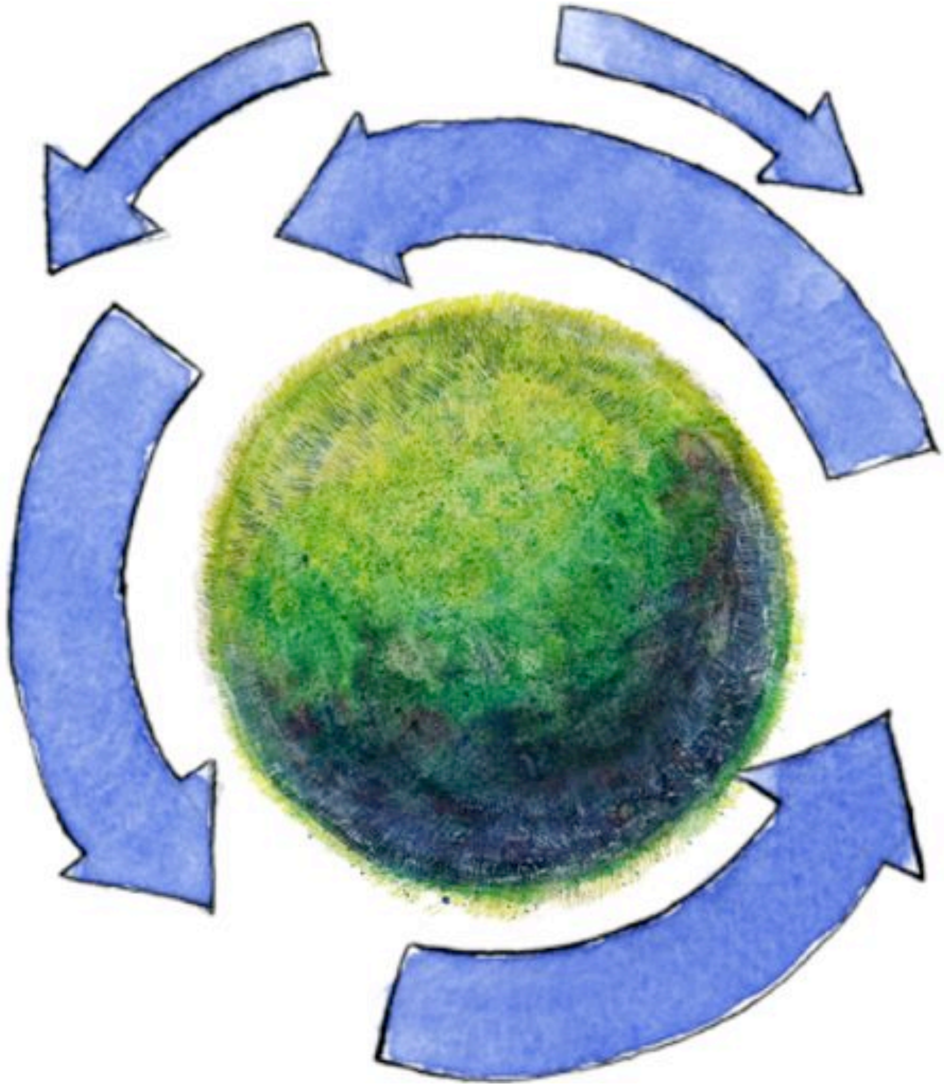
Árni Einarsson

The lake balls of Mývatn

in memoriam



Mývatn Research Station
Náttúrurannsóknastöðin við Mývatn

Árni Einarsson

The lake balls of Mývatn

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Kúluskíturinn í Mývatni

Minningarorð

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Myvatn Research Station 2014

Náttúrurannsóknastöðin við Mývatn 2014

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Myvatn Research Station
Náttúrurannsóknastöðin við Mývatn

Mývatn 2014

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Kúluskítur: Svo nefnist sjaldgæft kúlulaga vaxtarform grænþörungsins *Aegagropila linnaei*, sem nefnist *vatnaskúfur* á íslensku, en önnur vaxtarform þörungsins þekkjast í vötnum víða um norðurhvel jarðar. Samfélög stórra kúlna eru mjög sjaldgæf, auk Mývatns er aðeins vitað af þeim í tveimur vötnum í heiminum, annað er Akanvatn í Japan, hitt er í Úkraínu. Smærri kúlur þekkjast í fjölmörgum vötnum, þar af tveimur á Íslandi. Tvö önnur vaxtarform lifa í Mývatni, annað þeirra vex á steinum, hitt, svonefndur *vatnadúnn*, myndar breiður af lausum hnoðrum á stærð við fingurnögl og í félagi við skylda tegund, *Cladophora glomerata*, mynda þær víðfeðmt teppi á botni suðurhluta vatnsins, Syðriflóa. Teppi þetta var eitt af megineinkennum í lífríki Mývatns og myndaði undirlag fyrir nokkrar eftirsóttar átutegundir og skýldi botninum. Kúluskítur er friðlýstur á Íslandi og í Japan. Kúluskítssamfélögin í Mývatni hafa frá því þau uppgötvuðust af náttúrufræðingum í Mývatni árið 1978 vaxið í þremur megin flekkjum, einum í norðurhluta vatnsins,Ytriflóa, og tveimur í Syðriflóa. Samfélagið í Ytriflóa var gert úr smávöxnum kúlum en hin tvö úr 12-15 cm breiðum kúlum, sem lágu þétt saman og sums staðar í 2–3 lögum. Flekkirnir í Syðriflóa voru þar sem straumaskil myndast í vatninu í stormum. Ekki er vitað við hvaða skilyrði kúluskíturinn vex upp, en sést hafa grjóthellur í vatninu þaktar litlum áföstum hnoðrum og eru líkur á að uppeldisstöðvar hans hafi verið þar. Þessir hnoðrar hafi síðan slitnað frá undirlaginu er þeir stækkuðu og aldan náð betra taki á þeim og straumar síðan borið þá í flekkina.

Allir þeir grænþörungar sem að ofan eru nefndir hafa verið á hröðu undanhaldi síðustu ár. Kúluskítsbreiðurnar eru horfnar, og flest bendir til að kúluskítur sé nær allur horfinn úr Mývatni, þótt erfitt sé að leita af sér allan grun í þeim efnum. Grænþörungabreiðan er líka alveg að hverfa og á það jafnt við um báðar tegundirnar sem hana mynda. Um er að ræða lokastig þróunar sem greinilega var hafin um 1990.

Vatnaskúfur, þar með talinn kúluskítur, hefur verið á undanhaldi um heim allan vegna næringarefnamengunar frá mönnum og athöfnum þeirra um áratuga skeið. Mengunin veldur því m.a. að *blábakteríur* (Cyanobacteria, áður fyrr nefndir blágrænir þörungar) fjölga sér í stórum stíl í vatnsbolnum. Vatnið verður ógagnsætt, birta á vatnsbotninum minnkar og botngróðurinn hverfur. Grænþörungamottan á botni Mývatns hefur vaxið og dvínað í takt við sveiflur í blábakteríum, en bakteríublómar koma gjarnan nokkur ár í röð og í takt við öfgakenndar sveiflur í ýmsum öðrum meginþáttum lífríkisins. Grænþörungamottan rýrnaði ávallt eftir öflug blábakteríuár. Rannsóknir á borkjörnum úr setlögum vatnsins sýna einnig að á tímabilum með miklum bakteríugróðri hefur vatnaskúfur verið með minna móti. Hinar öfgakenndu sveiflur í lífríkinu eru raktar til röskunar vegna kísilnáms úr vatninu 1967–2004

og hafa þær haldið áfram eftir að starfseminni var hætt því að námugryfjan er enn á sínum stað og dregur til sín lífræn efni úr vatninu. Vinnslan hafði líka í för með sér talsverða næringarefnamengun í grunnvatninu. Orsakasamhengi milli sveiflna í blábakteríum og öðrum þáttum lífríkisins eru enn ekki ljós.

Athuganir á vettvangi atburða í kúluskítsbreiðunni í SV-horni vatnsins sýndu að breiðan var að grafast í leðju sem færðist eftir botninum til suðurs. Þessa atburðarás má rekja til þess að þörungamottan í vatninu var að rýrna svo mikið í heild sinni að leðjubotninn undir varð berskjaldaður fyrir álagi af völdum vindknúinna strauma sem liggja suður eftir miðju vatninu. Botnleðjan leitar þá í nýtt jafnvægi. Vaxandi vindasemi á tímabili gæti hafa flýtt fyrir þessari þróun og einnig sú staðreynd að efsta botnlagið verður mjög vatnskennt í mýleysisárum þegar mýlirfur er ekki til staðar að binda það.

Þótt næsta öruggt sé að hvarf grænþörunga á botni Mývatns stafi af auknum blábakteríum verður þess ekki vart af mæligögnum að skyggni hafi minnkað mikið vatninu á því tímabili sem mælingar ná yfir (1973–2013). Bendir það til þess að bakteríustig hafi verið komið í núverandi horf áður en mælingar hófust, eða að bakteríugróðurinn standi nú lengur fram á haust (fram yfir þann tíma sem mælt er). Sé það svo, hafa langtímaskilyrði þörunganna ekki verið lífvænleg um langa hríð, en þeir hafa náð að halda velli þó þetta lengi vegna blábakteríulausra tímabila sem gefa þeim færi á að rétta úr kútnum. Vatnaskúfurinn virðist því aðeins þrífast að veðurfar sé hæfilega vindasamt, en þó getur keyrt úr hófi fram í þeim efnum.

Sérstakar aðgerðir ofan í Mývatni sjálfu til að bæta lífskilyrði kúluskíts og endurheimta hann eru ekki raunhæfar. Eina raunhæfa leiðin til að snúa þeirri óheillaþróun við sem hér hefur verið lýst er sú að takmarka sem mest má verða að næringarefni (N og P) berist í grunnvatn og þaðan út í Mývatn. Næringarefni berast frá mannabyggð, skepnuhaldi, ræktun gróðurs og vinnslu dýraafurða og áður fyrr frá námuvinnslu kísilgúrverksmiðjunnar. Taka þarf þessi mál, einkum frárennsli frá byggð og gististöðum til gagngerrar endurskoðunar, og er ekki eftir neinu að bíða hvað það snertir. Jafnframt er brýnt að gera strax úttekt á næringarefnum í grunnvatninu og fara auk þess yfir fyrirliggjandi gögn um þau. Æskilegt að gera úttekt á ástandi kúluskíts í þeim vötnum á Íslandi sem hann finnst enn í.

Introduction

Lake balls are a growth form of the freshwater green algal species *Aegagropila linnaei.* This species, formerly known by the neame *Cladophora aegagropila*, is widely distributed in the northern hemisphere. The lake ball growth form is rather rare and requires a combination of several ecological factors to form, such as mobility by wave action in moderately shallow water with abundant light and moderate nutrients. Lake balls are round, green and fluffy, a set of characteristics that makes them aestetically appealing. The balls may occur in colonies on the lake bottom. Colonies of large lake balls (about 12 cm in diameter or more) have been described from Lake Akan, Japan and Lake Mývatn in Iceland. Colonies of such large lake balls, are extremely rare and probably rank among the most unusual plant communities in the world. The formerly extensive colony in Lake Mývatn has been contracting over a period of 30 years and has by now disappeared. The decline in the lake balls has been paralleled by a decline in another main growth form of *A. linnaei*, small free-floating tufts of algae (Fig. 1) and also *Cladophora glomerata*. This report describes the history of the species in Lake Mývatn, its discovery and the recent decline and discusses the possible causal factors in the light of a worldwide decline in the species.

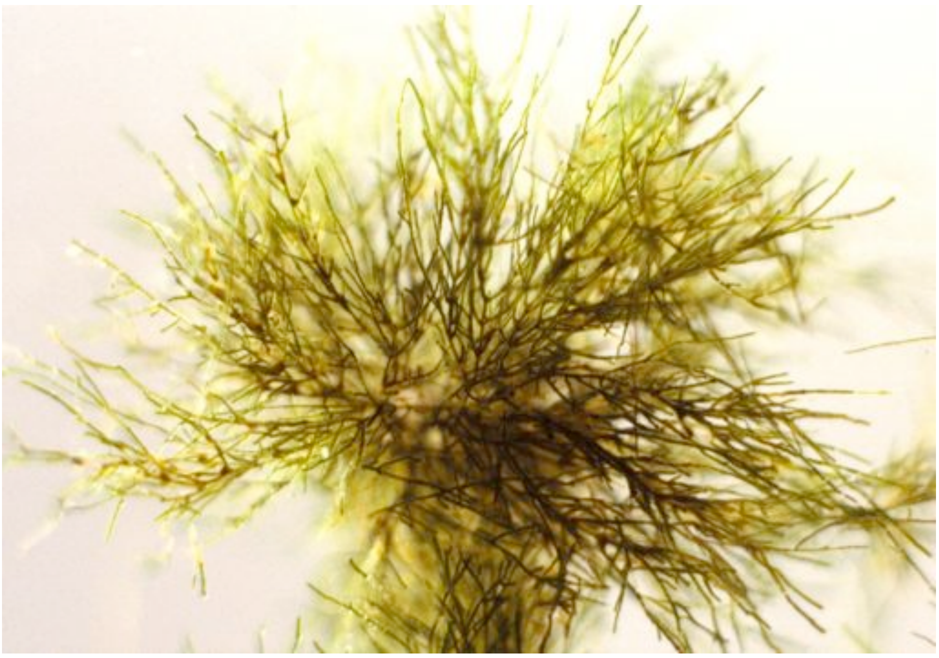


Fig. 1. A tuft of free-floating *Aegagropila linnaei* from Mývatn. Each branch is one cell in diameter. Magnification about ×10. *Nærmynd af vatnaskúfshnoðra úr Mývatni. Hver grein er ein fruma að þykkt. Um það bil tíföld stækkun.*

Fig. 2. ***Aegagropila linnaei*** **in Lake Laugabólsvatn in the West Fjords of Iceland.**
Vatnaskúfur í Laugabólsvatni við Ísafjarðardjúp.

Distribution in Iceland

In Iceland the species *A. linnaei* is known with certainty from a number of lakes. These are: Mývatn, Kringluvatn, Másvatn, Miklavatn, Víkingavatn and Snjóholtsvötn in NE Iceland, Vatnshlíðarvatn, Selvallavatn, Efstadalsvatn and Laugabólsvatn (Fig. 2) in NW Iceland. In SW Iceland the species is known from Lake Thingvallavatn (Jónsson 1992). Lake ball growth forms are known with certainty from Mývatn, Kringluvatn, Miklavatn, Vatnshlíðarvatn, Snjóholtsvötn and Selvallavatn. Unconfirmed records of lake balls are from Vestmannsvatn, Ólafsfjarðarvatn, Apavatn, Múlavatn (Snæf.) and Arnarvatn hið mikla. Large lake balls (>10 cm in diameter) are only known from Mývatn.

The lake ball story

Lake balls in Mývatn first became known to scientists during a systematic survey of the lake benthos in 1977 (see Gardarsson et al. 1987). The survey was carried out while the lake was turbid, with low visibility due to an extensive Cyanobacteria bloom (*Anabaena*) and only one lake ball was retrieved. In the following year the lake water was clear, which was a rather unusual situation, and an extensive lake ball patch

Fig 3. A lake ball patch in the SW area seen from the boat in 2006. The balls were about 12 cm in diameter. The grey patches at the lower corners of the photograph are due to glare on the lake surface. ***Kúluskítsflekkurinn í Bekraflóa séður úr báti árið 2006. Kúlurnar eru um 12 cm í þvermál. Ljósir fletir í hornum myndarinnar eru vegna glampa á vatninu.***

could be observed directly from the boat in the eastern part of the South basin. Soon, another smaller patch was discovered in the SW part of the lake (Bekraflói) (Figs. 3−5). Aerial photos from 1979, also a clear water year, allowed size estimates of the lake ball areas. The large eastern area was about 23.5 ha, the smaller SW patch was about 3.5 ha (Fig. 6). In 2006 the larger patch had all but vanished, but six tiny patches were located in its place. The areal of the SW patch had been reduced about half, from 3.5 to about 1.6 ha. In 2007 and 2008 this patch had been reduced to about 0.5 ha. The small eastern patches were not checked at this time. Overall, in 28 years the lake ball areas had shrunk to less than 2% of their 1979 size (Fig. 6).

In 2010 an attempt to collect lake balls for a local museum failed and so did further attempts in 2011. In early 2012 the lake was clear enough to allow direct observations from a boat and a lake ball expert from Japan, dr. Isamu Wakana, also spent some effort scuba diving in the SW lake ball area. Further observations were made from a boat at the largest of the remaining small patches on the east side of the South basin. These observations, in 2012, showed that the SW patch, as such, did not exist any more, Many lake balls had been covered by mud but scattered lake balls could still be seen on the surface of the muddy lake bottom but were clearly not thriving. One of the

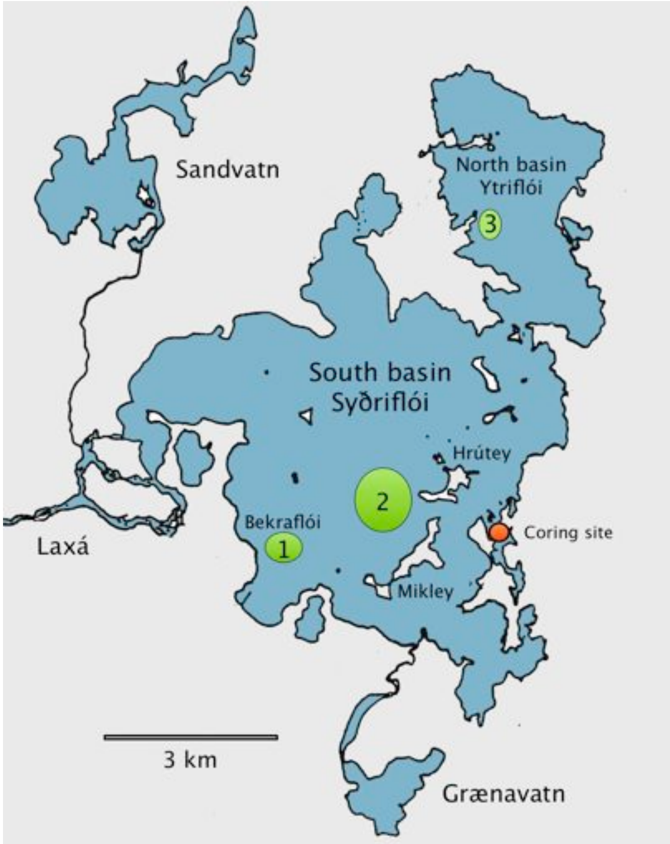


Fig. 4. A map of Lake Mývatn showing the locations of lake ball patches and the site of sediment coring. 1: SW-patch; 2: Eastern patch; 3: North basin patch. Kort af Mývatni sem sýnir staðsetningu kúluskítsflekkjanna (grænt) og staðinn sem setkjarnar voru teknir (rautt). 1: Flekkur á Bekraflóa; 2: Flekkir vestur af Hrútey; 3: Flekkur í Ytriflóa.

small eastern patches was found to be in good shape, but in the following year, in 2013, it had also disappeared. While some isolated lake balls may still exist in Mývatn it is by now (2013) clear that the communities of lake balls have vanished.

Other growth forms of *A. linnaei* in Lake Mývatn

Attached algae

Aegagropila linnaei has three main growth forms (Fig. 7). Apart from the two forms mentioned earlier, the lake balls and free-floating tufts (Fig. 1), there are algae that grow attached to a firm substrate. They may grow on any hard surface, most commonly on rocks, but in other countries also on large bivalves (which do not occur in Iceland). Epilithic (= growing on rocks) *A. linnaei* were first discovered in Mývatn

Fig 5. A healthy looking lake ball patch in Mývatn. SW-patch. ***Kúluskítsbreiða í góðu lagi í Bekraflóa í Mývatni.***

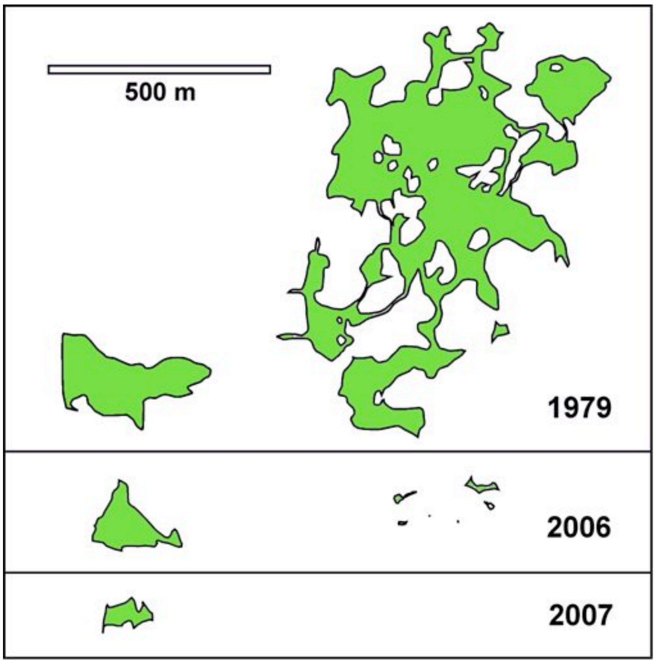


Fig. 6. Maps of lake ball areas in the South Basin of Lake Myvatn in 1979, 2006 and 2007. The areal extent in 2008 was similar as in 2007. The SW patch is to the left. The eastern patches were not visited in 2007, the largest patch seen there in 2006 still existed in 2012 but had disappeared in 2013. For the sake of illustration the distance between patches is reduced. North is up. ***Kort sem sýnir kúluskítsflekkina í Mývatni og breytingu með tíma (árin 1979, 2006 og 2007). Útbreiðslan 2008 var svipuð og 2007. Austurflekkirnir voru ekki heimsóttir 2007; stærsti flekkurinn þar árið 2006 var enn þar árið 2012 en var horfinn árið eftir (2013). Mælikvarðinn á myndinni á við um flekkina, en fjarlægð milli flekkja er mun meiri en myndin gefur til kynna.***

Fig. 7. Three well known growth forms of *Aegagropila linnaei*. *Þrjú vaxtarform vatnaskúfs: Kúluskítur, vatnadúnn og áfastur þörungur.*

during scuba diving studies in 1999. The epilithic algae have not been studied in detail in Mývatn, but in Lake Thingvallavatn, Iceland, their ecology was investigated by Gunnar Steinn Jónsson (Jónsson 1992). Observations indicate that in Mývatn, as in Thingvallavatn, they tend to grow on the sides or even the underside of rocks (Fig. 28 C). There is an indication that the epilithic algae play a role in the regeneration of lake balls (see later).

