· Review ·

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Limnology and ecology of lakes along the Sôya Coast, East Antarctica

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Abstract The Sôya Coast in East Antarctica has several ice-free areas where many small (<1 km^2) and shallow (<50 m depth) glacial lakes display various limnological features. Geological, biological, and ecological studies conducted by the Japanese Antarctic Research Expeditions since 1957 are reviewed herein. Most of the lakes along the coast are oligotrophic; however, water quality is highly variable depending on differences in lake morphology and history. Geophysical and paleolimnological studies suggest that most of the lakes appeared after the Last Glacial Maximum (LGM) and have since maintained a lacustrine condition. The ubiquitous occurrence of benthic microbial assemblages with low phytoplankton biomasses is a common feature of other Antarctic lakes. However, diverse benthic assemblages such as moss pillars and large pinnacle microbial structures are found in the lake basins. Frequent and continuous limnological studies have revealed three typical water circulation patterns, underwater light climate features (too much light, which includes UV radiation during the ice free season), and the structure of benthic assemblages based on their photosynthetic physiology. The phenomenon of mass floatation of benthic assemblages was observed in a lake during the ice-covered season; this was explained by seasonal environmental conditions. Thus, a hypothesis was formulated based on ecological matter cycling, eutrophication, and lake succession processes.

Keywords **glacial lakes, biological diversity, phytobenthos, polar ecosystem, photophysiology, circulation patterns**

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1 Introduction

Antarctica is an isolated continent. There are very few life supporting ice-free regions on the continent, so these regions are sometimes called polar oases within the polar desert. The ice-free areas are scattered along the coastal regions and around mountainous peaks (Nunataks) in continental Antarctica or concentrated on the Antarctic Peninsula in maritime Antarctica. They experience cold temperatures, the widespread effects of snow and ice, low annual inputs of solar radiation, and extreme seasonality in their light and temperature regimes. The biota is simple and lacks top predators. Primary producers such as cyanobacteria, algae, lichens, mosses, heterotrophic microorganisms, and metazoans dominate the sparse communities. The availability of liquid water is limited for most of the year, thus, active period of orgamisms is commonly very short in the polar oases. Although avian and mammalian fauna, such as penguins and seals, may symbolize Antarctica, they depend on food from the sea.

A remarkable diversity of lakes exists in Antarctica ranging from hypersaline with nearly 10 times the

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conductivity of seawater, to brackish, freshwater, sub-glacial, permanently ice-covered, and seasonally ice-covered[1]. Antarctic lakes provide a diverse range of aquatic habitats for biological communities, but often with a simplified food-web structure relative to temperate latitudes. The simplified complexity of these ecosystems, combined with their distinct physical and chemical features, has attracted scientists from many disciplines. Polar aquatic environments and their biota are proving excellent models for wider understanding in many fields including ecology, microbiology, paleoclimatology, astrobiology, and biogeochemistry, which has major implications for climate, colonization, and biodiversity.

Antarctic lakes are the most productive and diverse ecosystems in East Antarctica[1]. Most of these lakes were formed in ice-free areas during deglaciation after the Last Glacial Maximum (LGM)[2-3], and benthic phototrophs (cyanobacteria, algae, and aquatic mosses) developed as the major primary producers[4] and they generated the lacustrine ecosystem. There are many glacial lakes in ice-free areas of the Sôya Coast, in the vicinity of Syowa Station, and these areas have been subject to geological, limnological, and ecological studies by members of the Japanese Antarctic Research Expedition (JARE). Here, we review studies conducted by the JARE since 1957.

2 Limnological and morphometric variability of the Sôya Coast lakes

2.1 Location and general features

The Sôya Coast, with a shore line length of 138 km from Mukai-iwa (moraines, 69º03′S, 39º42′E) to Insteodden (a minor point, located at the eastern edge of Shirase Glacier, 69°59′S, 38°45′E), is a continental coast facing east of Lützow-Holm Bay (69°–70°S, 34°30′–40°E, Figure 1). There are several ice-free areas along the coast, which account for nearly half the total length of the coast line (68 km)[5]. Many lakes with basins created by glacial action and major islands in the bay, such as the East and West Ongul Islands, are found among these ice-free areas (Figure 2). The names, locations, and extent of the major ice-free areas and lakes are listed in Table 1.

Most of these lakes have shallow basins that were scraped by glacier movement or deepened by the weathering and erosive effects of ice freeze and thaw. They are fed by melt water from adjacent glaciers or snow and ice within their catchment basins (Figure 3). Some are marine relict lakes whose basins were in the shallow coastal sea; isostatic uplift of the present lake shores (sills) occurred after the retreat of the ice sheet when seawater was trapped within the basins. Thus, the former lakes are expected to have been freshwater and the latter saltwater; however, the salt content varies widely, even within both categories[6-10] . Some closed non-marine relict lakes with no apparent in/out flow streams display *athalassohaline* conditions (Akebi Ike, Langhovde; Figure 2b and Table 1). Whereas some marine relict lakes currently or historically fed by glacial melt water and those with a relatively large water catchment and supply of snow/ice melt water and an apparent out-flow stream in summer (open lakes) exhibit freshwater conditions (Oyako Ike, in Skarvsnes, Skallen Ôike in Skallen, and Maruwan Ôike in Rundvågshetta; Figures 2d, 2e, 2f, and Table 1). However, closed marine relict lakes with a narrow catchment basin exhibit hypersaline conditions (several times higher than marine salinity; Zakuro Ike and Itiziku Ike, Langhovde, Figure 2b, and Hunazoko Ike and Suribati Ike, Skarvsnes, Figure 2d).

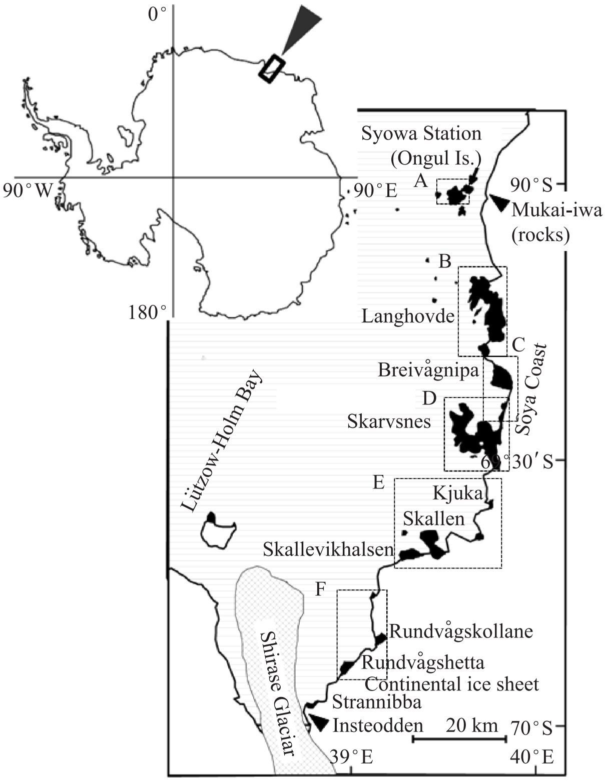

Figure 1 Study sites along the Sôya Coast, East Antarctica. Black areas represent ice-free areas. Areas enclosed by dotted lines (**a**-**f**) are shown in detail in Figure 2.

Salt content varies widely because of the precipitation of salt spray from the adjacent bay (wind-blown salt spray)[6], water supply/drainage and precipitation/evaporation balance[11-13], concentration process of trapped water under cold climate conditions[11], and classification of lakes by water quality and differences in the geological origin and morphometric features of their basins[9,14]. However, exact measurement of the water balance (in/out flow, precipitation/evaporation rates in their catchments, and residence time of lake water) in any of these lakes is yet to be conducted because of the technical difficulties associated with acquiring data in such remote and inhospitable locations.

