Restoration, conservation and phytoplankton hysteresis

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Phytoplankton growth depends not only upon external factors that are not strongly altered by the presence of phytoplankton, such as temperature, but also upon factors that are strongly influenced by activity of phytoplankton, including photosynthetically active radiation, and the availability of the macronutrients carbon, nitrogen, phosphorus and, for some, silicate. Since phytoplankton therefore modify, and to an extent create, their own habitats, established phytoplankton communities can show resistance and resilience to change, including managed changes in nutrient regimes. Phytoplankton blooms and community structures can be predicted from the overall biogeochemical setting and inputs, but restorations may be influenced by the physiological responses of established phytoplankton taxa to nutrient inputs, temperature, second-order changes in illumination and nutrient recycling. In this review we discuss the contributions of phytoplankton ecophysiology to biogeochemical hysteresis and possible effects on community composition in the face of management, conservation or remediation plans.

Key words: phytoplankton, physiological acclimation, eutrophication, Community hysteresis

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Phytoplankton in the Anthropocene

Aquatic ecosystems, including lakes, coastal waters or marine regions, have always been subject to changes in water exchange, nutrient inflows and sedimentation. These alterations can drive replacements of species, thereby shifting community compositions and ecosystem services (Contreras-Rosales et al., 2016). We now live in the Anthropocene with human activities altering terrestrial and aquatic systems worldwide (Falkowski et al., 2000; Crutzen, 2002; Ellis and Trachtenberg, 2014). Aquatic systems are therefore facing new, and faster changing, combinations of environmental factors, including altered hydrological flows, elemental flows and food webs (Rieglman, 1995; Cociasu et al., 1996; Kemp et al., 2005).

Fluxes of available carbon (C), nitrogen (N) and phosphorus (P) into the biosphere have increased by at least 13%, 100% and 400%, respectively, compared to pre-industrialized times (Vitousek et al., 1997; Falkowski et al., 2000; Smil, 2000). Horizontal N and P transfers are mediated in large part by industrialized agriculture, which increased N fertilization 7 times and P fertilization 3.5 times over 35 years (Tilman, 1999). These biosphere inputs will likely further increase during coming decades (Van Vuuren et al., 2010), even in the face of regional countermeasures and market shifts (van Dijk et al., 2016; Berthold et al., 2019a). Much of this additional agricultural input will eventually wash into aquatic ecosystems, as only fractions of the fertilizer end up in the crop (e.g. Liu et al., 2008). In parallel flows of sediment through rivers have been heavily regulated leading to altered
inputs of silica (Si) from weathering (reviewed in Jennerjahn, 2012). Nevertheless, even in the Anthropocene seasonally and latitudinally imposed photoperiods, incident photosynthetic active radiation (PAR) and water temperatures will remain as ultimate limiting factors on future phytoplankton community compositions and distributions.

Interacting with these abiotic factors are the differential physiological capacities of species, which undergo interspecific succession over seasonal, and longer periods. Seasonal community succession patterns have been widely studied (Lampert and Sommer, 2013) and are driven by combinations of temperature (Wasmund et al., 2019), current nutrient availability, water retention times (Garrido et al., 2016), grazer and virus pressure (Azam et al., 1983; Rohwer and Thurber, 2009). Water temperature often defines the onset and end of the growth period for a given taxon. Nutrient availability defines the carrying capacity of an ecosystem for blooms of given taxa, while grazer and virus densities interact with prey taxa densities to determine the net growth period for a taxon before it gets capped. Furthermore, (re)colonization of a taxon into an ecosystem depends upon re-growth of residual surviving cells, a local ‘seed bank’ or resting stages (Härnström et al., 2011; Kremp et al., 2016) or the capacity to naturally or anthropogenically (re)colonize a habitat, and perhaps form locally adapted sub-populations (Parmesan, 2006; Orsini et al., 2013).

**Eutrophication**

One of the direct effects of changing elemental fluxes is the human-induced eutrophication of aquatic ecosystems, which, in contrast to natural eutrophication, can occur within one human generation (e.g. de Jonge et al., 2002; Gulati and van Donk, 2002; Pael, 2006). The term eutrophication evolved over time, from an original usage for the capacity of bog systems to provide food based on their nutrient capacities (Naumann, 1931). Here we define the trophic state for aquatic systems in the most general sense, as intensity of organic photoautotrophic production (sensu Elster, 1958), with eutrophic systems showing a high phytoplanktonic photoautotrophic production. Eutrophication causes widespread changes not only in species composition, nutrient cycles and food web structures, but also in ecosystem services by altering commercial and recreational usage of water bodies around the globe (Lee, 1973; Vollenweider and Kerekes, 1982; Sas, 1989; Jochimsen et al., 2013).

The first recognition of increased primary production was noted in alpine lakes, with algal blooms noted at the end of the 19th century, which led to losses of clear-water fish species like pike (Hasler, 1947). Available N and P, as well as their seasonal patterns, were identified as causes of this eutrophication (Gessner, 1935). Not all primary producers benefited equally from the increased nutrient concentrations. Benthic macroalgae, adapted to clear water, and low nutrients (Kufel and Kufel, 2002), were firstly replaced by macrophytes forming canopies (Verhoestad et al., 2017), before most of submerged macrophytes were in turn replaced by high densities of phytoplankton (Blindow et al., 1993). This shift in main primary producers, from benthos to pelagial, was described as alternative stable states, for lakes (Blindow et al., 1993) and for coastal waters (Schiewer, 2007). Most recent studies suggest at least four stable states dominated by different primary producers: submerged macrophytes, emergent or floating macrophytes and then phytoplankton, each with different advantages and disadvantages regarding ecosystem services (reviewed in Janssen et al., 2021).

