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The importance of aquatic macrophytes in a eutrophic tropical shallow lake

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ABSTRACT

Inlay Lake is the second largest natural lake in Myanmar. Located in Shan State, in the eastern part of the country, it is a known biodiversity hotspot. The lake is negatively affected by an increasing local human population and rapid growth in both agriculture and tourism. In recent decades, several studies have listed faunistic and floristic groups in Inlay Lake, but there is still a general lack of knowledge about the aquatic macrophyte and phytoplankton community composition and abundance, and their interactions. To fill this knowledge gap, field surveys of biological and physical and chemical parameters were carried out in the period 2014–2017. They show that Inlay Lake is a shallow, clear water and calcareous lake, with nutrient concentrations indicating mesotrophic-eutrophic conditions. However, close to the shore, nutrient concentrations are generally higher, reflecting pollution from inflowing rivers, shoreline villages and floating gardens. Both the richness and abundance of aquatic macrophytes in Inlay Lake were high, with several species forming extensive stands in most of the lake over the whole survey period. Total phytoplankton and cyanobacterial biomass were low, but cyanobacteria included toxin-producing strains of *Microcystis*, suggesting that cyanobacterial and total phytoplankton biomass need to be kept low to avoid potentially harmful cyanobacterial blooms. Submerged macrophyte abundance and phytoplankton biomass were inversely correlated in the heavily vegetated northern lake area. Our survey suggests a great importance of the submerged macrophytes to the general water quality and the clear water state in Inlay Lake. Maintaining high macrophyte abundances should therefore be a goal in management strategies, both for Inlay Lake and other lakes in Myanmar. It is highly desirable to include macrophytes and phytoplankton in the lake monitoring in Myanmar.

1. Introduction

Submerged macrophytes play an important role in the structuring and functioning of aquatic freshwater systems (e.g. Carpenter and Lodge, 1986; Jeppesen et al., 1998; Timms and Moss, 1984; James and Barko, 1994; Vermaat et al., 2000; Burks et al., 2002) and are especially important for in-lake nutrient cycling and for stabilizing a clear water state in nutrient rich lakes (Phillips et al., 1978; Scheffer et al., 1993). In shallow lakes, submerged macrophytes can suppress algal growth and enhance water clarity through a number of mechanisms, including nutrient competition (Mjelde and Faafeng, 1997; Phillips et al., 1978) or release of allelopathic substances toxic to algae (Gross et al., 2007). Consequently, shallow lakes with macrophyte cover are more resistant to increasing nutrient load than lakes without or with limited macrophyte cover. Based on this, Scheffer et al. (1993) suggested two alternative stable states in temperate eutrophic lakes: a clear water state abundant in submerged macrophytes and a turbid and phytoplankton-dominated state. In addition, high macrophyte diversity seems to play a role in preventing the shift to phytoplankton dominance (Sayer et al., 2010).

Studies about excessive aquatic macrophyte growth and control have long been an issue everywhere, including in Asia (Pieterse and Murphy, 1990). However, while knowledge about the dynamics between physical and chemical water quality and biological communities in temperate lakes is large (e.g., Lyche-Solheim et al., 2013; Phillips et al., 2016), it is more limited for tropical lakes. The scattered studies, however, show that both physical and chemical conditions and biological interactions in tropical lakes differ from temperate lakes (Lewis, 2000; Meerhoff et al.,

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2003; Jeppesen et al., 2005), and it is not obvious that knowledge and conclusions from temperate areas can be transferred to tropical lakes.

A turbid state dominated by phytoplankton is considered undesirable, while water dominated by submerged macrophytes is regarded as better quality (EC, 2000). Knowledge about aquatic macrophyte growth and the mechanisms behind community shifts is therefore of considerable importance for management and for the establishment of good ecological status for lakes and reservoirs.

Large natural lakes are scarce in Myanmar and therefore given special attention under the Myanmar National Water Framework Directive (NWRC, 2014) (see Ballot et al., 2018; Nesheim et al., 2016). Phytoplankton and aquatic macrophytes are considered among the most important bioindicators for ecological status evaluation in lakes (EC, 2000). The use of these parameters is therefore desirable in monitoring and management strategies for Myanmar lakes. However, to develop appropriate tools it is necessary to increase the general knowledge about freshwater ecology in the country, including interactions between macrophytes and phytoplankton.

Recently, a few studies including phytoplankton and aquatic macrophyte composition and abundance have been conducted in some lakes and reservoirs in Myanmar (Ballot et al., 2020; Mjelde et al., 2021; Swe et al., 2021; Mjelde and Ballot, 2016; Mjelde et al., 2018). However, there is a general lack of knowledge about macrophyte–phytoplankton interactions in waterbodies in Myanmar, as well as in other Asian countries and in tropical and equatorial areas in general.

Inlay Lake is the second largest natural lake in Myanmar and is a known biodiversity hotspot. However, to date, only lists of macrophytes exist for Inlay Lake (Allen et al., 2012); there are no datasets describing macrophyte abundance, or investigations of phytoplankton communities and the interactions between the macrophytes and phytoplankton.

To our knowledge, the present work is the first detailed whole-lake study about the interactions between phytoplankton and aquatic macrophytes in Myanmar and their role in shaping the Inlay Lake ecosystem.

The aim of this study is to assess the richness and composition of the aquatic macrophyte and phytoplankton communities in Inlay Lake in Myanmar, and to discuss the importance of aquatic macrophytes as a stabilizing factor in a large and shallow eutrophic lake in a tropical area. Our hypothesis is that the submerged macrophytes control phytoplankton biomass and composition and hence stabilize a clear water state in the lake. However, due to the large climatic variations in a tropical lake, we expect large differences in the physical, chemical and biological conditions between the rainy and dry periods, which can be important for the stability. Inlay Lake is a large lake, and correlations between macrophytes and phytoplankton may differ between areas, i.e. from north to south and from littoral to middle part of the lake.

2. Methods

2.1. Study area

Inlay Lake is characterized by a high botanical and wildlife biodiversity and was therefore established as a Wildlife Sanctuary in 1985. In 2003, Inlay Lake became an ASEAN Heritage Park and was listed as an Important Bird and Biodiversity Area (IBA) in 2004. In 2015, it was designated as Myanmar's first UNESCO Biosphere Reserve and in 2018 it became Myanmar's fifth Ramsar site. Inlay Lake is considered as one of the freshwater biodiversity hotspots in Myanmar (Lwin and Sharma, 2012). The diverse fauna and flora, the unique location of the lake and the unique lifestyles and traditions of the local human population have also made it one of the primary tourist destinations in Myanmar (Lwin and Sharma, 2012), followed by an increasing need for tourist accommodation.

Inlay Lake is a freshwater lake located at 884 m above sea level in Shan State in the eastern part of Myanmar. It is the second largest natural lake in Myanmar, with a surface area that varies between 94.4 km^2 (May) and 126.1 km^2 (November) based on data from 2015 to 2016 (Michalon et al., 2019). The largest inlets are Tham Daung in the north and Belui in southwest, while the outlet river is in the south (Fig. 1). The total catchment area is estimated to be 3800 km^2 (Michalon et al., 2019). This gives a ~34.5:1 catchment:lake area ratio, strongly suggesting a high influence of the land use in the catchment area on the lake ecosystem (especially high runoff and siltation; Cooke et al., 2005).

The lake is shallow, with a maximum depth of around 3.2 m and an average depth varying between 1 m in the dry season and 2.2–2.5 m in the rainy season (Michalon et al., 2019). Generally, the water level is lowest from mid-April to mid-May and rises to its highest level between mid-September and mid-October. Based on monthly data from 2014 to 2017, average water depth in the middle of the lake in April-May and in September-October is estimated to be 1.28 and 2.35 m, respectively (data from Forest Department Myanmar). The lake is regarded as warm polymictic (Akaishi et al., 2006).

Floating tomato gardens have been the most important agricultural activity in the lake region since the 1940s, and in 2018 the total area of floating gardens was estimated to be 24.5 km^2 (Irrigation Department, Nyaung Shwe, Myanmar). Large amounts of chemical fertilizers and pesticides are used in these areas, but management practices are changing towards more sustainable alternatives, such as using submerged macrophytes from the lake as organic fertilizers. The main species used for this purpose are *Eichhornia crassipes* (Michalon et al., 2019), *Najas indica* & *Ceratophyllum demersum*, and filamentous algae. An application of a fertilizer species lasts for 7–20 days, depending on the species, before new plants must be added to the crops (Irrigation Department, Nyaung Shwe, Myanmar). The expansion of floating gardens and the occurrence of free-floating macrophyte species has caused a decrease in open lake surface area from 65.4 km^2 in 1967 to 50.1 km^2 in 2014 (Michalon et al., 2019).

In addition to fertilizer and pesticide use by floating gardens, lake water quality is affected by a growing human population and tourist activity in the area, combined with a lack of adequate sanitation infrastructure (Htwe, 2015). A recent study on surface water quality revealed eutrophic conditions in Inlay Lake and a high level of bacterial contamination (Akaishi et al., 2006).

Deforestation and agricultural practices in the catchment have also led to erosion and siltation in the lake. Total silt discharge from all subcatchments is estimated at ≈270,000 tonnes per year, of which 62 % is deposited in deltas, 20 % in marshes and 1 % in the lake itself (Furuichi, 2008). Silt discharge is considered an important component of eutrophication (Cooke et al., 2005; Everall et al., 2018).

