Responses of Antarctic Marine and Freshwater Ecosystems to Changing Ice Conditions

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Polar regions are warming more rapidly than lower latitudes, and climate models predict that this trend will continue into the coming decades. Despite these observations and predictions, relatively little is known about how polar ecosystems have responded and will continue to respond to this change. Two Long-Term Ecological Research (LTER) sites, located in contrasting environments in Antarctica, have been studying marine and aquatic terrestrial ecosystems for more than two decades. We use data from these research areas to show that the extent and thickness of ice covers are highly sensitive to short- and long-term climate variation and that this variation significantly influences ecosystem processes in these respective environments. Declining sea-ice extent and duration diminishes phytoplankton blooms as a consequence of reduced water stratification, whereas the thinning of lake-ice cover enhances phytoplankton blooms because of increased penetrating light into the water column. Both responses have cascading effects on upper trophic levels.

Keywords: sea ice, lake ice, ice phenology, ecosystem responses

Sea ice and lake ice are important ecological drivers structuring marine and freshwater ecosystems, respectively. The ice acts as an intermediary between the sub-ice ecosystem and the atmosphere, and its properties are shaped by how the water body (ocean or lake) responds to both short-term atmospheric changes and long-term climate variability (Fountain et al. 2016). Because of the direct coupling of water, ice, and atmosphere, the ice cover mediates links between climate change and the underlying aquatic ecosystem. Small changes in ice properties can have substantial and long-lasting effects on the sub-ice ecosystems. Long-term research on Antarctic marine (sea ice) and freshwater (lake ice) environments reveal the extent of these dynamics.

Sea ice is the principal physical property structuring Antarctic marine ecosystems (Smith et al. 2003). Globally, the maximum winter sea-ice extent is 16 million square kilometers (km^2) in the Arctic and nearly 20 million km^2 in Antarctica. The minimum sea-ice cover extent in summer is about 4 million km^2 in each of the polar regions. Continuous satellite observations of Antarctic Peninsula sea ice, which began in late 1978, have shown a decline in sea-ice extent and duration, reflecting changes over the wider region of the Bellingshausen and Amundsen Seas (Stammerjohn et al. 2012). Globally, the ecological implications of long-term sea-ice decline have been evident in the most rapidly changing locations (western Arctic and along the western Antarctic Peninsula) for more than a decade (Ducklow et al. 2012, Post et al. 2013).

Perennially ice-covered high-latitude lakes have been considered sentinels of climate change owing to their rapid response to air temperature (e.g., Paquette et al. 2015, Obryk et al. 2016). Small climatic changes alter the surface energy balance of the lakes leading to changes in ice thermal properties and associated hydrologic (Doran et al. 2002b) and ecosystem responses (Smol et al. 2005). For example, a shift from perennial to seasonal ice covers and lake-ice thinning in the Arctic, which has a rapid and cascading effect on the lakes' ecosystems, has been recently documented (Paquette et al. 2015). Presently in the McMurdo Dry Valleys, the thickness of perennial lake-ice covers ranges from approximately 3 meters (m) to 7 m, which decouples the underlying aquatic ecosystems from atmospheric interactions and restrict the transmission of photosynthetically active radiation (PAR) to the water column to less than 3% of incident, leading to the selection of highly shade-tolerant phytoplankton (Lizotte and Priscu 1992, Morgan-Kiss et al. 2016).

The Long-Term Ecological Research (LTER) program, funded by the US National Science Foundation,
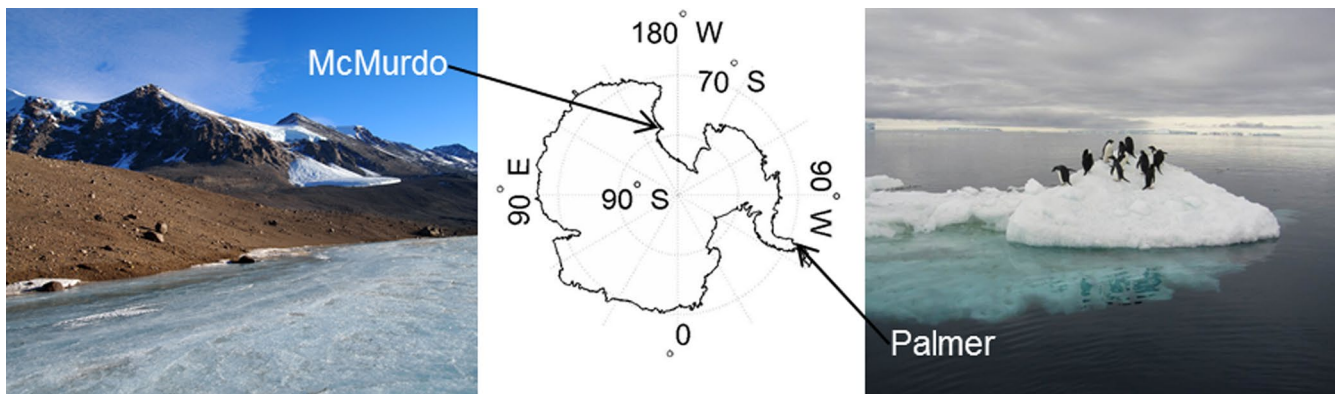
Figure 1. The location of the terrestrial (McMurdo) and marine (Palmer) Long-Term Ecological Research project sites in Antarctica. These photos depict typical landscape and seascape character. Photographs: Maciej K.Obryk (left) and Hugh W. Ducklow (right).

has been conducting strategically targeted observations at terrestrial (McMurdo Dry Valleys) and marine (Western Antarctic Peninsula) sites in Antarctica for over two decades (figure 1). Large differences in water column food-web components exist between the two sites. Prokaryotes (Bacteria and Archaea) and eukaryotic photoautotrophic plankton dominate the biomass of the McMurdo Dry Valleys lakes (Bowman et al. 2016); there is a paucity of crustacean zooplankton and no fish (Priscu et al. 1999). In contrast, the marine Western Antarctic Peninsula system includes a wide spectrum of organisms ranging from single-celled prokaryotes to large marine mammals. Each ecosystem responds uniquely to climate driven changes mediated by ice, largely because of the significant differences in community composition and associated food web dynamics. Here we synthesize both long-term and recently observed ecological responses at these two contrasting Antarctic sites as a consequence of changing ice properties. We focus on primary producers, a well-studied functional component common to the two systems (see Bowman et al. 2016 for Bacteria and Archaea). Phytoplankton cannot be addressed without reference to herbivores and their predators; the upper trophic levels at both sites are briefly discussed.

The Western Antarctic Peninsula (WAP) study site

The Palmer LTER study site (64–70°S, 64–78°W) extends 200 km from the nearshore coastal region (less than 100 m depth) to the continental slope region (more than 3000 m depth); the study area is poleward of the Antarctic Circumpolar Current and extends 700 km from near Palmer Station on Anvers Island in the north to the Charcot Island region in the south. Sea-ice duration ranges from 2–3 months in the north to more than 6 months in the south (figure 2), with much of the region now being ice free in summer. The mean air temperature is +4.1 degrees Celsius (°C) in summer and –2.4°C in winter (based on 2003–2014). Mean annual surface air temperature has increased by approximately 0.3°C per decade since 1950 (Ducklow et al. 2012). Warming is greatest in winter (+1.01°C per decade for

June, July, and August over 1974–2014; Fountain et al. 2016), with July showing the strongest trend (+1.7°C per decade over 1979–2007; Turner et al. 2013).