The identification of nutrient sources and maximum allowable inputs of nutrients into aquatic ecosystems (Lee, 1973; Vollenweider and Kerekes, 1982) helped to guide restoration measures. For lakes, the Plankton Ecology Group (PEG) defined models to describe seasonal changes in lakes under increased P loading (Sommer et al., 1986). The prediction of the PEG model was that depending on P status, several sequential phytoplankton blooms can appear throughout the year, with diatoms in the spring, cyanobacteria during summer and dinoflagellates in autumn. More recently the PEG model was re-evaluated and discussed against the background of global change (Sommer et al., 2012), highlighting the effects of increasing temperature on overwintering and spring bloom onset, and including more food web compartments. Nonetheless, despite our increased knowledge, phytoplankton blooms, including toxic blooms, now occur more frequently and at ever shorter intervals in more and more systems (Burke et al., 2001; Winder and Cloern, 2010; Winter et al., 2011).

Even though factors inducing eutrophication are well understood, it is less clear how to restore eutrophied systems towards either pre-disturbance conditions or towards (re)generation of favourable ecosystem services (Xu et al., 2018; Janssen et al., 2021). Such favourable ecosystem services could include a large stock of fish biomass for recreational or commercial fishing, high elemental sequestration capacities (e.g. blue carbon) or non-toxic, non-nuisance species assemblages in the water column (Janssen et al., 2021). Simply lowering inputs of the nutrient(s) that caused eutrophication will not necessarily lead towards some desired state (Duarte et al., 2009; Jochimsen et al., 2013). Such nonlinear, asymmetric responses to changing inputs, or hysteresis, derive from the internal resilience of a currently dominating community against internal and external perturbations. For example, submerged macrophyte species as dominating primary producers in oligotrophic systems sustain a set of buffering capacities against altered environmental conditions, acting as nutrient and sedimentation sinks in competition with phytoplankton (Kufel and Kufel, 2002). Likewise eutrophic systems dominated by a phytoplankton community buffer their continued dominance by, for example, lowering light availability for benthic primary producers.
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Figure 1: Importance of phytoplankton physiology defined by genotype and phenotype in restoration and management activities.

(Scheffer et al., 1997) or inorganic carbon availability for competing phytoplankters (Dam et al., 2018).

Therefore, to inform conservation and management goals, we review interactions of phytoplankton ecophysiology with our world of global change, through literature spanning both field and laboratory experiments. We hope to support management decisions in the face of multiple ecosystem stable states (see Table 1).

Biogeochemical and Trophic Hysteresis

Bottom-up and top-down effects of phytoplankton blooms

Phytoplankton blooms can affect the ecosystem bottom-up by decreasing euphotic depths, and thereby lower O$_2$-production at depth while simultaneously boosting O$_2$-consumption below the euphotic zone. The spread of hypoxia in freshwater systems is directly linked to human influences, through for example increased nutrient supply (Jenny et al., 2016). This elevated net O$_2$-demand at depth can lead to the loss of parts of the macrozoobenthos (Riemann et al., 2016), and affects the nutrient sequestration capacities of sediments. Suboxic sediments lose their capacities for storing P and Fe (Lampert and Sommer, 2007; Molot et al., 2014), which depend upon redox poise. Simultaneously suboxic sediments increase their denitrification capacities (Gruber and Sarmiento, 1997; Hietanen and Lukkari, 2007; Deutsch et al., 2010) as competition from aerobic respiration is suppressed. The resulting shift towards lower available N:P ratios and possibly higher Fe availability stimulates N-fixing species like cyanobacteria and helps keep the system within a cycle of internal fertilization (Lampert and Sommer, 2007; Molot et al., 2014) through water-column N fixation and P and Fe (re-)releases from sediments. This biogeochemical legacy effect can prolong system recovery by several decades after nutrient inflows are lowered to pre-disturbance concentrations (Chorus et al., 2020). Contrary, if eutrophic systems stay oxygen saturated, phytoplankton may experience Fe limitation (Geiß et al., 2004), especially in brackish waters with high co-precipitation capacities for Fe and P (Gunnars et al., 2002; Gunduz et al., 2011). If nutrient inflows are not lowered sharply, the post-eutrophication community may persist indefinitely (Nürnberg, 2009; Chorus and Spijkerman, 2021), in a hysteresis generated by biogeochemical interaction. Systems with such incomplete management actions remain in an unfavourable state, and knowledge on ecophysiological mechanisms may inform stakeholders about further steps (Fig. 1).

Phytoplankton blooms also affect the top-down control of ecosystems. Food webs are affected when phytoplankton secondarily provoke the loss of submerged vegetation through shading (Blindow et al., 1993; Scheffer et al., 1997). At the level of phytoplankton community composition blooms can provoke a drop, or variable abundances, of so-called high-quality phytoplankton that contain high amounts of polyunsaturated fatty acids (Taipale et al., 2019). There are also grazer-mediated changes in cell size and grazer-selection of non-toxic strains (see below, Ger et al., 2019; Lürling, 2020). Less palatable phytoplankton strains can then persist in a new stable state with lower grazing, in a hysteresis generated by trophic interactions.

Post-eutrophication restoration

Phytoplankton blooms and community structures can therefore not always be predicted from simple nutrient input–output models but are rather influenced by the physiological responses of diverse phytoplankton taxa to altered nutrient supply, temperature, second-order changes in illumination (Sas, 1989) and possibly to dissolved inorganic carbon (DIC). Therefore, interactions of biogeochemical and trophic mechanisms need to be considered when restoring phytoplankton-dominated systems (Ibelings et al., 2007). Depending upon the desired conservation or management goals, results of
resulting ecosystem consequences of nutrient input pulses and restoration may differ from the pre-disturbance ‘reference condition’, ranging from minimally disturbed to best attainable conditions (Stoddard et al., 2006) or possibly a desirable state distinct from the pre-disturbance reference condition. Current management strategies aim to lower nutrient fluxes into eutrophied systems (Paerl et al., 2011), with the focus on P, or N and P simultaneously, while bearing in mind economic feasibility (Conley et al., 2009; Lewis et al., 2011; Molinos-Senante et al., 2011).