Although salt concentration in the lakes in this area is highly variable, major nutrients required for phytoplankton

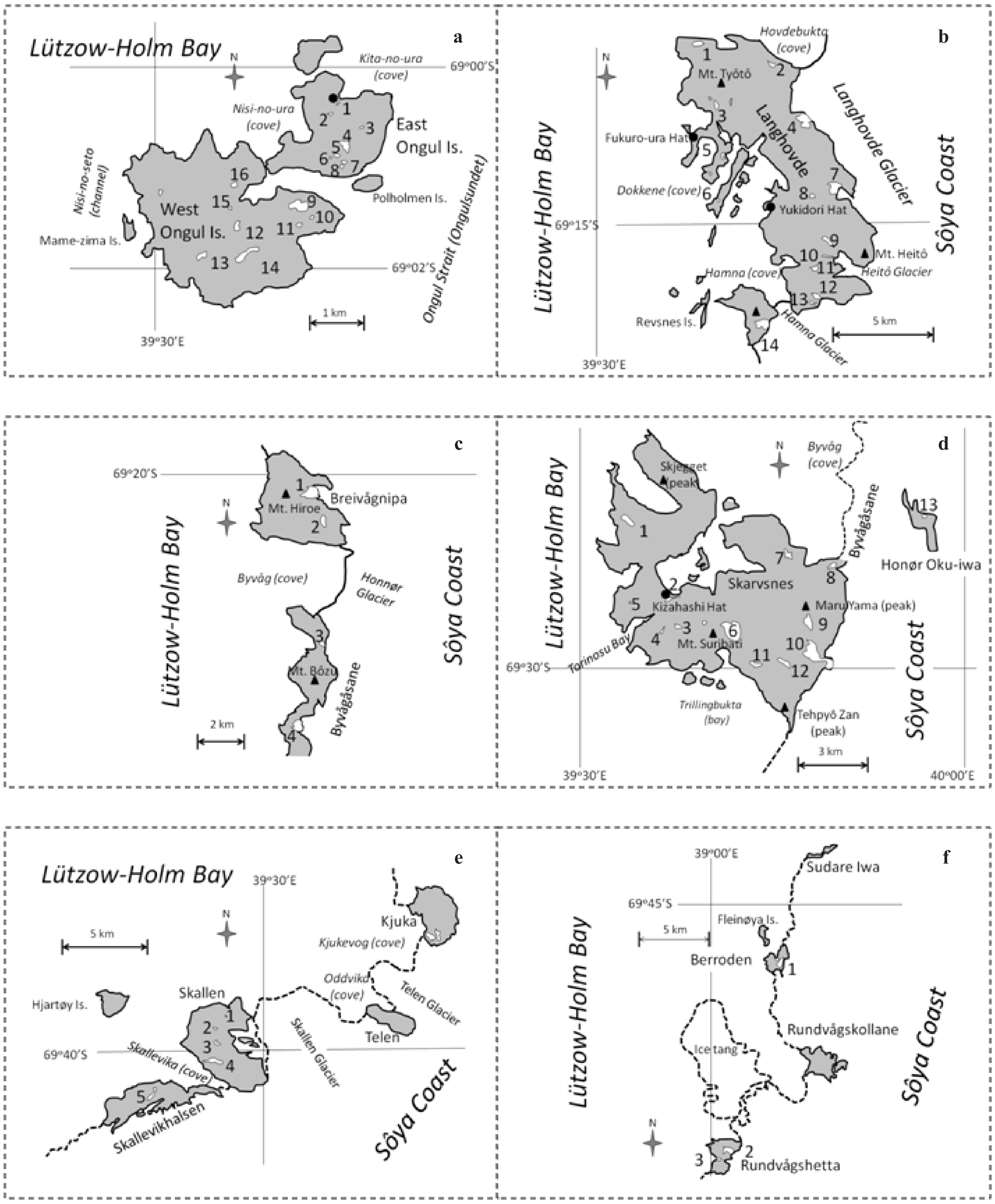

Figure 2 Location of major lakes in ice-free areas of the Sôya Coast. Gray areas in each map indicate ice-free areas and white closed areas within these indicate lakes. Numbers beside each lake in Maps **a**–**f** are explained in Table 1. **a**, East and West Ongul Islands; **b**, Langhovde; **c**, Breidvågnipa and Byvågåsane; **d**, Skarvsnes and Honnor Oku-iwa; **e**, Kjuka, Telen, Skallen and Skallevikhalsen; **f**, Sudare Iwa, Berroden, Rundvågskollne and Rundvågshetta.

Table 1 List of major ice-free areas (>3 km^2) and lakes along the Sôya Coast.

A lake water salt content of <5 ppt categorizes lakes as freshwater, 5–50 ppt as saline, and >50 ppt as hypersaline. Lake names with an * indicate the tentative name; Nd indicates that the value was not determined.

Map a: East Ongul Island (Higasi-Ongul Tô); 69°00′3″S, 39°35′30″E; area 3.4 km^2

Lakes	Position mark in Figure 2	Area/($\times10^4$ m^2)	Max. depth/m	Features
Aragane Dam*	a-1	0.5	4.0	Man-made reservoir
Daiichi Dam*	a-2	1.0	2.0	Man-made reservoir
Jagaimo Ike	a-3	0.2	0.5	Freshwater
Midori Ike	a-4	1.4	1.0	Freshwater
Kamome Ike	a-5	0.8	0.5	Freshwater
Ebosi Ike	a-6	0.1	0.5	Freshwater
Taratine Ike	a-7	0.6	0.5	Saline
Minami Ike	a-8	0.2	0.5	Freshwater

Map a: West Ongul Island (Nisi-Ongul Tô); 69°01′30″ S, 39º32′ E; area 8.0 km^2

Lakes	Position mark in Figure 2	Area/($\times 10^4$ m^2)	Max. depth/m	Features
Ô-ike	a-9	5.2	11.2	Freshwater
Higashi Ura Ike*	a-10	1.4	2.0	Freshwater
Ura Ike*	a-11	1.5	11.0	Freshwater
Yumi Ike*	a-12	2.6	5.6	Freshwater
Nisi Ike*	a-13	2.2	5.8	Freshwater
Nenjumo Ike*	a-14	5.0	Nd	Freshwater
Naka Ike*	a-15	1.4	4.5	Saline
Higashi Ike*	a-16	1.2	5.0	Freshwater

Map b: Langhovde; 69°10′30″–69º17′30″ S, 39°37′–39°49′ E; area 50.0 km^2

Lakes	Position mark in Figure 2	Area/($\times 10^4$ m^2)	Max. depth/m	Features
Zakuro Ike	b-1	6.9	4.6	Hypersaline, marine relict lake
Itiziku Ike	b-2	5.0	0.2	Hypersaline, marine relict lake
Akebi Ike	b-3	4.4	5.7	Saline
Nakanotani Ike*	b-4	27.1	17.5	Freshwater
Nurume Ike	b-5	3.5	16.5	Sarine, marine relict lake
Oyayubi Ike	b-6	2.5	5.2	Sarine, marine relict lake
Higasi-yukidori Ike	b-7	14.5	32.0	Freshwater
Yukidori Ike	b-8	4.1	8.0	Freshwater
Heito Ike	b-9	3.1	4.5	Freshwater, ice-dammed lake
Ten-no Ike	b-10	3.4	5.0	Freshwater
Kami-kama	b-11	4.4	3.5	Freshwater
Higasi Hamna Ike	b-12	12.3	22.7	Freshwater
Goku Ike	b-13	3.1	3.0	Freshwater
Nisi Hamna Ike	b-14	20.6	16.0	Freshwater

Map c: Breivågnipa; 69°20′–69°31′ S, 39°30′–39°45′ E; area 61.1 km^2(includes lakes in Byvågåsane)

Lakes	Position mark in Figure 2	Area/($\times 10^4$ m^2)	Max. depth/m	Features
Hiroe Ike	c-1	26.8	9.5	Freshwater
Burai Ike*	c-2	1.2	Nd	Freshwater
Tankobu Ike*	c-3	4.6	13.5	Freshwater, perennial ice cap
Bozu Ike*	c-4	11.0	18.5	Freshwater, perennial ice cap

Map d: Skarvsnes; 69°25′–69°17′30″ S, 39º37′–39º49′ E; area 50.0 km^2 (includes a lake in Honnor Oku-iwa)

Lakes	Position mark in Figure 2	Area/($\times 10^4$ m^2)	Max. depth/m	Features
Hunazoko Ike	d-1	14.4	9.2	Hypersaline, marine relict lake
Oyako Ike	d-2	6.5	8.0	Freshwater, marine relict lake
Hyotan Ike	d-3	5.3	12.4	Freshwater
Naga Ike	d-4	4.8	10.8	Freshwater
Hotoke Ike	d-5	0.6	3.0	Freshwater
Suribati Ike	d-6	51.5	32.0	Hypersaline, marine relict lake
Hama Ike*	d-7	8.2	1.5	Freshwater
Tsubaki Ike	d-8	14.0	15.0	Freshwater
Maruyama Ike	d-9	19.0	7.0	Freshwater
Kamino Ike	d-10	62.0	11.2	Freshwater
Namazu Ike	d-11	9.1	20.8	Freshwater
Dojo Ike*	d-12	11.1	2.0	Freshwater

Maps e and f: Skallen (14.4 km^2), Skallevikhalsen (7.6 km^2), and Rundvågshetta (2.5 km^2) (includes a lake in Berrodden).

