14.1 Introduction

The polar regions, both Arctic and Antarctic, show strong evidence of climate change affecting freshwater species, communities, and ecosystems, and are expected to undergo rapid and continued change in the future (IPCC, 2007). Diatoms in the freshwater and brackish habitats of inland waters of the Antarctic provide valuable records of their historic and modern environmental status. Antarctic habitats also contain a unique biodiversity of species many of which are found nowhere else on Earth. In this chapter, we review investigations using diatoms as indicators of environmental change in Antarctic and subantarctic island habitats, including lakes and ponds, streams and seepage areas, mosses and soils, cryoconite holes, brine lakes, and remarkable subsurface glacial lakes.

The Antarctic continent holds the vast majority of the Earth’s freshwater, but the water is largely inaccessible because it is in the form of ice. Life is dependent upon liquid water, a substance scarce in Antarctica. Less than 0.4% of the continent is ice free, and it is within these ice-free regions that freshwater lakes and ephemeral streams form, fed by the melting of snow and glacial ice and occasional precipitation. These ice-free regions are located primarily near the Antarctic coastline (Figure 14.1). Of these regions, the “desert oases” of East Antarctica are considered to be the coldest, driest regions on Earth. In the limited parts of these oases where liquid water is available, even if present for only a few short weeks of the year, there is life (McKnight et al., 1999).

Cyanobacteria (also known as blue-green algae) are the most widely distributed and abundant freshwater organisms, occurring as individuals, small colonies, or as cyanobacterial mats in lakes, ponds, and meltwater streams, and on moist soils. Higher plants occur only in lower latitudes of the Antarctic Peninsula. Diatoms are present in nearly all moist, wet to semi-dry, and some frozen habitats of the subantarctic islands and Antarctica. As in many other regions of the world, diatoms are often one of few organisms that are well preserved as subfossils.

14.1.2 Antarctic diatoms

The ability to use diatoms as environmental indicators to their greatest utility is dependent on accurate taxonomy, with the lowest prediction errors occurring in analyses using high and consistent taxonomic precision (Birks, 1994). The subantarctic and Antarctic diatom floras are remarkably regional, and it is important that future works rely on the latest primary literature from the Antarctic, rather than from other sources. We summarize the important resources in a historical and habitat context below.

Early exploration of the continent resulted in numerous collections of freshwater algae. Although diatoms were included in these surveys, they were often not of primary interest (Van Heurck, 1909; West and West, 1911). The most accessible subantarctic and maritime islands of Kerguelen and South Georgia were investigated early on (Reinsch, 1890; Carlson, 1913). Although the flora of Kerguelen Island had been the most studied of any of the Antarctic regions (Germain, 1937; Bourrelly and Manguin, 1954; Germain and Le Cohu, 1981; Le Cohu, 1981; Le Cohu and Maillard, 1983, 1986; Riaux-Gobin, 1994; Van de Vijver et al., 2001), a recent intensification of work on diatom taxonomy and biogeography has occurred. There has been renewed interest in taxonomic investigations of diatoms.
Species diversity of diatoms in Antarctica is low when compared to temperate regions (Jones, 1996), or even when compared to the Arctic (Douglas et al., 2004). This has been confirmed using a global taxonomically consistent data set at the genus level, which showed that at comparable latitudes, lakes in the Austral region consistently have lower local and regional diatom richness than similar water bodies in the northern hemisphere (Vyverman et al., 2007). Low diversity of the Antarctic flora is believed to be due, in part, to physical isolation of the continent and, thus, a limitation to dispersal. Antarctica is surrounded by circumpolar oceans, creating a barrier to colonization (Heywood, 1977). Furthermore, the number of algal species decreases with an increase in latitude (Jones, 1996), although a direct correlation between latitude and severity of the environment may not exist (Heywood, 1977). Nevertheless, areas that are conspicuously lacking in diatoms have been reported (Edward VII Peninsula (Broady,
antartic and subantarctic freshwaters

Figure 14.2 The late Pleistocene and Holocene history of Lake Terrasovoje, Amery Oasis from sediment biogeochemistry, total diatom abundance and most abundant diatom taxa (>5% of relative abundance) versus sediment ages. Sediment biogeochemistry shown includes total carbon (TC), total nitrogen (TN), carbon to nitrogen ratio (C/N), total sulfur (TS), and carbon to sulfur ratio (C/S). Shading of the biogeochemistry regions was considered of particular interest (see Wagner et al., 2004). The short bars between sediment biogeochemistry and diatom abundance indicate strata that were analyzed for diatom composition. The lower gray shaded areas show the period when the lake was overridden by glacial ice (prior to c. 12,400 cal yr BP), followed by the onset of biogenic sedimentation with production substantially reduced by long-lived snow fields and perennial ice cover limiting light penetration, and finally the establishment of a productive diatom assemblage (10,200 cal yr BP) due to early Holocene warming and a reduction in lake ice cover. The middle gray shaded area shows a period between 4900 and 3700 cal yr BP when diatom production was again restricted by a cool period and the return of snow-covered perennial lake ice (Wagner et al., 2004).

