



# Phytoplankton size- and abundance-based resilience assessments reveal nutrient rather than water level effects



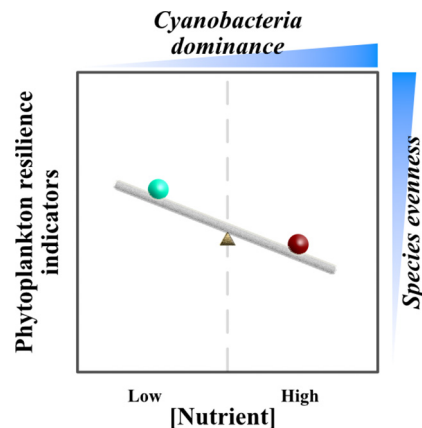
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## HIGHLIGHTS

- Resilience of phytoplankton to nutrients and water depth manipulations was assessed.
- Resilience was inferred and compared from size- and abundance-based approaches.
- Both approaches, size- and abundance-based resilience assessment, were comparable.
- Nutrient enrichment rather than water depth influenced resilience.

## GRAPHICAL ABSTRACT



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## ABSTRACT

The use of discontinuity analysis to assess resilience and alternative regimes of ecosystems has mostly been based on animal size. We so far lack systematic comparisons of size-based and abundance-based approaches necessary for assessing the performance and suitability of the discontinuity analysis across a broader range of organism groups. We used an outdoor mesocosm setup to mimic shallow lake ecosystems with different depths (1.2 m deep, “shallow”; 2.2 m deep, “deep”) and trophic status (i.e. low and high nutrient status characteristic of mesotrophic and hypertrophic lakes, respectively). We compared resilience assessments, based on four indicators (cross-scale structure, within-scale structure, aggregation length and gap size) inferred from the size and abundance (biovolume) structure of phytoplankton communities. Our results indicate that resilience assessments based on size and biovolume were largely comparable, which is likely related to similar variability in the size and abundance of phytoplankton as a function of nutrient concentrations. Also, nutrient enrichment rather than water depth influenced resilience, manifested in decreased cross-scale structure and increased aggregation lengths and gap sizes in the high-nutrient treatment. These resilience patterns coupled with decreased phytoplankton diversity and dominance of cyanobacteria in the high nutrient treatment support the use of discontinuity analysis for testing alternative regimes theory. Concordance of size-based and abundance-based results highlights the approach as being potentially robust to infer resilience in organism groups that lack discrete size structures.

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## 1. Introduction

The concept of ecological resilience was initially defined by Holling (1973) as the amount of change needed to force a system from being maintained by one set of self-regulated processes and structures to a fundamentally different system. The concept recognizes that ecological systems can reorganize in alternative states once disturbance thresholds are exceeded (so called “regime shifts”; Beisner et al., 2003). The socio-ecological outcomes following a regime shift are uncertain and generally difficult to predict (Folke et al., 2004; Jouffray et al., 2015), yet highly relevant considering that ecosystems are increasingly exposed to anthropogenic stressors (McLaughlin et al., 2013). Despite its usefulness in describing and capturing non-linear responses of ecosystems when critical stressors thresholds are surpassed (Scheffer et al., 2001), quantifying ecological resilience is challenging (Angeler and Allen, 2016). However, the discontinuity hypothesis (Holling, 1992) provides a framework to quantify resilience as it explicitly accounts for the intricate organization across multiple dimensions and non-linear behavior of ecosystems (Angeler et al., 2015a; Gunderson, 2000). This non-linear behavior is manifested in the discontinuous (scale-specific) distribution of body size across different groups of organisms and ecosystems (phytoplankton: Angeler et al., 2019; zooplankton; Baho et al., 2015; fish; Havlicek and Carpenter, 2001; mammals; Lambert, 2006; birds; Wardwell et al., 2008).

The discontinuity hypothesis postulates that scale-specific processes create discrete structures that are mirrored by species assemblages where resources are available to support subsistence and ecological functions (Holling, 1992). These scaling patterns are mostly inferred from organisms' body size (Allen et al., 2014; Nash et al., 2014). Size is recognized as the most important characteristic of an organism (White et al., 2007) as it integrates physiological and ecological processes (Brown et al., 2004; Elton, 1927; Peters, 1983), and it displays a relatively high degree of evolutionary conservatism across geological time scales (Polly, 2012). According to the discontinuity hypothesis, species falling within similar body size clusters operate at specific spatial and temporal scales that are different from the other scales in the system (Holling, 1992). Once the scaling structure has been quantified using discontinuity analysis (e.g. Barichiev et al., 2018), the distribution of species and their associated functions within and across scales can be evaluated. Resilience is predicted to increase when species having similar functional attributes are redundant within and across scales (Allen et al., 2005; Peterson et al., 1998). High functional redundancies increase the buffering abilities of ecosystems against stressors due to higher likelihood of compensating for loss of species or functions from the other (unaffected) scales (Angeler et al., 2015b; Peterson et al., 1998; Wardwell et al., 2008). Beside within- and cross-scale attributes, discontinuity analyses allow the quantification of two additional indicators of resilience, the aggregation length and gap size. The aggregation length is defined as the length of a specific scale in the system measured in terms of the range from lowest to highest body size of species comprising the scale, whereas a gap is an area in a body size distribution that is unoccupied by species, presumably due to the lack of resources (Holling, 1992; Stow et al., 2007). Changes in the within- and cross-scale structure, aggregation length, and gap size can indicate loss of resilience, regime collapse, and reorganization (Baho et al., 2015; Roberts et al., 2019b; Spanbauer et al., 2016). Discontinuity analysis is therefore useful for assessing and predicting alternative regimes and regime changes (Roberts et al., 2019a).

