

LETTER**From the Heroic Age to today: What diatoms from Shackleton's *Nimrod* expedition can tell us about the ecological trajectory of Antarctic ponds**

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Scientific Significance Statement

Many remaining “pristine” habitats are threatened by human activity, both directly and from the ongoing climate crisis. However, detecting change, and subsequently implementing protective measures, can be challenging given limited baseline data. This problem is highlighted in Antarctic freshwater systems, which have rapidly accumulated threats over the last century. By analyzing samples collected by Shackleton's *Nimrod* expedition nearly 100 yr ago, we evaluate changes in the pond diatom communities of Cape Royds on Ross Island by comparing them to samples collected during recent expeditions. We found limited evidence for species invasions and ecological change overall, though the diatom community of Pony Lake near Shackleton's hut was substantially restructured, indicating a need to investigate the cause of this shift to inform future monitoring and conservation efforts.

Abstract

Biological invasion and environmental change pose major threats to ecosystems. While long-term ecological change is commonly evaluated through sediment cores in lakes, it is generally not feasible for smaller ponds, and spatial resolution is limited. Here, we analyze pond diatom communities collected during Shackleton's *Nimrod* expedition at Cape Royds, Antarctica, to compare with the same waterbodies a century later. We find historical samples to be almost identical to modern counterparts, and provide no evidence of exotic

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Data Availability Statement: Data are available through the Environmental Data Initiative repository (<https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-mcm.9038.1>).

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introductions despite increasing human activity. However, a shift occurred in the pond nearest Shackleton's hut, Pony Lake, which was dominated by *Luticola muticopsis* a century ago, and was replaced by *Craspedostauros laevissimus*. Both are endemic species previously and currently present at Cape Royds, and we hypothesize that a shift in conductivity accompanying changing precipitation patterns may be responsible. Collectively, these results provide important data for assessing human and climate impacts among Antarctic lacustrine habitats.

At the dawn of the 20th century, Sir Ernest Shackleton's *Nimrod* expedition (1907–1909) made base at Cape Royds, on Ross Island, Antarctica, in their quest for the South Pole. While here, expedition biologist James Murray and geologist Raymond Priestley collected benthic samples from the abundant ponds on Cape Royds and vicinity. Upon their return to Europe (after achieving a new Farthest South), the samples were analyzed in London by a father/son team of biologists, William West and George Stephen West. The result was the pioneering report on Freshwater Algae in Antarctica (West and West 1911) which provided the world with one of its first glimpses into the phycological diversity of the last terrestrial frontier. The original microscope slides, now important type material and the taxonomic foundation for the entire region (Van de Vijver et al. 2012), have been carefully stored at the Natural History Museum in London over the last century, where they offer a unique glimpse into Cape Royds' pond diatom communities at the height of the Heroic Age of Antarctic Exploration.

The McMurdo Sound Region of Antarctica encompasses Ross Island and the McMurdo Dry Valleys (MDV), and is the largest ice-free area of the Antarctic continent. First sighted by James Clark Ross as part of the "magnetic crusade" of the 1840s, Ross Island provided a starting point for several famous "Heroic Era" campaigns in the early 20th century, including Robert Falcon Scott's *Discovery* (1901–1904) and *Terra Nova* (1910–1912) expeditions, and Shackleton's *Nimrod* expedition based at Cape Royds. Following a period of inactivity from the mid-1910s, major changes came to the region with the construction of the U.S. McMurdo Station and New Zealand's Scott Base as part of the International Geophysical Year of 1957–1958. Since then, scientific research and tourism has accelerated in the region, with > 9500 visitors to Cape Royds alone since 1992–1993 (IAATO 2020), making it one of the most frequented tourist localities on Continental Antarctica. While protective measures are in place to minimize human impacts on vulnerable Antarctic ecosystems (Antarctic Specially Protected and Managed Areas [ASPAAs and ASMAAs]), concerns over climate change and exotic species introductions persist (Chown et al. 2012).