1989), Dufek Massif (Hodgson et al., 2010) and Mt. Heekin Lakes (Spaulding, unpublished data) and there are periods in the development of some lakes where diatoms are absent, or near absent, on account of unfavorable conditions such as perennial snow and ice cover (Wagner et al., 2004, Figure 14.2). It will be of great interest to determine if these initial observations are supported by further investigation. Indeed, if diatoms do not occur in the highest latitudes of Antarctica, it may provide an important insight into diatom physiology and ecology.

The diatoms of the Antarctic Peninsula are more diverse than other regions, reflecting both its proximity to South America and more diverse aquatic habitats. An affiliation between the subantarctic and South American flora was recognized by several investigators (Frenguelli, 1924; Bourrelly and Manguin, 1954; Schmidt et al., 1990; Jones et al., 1993). For instance, many of the Achnanthes species found in King George Island lakes in moss habitats (Schmidt et al., 1990) have also been reported in similar Chilean habitats (Krasske, 1939). Furthermore, the diatom flora of the Antarctic is quite different from that of the Arctic; the polar regions have few taxa in common (Verleyen et al., 2009). While environmental conditions of the two poles may be extreme, the geographical isolation of Antarctica may limit the number of taxa to a greater extent than extreme environment (Vyverman et al., 2007). The importance of this geographical isolation in structuring...
Antarctic diatom communities have been revealed by multivariate analysis of diatom genera in 1039 freshwater bodies from both hemispheres (Verleyen et al., 2009), which showed that the diatom composition in Antarctic lakes is distinct from the other water bodies in both hemispheres, including Arctic regions (Figure 14.3).

Antarctic regions hold a large percentage of diatoms endemic to the continent, subregions, or even islands. The ratio of endemic to cosmopolitan taxa of Ross Island and several eastern Antarctic coastal regions was greatest between 68 and 77 degrees south (Hirano, 1965; Fukushima, 1970). Sixty-three percent of the diatoms of Antarctic Peninsula lakes were found to be endemic (Schmidt et al., 1990), while in the Larsemann Hills endemics account for about 40% of all freshwater and brackish taxa (Sabbe et al., 2003). While the presence of species endemic to a particular geographic region implies isolating processes that lead to species evolution, the presence of endemic lineages within the Antarctic and subantarctic implies geographic stability and the presence of glacial refugia during glacial maxima in which species could survive (Spaulding et al., 1999). At the same time, other work indicates diatoms are capable of rapid speciation (Theriot et al., 2006). Species within the genera Diadesmis, Luticola, Muelleria (Figure 14.4) and...
antarctic and subantarctic freshwaters

![Diagram showing depth zonation of microbial mat types in Antarctic lakes](image)

**Figure 14.5** Depth zonation of microbial mat types in the lakes from the Larsemann Hills and Böingen Islands (East Antarctica) showing the ecological threshold of 4 m of maximal lake-water depth above which well-developed microbial mats occur. Lakes shallower than 4 m are characterized by disturbed microbial mats and a different diatom flora due to the physical and chemical stress associated with yearly lake-ice formation (Sabbe et al. 2004).

Diatoms are considered to have evolved within geographically restricted regions, with eleven species of *Diadesmis* from Crozet Archipelago (Van de Vijver et al., 2002a) and twenty species of *Luticola*, several of which are restricted to the South Shetland Islands (Van de Vijver and Mataloni, 2008).

In addition to diatoms, the Antarctic Peninsula and East Antarctica form distinct biogeographical regions for several groups of other organisms (Andrassy, 1998; Gibson et al. 2008). Recent molecular data have shown that the modern Antarctic terrestrial biota have been continuously isolated on timescales of multimillion years, and pre-dates the break-up of Gondwana (Convey et al., 2008). This work supports the persistence of coastal ice-free habitats as refugia through multiple Cenozoic glacial cycles. Furthermore, convergence across taxonomic groups implies ancient distributions and also presents a paradox, because speciation of diatoms in other parts of the world has been tied to evolution within ancient water bodies or landscapes (Kociolek and Spaulding, 2000; Rossiter and Kawanabe, 2000; Mackay et al., this volume). Yet aerophilous habitats, which are common in the Antarctic, are habitats that are characterized by low moisture or periodic drying. Their existence is temporary and, therefore, the habitats are not geologically old. The high endemism of aerophilous diatoms in the Antarctic presents a question that is yet to be resolved.