Lakes	Position mark in Figure 2	Area/(×10^4 m^2)	Max. depth/m	Features
Daikei Ike*	e-1	0.9	6.5	Freshwater
Naka Ike*	e-2	1.8	8.3	Freshwater
Kita Ike*	e-3	3.2	2.7	Freshwater
Skallen Ôike	e-4	20.9	9.2	Freshwater, marine relict lake
Dairi Ike	e-5	13.7	0.8	Freshwater
Berroden Oike	f-1	6.0	Nd	Freshwater
Maruwan Oike	f-2	25.2	37.0	Freshwater, marine relict lake
Maruwan Minami Ike	f-3	2.0	Nd	Freshwater, marine relict lake

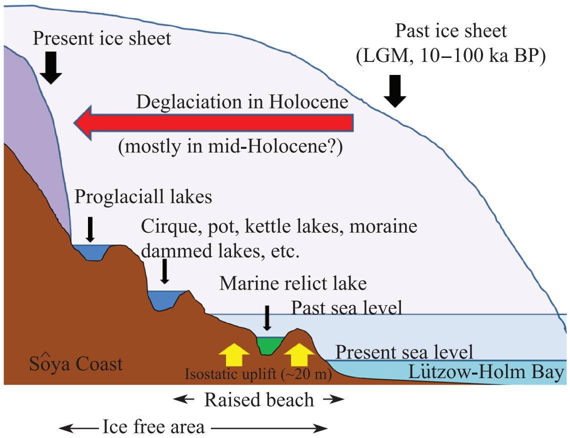

Figure 3 A schematic explanation of the origin of lakes along the Sôya Coast. An ice sheet extended over the entire area of the Sôya Coast during the LGM and present ice-free areas were fully covered by ice. After the LGM, the ice sheet diminished (deglaciation) and ice-free areas appeared. Many lake basins were created by glacial action. Lakes fed by snow and ice melt water appeared. Isostatic up-lifts trapped shallow seas and created several marine relict lakes near the coast.

growth, such as nitrate and phosphate, are quite low in most of the lakes along the coast, which are oligotrophic[8,15-17]. However, this is not the case in the hypolimnion of some saline marine relict lakes[14,18].

2.2 Geological history

The majority of marine relict lakes on this coast are located at <20 m altitude above present sea level. Fossils of marine organisms (e.g., bivalves, calcite nest-forming tube worms, and calcareous algae) are found in and around these lakes and raised beaches along the coast line. The age of these fossils has been estimated using the ^{14}C dating method and they have been categorized into two groups: 3–7 cal ka BP and 30–45 ka BP[19-21]. Most of the fossil samples collected from these areas belong to the former group (except for samples from the Ongul Islands and northern area of Langhovde in which both categories are found). This suggests that these lake basins were at the sea bed level at least 7 000 years ago and uplift of the coast or lowering of sea level has occurred at an average rate of a few mm per year since then. The presence of fossils from the Ongul Islands and northern area of Langhovde in the older category may indicate the absence of glacial coverage, movement, and erosion after 30–45 ka BP[21-22]. In addition, the absence of older fossils around marine relict lakes and raised beaches on the southern Sôya Coast could be attributed to the existence of an ice sheet or suggest the occurrence of deglaciation by 7 ka BP. Maemoku et al. suggested that the ice sheet overrode the southern part of Lützow-Holm Bay (nearly equal to the area of Sôya Coast) during the LGM and concluded that the evident deglaciation and isostatic uplift may have occurred both in the early and the mid-Holocene in the northern areas of the Sôya Coast, including the Ongul Islands[23]. However, based on radiocarbon analysis of fossils and modeling studies, full deglaciation in the present ice-free areas along the southern Sôya Coast occurred after the mid-Holocene[22,24-25].

Analysis of lake sediment cores from marine relict lakes of the southern Sôya Coast region have also indicated the existence of a clear transition from a marine to a lacustrine environment and dated the marine setting to ~1 000 cal a BP in Oyako Ike, Skarvsnes[26] and 2 900–3 500 cal a BP in Skallen Ôike and Maruwan Ôike on the southern Sôya Coast[26-29]. This analysis supports the hypothesis above that deglaciation and isostatic uplift events along the southern Sôya Coast occurred during or after the mid-Holocene Hypsithermal event, and indicates that the relict lakes became lacustrine environments after this event. Considering the above scenarios, most of the present lakes, including non-marine relict lakes, along the southern Sôya Coast may be a few thousand years old; however, this still requires paleolimnological confirmation.

2.3 Areal features: Lakes in the Ongul Islands

On East Ongul Island, where Syowa Station is located, there are several small and very shallow lakes that are occasionally dry. The lake floors are visible during periods of reduced snow accumulation and warm-dry summers, except for two dammed reservoirs (Aragane and Daiichi Dams, Figure 2a). All of the lakes, including the two reservoirs, store the snow melt water from their catchments. Because all of the lakes are shallow, except for Aragane Dam, they are entirely frozen during winter. During summer, lake water is slightly salty owing to wind-blown salt spray and evaporation[6-7,30]. However, there are also some relatively deep lakes (maximum depth of >2 m) on West Ongul Island. The thickness of the annual ice cap of freshwater lakes along the Sôya Coast never exceeds 2 m under current climate conditions; lakes deeper than 2 m can store liquid water below their annual ice cap even in winter.

2.4 Lakes in Langhovde

Several marine relict saline lakes and an *athalassohaline* lake (Akebi Ike) are found in the northern region of Langhovde (Figure 2b). Some of these marine relict lakes exhibit hypersaline conditions (Zakuro Ike and Itiziku Ike) and others have a similar salinity to the adjacent sea (Nurume Ike and Oyayubi Ike). Nurume Ike is a meromictic saline lake with a hypolimnion below ~10 m depth[18,31-32]. All life cycle stages of a benthic copepod (*Harpacticus furcatus* Lang.), which is likely distributed in the adjacent shallow sea, has been found to occur at a relatively high population density on the oxic lake sediment surface at 2–9 m depth[33]. In central and southern Langhovde, there are many cirques, pots, kettle lakes, and proglacial lakes (created in front of existing glaciers) with diverse conditions ranging from freshwater to slightly saline. Waters in proglacial lakes exhibit ultra-oligotrophic freshwater conditions. However, they contain silt derived from glacial deposits, have turbid water, and transparency is quite low. Lakes directly attached to glaciers tend to have perennial ice caps, which can exceed 3 m thickness in winter. An ice-dammed lake named Heito Ike (previously informally called Hyoga Ike) is located in central Langhovde, and the lake water is flushed out periodically by breaching of the perennial ice bank[34-35].

2.5 Lakes in southern ice-free areas

In southern ice-free areas, several marine relict lakes are located on the coastal side (e.g. Hunazoko Ike, Suribati Ike, and Oyako Ike, Skarvsnes, Figure 2d; Skallen Ôike, Skallen, Figure 2e; and Maruwan Oike, Rundvågshetta, Figure 2f). Many semi-closed lakes that occasionally overflow during heavy snow and warm summer years along U-shaped valleys (e.g. Naga Ike and Maruyama Ike, Skarvsnes), small cirques, pots, and kettle lakes are also located on the mountainous side. There are also proglacial lakes directly fed by glacial melt water (e.g. Hiroe Ike in Breidvågnipa, Tsubaki Ike, and Kamino Ike, Skarvsnes, Figures 2c, 2d). Many of the precise limnological features of lakes in these areas have been reported elsewhere[36-43] and are explained in detail in the following sections.