The climate in Myanmar is tropical and can be divided in three seasons: the dry winter or northeast monsoon season (November–February), the summer or hot (and dry) season (March – mid-May), and the rainy or southwest monsoon season (mid-May– October; Aung et al., 2017). The average annual maximum and minimum temperature for 1981–2010 at the Taunggyi weather station, 25 km north of Inlay Lake, were 25 °C (April) and 14 °C (December-January), respectively. The annual rainfall is about 1010 mm, and the precipitation is mostly confined to the rainy season (May–October). The overall predominant wind in the area is from the southeast, and the speed is generally low (less than 4−5 m/s; Aung et al., 2017).

Species lists of aquatic flora and fauna are available from earlier surveys in Inlay Lake (Allen et al., 2012). Around 30 species of aquatic macrophytes have been listed (Ito and Barfod, 2014; Lansdown, 2012; Nair, 1960), but no information about abundances exists. The fish community consists of 17 endemic and 15 widespread fish species (Kullander, 2012). The most important fish species for local people is the Inlé Carp (*Cyprinus carpio intha*), both as food source and as a cultural symbol of the ethnic Intha people (Allen et al., 2012). A high diversity of gastropods, mainly Viviparidae, Pachychilidae and Bithyniidae and bivalves from the families Unionidae, Cyrenidae and Sphaeriidae, is reported from the lake, however this information is from old studies (see references in Allen et al., 2012). The phytoplankton community has not been studied.

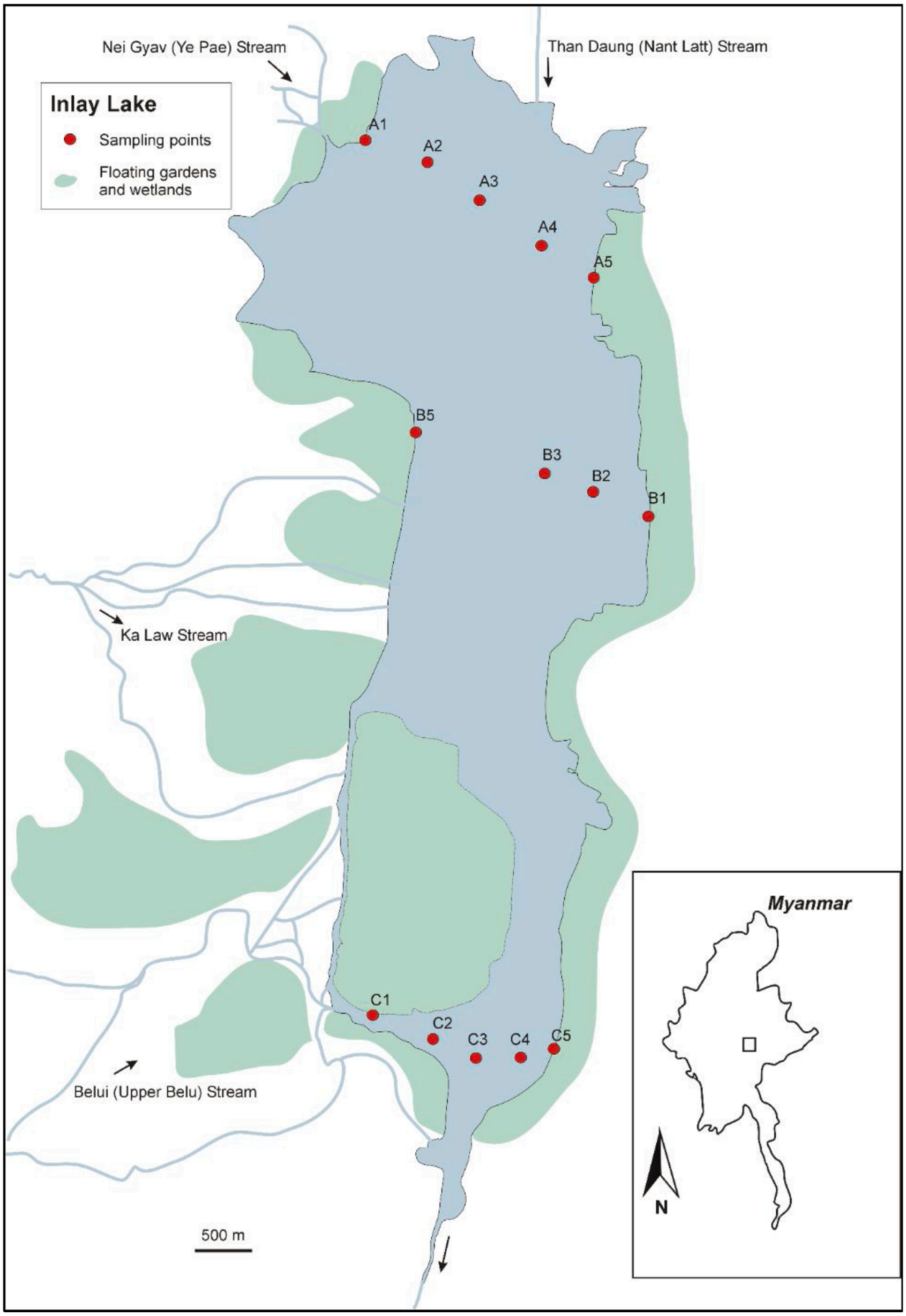

Fig. 1. Sampling sites in Inlay Lake in 2014–2017. Inlay Lake (square) is situated in Shan state in the eastern part of Myanmar (right).

2.2. Field and analysis methods

The field work was carried out in the period 2014–2017 with sampling conducted at four occasions, twice after the end of the rainy season (November 2014, 2015) and twice at the end of the cold dry winter period (February 2015 and March 2017). Physical measurements, water samples, phytoplankton and aquatic macrophytes were collected at 14 different lake sites (Fig. 1, Table 1) covering different areas, depths and habitats in the lake. The number and placement of sites captured most of the macrophyte and phytoplankton species (cf. the rarefaction curves later in the chapter) and reflected the main variations in physical, chemical and biological conditions in the lake. In March 2017, we sampled at a reduced set of open-water sites (A3, B3 and C3) and shore sites (A1, B1 and C1) in the northern, middle, and southern lake areas. Water samples from the main tributaries rivers Belui (Belu), Nei Gyar (Ye Pae) and Tham Daung (Nant Latt), and from the outlet river, were collected as part of the field work in 2014−2015. Physical and chemical data from tributaries from November 2017 are based on Eriksen et al. (2021).

Between November 29th and 30th 2017, water depth was determined using a handheld echosounder along 16 approximately east–west transects (211 depth measurements in total). The open water boundary of the lake was downloaded from OpenStreetMap (OpenStreetMap, 2018) and used to add an additional 400 points with zero depth around the lake's perimeter. The combined dataset of 611 points was then interpolated to a regular grid with 200 m resolution using Inverse

Table 1
Sampling localities in Inlay Lake in 2014–2017. Coordinates in decimal degrees.

Lake area	Loc. no	Latitude	Longitude	Quality elements
North	A1	20.603837	96.895600	P&W, PP, AM
	A2	20.602125	96.901859	P&W, PP, AM
	A3	20.593999	96.913220	P&W, PP, AM
	A4	20.589542	96.919611	P&W, PP, AM
	A5	20.58426	96.927998	P&W, PP, AM
Middle	B1	20.550628	96.935768	P&W, PP, AM
	B2	20.553565	96.926082	P&W, PP, AM
	B3	20.557946	96.918544	P&W, PP, AM
	B5	20.562589	96.902898	P&W, PP, AM
South	C1	20.48066	96.895886	P&W, PP, AM
	C2	20.477061	96.901475	P&W, PP, AM
	C3	20.473896	96.910144	P&W, PP, AM
	C4	20.470792	96.913435	P&W, PP, AM
	C5	20.47489	96.923759	P&W, PP, AM

P&W = physical measurements and water chemistry, PP = phytoplankton, AM = aquatic macrophytes.

Distance Weighting (Wong, 2017) to create the bathymetric map shown in Fig. 2. The Osgood Index (OI; Osgood, 1988) calculated from this gridded dataset and the lake area varies between 0.16 and 0.27, depending on variations in lake surface area. The index estimates the probability of partial or complete mixing of the lake, and the very low index values for Inlay lake indicate year-round polymixis and a high probability of internal phosphorus loading (Osgood, 1988; Mataraza and Cooke, 1997).