### 14.2 Lakes and ponds

Extent and duration of ice cover are typically the most influential variables controlling physical, geochemical, and biological features of high-latitude lakes and ponds (Smol, 1988; Wharton et al., 1993; Douglas et al., 2004; Foreman et al., 2004; Hodgson and Smol, 2008). Depending on latitude and elevation, the duration of ice-cover ranges from several months (e.g. northern Antarctic Peninsula lakes) to perennial (e.g. McMurdo Dry Valley lakes). Ice cover prevents wind-induced mixing and creates a stable water column, leading to perennial stratification (Spaulding et al., 1997). Ice cover reduces transmission of incident light, depending on the clarity of the ice. For example, the clear ice of Lake Vanda transmitted 18% of incident light, while the opaque ice of Lake Hoare allowed less than 2% of incident light (Hawes and Schwarz, 2000). Not only does ice cover reduce the photosynthetic flux density, it alters the spectrum of transmitted light available to diatoms in benthic-mat communities (Hawes and Schwarz, 2000; Moorhead et al., 2005). In addition, the physical and chemical stress associated with the yearly formation of lake ice largely determines the structure of the benthic microbial mats and associated diatom floras inhabiting the lakes (Sabbe et al., 2004; Figure 14.5). Well-developed, finely laminated and undisturbed mats typically form in coastal East Antarctic lakes with a lake-water depth exceeding 4 m.
In most cases, perennial ice cover prevents the development of a planktonic diatom community and allows benthic communities to dominate in Antarctic waters (Spaulding et al., 1997; Hodgson et al., 2001a). Diatoms, with their silica cell walls, require water-column mixing to maintain the dense cells in suspension. In ice-covered lakes, turbulence caused by wind mixing is reduced or absent (Light et al., 1981; Wharton et al., 1993; Spaulding et al., 1997). Although planktonic diatoms are also expected to be absent in perennially ice-covered lakes, a limited number of planktonic taxa have been reported from Antarctic freshwaters, under ice (for review see Jones, 1996). It might be expected that a planktonic flora would develop where open water is present for an extended period of time. However, even lakes that are ice free for a few months may not develop a plankton flora (Jones, 1996).

Based on investigations of diatoms in Arctic lakes, Smol (1988) proposed that the extent and duration of ice cover can be inferred from species composition and abundance of fossil diatoms (see Douglas and Smol, this volume). This model appears to be generally valid in Antarctic lakes. For example, changes in the diatom assemblages in the sediments of “Tiefersee” and “Mondsee” (unofficial names) on King George Island in the South Shetland Islands reflect differences in the extent of moat formation during the austral summer (Schmidt et al., 1990). Tiefersee, located away from a glacier, develops an ice-free moat. Correspondingly, the abundance of periphytic diatoms in the sediments is greater, and also more variable than in the more persistent ice cover of Mondsee, which possesses consistently lower diatom abundance. Further, fluctuation in the extent of moat development from year to year was interpreted based on the abundance of large pennate diatoms in sediment cores. Tiefersee showed stronger indication of an ice-free moat (more variation in periphyton abundance) than Mondsee (more constant diatom abundance). On a longer timescale, the benthic diatom community and presence of sediment deposits indicated that the ice cover of Lake Hoare (McMurdo Dry Valleys) has been perennial for at least 2000 years (Spaulding et al., 1997). In Lake Reid (Larsemann Hills, East Antarctica), a nearly monospecific diatom community of Staurastrum inermis Flower, Jones and Round occurred during the Last Glacial Maximum, likely related to perennial ice cover during this period (Hodgson et al., 2005).

In addition to ice cover, diatoms respond to a range of other environmental variables. By examining subfossil remains of diatoms in lake sediments, changes in environment can be tracked over time. In some cases, reconstructions are based on absolute diatom abundance or the ecological preferences of particular diatom species. For example, absolute diatom abundance calculated from identification and enumeration of frustules combined with analyses of preserved diatom pigments (fucoxanthin, diatoxanthin, diadinoxanthin) has been used to estimate total diatom primary production. Analysis of sediments from cores of isolation lakes in the Larsemann Hills showed that transitions from marine to lacustrine habitats were accompanied by a 2- to 26-fold decrease in marine diatom production and that these declines are not entirely compensated by increased production of benthic taxa in freshwater environments during lake evolution (Verleyen et al., 2004a). The ecological preferences of particular diatom species have also been used to qualitatively infer environmental changes. For example, the transitions between freshwater, brackish, and marine diatom assemblages in coastal lakes have been used to reconstruct relative sea-level changes from the isolation of lake basins at different attitudes, from which changes in ice-sheet configuration can be inferred (Wasell and Håkansson, 1992; Zwartz et al., 1998; Verkulich et al., 2002; Bentley et al., 2005; Verleyen et al., 2005; Hodgson et al., 2009). Deglaciation and subsequent warm periods are associated with increased nutrient supply to lakes, which strongly influences diatom species composition. Therefore, the onset and progression of glacial melt can be inferred from the colonization of lakes by benthic diatoms and the establishment of productive diatom communities (e.g. Björck et al., 1993; Björck et al., 1996; Hodgson et al., 2005; Wagner et al., 2004). In other cases, diatoms associated with specific substrates, such as mosses, have been used to infer the presence of these substrates in sediment cores, even when moss macrofossils are not preserved. For example, the diatom assemblage preserved in sediments deposited during the last interglacial (Marine Isotope Stage (MIS) 5e, 125–115 ka BP) in the Larsemann Hills, East Antarctica, includes species that are associated with soil and moss habitats (e.g. Diademia costei Le Cohu and Van de Vijver, Diatoma balfouriana Grev.) and aquatic mosses (e.g. Psmamthidium marquini Hustedt) of the warmer maritime–Antarctic biome. One of the species (D. costei) is considered endemic to the subantarctic (Hodgson et al., 2006b, Figure 14.6). This species assemblage is absent from the region and other ice-free oases in east Antarctica today (Verleyen et al. 2003) and suggests that temperatures were not only higher during the last interglacial, but present-day conditions have not warmed sufficiently for colonisation by species associated with the maritime and subantarctic biomes.