Free-floating tufts

The first observations of a mat of algae on the bottom of Mývatn were made by the biologist Finnur Guðmundsson in 1939 (unpublished). He took systematic grab samples and evaluated the volume of algae on a scale from 0−3 (Fig. 8). He found that most of the bottom of the South basin was covered by the algal mat. In an effort led by the University of Copenhagen around 1970 to describe and quantify the Lake Mývatn ecosystem (Jónasson ed. 1979) the algal mat was identified as *Cladophora aegagropila* which was the name used for *A. linnaei* at the time. Hunding (1979) measured the oxygen production of the species (with the attached diatoms) in Mývatn in relation to water depth and published a picture that confirmed the identification. A survey of the lake biota carried out by a team from the University of Iceland in 1977

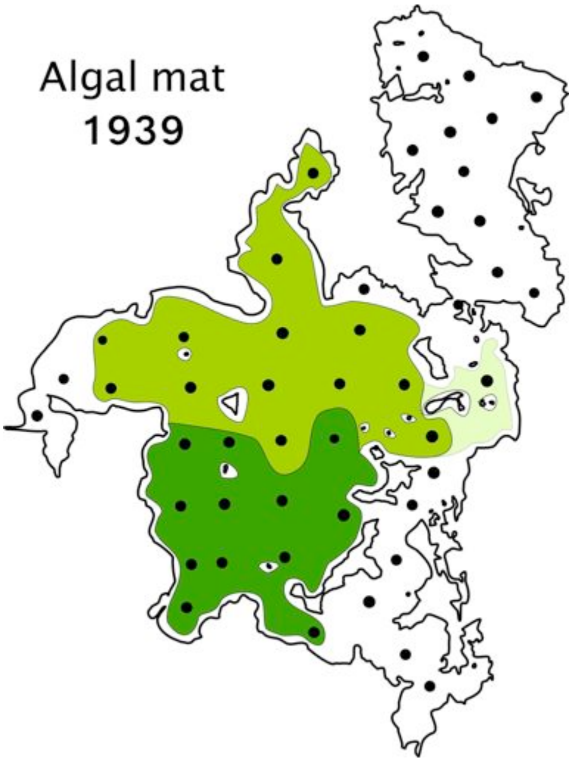


Fig. 8. Distribution of the mat of filamentous green algae in Mývatn in 1939. Sampling sites indicated by black dots. The relative volume of algae in the grab is indicated by the colour. White indicates no algae. Finnur Guðmundsson unpublished material. ***Útbreiðsla og magn þráðlaga grænþörunga í greiparsýnum af botni Mývatns árið 1939. Sýnatökustaðir merktir með punktum. Magn þörunga í hverju greiparsýni er gefið til kynna með lit. Hvítt merkir að engir þörungar hafi fundist í sýni. Finnur Guðmundsson, óbirt gögn.***

led by Arnthor Gardarsson, produced a map of the algal mat. The survey was partly repeated in 1981 and some sites were resampled in 1983 (Gardarsson et al. 1987). The average biomass of filamentous algae in 1977 was 53 g afdw/m^2 (afdw=ash-free dry weight, which is a measure of organic content) on the 24 sites where such algae were found. It was 78g/m^2 at comparable sites in 1981 but the difference was not statistically significant. There was an indication of reduced abundance in 1983, but again the difference was not statistically significant.

The survey of 1977 formed the basis of a vegetation map published in 1987 and in 1991 (Gardarsson et al. 1987, Gardarsson & Einarsson 1991) and revised in Einarsson et al. (2004) (Fig. 9). The map revealed large-scale variation in the macrophyte flora. The area influenced by cold-water springs had different macrophytes from those in the northern area which is influenced by mineral-rich water from the nearby geothermal area of Bjarnarflag. The mat of filamentous green algae was mostly confined to the South basin where the two types of inflowing water were mixed.

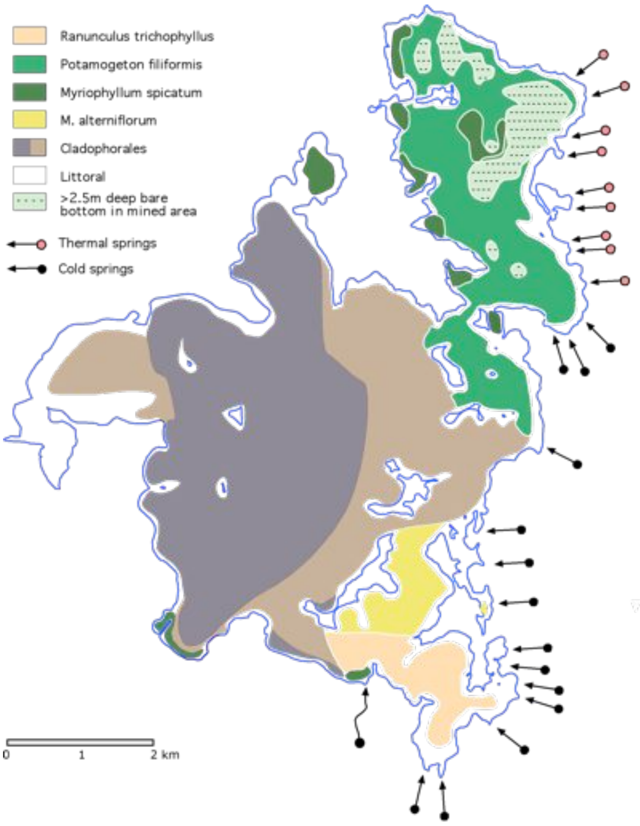


Fig. 9. A division of Lake Mývatn according to dominating macrophytes. Two shades of Cladophorales indicate different density of the algal mat. The main inflow of artesian springwater on the lake shore is also shown. From Einarsson et al. (2004). ***Myriophyllum spicatum*** **has now been identified as** ***M. sibiricum. Gróðurkort af Mývatni, byggt á ríkjandi plöntutegundum. Tveir tónar af Cladophorales (þörungamotta Syðriflóa) tákna mismunandi þéttleika.*** **Myriophyllum spicatum** ***(vatnamari) er nú talinn vera tegundin*** **M. sibiricum. M. alterniflorum** ***er síkjamari.*** **Ranunculus trichophyllus** ***er lónasóley og*** **Potamogeton filiformis** ***er þráðnykra.***

Studies of aerial photographs from clear-water years revealed much spatial and temporal variation in the algal mat (Einarsson et al. 2004), with 1963 showing the most extreme areal extension (Fig. 10). The temporal variation indicated that cyanobacterial blooms might be a controlling factor. In 1982 the algal mat was very extensive, suggesting that a clear-water phase in the period 1978−1982 had allowed the build-up of a large biomass of algae. In 1990−91 the mat was much reduced, most likely because of intense cyanobacteria blooms in 1988−1989. In recent years satellite photos have proved useful in monitoring the algal mat (Fig. 11). They have shown that the mat is heavily reduced and most of the South basin has no macroalgae any more.

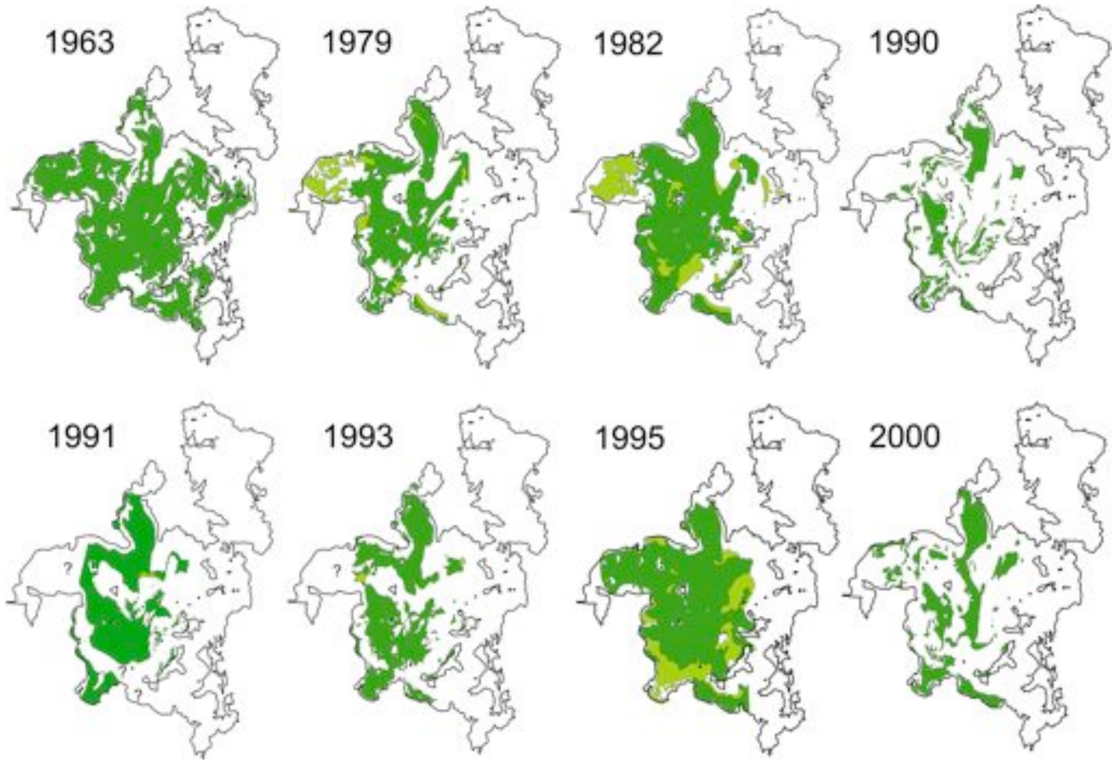


Fig. 10. Cover of the algal mat on the bottom of the South basin based on aerial photographs. Lighter colour indicates a lower density. From Einarsson et al. (2004). ***Þekja þörungamottunnar í Syðriflóa séð á loftmyndum teknum þegar vatnið er tært. Ljós litur gefur til kynna að þekjan sé ósamfelld. Úr grein Árna Einarssonar o.fl. 2004.***

The algal mat and its role in shaping invertebrate communities was studied in 1990−1991 by Gardarsson & Snorrason (1993) and in 2003 by Jensdóttir (2003, 2005). Gardarsson and Snorrason (1993) described three main types of muddy bottom in the South basin (Fig. 12): (1) the algal mat, showing some layering, with some of the algae buried in the topmost few cm of sediment and a layer of loose, fine algal filaments on top (Fig. 12); (2) a *Tanytarsus* bottom which has little or no algae but a dense layer of midge tubes, stabilizing the bottom, and (3) a bottom without a top layer of organisms described above. The invertebrate community associated with the algal mat was characterized by cladocerans and midge larvae that score high in the diet of fish and waterfowl at Mývatn (Gardarsson & Snorrason 1993).

Marianne Jensdóttir mapped the extent and characteristics of the algal mat in 2003 (Jensdóttir 2003, 2005). She confirmed an observation that had been made in a previous year by Isamu Wakana that the algal mat consisted of two species instead of one, namely *Aegagropila linnaei* and *Cladophora glomerata*. This discovery explained the vertical zonation described ten years earlier by Gardarsson & Snorrason

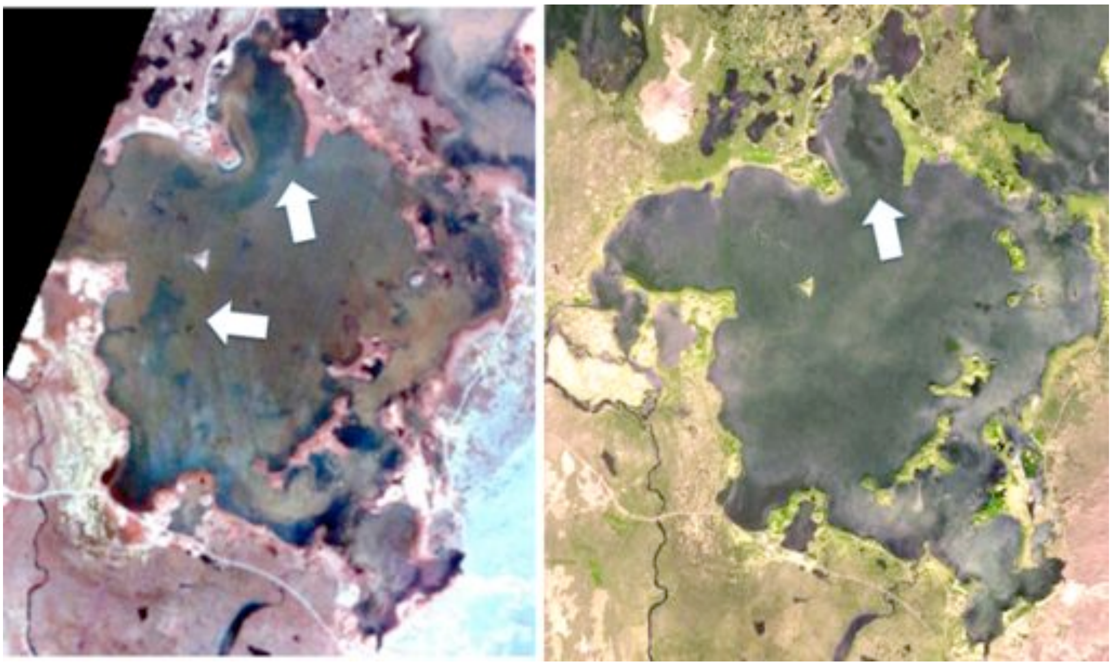


Fig. 11. Satellite images of the South basin of Lake Mývatn from 2008 (left) and 2013 (right) showing the final decline of the algal mat. Dark patches on the lake bottom west of the row of islands are mostly algal beds. The algal mat (arrows) has almost vanished. ***Gervitunglamyndir af Syðriflóa Mývatns frá 2008 (vinstra megin) og 2013. Dökkir flekkir á vatnsbotninum vestan eyja eru yfirleitt þörungar. Örvar benda á síðustu leifar þörunga-mottunnar.***

(1993) (cf. Fig. 12) so *C. glomerata* was clearly not a new species in the algal mat. Jensdóttir found *A. linnaei* to be both more frequent and more abundant than *C. glomerata*. *A. linnaei* was found at 102 sites but *C. glomerata* at 81 site. No algae were found at 2 sites. The average dry weight of algae (both species combined) ranged between 0.1 and 400 g/m^2. The dry weight of *A. linnaei*, where present, ranged from 2.5 to 357.8 g/m^2 (mean 123 g/m^2). The dry weight of *C. glomerata*, where present, ranged from 0.7 to 295 g/m^2 (mean 73 g/m^2). The difference in dry biomass between species was statistically significant ($P<0.001$). The highest biomass values occurred in the south-western part of the South Basin and in the Neslandavík bay at the north end of the South Basin (Fig. 13).

The biomasses of the two species were positively correlated on the 500 m grid but not on the finer 250 m grid, which was believed to reflect the influence of water currents at two different scales and acting differently on the two species. Strong currents will govern the overall distribution of the algal mat within the basin whereas smaller wave-induced currents will tend to separate the two species on the spot.

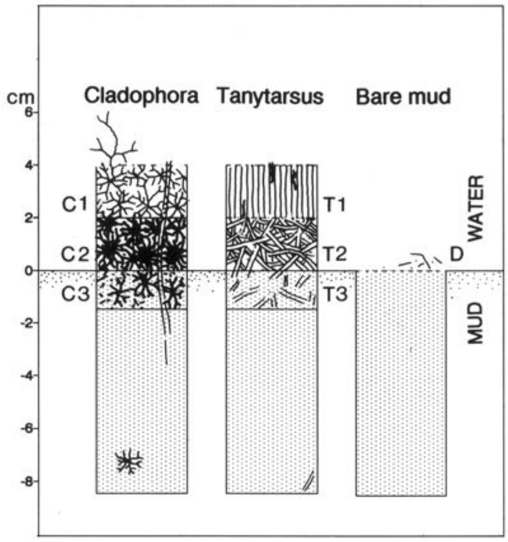


Fig. 12. Three types of mud bottom in the South basin of Lake Mývatn in 1990−1991. A "Cladophora" bottom has a mat of filamentous green algae of the species *Cladophora glomerata* (C1) and *Aegagropila linnaei* (C2 and C3). A "Tanytarsus" bottom has a dense layer of midge tubes, stabilizing the bottom. T1 is the active layer, T2 and T3 are tubes from the previous generation of midges. Bare mud is typical of low midge years and the mud surface is very watery and has no strength to support epibenthic organisms (organisms that sit on the sediment surface). From Gardarsson and Snorrason 1993. *Þrjár mismunandi gerðir botns í Syðriflóa Mývatns, séðar í þverskurði. „Cladophora"-botn er þakinn mottu úr tveimur tegundum grænþörunga,* A. linnaei *(vatnaskúfur) (C2 og C3) og* C. glomerata *(C1). „Tanytarsus"-botn er þakinn lagi af mýlirfupípum úr leðju og silki. Merki um tvær þrjár kynslóðir lirfa sjást (T1-T3). "Ber botn", lengst til hægri hefur hvorugt þessara lífrænu laga. Úr grein Arnþórs Garðarssonar og Sigurðar Snorrasonar (1993).*

The thickness of the epibenthic mat of algae, where present, ranged from 0.5 to 12 cm (mean 4.6 cm) and the mean proportions (by volume) of *A. linnaei* and *C. glomerata* were 14.6% and 81.0% respectively. In the subsurface part of the mat the corresponding figures were 76.8% and 23.2%. This difference in species proportions between the layers was statistically significant ($p < 0.05$).

Mean dry biomass for *A. linnaei* in the epibenthic layer and subsurface layer was 5.3 g/m^2 and 106.2 g/m^2 respectively and the difference was statistically significant ($P < 0.001$) (Fig. 14). Corresponding figures for *C. glomerata* were 17.2 g/m^2 and 20.7 g/m^2 in the epibenthic layer and the subsurface layer respectively (not a statistically significant difference).

There was a statistical difference in the dry biomass of *A. linnaei* and *C. glomerata* in both the epibenthic layer ($P < 0.002$) and the subsurface layer ($P < 0.001$). On the average 15% (3.5% *A. linnaei* and 11.5% *C. glomerata*) of the algal mat was located in the epibenthic layer and 85% (71.1% *A. linnaei* and 13.9% *C. glomerata*) in the

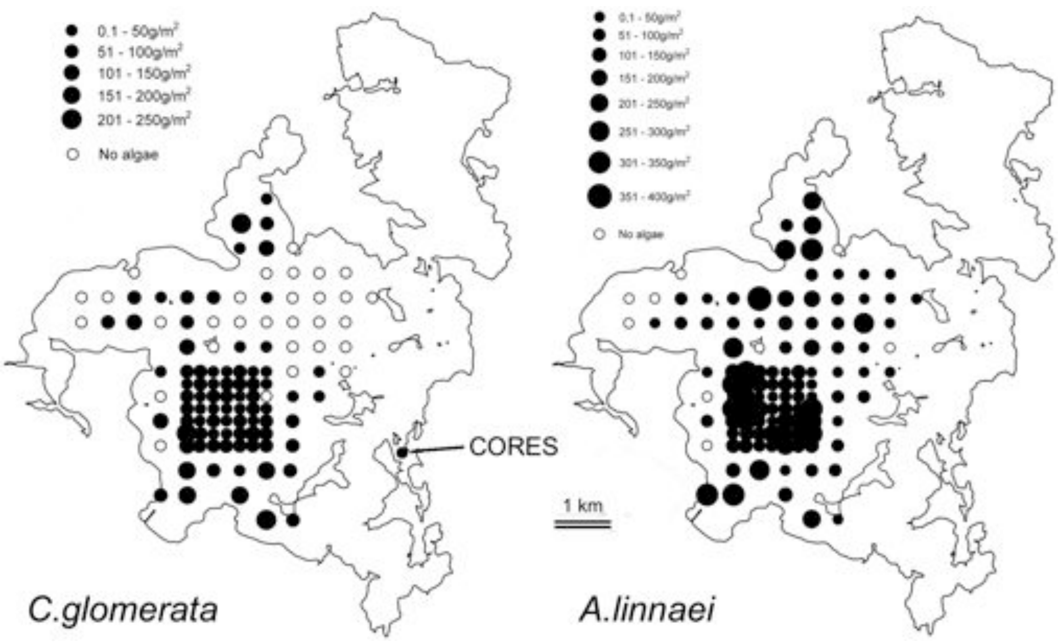


Fig. 13. Mean dry weight (gm^{-2}) of *C. glomerata* and *A. linnaei* in the South Basin of Lake Mývatn in July 2003. "No algae" includes sites where either no sample could be obtained because of a hard substrate or where no algae were found in an obtained sample. Coring site is also indicated. Redrawn from Jensdóttir (2005). ***Meðal lífmassi (g þurrvigt á fermetra) þörunganna*** **C. glomerata** ***og*** **A. linnaei** ***í Syðriflóa í júlí 2003.***

subsurface layer. Jensdóttir (2005) noted that the lake ball colonies and also relatively thick and long-lasting mats of free-floating tufts were located in areas where vortices occurred during southwesterly storms (the main storm direction) according to hydrological modelling developed by Kjaran et al. (2004) (see Fig. 17). Aerial photographs often show fine parallel streaks in the algal mat, suggesting that Langmuir circulation (vortices that go perpendicular to the wind direction) affects the distribution of algae on the lake bottom.