Diatoms (Bacillariophyceae), siliceous unicellular micro-eukaryotic algae, make excellent bioindicators due to their species-specific environmental preferences, ease in morphological identification, and excellent preservation (Smol and Stoermer 2010). They are especially useful in Antarctica where the continental flora consists of ~ 50 mostly endemic species (Esposito et al. 2008), and is distinct from the Maritime- and

sub-Antarctic regions (Verleyen et al. 2021). Reports on Cape Royds diatom communities are few, and largely consist of survey descriptions and checklists by West and West (1911), Fukushima (1964, 1967), and Broady (1989). On the other hand, diatoms have been intensively studied as part of the McMurdo Dry Valleys Long-Term Ecological Research Program for > 30 yr (Esposito et al. 2008). As part of this effort, Sakaeva et al. (2016) recently surveyed ponds throughout the McMurdo Sound Region, and demonstrated distinct differences in the diatom communities between Ross Island and the MDV. In the absence of substantial changes in dispersal and environmental conditions, we would expect pond diatom communities collected during the *Nimrod* expedition to be similar to those collected today. However, the influence regional change has had on resident diatom communities over the last century remains an open question.

While lake sediment cores are commonly used to reconstruct the past, interpretations from Antarctic sediments can be challenging (Píšková et al. 2019), and are inherently spatially limited, constraining our ability to observe ecological change across landscapes. Therefore, to investigate possible changes in Cape Royds pond diatom communities since the Heroic Age, we analyzed 14 of the original slides from West and West's collection at the Natural History Museum in London to characterize the diatom communities exactly as Shackleton's expedition found them. Count data from "historical" samples were compared with the "modern" communities in Sakaeva et al. (2016), using historical writings by Priestley (1908), Murray (1910), and West and West (1911) as a guide. These comparisons not only allow for inferences into the stability of diatom community structure and diversity since the departure of the *Nimrod*, but also humanity's environmental footprint in the McMurdo Sound Region over the last century.

Materials and methods

Study sites

Cape Royds is a coastal area located on the west side of Ross Island and across the McMurdo Sound from the MDV (Fig. 1A). In a majority of the numerous ponds at Cape Royds, brightly colored cyanobacterial mats carpet benthic sediments and provide habitat for diatoms. The historical samples were collected on various dates from 1908 to 1909. According to West and West (1911), "Most of the collections were made by Mr. James Murray in the near vicinity of the winter quarters of the Expedition at Cape Royds on Ross Island. One was

