Microbial Community Dynamics in Two Polar Extremes: The Lakes of the McMurdo Dry Valleys and the West Antarctic Peninsula Marine Ecosystem

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The Palmer and McMurdo LTER (Long Term Ecological Research) sites represent climatic and trophic extremes on the Antarctic continent. Despite these differences, the microbial components of the McMurdo lake and Palmer marine ecosystems share fundamental characteristics, including the production of organic carbon via autotrophy and its assimilation via heterotrophy. We leveraged 20+ years of observations at the Palmer and McMurdo LTERs to identify key differences in microbial ecosystem dynamics between these sites. Although the relationships between fundamental biological parameters, including autotrophy and heterotrophy, are different between these sites, recent climate events have influenced the coupling of these parameters. We hypothesize that for the lakes of the McMurdo LTER, decoupling is largely driven by physical processes, whereas in the coastal Antarctic, it is largely driven by biological processes. We combined this hypothesis with a new analysis of microbial community and metabolic structure to develop novel conceptual microbial food-web models.

Keywords: community ecology, limnology, oceanography, microbiology, climate change

The Antarctic continent is a polar desert, a vast zone of low terrestrial biomass surrounded by productive ocean waters. Where local climatic conditions on the continent allow for the presence of liquid water, life persists in isolated oases, such as the perennially ice-covered lakes of the McMurdo Dry Valleys (Priscu et al. 1999). These lake basins were inundated with seawater in the late Neogene, when sea level was higher, and have been modified to their present state by active hydrology, geochemical weathering, and biogeochemical processes (Doran et al. 1994). The region is largely free of glacial ice because of the damming effects of the Transantarctic Mountains, which block the flow of ice from the Polar Plateau. Low snowfall and warm foehn winds also contribute to the desert conditions (Fountain et al. 2010). The combination of year-round liquid water and a source of energy (i.e., transmitted sunlight) is rare in the Antarctic interior and supports truncated, microbially dominated food webs within the lakes of the McMurdo Dry Valleys.

In stark contrast to the Antarctic interior, the marine waters around the continent teem with life. At the continental margin, macronutrient-rich water from the Southern Ocean mixes with micronutrient-rich shelf water, resulting in high levels of primary production (PP) during the Austral summer that fuel a rich marine ecosystem. The coastal Antarctic is unique among coastal marine environments; with no major rivers, it receives very little carbon from the continental interior. As a result, the vast majority of carbon that enters the Antarctic marine food web is a product of *in situ* PP. Despite the profound differences between the McMurdo Dry Valley lake and Antarctic marine ecosystems, the importance of ice (see Obryk et al. 2016), the marine origin of the lakes, overlap in light regimes, limited allochthonous carbon sources, and mean annual water temperatures poised near 0 degrees Celsius (°C) provide an ecological intersection between these systems.

The microbial ecosystems within the McMurdo Dry Valley lakes and the Antarctic marine environment (figure 1) operate

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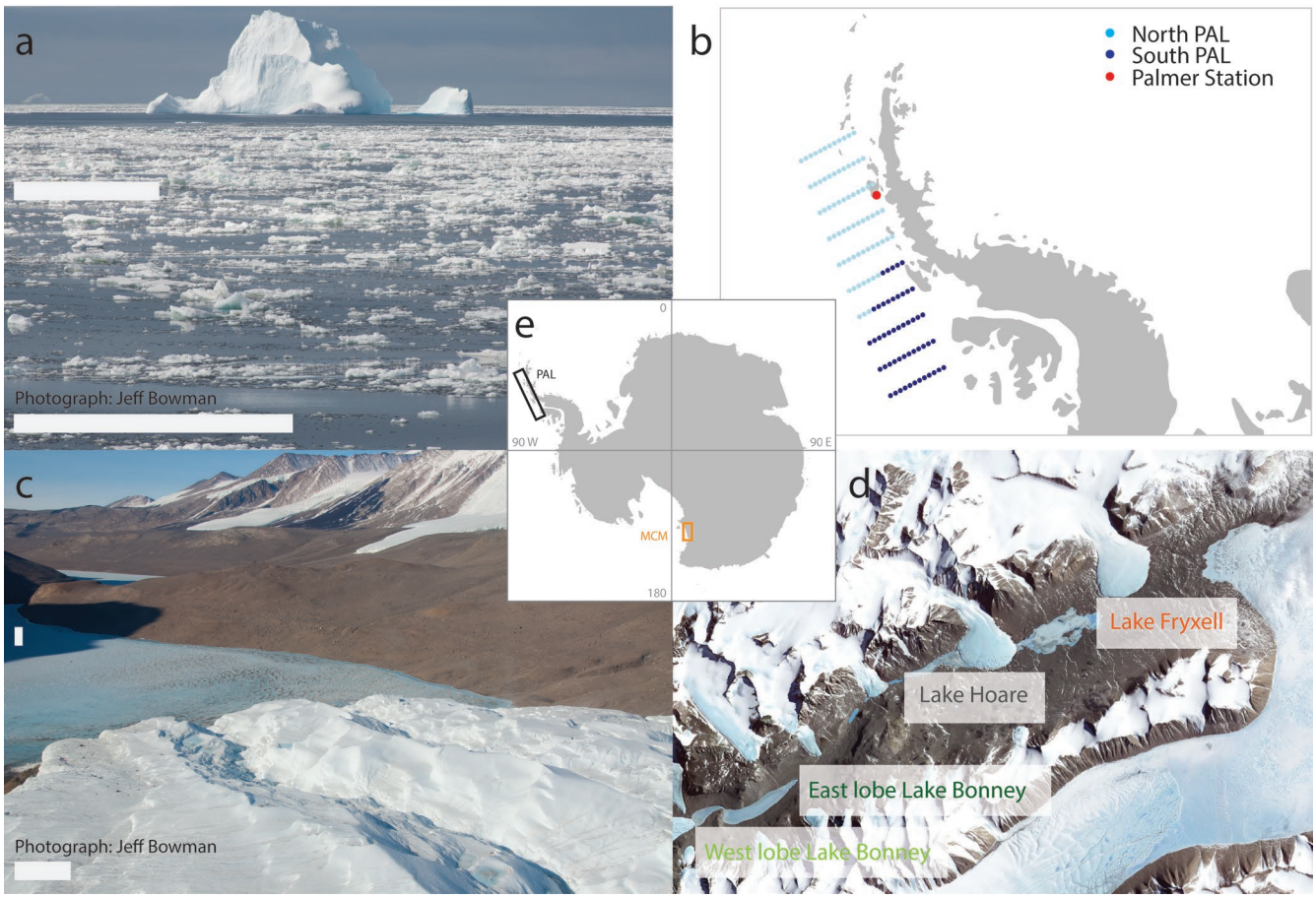

Figure 1. The Palmer (PAL; a, b) and McMurdo Dry Valley (MCM; c, d) LTERs. PAL covers a pelagic marine region along the West Antarctic Peninsula, extending from just offshore to a depth of over 3000 meters on the continental slope. For this reanalysis, PAL is split into north and south regions along latitude 66°S. MCM is located in Southern Victoria Land in East Antarctica and includes extensive data sets on the west and east lobes of Lakes Bonney, Lake Fryxell, and Lake Hoare. Inset (e) shows the location of both regions on the Antarctic continent. The image for PAL was taken on 12 January 2014 at approximately 66°S and 67°W. The image for MCM shows the tongue of Taylor Glacier and the west lobe of Lake Bonney (foreground) and the east lobe of Lake Bonney and the Sollas and Marr Glaciers (background); the photo was taken on 27 October 2011. The white bars in both images are 10 meters.

on the same basic bioenergetic principles but differ in their sources of nutrients, reduced carbon, trophic structure, and response to these variables (figure 2). In both environments, eukaryotic phytoplankton form the base of the food web, using light energy during the short summer to fix carbon dioxide (CO_2) into organic carbon as PP. Some of this carbon is released as exudate or lysate, providing a source of dissolved organic matter (DOM) to prokaryotic (Archaea and Bacteria) heterotrophs. Heterotrophs incorporate some fraction of this organic matter into new biomass as bacterial production (BP) and remineralize much of what remains, in the process reallocating nitrogen, phosphate, and inorganic carbon to the primary producers (Priscu et al. 1989, Karl et al. 1996). Light-dependent PP by photosynthetic eukaryotes is sufficient to meet the carbon demands of heterotrophic BP and respiration (R) in the coastal Antarctic environment (Morán and Estrada 2002). Within the MCM lakes, however, the amount of new carbon fixed annually by light-dependent PP can be insufficient to meet heterotrophic demand (R + BP > PP; figure 3). This deficit is met by the upward diffusion of relict carbon and inorganic nutrients from deep saline waters (Priscu et al. 1999), seasonal streamflow (Priscu 1995, Takacs et al. 2001), and the downward flux of aeolian sediments during the episodic partial melting of the lake ice cover resulting from solar radiation in summer (Priscu et al. 1995, Paerl and Prescu 1998). The carbon contribution of prokaryotic chemoautotrophy, a CO_2-fixing process driven by *in situ* chemical redox potentials rather than by light, to total PP is poorly quantified in both ecosystems.

An active microbial loop exists in both the McMurdo Dry Valley lakes and the coastal Antarctic, where bacterivorous protists graze on the prokaryotic population (Takacs and Priscu 1998, Garzio et al. 2013), excreting remineralized DOM and repackaging bacterial biomass for consumption

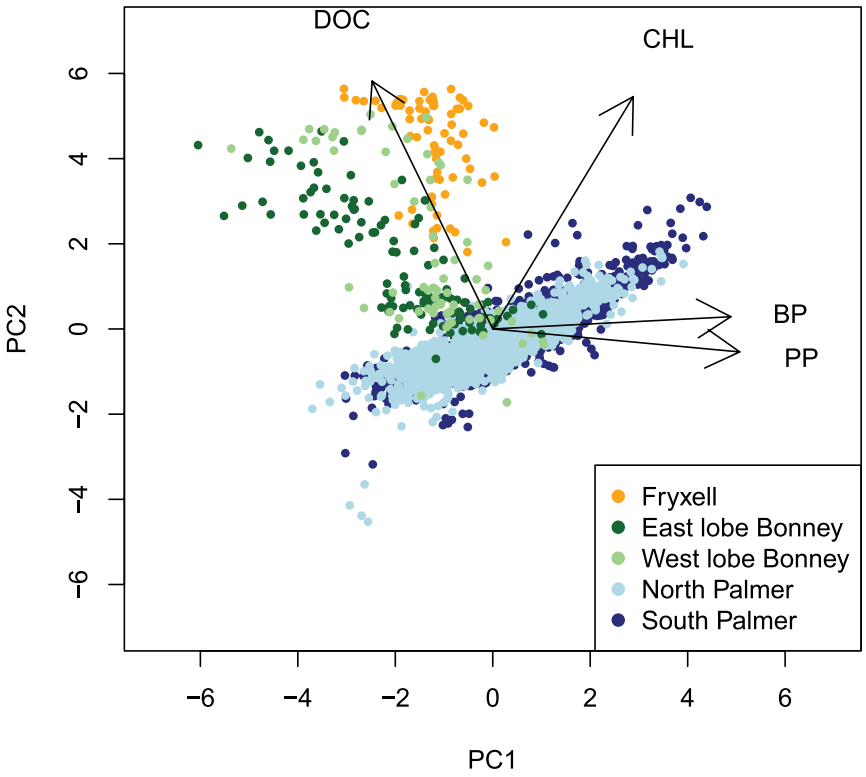

Figure 2. The principal component analysis (PCA) of all available discrete values for north and south Palmer, the east and west lobes of Lake Bonney, and Lake Fryxell based on chlorophyll a abundance (CHL), dissolved organic carbon concentration (DOC), primary production (PP), and bacterial production (BP). The data were log transformed to approximate a normal distribution and then scaled to have zero mean and unit variance.