To test if there was a difference in biomass with water depth the data set was divided into two depth categories, 1–3 m and >3 m. The first depth range was represented by 31 sites and the latter by 71 sites. Biomass of *C. glomerata* significantly decreased with depth ($P < 0.001$) whereas that of *A. linnaei* did not (Fig. 15).

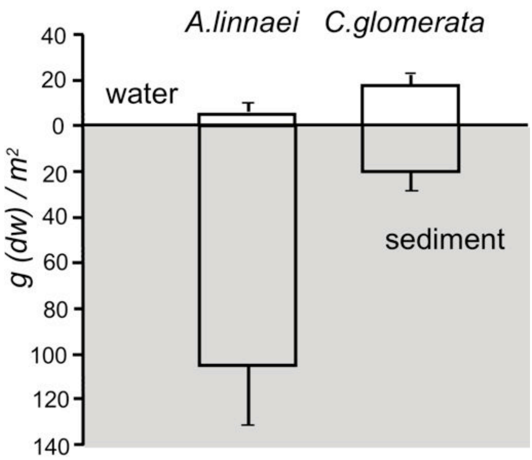


Fig. 14. Mean biomass (gdw/m^2) and 95 percent confidence limits of *A. linnaei* and *C. glomerata* in the algal mat on top of the sediment and in the uppermost 5 cm of the sediment. Modified from Jensdóttir (2005). *Meðal lífmassi (g þurrvigt á fermetra og 95% öryggismörk) vatnaskúfs og* C. glomerata *í þörungamottunni í Syðriflóa Mývatns. Gerður er greinarmunur á lífmassa ofan á botninum og ofan í leðjunni (efsta 5 cm laginu). Meginhluti lífmassa vatnaskúfs er ofan í leðjunni.*

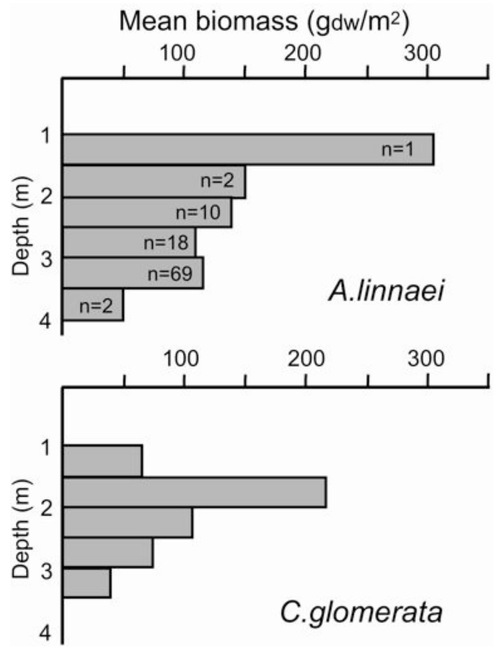


Fig. 15. Variation in mean biomass (gdw/m^2) of *A. linnaei* and *C. glomerata* with water depth in July 2003. From Jensdóttir (2005) (redrawn). *Meðal lífmassi (þurrvigt á fermetra) tegundanna* A. linnaei *og* C. glomerata *í Syðriflóa miðað við dýpi, 2003.*

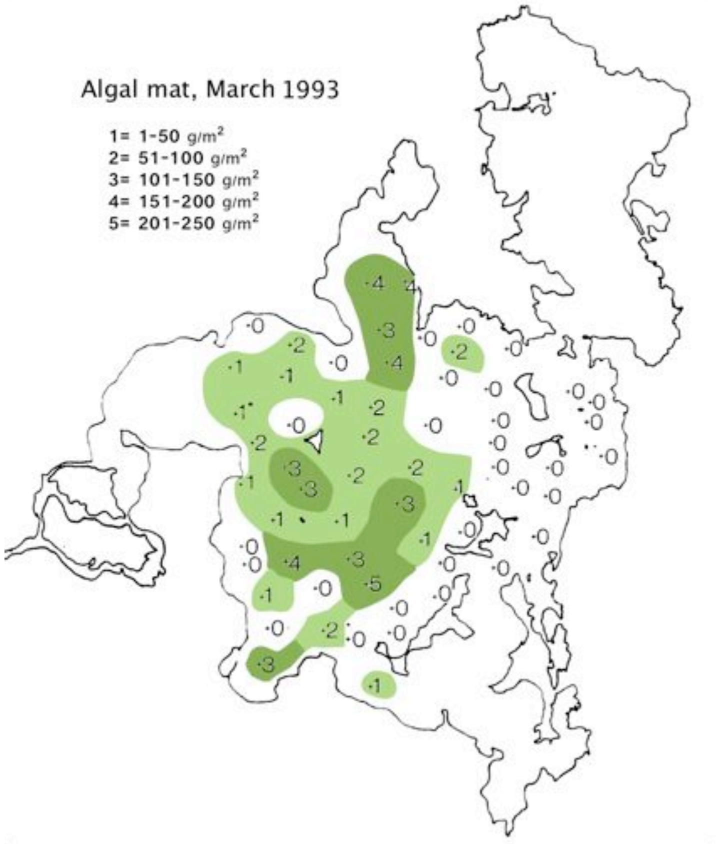


Fig. 16. Biomass of algal mat (g ash-free dry weight per m^2) under the ice in late March 1993. Modified from Einarsson et al. (1994). ***Lífmassi þörungamottunnar (g öskulaus þurrvigt á fermetra) undir ís í mars 1993. Úr skýrslu Árna Einarssonar o.fl. (1994), lítillega breytt.***

Jensdóttir (1993) tested the importance of substrate type for certain midge larvae and crustaceans which were preferred as food by fish and waterfowl and were known to be associated witht the algal mat.. She found that given the choice between a substrate of sand and an algal mat the animals preferred the algal mat. When allowed to choose between *A. linnaei* and *C. glomerata* they preferred the latter.

In March 1993 the algal mat was mapped under the ice, based on 61 station in the South basin (Einarsson et al. 1994). The biomass of algae represented the standing crop by the end of the winter, before the growing season (Fig. 16).

In 1980, when the author of this report was writing a tourist brochure about the nature of Mývatn, he found it appropriate to explain heaps of decaying algae commonly found on the lake shores. Such heaps were regularly forming in the ice-free period over a number of preceeding years (at least from 1973−74 when Carsten Hunding had a photograph published in Oikos 32, see p. 8 in Jónasson ed. 1979). In the late 1990s such deposits became increasingly rare and in the present century they have not formed, not even in the most powerful storms. This indicates that the abundance of algae has been reduced enormously since regular ecological observations started at Mývatn.

Storms have the potential to wash large quantities of algae ashore, but as mentioned before there is also indication that wind driven currents govern the overall distribution of the algal mat within the lake itself. The main storm direction at Mývatn is from the SW. A hydrological model has been developed that describes the currents in the lake during such storms (Tómasson & Kjaran 1993). Figure 17 shows a simplified version of the results of model calculations. The main pattern is that water is forced with the wind along the W and E shores and returns against the wind down the middle of the South basin. Vortices are created in the southwestern part of the lake as well as in the bay of Neslandavík which opens towards the main South basin on the north shore. The rather consistent spatial pattern of the algal mat seems to reflect this hydrological situation (Fig. 18).

The main lessons from the mapping studies described above are: (1) that there was variation in the spatial extent of the algal mat between multiyear periods, probably in response to cycles in Cyanobacteria blooms, (2) that the large scale pattern on the bottom was consistent across years and was heavily influenced by wind-induced currents, (3) that on a smaller spatial scale (250 m) species-specific differences aided by subtle wave-induced water motion lead to vertical zonation of the species both with respect to water depth and depth within the sediment, (4) the large variation between years concealed a trend that has lead to very small algal mats and the disappearance of the lake ball patches.

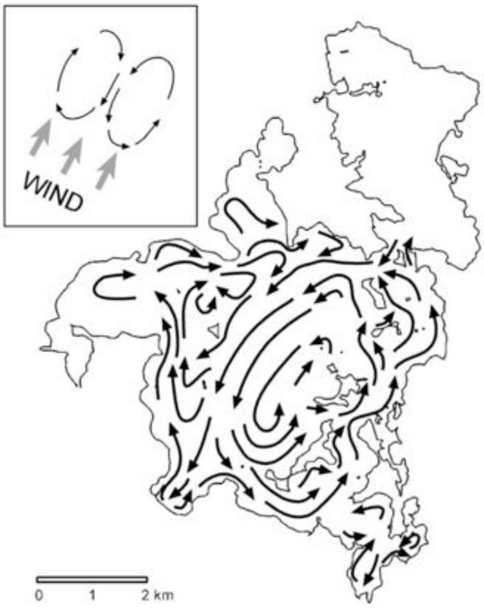


Fig. 17. Currents in the South Basin of Lake Mývatn during a storm from the southwest. A simplified diagram based on hydrological modelling (Tómasson and Kjaran 1993). The inset shows the general circulation pattern. From Einarsson et al. (2004). ***Straumar í Syðriflóa í suðvestan roki. Einfölduð mynd byggð á straumlíkani eftir Gunnar Tómasson og Snorra Pál Kjaran (1993). Innrammaða myndin til vinstri sýnir straumakerfið í hnotskurn. Úr grein Árna Einarssonar o.fl. 2004.***

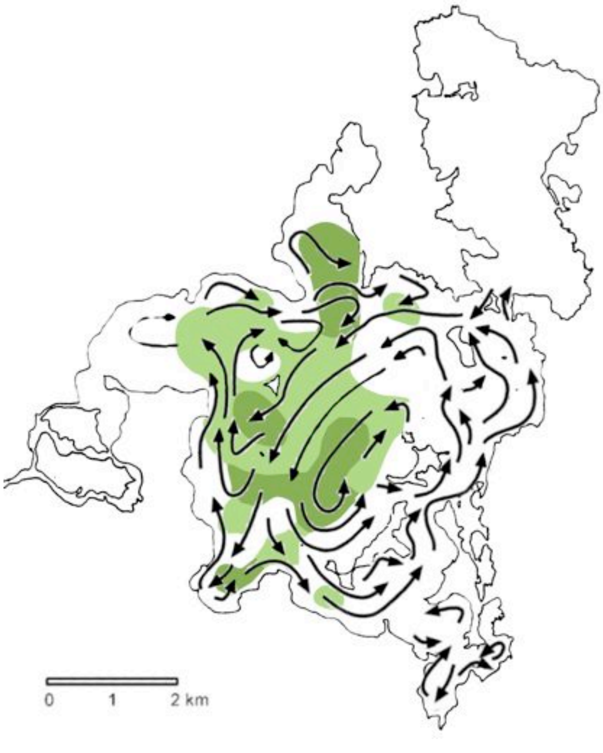


Fig. 18. The two preceeding figures combined, showing how storm-driven currents determine the spatial configuration of the algal mat. The mat is thickest where currents change direction and form vortices. ***Myndir 16 og 17 lagðar saman til að sýna hvernig straumakerfið mótar þörungateppið.***

Fig. 19. A cross section of a bleached lake ball from Mývatn, showing the radial arrangement of filaments. The ball is about 10 cm in diameter. ***Þverskurður af aflituðum kúluskít úr Mývatni. Takið eftir hvernig þræðirnir liggja eins og geislar út frá miðju. Kúlan er um 10 cm í þvermál.***

Ecology and fate of lake balls

How are they formed?

The lake balls are neither a bundle of entangled algal filaments (=threads), as one may think, nor are they formed by algae growing around an object like a small stone. Instead they grow radially from a centre in energy rich environment that rolls them about. A growing ball may increase its fresh weight about 50% in 6 months or 4−5 cm per year (Isamu Wakana pers. com). Regeneration of balls and ball patches is poorly understood. In Lake Akan regeneration takes place by recycling of fragmented balls (Isamu Wakana pers. com.). Regeneration of balls in Mývatn may partly be the same way, but the current working hypothesis is that the balls grow from tufts of algae detached from rocky substrate in energy rich environment (Figs. 19 and 20). If the growth rate cited above applies to Mývatn, the lake balls take only two to three years to form. This needs to be confirmed by experiments. A theoretical maximum of ball size is determined by light because of the unfavourable surface to volume ratio in the spherical organism (Yoshida et al. 1994, Nagasawa et al. 1994). Wave energy may break the balls before they reach this theoretical size. According to our working hypotheses lake balls can grow from either broken balls or from epilithic (=growing

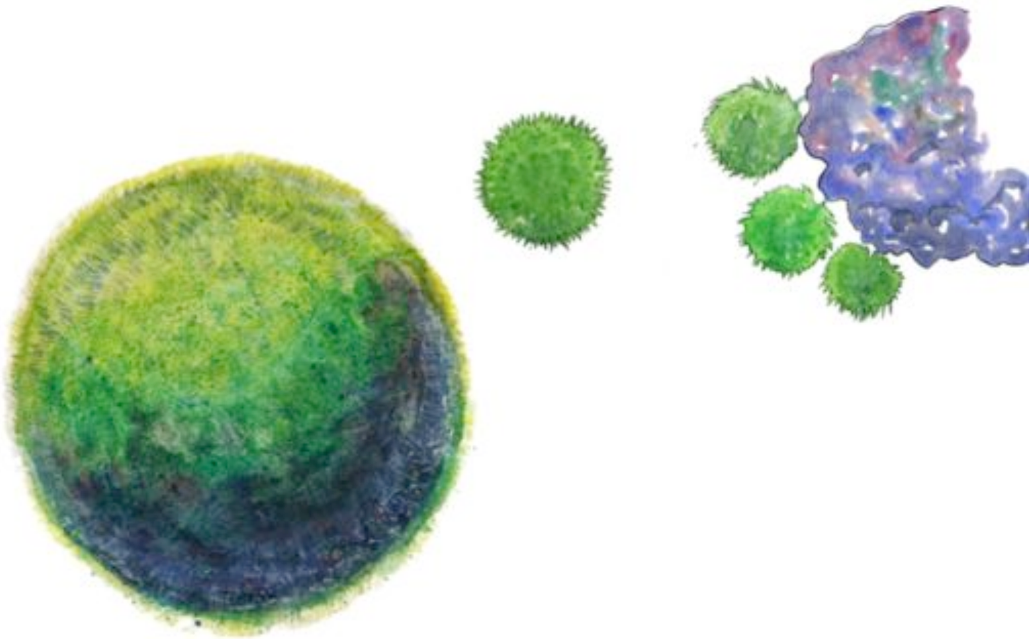


Fig. 19 It is likely that the lake balls form as small dense tufts on rocks in shallow water. Wave-induced currents rip them off as they grow and long-distance, wind-induced currents then accumulate them in areas of vortices. ***Talið er að kúluskíturinn í Mývatni myndist sem smáir dúskar á steinum. Aldan hrífur þá með sér er þeir stækka og straumar flytja þá síðan í flekki á stöðum þar sem straumar mætast í vatninu.***

on rocks) tufts. Balls do not grow from the free-floating tufts that form the bulk of the algal mat (Wakana pers.com.).

One organism?

Does a lake ball constitute a single organism? This is partly a matter of definition. A lake ball may grow from one individual alga, but even so, there is neither a proof nor is it likely that in a fully grown ball the filaments are all connected. Algae, unlike vascular plants, have no transport system of fluids and nutrients, so connectivity is not an issue. It is not unlikely that a lake ball originally grew up from more than one individual but this has never been investigated. Lake balls are not formed from a mixture of species. Lake balls are usually made of *Aegagropila linnaei* but other algal species may also form lake balls under certain circumstances (Wakana pers. com).

How are lake ball patches generated?

It is not known in detail how lake ball patches are generated, but the working hypothesis is that the small tufts detached from rocks gradually travel by storm-driven currents to places where circulation allows them to settle. The hypothesis is based on three main observations: (1) loosely attached dense-filament tufts have been observed on rocks in Mývatn (Fig. 20); (2) the main patches of the algae, including the lake balls, occur where storm-driven currents change direction, according to the hydrodynamic model of the lake (Fig. 18), and (3) the lake ball patches contained mainly full grown balls. There were some half-grown balls but no balls smaller than that. The last observation might indicate that either the lake ball patches were not recruited at all or, alternatively, that the balls were being sorted by the currents, i.e. only after reaching a certain minimum size the balls would be carried to the patch locations. A cross section of a thriving lake ball patch can be seen in Fig. 22.

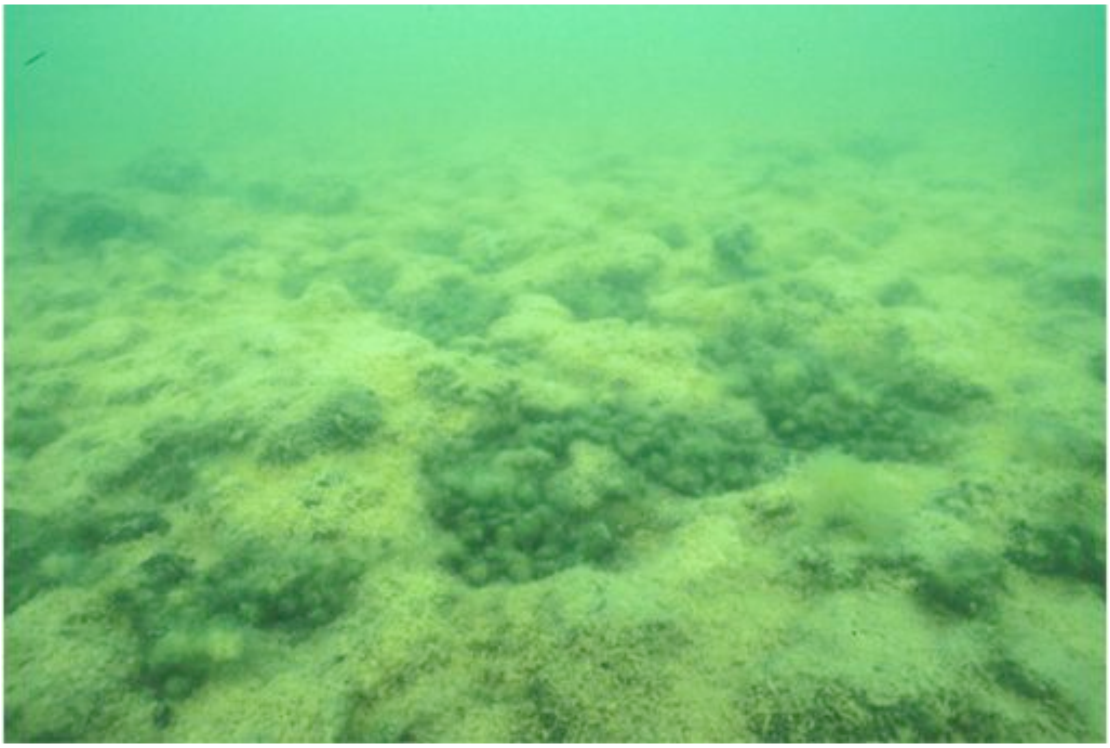


Fig. 20. Tufts of *A. linnaei* growing loosely attached to a rock slab in Lake Mývatn in 2001. Photo by Isamu Wakana. *Dúskar af vatnaskúf sitja fastir á klöpp í Mývatni. Myndin er tekin 2001 (Isamu Wakana).*

One working hypothesis that was tested but rejected was that the lake ball patches were somehow supported by underlying bedrock or sandy layers preventing the balls from sinking in the mud. Long sediment cores taken from the SW lake ball patch showed no such feature, but revealed metres of soft homogeneous sediment interrupted by the usual tephra layers. Mapping of the lake ball patches revealed, however, slabs of rock sticking out of the mud (cf. Fig. 29). Although the rock outcrops are small in comparison with the area of balls, it is conceivable that during episodes of strong wind-driven currents they create eddies that herd the balls together.