3 Biological and ecological studies

3.1 Floristic studies

Taxonomic studies of benthic samples collected from the shores of Sôya Coast lakes were conducted in the early stages of the biological survey by the JARE. They revealed the predominance of cyanobacterial benthic (epipelic) communities, e.g. the genera *Synechococcus*, *Dichothrix*, *Nostoc*, *Oscillatoria*, *Phormidium*, and *Nodularia*[44-46]. These cyanobacterial communities are common in Antarctic aquatic ecosystems and communities forming mat-like structures (termed microbial mats, mat assemblages, or simply cyanobacterial mats) at lakebed surfaces, where the physical environment is more stable, are well known. At the surface, nutrient supply is enhanced by sedimentation of nitrogen- and phosphorus-containing particles from above and degradation of organic matters from below[47-50]. Among these mat assemblages, subdominant communities comprising diatoms and some species of green algae (desmids and filamentous algae) have been recorded[44,46,51-52]. In addition to the similarity of the dominant communities to those of other lakes in East Antarctica, the mat assemblages were composed predominantly of green filamentous algae, *Oedogonium* sp.[46] and two species of moss, *Bryum pseudotriquetrum* and *Leptobryum* sp.[53-54]. These living and dead cyanobacteria, algae, and moss constitute the main biomass of thick (they can exceed 1 m) organic sediments in most lakes deeper than 2 m[26,28,37].

Isolation of cyanobacteria, green algae, and diatoms has revealed some precise morphological and taxonomic features[55-56]. Diatom assemblages tend to reflect the environmental factors that differentiate their distributions in Antarctic lakes[57], then the relationship between the limnological environment and diatom species composition in mat assemblages in several lakes has been studied[52,58]. Diatom flora is significantly affected by salinity or electric conductivity differences in lake water[59]. Green filamentous algae, *Ulothrix* spp., sometimes bloom in streams around lakes in summer[44]. Macroscopic colonies of *Prasiola crispa* (green algae) and *Nostoc commune* (cyanobacteria) are found on wet land and in some valleys, and snow algae (e.g., Volvocalean green algae) are visible on the snow remaining near birds' nests and rookeries in summer[60]. Many detailed floristic and distributional features have been summarized in a Japanese booklet published by the National Institute of Polar Research (NIPR)[61].

Similar to the oligotrophic lakes in East Antarctica, the proliferation of benthic assemblages is widely recognized; the biomass and photosynthetic production of phytoplankton in the water columns of these freshwater lakes are quite low, particularly in summer[62]. Time-course sampling or continuous recording of the changes in chlorophyll concentration in the water column throughout the year clearly indicate a bimodal increase in concentration in autumn (around April) and spring (around September) under ice cover and a decrease during winter and summer (polar night and midnight sun seasons)[36,63-64]. Tominaga experimentally demonstrated light inhibition of summer phytoplankton collected from a saline lake[62]. Tanabe et al. revealed a strong inverse correlation between underwater light intensity and chlorophyll concentration in the water column of a freshwater lake[36]. Both authors suggested photo-inhibition or photo-damage of phytoplankton communities under strong light conditions; similar phenomena have been suggested in other studies of shallow Antarctic lakes[65-67]. Because oligotrophic water contains low levels of photon-absorbing materials[48,68], the water is optically transparent. This is particularly true during the ice-free summer period, when underwater light intensity (light penetrating the water column) is higher and wind-induced vertical mixing combined with heat convection frequently carries suspended particles, such as phytoplankton, to the lake surface. Therefore, phytoplankton is likely frequently exposed to strong solar radiation, including UV.

Poor development of phytoplankton communities is a widely observed phenomenon in most lakes along the Sôya Coast. However, there are some exceptional cases of phytoplankton subsurface blooms reported at the boundary of the meta- and hypolimnion in meromictic lakes (oxic/anoxic boundary) or beneath the seasonal halocline of certain hypersaline lakes where sufficient macro-nutrients, such as phosphate and ammonium, are available[14,18]. These subsurface blooms are composed mainly of a flagellate, *Dunaliella* sp., and probably a green sulfur bacterium, *Chlorobium* sp., which have been reported in Hunazoko Ike, Suribati Ike, Skarvsnes and Nurume Ike, Langhovde[18].

It is well documented that benthic assemblages, depending on habitat depth or water quality differences, sometimes exhibit a wide variability of macroscopic life forms, such as epilithic, epiperic, flaky, laminated, lift-off, pinnacle, and prostrate[50,60-72]. Such diverse life forms have also been found among benthic assemblages in lakes along the Sôya Coast (Figure 4)[38]. Moreover, quite unique columnar or pillar-like structures have been discovered in lakes in the Skarvsnes area[73]. These structures sometimes stand more than 50 cm high above the mat assemblages, creating an underwater forest-like scene in several lakes[39,74]. The primary components of these structures are an aquatic moss, *Leptobryum* sp., and similar assemblages of mat-forming microbes such as cyanobacteria, green algae, and diatoms[74]. Another aquatic moss, *Bryum pseudotriquetrum*, previously reported as a member of phytobenthic assemblages in these lakes, is sometimes found in these structures. They are named moss pillars based on their structural features, and moss-microbial assemblages have been widely recognized in many freshwater and slightly saline lakes (athalassohaline lakes) along the Sôya Coast[10,75-76]. The distribution of aquatic mosses from lakes in Antarctica has been reported by several authors[10,77]; however, the pillar-like structures with microbial assemblages have not been reported in other Antarctic oasis lakes. The distribution of *Leptobryum* sp., the primary component of these moss pillars, has been reported in some lakes in the Schirmacher Oasis, near Indian Maitri Station[78], but whether or not similar structures are present on the lake bottom remains unknown.

The discovery of moss pillars has accelerated limnological and ecological studies of the lakes along the Sôya Coast. The focus has been on precise environmental features with continuous or comparative measurements of water quality and vertical structure[14,36,41,76,79-80] and paleolimnological studies using lake sediment cores[26-29]. Ecophysiological studies of the moss pillars[74,81] and mat assemblages[37-38,42], microbial studies using isolated fungi and yeasts from the lakes[82-84], and biodiversity studies of the lake ecosystems using a genomic approaches[85-88] have also been carried out. Continuous records of limnological parameters of typical lakes using mooring arrays are also published annually in the JARE data report Terrestrial Biology by NIPR[39-40,43,89]. Based on this research, some typical ecological features are explained below.

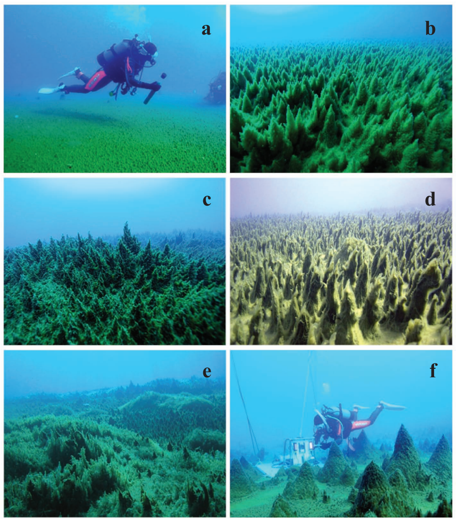

Figure 4 Visual diversity of benthic assemblages observed along the Sôya Coast lakes. **a**, mat-like assemblage distributed in the deepest part of Naga Ike (`10 m); **b**, soft, small (height: ~15 cm) pinnacle assemblages at 7 m depth in Naga Ike; **c**, small pinnacle (height: ~15 cm) assemblages at 5–8 m depth in Namazu Ike; **d**, soft, long (height: ~30 cm) assemblages at 10–15 m depth in Namazu Ike; **e**, grassy plain-like benthic community observed at 3–5 m depth in Namazu Ike, and **f**, moss pillars emerging from mat assemblage at 3–5 m depth in Naga Ike.

4 Limnological and ecological features

4.1 Physical environments surrounding the lake ecosystem

Circulation (vertical mixing) patterns and underwater light irradiance are essential physical parameters controlling lake ecosystems. The former strongly affects the vertical structure of lake chemistry (pH, ions, nutrients, and dissolved oxygen) and suspended matter (planktonic organisms and lithogenic particles), while the latter is an important energy source for biological (photosynthetic) production[48].

In lakes at high latitude, such as the High Arctic and Antarctica that briefly lose their annual ice cover in summer, water column circulation is induced by heat convection and wind-induced mixing during the ice-free period; whereas inverse stratification persists during ice-covered seasons. Circulation appears to only occur once a year in these lakes called cold monomictic lakes[90]. Most of the shallow freshwater lakes on the Sôya Coast belong to this category but circulation patterns are variable, even in lakes that lose their ice cap annually.