2.2.1. *Physical measurements and water samples*

Physical measurements and water samples were taken approximately 20 cm below the water surface at each locality. For the physical measurements we used a Hach, HQd Portable Meter (Hach, Loveland, CO, USA). For the chemical analyses, water samples were collected using a Ruttner sampler. One 100 mL water aliquot (preserved in the field with 4 M H_2SO_4 to 1 % final concentration) and one 100 mL aliquot (unpreserved) were stored at 4 °C. All samples were transported to and analysed at the ISO-certified NIVA laboratory in Norway. The physical and chemical parameters included water temperature, pH, conductivity, oxygen, colour, calcium (Ca), ammonium (NH_4), nitrate-nitrite

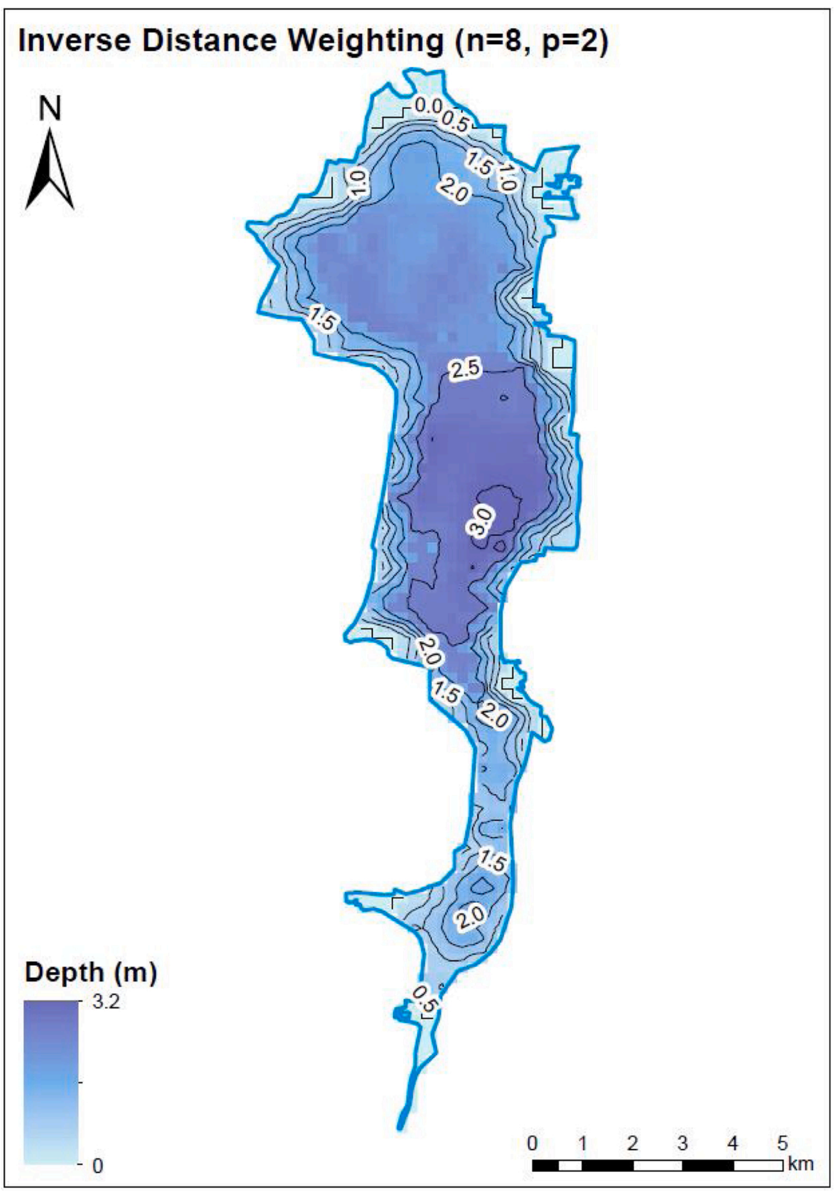

Fig. 2. Bathymetric map of Inlay Lake. The depth measurements were carried out 29-30 November 2017.

(NO_3+NO_2), ortho-phosphate (PO_4), total nitrogen (TN), total phosphorus (TP), total carbon (TOC) and silicate (SiO_2) concentrations. All chemical analyses were carried out according to Norwegian standard methods (see Supplementary Table S1).

2.2.2. Aquatic macrophytes

The surveys of aquatic macrophytes in Inlay Lake included only hydrophytes, i.e. species belonging to the submerged, floating-leaved and free-floating groups; emergent species (helophytes) were thus excluded. Hydrophytes reflect water quality much more directly than helophytes, making hydrophytes particularly important for ecological assessment in eutrophic lakes. They are therefore prioritized in assessment methods in EU WFD (e.g., Hellsten et al., 2014).

The plants were surveyed in an area of approx. 1 m^2 at each locality with an aqua scope and collected by dredging from the boat with a casting rake (e.g., Kolada et al., 2012). The abundances of the species were scored according to a semi-quantitative scale, where 1 = rare, 2 = scattered, 3 = common, 4 = locally dominant and 5 = dominant. Where possible, all taxa were identified to species level, using floras for the region (mainly Cook, 1996), in addition to updated or more specialised taxonomic work (e.g., La-Ongsri, 2008; Triest, 1988; Wiegleb, 1990; Wiegleb and Kaplan, 1998). Charophytes were identified based on Wood and Imahori (1965) and later verified by genetic analysis (Mjelde et al., 2021). In a few cases, identification to species could not be done with certainty, hence these taxa were identified to genus only. Sampling effort for macrophytes at species level was adequate according to a sample-based Coleman rarefaction curve with 50 runs without replication, constructed using the "EstimateS" software package (v8.20; Colwell, 2013). Ninety percent and 99 % of the 28 macrophyte species found in the 51 samples from 2014 to 2017 were found after 16 and 46 samples, respectively.

The estimated abundance of aquatic macrophytes is based on the semi-quantitative scores for all localities. We estimated the total abundance at each locality by adding the cubed five-level values for each species. The linear five-level scale commonly used for abundance estimation of aquatic macrophytes does not reflect the non-linear abundance increases, and using cubed 5-level values for total abundance is regarded as the "best possible" approximation for comparing abundances among macrophyte groups and among sites (Melzer, 1999; Schneider et al., 2018).

2.2.3. Phytoplankton

Quantitative water samples were taken at all localities using a Ruttner sampler. A 50-mL aliquot was taken for quantitative phytoplankton analysis (assemblage taxonomic composition and biomass) and preserved with acidic Lugol's solution. For qualitative phytoplankton analysis (taxonomic composition), a concentrated net sample (mesh size 20 μm) was collected and preserved by addition of formaldehyde (to 4 % final concentration). All samples for quantitative and qualitative analysis were stored in the dark until they were analysed. The Lugol-fixed samples were analysed for phytoplankton composition and biomass using Utermöhl sedimentation chambers (Utermöhl, 1958) and an inverted microscope (Olympus Optical Co-Ltd Japan Model CK2, Olympus, Tokyo, Japan). Sampling effort was more than adequate according to a sample-based Coleman rarefaction curve constructed as for macrophytes, with 99 % of the 14 major phytoplankton groups detected after 2 out of the total 46 samples collected. All taxa were identified to species or genus level, using selected identification keys (e.g., Büdel et al., 1978-2015; Huber-Pestalozzi, 1969; Komárek and Anagnostidis, 1999; Komárek and Fott, 1983; Skuja, 1949). However, some taxa could only be identified to family level. In addition, water samples (50 mL) were taken at each sampling point for isolation of cyanobacteria and kept in a cool shady place and gently shaken twice per day until processing at the Norwegian Institute for Water Research (NIVA) in Norway.

Using a microcapillary, single colonies of *Microcystis* were isolated. They were washed five times and placed in wells on microtiter plates containing 300 μL Z8 medium (Kotai, 1972). After successful growth, the samples were placed in 50 mL Erlenmeyer flasks containing 20 mL Z8 medium and maintained at 22 °C. Strains were classified based on morphological traits according to Komárek and Anagnostidis (1999). Morphological characterisations were conducted using a Leica DM2500 light microscope, Leica DFC450 camera and Leica Application Suite software (LAS; Leica, Oslo, Norway). The morphological identification was based on the following criteria: (i) size of vegetative cells, and (ii) nature and shape of colonies. Length and width of 50–250 vegetative cells were measured. All strains used in this study are maintained at the Norwegian Institute for Water Research, Oslo, Norway.

To test for the production of microcystins, fresh culture material of all four Microcystis strains was frozen and thawed three times using the Eurofins Abraxis microcystin enzyme-linked immunosorbent assay (ELISA) kits (Eurofins Abraxis, Warminister, PA, USA). The test is an indirect competitive ELISA designed to detect microcystins based on specific antibody recognition. The colour reaction of the ELISA test was evaluated at 450 nm on a Perkin Elmer1420 Multilabel counter Victor3 (Perkin Elmer, Waltham, MA, USA). All strains were also tested for saxitoxin, anatoxin-a and cylindrospermopsin using the Eurofins Abraxis anatoxin, saxitoxin and cylindrospermopsin kits (Eurofins Abraxis, Warminister, PA, USA).

2.2.4. Statistical analysis

To assess the relationship between environmental variables and biology, to describe the relationship between phytoplankton and macrophytes and to detect possible differences between seasons and/or lake areas we have analysed the data using multivariate, univariate and bivariate statistics.

Relationships between community composition and environmental variables were assessed using redundancy analysis (RDA). Analyses were done using the Vegan library (Oksanen et al., 2020) in R (R core team, 2020). Due to incomplete water chemistry from 2014 and a reduced sampling program in 2017, we only analysed community-environment relationships on the data from 2015. Data from November (end of the rainy season) and February (end of the dry season) in 2015 were analysed separately. Prior to analysis, all water chemical variables except pH (TP, TN, dissolved inorganic N (DIN; NO_3+NO_2), NH_4, PO_4, SiO_2, TOC and conductivity) were log-transformed to normalize the data. To assure that all the predictor variables were on comparable scales, all predictor variables (water chemistry, water temperature, depth, latitude and longitude) were also normalized by subtracting the mean and transformed to unit standard deviation. The RDAs of phytoplankton community composition were done using Hellinger-transformed abundances (square root of relative biovolumes) of the main phytoplankton classes. For macrophytes, we used Hellinger-transformed abundances based on species abundance (see Schneider et al., 2018).