With a focus on animal body size distributions as a quantifiable metric of resilience, Holling's discontinuity hypothesis emphasizes the role of relatively slow eco-evolutionary processes, and thus ultimate factors, for shaping resilience (Holling, 1992). However, there is also evidence that processes acting at more immediate or proximate ecological time scales, for instance biological interactions and environmental factors such as nutrients and temperature that influence the abundance or biomass structure of populations, can similarly lead to non-linear

structuring of communities (Gaedke et al., 2004; White et al., 2007; Yvon-Durocher et al., 2011). There is therefore a need to account for both ultimate and proximate factors for measuring resilience (Sundstrom et al., 2018). This is especially needed in current times of fast global environmental change. Ecological systems and disturbance regimes are changing rapidly leading to substantial alterations in diversity and communities' structures at time scales corresponding to human lifespans (Ellis et al., 2013; Hughes et al., 2013; McLaughlin et al., 2013). These changes are presumably occurring so fast that many species lack the ability to adapt evolutionarily to these changes (Bell and Collins, 2008). This can ultimately create a latent extinction debt that will manifest once species are lost (Dris et al., 2015). The implication for resilience assessments is that accounting for proximate factors of change by analyzing abundance-dependent matrices (such as biovolume) is likely more sensitive for revealing early signals of ecosystem change than analyses based on ultimate factors which are based on body size. This assumption is inspired by research in community ecology, which has shown that changes in the dominance structure (evenness) of communities are faster and more sensitive indicators of ecological change than species richness (Hillebrand et al., 2008). In reality, however, this picture can be more complex because different hypotheses (energetic, phylogenetic, biogeographical, textural discontinuity, and community interaction) can partially explain elements of discontinuity patterns, and interpretations can therefore vary among the hypotheses and scales of observation (Allen et al., 2006).

Despite the potential distinct role of ultimate and proximate factors for shaping resilience, research is currently based on either body size (Nash et al., 2014) or abundance/biovolume data (Angeler et al., 2012, 2019). There is only preliminary evidence from one study involving zooplankton that discontinuity analysis based on body size and abundance (biovolume) are comparable (Baho et al., 2015), which is at odds with a priori expectations that distinctly different ultimate and proximate factors shape ecological communities and thus resilience in different ways. Thus, more research is needed to systematically compare body mass and abundance data in resilience assessments, with the aim to reveal structuring forces that can lead to a manifestation of similar patterns of resilience. Such results are relevant because understanding the factors that shape natural communities is a fundamental aspect of ecology and ultimately resilience. From the applied side, congruence of resilience assessments based on body mass or abundance suggests that discontinuity analysis could be applied more universally by extending the approach to organism groups with body masses that are particularly challenging to measure (e.g. plants and fungi due to their modular growth) without violating the underlying theory (Angeler et al., 2015a; Holling, 1992). Furthermore, it could inform management and spur research towards the development of rapid and cost-effective measurement and quantification schemes of resilience; for instance, monitoring and assessments based on eDNA abundance in samples (Adams et al., 2019).

Phytoplankton have been shown to be useful models for resilience research (Folke et al., 2004; Scheffer et al., 2001; Scheffer and Carpenter, 2003), due to their diversity (Hutchinson, 1961), wide range of sizes and fast responses to environmental changes (McCormick and Cairns, 1994). Phytoplankton are also influenced by feedback mechanisms involving various biotic (grazing, competition) and abiotic (nutrients, seasonality, light) factors (Leibold and Norberg, 2004; Reynolds, 1984; Shigesada and Okubo, 1981). Phytoplankton are especially useful to understand how excessive nutrient enrichment, which is often related to agricultural practices, induces shifts in lakes from a desirable clear-water state to an undesirable turbid state (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Upon exceeding a nutrient threshold, lakes shift from a clear-water state characterized by the high abundance of submerged macrophytes to a degraded state with frequent cyanobacteria blooms that are generally toxic and detrimental to the provisioning of ecosystem services (Carpenter and Cottingham, 1997). Moreover, the effects eutrophication in lakes

ecosystems are contingent on water depth as shallow and deep lakes may behave differently to nutrient enrichment (Baho et al., 2017; Cooke, 2007). Water depth is an important factor that determines the distribution of both macrophytes (Fu et al., 2014; Ye et al., 2018) and phytoplankton (Jeppesen et al., 2007; Stroom and Kardinaal, 2016), especially cyanobacteria (Dokulil and Teubner, 2000). Habitat heterogeneity (including light regime, pH, temperature, oxygen, stratification profile) increases with increasing depth (Angeler et al., 2005; Diehl, 2002; Havens et al., 1998), which subsequently encompasses a wide range of optimum conditions for different groups of organisms; for example, the abundance of macrophytes tend to decrease with increasing depth (Ye et al., 2018), whereas some species such as cyanobacteria thrive with increasing depth due to their abilities to adjust their buoyancy allowing them to access nutrients from deeper layers (Dokulil and Teubner, 2000; Reynolds, 1987). Previous evidence showed that greater lake depth provides ideal conditions for shade tolerant cyanobacteria to bloom (Nöges et al., 2003; Nöges and Nöges, 1999). Thus, water level can mediate the impacts of nutrient enrichment on biodiversity (Baho et al., 2017). Accounting for such interactions (nutrient enrichment and water depth) is relevant for assessing the resilience of aquatic ecosystems (Baho et al., 2017), which can potentially lead to different results in size-based and abundance-based (phytoplankton biovolume) analyses of resilience.