by the higher trophic levels. Within the MCM lakes however, the top predators are restricted to microbial eukaryotes and, in at least one lake, rotifers and copepods (Priscu et al. 1999, Roberts et al. 2004). In the coastal Antarctic, bacterial protists are fed on by larger zooplankton (Ducklow et al. 2015), namely the Antarctic krill *Euphausia superba*, a temporally and spatially variable primary consumer that ultimately supports a rich and diverse megafauna and avifauna (Saba et al. 2014). Regardless of the height of the trophic pyramid, PP that is not directed to the upper trophic levels, remineralized, or released as DOM remains as particulate organic matter (POM) and sinks from the photic zone. As it sinks, this POM is colonized by chemotactic, copiotrophic bacteria, with the rate of the resulting bacterial degradation dependent on the lability of the POM and the functional capacity of the colonizers.

For over two decades, three lakes (Fryxell, Bonney, and Hoare; see figure 1) have been the focus of intensive study by the McMurdo Long Term Ecological Research (LTER) project (MCM; *www.mcmlter.org*), a component of the National Science Foundation's LTER network. A defining feature of both the MCM lake and coastal Antarctic ecosystems is the presence of ice (Obryk et al. 2016). Permanently covered by ice, the lakes maintain modest connections to the surrounding environment and each other (Dugan et al. 2014). The nature of the ice cover changes in response to air temperature (Obryk et al. 2016), and ephemeral streams provide climate-dependent pulses of glacial meltwater to the lakes, affecting lake levels as well as nutrient and dissolved organic carbon (DOC) availability. Thick (approximately 4–6 meter) permanent ice cover limits ventilation of the lakes with the atmosphere and prevents seasonal mixing, allowing the water columns to maintain strong, permanent chemoclines along which the microbial communities are vertically stratified (Dolhi et al. 2015). Importantly, the ice cover severely limits the light available to the photic zone, with less than 5% of solar photosynthetically active radiation (PAR) reaching the water columns of the lakes (Obryk et al. 2016).

In contrast with the MCM lake ice cover, much coastal Antarctic sea ice is seasonal, with the length of the season largely dependent on latitude. Along the West Antarctic Peninsula, changes to the timing and extent of ice cover are associated with recent ecological change, particularly at the north end of the peninsula (Ducklow et al. 2013). The Palmer LTER (PAL; *http://pal.lternet.edu/data*) has studied the marine ecosystem of the West Antarctic Peninsula since 1992. Primary production and the rich trophic structure of the PAL study region are, much like in the MCM lakes, closely linked to the presence of overlying ice. Sea ice controls the timing and strength of the spring phytoplankton bloom, allowing strong blooms to develop in a stable water column (Arrigo et al. 1998). Sea ice also serves as a substrate for the growth of ice algae, a crucial food source for juvenile krill (Saba et al. 2014), and as habitat for a number of ice-dependent species (Ducklow et al. 2006).

Together, the PAL and MCM projects have produced high quality, long-term data sets of key ecosystem parameters. These data sets have been invaluable in advancing our understanding of the function of these ecosystems, as well as their variability and responsiveness to changing climate across annual and decadal time scales. Despite many common attributes, the PAL and MCM study regions are fundamentally different (figure 2) and respond differently to annual and seasonal climate variability (Fountain et al. 2016). These fundamental differences serve to highlight important and unique ecological processes in each habitat and provide the framework for a natural experiment to test the long-term impacts of climate variability on polar microbial ecosystems. Here, we focus on the degree of coupling

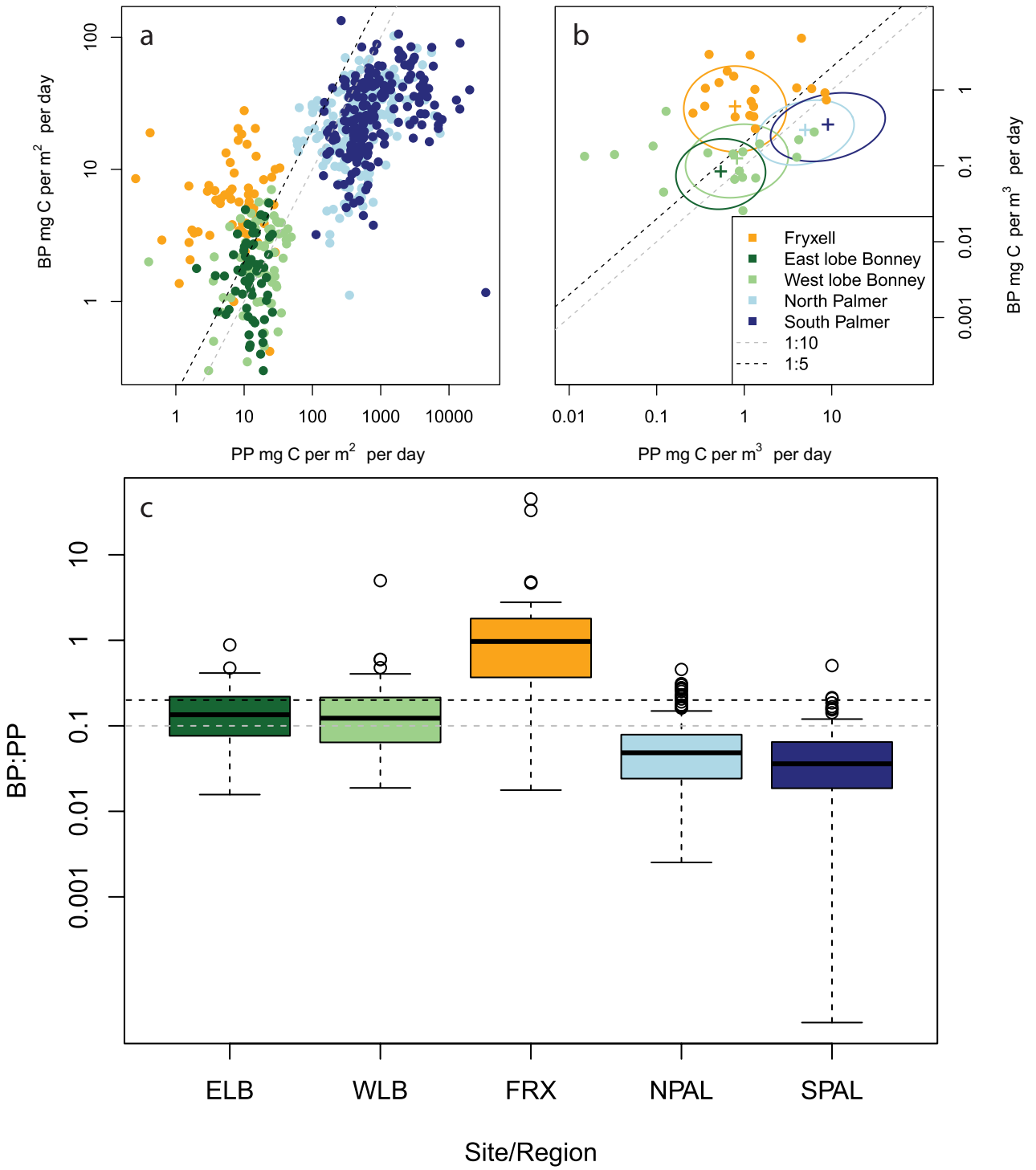

Figure 3. The depth-integrated bacterial production (BP) versus primary production (PP) for PAL and MCM. For all panels, the gray dashed line shows a 1:10 relationship of BP:PP, corresponding to the canonical relationship observed in the pelagic marine environment (Kirchman et al. 2009), whereas the black dashed line gives a 1:5 relationship of BP:PP, corresponding to the estimated point at which an external source of carbon is required to sustain bacterial growth (Anderson and Ducklow 2001). (a) Depth-integrated (to base of the photic zone) PP and BP. (b) Discrete (volumetric) measurements of BP:PP. The cross gives the mean for each site, the ellipse indicates the standard deviation, with the angle of the ellipse giving the slope of a linear model fit to log-normalized data. The north and south regions of PAL and the west lobe of Lake Bonney had a statistically significant fit to the linear model at $p << 0.001$. *For the west lobe of Lake Bonney and Lake Fryxell, the values from the 2001–2002 flood year are additionally shown as discrete points. (c) A boxplot of discrete values showing the range for all data.*

between primary producers and bacterial consumers in the context of recent climate events and consider the impacts of bacterial diversity and function on the microbial food web. All physical and biogeochemical data presented here are core measurements of the PAL and MCM LTER programs and are available from the PAL and MCM data repositories. For PAL, we used data obtained from the PAL sampling grid off the West Antarctic Peninsula (figure 1b). For MCM, we used data from Lakes Bonney and Fryxell, two chemically stratified lakes that lie at opposite ends of the Taylor Valley (figure 1d). The sample collection and processing were described previously for PAL (Ducklow et al. 2012) and MCM (Takacs et al. 2001, Foreman et al. 2004).

The coupling and decoupling of bacterial and primary production

The relationship between BP and PP has been extensively studied in marine and lake environments across latitudes (Cole et al. 1988, Ducklow 1988) and a canonical photic zone BP:PP relationship of 1:10 occurs throughout the world ocean (Kirchman et al. 2009). The variations around this mean are large however, and controlled by a variety of interacting physical and biological factors. These include top-down controls by bacterivorous protists and bacteriophage (Fuhrman and Noble 1995, Säwstrom et al. 2008), antagonistic or synergistic relationships between phytoplankton and bacteria (Amin et al. 2012), and various bottom-up controls, including temperature-driven effects on metabolism (Kirchman et al. 2009), the availability of allocthonous labile DOC (Barrera-Alba et al. 2009), and the production and lability of phytoplankton-derived DOC (Carlson et al. 1998).