To test which variables in the RDAs that significantly could explain variation in community composition, we did backward and forward selection using the set of predictor variables mentioned above. Only significant environmental variables ($p < 0.05$) were kept. Many of the environmental variables were correlated. Hence, if one variable was included in the model, other correlated variables would not explain much of the residual variation and therefore would likely be excluded from the model. The effect on community composition, however, might still be due to one or more of the correlated variables, even though another variable was "chosen" in the model selection. To assist interpretation of the RDAs, we therefore also analysed the environmental variables by PCA and plotted the main gradients in these variables along with the RDA-plots (see Figs. 5 & 9).

To disentangle spatial community gradients from effects from local environmental conditions (water chemistry, temperature and depth), we used variance partitioning by RDA (using function varpart() in vegan). We included the significant environmental variables as one group of predictors and latitude/longitude as another group of predictors. The analysis then calculates the fraction of variation explained by the environmental variables, spatial variables, and variation shared (confounded) by the two groups. Finally, we tested for significance of the environmental variables given that the spatial variables were included in the model, and vice versa.

Uni- and bivariate analyses were performed in addition and in support of multivariate analyses. Univariate analyses included two-way type I ANOVAs that were run to detect differences in average abundance/biomass among lake areas (north, middle, and south) and between sampling seasons (November, corresponding to the end of the rainy summer season, and February/March, corresponding to the dry winter season). Macrophyte and phytoplankton data from the same sites were collected six months apart and thus considered sufficiently distant and independent to be applied to ANOVAs. November 2014 and 2015 and February/March 2015 and 2017 were clumped to obtain a November (end of the rainy season) and a February/March (end of the dry season) data set, respectively, to increase replication and thus ANOVA reliability. A type I ANOVA was chosen as both factors were set by the investigators. Tukey HSD (Honestly Significant Difference) *post-hoc* multiple comparisons were run after significant ANOVAs to ascertain which average values were different from which. Among the plethora of *post-hoc* multiple comparison tests, Tukey HSD tests have the advantage of not increasing the risk of committing experiment-wide type I errors, as the test power is kept at the nominal level ($\alpha = 0.05$; e.g. Quinn and Keough, 2002: 199–200). When the ANOVA factor interaction was significant, factor levels within the ANOVA (two sampling seasons and three lake areas) were considered statistically different from one another (Zar, 2009).

Linear regressions were performed for selected data sets. We performed linear regressions between macrophyte abundance and phytoplankton biomass to see if the mutual exclusion of macrophytes and phytoplankton, typical in nutrient-rich, shallow temperate lakes (e.g., Jeppesen et al., 1998), also exists in tropical Inlay Lake. For such regressions, run for total, submerged, and floating-leaved macrophytes separately and for November and February/March separately, macrophyte abundance was treated as the independent variable based on the overwhelming evidence that macrophytes drive macrophyte–phytoplankton interactions (e.g., Timms and Moss, 1984; van Donk et al., 1993; Jasser, 1995; Mjelde and Faafeng, 1997; Pelton et al., 1998; Körner and Nicklisch, 2002; Hilt and Lombardo, 2010; Lombardo et al., 2013).

Uni- and bivariate analyses were performed with Addinsoft® XLSTAT®©, with significance assumed for $p < 0.05$. The assumptions of these parametric techniques were checked by visual inspection of data and residual distributions (Zar, 2009). However, ANOVAs and regressions are robust and give reliable results provided that non-normality and/or heteroskedasticity are not extreme (Zar, 2009).

3. Results

3.1. Physical and chemical variables

Inlay Lake is a shallow, clear and calcareous lake. However, some areas close to inflowing rivers and at macrophyte and sediment removal areas had higher turbidity and TOC than the rest of the lake (pers. obs.).

Water temperature measured during sample collection (central time of the day) was slightly but significantly higher in November and in the middle lake area (Table 2). Average pH was higher in February than in November. Conductivity was different across lake area and sampling season, with a significant lake area × season interaction, probably due to the small standard errors (Table 2). The dissolved oxygen in the surface layer was at or above 100 % saturation; and tended to be lower after the rainy period (November) than after the dry period (February/March) (Table 2).

TP and TN concentrations indicated mesotrophic conditions (Table 2) and were generally higher close to the shore (Supplementary Table S1), reflecting the pollution from inflowing rivers (Table 3), shoreline villages and floating gardens, while TOC was higher in the northern lake area (Table 2, Fig. 3).

The first two axes in a principal component analysis (PCA) of physicochemical variables from all sampling times and sites, explained 52 % of the total variation in the dataset (Fig. 3). The first axis was related to total nutrient concentrations (TN, TP, SiO_2 and conductivity) and pH, while the second axis was related to TOC and dissolved inorganic N (DIN; NO_3+NO_2), but also PO_4. The ordination did not show any separation between lake regions or sampling seasons, however, there was a general trend for northern sites to have higher TN concentrations and TOC than southern sites while dissolved nutrient availability (NO_3+NO_2, PO_4) was slightly higher at southern lake sites.

3.2. Aquatic macrophytes

The lake is surrounded by helophytes, dominated by *Phragmites karka*, and floating gardens, covering approximately 35 and 65 % of the shoreline, respectively. The average maximum depth for the helophytes is estimated to be 1.4 m (measured on 23 November 2015; not correlated to median water level). Maximum depth of submerged aquatic macrophytes was estimated to be 2.8–3 m (depth measured in November 2014).

A total of 28 species of aquatic macrophytes were identified during the survey period. The species included 16 submerged (including charophytes), 7 floating-leaved and 5 free-floating species (Supplementary Table S3). In general, the highest richness (as number of taxa) was

Table 2
Physical measurements and water chemistry from Inlay Lake, 2014–2017, by season (November and February/March) and lake area (north, middle and south); **average ± standard error**. Incomplete datasets and statistical analysis for complete datasets is in Supplementary Table S2.

			November			February/March		
variable[1]	abbrev.	unit	north	middle	south	north	middle	south
water temperature	T	°C	24.6 ± 0.5	25.8 ± 0.2	25.3 ± 0.3	23.3 ± 0.5	25.4 ± 0.3	24.1 ± 0.5
pH	pH	pH units	7.9 ± 0.1	8.1 ± 0.1	8.0 ± 0.2	8.5 ± 0.1	8.4 ± 0.1	8.3 ± 0.2
conductivity	cond	μS/cm	416.7 ± 14.3	363.6 ± 6.4	360.1 ± 4.4	351.4 ± 15.4	347.0 ± 8.5	349.3 ± 15.4
dissolved oxygen[c]	DO	mg O_2/L		6.4 ± 0.5			8.8 ± 0.5	
oxygen saturation	%DO	%		85.6 ± 6.8			115.4 ± 6.9	
calcium[c]	Ca	mg Ca/L		48.6 ± 1.9			40.1 ± 4.8	
total organic carbon[c]	TOC	mg C /L	6.4 ± 0.8	6.0 ± 0.3	3.8 ± 0.7	5.3 ± 0.5	5.0 ± 0.2	3.8 ± 0.6
total phosphorus[c]	TP	μg P/L	14.2 ± 3.1	18.2 ± 2.8	15.0 ± 1.9	9.1 ± 1.2	28.5 ± 18.9	16.3 ± 3.0
phosphate[c]	PO_4-P	μg P/L	3.3 ± 1.1	3.8 ± 0.7	4.3 ± 0.5	2.6 ± 1.1	3.0 ± 1.1	5.5 ± 2.1
total nitrogen[c]	TN	μg N/L	442.1 ± 23.8	450.0 ± 9.5	429.4 ± 42.6	530.0 ± 56.2	467.2 ± 74.7	446.4 ± 37.5
ammonium[c]	NH_4	μg N/L	53.4 ± 5.1	32.8 ± 3.0	32.8 ± 4.7	38.7 ± 6.5	35.7 ± 4.0	40.3 ± 4.5
nitrate + nitrite[c]	NO_x	μg N/L	24.2 ± 6.3	5.0 ± 0.4	52.0 ± 22.2	11.6 ± 2.1	10.3 ± 2.2	95.3 ± 56.5

[1] Superscript c denotes concentrations.

Table 3
Water chemistry from the main inlet rivers Belui (upper Belu), Tham Daung (Nant Latt), Nei Gyav (Ye Pae) and Ka Law (see Fig. 1). **Single values** from different dates. Nov.17-data from Eriksen et al. (2021), from slightly different sampling sites as the other dates.