Ultimately, P is assumed to be the limiting nutrient for most limnic systems (Liang et al., 2020), while an N and P co-limitation is common for coastal water bodies (Howarth and Marino, 2006). However, as N can be fixed from the atmosphere, management controls on water-borne P may be more feasible even in coastal systems, often in conjunction with upstream management of P for limnic systems. Nonetheless, aeolian and rain-borne P inputs can be substantial depending on regional land use (Tipping et al., 2014; Berthold et al., 2019b). In different habitat types including lakes and coastal water bodies, managed nutrient declines have not always led directly to improvements in water quality, species composition or system stability (Schindler, 2006; Conley et al., 2009; Schindler et al., 2016). Such delayed ecosystem reactions depend partly on the managed drops in external nutrient loading being countered by re-release of sequestered nutrients, particularly P, and can last decades (Nürnberg, 2009; Schindler et al., 2016; Chorus et al., 2020).

Shallow lakes, coastal ecosystems and even ocean basins (North Sea, Baltic Sea) may thus experience prolonged disruption during post-eutrophication, with increased Chl a, despite managed drops of total N (TN) and total P (TP) within the water column (Gulati and van Donk, 2002; McQuatters-Gollop et al., 2007; Schiewer, 2007). For example, in Lake Constance observed shifts in total phytoplankton biomass and composition happened rapidly only after a certain nutrient threshold was reached, with a simultaneous change from dominance by cyanobacteria to chrysophyte dominance (Jochimsen et al., 2013). Over a longer time frame of decades, the central basin of the Baltic Sea showed a shift in phytoplankton spring bloom composition from diatoms to dinoflagellates after lowering of external nutrient inputs (Hjørne et al., 2019). Coastal water bodies are challenging to manage as they usually receive the complete load of a catchment area and are especially prone to eutrophication-related problems. For such systems, biomimicry has been proposed to alter the food web structure to increase grazing pressure on phytoplankton (Fonseca et al., 1994; Schiewer, 2007), as for example ongoing re-planting of submerged vegetation (van Keulen et al., 2007) or removal of planktivorous and stocking of piscivorous fish (Jeppesen et al., 2007). Biomanipulation through changes in fish composition are discussed, but often fail if the overall nutrient inputs are not reduced accordingly (Søndergaard et al., 2007). Fish stock manipulations need to be constantly re-applied (~10 years) and may alter energy flow and fish species composition in the long term (Sváránta et al., 2011; Rogers and Allen, 2012). These methods depend therefore as much upon parallel restoration measures within the catchment as upon the application of the biomimicry. Other post-eutrophied systems developed communities of grazing resistant species upon mineral nutrient declines that lowered food web efficiency (Schiewer, 2007). Selective grazing by Daphnia can promote dominance of remaining toxic Microcystis (Ger et al., 2019), and furthermore different genotypes of Microcystis show different susceptibilities to grazing (White et al., 2011). This example emphasizes the importance of future studies on the impacts of zooplankton diversity on phytoplankton diversity. Thus, restoration measures can take anything from years to decades to be effective and may generate undesired outcomes.

| External driver | Consequence | Solution | References |
|-----------------|-------------|----------|------------|
| Increasing DOC  | Increasing re-mineralization in eutrophic waters | Decrease erosion and other nutrient inflows | Weyhenmeyer et al., 2014; Nieminen et al., 2018; Li et al., 2019b |
| Low NO₃⁻−NH₄⁺ | Toxic HAB | Decrease of NH₄⁺ input and maintenance of NO₃⁻ to decrease sediment P resolubility | Wauer et al., 2005; Newell et al., 2019 |
| Low DIP:DOP ratio | High APA turnover and source shift | Decrease overall P inflow and release from sediment | Zhang et al., 2017; Chorus et al., 2020 |
| Low Si inflow | Vanishing of diatom blooms | Increase fluvial matter transport | Cociasu et al., 1996; Jennerjahn, 2012 |
| High frequency of pulse disturbance | Fast-exploiting resilient blooms | Change pulse to press disturbance | Klappenbach et al., 2000; Shade et al., 2012 |
| Bloom persistence after nutrient input drop | Pulse-mediated stable phytoplankton | Determine and lower non-point sources and organic nutrient pools | Berthold et al., 2018; Li et al., 2019a; Chorus et al., 2020 |
**Hysteresis through Ecophysiological Acclimation**

The biogeochemical and trophic responses of phytoplankton communities involve members of at least 12 eukaryotic phytoplankton lineages and the ancient, diverse lineage of prokaryote cyanobacteria. Each of these lineages in turn comprises numerous genotypes, encoding numerous combinations of metabolic and physiological responses. It is thus difficult to define general practices to treat ‘nuisances’ like harmful algal blooms or undesired stable community states. When facing changing environmental conditions, individual cells rely on differential expression of their genotype to alter their phenotype (Fig. 1). When individual genotypic capacities for phenotypic acclimation are exhausted, other individuals with a slightly different genotype from the same population can be favoured or communities may shift composition towards taxa with different genotypes. After the overall community capacity to acclimate is exhausted, when conditions no longer support net growth, new sets of taxa may progressively dominate in a move towards a different community state, which will in its turn display acclimatory resilience in the face of external pressures. Of course, pressure on a specific phenotype is always a pressure on the genotype, which can cause evolutionary adaptation to the new environmental state on a generational timescale, within genomic or cytological limits for given taxa (Thomas et al., 2012; Reusch and Boyd, 2013; Aranguren-Gassis et al., 2019).