The McMurdo Dry Valleys (MCM) study site

The MCM LTER study site is a polar desert in Southern Victoria Land, East Antarctica (77–78°S, 160–164°E) receiving less than 5 millimeters of water-equivalent precipitation annually (Fountain et al. 2010). The MCM represent the largest ice-free expanse on the Antarctic continent resulting primarily from blockage of ice flow to the valleys from the Polar Plateau by the Transantarctic Mountains. A mosaic of soils, perennially ice-covered lakes, intermittent streams, and alpine and continental glaciers characterize the valleys (Spigel and Priscu 1998). Most of the lakes in the MCM are endorheic, so their water levels are controlled by gains of glacial ice melt in the summer and annual ablation processes. The mean annual surface air temperatures along the valley bottoms range from –14.8°C to –30.0°C, with summer temperature rarely rising above freezing (Doran et al. 2002a). Although the lake ice is controlled by the same regional climate, ice-cover thickness on each lake responds differently because of the unique chemical and thermal stratification of the individual water columns (Obryk et al. 2016). We focus our discussion on the west lobe of Lake Bonney (figure 3), a chemically stratified lake (Spigel and Priscu 1998) in the upper Taylor Valley as representative of stratified lakes in this region (most lakes in this valley are stratified). Its approximately 3.5-m-thick ice cover alters the attenuation of PAR reaching the underlying water column, resulting in extremely shade-adapted phytoplankton that form vertically distinct chlorophyll maxima (Lizotte and Priscu 1992, Fritsen and Priscu 1999, Morgan-Kiss et al. 2016). This lake is approximately 40 m deep, has a surface area of approximately 1 km², and receives most of its water from surface glacial melt and a small portion from saline flow emerging from underneath the Taylor Glacier, which terminates in this lake (Spigel and Priscu 1998, Mikucki et al. 2015).
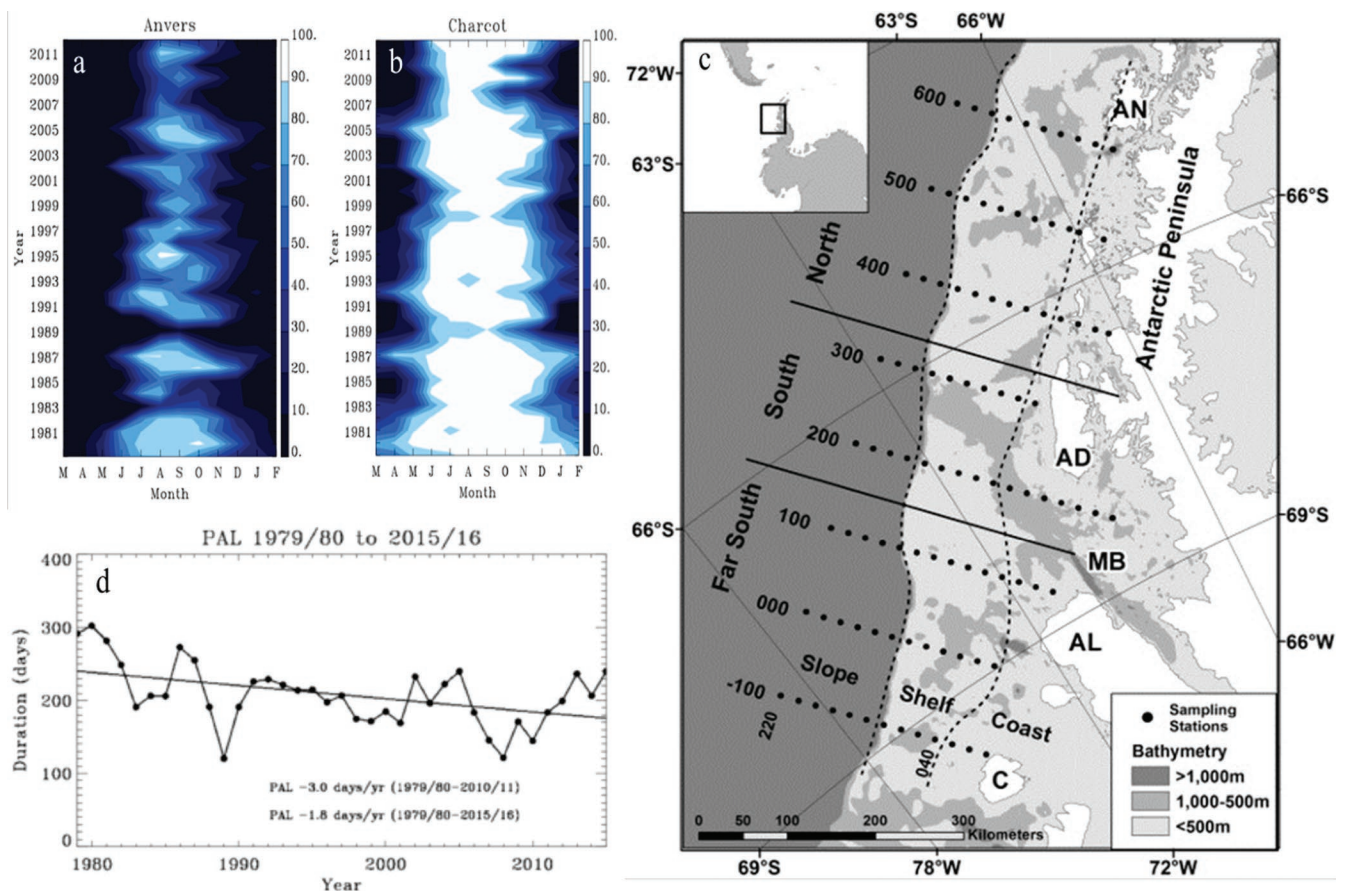
Figure 2. Temporal trends in sea-ice concentration and seasonal duration along the western Antarctic Peninsula. (a) and (b) Monthly mean sea-ice concentration (percentage of area covered by sea ice) between 1980 and 2012 in the near vicinity of Palmer Station (64°S, 64°W) and Charcot Island (70°S, 75°W). (c) A map of the Palmer LTER study region along the western Antarctic Peninsula. The onshore to offshore lines of oceanographic survey stations (black dots) are 100 kilometers (km) apart. Stations on a line are 20 km apart. Palmer Station is on Anvers Island (AN) near the northeastern corner of the study region. Charcot Island (C) is at the extreme southern end of the region. (d) The mean trend in the annual ice-season duration (days) for the greater Palmer LTER study region (200 km × 700 km, as we described in the text). The solid regression line has a slope of –18 days per decade (1979 and 1980 to 2015 and 2016). Sources: Panels (a) and (b) are adapted from Ducklow and colleagues (2013). The sea-ice concentrations were derived from NASA's Scanning Multichannel Microwave Radiometer (Stammerjohn et al 2008a).

Controls on sea and lake ice thickness

Ice cover influences ecosystem properties in these two ecosystems in different ways: Throughout an annual cycle, sea ice completely melts and re-grows, whereas lake ice thins and thickens. The seasonal melt and growth of sea ice along the WAP causes large changes in seasonal freshwater fluxes (freshwater influx in spring via ice melt and freshwater extraction in autumn, March–April–May, via ice growth) and therefore is responsible for strong seasonal changes in vertical water-column stratification (and ocean mixed layer depth). In turn, these seasonal changes affect temperature, salinity, nutrients, and light availability. In contrast, the largest impacts caused by the thinning of lake ice during austral summers in MCM are the strong changes in light transmission through the lake-ice cover.