			Belui (upper Belu)				Tham Daung		Nei Gyav		Ka Law
variable	abbrev.	unit	nov.14	febr.15	nov.15	nov.17	nov.15	nov.17	nov.15	nov.17	nov.17
total phosphorus	TP	µg P/L	57	18	57	27	27	68	42	93	10
phosphate	PO_4-P	µg P/L	29	13	29	19	14	50	20	11	1
total nitrogen	TN	µg N/L	530	635	690	1390	620	1600	560	142,000	885
ammonium	NH_4	µg N/L	19	19	30	13	14	215	60	75	31
nitrate + nitrite	NO_x	µg N/L	410	550	485	1300	500	920	130	>20,000	900

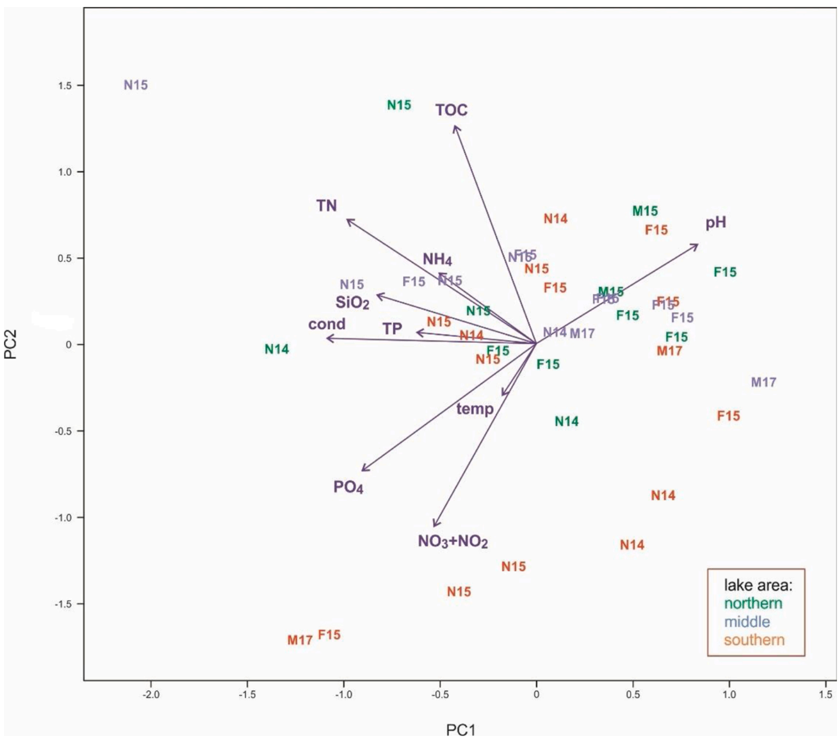

Fig. 3. PCA on environmental variables for all periods (2014–2017) and sites. Station coding/legend is as follows: Green = area "north"; orange: area "south"; blue: area "middle". The letter (F = February; M = March; N = November) and the number (14, 15, 17) are the month and year of sampling (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

recorded close to the shores while the central parts of the lake had the lowest richness, but macrophyte taxonomic richness in the observational plots was statistically similar across lake areas and sampling periods (two-way ANOVA for total macrophyte richness: $F_{period\,(1,1)} = 0.131$, $p = 0.720$; $F_{area(1,2)} = 2.721$, $p = 0.077$; $F_{interaction\,(1,2)} = 1.284$, $p = 0.287$; for submerged species: $F_{period(1,1)} = 0.266$, $p = 0.609$ $F_{area(1,2)} = 1.078$, $p = 0.350$; $F_{interaction(1,2)} = 0.272$, $p = 0.763$; for free-floating and floating-leaved species: $F_{period\,(1,1)} = 3.957$, $p = 0.053$; $F_{area(1,2)} = 0.616$, $p = 0.545$; $F_{interaction\,(1,2)} = 0.397$, $p = 0.675$) (Supplementary Table S3). Some protected bays close to hotels appeared to have a high taxonomic richness of floating-leaves species (pers. obs., not included in the survey).

The submerged vegetation, dominated by *Nechamandra alternifolia* and *Potamogeton lucens,* and to a lesser degree, *Ceratophyllum demersum, Myriophyllum verticillatum, Najas indica* and *Chara zeylanica,* made extensive stands in most of the lake and throughout the year, while the free-floating species, dominated by *Eichhornia crassipes*, formed small- to medium-sized moving islands (Supplementary Table S3). The floating-leaved species were very rare in the lake.

Total macrophyte and submerged species (elodeids and charophytes) abundance were lower in the middle and deepest part of the lake regardless of the sampling period (Fig. 4, Supplementary Table S4). Total abundance of floating-leaved and free-floating species (nympheids and lemnids) was lower than total submerged vegetation and remained similar across lake areas and sampling periods (Supplementary Table S4).

The community composition in November 2015 was not significantly related to any of the environmental variables (water chemistry, depth, temperature, latitude and longitude) in the RDA (data not shown). However, testing effects of latitude and longitude alone, there was a weak, but non-significant effect of latitude. A PCA on environmental variables in February 2015 revealed that the main gradient in environmental conditions (PC axis 1, Fig. 5A) was most strongly related to conductivity, PO_4, DIN, depth and pH (Fig. 5A). The second strongest gradient (axis 2, Fig. 5A) was related to longitude, TOC, and total phytoplankton biomass. The same analysis on the community composition in February 2015 revealed no significant effects of water chemistry, but depth and latitude were significant (Fig. 5B). Together, these variables explained 25 % of the variation in macrophyte community composition.

3.3. Phytoplankton

Phytoplankton taxonomic richness (as number of major groups) was

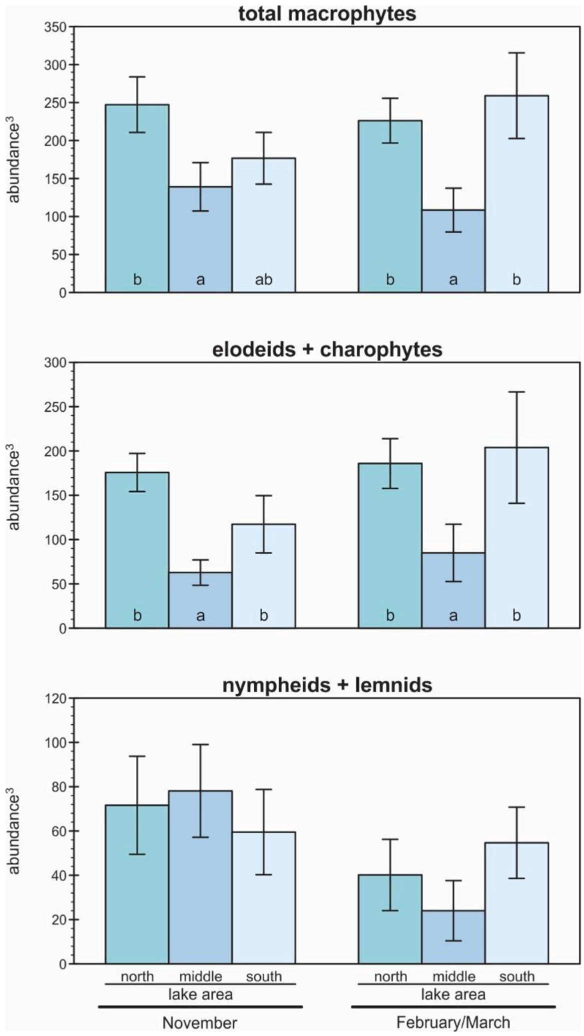

Fig. 4. Abundance of macrophytes (as cubed 1–5 scale) by lake area and sampling period for all periods (2014–2017). From top: total macrophytes; submerged forms (elodeids + charophytes); floating-leaved and free-floating forms (nympheids + lemnids). Abundance is expressed as cubed five-level values for each species (see Schneider et al., 2018). Average ± standard error; sample sizes: *n*north,Nov = 8, *n*middle,Nov = 8, *n*south,Nov = 10, *n*north, Feb = 7, *n*middle,Feb = 6, *n*south,Feb = 7. Different letters denote statistically different average values (in alphabetical order with a = lowest) according to multiple-comparison Tukey HSD tests after significant two-way ANOVAs; complete statistical results are in Supplementary Table S4. Please note the different *y* scales.

the same across lake areas and in both sampling periods (two-way ANOVA: period: $F_{1,40} = 0.407, p = 0.527$; area: $F_{2,40} = 1.508, p = 0.238$; period × area: $F_{2,40} = 1.382$, $p = 0.263$). At all localities, Bacillariophyceae, Cryptophyceae, Chlorophyceae, Euglenophyceae or Cyanobacteria were the dominating groups. The cyanobacterium *Microcystis* sp. was found in low amounts at almost all localities. Using ELISA, production of hepatotoxic microcystins was confirmed in four *Microcystis* cultures isolated from Inlay Lake.

In general, the phytoplankton biomass in Inlay Lake was low, with average biomasses less than 1 mg fresh weight (FW) L^{-1} (Fig. 6). However, higher biomasses (more than 2 mg/L) were observed at 3–4 localities close to the shore and floating gardens (Supplementary

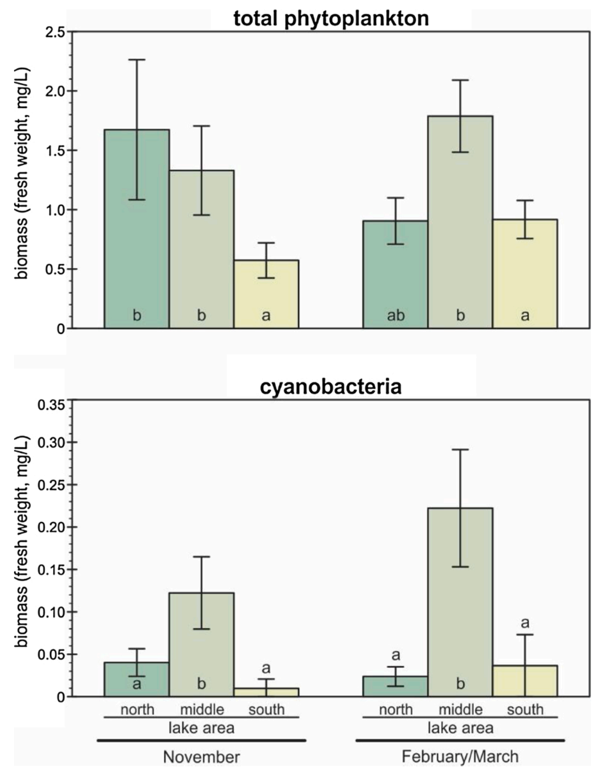

Fig. 6. Total phytoplankton biomass and cyanobacteria biomass (as mg L^{-1} of fresh biomass) by sampling season (Nov, Feb) and lake area (northern, middle, southern). Average ± standard error; sample sizes: *n*north,Nov = 8, *n*middle, Nov = 8, *n*south,Nov = 10, *n*north,Feb = 7, *n*middle,Feb = 6, *n*south,Feb = 7. Different letters denote statistically different average values according to multiple-comparison Tukey HSD tests after significant two-way ANOVAs; complete statistical results are in Supplementary Table S4). Please note the different *y* scales.