In this study, we used a mesocosm setup to mimic shallow lake ecosystems with different ecological conditions by manipulating water depth and nutrient levels. The nutrient manipulations mimicked mesotrophic and hypertrophic conditions. The aim of the study was to assess whether the resilience of the phytoplankton communities, that was allowed to develop over a growing season (May to early November 2011), was affected by the experimental manipulations. Using discontinuity analysis (Bayesian classification and regression trees), four indicators (cross-scale structure, within-scale structure, aggregation length, and gap size) of resilience were inferred from phytoplankton size and biovolume to assess the effects of the experimental treatments (water depth and nutrients). In addition, the results of discontinuity analysis obtained from phytoplankton size and biovolume were compared. We assessed the four indicators of resilience to test the following expectations:

- Resilience indicators differ across the nutrient treatments akin to ecosystem conditions that characterize alternative clear and turbid regimes of shallow lakes (Scheffer et al., 2001; Scheffer and Carpenter, 2003).
- Water depth mediates resilience because increased depth can increase spatial heterogeneity conducive to the development of harmful cyanobacteria blooms (Angeler et al., 2005; Diehl, 2002; Havens et al., 1998).
- Results from body size and biovolume differ because of the difference in information content of the data that emphasize ultimate (evolutionary) vs proximate (environmental factors, biological interactions) structuring forces, respectively. Size was deduced from measurements of maximum lengths of individual phytoplankton cells or colonies, whereas biovolume was calculated by combining the volume derived from geometrical shapes and the numerical abundances of phytoplankton present in the samples. More specifically, we expect that the size-based analysis discriminates between treatments, in accordance with the premise that our manipulations comprise alternative regimes. That is, this approach identifies different resilience characteristics between shallow and deep and nutrient rich and poor mesocosms (and potential interactions). But due to the eco-evolutionary feature of body size, proximate changes in mesocosms, as those occurring as a result of seasonal change during our experiment, may be less well captured compared to the abundance-based analysis. We therefore expect that the abundance-based analysis reveals the treatment effects as the size-based analysis, but in

addition shows significant temporal change, thereby capturing dynamic change over time associated with the proximate abiotic and biotic conditions present in the mesocosm.

## 2. Materials and methods

### 2.1. Site

An outdoor mesocosm experiment was set-up in Lake Erken, located in the south-east of Sweden, from May to early November 2011 (ca. six months). Lake Erken (59°49'59" N, 18°33'55" E) is meso-eutrophic (yearly average TP of 25 µg/L), with a surface area of 24.2 km<sup>2</sup>, a mean depth of 9 m and a maximum depth of 21 m (Weyhenmeyer et al., 1999).

### 2.2. Experiment design

A comprehensive description of the experiment can be found in Landkildehus et al. (2014). Briefly, the experiment design comprised a crossed factorial design with four treatments, which were replicated four times. The treatments consisted of two water depths (shallow; S, deep; D) crossed with two nutrients levels (low; L, high; H) resulting in a total of 16 experimental units. The mesocosms were attached to a floating wooden jetty where each tank was kept 20 cm above the water line. The floating jetty was anchored to a fixed position located within a wind sheltered bay and was approximately 25 m from the shoreline. The mesocosms were manufactured from impermeable and opaque fiberglass shaped into open top cylindrical tanks (diameter of 1.2 m and 4 mm thick) of two different heights (1.2 and 2.2 m) corresponding to the shallow and deep treatments, respectively. A bottom substrate (ca. 10 cm) consisting of a mixture of sand and mud collected from a nearby mesotrophic lake was added at the bottom of the tanks before adding filtered (500 µm) lake water to reach 1020 and 2150 L, representing the two contrasting water depths; shallow and deep. Diverse groups of organisms including; plankton (phytoplankton and zooplankton) collected from five neighboring lakes, submerged vegetation (Eurasian watermilfoil [*Myriophyllum spicatum*]), and planktivorous juvenile fish (roach [*Rutilus rutilus*]), were added to the mesocosms. The inoculations of aquatic organisms in each mesocosm were standardized using volume for phytoplankton (1 L well-mixed subsamples collected from the five neighboring lakes), number of apical shoots for watermilfoil (8 shoots ranging between 5 and 10 cm), and biomass (ca. 10 g) for roach.

The nutrient manipulations were achieved by adjusting the total phosphorus concentrations to 25 µg/L and 200 µg/L, for the low and high nutrient level simulating mesotrophic and hypertrophic conditions, respectively. Total nitrogen, on the other hand, was added to reach a phosphorus to nitrogen ratio of 1:20 by molecular weight. When the experiment began, nutrient additions were only required for the high nutrient' treatments. Thereafter, monthly nutrient additions were required to maintain the concentrations (low and high levels) constant throughout the experiment (see details about the monthly nutrient dosing in Landkildehus et al. (2014)). Standard 5-watt aquaria pumps were fitted inside each mesocosm to continuously mix the water. Commercial nylon nets, with relatively large mesh sizes (ca. 3 cm and 5 mm in diameter), were mounted on top of each tank to deter birds.

### 2.3. Sampling procedure and taxonomy analysis

The sampling campaign began on the 16th of May 2011, and samples were taken at regular intervals of two weeks until early November, resulting in a total of 13 sampling events. Depth integrated water samples, representative of the entire water column, were taken using a Plexiglass® sampler (length 60 cm and diameter of 9.5 cm). Well

homogenized subsamples of 50 mL were collected from each mesocosm and fixed with Lugol's solution (0.5 mL) for phytoplankton species identification.

Phytoplankton was identified using a modified Utermöhl protocol, commonly used in Scandinavia (Olrik et al., 1998), and an inverted microscope. Taxa were identified to the finest possible taxonomic unit (generally to species). The individual size ( $\mu\text{m}$ ) of each phytoplankton was deduced by measuring the maximum dimensions of cells or colonies (for example; diameter if the phytoplankton was spherical and length if rod shape). The average size of each taxon across each sample was used for subsequent resilience assessments. The total biovolume ( $\text{mm}^3 \text{L}^{-1}$ ) of each taxon was calculated based on the combination of volume inferred from geometrical shapes of phytoplankton and their abundances in the samples, using protocols described by Blomqvist and Herlitz (1998).