Ice thickness is primarily controlled by surface energy balance in both ecosystems. MCM lake-ice covers undergo an annual cycle of net growth during the dark, cold winter, and a net loss during the relatively warm austral summer, maintaining 3 to 7 m thick ice cover year round (McKay et al. 1985, Adams et al. 1998). The extent to which annual gains (ice growth) and losses (ice ablation) are out of balance leads to interannual variations in ice thickness. Unlike lake-ice covers, sea ice in the WAP region melts completely during summer (figures 3a and 3b) and re-grows in winter, reaching a thermodynamic thickness of approximately 70–100 cm. However, despite these differences, both lake and sea ice are driven by local climate variability, and both are thermodynamically affected by a heat flux from a deep temperature maximum in the water column (Martinson
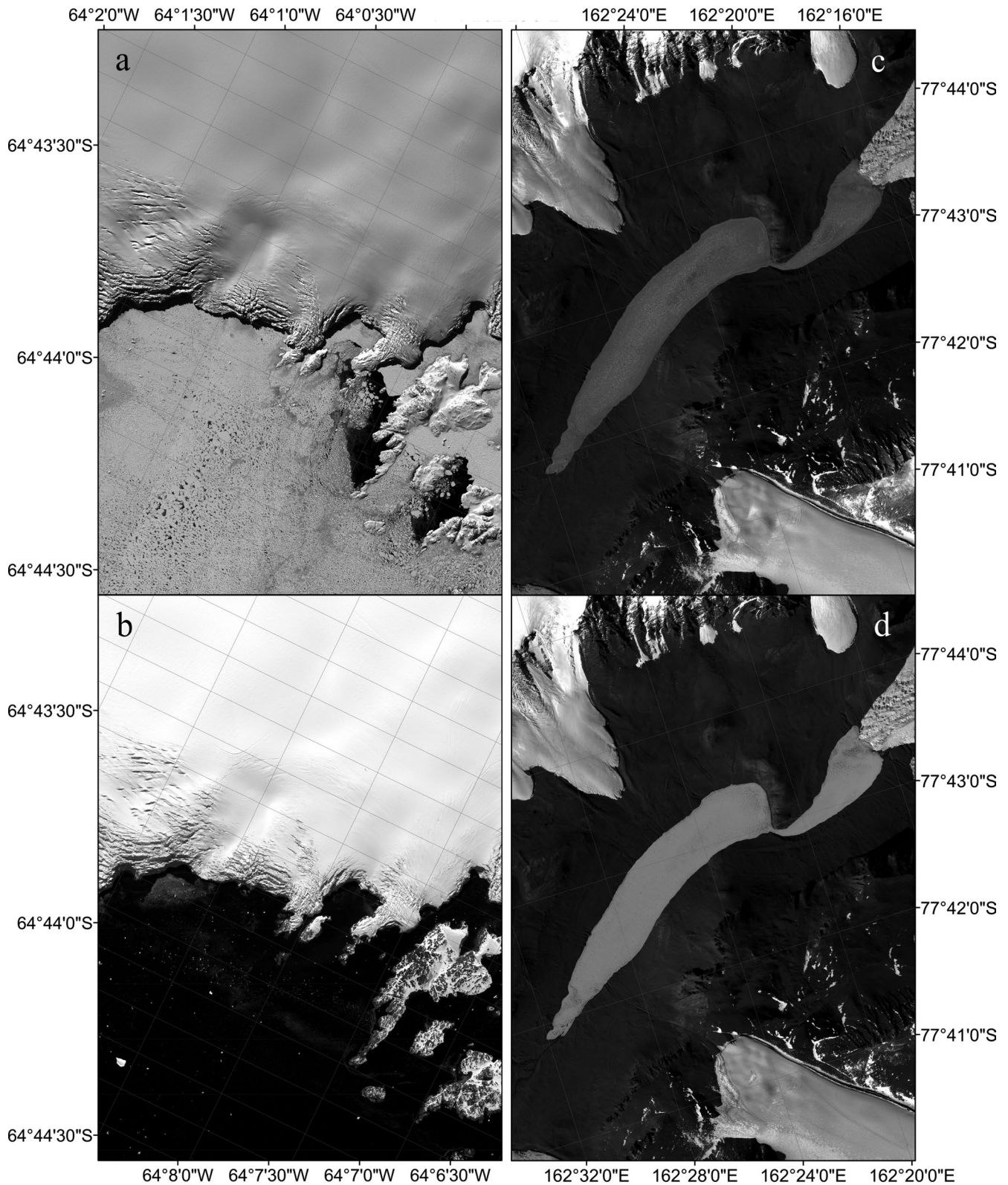
Figure 3. Satellite images representing seasonal ice changes at Palmer and McMurdo sites. (a) An example of seasonal sea-ice extent near Palmer Station in October and (b) ice-free seas in December. (c) Early season (December) relatively clear (i.e., less reflective) ice cover of Lake Bonney in McMurdo Dry Valleys in October and (d) opaque and highly reflective ice cover in December as a result of seasonal changes in optical properties in the lake ice (Howard-Williams et al. 1998).
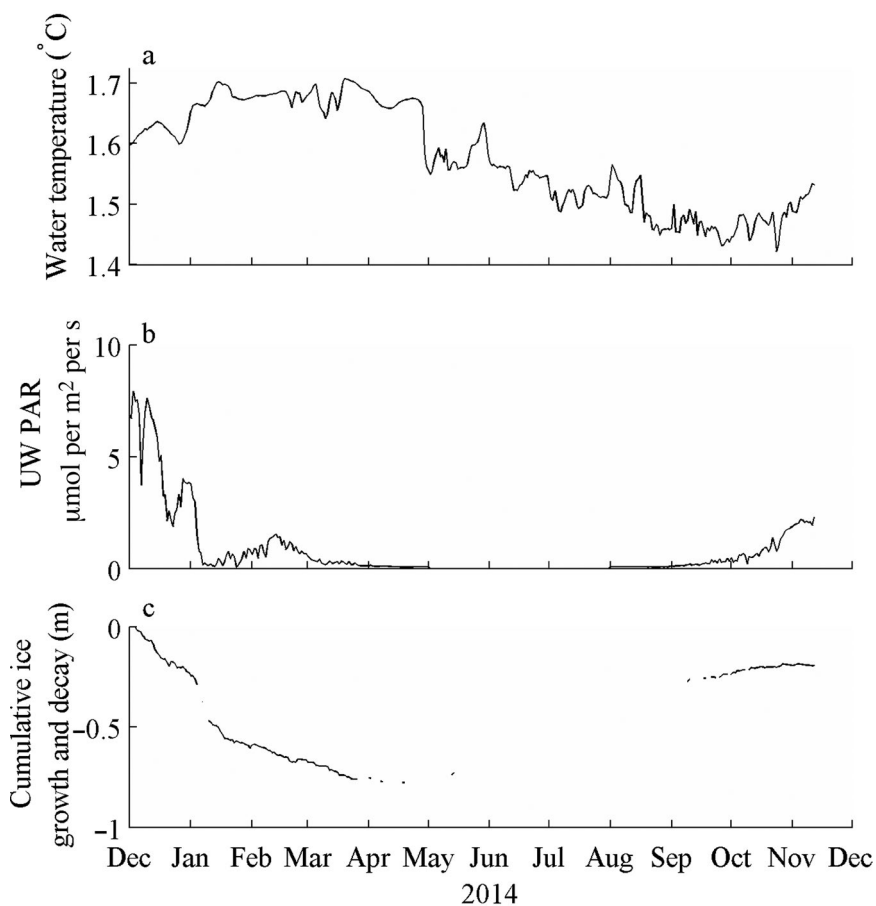
Figure 4. Seasonal changes in water-column temperature, underwater photosynthetically active radiation (UW PAR), and ice growth and decay for the west lobe of Lake Bonney. (a) Water temperature at approximately 11.5 meters (m) from the piezometric water level (the sensor is fixed from the bottom of the lake, and its absolute depth changes with seasonal lake level variations: up to 0.5 m in 2014). (b) UW PAR at 10-m depth from the piezometric water level. (c) Cumulative ice growth and decay (the decreasing values indicate ice decay, December to at least April, and the increasing values indicate ice growth). Data obtained using autonomous moored sensors deployed in the lake. For details, see www.mcmlter.org. Abbreviation: μmol per m² per s, micromols per square meter per second.

variability. Solar radiation (transmitted through the perennial ice cover) drives the thermal profile of the water column (Spigel and Priscu 1996), which controls heat exchanges at the ice–water interface (Obryk et al. 2016). Because water has a larger heat capacity than air, the seasonal warming of the water column persists until April (figure 4a). This warming is responsible for ice bottom decay until late autumn when little to no solar radiation penetrates the ice cover (figure 4b). Conversely, during the winter months, the cold atmosphere becomes a heat sink for the lakes, and the large temperature gradient between the top and the bottom of the ice cover drives new ice growth at the bottom of the ice cover. However, ice losses occur throughout the year via ablation, which includes sublimation, melt, and evaporation. During winter, ice removal is only via surface sublimation (which occur at the same time new ice is being added to the bottom). Winter ice ablation on all Taylor Valley lakes between 2001 and 2010 was relatively constant (0.07 m to 0.21 m between February and November), whereas summer ablation (including sublimation, surface and bottom ice melt, and evaporation), varied between 0.25 m to 1.62 m (between December and January; Dugan et al. 2013). Data on the rate of ice formation at the bottom of the ice are limited (Adams et al. 1998), and the maximum ice-formation rate so far recorded is on the order of tens of millimeters per day (figure 4c). On the basis of the mean annual ablation rates between 2001 and 2010 (0.64 m to 0.99 m per year), in concert with a steady state ice thickness of approximately 4 m, the bulk turnover time of the ice cover is between approximately 4 years and 6 years (Dugan et al. 2013).

Similarly to lake-ice thermodynamics, Antarctic sea-ice growth and melt processes are controlled by the surface energy balance, but these processes are also strongly influenced by the presence of a warm Circumpolar Deep Water, which can be 1 to 4 degrees above the *in situ* freezing point. Circumpolar Deep Water can be brought toward the surface through upwelling or by wind- or buoyancy-driven deep mixing (the latter occurring when brine is rejected during sea-ice formation). The presence of this warm water mass at depth moderates how much sea ice can thicken thermodynamically (Martinson and Iannuzzi 1998), particularly in areas of strong upwelling or ocean mixing (Martinson et al.

et al. 2008, Obryk et al. 2016). This in turn hinders ice growth during winter and facilitates melting in spring–summer. In contrast, ocean currents and winds also affect sea ice dynamically. Wind- or current-driven motion of the sea-ice cover causes either the opening of the ice cover or rafting, ridging, and mechanical ice thickening (Holland and Kwok 2012), depending on wind and current direction (see also Fountain et al. 2016).

The main thermodynamic factors controlling lake-ice thickness are heat loss via conduction from the ice cover and latent heat release at the ice-water interface (McKay et al. 1985). Therefore, annual ice growth and loss at the lake-ice bottom is a function of the temperature gradient between the atmosphere and ice–water interface. This gradient regulates seasonal and interannual ice thickness

2008, Martinson 2012). In addition (and as we described above), sea-ice extent and thickness is also strongly influenced by winds and ocean currents that drive ice motion. Over the last 3+ decades of continuous satellite observations, the annual ice season along the WAP is becoming shorter by up to several months (figure 2) largely because of delays in the start of the ice re-growth season in autumn (Stammerjohn et al. 2008a, 2012). In addition, the timing of the subsequent spring ice-edge retreat (or melt-back) is becoming earlier on average (thus, it also contributes to the shortening of the annual ice season duration), but the trend in the spring ice-edge retreat is not as strong as the trend in the autumn ice-edge advance because of more year-to-year variability. There is also a strong correspondence between anomalies in the spring ice edge retreat and the subsequent autumn ice edge advance (i.e., an earlier spring retreat is typically followed by a later autumn ice edge advance; Stammerjohn et al. 2008b, 2012). This is consistent with an ice-albedo and ocean heat feedback (Meredith and King 2005, Stammerjohn et al. 2012); the earlier the ice cover opens and retreats in spring, the greater the exposed ocean warms by solar insolation, the faster the ice cover continues to melt, and therefore the longer the surface ocean warms over summer. Consequently, ice growth in autumn is delayed by the need to cool a much greater heat reservoir. In addition to these feedbacks, winds also play a large role. Strong winds in spring help break up the ice cover to allow for solar warming of surface waters, and strong winds in autumn, in particular warm northerly winds, help delay the ice edge advance through wind-driven advection southward (Stammerjohn et al. 2008b, 2012, Holland and Kwok 2012).