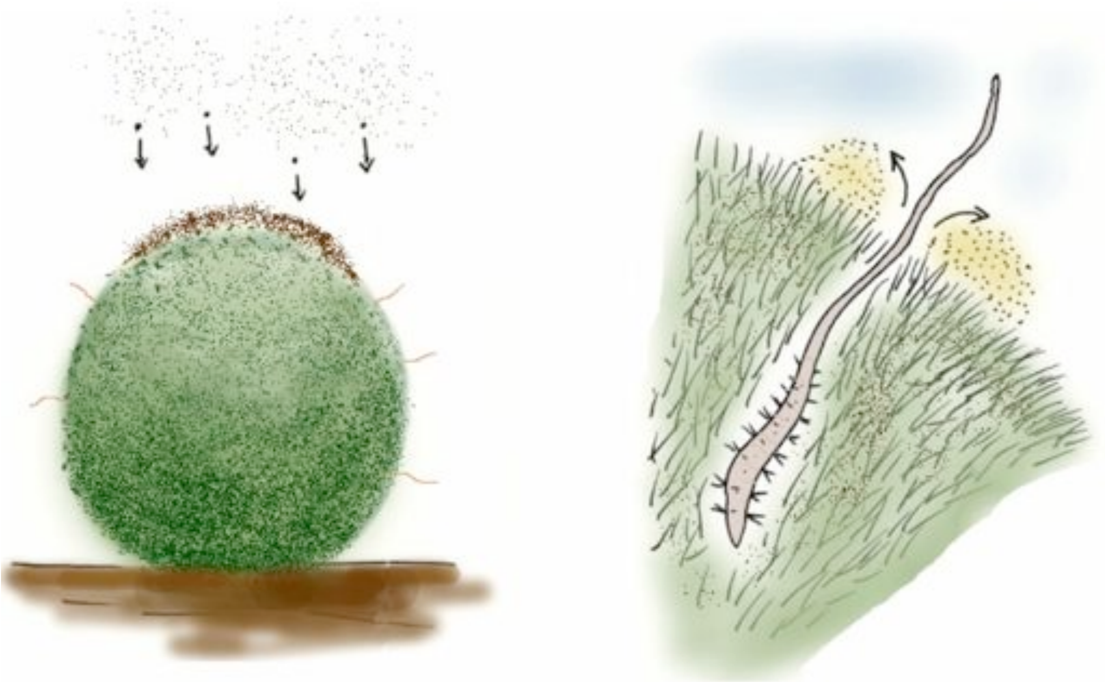
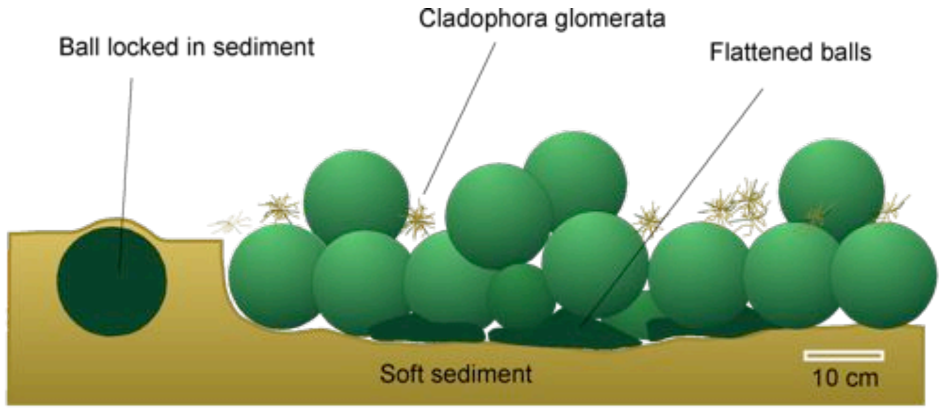


Fig. 21. Oligochaetes feeding on detritus trapped in the matrix of algal filaments. Fecal analysis indicates that the worms do not feed on *A. linnaei* but detritus only.
Ánar lifa í kúluskítnum og éta grot sem safnast saman í þörungaflókanum. Greining á saursýnum gefur til kynna að ormarnir éti eingöngu grot en ekki kúluskítinn sjálfan.

White lake balls

In the year, 2001, white lake balls were observed in the SW patch. The white balls were found scattered on top of the colony at the approximate density of one per 4 m^2 (Fig. 28 D). The white, or yellowish-white, colour was confined to the outermost 1-2 cm of the ball, the inside was naturally dark green. The only reasonable explanation for this phenomenon is sporulation (spore formation). Apparently it has never been observed in this species but in related species the normal cell contents, including the chloroplasts, are replaced by spores. Microscopic examination did reveal empty cells but not any spores. Whitish lake balls were searched for in the consecutive years but were never observed again in Mývatn.



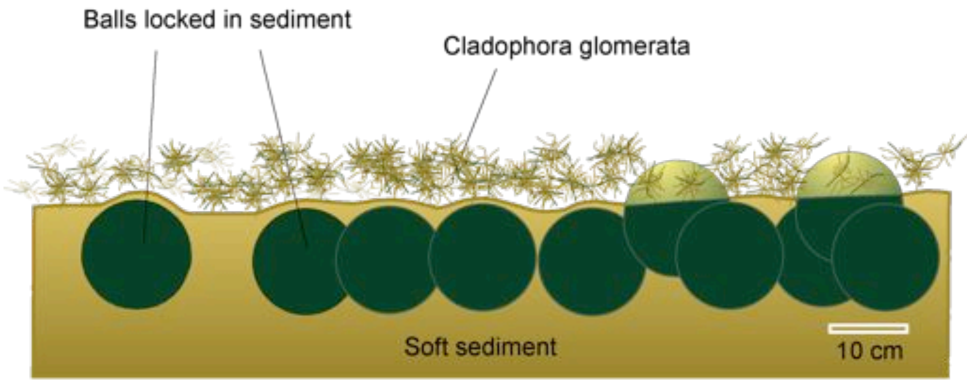


Fig. 22. Schematic cross sections of the SW lake ball patch in 2001 (upper figure) and 2012 (lower figure). Upper figure from Einarsson et al. (2004). ***Þverskurður af kúluskítsflekk í Bekraflóa 2001 (efri mynd) og 2012 (neðri mynd). Byggt á athugunum kafara. Efri myndin er úr grein Árna Einarssonar o.fl. (2004).***

The role of oligocheate worms

Lake balls in Mývatn are colonized by oligochaete worms which feed on the detritus that is caught in the algal matrix (Fig. 21). The worms defecate on the outside of the ball, creating heaps of feces on the surface and if a ball, cleaned on the outside, is left in a an aquarium overnight, a substantial amount of detritus accumulates on the bottom. The relationship seems to be a type of commensalism where the worms get shelter, but benefit the algae by cleaning them. The oligocheates have not been identified to species.

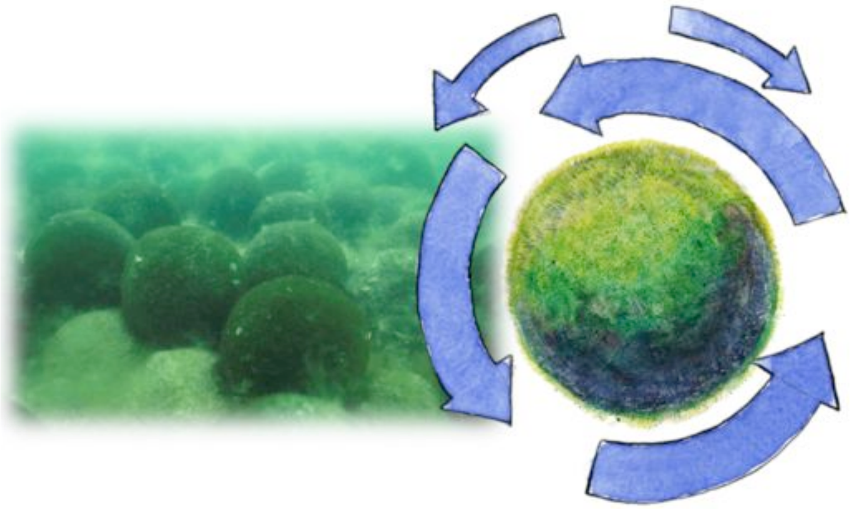


Fig. 23. Lake balls are kept clean by moderate wind-induced currents. Modest wave activity rolls the balls back and forth but stronger winds tumble the whole colony, bringing the detritus-covered lower layer back to the light. Light spots on the balls are oligocheate feces, cf. Fig. 21. ***Straumar í vatninu vegna ölduhreyfinga rugga kúluskítnum til og frá svo að hann nær að hreinsa sig af gruggi sem sest á hann. Sterkari straumar hræra upp í samfélaginu og losa undirliggjandi kúlur úr prísundinni. Ljósir dílar á kúlunum eru pínulitlar hrúgur af ánaskít, sbr. 21. mynd.***

A description of a lake ball colony and its demise

The first observation that indicated that the lake ball patches were contracting was made in 1999 when a visit to the eastern area revealed only a few small patches where huge colonies were observed in the 1980s. There was no clue as to the reason for this enormous decline. In contrast, a visit to the SW patch showed no sign of shrinking, and the density was about 150 balls per m^2. A cross section of the colony showed 2−3 layers of balls. The lowermost layer was consisting of flattened balls which formed a pavement on which the round balls were moving (Fig. 22). The round balls in the top layer were mostly fresh looking, dark green and clean, being free to move with the wave-induced current. The underlying balls tended to be stationary and covered by detritus to a varying degree, but not showing clear signs of decay. This seemed to indicate that moderate wave activity kept the uppermost layer clean and moving, but during storms the whole colony would be tumbled, shifting balls between the layers (Fig. 23). There was evidence that in places the whole colony had been covered by mud and then been freed again by water currents, leaving stacks of balls, cemented together by mud (Fig. 28 B). Outside the colony isolated balls were found buried in mud and unable to move. Some of the single balls were free to move and seemed to

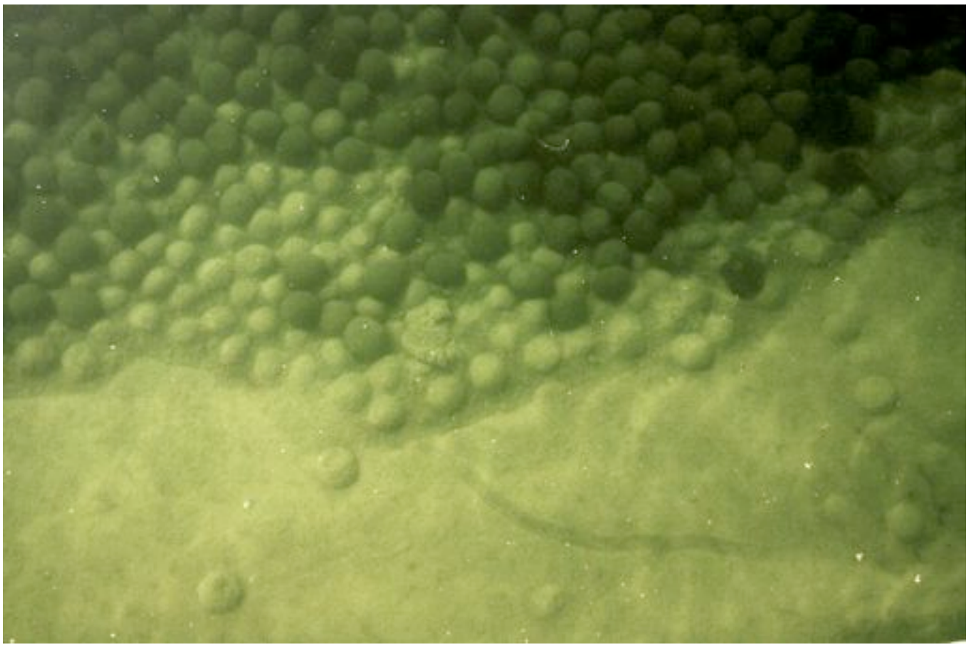


Fig. 24. Edge of the lake ball patch in the SW area seen from above in 2006. Note the sharp edge and how the mud is transported into the lake ball patch. The single ball outside the main patch has a pit in the top, indicating that it is hollow and decaying from the inside. ***Jaðar kúluskítsflekksins í Bekraflóa séð ofan frá í júní 2006. Takið eftir skörpum kanti og hvernig leðja berst inn á kúluskítsbreiðuna. Tvær kúlur utan flekks eru með holu, sem gefur til kynna að þær séu holar að innan og byrjaðar að rotna innan frá. Kúlurnar eru um 12 cm í þvermál.***

do so within a "footprint" or a small, oblong depression in the bottom, created and maintained by the moving ball itself. The edges of the colony were sharp, defined by the likewise sharp edges of the surrounding mud (Fig. 22 and 24). A thin layer of loose tufts of *Cladophora glomerata* was spread atop the *A. linnaei* ball colony. In 2006 all the known colonies were mapped. The SW colony had changed shape from what it was in the years before but remained similar in size. In 2007 and 2008 the size was reduced to about 50% of what it was in 2006 (Fig. 25).

In 2012 it became clear that the SW colony was vanishing. Only single balls were seen from the boat, and they formed a line from east to west and most were half buried in mud (Figs. 22 and 26 B). Scuba diving showed that many balls were lying just under the mud surface (Fig. 26 D), which was covered by a 2−4 cm thick mat of diatom-covered *Cladophora glomerata*. Shoots of *Myriophyllum sibiricum* were emerging in a few places (Fig. 26 C), something not seen before in the lake ball patches.

The scattered lake balls that reached out of the mud surface and were visible from the boat were half submerged in mud and unable to move. Most of the balls checked were soft and apparently hollow inside, which is a sign of decay.

To the north of the line of balls a large area of disintegrated balls was found (Fig. 26 A). This area is the northern part of the lake ball area mapped in 2006.

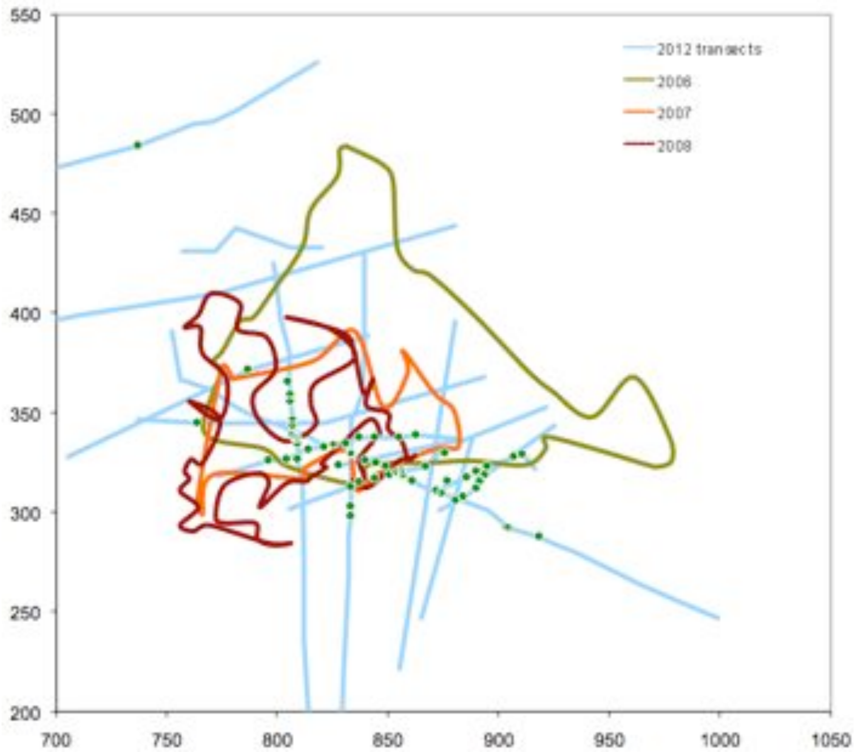


Fig. 25. The SW lake ball patch in 2006-2012. The outlines in 2006-8 were traced from a boat with a GPS equipment in clear water. The boat transects made in 2012 are shown with blue lines and observations of lake balls indicated with green dots. Scuba observations showed that the area immediately north (=up) of the green dot area had lake ball beds covered by mud and *Cladophora glomerata*. Further north the bottom was covered with lake ball fragments. Scale in m. ***Kúluskítsflekkurinn í Bekraflóa 2006-2012. Útlínurnar 2006-2008 eru dregnar eftir athugunum úr báti með aðstoð GPS-tækis í tæru vatni. Athuganir 2012 voru gerðar í grugguðu vatni þar sem ekki sást eins vel til botns og byggðust á sniðum (bláar línur). Grænir punktar merkja staði þar sem stakar kúlur sáust, en engir flekkir fundust. Athuganir kafara leiddu í ljós að rétt norðan við kúlusvæðið var flekkur sem hafði grafist alveg í leðju og var þakinn af*** **Cladophora glomerata*****. Skammt norður af honum var flekkur sem eingöngu samanstóð af sundruðum kúlum. Mælikvarðar á ásum sýna metra.***

What happened to the large eastern patch?

The patch was 23 ha in 1979 but aerial photographs indicate that by 1990 it had almost disappeared from the mud surface. The reason is not known, but scuba divers in the area in 1989 found lake balls covered by 5 cm of mud and no balls on top of it (Jóhannesson and Birkisson 1989). This seems to indicate that mud transgression was

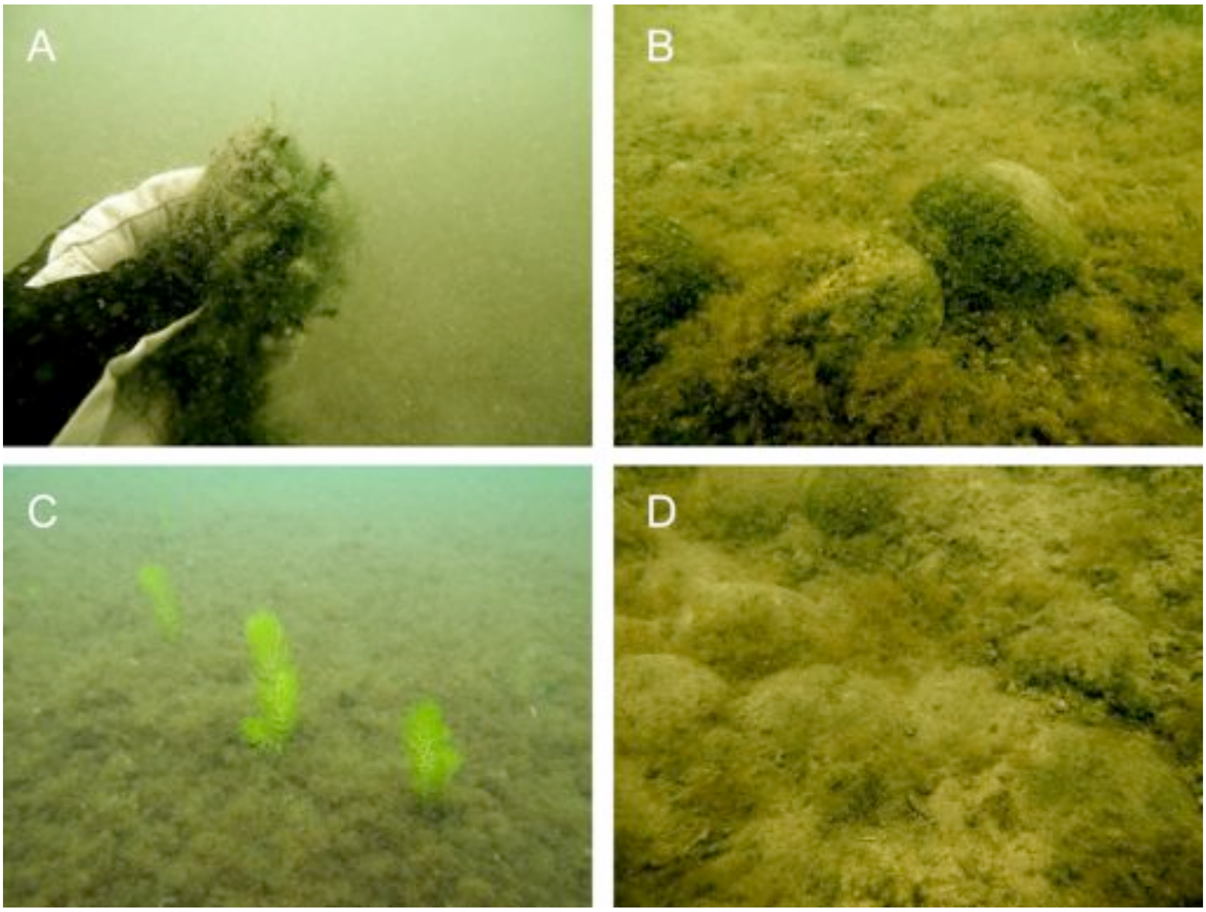


Fig. 26.

A. Disintegrated lake ball. SW area. Cyanobacteria bloom in the water.

B. Two lake balls half submerged in mud and surrounded by diatom-covered *Cladophora glomerata*.

C. *Myriophyllum* cf. *sibiricum* growing in a mat of diatom-covered *Cladophora glomerata*. SW lake ball area.

D. A lake ball bed covered by mud and *Cladophora glomerata*. SW area.

All photos taken in the SW lake ball area in June 2012 by Isamu Wakana.

A. Kúluskítur sem hefur leyst upp og myndar nú breiðu af sundurlausum þráðum á botni Bekraflóa þar sem áður var þétt breiða af kúlum. Blábakteríur grugga vatnið.

B. Tveir kúluskítar, u.þ.b. 12 cm í þvermál, að hálfu leyti í kafi í leðjunni.* Cladophora glomerata *myndar slikju yfir og umhverfis kúlurnar.

C. Botn, þar sem áður var þéttur flekkur af kúluskít, er hér þakinn teppi af* Cladophora glomerata*, sem sjálfur er þakinn kísilþörungum. Vatnamari byrjaður að vaxa.