## 2.4. Statistical analyses

### 2.4.1. Quantifying resilience

The relative resilience of the phytoplankton communities based on the taxonomy was quantified using Bayesian classification and regression tree (BCART) models to identify within and cross scale patterns in size (Allen et al., 2005; Stow et al., 2007) and biovolume (Angeler et al., 2012; Angeler and Allen, 2016). Species matrices from each mesocosm and time point were prepared for the size and biovolume datasets. Data were log-transformed and arranged in ascending order before being used in the analysis (BCART). BCART executes random searches considering all possible probabilistic combinations that a given split occurs and identifies homogenous groups of species that have similar size or biovolume by sequentially splitting groups (designated as "branching tree") (Chipman et al., 1998). The splits likelihoods are subsequently ranked where the final outcome represents the branching tree with the maximum likelihood where the terminal nodes indicate groups with highest homogeneity (Chipman et al., 1998). According to the discontinuity hypothesis (Holling, 1992), phytoplankton species that clustered in a particular (homogenous) group are presumed to operate at a specific scale that fundamentally differs in ecological patterns and processes from other scales (Allen et al., 2005; Holling, 1992). The final outcome (i.e. the model with the highest likelihood) of the analysis was used to derive the four indicators of resilience; defined as: 1) the number of groups or scales present (a measure of the cross-scale attributes of resilience), 2) the number of species present in each group (indicative of the within-scale attributes of resilience), 3) the aggregation length, i.e. the length of each group measured as the difference between the highest and the lowest log-transformed size or biovolume of species belonging to that given group, and finally 4) the distance between successive groups or scales where no species occur (gap length or discontinuities as defined by Allen et al. (2005)). The software used to run BCART was developed by Chipman et al. (1998) and can be downloaded (<http://www.rob-mcculloch.org/code/CART/index.html>).

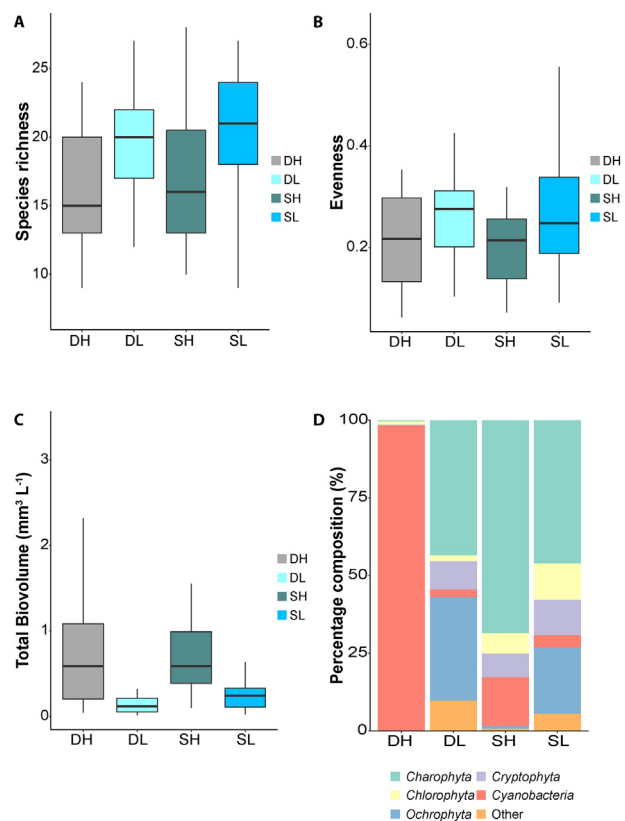
### 2.4.2. Statistical comparisons

The four resilience indicators (cross-scale structure, within-scale structure, aggregation length, and gap size) were analyzed individually and combined using permutational multivariate ANOVA (PERMANOVA) using PERMANOVA v.1.6 (Anderson, 2005). When PERMANOVA is used with single variables, the analysis becomes automatically a univariate ANOVA (Anderson, 2017). The only difference between univariate and multivariate analysis is that  $p$ -values in PERMANOVA are obtained by permutation and are not strictly bound to fulfill the assumption of normality (Anderson, 2017).

The parameters used to construct the model for univariate ANOVA and the multivariate analyses were identical and comprised the three following factors and their interactions: 1) the term "variable" (size vs. biovolume) tests for differences in resilience indicators that were

obtained from the analyses based on size and biovolume, 2) the term "treatment" tests for differences in our combinations of depth and nutrient manipulations (deep – high nutrient, DH; deep – low nutrient, DL; shallow – high nutrient, SH; shallow – low nutrient, SL), and 3) the term "time" tests for seasonal variation of our resilience indicators. Several terms and their interactions were crucial for hypothesis testing: 1) If according to our expectations, size-based and biovolume-based analyses indicate alternative regimes, the term "variable" is not significant. 2) If depth and nutrient manipulations affect phytoplankton distinctly, as has been shown in a previous taxonomic analysis (Baho et al., 2017), the term "treatment" is significant. 3) If the analysis based on biovolume is more sensitive to proximate changes in the mesocosm environments over the study period relative to size, which presumably embodies ultimate factors, the interaction term "variable  $\times$  time" is significant. 4) If our size-based and biovolume-based resilience analyses differ in detecting a treatment effect, the term "variable  $\times$  treatment" is significant. 5) If this is the case and also 3) is verified, the model should reveal a significant 3-factor interaction between variable, treatment, and time.