At both sites, the spring–summer phytoplankton bloom is mediated by the seasonal changes in the ice cover, but as we described above, the mediating controls on ice thickness (and areal coverage) are quite different between the two sites. For sea ice, air temperature, winds, ocean currents and vertical mixing processes determine ice extent and thickness, which in turn influence the timing and magnitude of the spring melt-back. Consequently, these processes affect the timing and extent of shallow freshwater stratification, which largely determines the timing, magnitude, and location of spring algal blooms (Venables et al. 2013). For lake ice, winter processes affecting ice thickness (air temperature, ablation rates, and heat fluxes from the water column) control the spring–summer transmission of solar radiation through the ice, which directly influences photosynthesis by the light-limited phytoplankton. Therefore, in summary, the influence of regional atmospheric and ocean circulation on sea ice makes WAP sea-ice extent more susceptible to large scale global climate variability (Fountain et al. 2016), whereas lake ice in MCM is controlled more by local atmospheric processes (McKay et al. 1985).

Ice-bound ecosystems

Sea and lake ice both harbor microbial ecosystems; however, because of differences in ice dynamics, their origin differs. Sea and lake ice have a complex, porous, three-dimensional structure, controlled by ice thermal regimes. Sea-ice structure is derived from brine rejection during the freezing process; and accommodates a dynamic biotic community of sea-ice algae, principally diatoms, bacteria and protozoa. It harbors distinct biotic assemblages in different parts of the ice column, including pools of seawater on the ice surface, dense accumulations on the underside, and layers within the ice itself. Lake ice, however, harbors a microbial ecosystem associated with deposition of aeolian sediment that melts into the ice (Priscu et al. 1998). The lake-ice morphology is characterized by melt ponds, weak candled ice, and ice pedestals up to 1 m high because of differential ablation resulting from aeolian deposition on the ice surface (Adams et al. 1998, Jepsen et al. 2010). There are comparatively few reliable measurements of primary production rates within sea and lake ice, and the integration of point measurements in space and time is especially challenging in these dynamic and remote environments.

Regional sea-ice primary productivity estimates come from remote sensing coupled with bio-optical modeling. Arrigo (2007) estimated that the mean annual net primary production in sea ice was 5–15 grams of carbon (C) per square meter (m^2) per year, but such estimates are severely hampered by the patchiness inherent in the sea ice, and also by chronic under sampling in space and time. Arrigo also concluded that even in the most favorable conditions, the annual production was probably less than 50 grams of C per m^2 per year, about the same as in the most oligotrophic parts of the open sea. The total annual production in the retreating sea ice of the marginal sea-ice zone (MIZ) around Antarctica (approximately 10 million km^2) is estimated to be 30–70 teragrams (Tg) C per year (Arrigo 2007). Within the pelagic MIZ, the annual production is about 1500 Tg C, or in other words, the sea-ice contribution is 3%. The annual production for the entire Southern Ocean (58 million km^2) is estimated to be approximately 8000 Tg C; therefore, the sea-ice contribution is less than 1% of the total. Chlorophyll stocks are extremely heterogeneous, ranging from less than 1 to more than 200 milligrams (mg) of chlorophyll (Chl) per m^2, characteristic of the most oligotrophic pelagic ocean regions and enriched estuaries, respectively. Biomass and detritus released from the melting ice sink through the water column and contribute to a seasonal pulse of organic matter to the water column. The role of the sea-ice algal community in triggering water column blooms remains unresolved. Much of the evidence in favor of sea-ice species as "seeds" is circumstantial and viable, successful "seeders" may be limited to just a few characteristic species. The actual contribution of sea ice to regional production, and its influence on the food web, are much greater than the direct subsidy of ice-borne production. For example, high phytoplankton biomass concentrations and high primary production rates are associated with diatoms corresponding with winters that have increased sea-ice extent and duration (Saba et al. 2014).

Perennial lake ice not only isolates the water column from direct interaction with the atmosphere, but, as we mentioned above, it also harbors microbial assemblages associated with aeolian sediment transport. Solar heating of the sediment entrapped in the ice forms inclusions of melt water (Jepsen et al. 2010) and a habitat for microbial life (Priscu et al. 1998). Priscu and colleagues (1998) showed this ice-bound ecosystem produces 229 mg of new particulate organic carbon (POC) per m^2 per year via in situ photoautotrophic activity and that a majority of this new carbon was incorporated into protein (Fritsen and Priscu 1998). Contribution of the POC produced from the ice cover to the water column varies from year to year depending on the rate of sediment loading on the ice surface, the extent of melt water inclusions and rates of its migration throughout, all of which are dependent on climatic conditions (Adams et al. 1998). This sediment and microbial ecosystem influences ice transparency and introduces organisms into the water column (Priscu et al. 2005). The distribution of aeolian sediment deposition on the surface of the ice surface has been shown to be spatially heterogeneous (Obryk et al. 2014), further complicating annual POC estimations. These ecosystems do not contribute substantially to primary productivity in the lakes (Fritsen and Priscu 1998). Priscu and colleagues (1999) showed water column community respiration on an annual scale exceeds photosynthesis and concluded that there must be another source of organic carbon to the lake. Relict organic carbon that accumulated in the deep saline waters may provide some of this carbon to drive heterotrophic processes (Takacs et al. 2001, Bowman et al. 2016), and chemolithoautotrophic processes may provide another source of new carbon (Vick-Majors et al. 2014). McMurdo LTER is now deploying autonomous limnological sampling equipment (Winslow et al. 2014) to examine ecosystem processes and community structure during the polar winter.

Seasonal ecosystem responses and associated photoacclimation

Despite the differences in ice dynamics, similarities between the two sites exist with respect to water column ecosystem responses. Both sites are exposed to strong seasonal solar variability (Fountain et al. 2016), which requires ice-bound and under-ice phytoplankton to photoacclimate to extreme solar radiation changes throughout the season, including photoprotective mechanisms (i.e., energy dissipation) under excess light and increasing photosynthetic efficiency (i.e., light absorption) during low-light conditions. Although some photoacclimation mechanisms are comparable in phytoplankton from both sites, photoprotection is less developed, and photosynthesis is saturated at relatively low PAR levels in lake phytoplankton because of the permanent nature of the ice covers (Morgan-Kiss et al. 2006). Comparatively, the seasonal marine phytoplankton bloom magnitudes are a result of fresh water influx from melted sea ice, analogous to the transparency of lake-ice covers. In austral spring and summer, the Antarctic MIZ and lacustrine environments are characterized by intense primary productivity concentrated in both space and time. Much of the annual primary production occurs during the spring–summer bloom at both sites; however, the exact timing and duration of blooms differs within regions and between the two sites (figure 5).

One of the largest (though brief) spring phytoplankton blooms observed at WAP since 1992 occurred in 2012 (figure 5). The bloom started in early November following the sea-ice retreat and reached a peak of 837 mg Chl per m^2 on 30 November. There was noticeable freshening but only slight warming in the same period, as the summer mixed layer shoaled to about 10 meters at the time of the bloom. Similarly, in MCM, on the basis of the longest seasonal temporal record, the bloom started mid-December (figure 5), when optical properties of the ice begun to change and ice started to thin. Chlorophyll-*a* reached a peak of 54.6 mg Chl per m^2 on 29 January, followed by a decline and an increase of up to 60.0 mg Chl per m^2 on 4 April (see below for explanation), based on depth integrated values between 4 and 20 m from figure 5 (no data exist beyond this date). The differences in timing and duration of seasonal blooms at both sites are reflected by differences in ecosystem–ice coupling and photoacclimation.

Sea ice represents an extreme light and nutrient environment for phytoplankton. It is well documented that cells have a range of photoacclimation responses to cope with these extreme light conditions (Morgan-Kiss et al. 2006, Rintala et al. 2006). For populations living on the surface of the ice, cells must cope with extremely high light levels that can inhibit the photosynthesis and growth and induce significant cellular damage (Arrigo et al. 2014). Phytoplankton respond by decreasing cellular concentrations of photosynthetic pigments while simultaneously increasing photoprotective pigments to decrease the overall absorptive cross-section of the photosynthetic apparatus (Robinson et al. 1997). The xanthophyll cycle represents a major photoacclimation strategy for dynamically adjusting the concentration of photoprotective pigments and allowing for rapid conversion of the photosynthetic apparatus from light absorption to energy dissipation (Demmig-Adams 1990, Robinson et al. 1997). To respond to high ultraviolet light levels, cells increase cellular concentrations of microsporine amino acids, which act as "sunscreen" (Hannach and Sigleo 1998).