D. Kúluskítsbreiða á kafi í ljósri botnleðju í Bekraflóa. Vel sést móta fyrir þremur kúlum vinstra megin. Þörungurinn* Cladophora glomerata *myndar gulbrúna slikju yfir.

Allar myndirnar teknar í Bekraflóa í júní 2012 (Isamu Wakana).

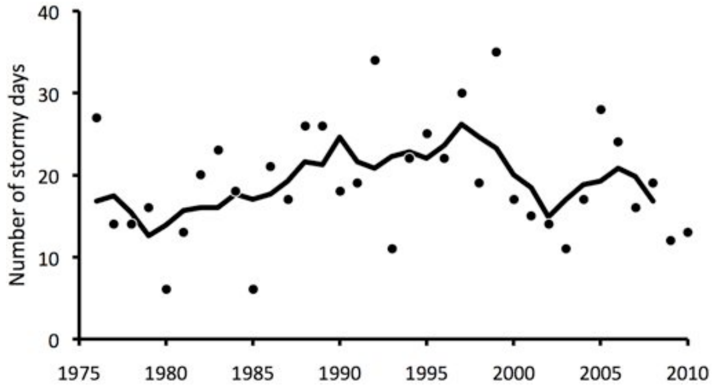


Fig. 27. Storminess in the Mývatn area in 1976-2010. Line shows 5-year running average. A stormy day is defined as a day with at least 6 Beaufort in the period June-September. ***Vindasemi við Mývatn árin 1976-2010. Línan sýnir 5 ára keðjumeðaltal. Vindasemin er gefin upp sem fjöldi daga með vind uppá a.m.k. 6 vindstig á tímabilinu júní-september (en þá er vatnið íslaust).***

taking place there too, but the scarcity of data must be emphasized. On 5 July 2012 one of the small patches from 2006 was visited. It is in the eastern part of the South basin, west of Hrúteyjarsund (Fig. 29). The patch looked healthy. Despite a close packing of balls they seemed free to move and did not show any obvious signs of decay. Most balls were unbroken and they did not have a depression in the top, indicative of a hollow inside. Lake balls were the only plants observed. They seemed to be thriving despite a thin layer of light coloured detritus on top of them. The areal of the colony was similar to that of 2006. North of the colony large outcrops of rock were protruding from the sediment and smaller slabs were seen in several places inside the colony and also some medium sized stones. Lake balls were not seen on top of the rocks, and there was no indication of algae attached to the rocks. The south edge of the colony was rather sharp and south of the edge the bottom appeared to be bare mud. When the 2006 map was superimposed on the 2012 map the north edge of the 2006 colony coincided with the south edge in 2012 (Fig. 29). It seems that the patch had moved its width in 6 years. Hydrodynamic modelling (Kjaran & Hólm 1991) yields southerly currents in this area during storms from the SW. These currents may have buried the southern part of the colony, or moved it towards the rocks. When the patch location was revisited in 2013 no trace of lake balls was found on the sediment surface. It had vanished.

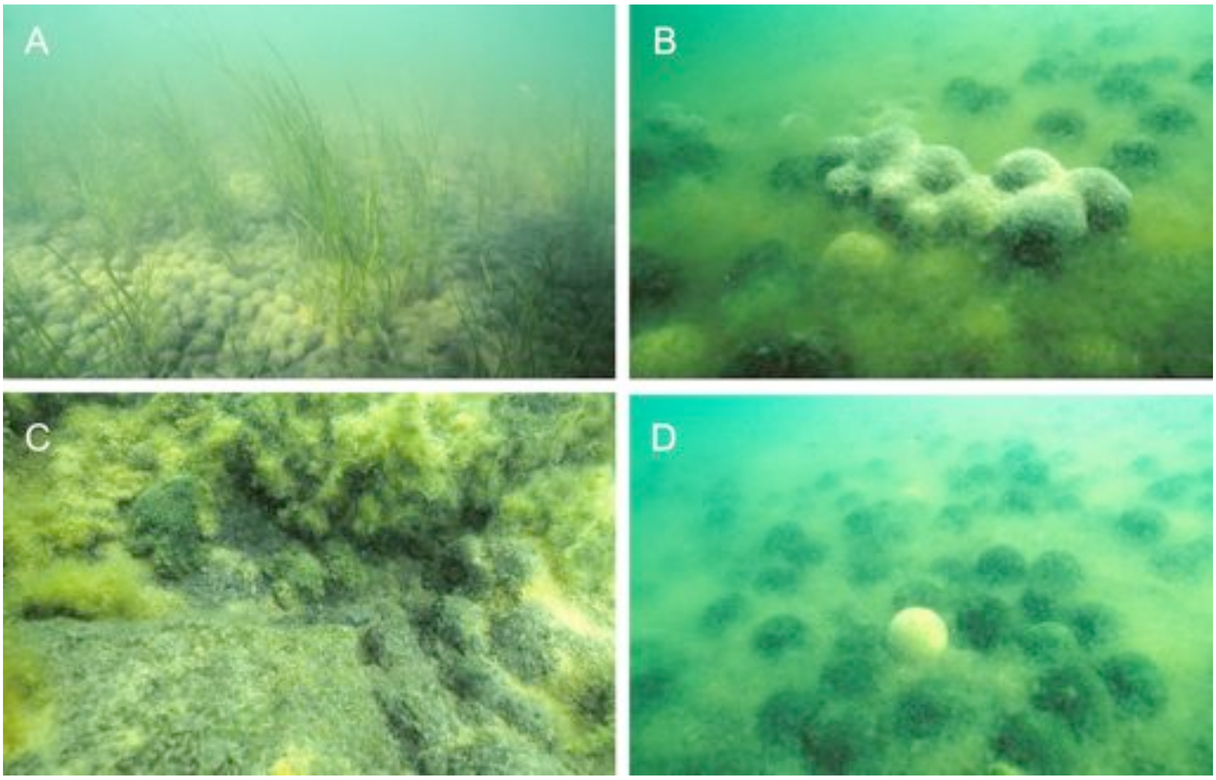


Fig. 28.

A. The lake ball patch in the North Basin in 1999, in a bed of *Potamogeton filiformis.*

B. A stack of lake balls "glued" together by muddy sediment. *Cladophora glomerata* covers the lake ball colony. SW area.

C. The epilithic form of *Agagropila linnaei* (dark green) growing on a rocky bottom with *Cladophora glomerata* (light green).

D. A lake ball bed covered by *Cladophora glomerata*. A discoloured lake ball in the foreground, another one in the distance. SW area.

All photos taken in Lake Mývatn (Isamu Wakana).

A. Kúluskítsbreiða í Ytriflóa innan um þráðnykru.

B. Stafli af kúluskít, "límdur" saman af leðju.* Cladophora glomerata *myndar slikju yfir kúluskítsbreiðunni.

C. Dökkgrænn botnfastur vatnaskúfur á grjótbotni.* Cladophora glomerata *(ljósgræn) í kring.

D. Kúluskítsbreiða í Bekraflóa. Þörungurinn* Cladophora glomerata *myndar gulgræna slikju yfir. Hvítur kúluskítur trónir í forgrunni, annar eins í fjarska.

Allar myndirnar eru teknar í Mývatni (Isamu Wakana).

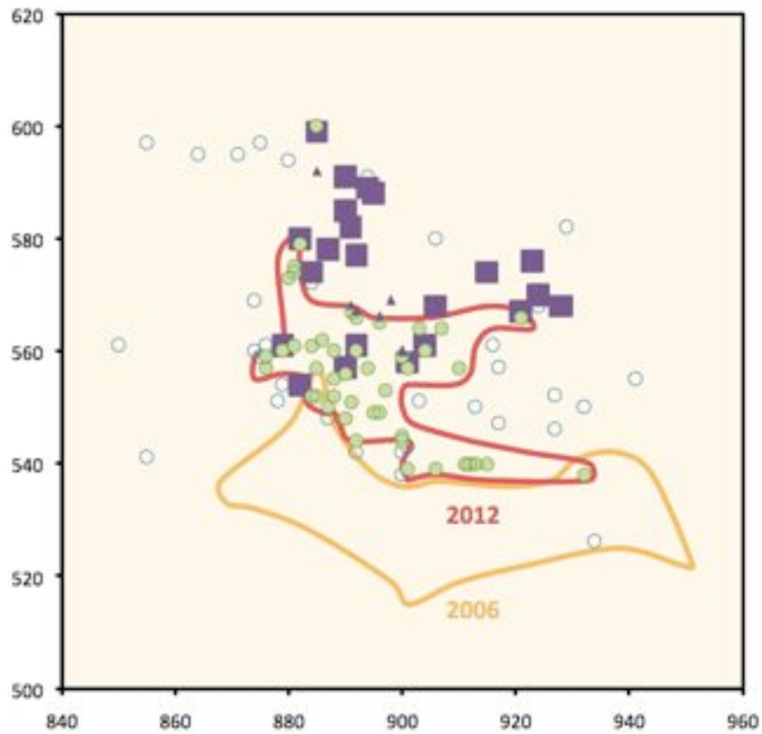


Fig 29. A map of a lake ball patch west of Hrúteyjarsund 5 July 2012. Symbols indicate observation points: Green circles (lake balls), open circles (bare mud bottom), squares (rock slabs) and triangles (stones). The outline of the patch in 2006 is also indicated. Scale in meters. North is up. This patch had disappeared in 2013. ***Kort af einum kúluskítsflekkjanna vestur af Hrúteyjarsundi 5. júlí 2012 (rauð lína). Fylltir hringir sýna staði þar sem kúlur fundust, opnir hringir þar sem engar kúlur voru. Ferningar sýna klappir og þríhyrningar staka steina. Útlínur sama flekks árið 2006 eru sýndar með rauðgulri línu. Sumarið 2013 fannst enginn kúluskítur á þessu svæði. Mælikvarði í metrum. Norður vísar upp.***

Lake balls in the North basin

Lake balls were discovered in the North basin of Mývatn around 1989. They only grow to a small size (3-4 cm) and grow attached to the rizomes of macrophytes such as *Myriophyllum*. Loose balls tended to accumulate in a small bay on the south shore of the basin (Fig. 28 A) but have not been found there for many years now. The balls in the North basin have neither a known nor a likely connection with those in the South basin.

Reason for the decline of the SW patch

Although reduced of light must be the overall reason for the shrinking of green algal beds, sediment movement is clearly one of the proximate factors involved in the

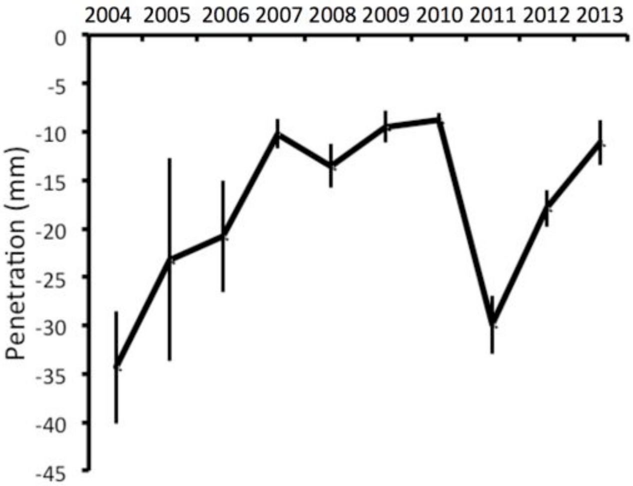


Fig. 30. The strength of the sediment surface (mean with 95% confidence limits) in the middle of the South Basin in the period 2004-2013. The graph shows how deep a standard object penetrates the sediment under its own weight. In years of high midge densities (2007-2010) the penetration was very short. The effect is due to silk spinning activities of the midge larvae. ***Burðarþol leðjunnar í efsta setlaginu á Mývatns árin 2004-2012. Burðarþolið fer eftir því hve mikið er af mýlirfum á botninum, en þær spinna silkiþræði sem binda leðjuyfirborðið saman. Línuritið sýnir meðaltal og 95% öryggismörk þess á stöð 33 um miðbik Syðriflóa.***

demise of the lake ball patches. Overall the change in the SW lake ball patch can be interpreted as an invasion of mud from north to south. The sediment kills the balls by covering them and preventing their movement. Sediment (mud) moves into the lake ball patches either by deposition of resuspended sediment or by lateral transport (drift) along the bottom. If a storm-driven current brings enough sediment into the patch to stop the motion of the balls a new storm, with less sediment transport, is needed to break them loose and restore their mobility. As long as the balls move relatively freely with the wave motion of the lake they will get rid of most of the settling sediment after resuspension events. Moderate storminess is likely to be beneficial for lake ball algae. It keeps the balls clean and does not translocate too much sediment.

The sharp edge of the bottom sediment on the north side of the colony (Figs. 22 and 24) is clearly the front of a propagating wave of mud moving in from the north-east, and it must be moved by wind-induced water current. As described earlier in this report, south-westerly storms are the most frequent. They force the lake water towards the north-east along the shores, but the water that accumulates at the north end forces its way back, against the wind, in a stream across the middle of the lake and hits the SW colony from the northeast (Figs. 17−18).

It must be assumed that the movement of the mud reflects a relatively recent change, either in the wind regime or the erodability of the bottom. Storminess has indeed changed over the observation period (Fig. 27), with the number of stormy days in the ice-free period increasing from about 15 to over 30 in the period 1977−1999, but since then wind activity has decreased again.

Midge larvae are another factor that influences sediment transport. In years when their density is high, the strength of the sediment surface is increased due to their silk-spinning activity (Ólafsson and Paterson 2004). Since 1970 the amplitude of the midge population cycles has increased, and now, during low midge years, i.e. every 6–9 years, the lake bottom is extremely loose and watery (Fig. 30) (see Einarsson et al. 2004). This may increase both resuspension and lateral drift of sediment. It also reduces the ability of the muddy sediment to support the weight of lake balls.

The most significant factor leading to sediment transport must be the lack of shelter when the algal mat is reduced. The changed sedimentation dynamics resulting from the combined effects of increased storminess, less shelter and the periodic loss of midges may have lead to the lateral sediment transport, killing the SW lake ball patch. The most simple hypothesis is, however, that the changed mud transport is only due to the removal of the algal mat. This leaves increased Cyanobacteria as a single causal factor of both algal mat reduction and the burial of lake balls.

The history of *A. linnaei* deduced from sediment cores

Aegagropila linnaei has chitinous cell walls, which is an unusual feature for green algae, but means that the cell walls are preserved in the sediment for centuries or longer. The history of the species in the lake can therefore be traced in cores from the sediment (Einarsson et al. 1993). Two studies have dealt with this. The first, published in 1993 is a long-term record from a 6 m long core covering the entire history of the present lake (Einarsson et al. 1993), the other is a detailed history of the lake over the last 150 years, as deduced from shorter sediment cores in a sheltered bay (Fig. 4) with high sedimentation rate (Hauptfleisch et al. 2010; Hauptfleisch 2012). The 6 m record shows that *A. linnaei* has always been present in the lake, ever since it was formed about 2300 years ago (Fig. 31). It showed a long term exponential increase with time, probably in response to increased light at the lake bottom due to sediment ation and less water depth.

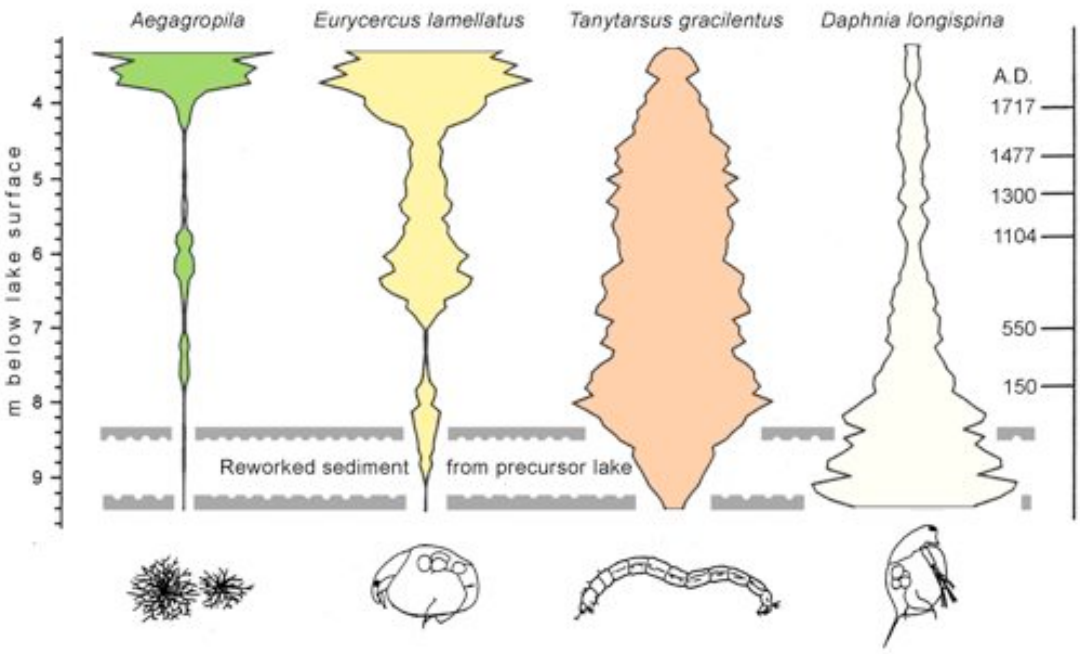


Fig. 31. Remains of *Aegagropila linnaei* and three invertebrates in a 6 m long sediment core from the South Basin of Lake Mývatn. The width of the columns reflects the number of fragments per g organic sediment. Modified from Einarsson et al. (2004). ***Leifar af vatnaskúf og þremur hryggleysingjum í 6 m löngum borkjarna úr setlagi frá Syðriflóa Mývatns. Breidd súlna endurspeglar fjölda leifa í hverju grammi af lífrænu seti. (Úr grein Árna Einarssonar o.fl. 2004).***

Superimposed on this trend were long term oscillations, the lows of which coincided with periods of high tephra deposition (Einarsson et al. 1993). The first low period is represented by the "landnam tephra sequence", which is series of four tephra layers from eruptions in Katla, Grímsvötn and Vatnaöldur in the two centuries before and shortly after *landnam* (Sigurgeirsson et al. 2013). The other period is around A.D. 1477 when a thick tephra layer was deposited in NE Iceland, and also includes a significant layer from A.D. 1717. Analyses of *myxoxanthophyll*, a sedimented pigment derived from Cyanobacteria, indicates that such bacteria flourished in the lake during these volcanic periods. Either the tephra carried nutrients (phosphate?) directly to the watershed or nutrients were released by soil erosion triggered by the tephra. *Aegagropila linnaei* would have suffered from the shading effect of the planktonic Cyanobacteria.

Einarsson et al. (1993) were unable to accurately time the rapid increase in *A. linnaei* in the uppermost 1 m of the sediment (Fig. 31), but it clearly occurred after 1700. In the detailed study of the last 150 years (Einarsson et al. in Hauptfleisch 2012) *A.*

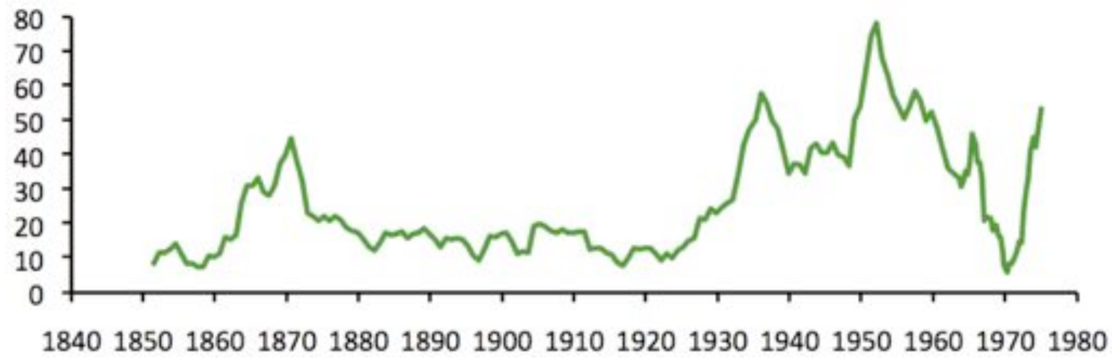


Fig. 32. Density of fragments (per mg organic sediment) of *Aegagropila linnaei* in a sediment core from Lake Mývatn. From Einarsson et al. in Hauptfleisch 2012. *Leifar* A. linnaei *í borkjarna frá vogunum við Höfða. Mælikvarðinn sýnir fjöda leifa í einu mg af lífrænu seti. Úr grein Árna Einarssonar o.fl í ritgerð Hauptfleish 2012.*

linnaei showed three well defined periods of growth. The earliest period was in 1860−1875 and the longest period of sustained density was 40 years in the middle of the 20th century, 1930−1970 (Fig. 32). Another core from the same location, showed a peak in *A. linnaei* in a ten year period, 1985–1995 (Fig. 33).

In the recent core studies a number of other variables were recorded alongside the fragments of *A. linnaei* and some observational data on weather, climate and biota were also available, allowing the testing of several hypotheses about which environmental factors govern the *Aegagropil*a-part of the algal mat.