Physiological acclimations include changes in buoyancy, nutrient uptake rates, orientation and content of light-harvesting pigments, cellular composition, enzymatic activities and use of different nutrient and energy sources, among other responses to temperature, light and nutrients. Such acclimations can happen over times of minutes to hours and are highly reversible, depending on the nature, amplitude and duration of the environmental signal.

**Temperature acclimation**

Temperature interacts on multiple levels with cell metabolism. Temperature, per se, is largely beyond management influence, but interacts strongly with other factors that are susceptible to management. Phytoplankton community growth rates show a response to a 10°C temperature increase ($Q_{10}$) of 1.4–1.9 (Eppley, 1972; Bissing et al., 2008; Edwards et al., 2016; Sherman et al., 2016), but only if other resources are not growth limiting. Increasing water temperatures will therefore be of limited direct importance in enhancing community growth rates in subtropical to temperate regions if nutrients in oligotrophic regions, or light in turbid or eutrophic regions, remain as limiting factors (Edwards et al., 2016; Marañón et al., 2018). Temperature increase can, however, affect the phytoplankton community species composition of temperate waters within days, by favouring, e.g. green algae or cyanobacteria (Weisse et al., 2016). With increasing temperatures an increase of blooms in shallow waters can be expected (Trombetta et al., 2019), as well as an earlier onset of blooms during spring and later autumn blooms (Wasmund et al., 2019). Several phytoplankton genotypes isolated from the tropics are already growing close to their maximum temperature, with risk of diversity losses with further increases in temperatures (Boyd et al., 2013). In polar regions water temperature strongly shapes the current phytoplankton composition by limiting enzyme turnover rates (Young et al., 2015) and membrane function (Nishida and Murata, 1996). Also, in polar regions, current species may be psychrophilic strains adapted to only cold temperatures or psychrotrophic strains that tolerate low temperatures. Diatoms can dominate cold waters, and most of these polar diatom species are psychrophilic strains (Suzuki and Takahashi, 1995; Boyd et al., 2013; Lacour et al., 2017). Even small increases in water temperature could profoundly influence future community compositions in such colder waters.

Acclimation and adaptation in diatoms rely on investments in key physiological mechanisms that determine growth temperature optima among ecotypes (Liang et al., 2019). Cold waters usually transport oxidized forms of N, like NO$_3^-$, as a result of upwelling events. Diatoms and dinoflagellates in particular prefer NO$_3^-$ (reviewed in Glibert et al., 2016), possibly because the enzyme nitrate reductase shows highest efficiencies at 5–25°C (Fan et al., 2003). These cold upwelling regions are thus niches for large, sinking-sensitive species (Cloern, 1996, 2018), as other phytoplankton groups grow better at higher temperatures and preferentially use different N sources. Interestingly, cyanobacteria seem to be absent from most cold-water marine areas (Vincent, 2000), yet dominate as mats or picoplankton in cold oligotrophic freshwater systems (Vézina and Vincent, 1997). Furthermore, these freshwater cyanobacteria seemed to be cold temperature tolerant rather than adapted (Vincent, 2000). These differences in strategies will influence the shape of future polar phytoplankton assemblages, as strains with wider temperature tolerance start to dominate with increasing water temperature at least in summer, whereas psychrophilic strains will be replaced, displaced poleward or seasonally restricted, leading to diversity shifts around the globe (Thomas et al., 2012; Barton et al., 2016). The acclimatory capacity of a phytoplankton assemblage, or meta-populations of several genotypes, depends on the intraspecific diversity. Recent studies with Arctic isolates suggest that a large intraspecific diversity may be as important as interspecific diversity for adaptation and selection in phytoplankton assemblages (Wolf et al., 2018). Diversity loss might lower the resistance of current phytoplankton communities to change while favouring species able to exploit decreasing nutrient levels (Allison and Martiny, 2009).

**Photoacclimation**

Photoacclimation comprises a complex, widely studied network of responses to changing light availability (Falkowski and Owens, 1980; Falkowski et al., 1981; Behrenfeld et al.,...
et al. (2016). From the view of wider conservation and ecosystem services, photosynthesis leads to fixation of C and release of O₂, which in turn affect all trophic levels and nutrient cycles. Across taxa, cells have variable capacities to control their internal pigment content (Graff et al., 2016) and even their pigment orientation to incoming light (Schuurges et al., 2016) to either protect themselves from over-saturating conditions (Bailey and Grossman, 2008) or to counter lower light availability (Geider, 1987). These photoacclimatory strategies interact strongly not only with availability of the nutrients needed to assemble the photosynthetic system (see below), but also with cell size. Small phytoplankton cells show a smaller self-shading (or packaging) effect at the cellular level, as there is not enough space (Ting et al., 2002) to stack large amounts of pigments within a small cell (Finkel, 2001). The lower packaging effect in small cells leads to a higher absorption cross section per pigment or per reaction centre, and therefore higher light absorption per pigment or per nutrient investment (Kirk, 1975). A community of small cells can thus pre-empt larger cells through better photosynthetic return upon limited nutrient investment, with Prochlorococcus in the open ocean a case in point. On the other hand, such small cells are intrinsically more prone to photoinactivation because of their same limited optical thickness (Key et al., 2010; Campbell and Seródio, 2020) and can thus suffer under variable light conditions.

The amplitude and rapidity of short-term acclimation to changing light varies widely across taxa, conferring differential capacities to withstand and exploit low or fluctuating light (Raven, 2011), thereby imposing different limits on the conditions where photosynthesis remains a viable strategy for different taxa (Murphy et al., 2017). Accumulation of cells in a community increases light attenuation, and the relation between biomass and light attenuation varies across taxa (Scheffer et al., 1997; Kemp and Villareal, 2018). Therefore, phytoplankton growth can itself impose light limitation on competing taxa, along with steep light attenuation gradients that secondarily generate a variable light environment. The growth of taxa able to exploit such low or fluctuating light can then maintain an alternate stable state by preventing the (re-)occurrence of other phytoplankton taxa or submerged macrophytes, which need higher or more stable light.