In contrast to surface conditions, cells residing in and under the ice must deal with extremely low light reflecting the efficient light attenuation by snow and ice (Arrigo et al. 2014). To respond, cells increase cellular concentrations of photosynthetic pigments, particularly accessory carotenoids and chlorophyll-*c*, which are effective at absorbing the blue and green light that can penetrate through snow and ice (Arrigo et al. 2014). In addition, cells employ a range of cellular adaptations to maintain high photosynthetic efficiencies (Mock and Kroon 2002, Rintala et al. 2006). Both sets of responses are nutrient dependent, and because nutrient limitation is not uncommon for the algae living in the ice, cellular responses are often constrained (Arrigo et al. 2014).
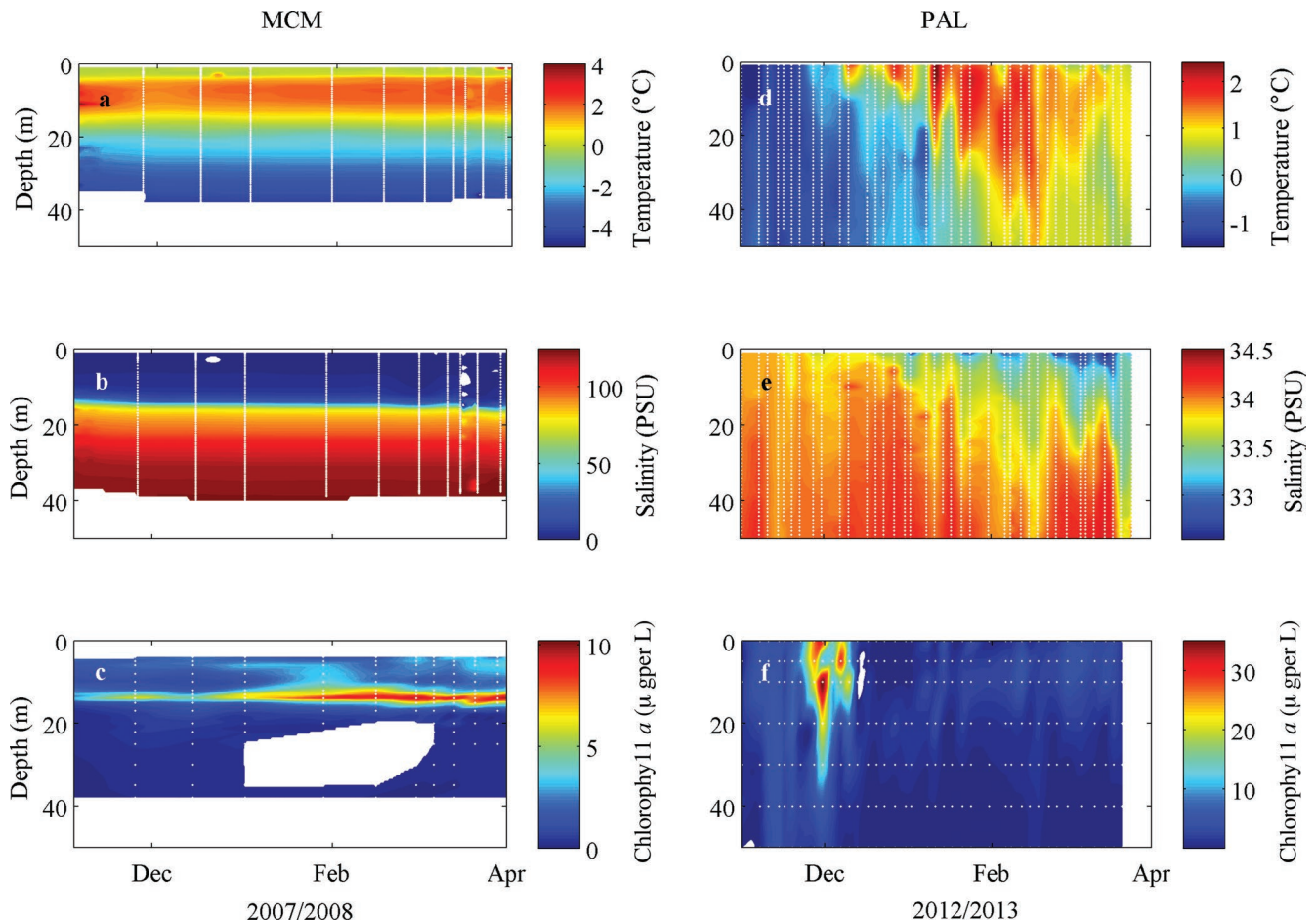
MCM

PAL

Figure 5. The seasonal evolution of the vertical distributions of temperature (a and d), salinity (b and e), and chlorophyll-a (c and f) at the McMurdo (MCM) LTER west lobe of Lake Bonney in 2007–2008 and at the Palmer (PAL) LTER, about 1 kilometer offshore of Palmer Station, Antarctica in 2012–2013. Sea-ice cover in the area ended around November 10, permitting regular, twice-weekly sampling by small boat. High-resolution (approximately one meter) temperature and salinity data were obtained with electronic sensors. Chlorophyll-a data were from discrete bottle samples at the depths and dates shown by white symbols at both sites. Temperatures and salinity were obtained using CTD profilers. Abbreviations: m, meters; µg per L, micrograms per liter; °C, degrees Celsius.

The high productivity of WAP waters tends to be dominated by diatoms (Prézelin et al. 2000) or cryptophytes (Rodriguez et al. 2002, Moline et al. 2004), with prymnesiophytes (Prézelin et al. 2000) being the next most prevalent phytoplankton taxon. Chlorophytes and phytoflagellates (pelagophytes, dinoflagellates, and prasinophytes) are sometimes present, but blooms are more an exceptional event (Bidigare et al. 1996, Moline and Prézelin 1996). WAP LTER time series measurements in coastal waters at Palmer Station indicate that dominant diatoms and cryptophytes are segregated in time and space (Saba et al. 2014). In contrast, prymnesiophytes are a relatively constant background population accounting for up to a quarter of the chlorophyll *a*. Cryptophyte blooms generally occur in January and are associated with cold, low salinity surface waters (Rodriguez et al. 2002, Moline et al. 2004). They are not associated with a shallow upper mixed layers consisting of purely marine waters suggesting light limitation is not the primary factor in

determining their success. As blooms occur after the sea-ice retreat in October and November, it is hypothesized that the cryptophytes are associated with glacial runoff. The glacial meltwater in the summer might possibly "seed" the water with a cryptophyte population from nearshore waters and/or the meltwater has a specific nutrient profile allowing cells to overcome micronutrient limitation. The shift from diatoms to cryptophytes represents a fundamental decline in the size spectrum of the phytoplankton community, which has significant implications for the grazer communities (Meyer and El-Sayed 1983, Quetin and Ross 1985, Sailley et al. 2013).

MCM lake ice changes in its extent, roughness, and transparency (Howard-Williams et al. 1998, Fritsen and Priscu 1999) over the year. Underwater PAR (UW PAR) peaks in December and is absent during the polar night between March and September (Priscu et al. 1999, Morgan-Kiss et al. 2016). Despite continuous summer solar input, a reduction of UW PAR occurs midsummer (December) as a result

of hoar frost formation within the air bubbles as ice temperature approaches an isothermal state (Adams et al. 1998, Howard-Williams et al. 1998, Fritsen and Priscu 1999). This optical change (figures 3c and 3d) reduces light transmission through the ice by approximately 50% (figure 4b; Howard-Williams et al. 1998). By autumn (March–April–May), the ice becomes more transparent as the lake water infiltrates the cover allowing the fading solar radiation to reach the water column with greater efficiency. Although solar radiation is directly responsible for internal ice melt because of the heating of entrapped sediment within the ice matrix (Jepsen et al. 2010), there is no obvious relationship between the penetrating solar radiation and ice decay and growth at the ice bottom (figures 4b and 4c). Despite high attenuation of PAR by the overlying ice column, sufficient light levels (figure 4b) penetrate the water column for a deep chlorophyll-*a* maximum to develop (between 12 and 15 m at Lake Bonney), associated with the depth of the thermocline and chemocline (figure 5). The upward flux of nutrients across the chemocline provides nutrients that fuel phytoplankton growth (Priscu 1995) as UW PAR increases in the austral spring. Seasonal trends in chlorophyll accumulation in dry valleys phytoplankton appear to be uncoupled from PAR levels and rates of primary production. Chlorophyll-*a* levels remain high during summer and autumn as solar radiation decreases (figure 5), while rates of primary production and expression of light-dependent C-fixation genes (RubisCO) rapidly decline during the same time period (Kong et al. 2012, Morgan-Kiss et al. 2016).

In MCM lakes, the underlying mechanisms for the apparent uncoupling of chlorophyll-*a* levels from light availability and photosynthesis during the polar night transition are likely driven by multiple processes across different phytoplankton groups. Obligate photoautotrophic phytoplankton (e.g., *Chlamydomonas* spp.), which dominate the upper water column of Lake Bonney, respond to declining light availability by photoacclimation processes, which involve the accumulation of chlorophyll to increase the efficiency of light-energy capture (Morgan-Kiss et al. 2016). Following this transient period of shade acclimation, lab experiments predict that the Lake Bonney alga *Chlamydomonas* sp. UWO241 maintains its photosynthetic apparatus in an intact, downregulated state for several weeks as an adaptive strategy to the short growing period during the austral summer (Morgan-Kiss et al 2006, 2016). However, phytoplankton capable of mixed metabolism (i.e., combined photosynthesis with heterotrophic ingestion of prey) could also contribute to the sustained chlorophyll-*a* levels during the onset of polar winter. Mixotrophy among dry valley lake protists appears to be a prevalent adaptive advantage to supplement carbon and energy acquisition during seasons of low to no light (Thurman et al. 2012, Li et al. 2016). Therefore, the occurrence of high chlorophyll-*a* levels during periods of low photosynthesis and low light availability reflect complex processes involving photoacclimation in obligate photoautotrophic phytoplankton as well as shifts in community metabolism, sustaining biomass of mixotrophic

species. Unfortunately, current models are based on projections from summer communities and laboratory manipulations on isolates. There are few chlorophyll-*a* data after the onset of polar night in April, but low levels in December indicate that much of the chlorophyll-*a* is degraded or sinks to the bottom during winter (Lizotte et al. 1996, Priscu et al. 1999). The deep chlorophyll layer acts as a biofilter, preventing upward diffusing nutrients from reaching the near-surface water layers. As a consequence, the phytoplankton in the upper water column are phosphorus deficient (Priscu 1995) and their biomass often declines early in the summer season.