Changes in entire species assemblages may occur in response to environmental variables and can be used qualitatively to reconstruct changes through time using inference.
models, or transfer functions, if the response relationships are well understood. In the Antarctic, diatom transfer functions have been developed to reconstruct changes in lake salinity (Roberts and McMinn, 1998; Verleyen et al., 2003), water depth (Verleyen et al., 2003), ammonium and chlorophyll a concentration (Jones and Juggins, 1995) and conductivity, soluble reactive phosphate, and silicate (Saunders et al., 2008). Transfer functions have then been applied to reconstruct historical conditions, such as lake-water salinity (or conductivity). In closed-basin lakes, the hydrologic balance reflects input through precipitation and snow and ice melt, and loss by evaporation, sublimation and ablation. The response of particular lakes depends on the Antarctic region. In most cases, when East Antarctic lakes have become less saline, warmer periods have been inferred due to increased precipitation and snow accumulation (Roberts and McMinn, 1999; Roberts et al., 2000; Roberts et al., 2004; Verleyen et al., 2004b, 2004c; Hodgson et al., 2005). Alternatively, warmer periods have been inferred when lakes become more saline, whereby reduced snow cover has led to decreased albedo, which in turn has caused increased evaporation of the lake water and sublimation of the lake ice (Hodgson et al., 2006a). In the McMurdo Dry Valleys, cold temperatures limit stream flow and lake water becomes more concentrated during colder periods (Lawrence and Hendy, 1989; Chinn, 1993; Doran et al., 2008). In Lake Fryxell, carbonate concentrations were associated with halophilic diatom taxa and allowed reconstruction of paleo lake levels (Whittaker et al., 2008). Peaks in stream discharge were also interpreted based on the occurrence of marine diatom fragments in lake sediments, because meltwater streams erode through ancient marine deposits, carrying marine fragments to the lake during periods of stream downcutting. Unlike diatom-inference models used in other parts of the world, Antarctic models are typically dependent on benthic diatoms alone (planktonic species are largely absent). Consequently, some of the major planktonic shifts associated with
climate change and water-column warming in lower latitude environments cannot be resolved in the Antarctic using fossil diatom assemblages. Further descriptions of the methods and applications of diatoms in Antarctic paleolimnology are summarized in two recent reviews (Hodgson et al., 2004; Hodgson and Smol, 2008).

14.3 Streams

Streams and rivers are unusual habitats in the Antarctic, because they are limited in their extent and hydrologically very different from flowing waters of the rest of the planet (McKnight et al., 1999). The McMurdo Dry Valleys contain waters that flow for less than 1 km to 30 km (Onyx River of the Wright Valley). While snowfall accumulates at high elevations, it sublimates or contributes to soil moisture but does not lead to runoff to feed stream flow (Chinn, 1993). Lacking precipitation and terrestrial runoff, the ephemeral streams are fed by melting glaciers, and flow in some regions for no more than 10 weeks of the year. Furthermore, flow is dependent on solar radiation and aspect of the source glacier; flow can vary 5 to 10-fold on a daily basis (Conovitz et al. 1998). Sediments are underlain by an active layer of permafrost of 0.1 m to 0.5 m depth, which freezes and thaws annually and influences the exchange of water and solutes across the hyporheic zone (McKnight et al., 1999). Finally, because streams drain to closed-basin lakes, hydrologic processes are reflected in lake-water level and solute chemistry (Chinn, 1993; House et al., 1995; Doran et al., 2008).

Diatoms are common in McMurdo Dry Valley streams and grow in benthic mats in association with cyanobacteria, chlorophytes, nematodes, tardigrades, and rotifers (Alger et al., 1997; Esposito et al., 2008). The benthic mats are colorful oranges, blacks, greens, and browns, reflecting photosynthetic and photoprotective pigments and an accumulation of biomass at values considered high even in comparison to temperate-zone biomass (McKnight and Tate, 1997). The algal mats are perennial and survive the long periods of the year when streams do not flow, overwintering in a freeze-dried state (McKnight et al., 1999). Diatoms within these ephemeral streams tolerate not only annual periods of desiccation and freezing, but can persist for decades or centuries without liquid water. Of the 38 species of diatoms identified in McMurdo Dry Valley streams (Alger et al., 1997) 60% were considered endemic. Common taxa include Diadesmis contenta (Grunow) Mann, Diadesmis perpusilla (Grunow) Mann, Hantzschia abundans Lange-Bertalot, Luticola austroatlantica Van de Vijver et al., Luticola gaussia (Heiden) Mann, Muellena praustralis (West and West) Spaulding and Stoermer, Psammothidium chlidanos (Hohn and Hellingman) Lange-Bertalot, and Stauroeis latistauras Van de Vijver and Lange-Bertalot. Diatom species composition, diversity, and endemism appear to be strongly tied to annual stream flow (Esposito et al., 2006), an observation that has direct application to quantifying climatic shifts. Under conditions of decreased solar radiation, temperature, and resulting reduction in stream flow, endemic Antarctic species become more dominant in stream assemblages (Figure 14.7). That is, cooling and the associated increase in ecological harshness of streams, favors Antarctic species over species that are more widespread. The McMurdo Dry Valleys experienced cooling trends over the 1990s (Doran et al., 2002; Torinesi et al., 2003), when diatom stream assemblages changed, a trend that may be reversed if warming occurs, as predicted (Shindell and Schmidt, 2004).
14.4 Mosses and soils