Figure 5 illustrates the vertical water temperature profiles of three different lakes during summer and winter. Vertically homogenous temperatures in summer and inverse stratification in winter is commonly observed in most freshwater lakes (Figure 5a). The vertically homogeneous temperature indicates that these freshwater lakes are holomictic in summer, which is a typical pattern of cold monomictic lakes (summer-holomictic type). Depending on the morphometric features or heat capacity of lakes, such as the difference in mean depth/surface area ratio, temperatures observed in summer exhibit quite large variation[14,37]; shallower lakes tend to be much warmer than deeper lakes. Continuous records of water temperature in such freshwater lakes clearly indicate that vertical mixing starts under ice-cover in spring (Figure 6)[36]. Seasonally increased solar radiation penetrates through the ice cover and heats the water nearly 2 months before ice-off. Surface water beneath the ice cover increases in density until water temperatures warm to ~4°C, at which point the warmed water at the surface starts to sink to the bottom. This inverse stratification is subsequently destroyed by heat convection in spring (October–November) and may accelerate ice thawing from beneath the ice cover. After the disappearance of the ice cap water temperature tends to decrease because of the acceleration of heat loss from the lake surface to the atmosphere with the aid of wind action. Wind-induced mixing occurs frequently in summer; however, short-term thermal stratification is observed on prolonged sunny, calm days.

The second circulation pattern is also categorized as holomictic and monomictic; however, circulation occurs during the ice-covered winter (winter-holomictic type, Figure 5b). This pattern is observed in hypersaline shallow lakes, e.g. Zakuro Ike, Langhovde and Hunazoko Ike, Skarvsnes. Because saline water is much denser in colder conditions, seasonally cooled surface saline water starts to sink and enhances vertical mixing creating a homogeneous thermal profile during winter. This is similar to the vertical mixing mechanism observed in high-latitude seas in cold seasons. Moreover, cold and dense brine rejection during ice cap formation may aid this vertical mixing and destroy the seasonal halocline observed between the epi- and hypolimnion in summer. The freezing point of saline water varies depending on salt content and is much lower than that of freshwater; therefore, water in such lakes reaches sub-zero temperatures in winter under ice cover[12], e.g. −15°C in Zakuro Ike and −18°C in Hunazoko Ike (September 2004, unpublished data). Similarly, extreme cold water temperatures were reported in Deep Lake in the Vestfold Hills in Antarctica, a hypersaline lake[91]. This lake has quite a high salinity of 270 PSU (seawater is ~35 PSU) and the water remains liquid and ice-free throughout the year. In summer, both melt water from the ice cap and influx from the catchment, which should be relatively light owing to a higher temperature and lower salt content, overlay the cold, hypersaline lake water and stop vertical holomictic circulation. These lighter waters create a seasonally stable epilimnion on the hypersaline water. A well-developed halocline was observed at ~2 m in Hunazoko Ike, and temperatures in subsurface waters exceeding 20°C were recorded in summer. This is despite water temperatures of

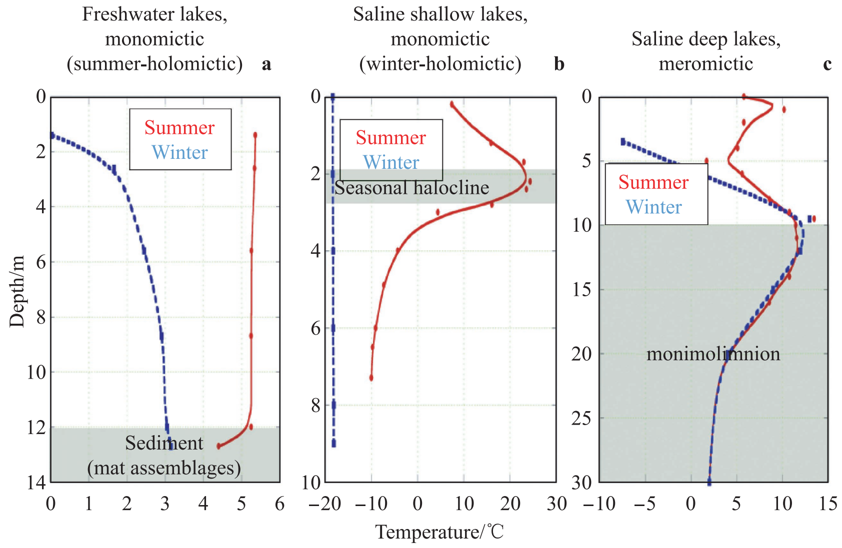

Figure 5 Three examples of vertical water temperature profiles measured in January (summer) and September (winter) indicate differences in seasonal circulation patterns. **a**, summer holomictic pattern (vertical mixing occurs in summer); most freshwater lakes with ice caps that thaw in summer have similar seasonal profiles; **b**, winter holomictic pattern (vertical mixing occurs in winter); observed in shallow hypersaline lakes; **c**, meromictic pattern observed in some saline lakes deeper than 10 m. Data were obtained by during the 45th JARE period (2003–2005) from Namazu Ike (**a**), Hunazoko Ike (**b**) and Suribati Ike (**c**).

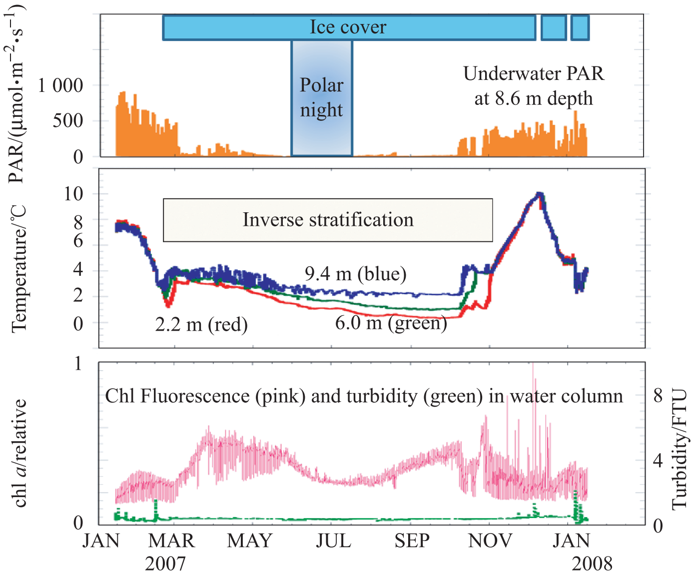

Figure 6 An example of the long-term lake environmental monitoring studies in Naga Ike, during the 48th JARE period. Design and settings of the mooring array are explained in Kudoh et al.[39-40]. During this observation period, the lake had an annual ice cap from the beginning of March to the end of December. Light reaching near the lake bottom during the ice-covered period showed both a wide seasonal decrease/increase and irregular fluctuations caused by snow on the ice. Inverse stratification, judged by water temperature at three discrete depths, started with ice-coverage in March and ended approximately 2 months before the ice cap disappeared. Chlorophyll fluorescence in the water column exhibited a bimodal seasonal increase in autumn and spring. However, the fluorescence signal diminished with a sudden increase in underwater PAR, particularly in spring. Turbidity in the water was higher in summer (December–February), probably because of an influx of silty melt water from the surrounding catchment basin.

approximately −10°C being recorded near the lake bottom (seasonal hypolimnion).

The third circulation pattern shown in Figure 5c is observed in some saline lakes deeper than 10 m with a meromictic circulation pattern. The perennially stable hypolimnion (monimolimnion) remains below 10 m and seasonal vertical mixing appears to occur within the surface epilimnion. Examples of lakes belonging to this category include the hypersaline lake Suribati Ike, Skarvsnes and the saline lake Nurume Ike, Langhovde. A distinct halocline exists that appears to prevent mixing between the two layers[14,33]. Anoxic conditions with large concentrations of macro-nutrients such as ammonium and phosphate are observed in the monimolimnion and hydrogen sulfide (H_2S) concentrations in the boundary layer are relatively high[14]. In Suribati Ike, the temperature in the epilimnion fluctuates seasonally from -7°C to 10°C, whereas temperatures at the anoxic/oxic boundary are rather mild throughout the year (~10°C). A dense phytoplankton bloom including photosynthetic bacteria (green sulfur bacteria) was observed in the boundary layer[14,18], as was a dimethyl sulfoxide respiring bacteria, which may play a role in sulfur cycling[85,92]. A similar meromictic system is widely recognized among other Antarctic oasis hypersaline lakes[48,93] and provides a unique habitable space for organisms within the vertical water column.