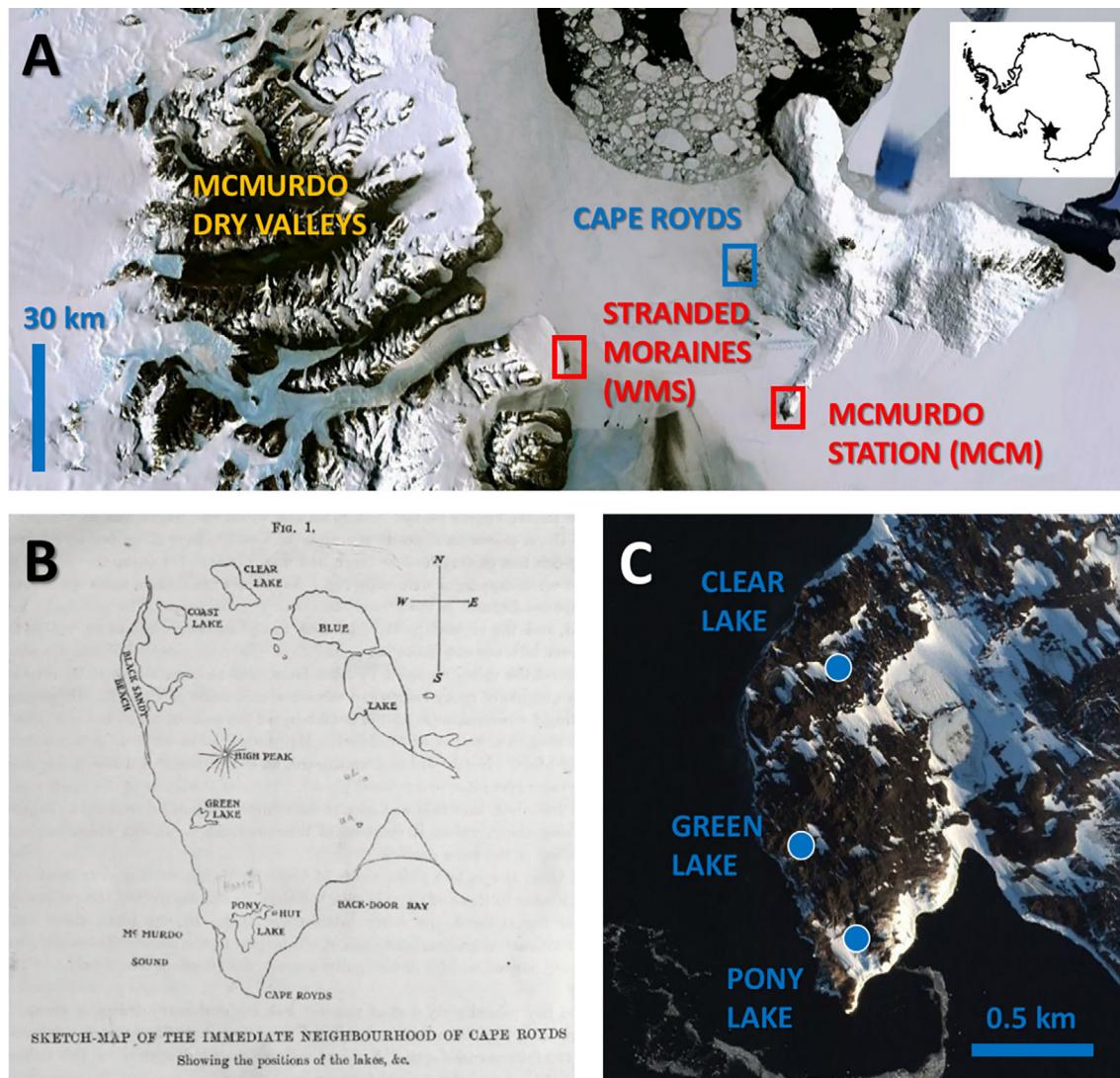


Fig. 1. (A) Satellite image of the McMurdo Sound Region. Indicated are Cape Royds and McMurdo Station on Ross Island, and the McMurdo Dry Valleys and the Stranded Moraines on the mainland. The location of the McMurdo Sound Region within the Antarctic Continent is provided as an inset (top right). (B) Map from the official report of J. Murray (Murray 1910), which was illustrated by Raymond Priestly during Shackleton's *Nimrod* expedition. (C) Recent satellite image of Cape Royds, with the locations of the resampled waterbodies (Clear Lake, Green Lake, and Pony Lake) indicated. See Sakaeva et al. (2016) and Supporting Information Table S1 for details on all other sampled sites. Images courtesy of the United States Geological Survey and Maxar Technologies, and accessed via Google Earth.

made by the leader of the Expedition at Hut Point, Ross Island, and two others on the mainland of South Victoria Land." Of these latter samples, labeled as "Lake on the west side of McMurdo Sound," both were collected by Raymond Priestly in January 1909 approximately "twenty-five miles from the camp at Cape Royds" at a lake near the so-called "Stranded Moraines" (West and West 1911; Fig. 1A).

Original scientific reports from the *Nimrod* expedition allowed us to discern with a high degree of confidence three lakes at Cape Royds where previous samples were taken: Pony Lake (sampled on 22 April 1908 and 04 January 1909), Green Lake (29 November 1908, 03 January 1909, 02 February 1909), and Clear Lake (April

1908), all collected by Murray (West and West 1911). Murray provided a description of the sample collection at Cape Royds, which includes a sketch map illustrated by Priestly (Fig. 1B; Murray 1910). This information is supplemented by archival material from the expedition at the Scott Polar Research Institute in Cambridge, England that includes a field notebook entitled "Observations on the lakes of Cape Royds" which also includes sketch maps of the region (1908). Both of these resources align remarkably well with modern satellite imagery of the area (Fig. 1C). However, the original documents did not provide adequate description to locate other sample locations on Cape Royds or the Antarctic mainland without speculation.

Pony Lake has received the most study at Cape Royds (McKnight et al. 1994; Brown et al. 2004; Dieser et al. 2013). Located within ASPA No. 121, it is most famous for being near Shackleton's hut (ASPA No. 157), and earned its name by serving as an exercise arena for the expedition's horses (Murray 1910). Oriented opposite an Adélie penguin (*Pygoscelis adeliae*) rookery, which is likely a source of nitrogen-rich aerosols, Pony Lake is by far the most likely on Cape Royds to be visited by tourists, though special permission must be acquired to physically access its southernmost section. Located near the coast, both Pony Lake and Green Lake (the latter named from the color of its ice, Murray 1910), have been previously reported to have high conductivities ($\sim 10,000 \mu\text{S}$), while Clear Lake (named for the transparency of its ice) has lower conductivity (845 μS ; Sakaeva et al. 2016).