Diatoms are abundant in wet, semi-wet soils, and non-aquatic moss ecosystems, habitats that are particularly abundant in subantarctic regions. On many of the subantarctic and maritime Antarctic islands of the southern Indian Ocean, mosses are the principal vegetation, covering large areas and rich in bryophyte species (Seppelt, 2004; Ochyra et al., 2008). Although moss habitats contribute a large proportion of terrestrial biomass, the diatoms living on these mosses and soils were relatively unknown until recently. Early studies of the diatom flora of Macquarie Island (Bunt, 1954) and Campbell Island (Hickman and Vitt, 1973) documented some taxa, but recent work reveals a well-developed, rich flora of more than 250 species (Van de Vijver and Beyens, 1999; Van de Vijver et al., 2002b, 2004; Gremmen et al., 2007). Other works have contributed to the discovery of the terrestrial diatom flora of King George Island (Van de Vijver 2008), Livingston Island (Chipev and Temniskova-Topalova, 1999, Zidarova, 2008) and Deception Island (Fermani et al., 2007, Van de Vijver and Mataloni, 2008).

The taxonomy of many of the subantarctic groups has recently been revised (Van de Vijver, 2008; Van de Vijver and Mataloni, 2008), demonstrating a diatom flora of regionally endemic species.

After accounting for regional differences, the composition and species richness of diatoms in mosses and soils is strongly influenced by moisture content (Chipev and Temniskova-Topalova, 1999; Van de Vijver and Beyens, 1999; Van de Vijver et al., 2002b, 2004). In dry habitats, species numbers are consistently lower than in wet habitats. Furthermore, only a limited number of species and genera appear to be capable of surviving xeric conditions (Van de Vijver and Beyens, 1999) and in those taxa, valve size typically decreases with decreasing moisture content. For example, valve size of *Navicula borealis* Ehrenb. on the island of South Georgia was significantly lower in the driest mosses than in wetter mosses. The environmental variables that influence the species composition differ across habitat types. That is, the species composition of diatom communities in moss habitats is related to habitat type (Van de Vijver and Beyens, 1999), while the species of diatom communities in soil habitats is influenced by nutrient concentrations (phosphate and nitrate). Animal-influenced habitats, such as the upper layer of the soil in penguin rookeries, are a clear example of this influence (Van de Vijver et al., 2002a; Fermani et al., 2007). All of these factors provide great potential for use of moss diatoms in interpreting shifts in moisture and habitat availability.

The Antarctic Convergence, or Antarctic Polar Front, is considered the climatic boundary between the Antarctic continent and several oceanic fronts (Broecker, 1996; Bard et al., 1997; Domack and Mayewski, 1999) and the subantarctic islands are located within this turbulent zone of the Antarctic Convergence. In this geographic position the islands are influenced by circumpolar winds, the Southern Westerlies, whose fluctuations influence ocean circulation and global climate. As a result, understanding species and environment relationships has allowed paleoclimatic reconstruction in this important region. The diatom species composition of moss habitats on Kerguelen Island has been related to elevation, a proxy for temperature (Gremmen et al., 2007). Regardless of the moss species composition, diatoms growing within moss habitats were related to altitude, with diatoms having colder optima also favoring higher altitudes. Accordingly, peat cores obtained from Île de la Possession (Crozet Archipelago) led to an environmental reconstruction of the past 6200 years using both moss remains and diatoms. Results indicate a major shift at 2800 yr BP to a wetter, windier climate attributed to an intensification, or latitudinal shift, or both, of the Southern Westerlies (Van der Putten et al., 2009).

14.5 Eolian transport of diatom valves

The presence of eolian marine and freshwater diatoms in ice cores of the polar plateau (Kellogg and Kellogg, 1996) can be used as tracers of air masses and circulation patterns. Atmospheric transport of freshwater diatom frustules is known to occur over long distances (Lichti-Federovich, 1984; Gayley et al., 1989; Chalmers et al., 1996); however, transport of valves does not imply that cells are viable. In the Antarctic, diatom valves were present in ice cores obtained from high elevations of the polar plateau, several hundred kilometers from freshwater sources (Burckle et al., 1988; Kellogg and Kellogg, 1996). In these studies, the diatoms were considered eolian, because no melt pools were known from the surface of the ice cap. However, the occurrence of diatoms in melt pools on the surface of glaciers is well established and can serve as a source of living populations (this chapter). The species found on the polar plateau were 98% lacustrine taxa, including *Luticola mutica* (Van Heurck) Mann, *Navicula shackletoni* West and West, *Luticola colnii* (Hilse) Mann, *N. delataica* Kellogg (Burckle et al., 1988), species known from freshwater and hypersaline lakes and deposits in Antarctica. The reconstruction of lake level in Lake Fryxell during the Holocene (Whittaker et al., 2008) was aided by recognition of a period in which deposition of eolian...
diatoms dominated the accumulation of sediments. Both sands and diatoms were blown onto the lake surface, and migrated through the lake ice cover.