The accumulation and maintenance of the photosynthetic system also imposes differential material (Finkel et al., 2010a) and energy costs across phytoplankton taxa. Some phytoplankters adopt a ‘just in time’ strategy of (re)building photosynthetic complexes rapidly, as required, which requires higher investment of energy into the metabolic systems to turn over proteins (Lavaud et al., 2016; Bonisteel et al., 2018). In contrast other phytoplankton adopt a ‘warehouse’ strategy of investing in excess stocks of the key proteins to support re-assembly of photosynthetic complexes (Campbell et al., 2013; Ni et al., 2017), which imposes a higher standing elemental investment, lower metabolic return upon invested nitrogen, but less immediate demands upon energy metabolism. These costs of accumulating and maintaining the photosynthetic system also interact with available nutrient levels (Loebl et al., 2010; Li et al., 2015) (see ‘Nitrogen’ below) thereby creating differential selections upon different taxa. Temperature strongly limits performance of the photosynthetic complexes and phytoplankton must increase their resource allocations to key metabolic complexes to maintain key fluxes at low temperature (Young et al., 2015; Ni et al., 2017).

At a higher level of organization, upon achieving dominance, filamentous cyanobacteria proportionately lower available light in lakes (Scheffer et al., 1997), through for example the high packaging effect of colonies that cause shading (Tilzer, 1987). This high shading within colonies can then support reducing micro-environments, which are more favourable for N fixation (Tilzer, 1987). Furthermore, the underwater light climate in shallow waters can be lowered to a point that the largest part of the water column remains net-heterotrophic, which favours species that can acclimatize fast to changing light (Berthold and Paar, 2021). In summary, differential capacities for photoacclimation contribute to niche partitioning across phytoplankton (Six et al., 2007a). It is intriguing that the prokaryotic cyanobacteria present by far the widest spectral diversity among phytoplankton lineages with distinct spectral profiles even within closely related taxa (Six et al., 2007b), in comparison to brown or green colours prevailing across most other lineages. Somewhat unexpected correlations among particular pigment gene clusters and adaptation to brackish environments show that spectral competition may be a major factor establishing niche boundaries (Larsson et al., 2014; Grébert et al., 2018).

Nutrient acclimation

Acclimation to changing nutrient concentrations is crucial to sustain growth rates and to buffer short-term limitations. Acclimation processes are not necessarily taxa specific, but rather depend on phenotypic plasticity, including changes in cell size, changes in cellular reserves or genetically encoded high- and low-affinity nutrient uptake systems. Nutrient limitation in field vs. laboratory studies is a highly controversial topic, since in principle minimum uptake thresholds for nutrients must be defined for certain taxa.

The regulation of uptake rates depends on the type of nutrient and storable reserves within cells, i.e. the cell quota Q (Droop, 1973). Cell sensing for limiting nutrients is regulated through the availability of the nutrient within the cytoplasm. Upon experience of altered nutrient amounts within the cell, phytoplankton cells react with short-term and long-term transcriptional changes. There are both high- and low-affinity transporter classes for N, P and Si with expression and therefore uptake rates depending on internal nutrient concentrations or elemental ratios (Thamdrakoln and Hildebrand, 2008; Glibert et al., 2016; Lin et al., 2016).
Nutrient ratios and competition

Beyond absolute availability thresholds for individual nutrients, elemental ratios that imply nutrient limitation have been derived from an empirical elemental ratio of C:N:P for particulate matter in the ocean (Redfield et al., 1963). This Redfield ratio concept has been widely used to describe apparent nutrient limitations of phytoplankton biomass (Elser et al., 1990; Hessen et al., 2013; Lee et al., 2015). Field ecologists usually apply the ratio of total nitrogen to total phosphorus (TN:TP) or the ratio of dissolved fractions (DIN:DIP) considering only directly measurable inorganic fractions, such as nitrate, ammonium or ortho-phosphate, to infer whether N or P is a limiting nutrient for phytoplankton growth. However, nutrient ratios are taxon specific and may even depend on the global availability of nutrients (Geider and La Roche, 2002; Finkel et al., 2010b; Talmy et al., 2014). For example, due to higher availability of iron and its possible stimulation of nitrogen fixation during glaciation, the Redfield ratio may once have been 25 N:1 P instead of the current 16:1, (Broecker and Henderson, 1998). Nutrient limitation predictions based on the empirical Redfield ratio may therefore only represent the current most widely distributed taxa and their average elemental composition, which can change in the future, across habitats or with shifts in community composition.

In laboratory experiments nutrient requirements follow ratios that are species and size specific (Marañón et al., 2013). For example, depending on cyanobacterial taxon N:P ratios can range from 13:1 to 50:1 (Finkel et al., 2010b). However, it is not clear if high N:P ratios in cyanobacteria derive from adaptation of at least some strains to generally lower P availabilities in oligotrophic ocean regions, therefore skewing the taxonomic interpretation of the ratio. Picocyanobacteria from oligotrophic parts of the ocean replace P with S in their cell membrane lipids (Van Mooy et al., 2006) to lower their P demand. Furthermore, N-fixing cyanobacterial species start to dominate at low N:P ratios (Karl et al., 2002). However, the occurrence of N-fixing cyanobacteria is not necessarily linked to low N:P ratios, as they can also occur at high N:P ratios, limiting generalizations (Chislock et al., 2014). Therefore, if certain N:P ratios could lead to exclusive domination by one or another group, that fails to account for the diversity of phytoplankton in aquatic ecosystems. This diversity is in part explained by a resource-based competition theory, where different species can coexist, if they are limited by different resources (Tilman, 1977), explaining diversity through chaotic conditions by resource competition for more than three resources (Huisman and Weissing, 1999). This interpretation may be complicated if cells limited by one resource engage in luxury consumption of another resource limiting to other cells. Larger cyanobacteria, like Nostocales, Aphani-zomenon or Nodularia, can, for example, luxury consume P and store it, rather than use it directly for growth (Vahtera et al., 2010; Hagemann et al., 2019). Similarly, diatoms like Chaetoceros and Ceratium can luxury consume NH₄⁺ at high rates, even at low DIN concentrations (Olofsson et al., 2019). This ‘ravenous’ nutrient uptake may prevent the seasonal or annual occurrence of other phytoplankton taxa (de Mazancourt and Schwartz, 2012).