We have no data from perennially ice capped proglacial lakes; therefore, whether or not they are of an amictic nature or if similar holomictic heat convection occurs during summer, as observed in annual ice-covered freshwater lakes, remains unknown.

The amount of light energy penetrating the water column and reaching lake bottoms is highly dependent on incident solar radiation, the attenuating effect of overlying snow and ice cover, and the nature of spectral transmission by the absorption and scattering of photons within the water column (Figure 7)[94-95]. Incident solar radiation in polar areas exhibits clear seasonality from continuous darkness in winter to continuous sunlight in summer, which should affect the annual photosynthetic production pattern[96-97]. On the Sôya Coast, the period of winter darkness (polar night), with no sun rise, lasts for nearly a month; however, a few µmol photons per square meter per second of photosynthetically active radiation (PAR) can reach a shallow lake bottom around noon during this period[76]. Thus, the winter darkness period in this area is a time of very weak radiation rather than a total absence of light. This weak radiation may still be insufficient for photosynthetic production. Continuous records of underwater light intensity at several lakes show an annual or lake-specific difference in the length of this weak winter light period, despite the fact that the lakes experience very similar seasonal changes in incident solar radiation. Underwater radiation during ice-covered seasons appears to be greatly affected by factors other than incident solar radiation, with several irregular peaks and dips during ice-covered seasons (Figure 6). These irregular fluctuations are attributed to the sudden coverage/disappearance of snow, which has a high albedo (reflection of sunlight) that can exceed 90%; snow coverage can reduce or eliminate the amount of sunlight reaching the ice surface by a factor of more than 10[94].

Once ice-off occurs in summer the amount of solar spectral radiation reaching the lake bottom is dictated largely by reflection at the water surface, absorption (colored or chromophoric dissolved organic matter, CDOM), scattering materials (mostly silts) in the water column, and depth. Measurement of spectral irradiance on the lake and just beneath the water surface gives a reflective property and the spectral irradiance measured at two discrete depths gives the diffuse vertical extinction property of the lake water (Figure 8). The relative ratio of reflection in calm conditions around noon is ~20% of the incident irradiance independent of wavelength difference. However, various vertical extinction properties (hereafter, *K*) among lakes have been detected. These range from that of pure water to UV-screened water owing to absorption of UV by CDOM, or in less transparent water the scattering of light by silt suspension (Figure 9)[37]. Differences in *K* and water depth result in a wide variation in light spectrum energy among lake bottoms, even under the same incident solar radiation and surface reflection; thus, benthic organisms living in different lakes or distributed at different depths within a lake may respond and grow under a diverse light spectrum.

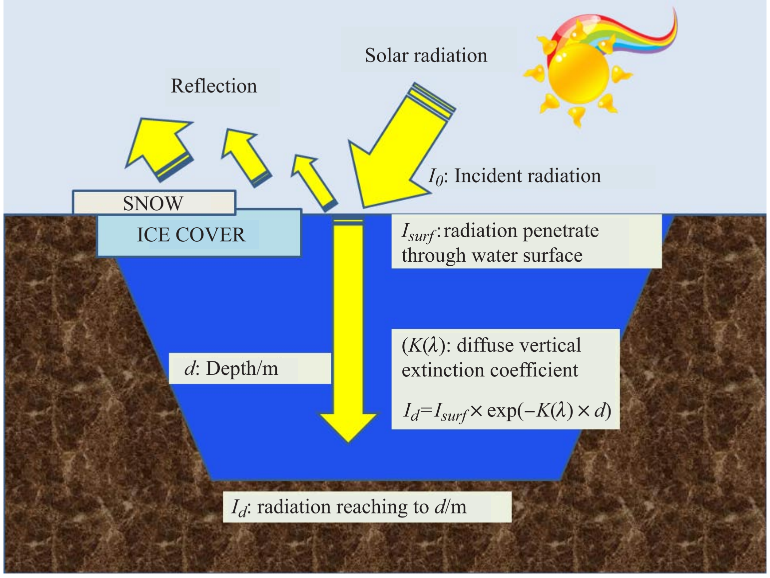

Figure 7 Schematic explanation of the light environment in a lake. Solar radiation reaching the lake surface (I_0) is partially reflected at the surface (reflection) and the remaining radiation penetrates the water column (I_{surf}). Radiation (I_d) reaching a given depth (d/m) is expressed using the Lambert–Beer equation: $I_d = I_{surf} \times \exp(-K(\lambda)\,(dm)i)$, where *K* is the diffuse vertical extinction coefficient.

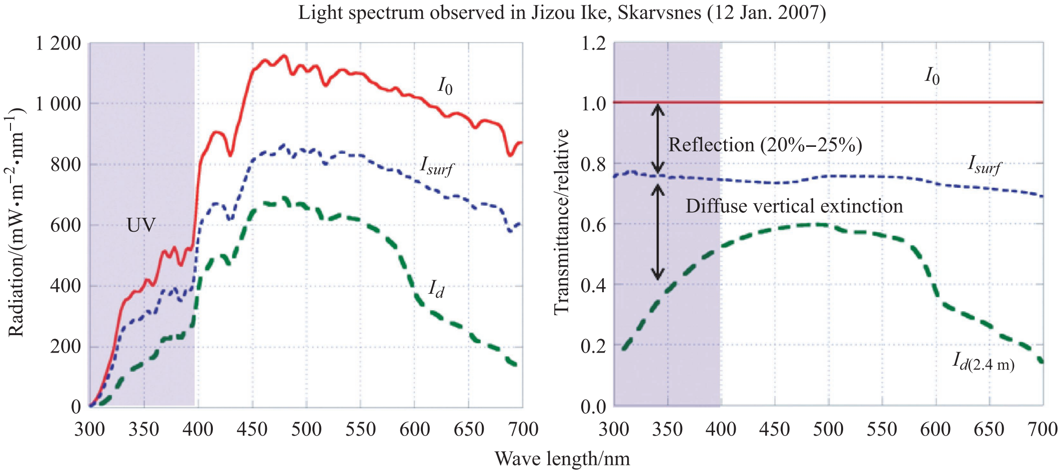

Figure 8 Spectral radiation intensity measured at the lake surface (I_0), beneath the surface (I_{surf}), and near the lake bottom (I_d, d = 2.4 m) in Jizou Ike on 12 January2007. Reflection at the lake surface appears to be ~20% independent of light wave length. Light spectrum energy of shorter (UV-band) and longer visible wave lengths show lower levels of transmittance in the water column than the blue-green light band (right panel). Similar results and more precise methods are reported in Tanabe et al.[37].

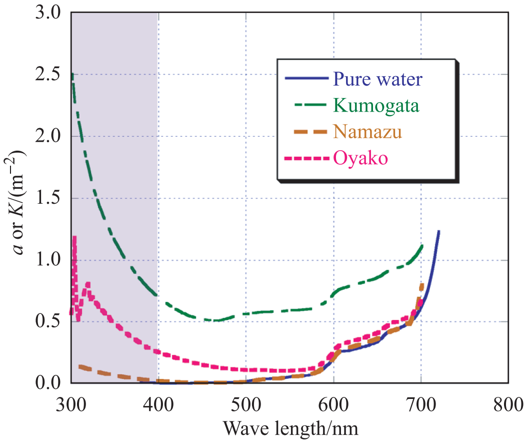

Figure 9 Diffuse vertical extinction coefficient (K) measured in Kumogata Ike, Namazu Ike, and Oyako Ike in Skarvsness (January, 2007), and an example of the absorption coefficient of pure water (a, data from reference [102]). K is highly variable among lakes, ranging from nearly the same absorption property of pure water (Namazu Ike), a high extinction of the UV-band (Oyako Ike), to rather high extinction at all wave lengths, probably owing to silt suspension in the water (Kumogata Ike).

4.2 Biological responses

Collection and analysis of mat assemblages from several lakes along the Sôya Coast have indicated that the top surface of these assemblages are usually heavily pigmented with carotenoids, UV-screening scytonemin, and mycosporine-like amino acids (MAAs)[37]. As mentioned in the previous section, underwater light intensity and spectrum composition at the benthic surface of each lake varies widely depending on differences in depth and K. A general tendency of a positive correlation between the photo-protective pigments, including substances such as MAAs, on the surface of the assemblages and incident radiation has been reported (Figure 10). Samples of structurally different mat assemblages (firm and loose) collected and immediately vertically sliced were different in their photo transmittance capacity and photochemical reactions; this suggests that mat assemblages can photosynthesize by modifying a light-protection/utilization balance in each habitat[37].

