Flood Events and Carbon Burial: Taiwan as Instructional Source Area James T. Liu, Shuh-Ji Kao, Chih-An Huh, and Chin-Chang Hung
A Deep-Time Perspective of Land-Ocean Linkages in the Sedimentary Record <i>Brian W. Romans and Stephan A. Graham</i>
Remote Sensing of the Nearshore Rob Holman and Merrick C. Haller
High-Frequency Radar Observations of Ocean Surface CurrentsJeffrey D. Paduan and Libe Washburn115
Lagrangian Motion, Coherent Structures, and Lines of Persistent Material Strain <i>R.M. Samelson</i>
Deglacial Origin of Barrier Reefs Along Low-Latitude Mixed Siliciclastic and Carbonate Continental Shelf Edges André W. Droxler and Stéphan J. Jorry
The Trace Metal Composition of Marine Phytoplankton Benjamin S. Twining and Stephen B. Baines
Photophysiological Expressions of Iron Stress in Phytoplankton Michael J. Behrenfeld and Allen J. Milligan 217
Evaluation of In Situ Phytoplankton Growth Rates: A Synthesis of Data from Varied Approaches <i>Edward A. Laws</i>

Icebergs as Unique Lagrangian Ecosystems in Polar Seas K.L. Smith Jr., A.D. Sherman, T.J. Shaw, and J. Sprintall	269
Ecosystem Transformations of the Laurentian Great Lake Michigan by Nonindigenous Biological Invaders <i>Russell L. Cuhel and Carmen Aguilar</i>	289
Ocean Acidification and Coral Reefs: Effects on Breakdown, Dissolution, and Net Ecosystem Calcification Andreas J. Andersson and Dwight Gledhill	321
Evolutionary Adaptation of Marine Zooplankton to Global Change Hans G. Dam	349
Resilience to Climate Change in Coastal Marine Ecosystems Joanna R. Bernhardt and Heather M. Leslie	371
Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone William F. Gilly, J. Michael Beman, Steven Y. Litvin, and Bruce H. Robison	393
Recalcitrant Dissolved Organic Carbon Fractions Dennis A. Hansell	421
The Global Distribution and Dynamics of Chromophoric Dissolved Organic Matter Norman B. Nelson and David A. Siegel	447
The World Ocean Silica Cycle Paul J. Tréguer and Christina L. De La Rocha	477
Using Triple Isotopes of Dissolved Oxygen to Evaluate Global Marine Productivity <i>L.W. Juranek and P.D. Quay</i>	503
What Is the Metabolic State of the Oligotrophic Ocean? A Debate Hugh W. Ducklow and Scott C. Doney	525
The Oligotrophic Ocean Is Autotrophic Peter J. le B. Williams, Paul D. Quay, Toby K. Westberry, and Michael J. Bebrenfeld	535
The Oligotrophic Ocean Is Heterotrophic Carlos M. Duarte, Aurore Regaudie-de-Gioux, Jesús M. Arrieta, Antonio Delgado-Huertas, and Susana Agustí	551

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at http://marine.annualreviews.org/errata.shtml