PERMANOVAs were based on the Euclidean distances and 9999 unrestricted permutations. Pairwise comparisons across treatments were performed to determine which of the treatment manipulations (DH, DL, SH, SL) mostly differed in resilience structure. Some mesocosms (one SL and one DL) were excluded from the statistical analyses due to unforeseeable circumstances that upset the desired nutrient balance. One end of wooden jetty was used by birds as resting ground, which disturbed the experimental nutrient balance with their excrements. In one tank (DL), a non-stocked fish (an adult perch [*Perca fluviatilis*], 150 g) was discovered. The influence of the birds (despite using nets as a deterrent) and the non-stocked fish could be detected by means of non-metric multidimensional scaling ordination of water quality variables,



**Fig. 1.** Comparison of time integrated community metrics: (a) species richness, (b) evenness, (c) total biovolume (scaled using common logarithm), and (d) percentage composition across treatments: DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient, and SL: shallow mesocosm - low nutrient. Figures modified from Baho and others (2017).

causing these two low nutrient tanks to cluster around the high nutrient ones. As a solution to obtain a balanced experimental design, one replicate from the other two treatment (shallow – high nutrient and deep – high nutrient) was randomly removed and our final analyses are based on three replicates per treatment.

### 3. Results

#### 3.1. Phytoplankton community structure

A detailed taxonomic analysis has been reported previously (Baho et al., 2017) and a summary overview of these results is given here to contextualize the resilience analysis. Briefly, the effects of the nutrient enrichment on species richness, evenness and total biovolume (Fig. 1A–C) were more apparent than the water depth manipulation. Regardless of the water depth, species richness and evenness of phytoplankton were higher in the low nutrient mesocosms compared to the high nutrient ones. Total biovolumes were consistently higher in the high nutrient than the low nutrient treatments. The deep – high nutrient mesocosms had the highest phytoplankton biovolume and was followed by the shallow – high nutrient treatment, while the two types of low nutrient (DL and SL) treatment had comparable biovolume. The biovolume of the high nutrient treatments peaked during the month of August.

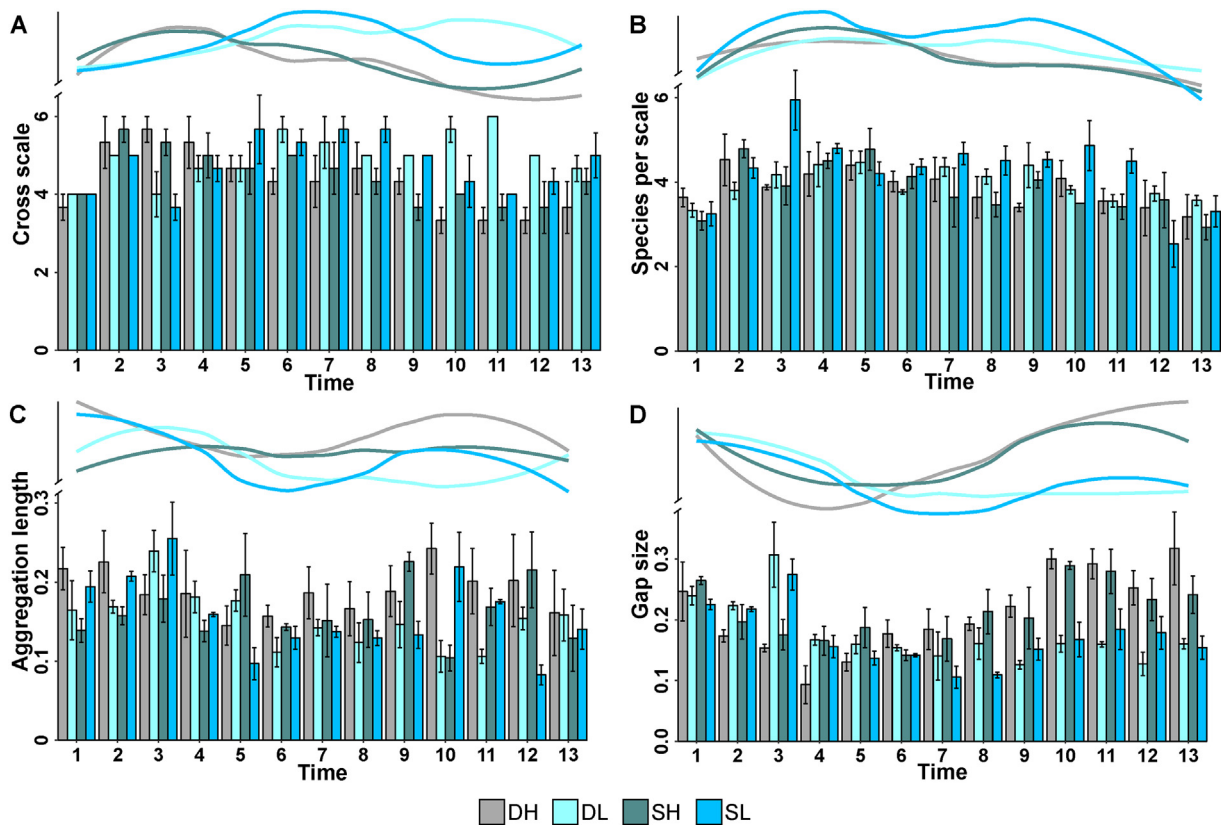
The four experimental manipulations (DH, DL, SH, SL) yielded phytoplankton communities' composition that significantly (PERMANOVA,  $P < 0.05$ ) differed from each other (Fig. 1D). Cyanobacteria were predominant in the deep and high nutrient treatment, whereas Charophyta were the most abundant group in the shallow and high nutrient mesocosms. Cyanobacteria reached their maximum abundances in the high nutrient treatments during the month of August. The communities' structure of the two low nutrient treatments were generally similar to

each other with the exception of Chlorophyta, which reached relatively high biovolume in the shallow compared to the deep mesocosms, while an opposite trend was observed for phytoplankton belonging to the Ochrophyta group.