In situ measurement of mat assemblage and aquatic moss photochemical activity was performed on SCUBA, revealing depth-related distributional differences among the dominant assemblages; mosses were more active in shallower water, but microbial mat assemblage activity was comparatively higher at depth. Moss pillars, which are complex assemblages of aquatic mosses and microbial assemblages, are thought to be well developed at intermediate depths (Figure 11)[38].

4.3 An explanation of the lift-off and floating phenomenon

Phytobenthic assemblages sometimes fragment, lift-off, and are often found floating on Antarctic lake surfaces in summer[98-101]. In Lake Skallen Ôike, considerable portions of these assemblages drift to the lake shores every year and are blown over the surrounding landscape by strong winds[42]. There has been speculation on the possible mechanisms responsible for floatation and the ecological implications based on comparative data from floating and benthic assemblages collected during summer open water periods. However, more substantial evidence is required to identify the mechanisms, particularly in the case of floatation under ice. Repeated limnological observations by the overwintering team of the 51st JARE (2009–2011) during seasons of ice cover revealed massive phytobenthic assemblages floating under lake ice cover in mid-October 2010, when the frozen surface layer maintained a stable thickness.

The first observations in Skallen Ôike were performed between 11–13 October 2010; the lake was completely covered with ice and almost half of the surface area was randomly covered by drifting snow (Figures 12a and 12b). The other half of the lake surface was transparent, allowing visual observation of the floating material below

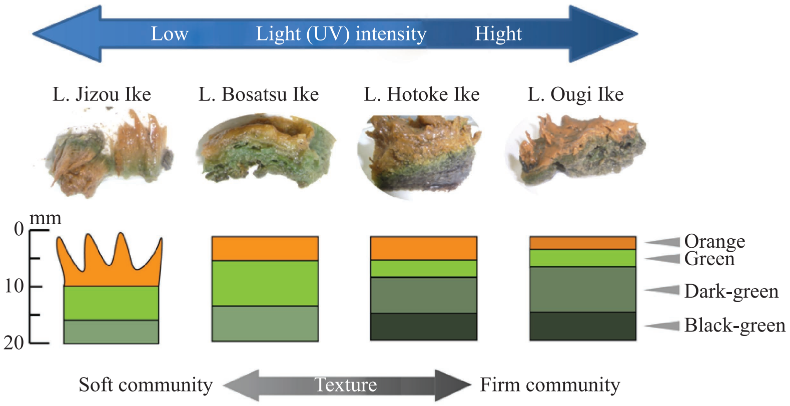

Figure 10 Photographs and schematic diagrams of vertical sections through benthic assemblages in four lakes (redrawn after reference [37]). Structural and pigment variability among assemblages from different lakes along the Sôya Coast are the result of adaptation to ambient light conditions.

the surface. A search over the ice cover was attempted, but no assemblages were found. During the second survey on 21 October 2010, no notable change was observed in either ice conditions or snow cover. However, many floating phytobenthic assemblage fragments were observed below the ice cover (Figures 12c and 12d); these were visible through the transparent ice (1.8 m thickness) from the central area of the western basin to approximately the entire area of the eastern basin, where water depth exceeded 2 m (Figure 12a). The relative assemblage coverage was 77% (*SD* 0.9%, *n* = 25) of the lake surface area, where they were seen through the transparent ice (Figure 12c).

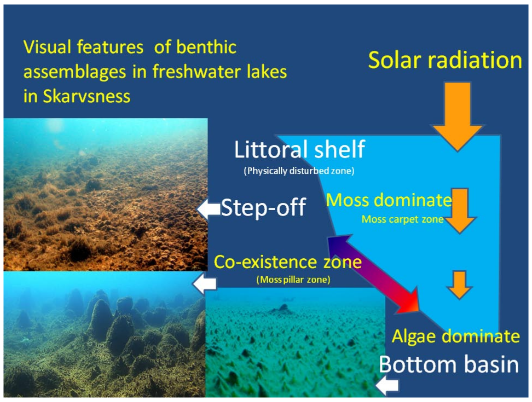

Figure 11 A possible explanation for the depth-related distribution pattern of dominant benthic assemblages. Photosynthetic activity of aquatic mosses is relatively higher in shallow basins and lower in deep basins than microbial phototroph activity[38]. Physical disturbance by ice cap movement during ice development/disappearance seasons is intensive in the shallow littoral shelf zone, and therefore, almost no macroscopically visible benthic assemblages develop. Aquatic mosses dominate in the shallower step-off zone of the lake and microbial mat assemblages dominate in the deeper part of the lake basin. Moss pillars, the complex assemblage of aquatic mosses and microbial assemblages, are able to develop well at intermediate depths.

Such mass floatation occurred under the physical conditions described here. Daily average solar radiation in the central area of the Sôya Coast (Skarvsnes) in October 2010 reached a seasonal maximum of more than 200 W· m^{-2} on sunny days. This value was close to 50% of the yearly maximum, but daily average atmospheric temperature was still less than −10°C (Figure 13a). Acceleration of photosynthesis with seasonal increases in PAR may be the main process leading to the detachment of phytobenthic assemblages via the formation of oxygen bubbles and attainment of positive buoyancy, as suggested by Pearce and Galand[100] and Tanabe and Kudoh[42].

Seasonal increases in solar radiation and subsequent PAR penetration through the ice cover also induced heating of the lake water in spring (Figures 13b and 13c). In early October 2010, well-developed inverse thermal stratification of the water column was evident (~2°C at 2 m and ~4°C near the bottom). However, the colder upper water gradually warmed and the temperature differences between depths had disappeared by mid-October 2010. According to the density-temperature relationship of freshwater, when surface cold water warms to ~4°C, density increases and the water sinks causing vertical mixing, as discussed in the previous section. Thermal convection in Skallen Ôike began in mid-October in 2010 (the study year).

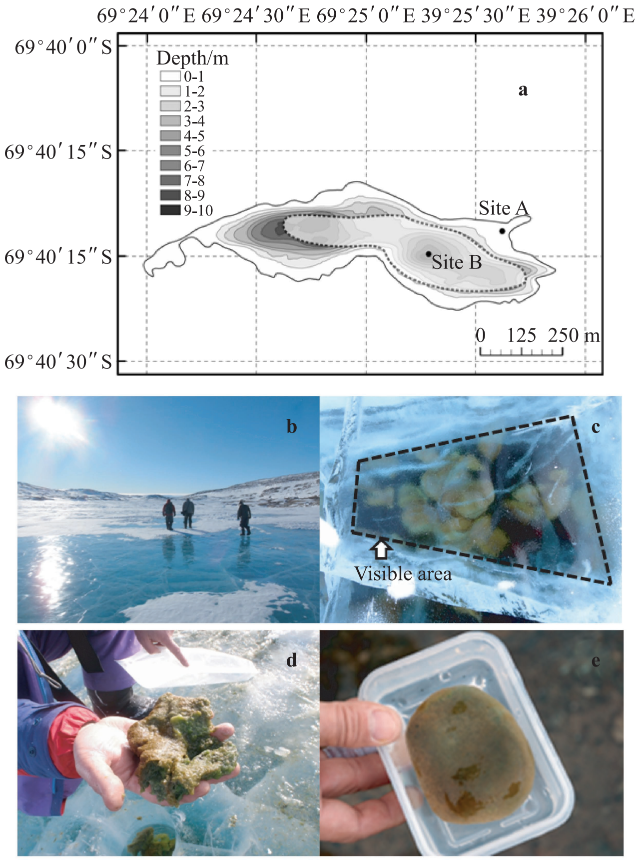

Figure 12 Area where mass floatation of benthic assemblages occurred beneath the ice is marked on a bathymetric map of Skallen Ôike (gray area enclosed by dotted line in **a**). Photographs of ice-covered Skallen Ôike in October, 2010 (**b**), floating assemblages observed through transparent ice (**c**), the floating assemblage collected from the water beneath the ice in October (**d**), and the floating assemblage collected in January (**e**).

The onset of vertical mixing and slight increase in water density due to heating (physical events) may aid the floatation of phytobenthic assemblages. To date, there is no evidence of quantitative influences on the buoyancy of benthic assemblages, such as physical events or physiological acceleration of photosynthetic activity. Nevertheless, the timing of massive phytobenthic floatation and the collapse of inverse stratification occurred simultaneously in the lakes studied. No other factor is expected to have assisted the process in mid-October. The thick ice cap prevented direct wind mixing of lake water; the ice was stable. Therefore, disturbance induced by ice movement would have been negligible and melt water intrusions from the catchment area minimal at such low air temperatures.