The results were that growth periods of *A. linnaei* were evidently not ininfluenced by low oxygen conditions (a trigger of nutrient release from the sediment), sandiness of the sediment (making it more firm) (Fig. 34) or diatoms (competition for light and nutrients). The growth of *A. linnaei* in the period 1920–30 coincided with a significant long-term climate warming (Fig. 34), but overall there was no clear relationship with temperature, and the peak in the 19th century was apparently not parallelled by a rise in temperature. The peak in 1985–1995 could be compared with many other variables because the period covered by the core coincides with good meteorological records and detailed ecomonitoring of the lake (Fig. 35). This peak did not correspond to variation in temperature, cloudiness or minerogenic matter (sandiness), and not with midge abundance either (firmness of the sediment surface). There was a negative correspondence between *A. linnaei* and variation in grazing pressure from ducks (Fig. 35) but the grazing pressure was generally low so it is rather unlikely that the algae were grazed down by the ducks.

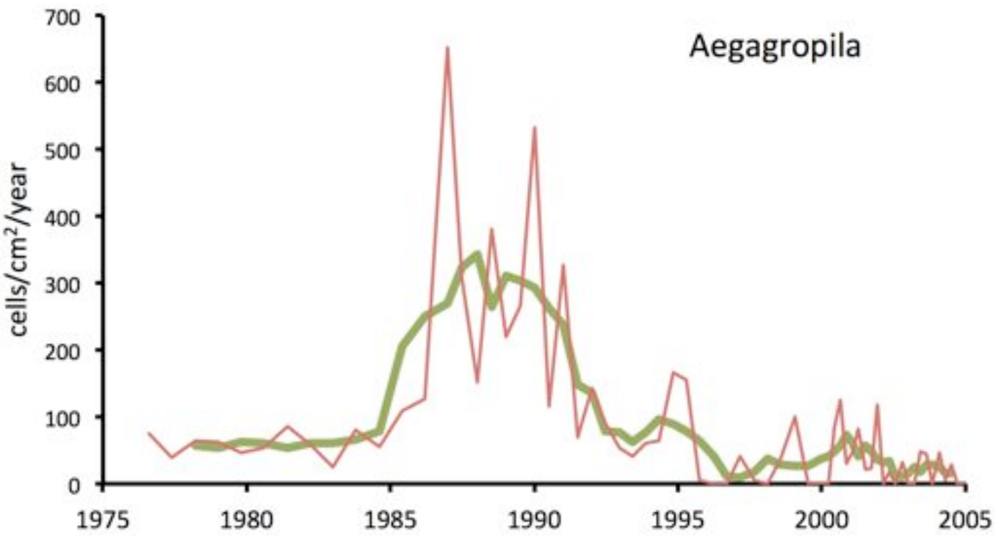


Fig. 33. Deposition rate of fragments of *Aegagropila linnaei* in a sediment core from Lake Myvatn. Fat line is 5 point running averages. From Einarsson et al. in Hauptfleisch 2012. ***Ákoma (fjöldi frumna á fersentimetra á ári)*** **Aegagropila linnaei** ***í borkjarna úr Mývatni. Segir til um hve mikið botnfell af leifum þörungsins á flatareiningu. Feita línan er 5 punkta keðjumeðaltal.***

In the 150 year record there was no relationship between *A. linnaei* and the large scale ecosystem fluctuations in the period 1860–1930 manifested in large fluctuations in fish catch and duck egg harvest, synchronized with periods of alternating high Si-Ca vs. Fe-S concentrations interpreted as alternating periods of benthic production and benthic anoxia (Einarsson et al. in Hauptfleisch 2012).

The last 35 years of ecomonitoring have also seen large scale fluctuations in the biota, characterized by alternating 3-4 year periods of high midge (chironomid) densities and clear water and periods of low midge abundance and turbid water (Ives et al. 2008; Einarsson et al. 2004). These fluctuations affect the sediment, light and nutrients in various ways that might be expected to influence the growth potential of *A. linnaei* or its competitor *C. glomerata*. Surprisingly, *A. linnaei* was not readily related with these fluctuations. This contrasts with the mapping from aerial photographs which suggest that the algal mat is much reduced after periods of cyanobacterial blooms. This discrepancy may be due to the fact that the algal mat is not composed of only one, but two species. One of them is preserved in the fossil record and the other may be more sensitive to Cyanobacteria.

While the long term fluctuations in abundance do not correspond to periods of Cyanobacteria, the fossil record does show the impact of individual bloom years (Fig.

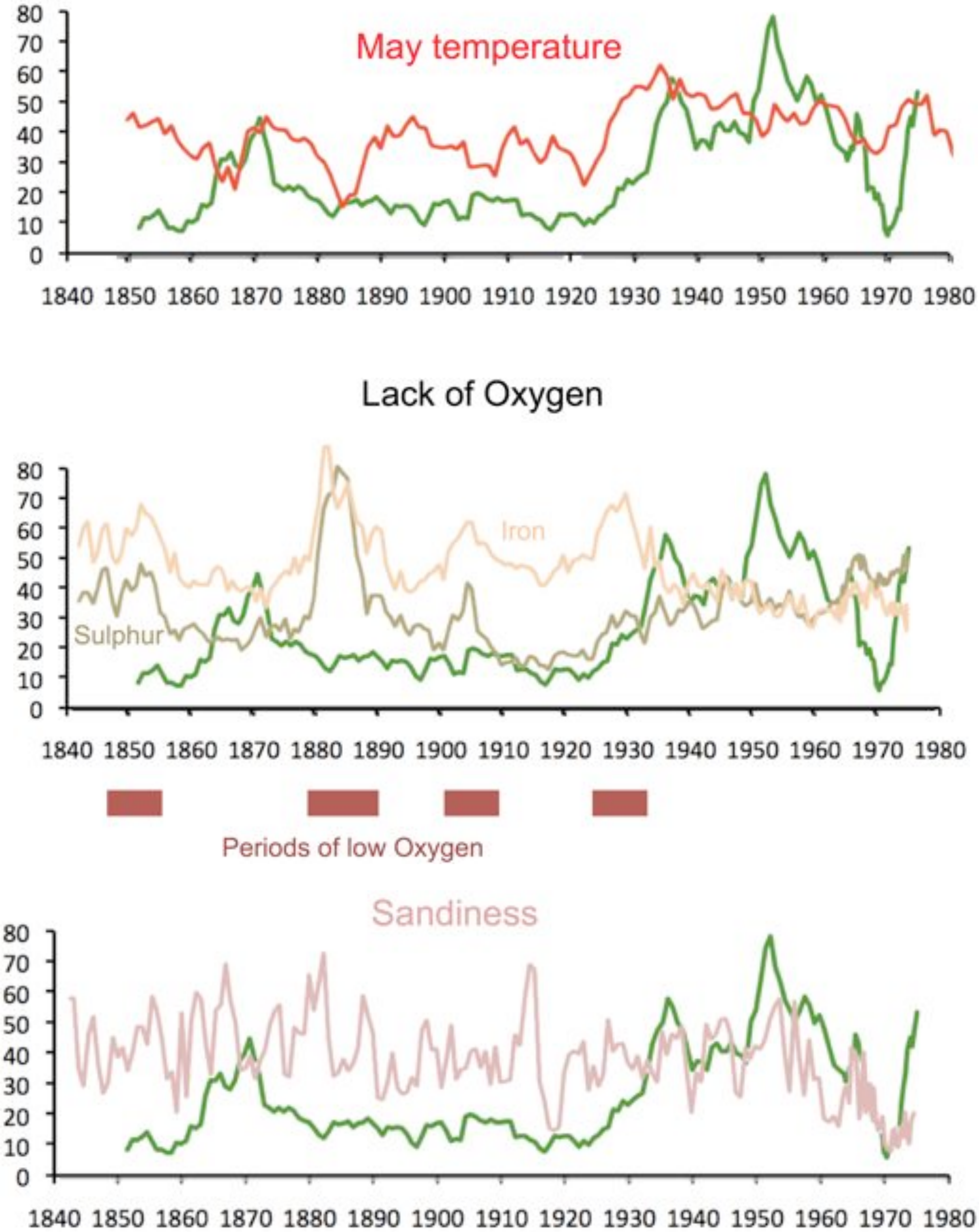


Fig. 34. ***Aegagropila linnaei*** **remains (green line) in a sediment core from Mývatn covering the period c.1850-1975. Also plotted are variables that may influence the species: average May temperature (instrumental from Stykkishólmur, W. Iceland, Jonsson & Gardarsson 2001), Iron and Sulphur in the sediment core (peaks in which indicate lack of oxygen at the sediment surface), and sandiness in the core (which may affect the mechanical properties of the sediment). (From Einarsson et al. in Hauptfleisch 2012).** ***Leifar vatnaskúfs (græn kúrfa) í borkjarna úr Mývatni sem nær yfir tímabilið milli 1850 og 1975. Einnig eru sýndar nokkrar breytur sem gætu haft áhrif á vatnaskúfinn. Efst er meðalhiti í maí (mælt í Stykkishólmi). Í miðið er járn og brennsteinsinnihald setsins í kjarnanum. Toppar í þessum efnum benda til súrefnisskorts við botninn. Neðst er sandmagn í kjarnanum, en það gæti haft áhrif á eiginleika setsins. (Úr ritgerð Árna Einarssonar o.fl í Hauptfleisch 2012).***

Fig. 35. ***Aegagropila linnaei*** **and midge egg remains in a sediment core from Mývatn covering the period c.1975–2005. Also plotted are estimates of duck grazing pressure and data on cloudiness and air temperature (From Einarsson et al. in Hauptfleisch 2012).** ***Efstu tvö línuritin sýna gögn úr borkjarna úr Mývatni (vatnaskúfsleifar ofar og mýfluguegg neðar). Í miðið er línurit sem sýnir beitarálag anda á vatnsbotninum og neðstu línuritin sýna skýjafar og lofthita skv gögnum Veðurstofunnar (Úr ritgerð Árna Einarssonar o.fl í Hauptfleisch 2012).***

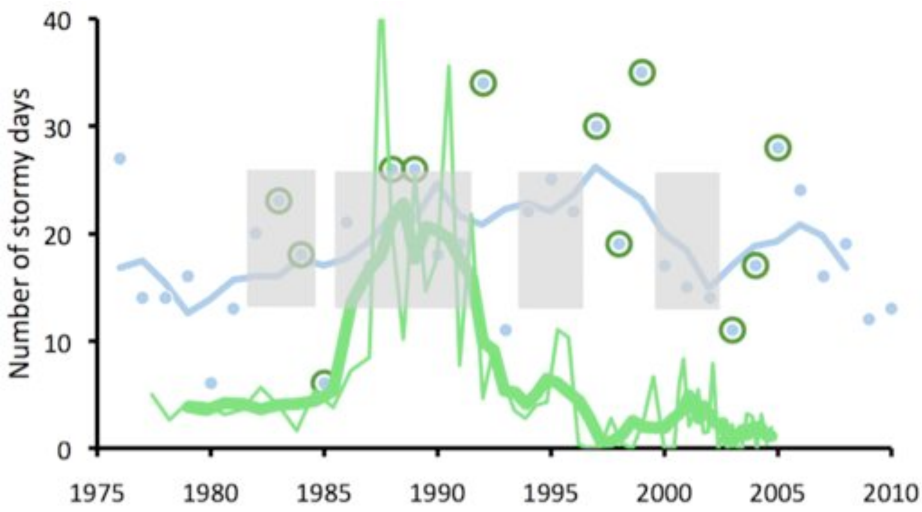


Fig. 36. Periods with moderate winds and low abundance of Cyanobacteria are favourable for the growth of I. Density of fragments of *Aegagropila linnaei* in a sediment core from Lake Myvatn (thin green line). Fat green line is based on 5 point running averages. Blue points are the numbers of stormy days in the ice-free period (May-September) (blue line is 5 point running average). Green rings circle years with Cyanobacteria blooms. Grey boxes indicate periods (3 years or more) characterized by moderate wind activity. Growth periods of *A. linnaei* seem to be limited to clear-water years with moderate wind activity. From Einarsson et al. in Hauptfleish (2012). ***Tímabil með hóflegum vindi og litlu magni blábaktería eru vatnaskúfnum hagstæð. Grænar línur sýna vatnaskúfsleifar í borkjarna úr Mývatni (feita línan er 5 punkta keðjumeðaltal. Punktar merkja fjölda stormdaga að sumarlagi. Ár með blábakteríum eru hringmerkt. Skyggð svæði eru tímabil (a.m.k. 3 ár í röð) með hóflegum vindi. (Úr ritgerð Árna Einarssonar o.fl. í Hauptfleisch 2012).***

36). This indicates that no single factor explains the variation in *A. linnaei*, and an explanation is to be sought in the combined effects of two or more factors. As an example, the abundance of *C. glomerata* in the Great Lakes of N. America has been successfully modelled, based on how the algae respond simultaneously to light, temperature and nutrients (Tomlinson et al. 2010; Canale and Auer 1982).

The most promising combination for *A. linnaei* is that of wind and cyanobacterial blooms. The data from 1977–2005 suggests that *A. linnaei* only thrives at intermediate levels of wind action, and then only if light is not limited by blooming Cyanobacteria (Fig. 36). The reason for this seems logical. The lake is shallow enough that wind ≥ 8 m/s stirs up bottom sediment (Einarsson et al., 2004). In the algal mat *C. glomerata* tended to dominate its upper part whereas the underlying *A. linnaei* was within the sediment where light cannot penetrate. With no wind the underlying algae will die. Moderate wind and wave action is needed to break the mat and bring *A. linnaei* to the light. Obviously the wind is also important for the *lake ball* colonies. The colonies have multiple layers of balls, sometimes covered by a thin layer of *C. glomerata* and clearly have to be reshuffled from time to time to thrive (Einarsson et al. 2004).

Worldwide distribution and decline of *A. linnaei*

A recent overview by Boedeker et al. (2010) describes the distribution and worldwide decline of *A. linnaei*. The species is widespread in the northern hemisphere. It has been found in the eastern North America, Iceland, the British Isles and on the mainland of Europe. It is especially common along the Baltic coast. It has been recorded in the western part of the former Soviet Union, Lake Baikal, and a few places in eastern Asia including Japan. The *lake ball growth form* has been recorded in numerous lakes. Currently it is known from a few lakes in Iceland, in the U.S. (Lake Bemidji, Minnesota), Estonia (Lake Öisu) and Scotland (Loch Watten), Ukraine (Lake Svityaz) and in Japan (Lake Akan). Other lakes have been recorded to have lake balls, but the details are unclear. Colonies of large lake balls were formerly known in a few lakes but in recent years only in Lake Mývatn, Lake Akan (Japan) and in Lake Svityaz in Ukraine. Some regions of the world are well sampled, such as (western) Europe, but the largest parts of the globe are not. The absence of *A. linnaei* in northern North America and Siberia (Fig. 37) could be an artifact of undersampling, despite efforts to locate records from those areas (Boedeker et al. 2010).

Many states have paid special attention to the species because of the popularity of lake balls or because the species is rare or becoming so. *A. linnaei* is included in the national red lists of Belarus, Estonia, Germany, Japan, Russia and Sweden. In addition, *A. linnaei* is explicitly mentioned in the Ramsar specifications of Lake Akan, Japan and Lake Myvatn, Iceland and is officially protected in those two countries. In the United Kingdom, *A. linnaei* is included in the list of rare algae and in assessments of Imortant Plant Areas (Boedeker et al. 2010).

The following account is based entirely on Boedeker et al. (2010), and the references given are from their paper: At several locations *A. linnaei* is already assumed to be extinct. In four out of the five locations in The Netherlands where *A. linnaei* was found 60 years ago, it is now absent, and the unattached forms seem to have disappeared altogether due to the effects of eutrophication (Boedeker and Immers 2009). Balls of *A. linnaei* have been extinct in Lake Zeller in Austria since around 1910, most probably due to effects of human activity (Nakazawa 1974), and only the attached filamentous form has been reported since then (Kann and Sauer 1982). The attached growth form is still present in several larger rivers of northern England and

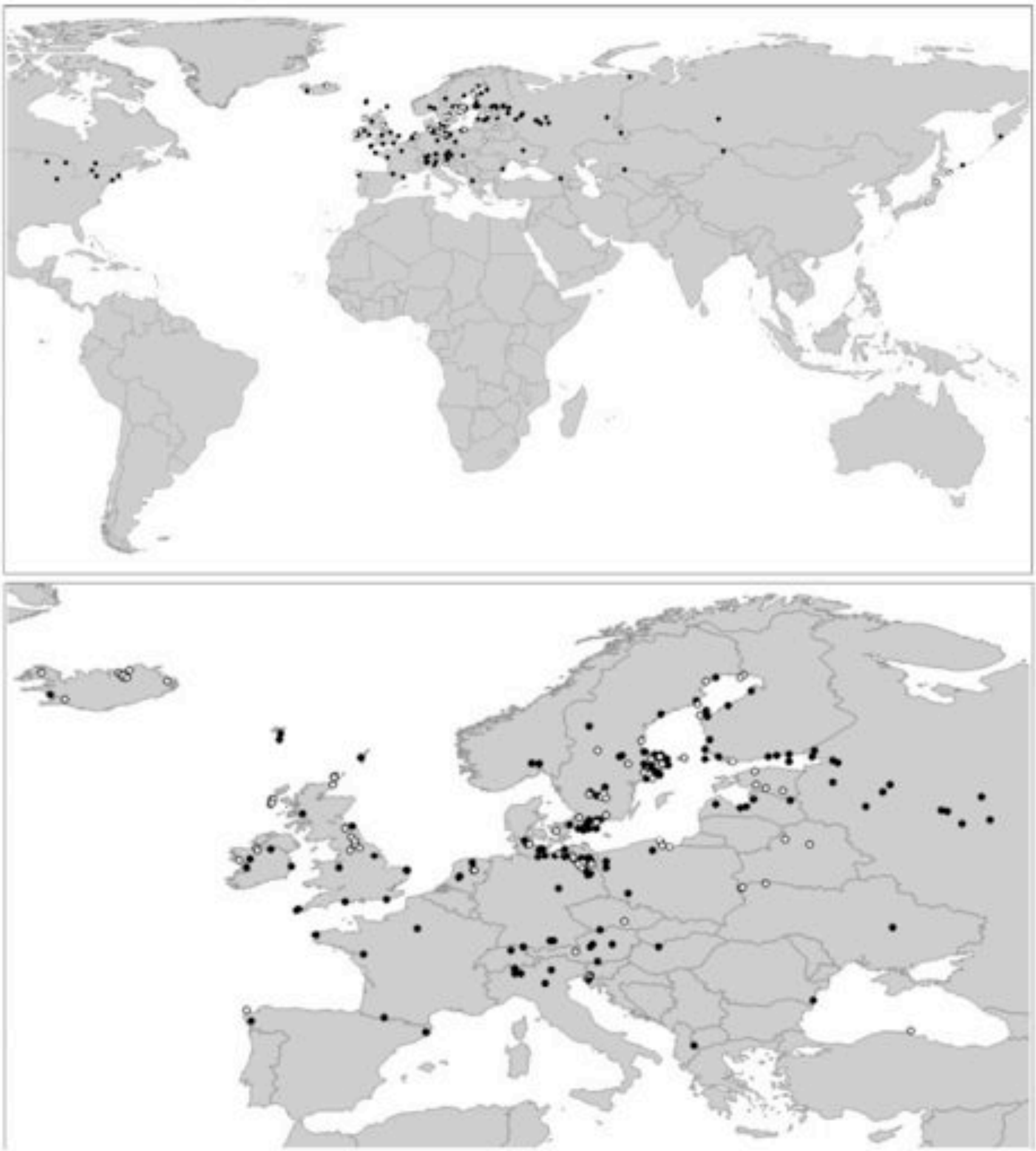


Fig. 37. All known locations of *Aegagropila linnaei.* The lower map shows Europe in more detail. From Boedeker et al. (2010). *Þekktir fundarstaðir vatnaskúfs. Úr grein Boedeker o.fl. (2010).*

Fig 38. A Cyanobacteria bloom (*Anabaena* sp.*)* in the bay at Höfði, a spring water bay on the east side of Mývatn in 2005. This is the first (and only) time that such a bloom has been recorded there. ***Blábakteríublómi („leirlos") í Mývatni við Höfða sumarið 2005. Ekki er vitað til að slíkur blómi hafi borist þangað áður. Pho***

Scotland, but the ball-shaped growth form is found only in a few unchanged locations (John 2002). There is only one location in Denmark (Sorö Sö, Sjæland) where *A. linnaei* occurs, but the species had been found previously in more locations (van den Hoek 1963). In Lake Galenbecker, in northeastern Germany, carp cultivation and intensified agriculture in the 1960s led to eutrophication and extinction of the species (Pankow 1985). Also, in Japan, where the species is still relatively widespread, human activities have led to the destruction of many of natural habitats of *A. linnaei*. Populations of *A. linnaei* have disappeared from two bays in Lake Akan (Wakana et al. 2006). Population declines (both in population density and distribution) have been monitored in Lake Takkobu, Japan, between 1996 and 2004, and are probably a result of eutrophication, such as higher nutrient load, accumulating layers of mud and silt on the marsh bottom, shading by phytoplankton blooms, and an increase in the depth limit of freshwater bivalves (Wakana et al. 2005). Declining populations have also been observed in several other swamp lakes for the same reason (Wakana et al. 2001).