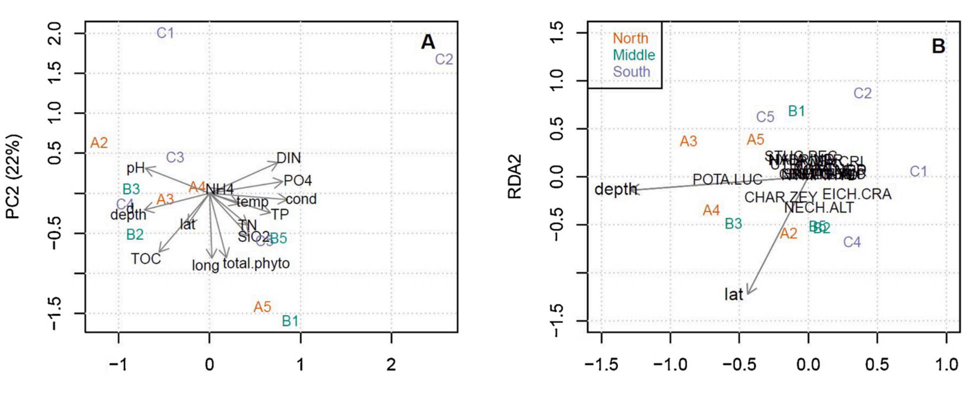

Fig. 5. A) PCA on environmental variables, and B) RDA on macrophyte community composition from February 2015. Only significant variables were included in the RDA plot. Station coding/ legend is as follows: Orange = area "north", green = area "middle", purple = area "south". Abbreviations: TN: Total Nitrogen, TOC: Total Organic Carbon, TP: Total Phosphorous, PO_4: Phosphate, DIN: dissolved inorganic N (NO_2+NO_3), SiO_2: silicate, cond: conductivity, lat: latitude, long: longitude. Species abbreviations: see Supplementary Table S3 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table S5).

Total phytoplankton biomass (mg of fresh weight L^{-1}) was relatively variable across sites. The highest total phytoplankton biomass was found in the northern area in November while in February-March the middle area had the highest biomass. The biomass was lowest in November in southern area (Fig. 6). Cyanobacteria were significantly more abundant in the middle lake area, regardless of sampling period (Fig. 6).

A PCA on the environmental variables from November 2015 revealed that the main gradient in environmental conditions (PC axis 1, Fig. 7A) was most strongly related to TOC, TN, latitude, and DIN. The second strongest gradient (axis 2) was related to temperature, DIN, NH_4, conductivity and TP. Two variables could significantly explain variability in phytoplankton community composition in November 2015, namely TOC and TN (Fig. 7B). Latitude and longitude did not come out as significant in the model selection or in the variation partitioning procedure. Hence, most of the explained variation in phytoplankton community composition in November 2015 was related to environmental factors, not spatial position. The fraction explained by TOC and TN was 24 % according to the adjusted R^2 of the RDA. There were, however, few strong relationships between relative abundances of specific phytoplankton classes and the significant variables (Fig. 7B). A PCA on environmental variables in February 2015 revealed that the main gradient in environmental conditions (PC axis 1, Fig. 7C) was most strongly related to conductivity, PO_4, DIN, TP and pH (Fig. 7C). The second strongest gradient (axis 2, Fig. 7C) was related to longitude, TOC, SiO_2 and TN. Three variables came out as significant predictors of phytoplankton community composition in February 2015: PO_4, SiO_2 and TOC (Fig. 7D). Latitude and longitude were not significant in the model selection or the variation partitioning. According to the adjusted R^2 of the RDA, 32 % of the variation in phytoplankton community composition was explained by environmental factors in February 2015, which was higher than in November. There were, however, no strong relationships between relative abundances of phytoplankton classes and single variables.

3.4. Phytoplankton vs. aquatic macrophytes

In November, total phytoplankton biomass was negatively associated with total macrophyte abundance in the northern lake area and positively associated in the middle area (Fig. 8, Supplementary Table S7). No relationship was found in February. Submerged macrophytes in the northern lake area explained 69 % of phytoplankton biomass, and their relationship was negative both in November and in February. In the

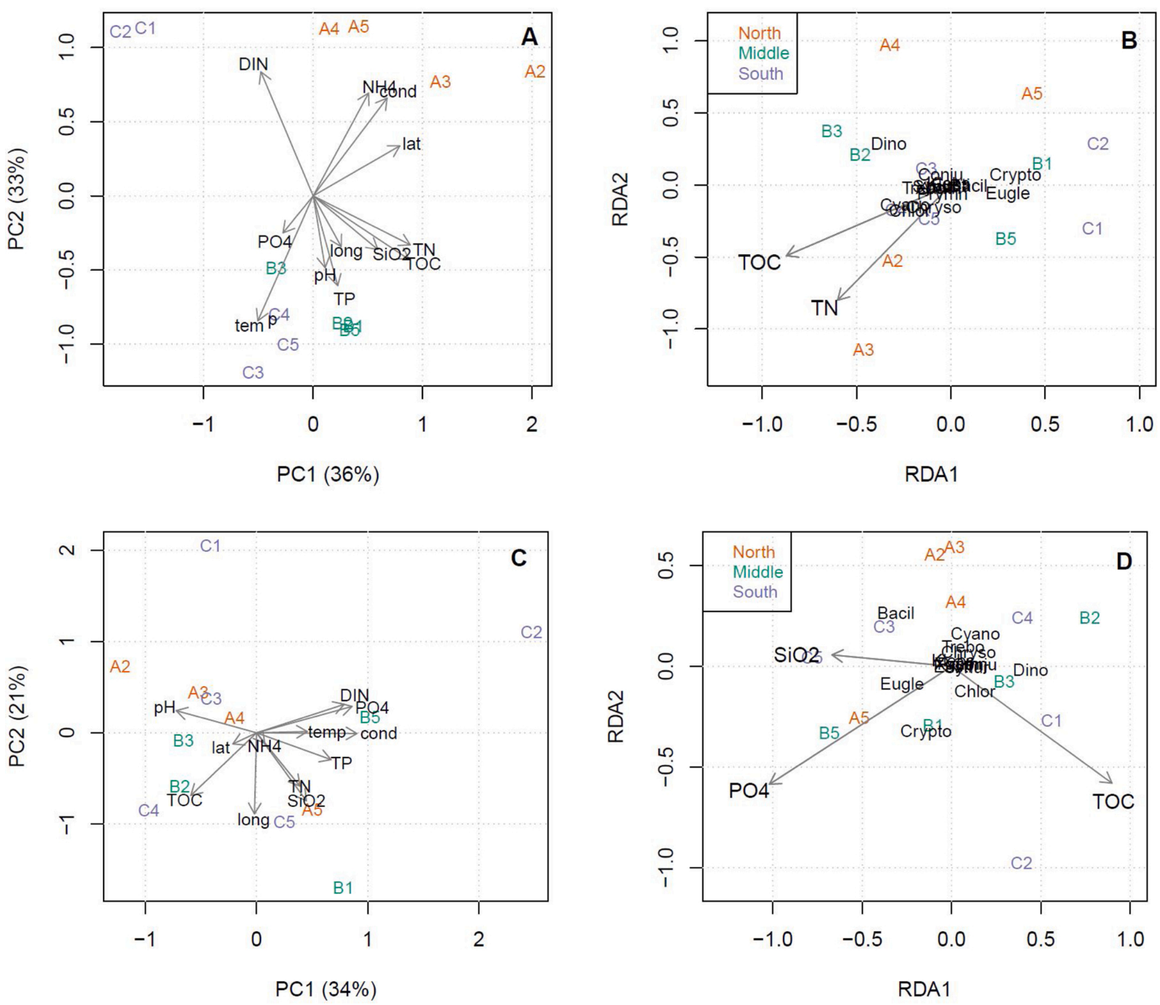

Fig. 7. A) PCA on environmental variables, and B) RDA on phytoplankton community composition from November 2015. C) and D) show the same plots from February 2015. Only significant variables were included in the RDA plots. Station coding/legend is as follows: Orange = area "north", green = area "middle", purple = area "south". Abbreviations: Crypt: Cryptophyceae, Xanth: Xanthphyceae, Chlor: Chlorophyceae, Klebs: Klebsormidiophyceae, Eusti: Eustigmatophyceae, Cyano: Cyanophyta, Chrys: Chrysophyceae, Prymn: Prymnesiophyceae, Conju: Conjugatophyceae, Dinop: Dinophyceae, Synur: Synurophyceae, Bacil: Bacillariophyceae, Eugle: Euglenophyceae, TN: Total Nitrogen, TOC: Total Organic Carbon, TP: Total Phosphorous, PO_4: Phosphate, DIN = dissolved inorganic N (NO_2+NO_3), SiO2 = silicate, cond = conductivity, lat = latitude, long = longitude (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