Marine forms are not likely to be transported by wind over long distances (Burckle et al., 1988), and glacial ice is dominated by freshwater forms (lakes make up only 0.32% of the Antarctic terrestrial surface area) rather than marine forms. Yet, a crucial component of eolian transport is that subfossil diatoms of terrestrial deposits are most easily transported (Sancetta et al., 1992), as compared to live cells. While empty diatom valves of marine and freshwater species may be transported considerable distance, living forms may not be so easily entrained in the atmosphere. For example, onshore winds were found to be effective in lifting marine diatoms from the sea surface, but there was no support for transport beyond the nearshore region (Maynard, 1968). A similar study from the Ross Sea, Antarctica, found that while marine particles were transported with aerosols, fragments or whole diatom valves were not included (Saxena et al., 1985). The transport of living marine diatoms for any distance has not been demonstrated, presumably because living cells have difficulty becoming airborne, as they often form long chains, have external organic coatings, and contain dense internal protoplasm (Burckle et al., 1988). The combination of diatom species that are endemic to narrow regions and eolian transport has the potential to be utilized to a greater extent.

14.6 Cryoconite holes
Cryoconite holes are depressions on glacier surfaces filled with water and sediment, named for the “cold rock dust” they contain (Nordenskjöld, 1875). Wind-blown sediment is transported onto glacier surfaces and collects in depressions in the ice. The lower albedo of the sediment causes the ice to melt more quickly than its surroundings, forming a hole. Over time, wind-blown sediment and organic matter accumulates and enhances the melting process. Organisms transported into cryoconite holes can increase expansion of the holes through absorption of solar energy and metabolic activity (GerdGel and Drouet, 1960; McIntyre, 1984). Cryoconite holes may be significant on glaciers, accounting for up to 6% of the surface area of the accumulation zone (GerdGel and Drouet, 1960; Fountain et al., 2004; Hodson et al., 2007), ranging from 5-145 cm in diameter to 4-56 cm in depth. In the Antarctic, meltwater from cryoconite holes generates as much as 13% of glacial runoff (Fountain et al., 2004). In addition to their importance in glacial mass balance, cryoconite holes may serve as refugia for biota and play an important role in re-seeding neighboring lakes or streams (Wharton and Vinyard, 1983; Wharton et al., 1981; Porazinska et al., 2004). In lieu of the extreme physical and chemical conditions within cryoconite holes, researchers consider these systems to be analogs of refugia on Earth during cold periods and other icy planets (Tranter et al., 2004; Säwström et al., 2002).

Although the organisms in cryoconite holes typically reflect the aquatic biota of surrounding areas, containing cyanobacteria, green algae, metazoans, and diatoms (Wharton, 1981, 1985; Mueller et al., 2001; Christner et al., 2003; Porazinska et al., 2004; Stibal et al., 2006), there may be important differences. The microhabitat appears to favor species that can withstand the extreme changes in physical and chemical conditions and, in the McMurdo Dry Valleys, contain high abundances of the diatom *Muelleria cryoconitola* Stanish and Spaulding, which appears to be endemic to these microhabitats (Van de Vijver et al., 2010). Although these microhabitats have not been used in terms of interpreting environmental conditions yet, the unique species within them are of potential use in detecting environmental change to glacial surfaces.

14.7 Brine lakes
While a few brine, or hypersaline, lakes are extant in the McMurdo Dry Valleys (Doran et al., 2003), many closed-basin lakes (including lakes Vanda, Bonney, and Fryxell) were reduced to brine lakes in the past (Lyons et al., 2006; Whittaker et al., 2008). The present brine lakes include Lake Vida, which is considered to be at the extreme end of lacustrine types (Doran et al., 2003). The ice cover of Lake Vida is 19 m thick and the water column is composed of a sodium chloride (NaCl) brine, seven times as saline as seawater. The brine is considered to have been isolated for at least 2800 years, based on 14C dates. Because of its extreme salinity, the brine remains liquid below −10 °C. Although the surface ice contains viable microbial mats, there has been no effort to date to determine if diatoms are present. Large glacial lakes existed in the McMurdo Dry Valleys during the last glacial maximum (Stuiver et al., 1981; Hall and Denton, 2000; Whittaker et al., 2008) and an understanding of present-day brines may help understand sediment records of the past. While sediments of Lake Vanda contain well-preserved diatoms (Spaulding, personal observation), to date they have not been used to add to interpretation of the paleoclimate of the region.