Ecological response to long-term changes in ice phenology

The long-term ecological response to changes in ice phenology (temporal patterns in thickness and extent) is complex at both LTER sites. Conceptually, thicker lake ice is associated with lower primary productivity, and thinner lake ice is associated with higher primary productivity as a consequence of PAR attenuation in the lake-ice cover (figure 6). This relationship is also modulated by the residence time of the sediment on the surface and within the ice, as well as seasonal stream water influx, which affects the turbidity of the water column and nutrient influx. In contrast, the effect of sea ice on phytoplankton bloom formation and magnitude is twofold. In the northern WAP, blooms are larger following thicker sea-ice winters because more ice supplies more freshwater and therefore more stable conditions after the ice melt (figure 7; Saba et al. 2014). This explanation is consistent with declining sea ice that has led to lower stability and greater water column mixing, lowering the average light intensity experienced by phytoplankton (figure 7). In the south, sea ice formerly covered most of the region for most of the year (figure 2b), preventing light from reaching the water column, and exposing little open water for bloom development (figure 7).

The long-term ecological response at both sites is also modulated by local weather conditions and teleconnections to hemisphere-scale climate modes such as the El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (Stammerjohn et al. 2008b, Saba et al. 2014). Heavy winter sea ice presents a barrier to wind mixing: Deeper mixed layers form in winters when sea-ice cover is light, intermittent, or even absent, leading to less vertical stability and more mixing in summer, inhibiting phytoplankton blooming (Venables et al. 2013). In MCM, unusually warm seasons (local weather climate) can have large ecological responses. For example, an unusually warm season in 2001–2002 coincided with a rapid lake level rise (Foreman et al. 2004). Large volumes of glacial melt water inflow are linked with increased turbidity in the water column (Fountain et al. 2016) and reduced primary productivity (Foreman et al. 2004). Details on climate teleconnection for both sites and on the warm season, hereafter referred to as the flood year, are described from a climatological perspective in Fountain and colleagues (2016).
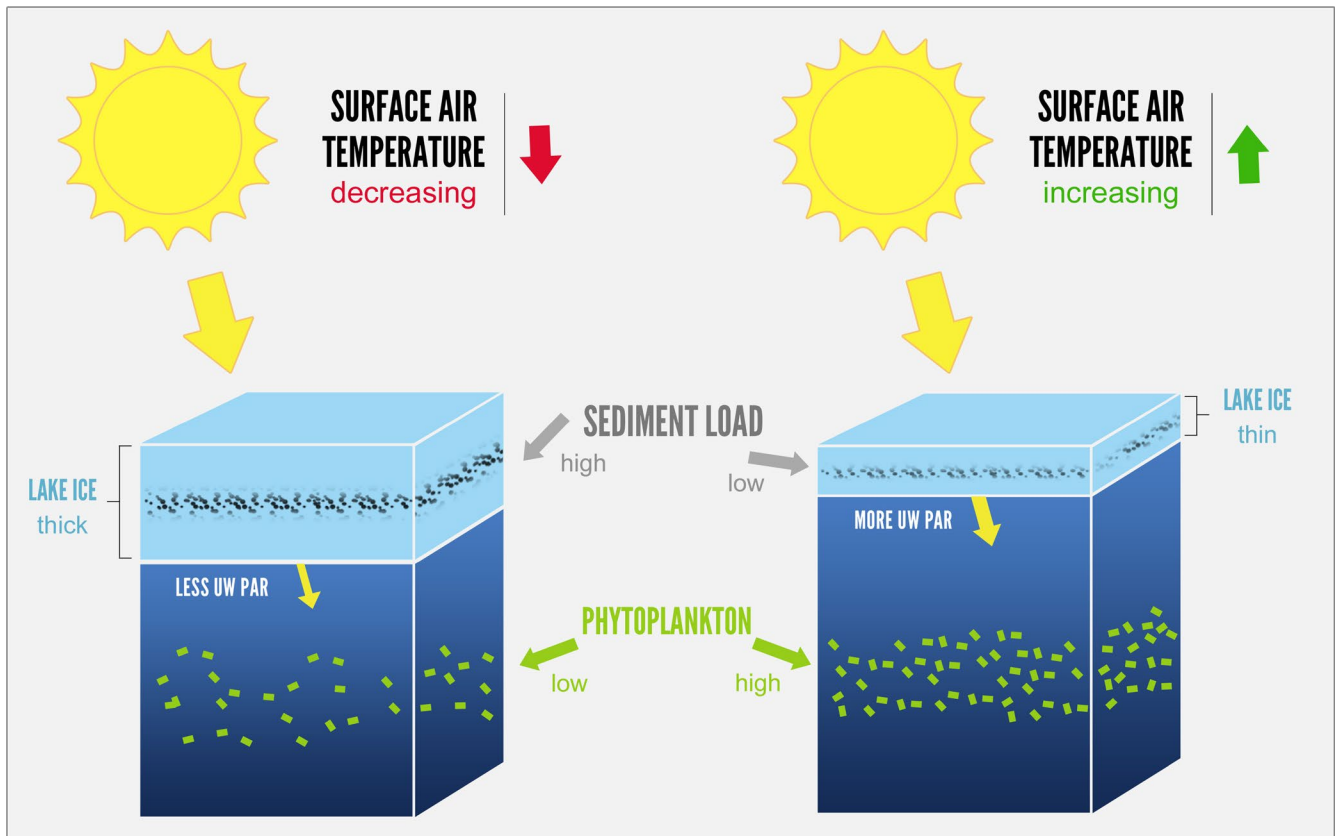
Figure 6. A generalized schematic representing bimodal ecological response to phytoplankton in stratified perennially ice-covered Antarctic lakes to changing ice thickness. Thinner ice is associated with higher primary productivity due to increased penetration of solar radiation into the water column.

Along the WAP, although sea-ice cover has declined by as much as 90 days (figure 2; Stammerjohn et al. 2008a), spatial and short term temporal variability complicate and obscure detection of ecological trends through discrete sampling. An interdecadal comparison of chlorophyll standing stocks determined from satellite ocean color imagery confirms that phytoplankton blooms declined by up to 90% in 1998–2006 compared with in 1978–1986 in the northern WAP region (Montes-Hugo et al. 2009). However, by the 2000s, sea-ice loss had actually opened new areas of the ocean in the south for phytoplankton growth (figure 7; Montes-Hugo et al. 2009). This effect of a warming climate could be a negative (self-limiting) feedback loop, whereby warming produces larger blooms that store more carbon, alleviating future warming (Peck et al. 2010). However, we do not know the probable direction of continued sea-ice loss in the north or south. Both trends—currently decreasing phytoplankton blooms in the north and increases in the south—appear to be a response to declining sea ice.