We evaluated phytoplankton–bacteria coupling at PAL and MCM by comparing the time series records of BP and PP. BP was measured by the uptake of ^{3}H-labeled leucine at PAL (Ducklow et al. 2012) and incorporation of ^{3}H-labeled thymidine into DNA at MCM (Takacs et al. 2001). These assays measure protein and DNA synthesis, respectively—separate but related physiological processes (Chin-Leo and Kirchman 1988). Although thymidine incorporation rates and leucine uptake rates vary according to the composition and physiological state of the bacterial assemblage, an evaluation of these assays carried out at PAL during the 2003–2005 summer seasons demonstrated good agreement after conversion to units of carbon (data not shown, slope of linear regression = 1.02, $R^2 = 0.85$, $n = 524$). PP was measured at both sites by the uptake of carbon-14 (^{14}C)-labeled bicarbonate (Foreman et al. 2004, Ducklow et al. 2012). At PAL, the PP record goes back to 1995, and BP records go back to 2003. At MCM, measurements of BP and PP extend back to 1993.

Photic zone values of BP and PP are generally at least one order of magnitude greater at PAL compared lakes Bonney and Fryxell (figure 3a and 3b), whereas the ratio of BP:PP is higher in the lakes (figure 3c). The depth-integrated BP:PP relationship for PAL is generally below 1:10 (mean [M] = 0.07, standard deviation [SD] = 0.07, for north and M = 0.05, SD = 0.05, for south of 63°S latitude; figure 3a) and consistent with those expected for polar marine waters (Kirchman et al. 2009), indicating that heterotrophic demand in the photic zone can be met by PP (Anderson and Ducklow 2001). Although the BP:PP ratios in the east and west lobes of Lake Bonney are higher, they are generally below 1:5 (M = 0.17, SD = 0.14, for east and M = 0.23, SD = 0.63, for west), indicating that heterotrophic demand in the photic zone can also be met by PP in Lake Bonney (Anderson and Ducklow 2001). By contrast, Lake Fryxell has a greatly elevated BP:PP ratio (M = 2.44, SD = 7.14), with the estimated rate of depth-integrated BP exceeding PP in some cases (figure 3a and 3c). This is indicative of a carbon deficit in the photic zone of Lake Fryxell that must be subsidized by external inputs, as well as a weak coupling between primary producers and bacterial consumers. The relationship between these trophic levels is further supported by the correlation of BP to PP (figure 3b). Although (log normalized) BP and PP are correlated for both regions at PAL ($R^2 = 0.53$ and 0.61 for north and south, respectively), these parameters exhibited a much weaker correlation for the east and west lobes of Lake Bonney ($R^2 = 0.16$ and 0.08 for east and west lobes, respectively) and are uncorrelated for Lake Fryxell ($R^2 = 0$). The tight coupling between BP and PP at PAL and weaker (or nonexistent) coupling at MCM suggest that fundamentally different processes are driving the relationship between carbon fixation and organic-carbon uptake within these two ecosystems.

The relationship between community respiration (net CO_2 production) and primary production (R:PP) further emphasizes the elevated BP:PP ratios in Lake Fryxell. On the basis of R:PP, the MCM lakes have been identified as net heterotrophic (i.e., R:PP > 1), particularly when R and PP are integrated over the entire water column and throughout the year, with Lake Fryxell exhibiting the highest R:PP ratios (Lyons et al. 43). Although disproportionately higher respiration rates are indicative of low bacterial growth efficiencies in oligotrophic clear-water lakes (Pålsson et al. 2005), high BP:PP values suggest that bacterial growth efficiencies are not necessarily low in Lake Fryxell. Rather, they highlight the reliance of the heterotrophic community in the photic zone of Lake Fryxell on alternate sources of carbon. The most significant of these sources may be the upward diffusion of relict DOC from the stratified saline waters below the photic zone (Priscu et al. 1999, Takacs et al. 2001), but it also includes the release of organic material from lake ice (Priscu et al. 1999), streamflow (Lyons et al. 43), and nearshore benthic mats (Lyons et al. 43).

The influence of different DOC inputs on the coupling of BP to PP can also been seen in PAL and the other MCM lakes, with differing BP:PP ratios potentially influenced by the different sources of DOC in these ecosystems. Lacking terrestrial inputs, the principal sources of DOC to support heterotrophy in the coastal Antarctic environment are phytoplankton exudates (Morán and Estrada 2002), lysates (Sala et al. 2005), and the decomposition of phytoplankton and ice

algal particles (Ducklow et al. 2006). Doval and colleagues (2002) also noted an accumulation of DOC above the seafloor in some regions of the PAL study area, suggesting that methane or DOM reprocessed in sediment can contribute to the DOC pool, a process analogous to the major DOC source predicted for MCM; however, the total possible contribution from this source to the marine environment is small.

For both PAL and the MCM lakes, the quality and quantity of DOC derived from individual phytoplankton cells are important factors in the BP:PP relationship. Phytoplankton exudate quantity and composition are dependent on phytoplankton taxonomy and physiology, both of which are influenced by environmental factors such as nutrient limitation, light availability, and temperature (Takacs et al. 2001). Although the lability of DOC derived from different sources or phytoplankton functional groups is not well understood for either PAL or MCM, there are seasonal changes in phytoplankton community composition at PAL and spatial differences within and between the MCM lakes that influence the availability of labile DOC. Diatoms are the major primary producers in the PAL water column and dominate the euphotic zone in the early summer bloom (Goldman et al. 2015). Later in the season this diatom bloom gives way to a mixed bloom of cryptophytes, *Phaeocystis*, and diatoms (Goldman et al. 2015), with the abundance of cryptophytes greater in near-shore, meltwater-influenced regions of the study area (Moline et al. 2004, Luria et al. 2014). In contrast, the phytoplankton functional groups that reside in the vertically stratified water columns of the MCM lakes are typically flagellated, with diatoms restricted to streams, sediments, and benthic mats (Spaulding et al. 1994). In the nutrient-poor, upper photic zone of Lake Bonney, for example, large chlorophytes dominate the phytoplankton community, whereas the region just above the chemocline, where maximum PP levels occur, is occupied by smaller haptophytes and stramenopiles (Bielewicz et al. 2011).

Temporal variability in bacterial and primary production

The Antarctic continent as a whole is undergoing a profound ecological shift brought on by changing climate. Surface air temperatures have steadily increased across West Antarctica since 1957, whereas East Antarctica underwent a cooling period from 1996 to 2000 (Doran et al. 2002) before entering a warming phase (Steig et al. 2009, Fountain et al. 2016). For PAL, the steady increase in temperature is reflected in the loss of sea-ice duration and extent, with well-documented impacts on both primary producers and the higher trophic levels (Saba et al. 2014, Obryk et al. 2016). Decreased ice cover poses several detrimental effects to the PAL krill population, the crucial link between primary producers and the upper trophic levels. Juvenile krill are directly dependent on lipid-rich ice algae for food. Consequently, reduced sea ice, particularly during the Austral spring, means fewer prey and therefore lower krill recruitment (Saba et al. 2014). The earlier retreat of sea ice also allows deeper mixing of the water column by late-winter storms, suppressing bloom formation by transporting phytoplankton below the depth at which photosynthesis can no longer balance respiration. This wind-driven suppression of the phytoplankton bloom leads to less food for adult krill; observations of chlorophyll *a* concentration, BP, and krill size classes since 1987 have revealed a 4- to 6-year cycle coincident with the southern annual mode (SAM), a relatively short-term Southern Hemispheric pattern of climate variability that exerts a strong control on sea-ice duration and extent (Fountain et al. 2010, Fountain et al. 2016).

The thickness of the perennial ice cover over the MCM lakes is directly related to air temperature, which is influenced by the same modes of climate variability that control ice cover at PAL (Fountain et al. 2016, Obryk et al. 2016). In addition, air temperature and the albedo of glacier surfaces control the influx of glacial meltwater to the lakes, which varies annually and has a profound impact on lake ecology. During the austral summer of 2001–2002, a positive SAM preceded by a strong La Niña caused unusually warm temperatures for weeks across the continent, affecting both PAL and MCM (Obryk et al. 2016). MCM experienced average air temperatures and windspeeds 1.9°C and 0.4 meters per second higher than those in the previous year (Doran et al. 2008), resulting in meltwater inflow twice the volume of the previous eight summers combined (Foreman et al. 2004). The legacy of this flood year affected the physical characteristics of the lakes for more than 10 years. This single flood event restored lake levels that had been decreasing over the preceding 14 years (Doran et al. 2008). Glacial meltwater is a significant source of water and nutrients to the lakes (Dore and Priscu 2001); however, during the flood year, meltwater also increased lake turbidity, reducing PP in the lower reaches of the photic zone of the west lobe of Lake Bonney (Foreman et al. 2004). Because temperature-driven flood events also result in thinner lake ice cover, the reduction in PP at the base of the photic zone was partially offset by increased light transmittance at the top of the photic zone (Obryk et al. 2016).

To examine the impact of the 2001–2002 flood and other discrete climate events on recent time trends for BP:PP and the concentration of DOC in the PAL (north and south regions) and MCM (west lobe Lake Bonney and Lake Fryxell) ecosystems (figure 4), we applied generalized additive (BP:PP) and generalized least-squares (DOC) models. The generalized additive models accounted for the time-series, nonlinear, additive nature of the BP:PP data, whereas the generalized least-squares models allowed us to describe linear or polynomial trends in the DOC data. The major trends in both DOC and BP:PP were consistent between the two regions at PAL (only N region shown), but they differed between PAL and MCM and between the west lobe of Lake Bonney and Lake Fryxell.