Sample collection and analyses

Methods for the sampling and analysis of modern material are outlined in Sakaeva et al. (2016). Briefly, pond microbial mats were sampled from Cape Royds on 24 January 2013, 21 December 2013, and 02 January 2014, while the MDV ponds were sampled over various summer dates from 2013 to 2014 (Supporting Information Table S1). Samples were preserved in $\sim 5\%$ formalin (final concentration), digested using heat and hydrogen peroxide (H_2O_2), and rinsed to a neutral pH with distilled water. Digested material was dried onto cover slips, mounted onto glass microscope slides with Zrax[®] medium (W. P. Dailey, University of Pennsylvania), and analyzed by light microscope at $\times 1250$ magnification. Results are described in detail by Sakaeva et al. (2016).

The West and West (1911) slides are stored at The Natural History Museum (NHM), London, and have been recently utilized by several investigators to resolve issues of diatom taxonomy, including Cavacini et al. (2006), Van de Vijver et al. (2012), Levkov et al. (2013), and Kohler et al. (2015) (Supporting Information Table S2). However, to the best of our knowledge, these slides have never been analyzed for diatom community composition or used in an ecological study. In total, we enumerated diatoms from 14 of the available historical slides, which are listed in Supporting Information Table S2 along with their NHM accession numbers and descriptions. Because of the preparation method used in making the historical slides (some had thick coverslips, see Supporting Information Fig. S1), several of these were counted at $\times 650$ or $\times 850$ magnification (i.e., Green Lake, Lake west side of McMurdo Sound). However, due to the simplicity of the flora, adequately large size of frustules, and regional experience of the analysts, this was not likely to affect count quality.

For both modern and historical material, at least 300 valves were counted from each slide, and relative abundance of species were calculated (slides were also briefly scanned afterward for rare species). Scanning electron microscopy (SEM) images were made from modern samples after being air-dried onto

aluminum stubs, which were then sputter-coated with 50 nm of Au and photographed on a JEOL JSM-6380LV at 25 kV. Species identifications were made according to the species list in Sakaeva et al. (2016), the Antarctic Freshwater Diatoms website (<http://huey.colorado.edu/diatoms>), and the original West and West (1911) publication. A full report on the diatom communities, water chemistry, physical conditions, and GPS coordinates of sites are given in Sakaeva et al. (2016).

Statistical analyses

To compare historical and modern communities, we created a non-metric multidimensional scaling (NMDS) ordination by combining data from Sakaeva et al. (2016) and the 14 newly counted historical slides using the *vegan* R package (Oksanen et al. 2017) to visualize relationships between samples and among regions. Replicates were averaged by site and sample period, and a Morisita-Horn distance matrix was calculated using the untransformed, unfiltered relative abundances as in Sakaeva et al. (2016). For Clear Lake, Green Lake, and Pony Lake, a direct comparison of historical vs. modern samples was made with a dot plot. Statistical analyses were performed using R version 3.4.3 (R Core Team 2017), and all data are available through the Environmental Data Initiative repository (Kohler et al. 2021).

Results and discussion

Cape Royds historical diatom communities were remarkably similar in composition to their modern counterparts. No diatoms observed in the historical material were absent in the modern material (i.e., no extirpations), and likewise, all of the common modern diatoms at Cape Royds were also present in the historical material (i.e., no exotic introductions, although we cannot rule out the possibility of rare species). This suggests that the species pool has remained essentially unchanged since the Heroic Age despite growing traffic in the area. Furthermore, the historical samples cluster with modern Cape Royds communities in the NMDS rather than with the MDV (Fig. 2A), indicating that the biogeographical pattern demonstrated in Sakaeva et al. (2016) has been stable for at least a century. Briefly, Cape Royds was characterized as having higher relative abundances of *Craspedostaurus laevissimus*, *Luticola muticopsis*, and *Sabbea adminii*, while genera *Muelleria*, *Hantzschia*, and *Humidophila* were more common in the MDV (Fig. 2B). Interestingly, samples from "across McMurdo Sound" at or near the Stranded Moraines also clustered with the Ross Island samples (notably those taken from near McMurdo Station; Fig. 2A), indicating that proximity to McMurdo Sound may play a large role in assembling diatom communities.