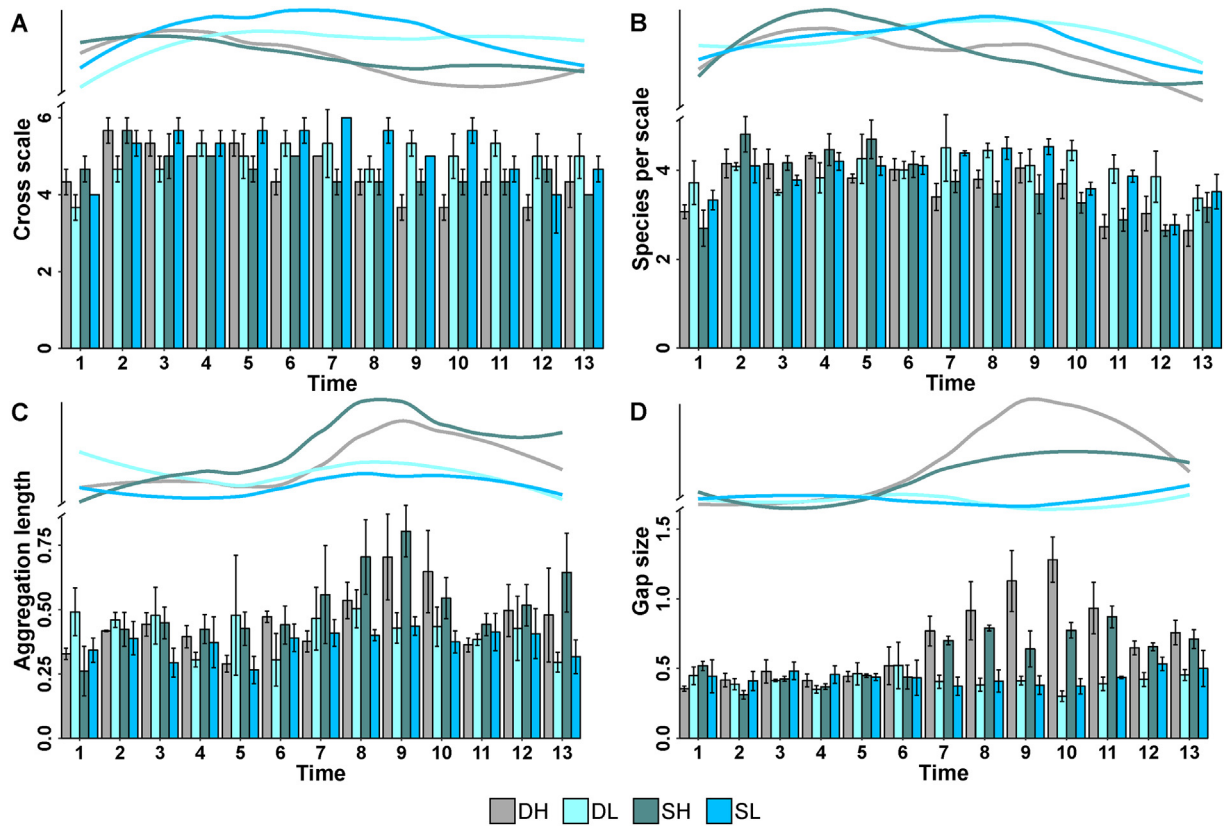
#### 3.2. Resilience analysis

The four indicators of resilience inferred from discontinuity analysis based on phytoplankton size and biovolume gave comparable cross-scale structure, within-scale structure, aggregation size and gap size (Figs. 2–3). In addition, the temporal patterns for each indicator tend to follow the same trend according to the nutrient manipulations (Figs. 2–3), where the high nutrient treatments followed similar temporal trajectories that were distinct from the low nutrient treatments. For instance, in the size dataset, the low nutrients had higher number of scales (cross-scale structure), whereas the high nutrient treatments had larger gap (Fig. 2). These similarities in trends were also visible for aggregation length and gap size obtained from biovolume (Fig. 3). The aggregation length and gap size from the high nutrient treatments initially peaked at time point 7 (corresponded to the month of August) and thereafter remained consistently higher than the low nutrient treatments (Fig. 3). The gap size from the size dataset followed a similar pattern as the gap size from the biovolume dataset, where both initially peaked at time point 7 for the high nutrient treatment (Figs. 2–3).

The results of the PERMANOVA based on the individual (Table 1 and Tables S1–S4) and combined (Table 2) resilience indicators that were derived from phytoplankton size and biovolume did not statistically differ. The treatment manipulations, time effects and their interactions (treatment  $\times$  time) were consistently significant when considering either the individual (Table 1) or the combined indicators (Table 2). The interaction between variable (size vs biovolume) and treatment was



**Fig. 2.** Comparison of the four attributes of resilience derived from phytoplankton size across different time points: (a) cross scale (number of scales) and (b) within scale (number of species per scale), (c) aggregation length, and (d) gap size. Shown are the bar charts (mean  $\pm$  standard error) with overlaid trend lines across treatments: DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient, and SL: shallow mesocosm - low nutrient.



**Fig. 3.** Comparison of the four attributes of resilience derived from phytoplankton biovolume across different time points: (a) cross scale (number of scales) and (b) within scale (number of species per scale), (c) aggregation length, and (d) gap size. Shown are the bar charts (mean  $\pm$  standard error) with overlaid trend lines across treatments: DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient, and SL: shallow mesocosm - low nutrient.

significant for two indicators; cross-scale structure and gap size, and when all indicators were combined. However, the interactions involving variable and time, and all three factors combined (variable  $\times$  treatment  $\times$  time) were not significant for the individual (Table 1 and Tables S1-S4) or the combined resilience indicators (Table 2). Post-hoc analyses performed on the individual (Tables S5-S8) and combined (Table 3) indicators revealed that the differences induced by nutrient enrichment were more common than those from the depth manipulation. The effects of the depth manipulations were only significant for the low nutrient mesocosms when considering both the individual (Tables S5-S8) and the combined resilience attributes (Table 3).