Following an apparent increase from 1996 to 2000, the concentration of DOC declined at a rate of 0.4 grams per square meter per year in the west lobe of Lake Bonney from

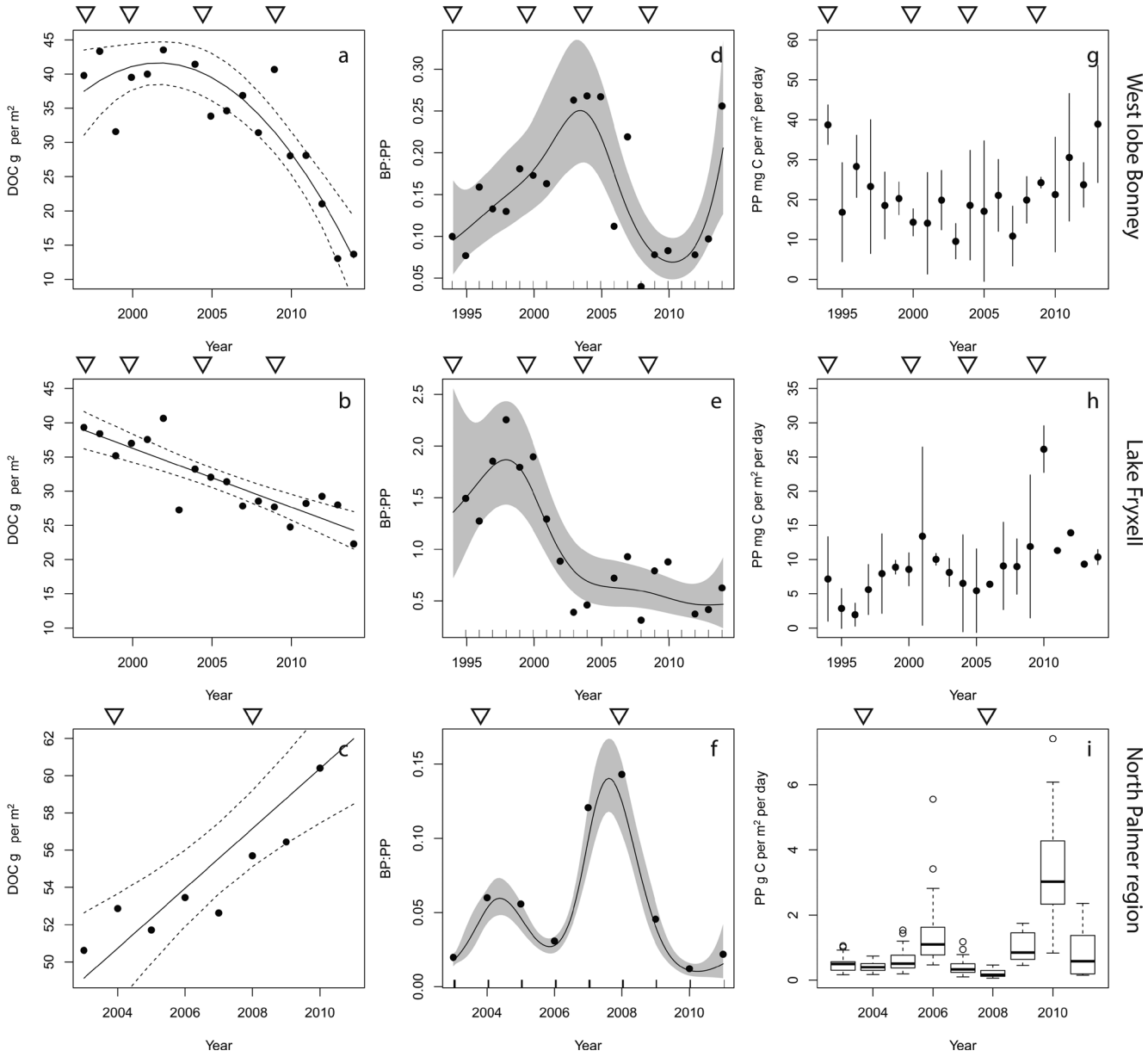

Figure 4. Additive and linear models describing time trends of depth-integrated photic zone DOC concentration and BP:PP and the distributions of depth-integrated PP values in the west lobe of Lake Bonney and Lake Fryxell and north PAL. DOC time-series trends are the following: (a) west lobe Lake Bonney (t(15) = −3.72, p = 0.0021); (b) Lake Fryxell (t(16) = −6.68, p << 0.001); and (c) the north region of PAL(t(7) = 5.15, p = 0.0013). BP:PP time-series trends are the following: (d) west lobe Lake Bonney (F(4.96) = 3.20, p = 0.002, deviance explained = 71.3%). In the summer of 2001–2002, BP:PP reached 1.7 in the west lobe of Lake Bonney, but this value is not shown on the plot; (e) Lake Fryxell (F(3.96) = 4.15, p = 0.0002, deviance explained = 74.9 %); (f) the north region of PAL (F(7.35) = 30.33, p << 0.01, deviance explained 63.9%). Depth-integrated PP is (g) West Lake Bonney, (h) Lake Fryxell, and (i) North PAL. PAL depth-integrated PP values are shown using a boxplot, with the median value given by the dark band in each box. Because each lake is sampled only two to four times each year, a box plot was not appropriate for the MCM data; instead, the mean value for measurements made in November and December of each year is given by the point and the standard deviation by the vertical lines. Positive SAM events are indicated by the triangles above each panel after Bers and colleagues (2013).

2000 to 2013 (figure 4a). In addition, a significant amount of the variability in the photic zone BP:PP relationship was accounted for by time trends for the west lobe of Lake Bonney (figure 4d). BP:PP increased from 1995 to 2005, followed by a decrease to a minimum in 2010. Notably, during the 2001–2002 flood year, BP:PP increased 10-fold. This was the only time point for which BP:PP exceeded 1 (this year could not be modeled and was excluded from the time-series model in figure 4d). From 2003 until 2004, BP:PP in the west lobe of Lake Bonney remained at nearly twice pre-2001

levels. A second warm summer in 2008–2009—also the result of a coupled positive SAM and La Niña—had different effects, with no BP:PP spike and no decreased PP in the years following the event. Rather, BP:PP reached a minimum in 2010 as a result of high PP (figure 4d) before increasing in 2011 and 2012. The PAL BP:PP record also showed a significant trend in variability from 2003 to 2011 (figure 4f); however, the response of the BP:PP ratio to the warm summer of 2008–2009 contrasted sharply with that observed in the MCM lakes. There was an increase in BP:PP during 2007 and 2008, with BP:PP reaching a maximum in excess of 0.1 driven by low PP. This was followed by increasing PP in 2009 and 2010 (figure 4i), with high PP values driving BP:PP below 0.05 (figure 4f).

Consistent with the trend observed for the Lake Bonney photic zone, the DOC concentration in the photic zone of Lake Fryxell has been in a steady decline since 1996 (figure 4b). No increase in DOC was observed for either the 2001–2002 or 2008–2009 flood years. The ratio of BP:PP also declined over this period, although BP:PP has stabilized near 0.5 since 2005 (figure 4e). This value is more than twice the median BP:PP calculated for the east and west lobes of Lake Bonney (figure 3d). The 2001–2002 and 2008–2009 flood years resulted in high but highly variable PP values for the Lake Fryxell photic zone, with maximum PP occurring the year following the 2008–2009 flood (figure 4h). These flood events did not have a noticeable effect on BP:PP for those years, indicating a concurrent increase in BP.

The BP:PP and DOC time trends confirmed the previously observed connections among hydrology, BP, and PP for the MCM lakes (Takacs et al. 2001, Foreman et al. 2004), and the significance of transient climate events on this ecosystem. The 2001–2002 flood event produced a transient, high BP:PP signal in the west lobe of Lake Bonney resulting from a rise in the depth of the photic zone as light transmittance decreased (Foreman et al. 2004). PP remained high (figure 3b) at depths to which light could penetrate and was stimulated by the influx of nutrients (Foreman et al. 2004) for several years after the flood. BP was not stimulated during this period, and BP:PP values remained low (figure 4d). In contrast to the west lobe of Lake Bonney, BP in the photic zone of Lake Fryxell had a positive response to the flood years. Previous work identified stream algal mats as a source of labile DOC to Lake Fryxell (Lyons et al. 43); increased streamflow may have added organic carbon to the Lake Fryxell photic zone while concomitantly increasing inorganic nutrient loads that enhanced PP. Because BP in the photic zone of both Lake Fryxell and Bonney are supported in part by relict carbon, it is buffered from the climate events that directly affect PP. The impact of the long-term decline in photic zone DOC (figure 4a and 4b) on BP remains uncertain.

In marked contrast to the trends observed for the MCM lakes, the northern region of PAL exhibited a linear increase in DOC levels from 2004 to the present (1.6 g per square meter per year; figure 4c). The ratio of BP to PP reached local minima in 2006 and 2010 as a result of high PP (figure 4f and 4i). Although the PAL ecosystem is influenced by the same climate events that affect MCM, there is an important difference in timing that is directly related to sea ice extent. In contrast to MCM, PP at PAL is influenced more by winter than by summer conditions. A negative SAM in winter and spring typically leads to conditions of low wind, high ice, and high PP in the spring and summer (Saba et al. 2014, Fountain et al. 2016). A positive SAM phase in winter and spring produces opposite conditions: low sea ice extent, high winds, and suppressed PP. The 2001–2002 event at PAL resulted from a persistent positive SAM (May–December monthly mean = 0.63) preceded by La Niña conditions (Bers et al. 2013), producing warm winds and rapid ice retreat (Fountain et al. 2016). During the winter and spring of 2008, SAM was again largely in a positive phase (May–December monthly mean = 0.75) following a La Niña (Bers et al. 2013), with a corresponding weak 2009 summer bloom. In the winter and spring of 2009, SAM was strongly negative (May–December monthly mean = −0.55), leading to high PP in the Austral summer of 2010.

The coupling of BP and PP is complicated by the presence of large grazers at PAL, a feature absent from MCM, which can contribute to low BP:PP values during years of high PP. The abundance of *E. superba* and related species is cyclical, with peaks in abundance occurring every 4–6 years in concert with peaks in PP (Saba et al. 2014). Although "sloppy" krill feeding can have an immediate positive impact on BP by producing DOC, higher krill-grazing rates ultimately channel more carbon into upper trophic level respiration and biomass and away from BP. Carbon excreted by krill in large fecal pellets quickly leaves the photic zone, and the large vertical range of krill, which can extend over hundreds of meters on the continental shelf, further transports carbon away from bacteria in the photic zone. Krill size classes peaked during the summer of 2005–2006 and 2009–2010 (Saba et al. 2014), corresponding to years of high PP (figure 4i). The decoupling of BP:PP during those years may result from the channeling of labile carbon away from bacteria and to the higher trophic levels. Therefore, a fundamental difference in microbial ecosystem function between MCM and PAL may be that BP:PP uncoupling within the MCM lakes is driven by physical processes, primarily the balance between advective DOC and nutrient input and upward diffusion (Foreman et al. 2004), whereas uncoupling within the PAL water column is driven (in the first order) by biological processes, primarily phytoplankton grazing by higher trophic levels. Continued observations over more flood cycles at MCM and krill abundance cycles at PAL will clarify the relationship between these factors.

Microbial community structure and function

Although a number of DNA sequence–based studies of prokaryotic microbial community structure and function have taken place at PAL and MCM, these data have not yet become part of the long-term core data collection at either

site. Consequently, it is not possible to directly assess the impact of climate events on the structure and function of these communities. Nonetheless, the available data do provide important insights into ecosystem processes. Several studies at PAL and MCM have made use of the 16S rRNA taxonomic marker gene to describe community structure between locations or along seasonal and depth gradients. Fewer studies at either site have evaluated the abundance of functional genes beyond the 16S rRNA gene. At PAL, fosmid (Grzymski et al. 2012) and clone (Kalanetra et al. 2009) library studies identified the genetic potential for prokaryotic chemoautrophy from wintertime samples and linked this process to the Archaeon *Nitrosopumilus maritimus* and Alphaproteobacteria *Ruthia magnifica*. Functional gene studies in the MCM lakes have used targeted approaches to identify specific genes hypothesized to play roles in key biogeochemical cycles. These include the analysis of the *amoA* gene for ammonia oxidation (Voytek et al. 1999), the *pufM* photosynthesis gene unique to the purple nonsulfur bacteria (Karr et al. 2003), the *dsrA* gene for dissimilatory sulfate reduction (Karr et al. 2005), and the *rbcL*, *cbbM*, and *nifJ* genes that code for proteins associated with inorganic carbon fixation (Dolhi et al. 2015). The distributions of these genes were found to be remarkably specific to lake and depth. Although *amoA* genes were widely present across the MCM lakes for example, they were limited to oxic waters above the chemocline and associated with elevated concentrations of nitrite (Voytek et al. 1999). Form II Rubisco (*cbbM*) associated with sulfur-oxidizing bacteria appear exclusively in Lake Fryxell and the west lobe of Lake Bonney, suggesting that sulfide oxidation is related to those lakes' specific geochemistries (Dolhi et al. 2015). Sulfate reduction has only been examined in Lake Fryxell, where *dsrA* gene copies were shown to vary in abundance and diversity with depth through the water column, reaching a minimum in the oxic waters above the chemocline (Karr et al. 2005).