Two of the three Cape Royds ponds that were directly compared, Green Lake and Clear Lake, were essentially identical to those sampled a century ago (Fig. 3). For Clear Lake, mean richness was comparable between samplings (12.3 and

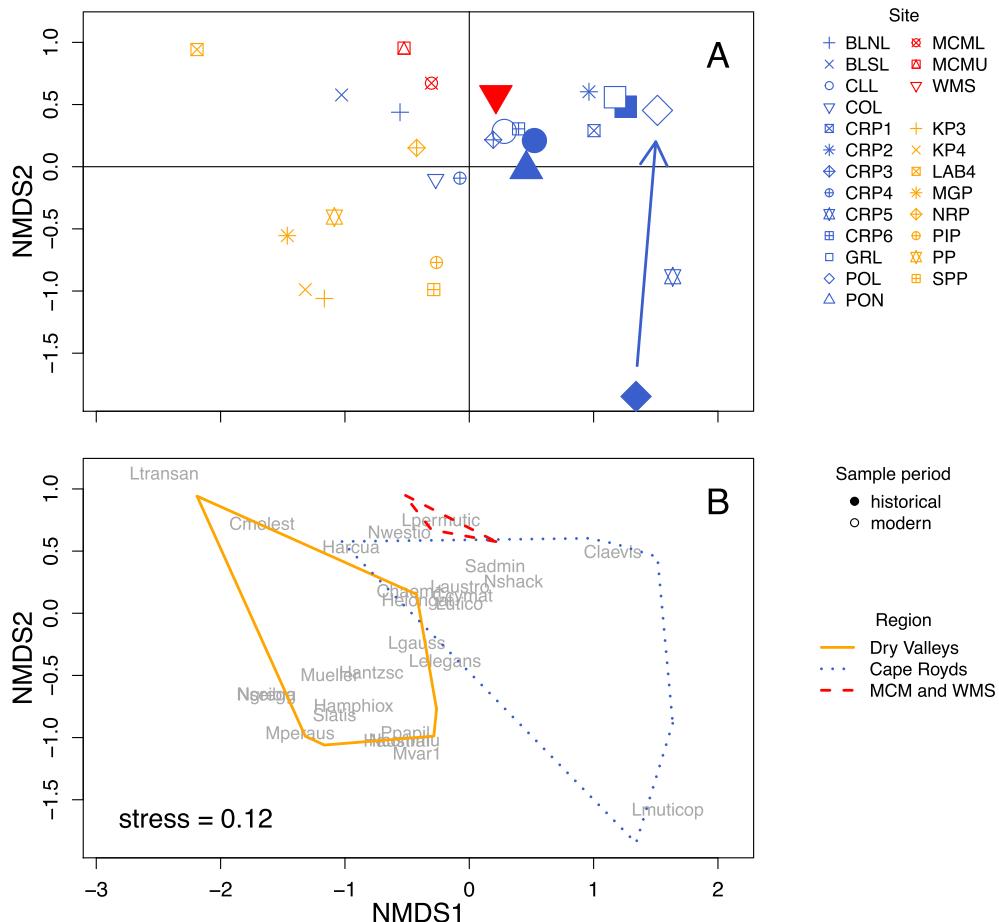


Fig. 2. NMDS ordination of (A) all sites (symbols indicating mean values) showing the historical (filled symbols) and modern (empty symbols) diatom communities. Cape Royds sites are given as blue symbols, Dry Valleys in orange, and West McMurdo Sound and McMurdo Station in red. The blue arrow indicates the change in position from historical to modern Pony Lake. Symbol abbreviations include BLNL, Blue Lake North Lobe; BLSL, Blue Lake South Lobe; CLL, Clear Lake; COL, Coast Lake; CRP1–6, Cape Royds Pond 1–6; GRL, Green Lake; KP3–4, Kaki Pond 3–4; LAB4, Labyrinth Pond 4; MCML, McMurdo Pond Lower; MCMU, McMurdo Pond Upper; MGP, Many Glaciers Pond; NRP, Nussbaum Riegel Pond; PIP, Picture Pond; POL, Pony Lake; PON, unknown Cape Royds pond; PP, Parera Pond; SPP, Spaulding Pond; and WMS, Stranded Moraines at West McMurdo Sound. (B) Species loadings for diatoms with at least 5% relative abundance are plotted. Diatom codes are as follows: Ccymat, *Chamaepinnularia cymatopleura*; Chaem1, *Chaemaepinnularia* sp. 1; Claevis, *Craspedostauros laevissimus*; Cmolest, *Craticula molestiformis*; Hamphiox, *Hantzschia amphioxys*; Hantzsc, unknown species of *Hantzschia*; Harcua, *Humidophila arcuata*; Hastral, *Humidophila australis*; Helongat, *Hantzschia elongata*; Laustro, *Luticola austroatlantica*; Lelegans, *Luticola elegans*; Lgauss, *Luticola gaussii*; Lmuticop, *Luticola muticopsis*; Lpermutic, *Luticola permucitopsis*; Ltransan, *Luticola transantarctica*; Lutico, unknown species of *Luticola*; Mperaus, *Muelleria peraustralis*; Mueller, unknown species of *Muelleria*; Mvar1, *Mayamaea atomus* var. 1; Ncommu, *Nitzschia commutata*; Ngrega, *Navicula gregaria*; Nseibig, *Navicula seibigiana*; Nshack, *Navicula shackletoni*; Nwestio, *Nitzschia westiorum*; Ppapil, *Psammothidium papilio*; Sadmin, *Sabrea adminii*; Slatin, *Stauroneis latistauros*. Ordination hulls are given to show the placement of samples by region, with Dry Valleys in orange, Cape Royds in blue, and McMurdo Station and the Stranded Moraines in red.