Long-term drops in nutrients can favour a community shift towards dominance by mixotrophs such as chrysophytes (Jochimsen et al., 2013), which can alleviate nutrient limitation through mixotrophy (Lewitus and Kana, 1995; Krom et al., 2003). Bacterioplankton competes directly with phytoplankton for N and P (Joint et al., 2002), but bacterioplankton can be subsequently grazed by mixotrophic phytoplankton, especially under limited light and increased temperature (Wilken et al., 2018). Monitoring phytoplankton diversity is therefore necessary not only to identify harmful taxa, but also to track highly competitive bloom-stabilizing taxa and shifting life strategies.

Carbon

DIC is rising as a result of anthropogenic releases of CO₂ (Royal Society (Great Britain), 2003). Phytoplankton responses to this increase in DIC are complex and diverse, varying with taxa and interacting with other environmental factors (Gao et al., 2012; Gao and Campbell, 2014), placing predictions of potential winning and losing taxa under higher pCO₂ beyond the scope of this review. A perhaps unexpected secondary effect of eutrophication is, however, the onset of intermittent limitations upon phytoplankton growth by lowered DIC in some habitats, including estuaries (Fogel et al., 1992) as well as in brackish waters during red tide episodes (Hansen et al., 2007) or hypereutrophic lakes (Dam et al., 2018). Rapid phytoplankton growth can, under such conditions, place local limitations upon the delivery of DIC into cells for assimilation.

DIC limitation directly limits the assimilation of carbon and thus imposes feedback limitations upon photosynthetic electron transport. DIC limitation also interacts with requirements for other nutrients, altering cellular responses to changing nitrogen availability (Barker-Aström et al., 2005). Although many freshwater taxa have multiple systems for uptake and accumulation of DIC (Raven, 2003; Raven et al., 2014), some marine taxa, which evolved for life under stable, high DIC and pH, have only limited systems for DIC accumulation encoded within their genomes (Price et al., 2008; Shen et al., 2017). Thus, eutrophication of a habitat can, secondarily, alter the prevalent DIC regime from a high, stable geochemically defined DIC to a lower, more variable DIC under dynamic biogenic influence, thereby imposing at least intermittent limitations upon growth of some phytoplankton taxa. These effects may interact with changing delivery of dissolved organic carbon (DOC), as increasing numbers of storms may transport pulses of excess DOC into water bodies (Asmala et al., 2021). Such elevated DOC can persist up to 200 days and can be remineralized faster through bacterial respiration under elevated P inputs (Allesson et al., 2020). Nutrient-rich water bodies may therefore act as net-carbon sources, as more C-compounds can be remineralized.
rather than sequestrated in the sediment (Thingstad et al., 2008). Monitoring of the biological oxygen demand after addition of N, or P, might be a feasible approach for state agencies to identify such seasonal C-source conditions within an ecosystem (Mallin et al., 2004; McCormick et al., 2006).

In general, coastal and bloom-forming taxa may be pre-adapted to cope with moderate decreases in DIC and pH, through their evolution under the influence of short-term biogenic fluctuations (Li et al., 2016). Biogenic shifts in carbonate regime can thus act to exclude taxa adapted to high, stable DIC from persisting in environments with fluctuating DIC and thereby contribute to a hysteresis of phytoplankton community responses to changing nutrient inputs (O’Neil et al., 2012; Dam et al., 2018).

Nitrogen

There are NH$_4^+$ and NO$_3^−$ transporters, with either high or low affinities (reviewed in Glibert et al., 2016). The availability of NH$_4^+$ reducing enzymes, but NO$_3^−$ does not, however, lower NH$_4^+$ assimilation, because NO$_3^−$ necessarily passes through NH$_4^+$ during assimilation (Dortch, 1990). Furthermore, NH$_4^+$ is sometimes considered a preferred N source for phytoplankton, but concentrations above 30 μmol l$^{-1}$ can be growth suppressing (Glibert et al., 2014). NH$_4^+$ uptake is therefore regulated with fewer NH$_4^+$ transporters at increasing NH$_4^+$ concentrations (Post et al., 2012). The ratio of available NO$_3^−$ to NH$_4^+$ can further affect phytoplankton community composition, as NO$_3^−$ assimilation enzymes are cold-temperature adapted (see above; Fan et al., 2003). Contrarily, higher NH$_4^+$ and temperature can lead to dominance by cryptophytes and cyanobacteria (Glibert et al., 2016). This selective pressure was observed to act seasonally on phytoplankton compositions in eutrophic reservoirs (Andersen et al., 2020) and even over decades in lake fertilization experiments (Swarbrick et al., 2019). Low NO$_3^−$:NH$_4^+$ can therefore promote harmful cyanobacterial blooms (Newell et al., 2019). On the other side, in systems with high but fluctuating NO$_3^−$:NH$_4^+$, larger taxa with vacuoles tend to dominate, as stored NO$_3^−$ does not inhibit uptake rates (Stolte and Riegen, 1995).