#### 4. Discussion

In this study, we assessed the congruence of resilience assessments based on the size and biovolume structure of phytoplankton communities in mesocosms of different depths and nutrient concentrations. We

expected that size and biovolume are presumable surrogates of ultimate (evolutionary) and proximate (environmental factors, biological interactions) factors, respectively, and therefore anticipated different results. However, the resilience results obtained from the phytoplankton's size and biovolume datasets, were largely comparable (Tables 1–2), reflected in non-significant terms in our PERMANOVA models that involved the factor “variable” (size vs biovolume). These results supported our expectation that both size-based and biovolume-based resilience assessments discriminate between our manipulations of nutrients and depth as they are important features of alternative regimes of lake ecosystems that are characterized by different sets of abiotic and biotic environments (e.g. Baho et al., 2017; Beisner et al., 2003), including resilience features (Sundstrom et al., 2018). In contrast, the expectation that biovolume discerns temporal variability inherent in the dynamics of the proximate environment during seasonal change better than size was not supported. Overall, these findings are similar to those of a previous study on zooplankton communities (Baho et al., 2015).

**Table 1**  
Summary of the of permutational ANOVA analyses for each resilience indicator i.e., cross-scale, species per scale, aggregation length, gap size, obtained from biovolume and size, treatment (DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient and SL: shallow mesocosm - low nutrient) and time. Significant terms ( $P < 0.05$ ) are emphasized in bold.

Effect	Resilience indicators							
	Cross-scale		Species per scale		Aggregation length		Gap size	
	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Variable (size vs. biovolume)	0.94	0.33	0.98	0.33	0.10	0.75	3.13	0.08
Treatment	<b>33.23</b>	<b>&lt;0.01</b>	<b>23.22</b>	<b>&lt;0.01</b>	<b>10.10</b>	<b>&lt;0.01</b>	<b>75.09</b>	<b>&lt;0.01</b>
Time	<b>1.76</b>	<b>0.05</b>	<b>3.18</b>	<b>&lt;0.01</b>	<b>2.95</b>	<b>&lt;0.01</b>	<b>6.27</b>	<b>&lt;0.01</b>
Variable $\times$ Treatment	<b>2.70</b>	<b>0.04</b>	1.64	0.18	0.90	0.43	<b>5.08</b>	<b>&lt;0.01</b>
Variable $\times$ Time	0.71	0.75	1.02	0.43	0.39	0.97	1.21	0.28
Treatment $\times$ Time	<b>2.92</b>	<b>&lt;0.01</b>	<b>3.90</b>	<b>&lt;0.01</b>	<b>13.40</b>	<b>&lt;0.01</b>	<b>26.78</b>	<b>&lt;0.01</b>
Var. $\times$ Treat. $\times$ Tim.	1.22	0.19	1.24	0.18	0.86	0.69	1.33	0.11

**Table 2**

Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) based on the combined resilience indicators (cross-scale, species per scale, aggregation length, gap size) comparing: resilience structures obtained from size and biovolume, treatment (DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient and SL: shallow mesocosm - low nutrient) and time. Shown are degrees of freedom (df), mean squares, F ratios and significance levels (P). Significant terms ( $P < 0.05$ ) are emphasized in bold.

Effect	df	Ms	F-value	P-value
Variable (size vs. biovolume)	1	0.84	0.98	0.37
Treatment	<b>3</b>	<b>25.32</b>	<b>29.40</b>	<b>&lt;0.01</b>
Time	<b>12</b>	<b>2.08</b>	<b>2.42</b>	<b>&lt;0.01</b>
Variable × Treatment	<b>3</b>	<b>1.96</b>	<b>2.28</b>	<b>0.03</b>
Variable × Time	12	0.72	0.84	0.70
Treatment × Time	<b>36</b>	<b>3.28</b>	<b>3.82</b>	<b>&lt;0.01</b>
Var. × Treat. × Tim.	36	1.06	1.23	0.11

Our results suggest that, at least in the case of phytoplankton, a categorical differentiation of size and biovolume into ultimate and proximate factors is problematic. This difficulty arises from different factors that have been shown to structure size distributions in communities at disparate scales ranging from local biological interactions to landscape and biogeographical features (Allen et al., 2006). Such structuring forces can influence communities individually and collectively leading to context-dependent patterns. Specifically, although size is considered to be an evolutionary constrained trait that changes over relatively long time scales (Polly, 2012), it can also be a plastic trait that responds to environmental variations (Paaby and Testa, 2018; Pichancourt and van Klinken, 2012; Richards et al., 2006; Weithoff and Beisner, 2019). Organisms' size can vary as a function of nutrient availability (Massie et al., 2010; Paaby and Testa, 2018; Richards et al., 2006), and organisms can grow larger or remain small depending on nutrients. For example, Massie et al. (2010) found that the normal cell cycles of phytoplankton ceased in nutrient limiting conditions that led to a reduction in size of individuals. In this context, plastic responses in phytoplankton size due to nutrient enrichment may drive similar changes in the phytoplankton biovolume. This suggests, again coherent with alternative states theory in lakes, and supporting Holling's (1992) claim that a few key variables can drive ecosystem dynamics, that nutrients have a profound effect on lake ecology. We acknowledge that phytoplankton is a highly dynamic group of organisms with short generation times, fast community turnover, and malleable sizes of individuals that respond fast to ecological change (McCormick and Cairns, 1994), and this dynamism might ultimately have prevented us from detecting a difference between size-based and abundance-based (such as biovolume) resilience assessments.