Ice thickness trends for the west lobe of Lake Bonney show two distinct patterns; an ice thickness increase since the early 1990s to approximately 2001 (Doran et al. 2002b), followed by an ice thickness decrease (around 2003) thereafter (figure 8a; Obryk et al. 2016). Between 1993 and 2013, primary productivity was negatively correlated with ice thickness ($r = -.66$, $p < .001$, $n = 20$), with a particularly strong negative relationship before 2001–2002 flood year ($r = -.84$, $p < .01$, $n = 8$), indicating a state change in the ecosystem following the large pulse of melt water input ($r = -.54$, $p = .07$, $n = 12$). The flood year increased turbidity, nutrient flux, and associated light attenuation in the lake as a result of larger melt-water influx (Fountain et al. 2016). As a result of diminished UW PAR, an increase of chlorophyll-a is observed, representing a photoacclimation response (figure 8b), similar to the impact of declining PAR on phytoplankton communities during the polar night transition (Morgan-Kiss et al. 2016). The legacy of the flood year (increased turbidity of the water column) is shown by chlorophyll-a concentration (photoacclimation), which increased a season following the flood year and has declined since (figure 8b). Only recently did chlorophyll-a return to preflood season values. The observed long-term trends in Lake Bonney show that ice thickness variation influences primary productivity; however, this response can be modulated by changes of phytoplankton physiology by regulating UW PAR because of changes in the optical properties of the water column. Principal component analysis reveals that lake-ice thickness has a strong negative relationship with primary productivity, and that primary productivity is positively related to lake-level fluctuations,
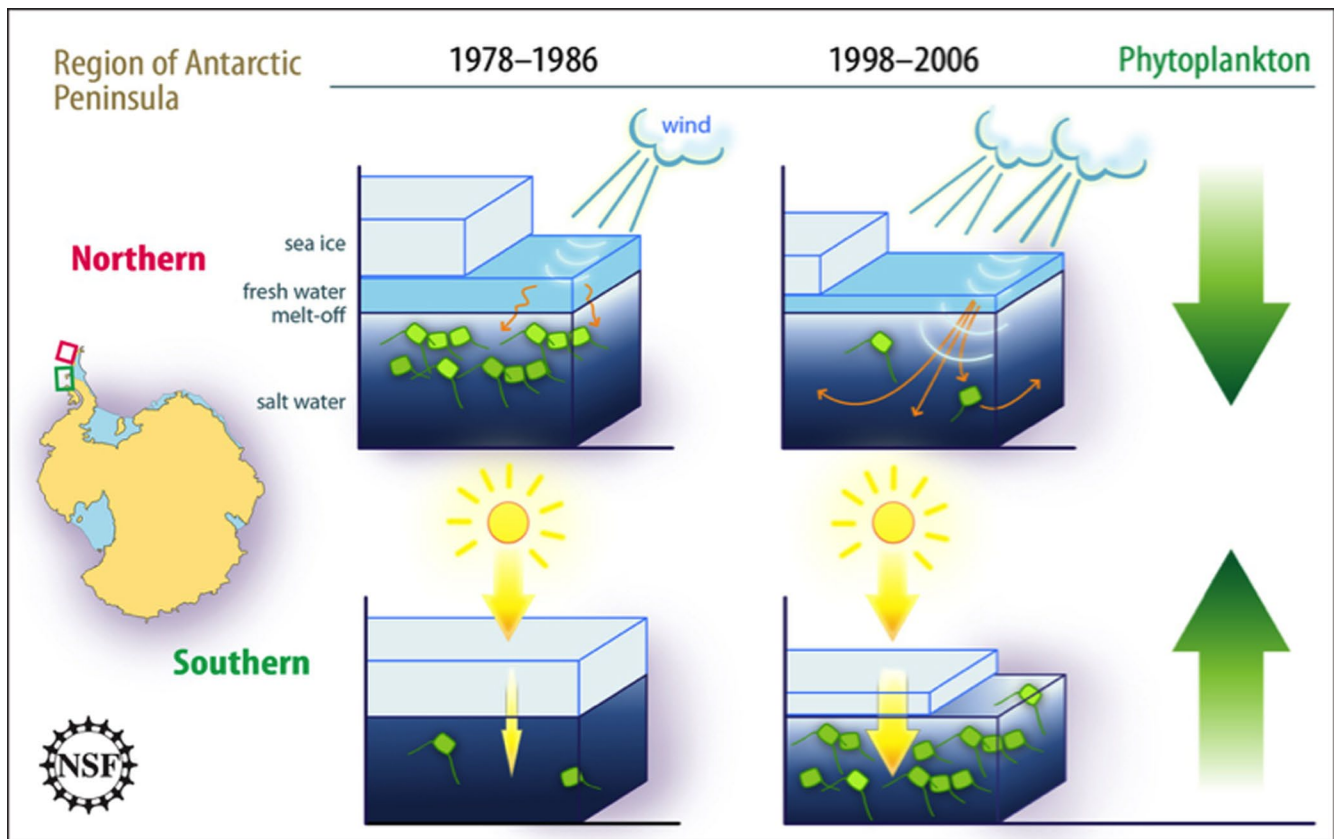
Figure 7. Changes in sea-ice influence on ocean mixed layer along WAP, 1975–2006, generalized from Montes and colleagues. (2009). In the north region, declining sea-ice cover has caused declines in phytoplankton because of less freshwater input and greater vertical mixing. In the south, loss of ice has exposed the new ocean surface to sunlight, leading to phytoplankton increases. Source: Z. Deretsky and American Association for the Advancement of Science.
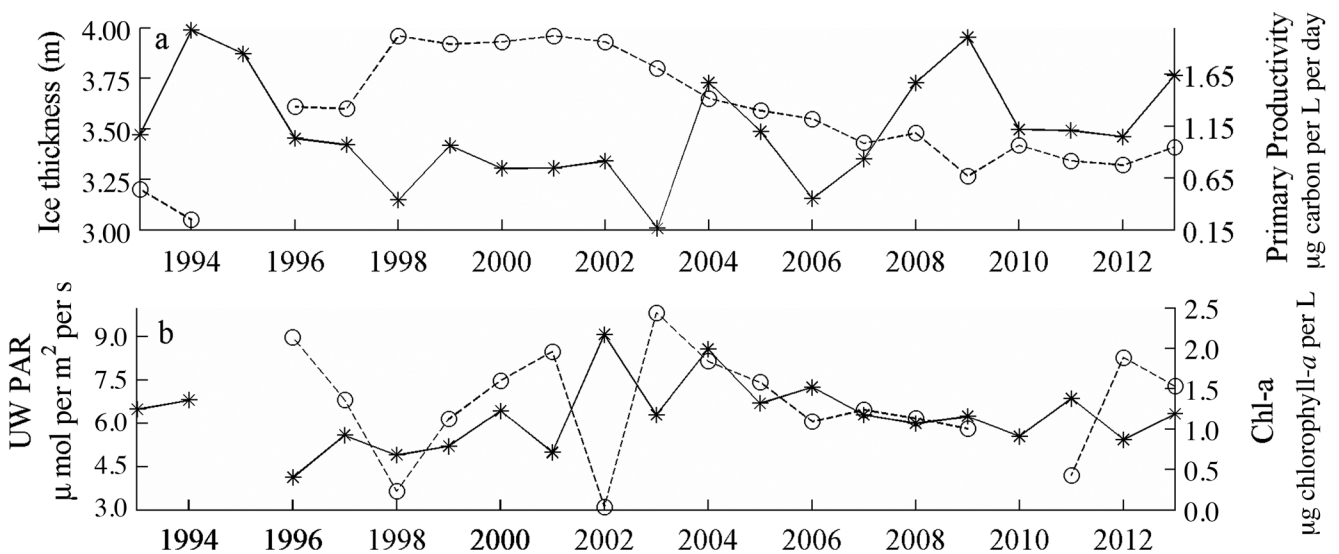

*Figure 8. Long-term trends in (a) ice thickness (the circles corresponding to the left y-axis) and primary productivity (the asterisks corresponding to the right y-axis) and (b) underwater photosynthetically active radiation (UW PAR, the circles corresponding to left y-axis) and chlorophyll-*a (Chl-a, the asterisks corresponding to right y-axis) concentration from the west lobe of Lake Bonney. The primary productivity, chlorophyll-*a*, and UW PAR are from a 10-meter depth. The years along the x-axis denote the beginning of austral summer (the data were obtained in November, with an exception of 1993 and 1994 to 1995, which were obtained in December and October, respectively). Abbreviations: L, liters; m, meters; s, seconds; µg, micrograms; µmol, micromols.*
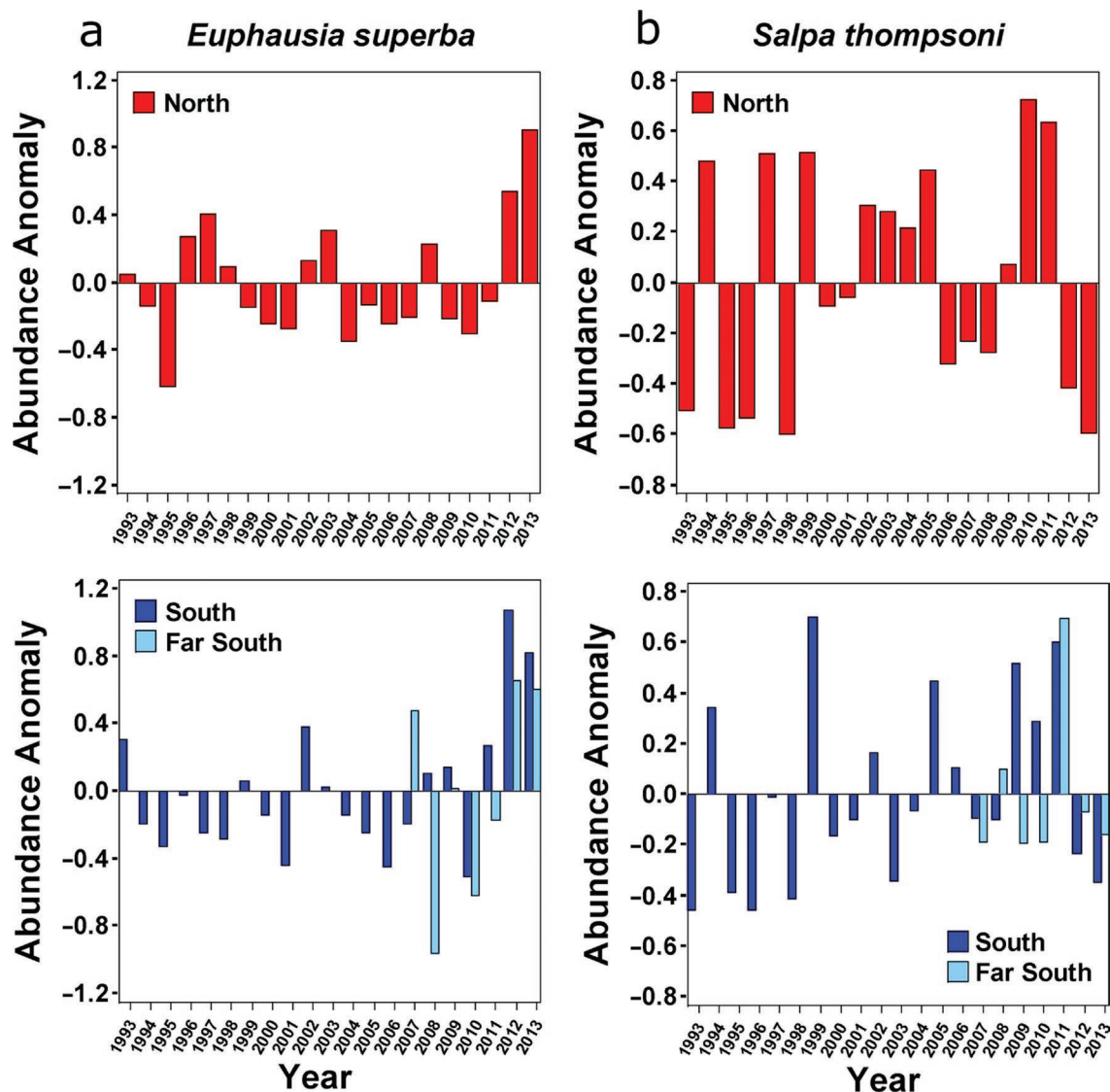
*Figure 9. Abundance anomalies (1993–2013) for (a) Antarctic krill (*Euphausia superba*) and (b) salp (*Salpa thompsoni*). The northern subregion of the LTER study area extends from Palmer Station (64°S) to 67°S. The south and far south region extends from 67°S to Charcot Island (70°S). There is no significant long-term, directional trend for either species over the time period examined. Source: Reprinted from Steinberg and colleagues (2015).*