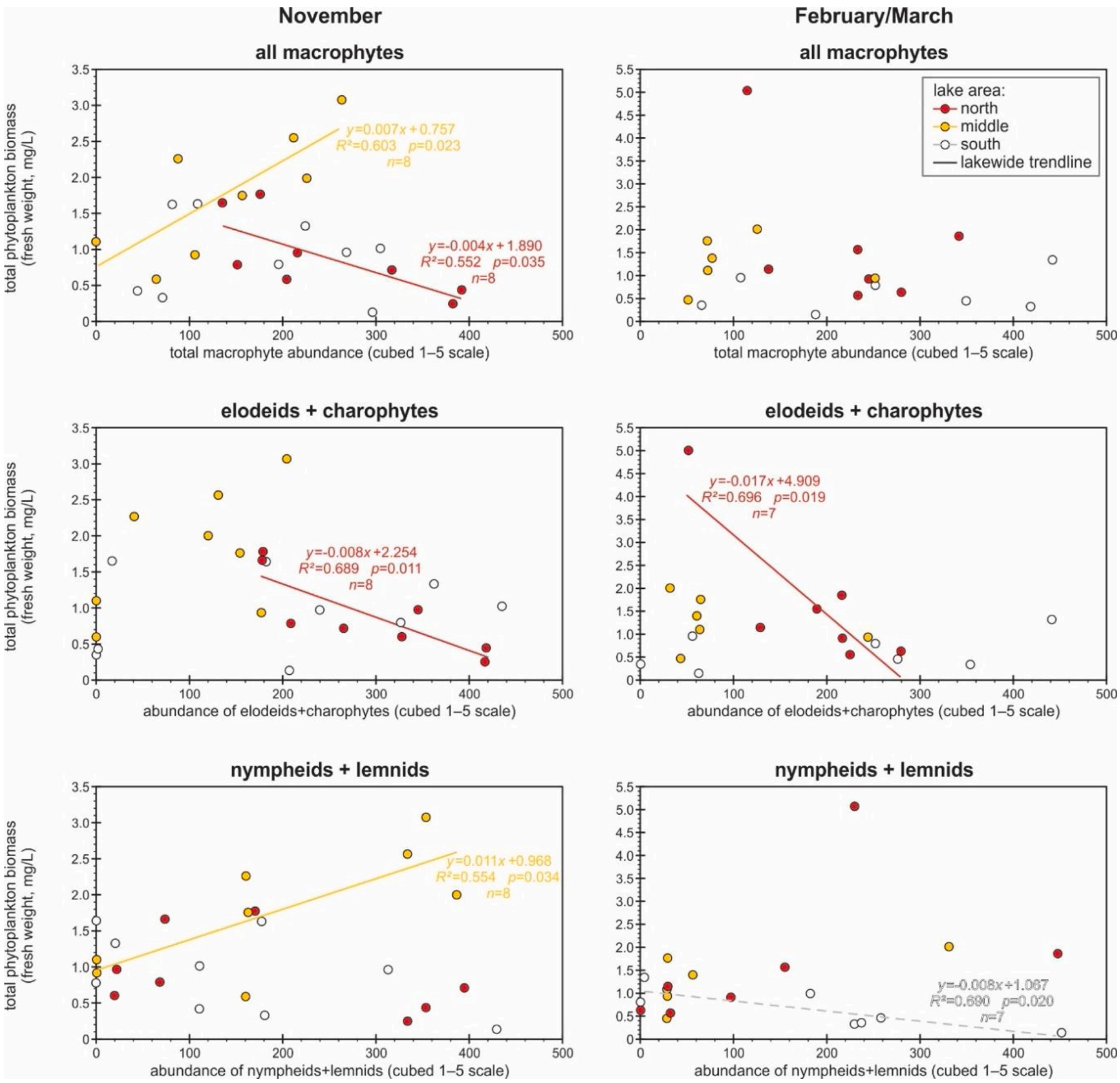

Fig. 8. Relationships (as linear regressions) between total, submerged (elodeids + charophytes), and floating-leaved (nympheids + lemnids) macrophyte abundance (cubed five-level scale) and total phytoplankton biomass by lake area and sampling period. Complete regression results are in Supplementary Table S7.

middle of the lake, the floating-leaved and free-floating macrophytes had a positive relationship with total phytoplankton biomass in November.

Cyanobacteria biomass was negatively correlated with total and submerged macrophyte abundance in the northern lake area in February (Supplementary Table S7).

4. Discussion

In contrast to earlier water chemistry data (Akaishi et al., 2006), we found relatively low nutrient concentrations in Inlay Lake. However, data from the tributaries show periodically very high nutrient input, indicating potentially eutrophic conditions. In addition, studies of benthic macroinvertebrates in the tributaries in November 2018 showed that communities in some places were dominated by organisms having high tolerances to low oxygen, which may also indicate high nutrient inputs at least in some parts of the year (Eriksen et al., 2021). The contradicting results between our survey and earlier data indicate large temporal and spatial variations in nutrient concentrations in the lake. In addition, a large amount of nutrients is bound in the rich macrophyte vegetation (Mjelde and Faafeng, 1997; Schneider et al., 2014; Van Donk et al., 1993).

The species richness of hydrophytes in Inlay Lake seems high compared to other tropical lakes (e.g., Dalu et al., 2012; Dong et al., 2014; Lacoul and Freedman, 2006; Ondiba et al., 2018; Saluja and Garg, 2017), and higher than in other lakes in Myanmar (pers. obs.). However, the species richness is only medium-high compared to the species richness in lakes of similar size and type in low-altitude temperate areas in Europe (e.g., Rørslett, 1991; Viana et al., 2014). The high tropical diversity of freshwater flora (e.g., Chambers et al., 2008) typically belongs to the wetland flora and helophytes (which were not included in our study), and not the hydrophyte flora. In addition, the massive helophyte-covered littoral zone and eutrophic water prevent growth of more pollution-sensitive submerged species in Inlay Lake.

The high aquatic macrophyte diversity and species richness is mainly due to submerged species, which constitute 53 % of the total richness. Most of the submerged species, e.g., the dominant *Nechamandra alternifolia, Potamogeton lucens*, *Ceratophyllum demersum, Myriophyllum verticillatum* and *Najas indica* are bicarbonate users (e.g., Madsen and Sandjensen, 1991), and their abundances reflect and depend on the high alkalinity (calcium concentration) in the lake (e.g., Vestergaard and Sand-Jensen, 2000). In addition, most of the submerged species in Inlay Lake tolerate high nutrient conditions and turbid waters, due to low-light tolerance, canopy forming ability, etc. (Mjelde and Faafeng, 1997; Sand-Jensen and Madsen, 1991; Tóth and Herodek, 2011). Because of their elongated and canopy-forming growth form (Frodge et al., 1990), these species occupy a large part of the water column in shallow areas in Inlay Lake. The submerged species have different flowering and fruiting periods (Panda et al., 2016) and show some seasonality in their abundance. So, due to high species richness with different functional traits and phenology, the lake maintains a continuous submerged macrophyte community throughout the year in most parts of the lake, especially in the northern and southern areas.

The dominating free-floating *Eichhornia crassipes* is an invasive South American species and was introduced to the lake as an ornamental plant probably during the early 1900s (Su and Jassby, 2000). It is today considered as the most harmful aquatic weed throughout the tropics and subtropics (Cooke et al., 2005; Gopal, 1990). The abundance of this species is low in Inlay Lake and it may be nutrient limited by submerged species and constrained by wind erosion and heavy boat traffic on the lake. *E. crassipes* is also used as a fertilizer on the floating gardens which can affect its abundance. Several of the floating-leaved species are used for ornamental purpose (*Nymphaea*) and for weaving products (mainly *Nelumbo*), which may be the reason for their very low abundance in the lake.

Reduced abundance of free-floating species in the middle lake areas from November (after rainy period) to February/March (after dry period) may be due to decreased water depth and hence increased competition with submerged species. No significant differences between sampling periods for total macrophytes or submerged macrophytes indicate stability throughout the year independent of dry or wet period. This in contrast to a eutrophic Myanmar lowland reservoir (Moeyingyi) where both richness and abundance of macrophytes were markedly reduced in the dry period (pers. obs., see also Mjelde and Ballot, 2016). No significant associations between macrophytes and physical and chemical variables indicates that the water quality in all areas is suitable for submerged macrophytes, which is important for lake resilience, and hence, for lake management. The significant associations between macrophytes and spatial factors (latitude, i.e. lake area, and depth) probably reflect the lower abundance of submerged macrophytes in the deeper central area, indicating a maximum growing depth of submerged species at approx. 3 m depth. In addition, the spatial factors probably reflect the differences in functional traits and habitat preferences, e.g., *Nechamandra alternifolia* seems to prefer the northern area while *Chara zeylanica* had highest abundance in the southern part.