To explore bacterial structure and function in greater detail, we applied the paprica v0.3.0 metabolic inference technique (Bowman and Ducklow 2015) to rRNA gene data collected as part of the Microbial Inventory Research Across Diverse Long Term Ecological Research Sites (MIRADA LTERS) at PAL (south and north stations; Luria et al. 2014) and MCM (west lobe of Lake Bonney and Lake Fryxell; Vick-Majors et al. 2014). Paprica assigns the predicted metabolic pathways associated with the most closely related sequenced genome (closest completed genome, CCG), or ancestral "consensus" genome (closest estimated genome, CEG), to each 16S rRNA gene read. This metabolic inference approach was designed to be conservative; therefore, although the inference of a specific metabolic pathway is good evidence for the presence of that pathway in a strain closely related to one observed, the absence of a metabolic pathway does not constitute evidence of the absence of a metabolic process. Because heterotrophy is ubiquitous at PAL and MCM and aerobic respiration is ubiquitous wherever oxygen is not limiting, we have focused our discussion on metabolisms that rely on alternative electron donors and acceptors other than organic carbon and oxygen, respectively. An exception was made for metabolism involving C_1 compounds, such as methane, because these processes may be significant in both environments but have received comparatively little attention (except see (Karr et al. 2006)).

From a community structure perspective, the most abundant bacterial 16S rRNA gene phylotype observed within the MCM lakes was associated with the actinobacterial CCG *Rhodoluna lacicola* (figure 5). *R. lacicola* was isolated from a hypertrophic lake but is related to the Actinobacteria clade ACK-M1, which is highly abundant in oligotrophic lakes (Newton et al. 2011), and *Alpinimonas psychrophila*, a bacteria isolated from glacier cryoconite holes (Schumann et al. 2012). No genomes are available for the ACK-M1 clade or genus *Alpinimonas*. A BLASTN search of representative reads associated with *R. lacicola* and the placement of these reads on a reference tree constructed from 16S rRNA genes from all typed Actinobacteria confirmed that they belong to a close relative of *A. psychrophila* (sequence identity of 96%). The dominant members of many of the Lake Fryxell sample communities included a Spirochaetales CEG and additional Actinobacteria CCGs. One sample from West Lake Bonney was compositionally distinct from the remainder of the MCM samples because of a high abundance of a *Saccharibacteria* CEG from the candidate division TM7 (figure 5). The between-sample diversity among the most common phylotypes was lower at PAL than at MCM, with all samples dominated by the CCGs *Candidatus Pelagibacter ubique* HTCC1062 and *Candidatus Thioglobus singularis* PS1. *Candidatus T. singularis* PS1 belongs to the widely distributed SUP05/Arctic96BD-19 clade of gammaproteobacterial sulfur oxidizers (Marhsall and Morris 2013) previously recognized as abundant in Antarctic surface waters (Kim et al. 2013, Bowman and Deming 2016), whereas the *Pelagibacter* genus is ubiquitous in the global ocean. Despite the wide phylogenetic distance between *R. lacicola* and *P. ubique* HTCC1062, these dominant taxa point to some key ecological similarities. Both *R. lacicola* (and related strains) and *P. ubique* HTCC1062 are nonmotile, small-celled bacteria with streamlined genomes, suggesting a nonparticle associated lifestyle adaptable to oligotrophic conditions.

The waters above the chemocline in the west lobe of Lake Bonney contained a significant number of a Firmicutes phylotype associated with syntrophic bacteria CCG *Syntrophomonas wolfei* Goettingen, which is often found in consortia with methanogenic archaea. This CCG was an interesting piece of our comparison because it represented one the greatest taxonomic overlaps between MCM and PAL; after *P. ubique* HTCC1062 and *T. singularis* PS1, *S. wolfei* Goettingen was the dominant CCG in most of the PAL summer surface samples. In Lake Bonney, the appearance of this putatively anaerobic phylotype in the oxygenated waters above the chemocline is consistent with previous observations of methanogenic Archaea (Vick-Majors et al. 2014), with which it is known to form syntrophic partnerships

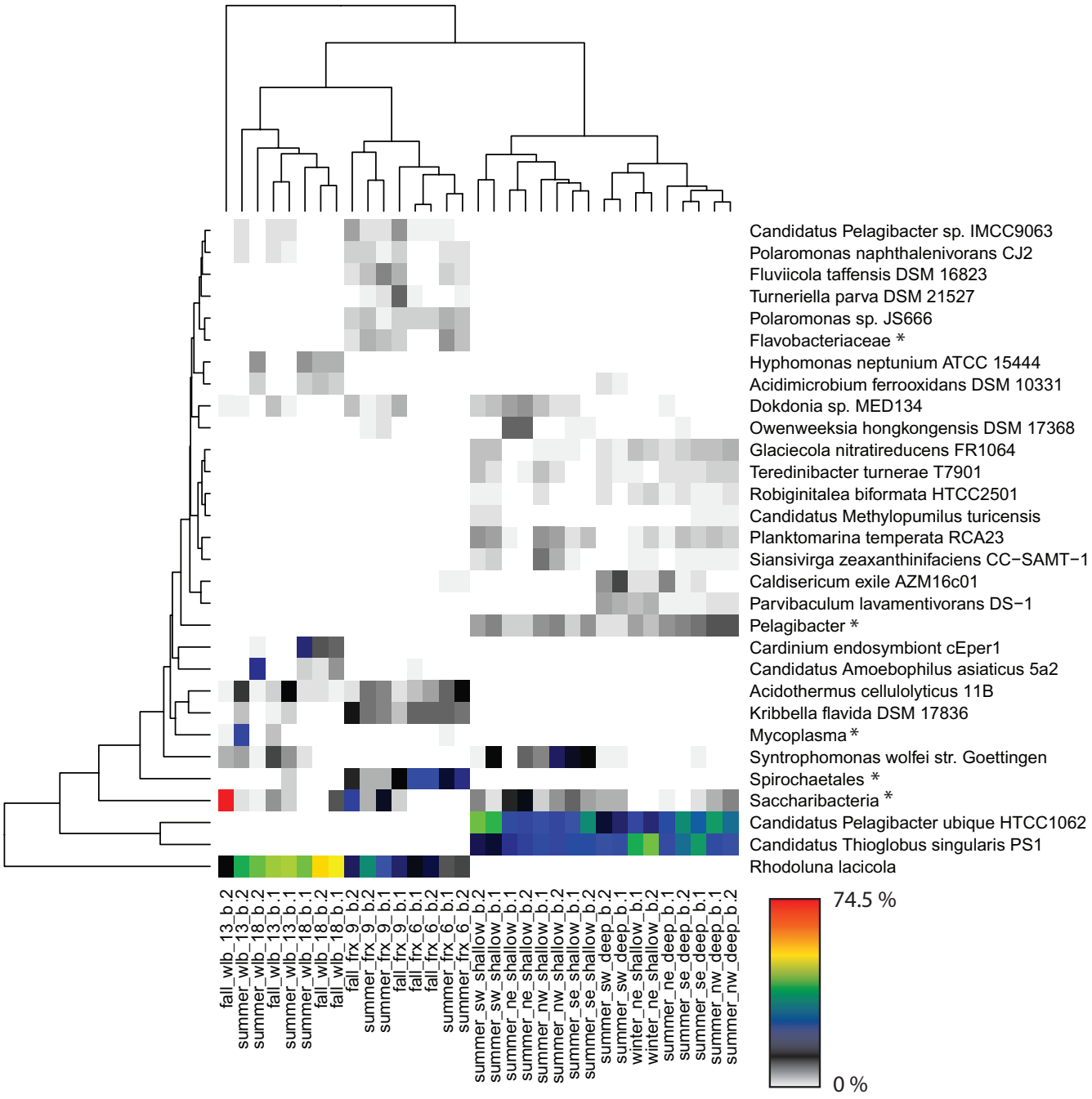

Figure 5. A heat map of the most abundant phylotypes in PAL and MCM samples as determined by phylogenetic placement. The data were previously published as part of the MIRADA LTERS project (Luria et al. 2014, Vick-Majors et al. 2014) and processed as described previously with the following modifications. Samples were subsampled to a depth of 1977 reads (the size of the smallest library), and edge abundance was normalized for 16S rRNA gene copy number within paprica v0.3.0. Because of the difficulty of distinguishing between chloroplast and cyanobacterial 16S rRNA genes, all 16S rRNA genes that placed to the cyanobacteria were removed from this analysis. Each row of the heat map is a phylogenetic edge representing a closest completed genome (CCG) or closest estimated genome (CEG) used for metabolic inference. Names that are not species names (identified by asterisk) indicate a CEG and are named according to the lowest taxonomic level shared by all daughter taxa. The color of the heat map gives the number of query reads that placed to each genome (i.e., the 16S rRNA gene of that genome is the closest phylogenetic relative of the genomes used). The clustering on the x and y axes follows the defaults of the heat map command in R; Euclidean distance and the complete clustering method.