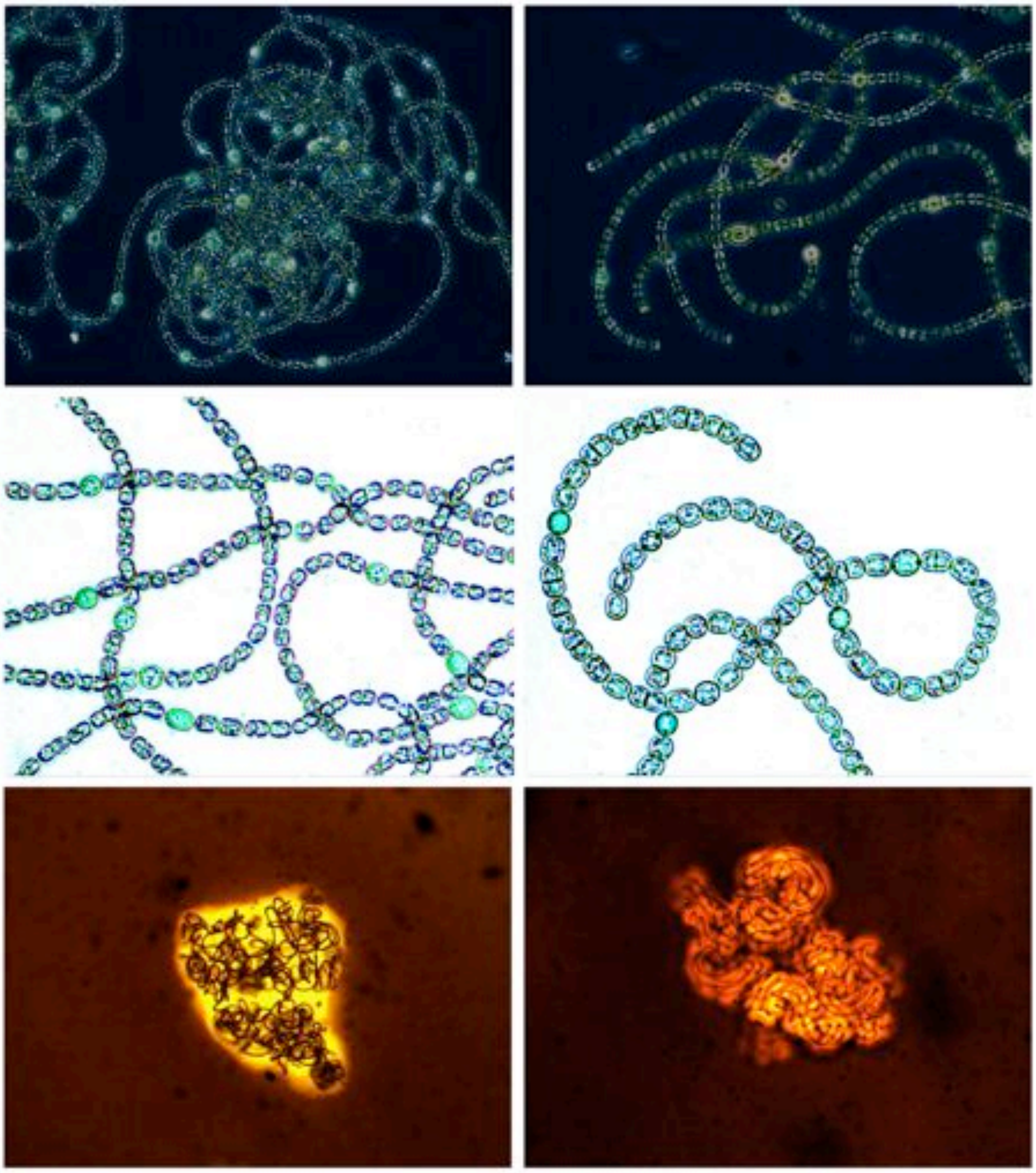


Fig. 39. Bloom-forming Cyanobacteria from Mývatn in 2013. ***Anabaena flos-aquae*** **on the left,** ***A. circinalis*** **on the right. The bottom figures show the gelatinous sheath.** ***Blábakteríur sem mynduðu vatnablóma („leirlos") í Mývatni sumarið 2013.*** **Anabena flos-aquae** ***vinstra megin;*** **Anabaena circinalis** ***til hægri. Neðstu myndirnar sýna hlauphjúp sem umlykur frumusambýlin. Photos by the author.***

The Red Data Book of Estonia lists eutrophication, changes in water hydrology, and dredging as factors that threaten the survival of *A. linnaei* (Lilleleht 1998).

The following account from Boedeker et al. (2010) is so important for the subject of this report that it is cited in full (italics):

"Eutrophication as the main cause for the decline of **A. linnaei.** *Human activities increase and accelerate the external supply of nutrients to aquatic ecosystems worldwide (e.g., Smith et al. 1999, MEA 2005). Freshwater habitats especially face increasing threats from physical alteration, changes in water level and salinity, overexploitation, introduction of non- native species, herbicide and other biocide runoff, airborne pollution, and nutrient loading (MEA 2005, Revenga et al. 2005). Eutrophication of aquatic ecosystems is a common process worldwide and leads to the loss of unique habitats and a reduction in biodiversity (e.g., Bayly and Williams 1973, Smith et al. 1999).*

Enrichment of nitrogen and phosphorus loadings selects for fast-growing algae (phytoplankton, macroalgae such as Ulva *or* Cladophora *species) at the expense of slower-growing species (Duarte 1995), such as some charophytes, for example, or A. linnaei. Shallow lakes are especially prone to the regime shift from aquatic macrophytes to phytoplankton dominance.*

The decline of several freshwater algal groups has been attributed to eutrophication effects; such groups include macroscopic Nostoc *species (Mollenhauer 1998, Mollenhauer et al. 1999), desmids (Coesel et al. 1978, Geissler 1988), and charophytes (Geissler 1988, Blindow 1992, Nagasaka et al. 2002). A number of reports on the local decline or extinction of populations of* A. linnaei *mention eutrophication as a responsible factor (Pankow 1985, Wakana et al. 2001, 2005, 2006; Boedeker and Immers 2009).*

Our literature study showed that A. linnaei *occurs in several different lake types, but most typically in shallow, oligomesotrophic, glaciofluvial lakes with reed stands, dense charophyte vegetation, a pH greater than 7, and moderate to high calcium levels. However, the ecological preferences or requirements of* A. linnaei *have never been fully characterized, and conflicting views can be found in the literature with regard to nutrient levels. In a classic volume on European* Cladophora *species, van den Hoek stated that* A. linnaei *(as* Cladophora aegagropila*) "seems to occur only in more or less eutrophic water" (1963). In this study, we collected information on trophic-level changes for a considerable number of lakes where* A. linnaei *occurred historically or still occurs (summarized in table 2). Information on the pristine state (i.e., the trophic level of a water body without anthropogenic influences) was available for 74 lakes (table 2). Ninety-two percent of these lakes were either oligo- or mesotrophic in their pristine state, indicating typical habitats of A. linnaei (with* *regard to the trophic level) that contrast with van den Hoek's conclusion, above. For 61 lakes, information on both the pristine state and the current trophic level could be compared. Of these lakes, 92% were originally oligo- or mesotrophic, but more than half of those 61 lakes (57%) are currently eutrophic; therefore, dramatic changes have occurred in the recent past in many habitats of* A. linnaei. *When looking at all lakes with available information on the current trophic state (n = 80), the numbers are even more dramatic. Sixty-six percent of the lakes are now eutrophic, or had been in the recent past, and* A. linnaei *still occurs in only 39% of those 80 lakes. These numbers correspond to the general findings presented in figure 2, and strongly suggest that* A. linnaei *occurs mainly in oligomesotrophic habitats, and that eutrophication is correlated with the observed decline of* A. linnaei *populations.*

Seemingly contrary to this inferred habitat preference is the finding of populations of A. linnaei *in 15 eutrophic locations (each addressed below). However, in five of these locations (Takkobu marsh, Pon swamp, Kimoma swamp, Lake Akan, and Boven Wijde; see S3 and S4 at www .nationaalherbarium. nl/supplements/boedeker/ BioScience_2010) a strong decline in population size has been observed (Wakana et al. 2001, 2005, 2006, and Boedeker and Immers 2009, respectively), and the future of these populations must be regarded as uncertain. Generally, most eutrophic lakes are turbid and have a poor underwater light climate, but eutrophic clear-water lakes also exist. Shallow lakes, with abundant submerged macrophyte vegetation, may have very clear water with sparse phytoplankton despite relatively high nutrient loadings in lowland areas with soft rock (Phillips et al. 1978). Biological interactions in clear-water lakes differ markedly from "regular" eutrophic lakes (e.g., Jeppesen et al. 1999). The eutrophic clear-water lake Mývatn (Iceland) is well known for its population of* A. linnaei *balls (Einarsson et al. 2004). In Germany, A. linnaei has been found in a couple of eutrophic clear-water lakes (Neuklostersee and Teterower See). In Lake Biwa and Lake Kawaguchi (both in Japan), only restricted parts of the lake are eutrophic, while large parts are still mesotrophic (Nagasaka et al. 2002). Two brackish locations of* A. linnaei *are classified as (slightly) eutrophic (Pojo Bay, Finland, and Lake Mälaren, Sweden), as well as one river (River Wear, Scotland). The only "regular" eutrophic lakes where* A. linnaei *was found were Lake Ülemiste (Estonia) and Lake Tiefwarensee (Germany), but the latter had been recently restored to mesotrophic conditions. Even though the evidence is correlative, these numbers strongly suggest that* A. linnaei *occurs mainly in oligomesotrophic habitats but can persist in eutrophic, clear-water lakes, and that indirect effects of eutrophication* *caused the observed loss of* A. linnaei *populations*."

After dismissing acidification as a significant factor in the decline of *A. linnaei*, because the vast majority of habitats are well buffered and with pH between 7 and 9, Boedeker et al. (2010) conclude that "*Although the exact effects of eutrophication that cause a decline in populations of* A. linnaei *are unclear and require further experimental studies, it seems evident that the decline is correlated with eutrophication*. *This of course is a general problem that is not easily solved, since the process is closely linked to agriculture, tourism, and human demand and population growth, and is therefore linked to politics and economies*."

The reason for decline

The decline in the algal mat, both *A. linnaei* and *Cladophora glomerata*, has occurred all over Lake Mývatn. The mat has been reduced to a fraction of the previous biomass and distribution. The reduction has a parallel in a worldwide decline in *A. linnaei*, which has been attributed to nutrient enrichment from human activity (eutrophication) (see above). Of the many effects of eutrophication, shading by cyanobacterial blooms is most likely to impact the mat-forming green algae. The transparency of the water in eutrophic lakes and ponds is primarily controlled by bloom-forming cyanobacteria. Cyanobacteria influence the algal mat in Mývatn. The algal mat was rapidly reduced in periods of cyanobacterial blooms in the past (see 1990 and 2000 in Fig. 10, p. 17) and sediment core studies indicate a negative relationship between *A. linnaei* and Cyanobacteria on a long time scale (Einarsson et al. 1993). The contraction of the algal mat exposes the underlying muddy bottom substrate to wind driven currents, which leads to relocation of the sediment. The sediment is pushed towards the south by the currents, burying the lake ball colonies on its way, colonies already weakened by the low light.

The blooms show intense fluctuations, more or less in synchrony with midge fluctuations, which have a variable period of 6–9 years. Blooms persist for 2–3 consecutive summers (Fig. 40) but in between the lake is more clear. There is no apparent trend in water transparency over the last four decades (1973–2011, Fig. 40). This may indicate that it was the *long-term eutrophic level* rather than a *trend in eutrophication* that caused the algal mat to disappear. It is possible that the intense and repeated blooms have gradually reduced the algal mat beyond recovery. The

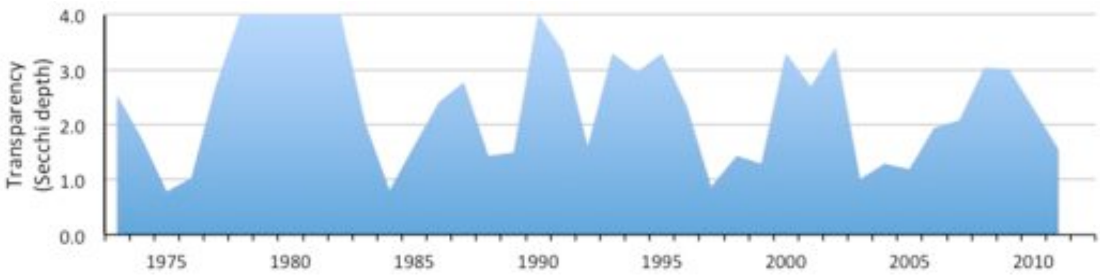


Fig. 40. Transparency (as mean Secchi depth in m in July and August) in the middle of the South Basin of Lake Mývatn in 1973-2011. In the period 1977-88 the transparency is calculated form the catch of *Simulium vittatum* in late summer, based on an unpublished correlation analysis. The maximum value, 4.0, means that lake bottom is clearly visible from the surface throughout July and August. Values 1973-76 are based on fig. 4 in Jónasson and Aðalsteinsson (1979). *Meðalrýni (í metrum) í miðjum Syðriflóa í júlí og ágúst 1973-2011. Hámarksgildum (4 m) er aðeins náð ef vatnið er tært í botn í júlí og ágúst.*

clear-water periods have not lasted long enough for its recovery. Variation in storminess may have helped this development.

The first evidence of the lake ball decline came around 1990 (eastern colony disappearing) which means that the cyanobacterial blooms must already have become too intense by that time. According to the sediment cores the biggest decline occurred earlier, in the late nineteen-sixties. Historical records, summarized in Hauptfleisch (2012) indicate, however, that cyanobacterial blooms were not new to the ecosystem. But possibly the cyanobacterial blooms are more intense, more frequent or more prolonged than before. The timing suggests that the change took place with the industrialization in the lake and its surroundings. No continuous record exists from before the industrial age that allows direct comparison with the current (post 1970) situation.

Management action

Is there a management action that could possibly reverse the situation? First of all it should be made clear that the changes we observe are large-scale, and no in-lake actions seem feasible. Intensified Cyanobacteria blooms are very probably causing the decline. The ecology and dynamics of the blooms in Mývatn are complex and not well understood. It is likely that the blooms result from eutrophication triggered by the mining operation. The mining ceased in 2004 but the lake ecosystem continues to oscillate dramatically, producing periodic blooms of Cyanobacteria. This may be beyond our control but a wise step would be to reduce the present discharge of human derived nutrients as much as possible. It might not reverse the development in the lake but has to be done to prevent further eutrophication in this vulnerable area. Detailed mapping and monitoring of N and P in the groundwater is necessary, and this should be launced as soon as possible. As for lake balls, a survey of their status in other lakes is needed.

Summary

- The lake balls in Mývatn are a growth form of a rather widely distributed species *Aegagropila linnaei* in the northern hemisphere.
- This growth form is rare, and colonies made of large lake balls are only known from three lakes, apart from Mývatn only in one lake in Japan and another in Ukraine. Small lake balls are known to exist in three other lakes in Iceland.
- Two other growth forms live in Mývatn, one grows on rocks the other forms an extensive mat of loose tufts in association with a related species *Cladophora glomerata* on the muddy lake bottom.
- The lake ball colonies in Mývatn were located in areas where wind-induced water currents formed eddies. It is not well known how the lake balls were formed, except that they grew radially from a small tuft, probably originating as attached algae growing in energy rich environments (shallow rock slabs).
- Both the loose algal mat (both species) and the lake ball colonies have declined dramatically in recent years. The lake ball colonies have now vanished and the mat is reduced to a tiny fraction of what it was. Lake ball colonies were first observed to fail around 1990.
- The decline of lake balls is in line with a global decline in *A. linnaei* where eutrophication has been identified as the main cause.
- The algal mat in Mývatn showed large variation in response to changes in cyanobacterial blooms. The mat was much reduced after multiyear periods of intense blooms, and was expanding during clear-water periods. In the long run *A. linnaei* appears to be thriving best under moderately windy conditions.

- The lake ball colonies may have been reduced by poor light conditions but detailed observations of one recently extinct colony indicate that it was buried by mud that was creeping slowly along the bottom from the north.

- Evidently the reduction of the algal mat exposes the underlying mud-water interface, making it vulnerable to wind-driven currents and alters the sedimentation dynamics in the lake. The process may be supported by periodic declines in the firmness of the mud when midge populations crash and also by multiyear periods of increased storminess.

- The most likely single cause for the collapse of the algal mat and the lake ball colonies is increased intensity or duration of cyanobacterial blooms. There is no observed trend in such blooms since 1973. There are, however, pulses of blooms, coinciding with enormous fluctuations in the midge populations and several other components of the ecosystem.

- The intense pulsing of the ecosystem is attributed to a mining operation in the lake in 1967–2004 and this operation may have altered the characteristic of cyanobacterial blooms from the beginning, to make the lake uninhabitable for the algae in the long run.

- There is no straight forward management action to take, other than reducing nutrient (N and P) input from humans as much as possible. N and P levels in the groundwater need to be mapped and monitored. The status of lake balls in other lakes in Iceland should be explored.

EPILOGUE – Canary in the mine

For the author of this report the saga of the lake balls in Mývatn is very much a personal story. Now, when they have disappeared, there is room for some nostalgic thoughts. I remember when it all started. It was on a bright and calm summer day in 1978. I was consciously motoring on a small boat across the lake to a place where the year before a university team of scientists had pulled up a single lake ball during a mapping survey of the bottom. The lake had been turbid with *Anabaena*, and nothing could be observed directly from the boat. But this summer, 1978, the lake was crystal clear. I had spent some time enjoying this new situation, using a glass bottomed box to view the bottom, seeing all the rocks and skerries that the propeller had miraculously escaped in the past years, watching the beds of pondweed and water milfoil, the shoals of three-spined sticklebacks shooting back and forth, the muddy bottom with myriads of midge larvae and the network of tracks made by thousands of ducks trying to scoop them up. I thought it might be worth the while on such a fine day to check if any lake balls could be spotted where that odd ball was fished up last summer. The consensus among the group of scientists working on the lake at the time was that such balls were rare and accidental, − made by filamentous algae rolled up by currents. The catch of that ball in 1977 had to be an unlikely coincidence, − it was caught by a small bottom grab, a device that carves out a 20 by 20 cm piece of the muddy bottom and brings it to the surface along with all the tiny invertebrates that live there. What I saw on this fine day in 1978 when I leaned over the gunwale and looked through the viewer was just mindblowing: a huge field of dark green lake balls, like all the tennis balls in the world had gathered for their annual meeting (Figures 3 and 24 may give you an idea) .

The lake ball saga spans 35 years, which is more or less the time I have spent at Mývatn, monitoring the wildlife from top to bottom, constantly worried about its welfare in this modern world of human progress. And now, when such a prominent feature of the ecosystem has vanished it is time to look back. This period was an adventure. Recalling first the joy of introducing lake balls to the public, share those miraculous plants with visitors, local school children and their parents, and experiencing how easily people were captivated by those round, fluffy, soft and friendly looking algae. The lake balls quickly became well known all over Iceland. One day a class of 13−14 year old children came from far away to visit the lake and the Myvatn Research Station. The children were all allowed to hold a lake ball in their hands. A boy who had just done so raised his hand and said: “May I use your phone, please. I would like to call my mother and tell her that I just held a lake ball in my hand." Everybody was fascinated by lake balls, and it was always easy to use them as a starting point for a discussion about lakes, how they work, their wildlife, and problems with conservation. The lake ball is an organism that is exceptionally vulnerable to changes in external conditions caused by human activities. There it rests on the lake bottom, bathed in nutrient rich water but surviving only of it is moved gently by the wave action and reaches sufficient light. It is adapted to dimly lit environment, but its shape makes it exceptionally sensitive to low light. A normal plant spreads out its flap-like leaves and grows into the light. A spherical plant-like organism such as the lake ball has the lowest surface-to-volume ratio possible and that limits its growth to a certain maximum size. If, at this point, the light is reduced for some reason, – this could be through excessive plankton growth due to nutrient enrichment, – the lake ball begins to rot from the inside. This weakens its structure, and the previously refreshing water currents now become a deadly threat to their survival. The current that rolled the balls gently around now rips them to pieces. The lake balls are like a canary in the mine. When they thrive, we have little reason to worry, but when something is wrong they will be the first to tell us.

I am also recalling my surprise when Isamu Wakana contacted me with the information that lake balls were famous in Japan and that there was a person who had dedicated his life to them, namely himself. This led to four trips to Japan to participate in field trips, symposia, and festivals dedicated to this wonderful alga. I think fondly of the Japanese interpreter who was most reluctant to translate the Icelandic name of a lake ball ("kúluskítur", literally "ball-shit") to our audience at Lake Akan because he found it rather rude, and I had to convince the audience that the Icelandic name was almost identical to the Japanese name Marimo, meaning round weed (or round algae). I am recalling a two day climb to the top of Mount Fuji with Japanese lake ball scientists after a field trip to the Marimo lakes below. I am also recalling the Ainu people, living by Lake Akan, who have developed a special relationship with the algae. Recalling my surprise in 2012 when I was snorkelling in Lake Akan and found out that its lake balls had grown enormously, to almost football size, in response to successful management, – simply by diverting sewage from the lake and increasing the water clarity. Isamu Wakana has been to Mývatn many times and, and no one has been more helpful in solving the mystery of the lake balls but him. Without his everlasting enthusiasm and knowledge we would still be fumbling around in the murky water of Mývatn.