14.8 Subglacial lakes
In the future, diatoms near, and in, subglacial lake sediments will be of great interest in interpreting past conditions. Evidence from perennially ice-covered lakes, or periods in lake-sediment
The debate concerning the paleoclimate of Antarctica during the glacially deposited Sirius Formation (Webb et al., 1984) raising global sea level by more than 25 m during the Pliocene. II, 400 ka, an unusually long interglacial when the Southern Ocean was warmer than at present and global sea levels were 4–6 m higher (Jansen et al., 2007). A long-standing controversy continues over the East Antarctic Ice Sheet and whether it was stable, or warmed and melted, raising global sea level by more than 25 m during the Pliocene. The debate concerning the paleoclimate of Antarctica during the Pliocene centers on the interpretation of diatoms in the glacially deposited Sirius Formation (Webb et al., 1984; Denton et al., 1991; Webb and Harwood, 1991; LeMasurier et al., 1994; Wilson et al., 2002). The “dynamic” hypothesis proposes that the Sirius deposits contain reworked marine diatoms that were deposited within basins in East Antarctica during a warm interval in the Pliocene, when the East Antarctic Ice Sheet retreated to about one-third of its present size (Webb et al., 1984; Webb and Harwood, 1991). According to this hypothesis, grounded ice scoured the marine basins during a later cold period, incorporated marine sediments and diatoms, and deposited the reworked material in the Transantarctic Mountains (in the Sirius Formation). Alternatively, the “stable” hypothesis proponents contend that the East Antarctic Ice Sheet has remained essentially unchanged for millions of years (Denton et al., 1991; LeMasurier et al., 1994), and that diatoms in the Sirius deposits are the result of surface (eolian) contamination (Burckle and Potter, 1996). Burckle and Potter discovered Pliocene–Pleistocene diatoms within fractures of Devonian rocks, and concluded that the younger diatoms were transported by wind and deposited within the much older rocks. Mahood and Barron (1996) point out that controversies such as that surrounding the Sirius Formation could be resolved by closer taxonomic scrutiny of diatom taxa used as markers of biostratigraphy and environmental conditions. With such detailed examination of taxa, misunderstandings of the identity, age, and source of diatoms would be far less likely. Indeed, the most recent efforts to resolve the age and origin of glacial deposits of the Sirius Formation has revealed a complex glacial history supporting temperate climatic conditions in the Mount Feather region until the Late Miocene (Wilson et al., 2002). The non-marine diatoms of the Mount Feather Diamicton are dominated by Anomoeoneis costata Hust. and Stephanodiscus sp., species whose presence implies a temperate climate. These taxa no longer grow under the current glacial conditions of the Antarctic continent. Additional work to characterize the diatom assemblages promises to further identify and constrain the sources of glacial deposits.

14.9 Fossil diatoms in glacial deposits to reconstruct ice-sheet and climate history

The presence of subfossil marine diatoms has provided crucial evidence for the extent of the Antarctic ice sheets, and the age of these diatoms (determined by biostratigraphy and cosmogenic 10Be concentrations in the sediment matrix) indicates time periods when the ice sheet was absent. This is particularly pertinent for the West Antarctic Ice Sheet, whose partial or complete collapse in previous interglacials may have resulted in substantial contributions to global sea-level rise (Denton and Hughes, 2002). Knowledge of how this ice-sheet configuration changes during periods of relatively well-known paleoclimatic conditions critically advises our ability to predict future behavior. Several studies have proposed West Antarctic Ice Sheet collapse at least once in the last 600 ka (Hearty et al., 1999; Scherer et al., 1998), with candidate periods being MIS 11, 400 ka, an unusually long interglacial when the Southern Ocean was warmer than at present, and even (for partial collapse) MIS 5e (Scherer et al., 1998), when temperatures were between 2 and 5 °C higher than today and global sea levels were 4–6 m higher (Jansen et al., 2007).

A long-standing controversy continues over the East Antarctic Ice Sheet and whether it was stable, or warmed and melted, raising global sea level by more than 25 m during the Pliocene. The debate concerning the paleoclimate of Antarctica during the Pliocene centers on the interpretation of diatoms in the glacially deposited Sirius Formation (Webb et al., 1984; Denton et al., 1991; Webb and Harwood, 1991; LeMasurier et al., 1994; Wilson et al., 2002). The “dynamic” hypothesis proposes that the Sirius deposits contain reworked marine diatoms that were deposited within basins in East Antarctica during a warm interval in the Pliocene, when the East Antarctic Ice Sheet retreated to about one-third of its present size (Webb et al., 1984; Webb and Harwood, 1991). According to this hypothesis, grounded ice scoured the marine basins during a later cold period, incorporated marine sediments and diatoms, and deposited the reworked material in the Transantarctic Mountains (in the Sirius Formation). Alternatively, the “stable” hypothesis proponents contend that the East Antarctic Ice Sheet has remained essentially unchanged for millions of years (Denton et al., 1991; LeMasurier et al., 1994), and that diatoms in the Sirius deposits are the result of surface (eolian) contamination (Burckle and Potter, 1996). Burckle and Potter discovered Pliocene–Pleistocene diatoms within fractures of Devonian rocks, and concluded that the younger diatoms were transported by wind and deposited within the much older rocks. Mahood and Barron (1996) point out that controversies such as that surrounding the Sirius Formation could be resolved by closer taxonomic scrutiny of diatom taxa used as markers of biostratigraphy and environmental conditions. With such detailed examination of taxa, misunderstandings of the identity, age, and source of diatoms would be far less likely. Indeed, the most recent efforts to resolve the age and origin of glacial deposits of the Sirius Formation has revealed a complex glacial history supporting temperate climatic conditions in the Mount Feather region until the Late Miocene (Wilson et al., 2002). The non-marine diatoms of the Mount Feather Diamicton are dominated by Anomoeoneis costata Hust. and Stephanodiscus sp., species whose presence implies a temperate climate. These taxa no longer grow under the current glacial conditions of the Antarctic continent. Additional work to characterize the diatom assemblages promises to further identify and constrain the sources of glacial deposits.