11, historical vs. modern), and both had high relative abundances of *C. laevissimus*, *S. adminii*, and *Chamaepinnularia cymatopleura* (Fig. 3). Green Lake was furthermore comparable in mean species richness between periods (6.7 and 5.7, historical vs. modern), and at both times dominated by *C. laevissimus*, with lower relative abundances of *Nitzschia shackletoni* and *S. adminii*. West and West (1911) also reported high numbers of *C. laevissimus* from these two ponds (as *Tropidoneis laevissimus*; Supporting Information Table S3) along with the pond on the west side of McMurdo Sound,

noting "this diatom was one of the most abundant species in the Antarctic collections, occurring in great quantity in several of the lakes, both freshwater and strongly saline." In line with our observations from both periods, West and West (1911) also found *C. cymatopleura* (as *Navicula cymatopleura*), *S. adminii* (as *Navicula perlepida*), and *N. shackletoni* to be abundant in Clear Lake (Supporting Information Table S3).

In the case of the third waterbody, Pony Lake, a fundamental shift in the dominant species, was observed. A century ago, Pony Lake was dominated by *L. muticopsis*. This taxon was

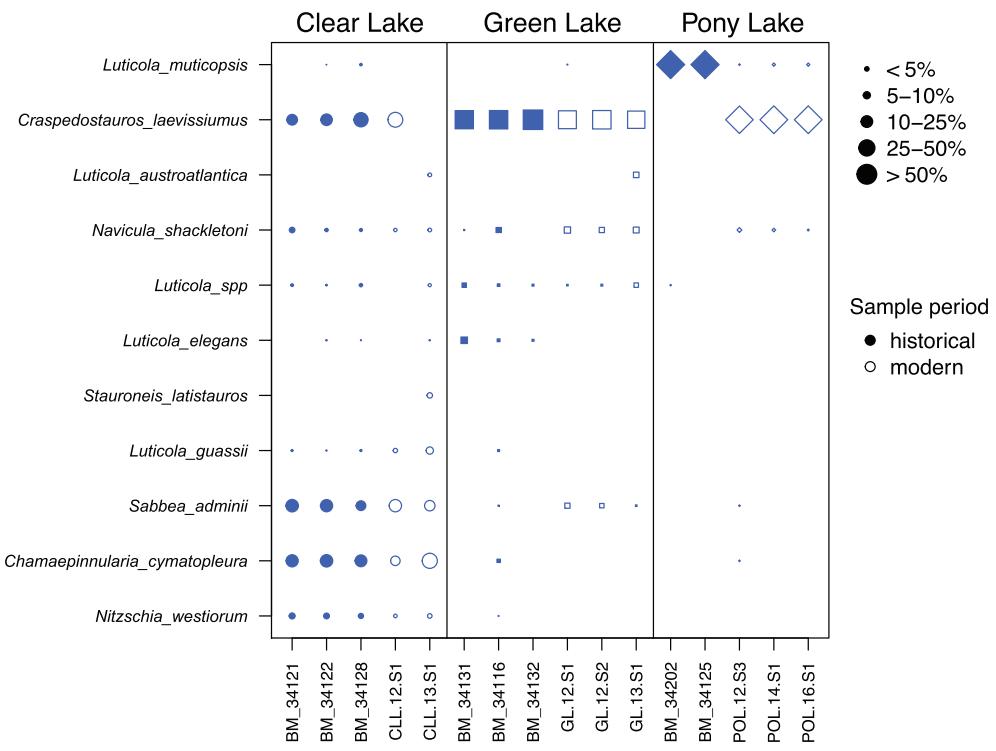


Fig. 3. Dot plot showing the relative abundances of diatom species (all with a relative abundance of at least 5%) from the three lakes with paired historical (filled symbols) and modern (empty symbols) samples. All replicates are shown with the exception of Pony Lake, where one sample is shown (at random) from each of January 2013, 2014, and 2016.