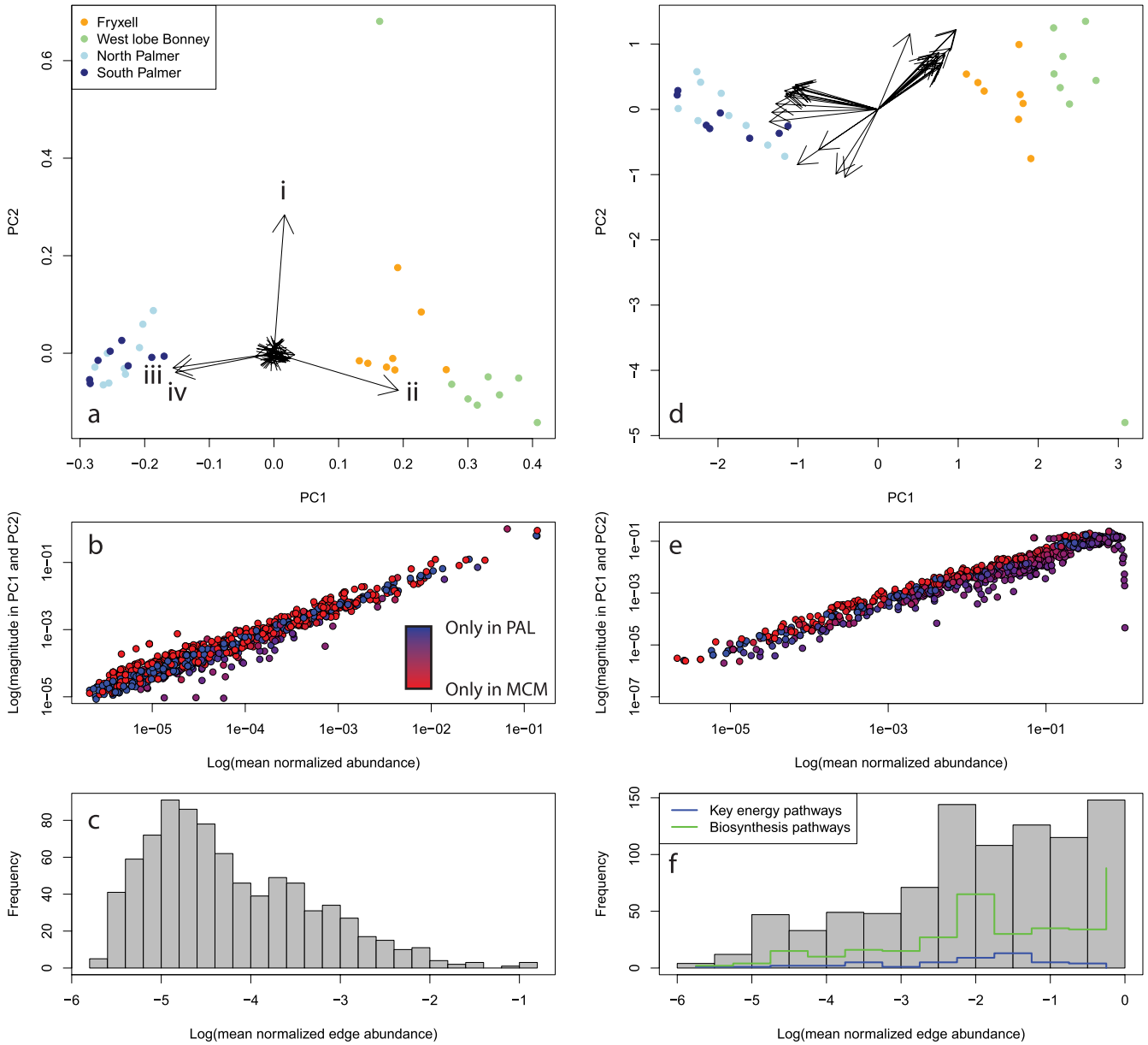

Figure 6. The compositional and functional differences between PAL and MCM microbial communities. (a) The PCA of MCM and PAL samples based on the relative abundance of closest completed genomes (CCG) and closest estimated genomes (CEG) associated with the MIRADA LTERS data set; i, Saccharibacteria; ii, Rhodoluna lacicola; iii, Thioglobus singularis PS1; iv, Pelagibacter ubique HTCC1062. (b) The variance of phylogenetic edges as a function of edge abundance. Variance is correlated to edge abundance at $R^2 = 0.82$. The standard anomaly of each edge for PAL and MCM is given by the color of the point, with blue indicating the edge was found only at PAL and red indicating that the edge was found only at MCM. (c) A histogram of normalized edge abundance. (d) The PCA of MCM and PAL samples based on the abundance of metabolic pathways inferred from the analysis of the MIRADA LTERS data set (see text). (e) The variance of metabolic pathways as a function of pathway abundance, points are colored as for b. Variance is correlated to pathway abundance at $R^2 = 0.66$. (f) Histogram of normalized pathway abundance. The abundance of key energy pathways (see figure 7) and biosynthesis pathways are shown in blue and green, respectively.

(Sieber et al. 2010), and suggests that anaerobic populations may live in suboxic microzones within suspended particles. Although less abundant than *S. wolfei* Goettingen, the Bacteriodetes CCGs *Owenweeksia hongkongensis* DSM 17368 and *Dokdonia* sp. MED134 were also found at PAL and MCM. The Bacteriodetes are well known for a particle-associated lifestyle. Therefore, although the free-living bacterial communities at PAL and MCM are dominated by taxonomically distinct (figures 5 and 6a) but potentially functionally similar groups (figures 6d and 7), suspended

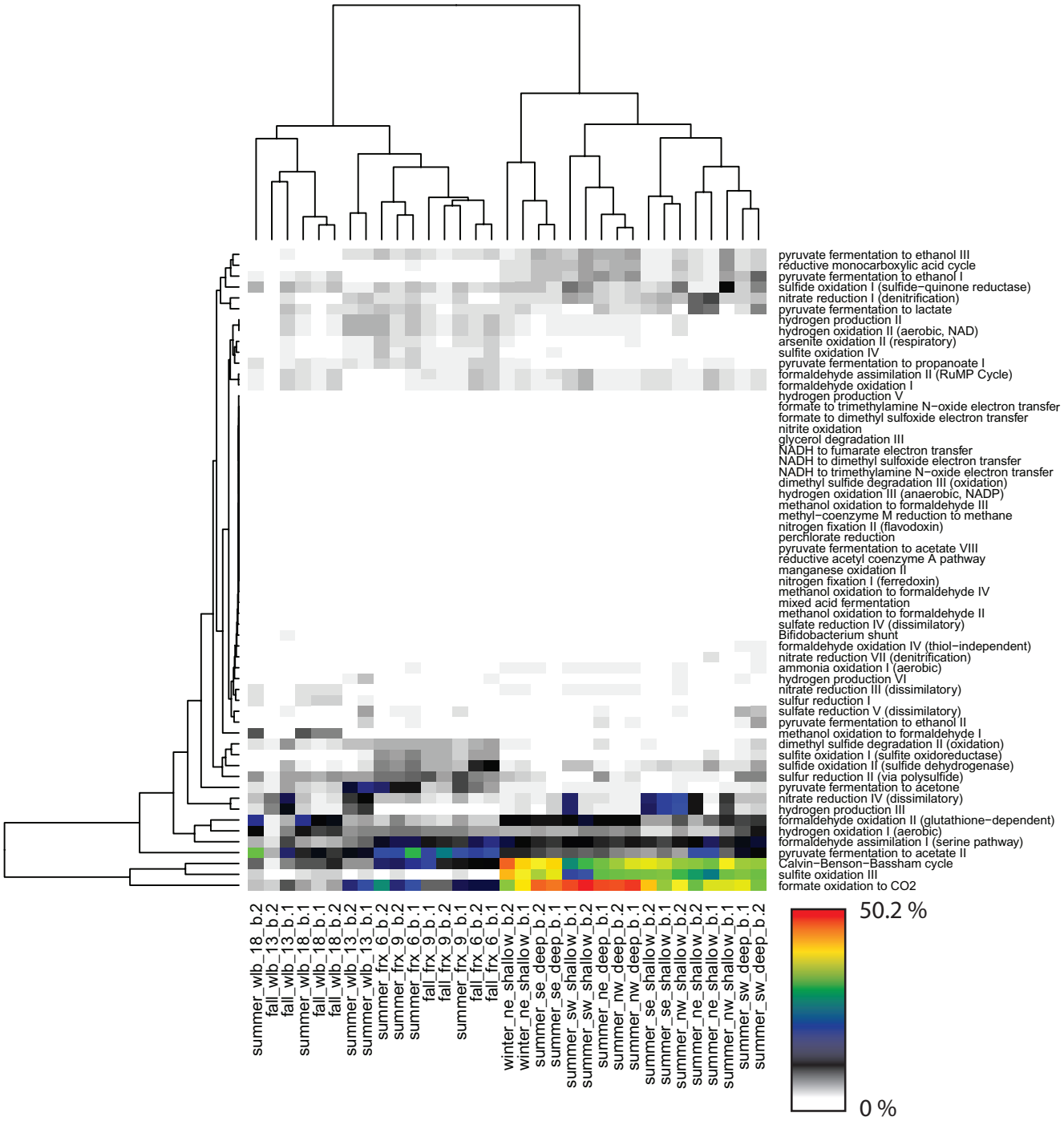

Figure 7. The abundance of pathways involved in energy acquisition and carbon fixation. The paprica metabolic inference technique (Bowman and Ducklow 2015) was used to predict functional potential of microbial communities from 16S rRNA gene data previously obtained for the MCM and PAL sites (Luria et al. 2014, Vick-Majors et al. 2014). The pathways involved in the aerobic respiration of organic substrates are not shown. The data were normalized to a fraction of the most abundant pathway for each sample prior to hierarchical clustering. The clustering on the x and y axis follows the defaults of the heat map command in R; Euclidean distance and the complete clustering method.

particles may constitute similar microenvironments across the two sites where taxonomically and functionally similar bacterial communities can thrive. Although the CEG *Saccharibacteria* was also found at PAL and MCM and the parent candidate phylum TM7 is widely distributed in the marine environment (Bowman et al. 2012, Ferrari et al. 2014), comparatively little is known about the ecology of this group. A particle-associated lifestyle is plausible however, on

the basis of previously observed associations with marine sponges (Ferrari et al. 2014), fecal material (Ferrari et al. 2014), and sea ice (Bowman et al. 2012).

Overall, the most abundant phylotypes were largely responsible for the variations in structure between and within the PAL and MCM communities (figure 6a and 6b). The CCGs *R. lacicola*, *P. ubique* HTCC1062, *T. singularis* PS1, and CEG Spirochaetales accounted for much of the difference between PAL and MCM, whereas within-site variation was additionally driven by the CEG Saccharibacter. Although the differences in community structure between the MCM samples were greater than between PAL samples—reflecting the physiochemical diversity of the lakes and greater connectedness of the PAL ecosystem—this was largely due to the single west lobe Lake Bonney sample dominated by the *Saccharibacter* CEG (figures 5 and 6a). The distribution of samples according to inferred metabolic pathways closely followed that of community structure, with the west lobe Lake Bonney sample a clear outlier (figure 6d).