In addition, our results suggest that size and biovolume data for phytoplankton might, to a certain degree, be collinear because size measurements were also used to estimate biovolume based on geometric shapes. This collinearity is interesting because our size-based approach does not include the abundance component, which is accounted for in the biovolume measurements. Both approaches therefore differ in their resolution regarding biological hierarchy with the size-based and

**Table 3**

Pairwise comparison across treatment (DH: deep mesocosm - high nutrient, DL: deep mesocosm - low nutrient, SH: shallow mesocosm - high nutrient and SL: shallow mesocosm - low nutrient) combining all four resilience indicators.

Treatment comparisons	$\Delta$	P-value
DH - DL	<b>6.36</b>	<b>&lt;0.01</b>
DH - SH	0.28	0.95
DH - SL	0.85	0.49
DL - SH	<b>6.27</b>	<b>&lt;0.01</b>
DL - SL	<b>6.59</b>	<b>&lt;0.01</b>
SH - SL	0.95	0.40

Significant terms ( $P < 0.05$ ) are emphasized in bold.

biovolume-based approach inferring resilience at the level of individuals and the entire population, respectively. While we can currently not identify mechanistic relationships leading to the observed results, we speculate that conservative structuring forces lead to similar phenomenological ecological responses despite different emphases on putative patterns-process relationships. However, from an applied perspective, the congruence of results between size and biovolume suggest an advantage for resilience assessments. Specifically, monitoring data are frequently based on biovolume only, and our results suggest that extending Holling's resilience assessment approach beyond traditionally used body size or mass data is warranted. However, we caution against a premature generalization of this speculation because differences between size-based and biovolume-based resilience assessments might vary under different environmental stress scenarios and therefore be context specific. Further research using other organism groups, ecosystems and stressors are needed.

Although nutrient and water level are important factors influencing the ecology of lakes (Baho et al., 2017; Cooke, 2007; Janssen et al., 2014), our experimental manipulations showed that the effects on resilience of the nutrient enrichment were generally more apparent than water depth. The comparison of results of the taxonomic community metrics (Fig. 1) combined with the resilience indicators (Figs. 2-3 and Table 3) indicate that nutrient enrichment might have created regime conditions that are consistent with a large number of taxonomic studies and alternative state and regime shift theory (Beisner et al., 2003; Scheffer et al., 2001; Scheffer and Carpenter, 2003). These conditions were reflected in reduced phytoplankton diversity and increased dominance of cyanobacteria, lower cross-scale and within-scale structures and larger aggregation length and gap size, compared to the lower nutrient treatments (Figs. 1-3). At least the increase in gap size and the lower number of species within scales provide insights on biodiversity regulation mechanisms that are supported by ecological complexity theory. Specifically, previous studies have shown that extinction is generally non-random with species occurring at the edges of aggregations within size distributions going earlier extinct or tending to be more vulnerable to extinction relative to species located at the center of aggregations (Allen et al., 1999; Allen and Saunders, 2002). This highlights that traditional metrics of biodiversity, particularly species richness, can be mechanistically related to features of complex systems that have so far received little attention by ecologists.

The relationship between taxonomic and resilience-based results is further captured in the seasonal developments. That is, the significant time effects from the PERMANOVA results reflect seasonal change. The temporal phytoplankton community development shown in our previous study (Baho et al., 2017) followed the seasonal succession model proposed by Reynolds (Reynolds, 1980, 1984). The community composition gradually changed from green-algae to cyanobacteria (Baho et al., 2017), representative of the transition from late spring - early summer to late summer conditions (Angeler et al., 2019). However, cyanobacteria reached higher biovolumes in high nutrient treatments compared to the low nutrient treatments. The onset of the cyanobacteria bloom was concomitantly captured by the resilience indicators. For instance, the increase in the aggregation length and gap size obtained from the phytoplankton size and biovolume from the high nutrient coincided with the start of the cyanobacteria bloom, while the number of cross-scales tended to decrease. Freshwater cyanobacteria are known to produce bioactive metabolites during blooming events that can inhibit other phytoplankton species, which can potentially account for some of the changes observed in the resilience indicators (Leão et al., 2009).

## 5. Conclusions

A striking difference between our earlier taxonomic and present resilience-based studies is the importance of interaction between water level and nutrient enrichment. Such effects were evident for

structuring phytoplankton diversity and community structure, but they played a marginal role in shaping resilience. This suggests that while observational patterns of taxonomic and resilience-based assessment can be well aligned, phenomena can occur that limit mechanistic explanations. We therefore conclude by highlighting that further research can explore mechanistic relationships between resilience-based and taxonomic studies of ecosystem patterns and processes. Such comparisons are important because complementary, management-relevant information about the stability of ecosystems in a rapidly changing world can be obtained (Roberts et al., 2019b). Future research can also capitalize on our finding that resilience assessments based on size and biovolume provide similar results. This suggests that Holling's (1992) discontinuity hypothesis, which has so far been limited to organisms with discrete body sizes, can be extended to organism groups with different architectures, such as plants that show modular growth (Angeler et al., 2015a). Given the importance of resilience assessments in recent time, and the potential that discontinuity analysis offers, further explorations about the performance of metrics that emphasize abundance (e.g. biovolume, coverage, density, plant stem diameter) in resilience assessments seems warranted.

### CRedit authorship contribution statement

**Didier L. Baho:** Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Stina Drakare:** Methodology, Investigation, Project administration, Writing - review & editing. **Richard K. Johnson:** Methodology, Project administration, Writing - review & editing, Funding acquisition. **David G. Angeler:** Methodology, Conceptualization, Investigation, Supervision, Project administration, Writing - review & editing.

### Declaration of competing interest

The authors declare no conflicts of interest.

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### Data accessibility statement

Data presented in the result section is deposited in figshare (<https://doi.org/10.6084/m9.figshare.12719798.v2>).

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.141110>.

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