which are responsible for nutrient flux during the summer inflows via stream flow.

Food-web responses to ice variability

Responses to variability in ice cover cascade through the trophic levels of each ecosystem. Changes at the producer level may cascade to higher trophic levels, and there may be direct effects on herbivores and predators, whose life cycles are also attuned to ice phenology. MCM and WAP ecosystems contrast starkly in the importance of upper trophic level organisms. The strong dependence of Antarctic krill (*Euphausia superba*) on sea ice, and the unambiguous decline of sea ice over the past several decades suggest that krill should have declined as well, and they have, at least over large space and time scales in the Southern Ocean (Atkinson et al. 2004).

Antarctic krill have declined by 38%–75% per decade since 1976, apparently in response to declining sea ice. Salps, gelatinous pelagic tunicate filter feeders (*Salpa thompsoni*), are typically found in warmer, lower-productivity, and more ice-free Southern Ocean regions than krill. Salps have increased over the SW Atlantic region since 1926 (Atkinson et al. 2004).

Like phytoplankton, these patterns are more complicated at smaller spatial and temporal scales. Steinberg and colleagues (2015) analyzed long-term trends in zooplankton along the WAP during 1993–2013. There was no directional trend in Antarctic krill abundance; rather, krill showed a 5-year cycle of positive and negative abundance anomalies (figure 9a) and a strong positive correlation with primary production lagged by 2 years. *Salpa thompsoni* showed no
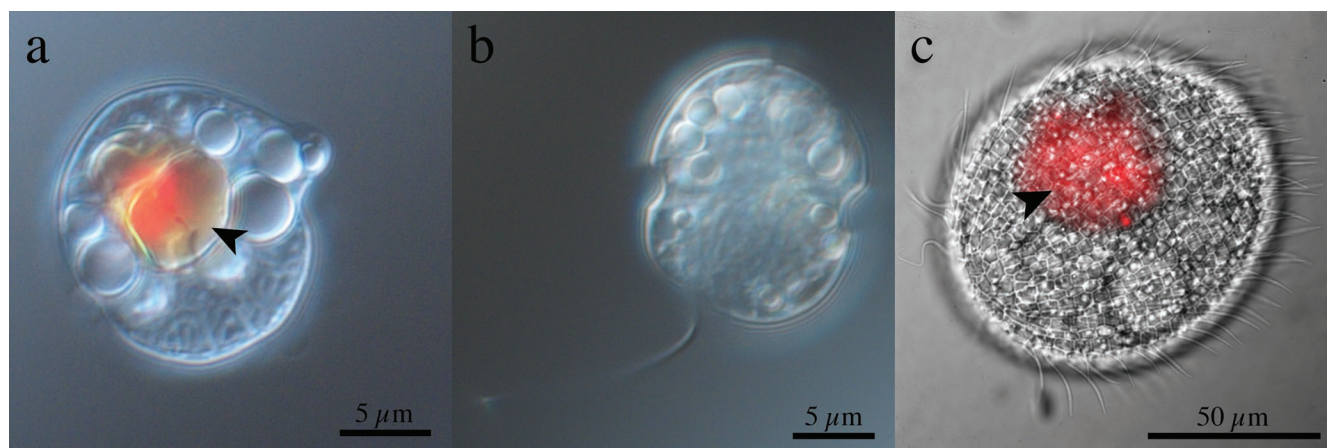
Figure 10. Micrographs of dinoflagellates and a ciliate. (a) Dinoflagellate with photosynthetic prey engulfed. Stack of differential interference contrast (DIC) and epifluorescence images. (b) DIC image of a dinoflagellate without pigmented prey inside. (c) A ciliate with photosynthetic prey engulfed. Stack of bright field and epifluorescence images. Chlorophyll autofluorescence is indicated by the red-colored areas (color online only). Arrows indicate food vacuoles in the cells.

abundance trend in the northern part of the study region, but there was an increasing trend of positive anomalies in the south (figure 9b), possibly reflecting the same response to sea-ice loss as phytoplankton (Montes-Hugo et al. 2009). The shelled pteropod *Limacina helicina*, an important herbivore in the WAP region (Bernard et al. 2012), was also negatively correlated with sea ice and increased in abundance over time in the south. This trend bears watching as pteropods have calcium carbonate shells and are predicted to be vulnerable to ocean acidification.

Taken altogether these zooplankton results suggest that although the WAP environment is undoubtedly changing rapidly, it is difficult to discern trends in smaller areas, and over shorter (two decades) periods. This points to the importance of annual surveys with autonomous systems over larger regions to document and understand food-web responses to climate change. The predicted regional decline in krill, and their replacement by nonpalatable salps, would be an ominous trend for upper trophic level consumers such as Adélie penguins, seals and whales. Adélie penguins have declined in the northern WAP by over 80% since 1975 (Ducklow et al. 2013), possibly in response to a declining krill (prey) population (Trivelpiece et al. 2011). But other factors besides a declining food supply are also affecting the Adélie population negatively (Fraser et al. 2013). Over the same period, subpolar, ice-tolerant species such as gentoo penguins and Humpback whales are increasingly present in the region as the sea-ice cover declines.

The impact of ice thickness changes on the MCM food web and community dynamics in photic and aphotic zones is still an open question. As we discussed above, light availability has a complex effect on the phytoplankton communities, potentially affecting photobiology, carbon and energy acquisition, and community composition. Current dry valley food-web measurements reveal that phytoplankton communities in the photic zone of Lake Bonney are dominated by mixotrophic pico- and nano-plankton such as haptophytes and cryptophytes (Kong et al. 2012, Dolhi et al. 2015, Bowman et al. 2016). These smaller phytoplankton are key prey for larger heterotrophic protists such as dinoflagellates and ciliates, which represent the top predators in these truncated food webs (figure 10; Thurman et al. 2012). Heterotrophic nanoflagellates (e.g., choanoflagellates, chrysophytes) and mixotrophic haptophytes dominate eukaryote communities in the aphotic zone of Lake Bonney, where chemolithoautotrophic and heterotrophic bacteria are abundant (Kong et al. 2012, Dolhi et al. 2015). Reduced ice thickness and increased PAR during warmer summers can favor larger obligate photoautotrophic phytoplankton, including *Chlamydomonas* spp., which are major hosts for parasitic nanoflagellates and are unsuitable prey for the larger protist grazers (Li et al. 2016).

Conclusions

Despite the disparate nature of the ice cover and food webs in the marine and freshwater Antarctic ecosystems described in this article, some striking similarities emerge. At both sites, physical habitat characteristics in summer are affected by winter climate dynamics, which sets precedence for the summer ice conditions that ultimately drive these ecological systems. The austral summer phytoplankton blooms are responsive to changes in ice phenology at both sites and represent a good proxy of climate change because they do not integrate interannual climate variability.

The hemispheric-scale climate teleconnections within each site (Fountain et al. 2016) indicate that loss of winter sea ice will lead to declines in phytoplankton bloom magnitude, whereas the thinning of the lake-ice covers will lead to an increase in bloom magnitudes. Observations in the WAP suggest declining blooms now and into the future

with continued decreases in the annual ice season duration. However, continued glacial melting—enhancing water-column stability and possibly contributing limiting micronutrients—complicates such projections. In MCM, although ice thinning is correlated with elevated water column PAR and associated higher primary production, these systems are also nutrient limited, suggesting that the ecological response of these lakes to changes in ice phenology, associated with climate change, is self-limiting as long as the perennial ice cover persists.

Although both sites show a sensitivity of ecological response to climate-driven changes associated with ice phenological changes, they are also on a threshold of dramatic change. Disappearing sea ice along the WAP and increasing UW PAR in nutrient-limited lakes as a result of lake-ice thinning will soon change the quasi-stable status quo of these systems into a new and unknown state. Continued long-term data collection at the PAL and MCM sites as part of the LTER network will allow us to follow these dynamic changes in the ecosystem caused by changing climate.

Acknowledgments

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