As expected, we found significant associations between phytoplankton and water quality factors. However, the general low phytoplankton biomasses and the negative relationship between phytoplankton and submerged macrophytes, especially in November, most probably indicate competition with the submerged macrophytes. The higher standing crop typically allows macrophytes to outcompete and control microscopic algae development despite the latter's higher uptake rates (e.g., Körner and Nicklisch, 2002; Pelton et al., 1998). The higher biomass of some phytoplankton groups observed close to the floating gardens (longitude) can indicate higher nutrient and/or organic matter concentrations in those areas (Novarino, 2011; Rosén, 1981; Wolowski, 2011).

Although we could not quantify the cyanobacterial–total phytoplankton relationship due to overall low biomass values and a high datapoint scatter, our observations suggest that cyanobacteria biomass in Inlay Lake may be directly related to total phytoplankton biomass as it has been observed in subtropical (Canfield et al., 1989) and temperate lakes (Downing et al., 2001). Among the most common cyanobacteria species in Inlay Lake there were four toxin-producing strains of *Mycrocystis*, strongly suggesting that Inlay Lake could experience potentially harmful cyanobacterial blooms should in-lake nutrient concentrations increase to a full-blown eutrophic state. However, our data suggest that total phytoplankton and cyanobacterial biomass were inhibited by total and submerged macrophytes in the heavily vegetated northern lake area, in agreement with findings from subtropical and temperate lakes (e.g., Timms and Moss, 1984; Canfield et al., 1989; Scheffer, 1998; Downing et al., 2001). Such relationships suggest that cyanobacteria might become dominant in Inlay Lake if nutrient concentrations increase and/or loss of submerged macrophyte abundance occur in the future, as it happens in temperate lakes (e.g., Timms and Moss, 1984). Cyanobacterial dominance may be further exacerbated by global warming (e.g., Newcombe et al., 2012).

The dominating submerged species in Inlay Lake may be capable of removing and storing large quantities of nutrients from the water by foliar and root uptake, as it was observed from temperate lakes (Pelton et al., 1998; Phillips et al., 1978; Van Donk et al., 1993). Several studies demonstrate how macrophytes affect the nutrient concentrations in the water and suppress phytoplankton biomasses (e.g., Hilt and Lombardo, 2010; Scheffer et al., 1993). Based on the physical, chemical, macrophyte, and phytoplankton patterns that we have observed in Inlay Lake, we suspect a co-involvement of competitive nutrient uptake by macrophytes behind the very low phytoplankton biomasses also in Inlay Lake.

The middle and deepest part of the lake, around 3 m depth in the rainy season, has low abundance of both submerged macrophytes and the free-floating species *E. crassipes*. The relatively low macrophyte abundance in relation to water volume might prevent the macrophytes from exerting their control on phytoplankton growth. This is supported by the relatively high abundance of cyanobacteria in the middle lake area, as cyanobacteria are typically more susceptible to macrophyte allelopathy than other phytoplankton groups (Gross et al., 2003; Jasser, 1995; Lombardo et al., 2013). Therefore, we suggest that, in addition to nutrient competition, allelopathic compounds released from *Myriophyllum verticillatum*, *Ceratophyllum demersum* and *Chara* species (Gross et al., 2003, 2007; Hilt et al., 2006) may be important in inhibiting the growth of cyanobacteria. *Nechamandra alternifolia*, which dominates the submerged vegetation in the northern area, also might inhibit phytoplankton growth in general and especially cyanobacteria. The leaves in this species possess large secretory cells (Cook and Lüönd, 1982), which make the whole plant slippery (pers. obs.). The secretion from the cells may have an allelopathic effect on phytoplankton, however no studies about this seem to exist, and our hypothesis remains untested. Toxic compounds from other species, e.g., *E. crassipes* (Gross, 2003; Sharma et al., 1996), may also affect phytoplankton in Inlay Lake.

Despite the gaps in the knowledge of the Inlay Lake ecosystem, our study indicates that the high abundance of submerged macrophytes play an important role for maintaining a clear water state in Inlay Lake. In addition, the high number of submerged species with different seasonal strategies, functional traits, and phenology allows high submerged abundance in different areas and throughout the year, and may contribute to maintaining the resilience and stability of the ecosystem, as suggested earlier (Moss, 1998; Scheffer, 1998; Sayer et al., 2010; Liu et al., 2020). Fish, invertebrates, zooplankton and periphyton algae certainly play a role in the lake ecosystem stabilization, however, no comprehensive studies on these groups in Inlay Lake exist, and their importance in Inlay Lake remains unknown. The shallowness of the lake, which enables the submerged vegetation to cover a large bottom area also during periods with more turbid water, is a prerequisite for a macrophyte-dominated clear water state.

No comprehensive management plan for decreasing nutrient loads to the lake has been established. Considering the high catchment:lake surface area and the deforestation and hotel plans in the catchment area, which most probably will increase sediment and nutrient loads (Cooke et al., 2005), Inlay Lake may be close to or within the nutrient level range where alternative states can exist (Phillips et al., 2016). The richness and abundance of submerged macrophytes has been and is still an important characteristic of Inlay Lake. However, continued or increased nutrient load can result in decreased submerged species abundance and richness which makes the lake more vulnerable to cyanobacteria blooms (Cooke et al., 2005; Downing et al., 2001).

In temperate lakes, species richness of submerged and floating-leaved species seems to decrease when winter nitrate concentrations –

a proxy for nitrate loading – rise above 1–2 mg NO_3-N L^{-1} (Barker et al., 2008; James et al., 2005). We do not know if these values also apply to tropical lakes, but one should be aware that nutrient concentrations in Inlay Lake, at least in some areas of the lake, may at times be close to such thresholds.

The use of lake macrophytes as mulch and fertilizers in the floating gardens is increasingly replacing the use of chemical fertilizers. This means that large amounts of lake macrophytes are harvested (Michalon, 2014). During our study period, we did not see any reduction in macrophyte biomass due to the harvest of submerged macrophytes, however no study on this aspect were conducted. The use of macrophytes may be minor compared to their abundance and regrowth. However, increasing this practice may endanger the natural balance between aquatic macrophytes and phytoplankton in Inlay Lake which can trigger a shift from the current macrophyte dominance towards a phytoplankton dominated lake (Scheffer et al., 2001).

We suggest that a year-long growing period and no dieback in autumn favour submerged macrophytes, which can thus maintain a heavy presence throughout the year. Since macrophytes do not have to compete with phytoplankton every spring as in temperate lakes, we suppose that their presence may be more stable than in temperate systems at similar nutrient level. Conversely, once a turbid phytoplankton-dominated state is established, it may be more stable in tropical areas compared to temperate areas. Stability in Inlay Lake may also be influenced by its extreme shallowness. The Osgood Index (OI) for Inlay Lake is 0.2–0.3 which is way below the OI≈6 threshold for polymixis (Mataraza and Cooke, 1997), strongly suggesting that Inlay Lake is particularly prone to storm-related mixing that could resuspend nutrients making them available for phytoplankton growth. Conversely, the heavy presence of submerged plants may reduce sediment resuspension despite the frequent polymixis (e.g., James and Barko, 1994; Vermaat et al., 2000).

To assess the consequences of increasing pressures, mainly nutrient load (from growing human population, agricultural areas, tourism and hotel establishments) and sedimentation load (due to deforestation) it is important to increase the knowledge about the Inlay Lake ecosystem and its catchment area. In addition, continuation of management activities in the lake (MOECAF, 2014, 2015) followed by further monitoring are needed. Aquatic macrophytes and phytoplankton respond to nutrients which enter the lake only periodically. Therefore, monitoring of these groups is desirable to assist in the management of Inlay Lake, as well as for other Myanmar lakes. The high alkalinity water in Inlay Lake is a premise for the high diversity of submerged species. We expect that increased eutrophication in low alkalinity lakes, e.g., more typical lakes in the lowland dry area in Myanmar (pers. obs.), may favour free-floating macrophyte species, which seem to have a weaker structuring role than submerged vegetation (Meerhoff et al., 2003).

Myanmar currently lacks systems for evaluating the ecological status of its surface waters, though there have been attempts to adopt Integrated Water Resources Management (IWRM) for this purpose through a number of recent government initiatives, including the Myanmar National Water Policy (NWP) and the Myanmar National Water Framework Directive (NWRC, 2014), inspired by the EU Water Framework Directive (EC, 2000; WFD, 2000). However, the success of the Myanmar National Water Framework depends on the knowledge about the different freshwater ecosystems in the country, with different biodiversity and stability drivers. The examination and maintenance of biodiversity and water quality in other lakes and reservoirs in Myanmar should be given more attention. Knowledge about aquatic macrophyte growth and understanding the mechanisms behind community shifts is of considerable importance for the management and the establishment of good ecological status for Myanmar's lakes and reservoirs.

CRediT authorship contribution statement

Thida Swe: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Paola Lombardo:** Formal analysis, Visualization, Writing - review & editing. **Andreas Ballot:** Conceptualization, Methodology, Visualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Supervision. **Jan-Erik Thrane:** Formal analysis, Visualization. **James Sample:** Formal analysis, Visualization. **Tor Erik Eriksen:** Writing - review & editing. **Marit Mjelde:** Conceptualization, Methodology, Visualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors report no conflict of interest

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2021.125910.

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