Picocyanobacteria use different (N-free) compatible solutes for salinity acclimation, as an adaptation to different N limitation (Klähn et al., 2010). Prolonged N limitations can furthermore induce the production of N-scavenging enzymes (see Fig. 2A), including amino acid oxidases and proteases, either membrane bound or extracellular (see list in Berges and Mulholland, 2008) to access dissolved organic N (DON).

DON is an important N source for phytoplankton but is difficult to characterize as it consists of complex, partly undescribed molecules within the pool of dissolved organic matter (Mulholland and Lomas, 2008). Autochthonous DON derived from phytoplankton was found to be the preferred DON source for natural phytoplankton assemblages, whereas bacterioplankton preferred allochthonous DON material (Korth et al., 2012). Recycling of DON prolongs support of phytoplankton growth before N forms eventually exit the system through pathways of denitrification or anaerobic ammonium oxidation (Deutsch et al., 2010; Jäntti et al., 2011). N-fixing cyanobacteria can overcome the onset of N-limitation by developing heterocyst or by scheduling N fixation during the nighttime (Toepel et al., 2008; Grover et al., 2020) to limit inhibition of nitrogenase by the O$_2$ released from photosynthesis. An increase in the HetR protein is responsible for heterocyst development within 3 hours of the onset of N limitation, with the N status intracellularly sensed by changing levels of 2-oxoglutarate (Zhou et al., 1998; Muro-Pastor et al., 2001). In species with heterocyst, the amount of heterocyst per colony is therefore a good estimator of bloom reliance on N$_2$, as cyanobacteria can dominate by acquiring other N sources (Berber et al., 2004; McCarthy et al., 2013). The release of excess fixed N from N-fixing cyanobacterial blooms further stimulates other phytoplankton compartments and the whole food web (Karlson et al., 2015), further increasing the ecosystem N burden even after an initial cyanobacterial bloom collapse.

N limitation interacts with upkeep of photosynthesis since photosynthetic pigments and catalytic complexes represent major standing investments of N (Li et al., 2015), which can accumulate well above instantaneous requirements for catalysis of photosynthesis. These large pools can then support generations of cell division without net accumulation of new protein, enabling cells to temporarily offset biosynthetic accumulation of key proteins from rounds of subsequent division after dissolved N resources are depleted. Cells thereby indulge in luxury accumulation and sequestration of N resources to support later generations of growth, excluding other taxa from exploiting the habitat (de Mazancourt and Schwartz, 2012). In turn, the N costs and investments to maintain photosynthesis in a taxon shifts depending upon other external factors, notably including pCO$_2$ (Li et al., 2015). Other strategies to cope with N limitation, for example loss of pigments (chlorosis), support survival of intermittent limitations under unfavourable conditions (Barker-Aström et al., 2005; Klotz et al., 2016).

Management efforts should therefore focus on lowering NH$_4^+$ (Newell et al., 2019), possibly in conjunction with maintenance of NO$_3^−$ in deeper, stratified waters to preempt redox-sensitive P reflux from sediments (Wauer et al., 2005). Simultaneous lowering of P should be considered, as most toxic N-fixing species thrive at elevated P concentrations during high temperatures and at low NH$_4^+$:NO$_3^−$-ratios (see above and following). Inorganic N will eventually be removed from the system through various microbial pathways, but DON may remain accessible to phytoplankton. Thus, organic N sources should be preferably lowered instead of focusing solely on total N (Lewis et al., 2011).
Phosphorus

The thresholds for P-deficiency responses range from 0.1 to 0.4 μmol ortho-P L⁻¹ (dissolved inorganic phosphorus, DIP) in laboratory cultures, lakes, lagoons and marine waters (Grillo and Gibson, 1979; Nausch, 1998; Li et al., 2019a; Berthold and Schumann, 2020). This threshold range for P deficiency is consistent with growth saturating concentrations ranging from 0.4 to 0.8 μmol l⁻¹ measured in laboratory cultures (Grover, 1989). However, these apparently high concentrations for onset of P deficiency are in stark contrast with low, sometimes undetectable P concentrations in lakes, coastal waters and even oceans during summer or in general (Hudson et al., 2000; Martin et al., 2014; Berthold et al., 2019a).

Environmental samples contain, however, a variety of dissolved organic P (DOP), which is only partly accessible through the colorimetric determination used to determine soluble reactive phosphorus (SRP). DOP concentrations are rarely monitored, but they can make up to 99% of dissolved P fractions (Karl and Björkman, 2015). This fraction is assumed...
to support phytoplankton growth even under non-detectable DIP or SRP concentrations.

Uptake of PO₄ in lakes imply high turn-over rates of P among cells (Hudson et al., 2000). However, P uptake is an energy-demanding process and very low P concentrations can be at the threshold of thermodynamically feasible P uptake (Grillo and Gibson, 1979; Ritchie et al., 2001). Uptake of PO₄ in cultures of Synechococcus R-2 is ATP driven with a demand of one ATP per molecule PO₄ (Ritchie et al., 2001). It is assumed that the very low traces of P found in oligotrophic lake water or growth media represent a steady state between cells and surrounding media, due to P leakage or turn-over (Hudson et al., 2000; Isvánovics et al., 2000).

To overcome persistent nutrient limitation, cells can produce cell-bound and extracellular phosphatases, as a second-tier response, up-regulated as the cell P quota drops below the level at which high-affinity transporters are expressed (Litchman and Nguyen, 2008; Ostrowski et al., 2010). It is possible that under severe P-limiting conditions, P uptake happens so fast that every P molecule released from DOP by alkaline phosphatase activity (APA) is taken up nearly instantaneously, leaving no detectable DIP in the water column (Wynne and Rhee, 1988; Hudson et al., 2000; Berthold and Schumann, 2020; Fig. 2).