For both community and metabolic structure, the more abundant edges and pathways generally accounted for more variance between samples (figure 6b and 6e). However, the abundance distribution differed between metabolic and community structure, with a few abundant CCG and CEG largely defining taxonomic structure (figure 6b and 6c) followed by a long "tail" of rare taxa, whereas a greater number of abundant metabolic pathways defined metabolic structure (figure 6e and 6f). The metabolic pathways involved in energy acquisition and conversion (figure 7) were relatively low in abundance (figure 6f) and accounted for little variation between the samples, although they had a largely heterogeneous distribution (figure 7). One notable exception was the formate oxidation to CO_2 pathway, a C_1 metabolic pathway inferred for the CCG *P. ubique* HTCC1062 at PAL (table 1). Although inferred less frequently for the MCM lakes, the pathway was inferred for several CCG in Lake Fryxell, including the abundant Actinobacteria CCG *Acidothermus cellulolyticus* 11B (table 1) also found in the west lobe of Lake Bonney. Lake Fryxell is known to host an active methane cycle (Bers et al. 2013) despite the absence of *S. wolfei Goettingen* (putatively associated with methanogenesis in the west lobe of Lake Bonney; figure 5); the relatively low frequency of the formate oxidation pathway may be related to the shallow MIRADA sampling depths in this lake (no samples were retrieved from the deep, highly reduced waters).

The available taxonomic, functional, and geochemical observations were used to produce conceptual models of the PAL and MCM (the west lobe of Lake Bonney) microbial food webs and associated biogeochemical transformations under warmer and cooler climate scenarios (figures 8 and 9). Water column solar radiation, which is directly linked to climate-related ice properties, is the basal source of metabolic energy for the PAL and MCM ecosystems, with both environments showing a strong taxonomic and functional response to the polar night and to ice cover (Bielewicz et al. 2011, Grzymski et al. 2012, Vick-Majors and Priscu 2012, Luria et al. 2014, Vick-Majors et al. 2014, Bowman and Ducklow 2015). In addition to driving PP by eukaryotic photoautotrophs, solar radiation supports prokaryotic photosynthesis and photoheterotrophy, which are differentially important in the MCM lakes. Phototrophic *Chloroflexi* and Gammaproteobacteria spp. related to green and purple phototrophic bacteria are present in Lake Fryxell (Karr et al. 2003) but have not been detected in the west lobe of Lake Bonney. Certain phylotypes of Actinobacteria in Lake Fryxell are related to photoheterotrophic *Planktophila* (Vick-Majors et al. 2014); proteorhodopsin-driven photoheterotrophy may confer a competitive advantage during carbon-limited periods to Actinobacteria in the MCM lakes. This advantage may have increasing importance if DOC levels continue to decline in the photic zones of the MCM lakes (figure 4).

At PAL and MCM, lithogenic redox potentials provide a secondary energy source for microbial chemoautotrophic metabolism within the aphotic zones during the summer season (figures 8 and 9) and a primary source during polar night (Dolhi et al. 2015). Although considered to be a small fraction of total PP, contributions of chemoautotrophic inorganic carbon fixation and associated elemental transformations are likely important when integrated along the entire water column over the annual cycle (Priscu et al. 1990). In our analysis, the Calvin-Benson-Bassham cycle, a key pathway for CO_2 fixation, was inferred to be more abundant at PAL than in the MCM lakes, although other CO_2 fixation pathways are rare at both sites (figure 7). The lack of alternate carbon fixation pathways may reflect the importance of Archaea (not included in this reanalysis) in prokaryotic CO_2 fixation, as has been suggested by other studies at PAL (Grzymski et al. 2012) and MCM (Karr et al. 2006, Vick-Majors et al. 2014). The putatively particle associated CCG *S. wolfei* Goettingen is known to fix carbon (Sieber et al. 2010); however, none of the carbon-fixation pathways met our criteria for prediction in the *S. wolfei* Goettingen genome.

Because of the high concentration of reduced inorganic and biogenic sulfur in the MCM lakes, sulfur oxidation may be an important energy source for prokaryotic carbon fixation there. Similarly, the high abundance of the CCG *T. singularis* PS1 at PAL suggests an active sulfur cycle and accounted for nearly all inferred carbon fixation pathways (table 1). By contrast, our metabolic inference methods identified only limited numbers of pathways involved in nitrogen cycling beyond dissimilatory nitrate reduction, despite the ubiquity of nitrogen species conversions in the global ocean. This disparity is likely partially artefactual; many pathways for nitrogen metabolism are poorly defined and difficult to predict in even completed genomes. Within the MCM lakes however, unusual geochemistry can limit nitrification. Although nitrifiers (Voytek et al. 1999) and partial nitrification (i.e., ammonia oxidation; Priscu 1997) have been observed in the MCM lakes, nitrite is not oxidized completely to nitrate. This may be the result of high concentrations of hydrogen sulfide or metals and/or the general lack of oxidants below the chemocline (Voytek et al. 1999).

Table 1. The major and minor contributors to select metabolic pathways predicted by metabolic inference for summer_se_shallow_b.1 (PAL), summer_wlb_13_b.2 (WLB) and summer_frx_6_b.2 (FRX; figure 5).

Pathway	Function	PAL	FRX	WLB
Calvin-Benson-Bassham cycle	carbon fixation	***Candidatus Thioglobus singularis PS1***	*Polaromonas sp. JS666* *Rhodoferax* *Polaromonas napthalenivorans CJ2* *Bordetella bronchiseptica MO149* *Niastella koreensis GR20-10*	*Acidimicrobium ferrooxidans DSM 10331* *Gammaproteobacteria* *Thiomicrospira crunogena XCL-2*
formaldehyde assimilation I (serine pathway)	C_1 metabolism		*P. sp. JS666* *Rhodoferax* *P. napthalenivorans CJ2*	
formaldehyde oxidation II (glutathione-dependent)	C_1 metabolism	*Dactylococcopsis salina PCC 8305*		*Hyphomonas neptunium ATCC 15444* *Marinobacter psychrophilus* *Stentrophomonas*
formaldehyde oxidation I	C_1 metabolism			*Clavibacter michiganensis NCPPB 382*
formate oxidation to CO_2	C_1 metabolism	***Candidatus Pelagibacter ubique HTCC1062***	***Acidothermus cellulolyticus 11B*** *P. sp. JS666* *B. bronchiseptica MO149* *Haliangium ochraceum DSM 14365*	*A. cellulolyticus 11B*
hydrogen oxidation I (aerobic)	*chemoautotrophy*		*Rhodoferax* *P. napthalenivorans CJ2*	*H. neptunium ATCC 15444* *Gammaproteobacteria*
hydrogen production III	*anaerobic metaboli*sm	***S. wolfei* Goettingen**		
nitrate reduction IV	anaerobic metabolism	***S. wolfei* Goettingen**		
pyruvate fermentation to acetone	anaerobic metabolism		***A. cellulolyticus 11B***	*A. cellulolyticus 11B*
pyruvate fermentation to acetate II	anaerobic metabolism		*Kribbella flavida DSM 17836* *Flavobacteriaceae* *B. bronchiseptica CJ2 3067*	*Candidatus ameobophilus asiaticus 5a2* *Leifsonia xyli CTCB07* *C. michiganensis NCPPB 382*
pyruvate fermentation to ethanol I	*anaerobic metabolism*			*Lactococcus*
pyruvate fermentation to lactate	anaerobic metabolism		*B. bronchiseptica CJ2*	*Lactococcus*
sulfide oxidation I (sulfide-quinone reductase)	chemoautotrophy		*Rhodoferax*	*M. psychrophilus*
sulfite oxidation I (sulfite oxidoreductase)	chemoautotrophy		*P. sp. JS666*	*P. napthalenivorans* *N. defluvii*
sulfite oxidation III	*chemoauto*trophy	***Candidatus T. singularis PS1***		*Gammaproteobacteria*
sulfur reduction II (via polysulfide)	anaerobic metabolism		*H. ochraceum DSM 14365*	*Gammaproteobacteria*

Note: Bold means more than 5% of all reads for that sample. No entry indicates that no community member with an abundance greater than 0.5% of total reads was predicted to have that pathway. For brevity, a maximum of five genomes—and only genomes predicted at more than 0.5% of the total population—are listed for each sample.

Following the classic microbial loop, phytoplankton-derived DOC at PAL and a combination of phytoplankton-derived and relict DOC at MCM are consumed by the heterotrophic community. The prokaryotic communities of the PAL water column and MCM lakes interact differently with this (primarily) eukaryotic biomass. The relatively deep photic zone and water column at PAL facilitate POM degradation by particle-associated bacteria and extracellular enzymes; the resulting DOC (also sourced from phytoplankton lysates and exudates) fuels BP of both particle-associated and free-living bacteria. In contrast, phytoplankton extracellular release is estimated to be low relative to BP for the MCM lakes (Takacs et al. 2001).

Previous work suggests that the DOC deficit in the MCM lakes, resulting from low PP and potentially by lower extracellular release (Takacs et al. 2001), is partially met by the