also reported here by West and West (1911), and “*Navicula muticopsis*” is even written on both Pony Lake slides (Supporting Information Fig. S1, Table S2). Today, Pony Lake is dominated (> 95%) by *C. laevissimus*, while *L. muticopsis* only represents ~ 1% of the relative abundance (Sakaeva et al. 2016). Species richness was also lower in historical Pony Lake slides due to the dominance of *L. muticopsis* (average 1.5 vs. 4.25). The morphologies of *L. muticopsis* and *C. laevissimus* are distinct, ruling out the possibility of mistaken identity (Fig. 4; Supporting Information Fig. S2). While we did not observe *C. laevissimus* in the historical Pony Lake slides (and none were mentioned by West and West), it was observed in other historical slides (e.g., Clear Lake and Green Lake), thus ruling out the possibility that this species is new to Cape Royds. After this initial analysis, we gained permission to resample Pony Lake inside the ASPA at its northern and southern margins on 04 January 2016 to confirm our observations and ensure differences were not related to patch heterogeneity (Supporting Information Table S1). Indeed, these samples were also dominated by *C. laevissimus* (> 95% in all four samples, mean richness = 3.75). Thus, the restructuring of the Pony Lake diatom community indicates that, at least here, change has taken place.

What happened at Pony Lake? A modern diatom mystery

Given our data set, it is challenging to definitively identify the cause of the community shift at Pony Lake. We

nonetheless offer three possibilities: First, the disproportionate human presence at Pony Lake compared with all other waterbodies on Cape Royds is too conspicuous to overlook. However, the mechanism by which it would influence the diatom communities is not obvious, especially because there was no introduction of an invasive species, and the dominant phytoplankton species in the pond remains unchanged (*Chlamydomonas intermedia*, McKnight et al. 1994). Furthermore, this site is protected as an ASPA requiring special permission for entry (although Shackleton's and his crew likely took few environmental precautions). More importantly, any potential anthropogenic nutrient impacts would have to compete with remobilization of nutrients from the flocculent sediments and the influence of the adjacent penguin rookery.

Second, the Cape Royds penguin colony is similarly impossible to ignore due to its proximity and number of individuals. West and West (1911) found *L. muticopsis* to be common in samples near the Cape Royds rookery, which is thought to have been around 1500 breeding pairs during Shackleton's expedition (Ainley 2002) and remained about this size until the 1980s, after which the population increased to a maximum of about 4000 (Wilson et al. 2001). While the population declined around 2001–2005 due to icebergs in McMurdo Sound preventing sea ice retreat, the population rebounded to ~ 3000 in 2012 (Lyver et al. 2014), approximately when our samples were collected. Therefore, a response to changing