I am recalling the excitement when my colleagues, most notably my mentor Arnthor Gardarsson, found out that the algal mat was an important habitat for invertebrates that were fed on by ducks and fish. Also recalling the joy when I realized that microscopic membranes in old sediments were the remains of long gone algae, which meant that the history of the algal mat could be traced centuries back in time.

Right from the beginning researchers, myself included, observed big fluctuations in the distribution of *A. linnaei*, but I think we never seriously thought that one day the lake balls would be gone, and most of the algal mat too. In retrospect, however, this development looks familiar. It has happened in almost every lake ball habitat around the world and the reason is clear: eutrophication because of human activities. Sadly, Lake Mývatn has now joined the group of lakes that have lost their lake balls because of nutrient enrichment by us humans. The situation at Mývatn is more complex than in other lakes because of the mining operation in 1967–2004 that upset the ecological balance and amplified natural fluctuations. Despite the complexity of the situation we must make an effort to see the broad picture. It has to be a warning sign when the green algal beds disappear. The canary has died. □

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APPENDIX

Chemistry of water in and above the sediment in Bekraflói (near the lake ball colony). Station 1, 24 June 1998. From Gíslason et al. (2004). The paper describes the chemical composition of near-bottom water close to the SW lake ball patch while it was still present. It also describes chemical gradients in the sediment water and the diffusive flux of elements between the lake and the sediment. The data is reproduced here for descriptive purpose, to illustrate the amount of chemical data available for the lake ball environment.

Gögn um efnasamsetningu og efnaflæði í vatni í og yfir setinu í grennd kúluskítsflekk á Bekraflóa (Stöð nr. 1), 24. júní 1998. Úr grein Sigurðar Reynis Gíslasonar o.fl. 2004.

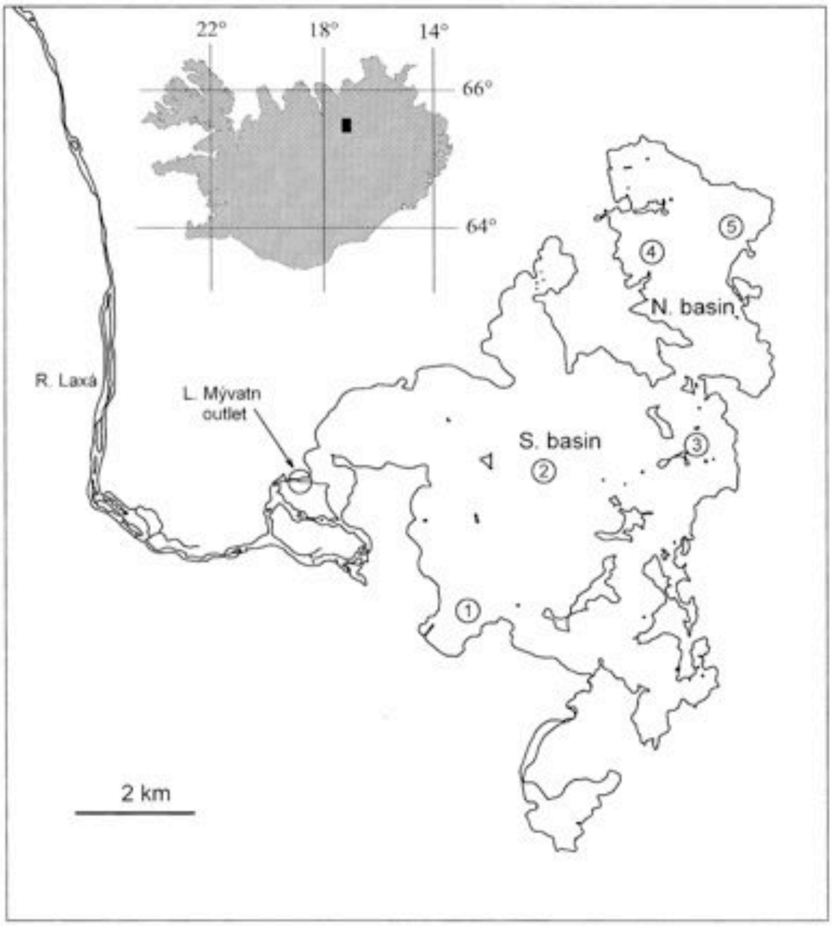


Figure 1. Sampling sites in Lake Myvatn (station 1) and at the Geirastadaskurdur outlet. Previous sampling sites (1–5) of Ólafsson (1991b) are also shown.

Styrkur uppleystra efna í setvatni í Bekraflóa og í útfalli Mývatns. Úr grein Sigurðar Reynis Gíslasonar o.fl. (2004).

Appendix 1. Concentration of dissolved elements in the interstitial water within the sediment, 16 cm above the sediment-water interface, and at the lake outlet.

Sample number		98-M006	98-M005	98-M004	98-M003	98-M002	98-M001
Sampling station		Outlet	Lake wat.	Sed.water	Sed.water	Sed.water	Sed.water
Depth	(cm)		−16	25	55	100	150
Cond.	μS/cm	165	162	378	505	535	518
pH		10.03	9.81	7.26	7.16	7.30	7.26
Eh	mV	100.0	39.5	−25.9	−45.0	−20.8	−26.0
T[1]	°C	17.8	20.0	20.4	19.7	19.8	19.8
O_2	mmol[2]	0.319	0.268	0.195	0.161	0.202	0.224
Si	mmol	0.132	0.094	0.701	0.719	0.609	0.580
Na	mmol	1.013	0.966	1.348	1.501	1.583	1.670
K	mmol	0.038	0.033	0.142	0.164	0.165	0.176
Ca	mmol	0.190	0.176	0.526	0.778	0.958	1.095
Mg	mmol	0.158	0.145	0.440	0.658	0.778	0.848
Cl	mmol	0.155	0.156	0.176	0.164	0.172	0.181
S	mmol	0.160	0.149	0.006	0.007	0.004	0.003
Alk.	meq.[2]	1.27	1.18	4.17	5.79	6.22	6.41
F	μmol[2]	18.2	17.9	17.5	16.3	15.9	13.7
PO_4	μmol	0.105	0.125	63.406	14.518	5.238	0.246
P_{total}	μmol	0.297	0.272	83.0	27.5	9.07	2.30
NO_3	μmol	0.426	0.281	0.187	0.138	0.195	0.158
NO_2	μmol	0.059	0.065	0.113	0.123	0.193	0.176
NH_4	μmol	0.473	0.375	985	1369	1306	934
Al	μmol	0.930	1.041	0.0195	0.0563	0.0179	0.0511
Fe	μmol	0.168	0.192	10.64	18.98	6.41	18.4
Mn	μmol	0.0167	0.0134	4.51	7.70	9.14	11.6
Li	nmol[2]	224	209	383	498	541	508
Be	nmol	0.599	0.566	0.422	0.821	0.200	0.621
Sr	nmol	108	91.3	377	423	616	742
Ba	nmol	1.59	2.13	3.36	0.328	1.43	4.92
V	nmol	0.917	1.088	0.503	0.0921	0.271	0.174
Ti	nmol	2.42	6.20	6.49	7.20	6.99	4.66
Cr	nmol	17.0	15.7	6.23	6.56	7.60	6.15
Co	nmol	0.462	0.509	12.7	19.0	18.5	12.6
Ni	nmol	4.11	4.72	30.3	16.9	18.2	15.4
Cu	nmol	7.65	8.47	12.0	2.28	2.57	3.21
Zn	nmol	7.63	15.1	88.3	20.3	74.0	61.0
As	nmol	<0.013	<0.013	1.268	<0.013	1.081	<0.013
Mo	nmol	9.69	9.94	4.50	4.54	8.04	3.41
Cd	nmol	0.0480	0.0329	0.110	0.0641	0.414	0.227
Sn	nmol	0.066	0.174	0.098	0.106	0.127	0.190
Hg	nmol	<0.01	<0.01	0.011	0.012	<0.01	<0.01
Pb	nmol	0.108	0.181	0.109	0.109	0.131	0.297
U	nmol	0.220	0.226	0.053	0.028	0.052	0.036
Sb	nmol	0.050	0.076	<0.008	0.011	0.030	0.013

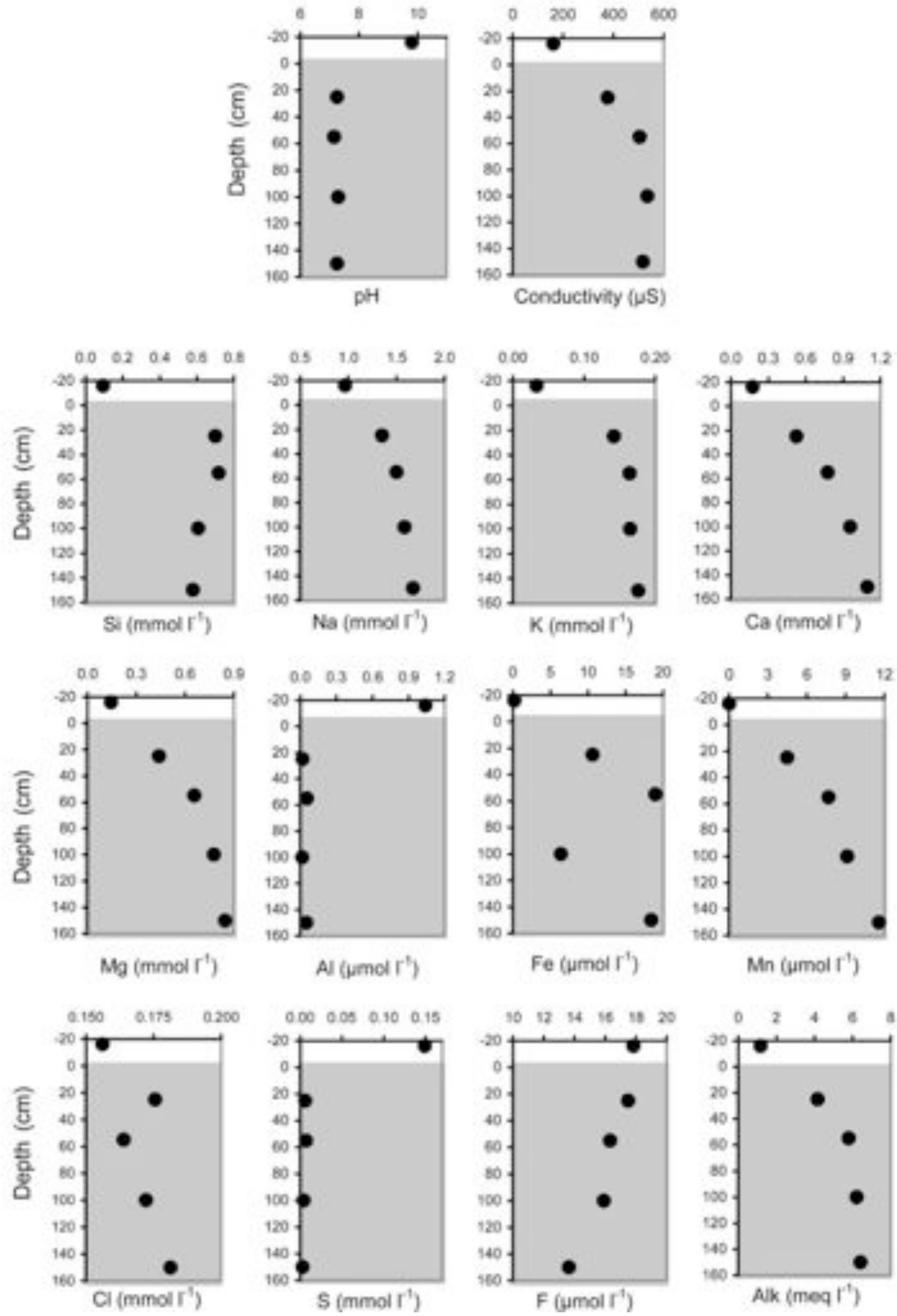
[1]Temperature at which conductivity, pH and Eh were measured.
[2]Concentrations are given in mmol l^{-1}, meq. l^{-1}, μmol l^{-1} and nmol l^{-1}.

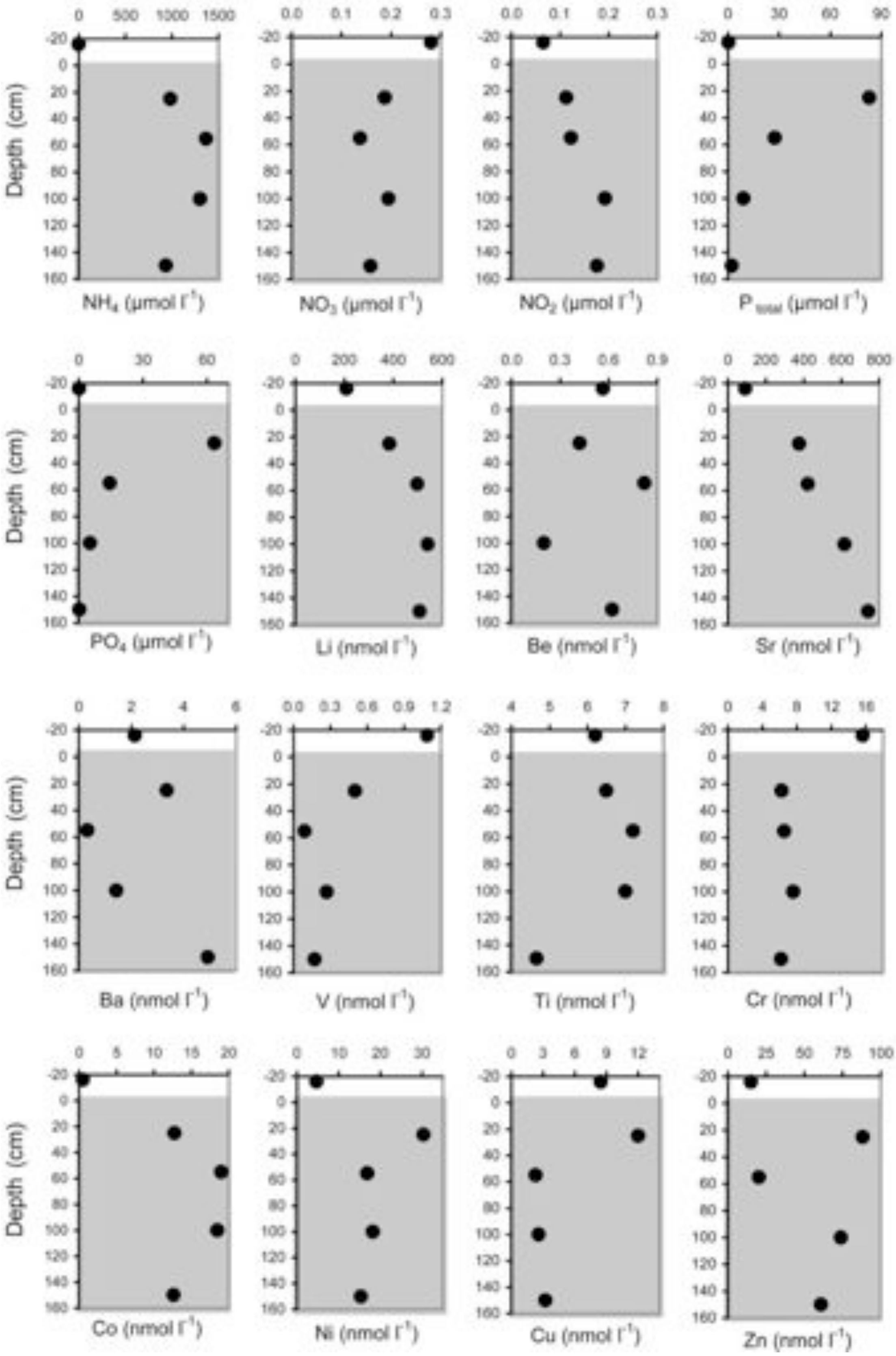
Concentration gradient in the interstital water and diffusive flux at 10 °C in descending order. From Gíslason et al. 2004. *Styrkfallandi og flæði efna í seti Bekraflóa (Sigurður Reynir Gíslason o.fl. 2004).*

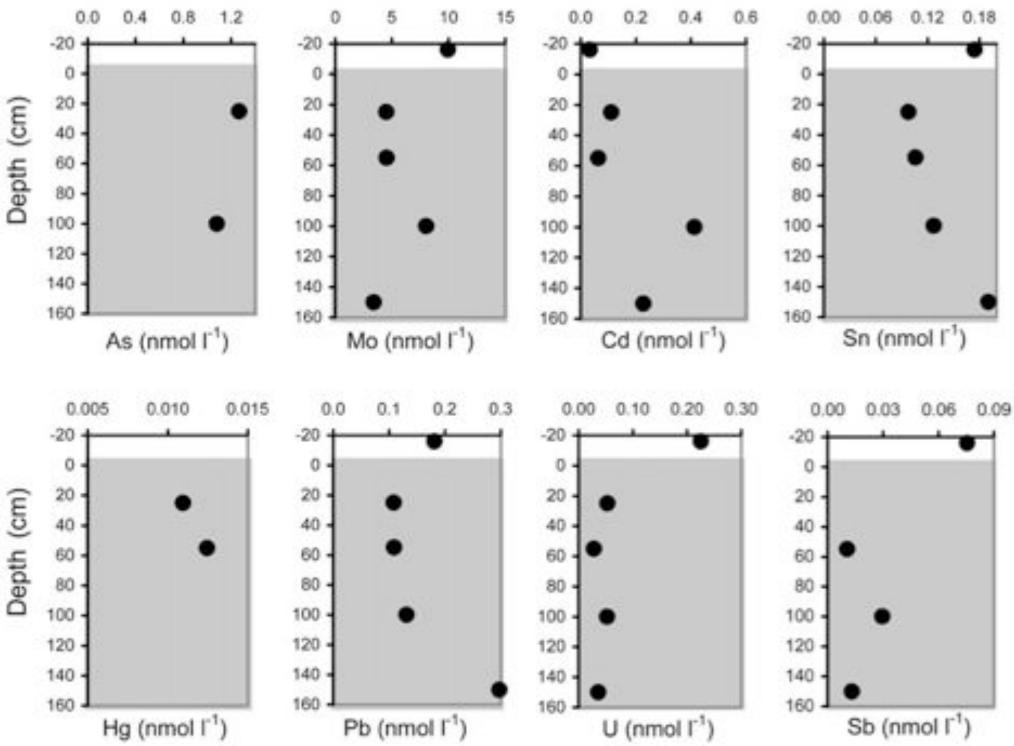
Sample	dC/dz molcm^{-3}cm^{-1}	Flux* molcm^{-2} s^{-1}
Alk.	1.49E-07	−6.49E-13
NH_4^+	4.93E-08	−4.29E-13
$H_4SiO_4^o$	3.26E-08	−1.42E-13
Na	1.91E-08	−8.33E-14
Ca	1.75E-08	−7.62E-14
Mg	1.48E-08	−6.42E-14
S	−7.16E-09	3.12E-14
K	5.45E-09	−2.37E-14
$P_{total.d.}$	4.14E-09	−1.80E-14
PO_4	3.16E-09	−1.38E-14
Cl	9.72E-10	−4.23E-15
Fe	5.22E-10	−2.27E-15
Mn	2.25E-10	−9.79E-16
Al	−5.11E-11	2.22E-16
F	−1.75E-11	7.63E-17
Sr	1.43E-11	−6.21E-17
Li	8.70E-12	−3.78E-17
NO_3	−4.67E-12	2.03E-17
Zn	3.66E-12	−1.59E-17
NO_2	2.37E-12	−1.03E-17
Ni	1.28E-12	−5.57E-18
Co	6.12E-13	−2.66E-18
Cr	−4.71E-13	2.05E-18
Mo	−2.72E-13	1.18E-18
Cu	1.77E-13	−7.70E-19
Ba	6.12E-14	−2.66E-19
V	−2.92E-14	1.27E-19
Ti	1.46E-14	−6.36E-20
U	−8.63E-15	3.76E-20
Be	−7.21E-15	3.14E-20
Cd	3.87E-15	−1.68E-20
Sn	−3.83E-15	1.67E-20
Pb	−3.64E-15	1.59E-20

*Negative flux is out of the sediment to the bulk water and *vice versa*.

Variation with depth in pH, conductivity, alkalinity, and the concentration of major and trace elements in the interstitial water within the sediment and in the lake water 16 cm above the lake bottom at the sampling site.24 June 1998. From Gíslason et al. (2004). *Breytileiki með dýpi í ýmsum efnafræðlegum þáttum í seti Bekraflóa 24. júní 1998. Úr grein Sigurðar Reynis Gíslasonar og fl. (2004).*




Depth (cm)
NH$_4$ (µmol l^{-1})
NO$_3$ (µmol l^{-1})
NO$_2$ (µmol l^{-1})
P$_{total}$ (µmol l^{-1})
PO$_4$ (µmol l^{-1})
Li (nmol l^{-1})
Be (nmol l^{-1})
Sr (nmol l^{-1})
Ba (nmol l^{-1})
V (nmol l^{-1})
Ti (nmol l^{-1})
Cr (nmol l^{-1})
Co (nmol l^{-1})
Ni (nmol l^{-1})
Cu (nmol l^{-1})
Zn (nmol l^{-1})



Depth (cm)
As (nmol l^{-1})
Mo (nmol l^{-1})
Cd (nmol l^{-1})
Sn (nmol l^{-1})
Depth (cm)
Hg (nmol l^{-1})
Pb (nmol l^{-1})
U (nmol l^{-1})
Sb (nmol l^{-1})