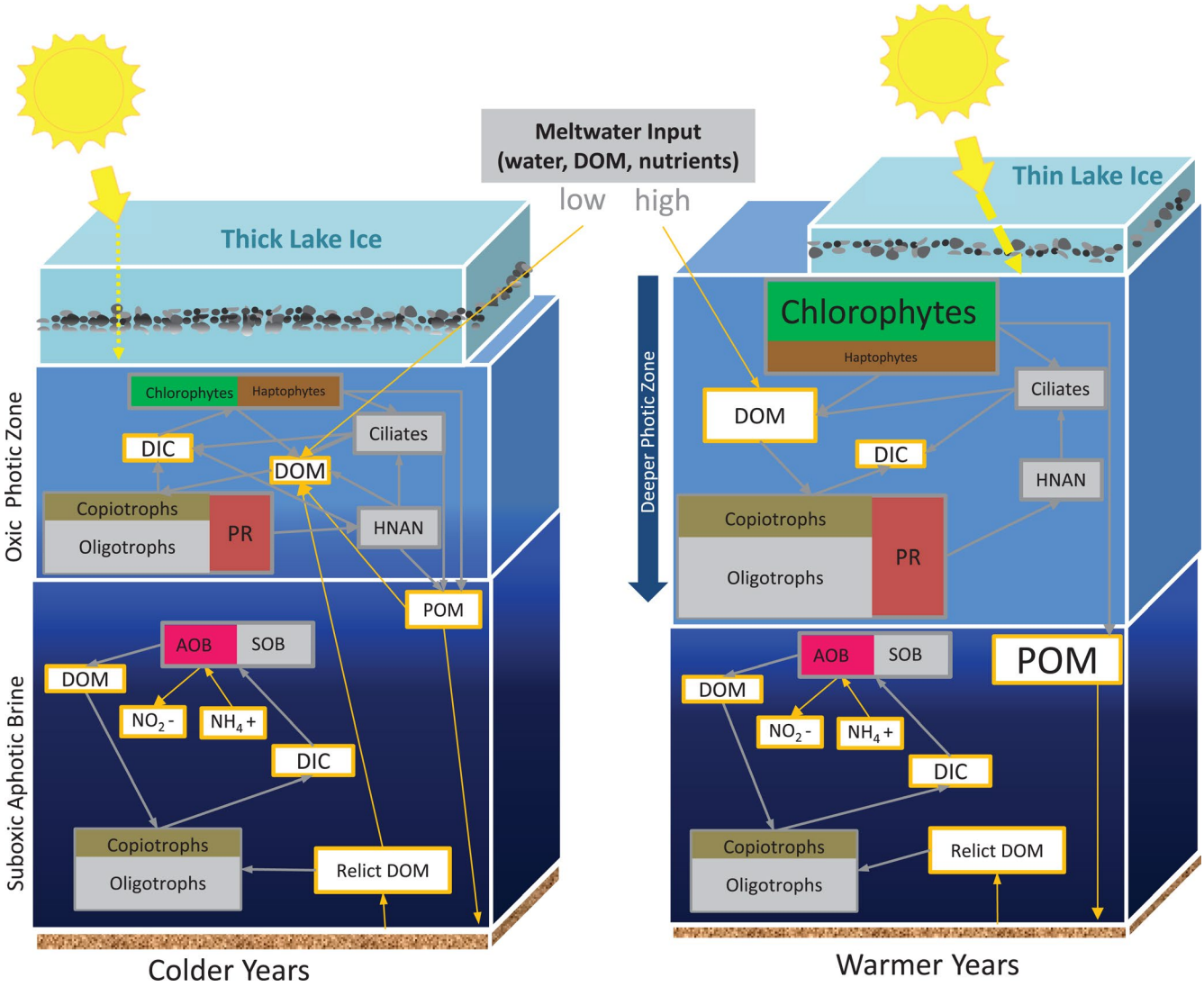

Figure 8. A conceptual microbial food-web model for MCM, including trends in carbon and energy cycling in the west lobe of Lake Bonney in a cooler year versus a warmer year. The boxes with gray outlines indicate functional groups (e.g., primary producers) composed of distinct functional subgroups (e.g., Chlorophytes, Haptophytes—although functional groups and subgroups are not necessarily taxonomically coherent), with the gray arrows indicating the inputs and outputs that can be attributed to the whole functional group. The boxes outlined in orange indicate reservoirs. The orange arrows indicate abiotic transfers between reservoirs or transfers that are attributable to singular subgroups within a functional group (e.g., the transfer of NH_4^+ to ammonia oxidizing bacteria). Abbreviations: AAnPs, aerobic anoxygenic phototrophs; AOA, ammonia oxidizers; DIC, dissolved inorganic carbon; DOM, dissolved organic matter; HNAN, heterotrophic nanoflagellates; NOB, nitrite oxidizers; POM, particulate organic matter; PR, proteorhodopsin groups; SOB, sulfide oxidizing bacteria. Copiotrophs and oligotrophs refer to heterotrophic bacteria optimized to high and low carbon concentrations, respectively.

upward diffusion of relict DOC from below the photic zone (Priscu et al. 1999). During warmer summers however, high flood years combined with thinning ice in the MCM lakes may stimulate PP by an influx of nutrients to nutrient-poor surface waters. In these years, elevated inputs of freshwater melt may also raise lake levels, increasing the depth of the photic zone and resulting in higher rates of depth-integrated PP (figure 8). Allocthonous DOC introduced with meltwater and higher PP can also increase the availability of DOC for BP, thereby temporarily reducing bacterial reliance on relict carbon.

Regardless of whether DOC is allocthonous or autochthonous, the combination of POC and DOC may support similar ecological strategies among PAL and MCM heterotrophs. Two trophic strategies are recognized for marine heterotrophs: nonmotile, small-bodied oligotrophs are often numerically dominant and optimized for opportunistic encounters with DOC, whereas motile, large-bodied

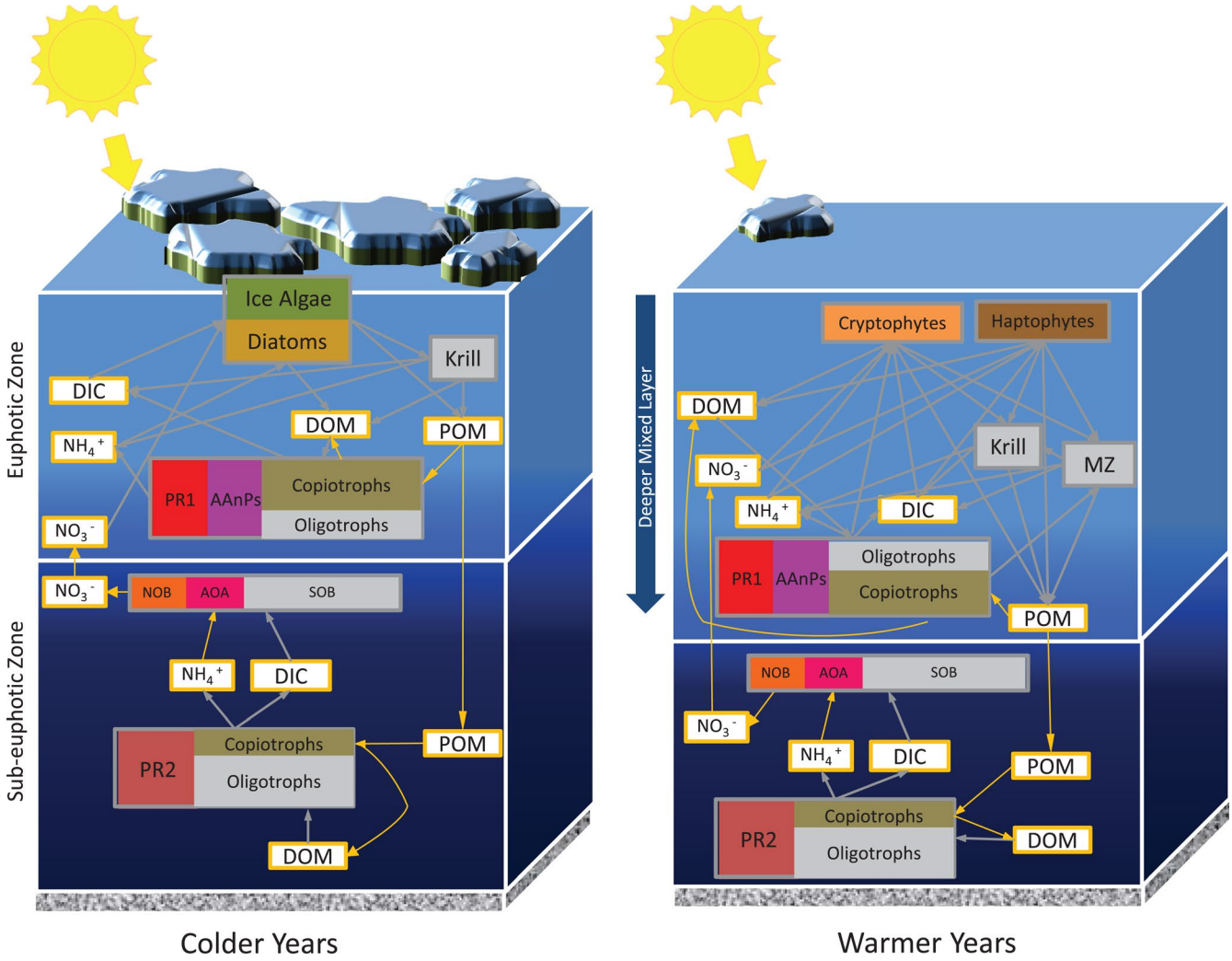

Figure 9. A conceptual microbial food-web model for PAL, including trends in carbon and energy cycling at PAL in a cooler year versus a warmer year. The boxes with gray outlines indicate functional groups (e.g., primary producers) composed of distinct functional subgroups (e.g., diatoms, ice algae), with gray arrows indicating the inputs and outputs that can be attributed to the whole functional group. The boxes outlined in orange indicate reservoirs. The orange arrows indicate abiotic transfers between reservoirs or transfers that are attributable to singular subgroups within a functional group (e.g., the transfer of NH_4^+ to ammonia oxidizing bacteria). Abbreviations: AAnPs, aerobic anoxygenic phototrophs; AOA, ammonia oxidizers; DIC, dissolved inorganic carbon; DOM, dissolved organic matter; NOB, nitrite oxidizers; POM, particulate organic matter; PR, proteorhodopsin groups; SOB, sulfide oxidizing bacteria. Copiotrophs and oligotrophs refer to heterotrophic bacteria optimized to high and low carbon concentrations, respectively.

copiotrophs are optimized to particle colonization and degradation (Stocker 2012). At PAL and MCM, the dominant bacteria (*P. ubique* HTCC1062 and various Actinobacteria, respectively) may take on the role of oligotrophic specialists, whereas other less abundant taxa associate with particles. Low-oxygen microenvironments in these particles could account for some of the anaerobic pathways inferred for these samples, including hydrogen production, nitrate reduction, and fermentation pathways (table 1).

Following the microbial loop, heterotrophic prokaryotes at PAL and MCM are presumed grazed by bacterivorous protists. Although haptophytes and chlorophytes dominate the photic zone of Lake Bonney through the summer, mixotrophic cryptophytes and dinoflagellates are abundant during the seasonal transition from summer to winter (Bielewicz et al. 2011). Limited studies of bacterivory at PAL have revealed that microzooplankton grazers—including seasonally abundant cryptophytes—can remove 100% of daily BP (Garzio et al. 2013). In addition to bacterivorous nanoflagellates, bacteriophage-mediated lysis of bacteria appears to be a major contributor to bacteria mortality in the MCM lakes (Lisle and Priscu 2004). Because cryptophytes and dinoflagellates dominate late-season blooms and blooms in the expanding meltwater-influenced regions at PAL (figure 9)

and viral lysogeny is prevalent in the Antarctic coastal environment (Brum et al. 2015), grazing and infection dynamics in the MCM lakes may provide some insight into future changes to the PAL microbial loop.

Conclusions

Since their inception, the PAL and MCM LTER sites have collected rich biogeochemical data sets across a period of intense climate-driven ecological change. Although the temporal extent of these data sets are in many cases sufficient to capture only one or two cycles in the natural oscillations for most measured parameters, they do reveal how certain aspects of Antarctic coastal marine and permanently ice-covered lake ecosystems respond to climatic perturbations. Clearly, the influence of ice cover on physical processes, including mixing and the flux of photosynthetically available solar radiation, play a key role in the structure and function of these polar ecosystems. Thinner and lower ice cover changes the abundance and diversity of photoautotrophic members of the ecosystems and influences the flow of organic carbon through the microbial loop and eventually to higher trophic levels. Discrete climate events can produce tipping points in these systems that have long-lasting effects on the patterns and coupling of PP and BP. Although observations are limited, biodiversity may also be altered significantly, culminating in the changes in trophic structure described here. Long-term time-series observations of community structure and function are needed to test the influence of these events on ecosystem function. Superimposed on top of the climate-driven aspects of these ecosystems and amplifying their effects is the strong biomodal solar cycle that occurs at high latitudes. As climate continues to warm in Antarctica we can expect to see new, unknown tipping points reached that may lead to further changes in the structure and function of these ice-dependent ecosystems.

Acknowledgments

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