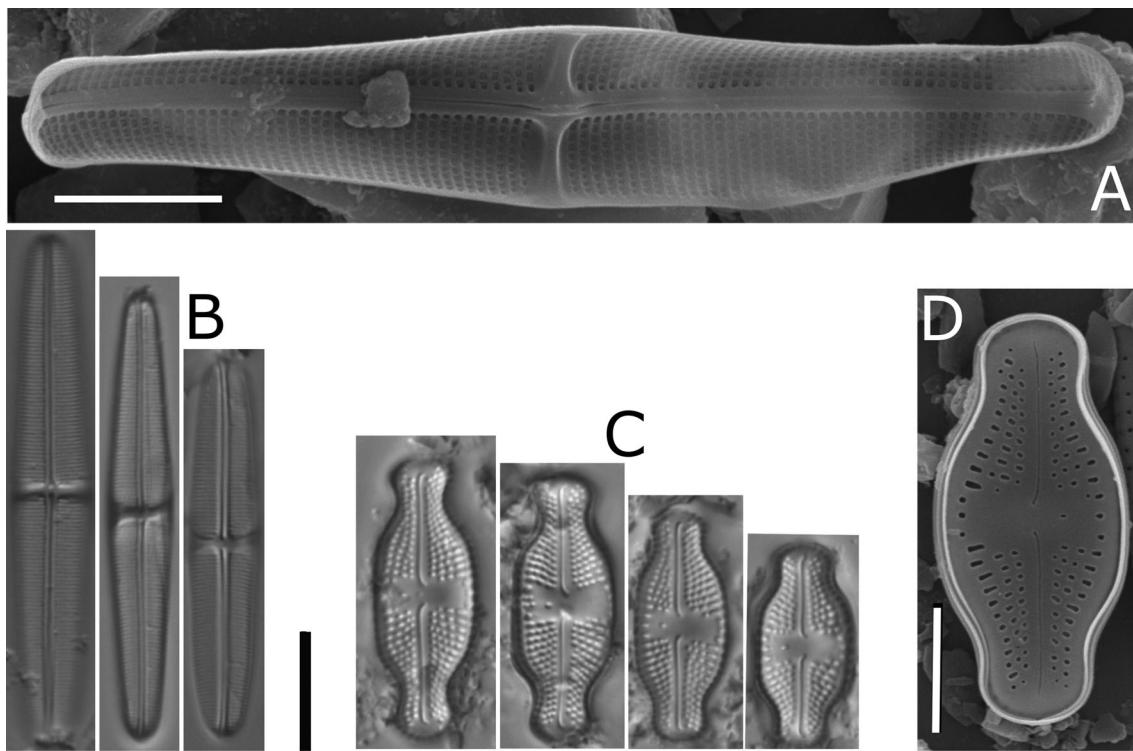


Fig. 4. *Craspedostauros laevissimus* (**A, B**) and *Luticola muticopsis* (**C, D**), the two dominate species in modern and historical Pony Lake samples, respectively. Light microscope (LM) images of the *C. laevissimus* population (**B**) were taken from modern Pony Lake, and LM images of the *L. muticopsis* population (**C**) were taken from modern Green Lake. Both SEM images (**A, D**) were taken from modern Green Lake. Scale bars for LM and SEM images are 10 μm and 5 μm , respectively. The modern morphological concept of *L. muticopsis* (from Van de Vijver and Mataloni 2008 and Levkov et al. 2013) is used here. The newly dominant taxon, *C. laevissimus*, was described as a new species, *Tropidoneis laevissima*, in West and West (1911), and was transferred to *Craspedostauros* by Sabbe et al. (2003). Both are brackish taxa endemic to Antarctica.

rookery size, or changes in the connectivity between rookery and pond, is possible. However, Pony Lake is already hypereutrophic, and contributions from the rookery are thought to be primarily from aerosols due to high rates of evaporation and the microbial signature of the dissolved organic matter (Brown et al. 2004; Dieser et al. 2013).

A third, and we argue most likely, possibility is a change in non-nutrient ions through concentration and dilution with varying snow and ice-cover. In the few surveys of Cape Royds conducted since West and West (1911), both Broady (1989) and Fukushima (1964, 1967) noted that *C. laevissimus* was found at higher salinities than *L. muticopsis*. Furthermore, Sakaeva et al. (2016) found *L. muticopsis* to dominate in nearby Cape Royds Pond 5, which had high nutrients like Pony Lake, but almost half the conductivity. As a result, Pond 5 may represent a remnant of the habitat type historically characteristic of Pony Lake. In contrast, the high-conductivity Green Lake is, and was, dominated by *C. laevissimus*. West and West (1911) stated that Pony Lake was “Never clear of ice except in small parts between 28 November 1908 and the end of January 1909.” The samples themselves were collected in January and April, and for the latter the samples were “obtained from under the ice” (communities were nonetheless

identical). In modern times, Pony Lake was ice-free in late January during the 1990s (McKnight et al. 1994; Brown et al. 2004), and while filled with snow and ice from about 2003–2012, it has recently had ice-free periods and lowered lake levels due to reductions in winter snowfall (D. Ainley pers. comm.). Because Pony Lake is primarily snowpack-fed (Dieser et al. 2013), we hypothesize that changes in local winter precipitation patterns may have led to the prominence of *C. laevissimus* through potential increases in conductivity.

Conclusions

Consistent with recent studies that have also made use of historical material to assess change in the McMurdo Sound Region (Jungblut and Hawes 2017; Jungblut et al. 2018; Velasco-Castrillón et al. 2018), our work suggests that the regional diatom metacommunity has remained essentially stable over the last century. Our inability to detect evidence of exotic or extirpated diatom species in one of Continental Antarctica’s most accessed areas is a bit of good news among myriad reports on ecological collapse and biological invasions. However, the dramatic shift at Pony Lake deserves further attention, and our results will aid in informing, revising, and

planning future ASMAs and ASPAs to ultimately protect microbial communities of the final terrestrial frontier.

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