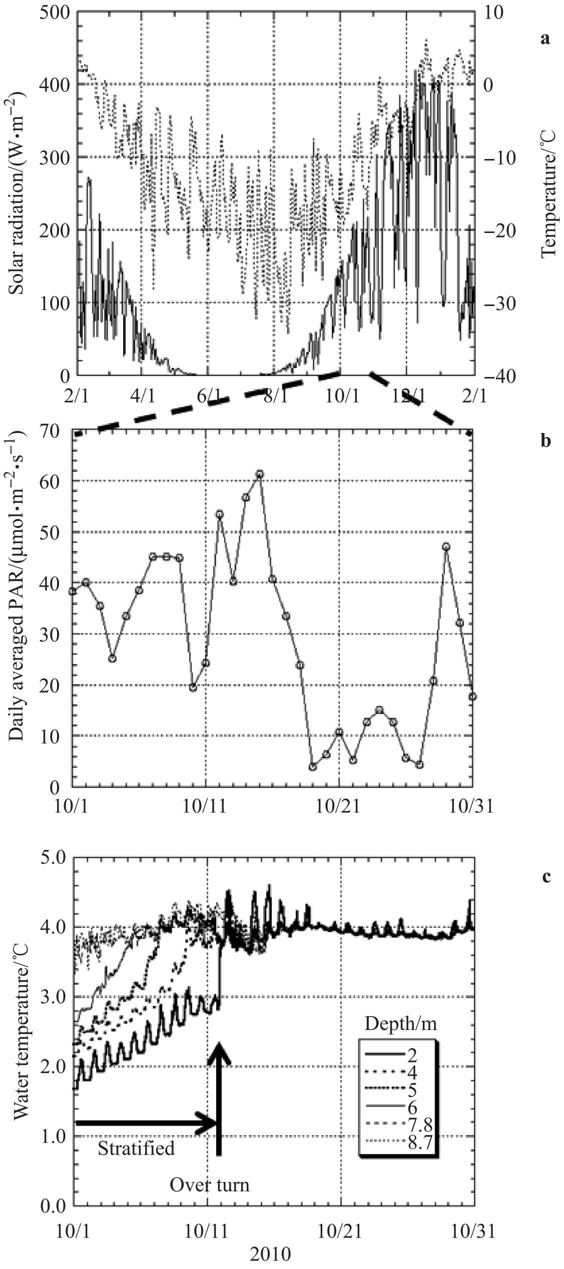

Figure 13 Daily average solar radiation and air temperature data recorded by an automated weather station (AWS) set at the central ice-free area of the Sôya Coast (Skarvsnes) during the 51st JARE (**a**), underwater PAR intensity measured near the bottom (9.3 m) of Naga Ike in October , 2010 (**b**), and water temperature changes measured at 30-min intervals in Naga Ike at six discrete depths in October (**c**). These data were measured continuously on one of the long-term monitoring JARE program studies and are published in the JARE-Data Reports series from the NIPR[39-40,43,89]. Inverse thermal stratification under ice-cover developed by early October but was destroyed in mid-October when massive floatation of the benthic assemblages was discovered.

When assemblages are transferred from the lake bottom to the surface, they experience very different physiological conditions. Tanabe and Kudoh considered the properties of benthic and floating assemblages during summer and postulated that assemblages adapt by changing their morphology, pigmentation, and photophysiology in response to increased illumination[42]. By the onset of the ice-free summer, they have been floating for approximately 3 months, during which time they may have adjusted their morphology and photophysiology to the lake surface environment before thawing takes place in the summer. Definite oblate, spheroid assemblages are found in this lake every summer (Figure 12e); this form may be adapted for survival on the lake surface. Although they may respond to the lake surface environment, most floating assemblages lose photosynthetic activity by the end of the summer open water period because of drifting ashore, freezing, desiccation, and transport by wind to the surrounding landscape (Figure 14). Massive floatation of phytobenthic assemblages that covered almost half of the lake surface area were simply destroyed, but nevertheless would have contributed to transporting lake production to the surrounding ecosystems[101]. If such a phenomenon spontaneously induces seasonal activation of photosynthesis every year, a large number of photosynthetically active assemblages would be detached from their natural habitat. This can be disadvantageous for the maintenance and sustainability of assemblages in benthic lake habitats. However, it also provides an opportunity for benthic subsurface communities in dark regions to reactivate (e.g., gap regeneration in the case of climax forests) and also allows floating assemblages to restart photosynthesis at the top of sediments by resinking[42]. The evolutionary advantages for the floating assemblages involved in this annual transfer and consequent loss of production remain unknown. Further studies to elucidate the reasons behind such trophic transfer and cycling between Antarctic ecosystems are required.

5 Summary and conclusion

Limnological and ecological studies conducted around glacial lakes in Sôya Coast by JARE were reviewed and some of their features were described:

(1) There are many glacial lakes where aquatic (benthic) organisms proliferate. The benthic organisms comprise diverse assemblages on the lake sediments and contain unique and different life-forms among lakes. Despite them having similar origins and length of historical time under the same climatic conditions.

(2) Among the annually ice-covered lakes, three typical circulation patterns, which are generated by differences in salinity, were identified through repeated and continuous observational studies.

(3) Photophysiological studies suggest that the photosynthetic organisms inhabiting the water column and benthic surface were exposed to strong light, including UV in summer. They may be responding to ambient light conditions with structural and pigmentation adaptations. Because there are the differences in ambient light conditions owing to

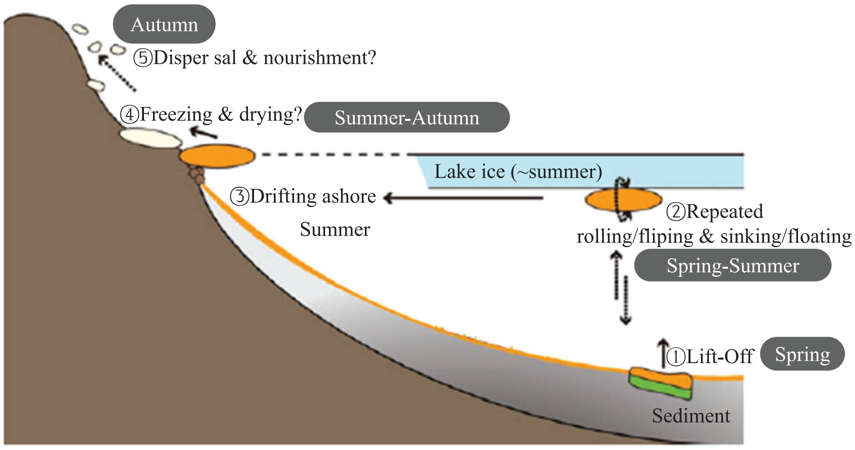

Figure 14 Schematic diagrams of the formative mechanism and possible ecological implications of the floating assemblages (after reference [42]). Floatation of amorphous mat assemblages occurred in mid-October. Repeated sinking and floating, with rolling and flipping, under lake ice coverage may occur depending on assemblage buoyancy. The floating assemblages become spheroid in shape and the surface of the assemblages is heavily pigmented because of increments of UV and strong light-protective pigments (photo-adaptation response). The spheroid assemblages during the non-ice covered summer were found drifting ashore and some portions are blown away from the lake to the surrounding landscape.

differences in light attenuation properties and lake depth, adaptations likely differ among lakes and this in part results in the diversity of life-forms seen in the benthic assemblages of Sôya Coast lakes.

(4) Spontaneous mass floatation of benthic assemblages was observed under ice-covered lakes in spring. Seasonal acceleration of photosynthesis and vertical circulation are possible mechanisms. This phenomenon causes production matter transportation from lakes to adjacent terrestrial habitats, linking the lakes and surrounding terrestrial ecosystems.

Most lakes in the Antarctic continent were created after the LGM, have experienced recent global climatic changes, and offer the most productive habitat for Antarctic organisms as a result of primary succession. Future comparative studies of Antarctic Oases, combined with detailed long-term monitoring studies will yield new perspectives on the structure, function, and succession processes of not only Antarctic lakes, but also aquatic ecosystem.

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