14.10 Summary

Diatoms of the Antarctic and subantarctic islands are part of a unique flora that are exposed to high gradients of solar radiation, short growing seasons, extreme temperature ranges, changing amounts of moisture, strong salinity gradients, and vulnerability to climate change. The species diversity of diatoms of inland habitats in Antarctica is low compared to both temperate and Arctic regions, due, in part, to physical isolation of the continent. Within the continent, diatoms of the Antarctic Peninsula are more diverse than other regions, reflecting both
the proximity to South America and the more diverse aquatic habitats of the warmer peninsula region. Despite the cold conditions, Antarctic regions have also been recognized as sites that contain a large percentage of diatoms endemic to the continent, small subregions, or even islands.

Diatoms have been used to determine environmental change in the Antarctic from a variety of habitats, including lakes, streams, mosses and soils, and fossil deposits. In some sites, the history of lake ice cover has been inferred. Because perennial ice cover prevents the development of a planktonic diatom community, the composition of diatom assemblages in the sediments can be used to detect differences in the extent of melting of ice cover and the formation of a moat during the austral summer. The sediments of Lake Hoare (McMurdo Dry Valleys) revealed a benthic diatom community and the presence of sediment deposits indicated that the ice cover has been perennial for at least 2000 years. Several of the coastal lakes have been influenced by marine inflows, or were entirely marine. Lake sediment cores allow estimates of marine diatom production and shifts to increased production of benthic taxa in freshwater environments as glaciers retreated during the Holocene. Deglaciation and subsequent warm periods are associated with increased nutrient supply to lakes, which strongly influences diatom species composition. Therefore, the onset and progression of glacial melt can be inferred from the colonization of lakes by benthic diatoms and the establishment of productive diatom communities. Diatom transfer functions have been developed to reconstruct changes in lake salinity, water depth, ammonium and chlorophyll a concentration, conductance, soluble reactive phosphate, and silicate.

The response of particular lakes to changes in temperature depends on the Antarctic region. In most cases, when East Antarctic lakes have become less saline, warmer periods have been inferred due to increased precipitation and snow accumulation reflecting input through precipitation and snow and ice melt, and loss by evaporation and ablation. Alternatively, warmer periods have been inferred when lakes become more saline, whereby reduced snow cover has led to decreased albedo, which in turn has caused increased evaporation of the lake water and sublimation of the lake ice. Unlike diatom-inference models used in other parts of the world, Antarctic models are typically dependent on benthic diatoms alone because planktonic species are largely absent.

In streams, diatom species composition, diversity, and endemism appear to be strongly tied to annual stream flow, an observation that has direct application to quantifying climatic shifts. Under conditions of decreased solar radiation, temperature, and resulting reduction in stream flow, endemic Antarctic species become more dominant in stream assemblages. In moss and stream habitats, the diatom species composition on Kerguelen Island has been related to elevation, a proxy for temperature. Regardless of the moss species composition, diatoms growing within moss habitats were related to altitude, with diatoms having colder optima also favoring higher altitudes.

A debate concerning the paleoclimate of Antarctica during the Pliocene centers on the interpretation of diatoms in the glacially deposited Sirius Formation. The dynamic hypothesis proposes that the Sirius deposits contain reworked marine diatoms that were deposited within basins in East Antarctica during a warm interval. According to this hypothesis, grounded ice scoured the marine basins during a later cold period, incorporated marine sediments and diatoms, and deposited the reworked material in the Transantarctic Mountains. Alternatively, the stable-hypothesis proponents contend that the East Antarctic Ice Sheet has remained essentially unchanged for millions of years.

Future work may utilize the understanding of eolian transport, cryoconite holes, brine lakes, and subglacial lakes to apply diatoms as tools for understanding aspects of Earth's history. The polar regions, both Arctic and Antarctic, show strong evidence of climate change in freshwater species, communities, and ecosystems, and are expected to undergo rapid and continued change in the future. Diatoms in the freshwater and brackish habitats of inland waters of the Antarctic hold valuable records of historic and modern environmental status, as well as containing a unique biodiversity of species found nowhere else on Earth.

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