P turn-over mediated by phosphatase can be quite high and is usually negatively correlated with available dissolved inorganic P (Nausch, 1998). Such high activities can turn over the complete pool of DOP in 11 hours to 200 days, depending on biomass, season and available PO₄⁻ (Nausch, 1998; Labry et al., 2005). Total phosphatase activity depends additionally on the amount of bacterioplankton in the water column. Indeed, it is not technically possible to discriminate between the phosphatase activities from phytoplankton and bacterioplankton using the common bulk community assay of 4-methylumbelliferyl phosphate-fluorescence and even size-class filtration prior to the assay may show some carry-over effects (Hoppe, 2003; Labry et al., 2005). A possible approach is enzyme-labelled fluorescence markers and the use of an epifluorescence microscope (González-Gil et al., 1998; Dyhrman and Palenik, 1999; Štrojsová et al., 2003). However, this approach is time-consuming. Furthermore, long-term data sets on DOP are rare (van Beusekom and de Jonge, 2012; Karl and Björkman, 2015), as DOP is not usually monitored as part of water quality programs. Including DOP would be a feasible variable for monitoring agencies to better determine actual P supply status within a system, compared to e.g. enzyme kinetics assays or epifluorescence microscopy.

In terms of anthropogenic control phosphatase production and stability is light dependent, in that light is necessary for phytoplankton to produce phosphatase (Wynne and Rhee, 1988). At the same time, however, phosphatase stability decreases upon exposure to light and shading by DOM can protect phosphatase from degradation (Janssen and McNeill, 2015), allowing more prolonged phosphatase activity. Such DOM is either allochthonous or autochthonous. Scenarios in lakes points towards an increased brownification through increased DOM and iron (Weyhenmeyer et al., 2014), leading to possibly enhanced phosphatase half-life times, and therefore increased capacity for P recycling. This enhanced P recycling in the water column could then in turn favour bacterioplankton and phytoplankton communities and sustain their biomass, possibly prolonging their post-eutrophication persistence.

Cells can form PolyP granules even against strong concentration gradients, as described for lakes, oceans and cultures (Martin et al., 2014; Diaz et al., 2019; Hagemann et al., 2019; Li et al., 2019a). Under P-limiting conditions phytoplankton assemblages may show a luxury consumption of P as a response to previous deficiency. There seems to be no size pattern, as filamentous cyanobacteria, as well as picophytoplankton can accumulate large amounts of PolyP (Hagemann et al., 2019; Li et al., 2019a). Picophytoplankton recycling of PolyP seems to support other blooming algae in eutrophic waters of Lake Ontario, therefore mediating P fluxes from smaller to larger phytoplankton (Li et al., 2019a). Uptake-efficient picophytoplankton could act as short-term, small-scale P storage under low P conditions, until PolyP is liberated again to support other phytoplankton in eutrophic waters. This community-scale resource allocation may therefore buffer seasonal P deficiencies, or from a management perspective, temporal restoration measures.

Scenedesmus does not show variation in its intracellular P concentrations under N limitation but does show an 8-fold lower P uptake rate (Rhee, 1974). Similar results were found for N-limited Synechococcus (Grillo and Gibson, 1979), pointing to an energy-saving mechanism of down-regulation of P uptake when N is limiting. Chl fluorescence is quenched after a P pulse delivered to P-limited cells of Dunaliella tertiolecta (Roberts et al., 2008). This fluorescence signal could potentially be used as a monitoring tool to detect P limitation in cultures, and possibly in natural systems, if the fluorescence signal could be taxonomically resolved. A similar approach was tested in coastal waters by combining an HPLC with ChemTax and FRFR to track responses during the addition of either N or N + P to a natural phytoplankton assemblage (Zhao and Quigg, 2014). The approach allowed tracking of shifts in phytoplankton composition and therefore determination of groups competitive under pulsed nutrient supply.

Nutrient pulses are probably the rule in most systems, as phytoplankton cells experience pulse-wise exhaustion and resupply of nutrients within their diffusive boundary layer (Aubriot et al., 2000). High uptake rates and nutrient-limited boundary layers around a cell can lead to a transport limitation, where the uptake is regulated by motion of the medium relative to the cell, and a diffusion quotient, rather than by bulk nutrient concentration (Pasciak and Gavis, 1974; Ploug
et al., 1999). Such diffusional limitation is influenced by cell size and, in larger cells, by motility or buoyancy control (Gemmel et al., 2016). The determinations of physiological uptake rates may therefore differ from in situ uptake rates, depending on experimental setting, as for example mixing of the medium. The regulation of P uptake depends therefore on the timing of re-supply. If the amount of available external P does not drop after 15–25 minutes, cells down-regulate their uptake rates (Aubriot and Bonilla, 2012). However, down-regulation for genes for high-affinity P transporters only occurs if cells start to recover from P starvation (Solovchenko et al., 2020). Such high-affinity P-uptake systems include the sphX gene in Synechococcus PCC7942, which enables cells to show pre-acclimated uptake kinetics to re-occurring P pulses, depending upon gene expression induced under earlier cycles of P pulses (Falkner et al., 1998). These mechanisms enable some cells to exploit low, pulsed nutrient concentrations with high-affinity transporters, and thereby persist even when measures of bulk dissolved inorganic P are low. In contrast, a high background nutrient concentration will lead to expression of lower affinity systems to support a steady growth rate (Aubriot and Bonilla, 2012).

Monitoring external nutrient concentrations will not, therefore, on their own reveal nutrient limitations of the phytoplankton community. Monitoring nutrient concentrations needs to be complemented by knowledge of the physiological response capacity of the relevant phytoplankton assemblage, including capacities for luxury storage of nutrients (Hagemann et al., 2019), recycling of organic nutrient sources (Labry et al., 2005) or functional substitutions of nutrients (Van Mooy et al., 2006) in cell compartments.

Silicate

In diatoms there are high- and low-affinity systems for Si, which in turn depend on intracellular binding components to incorporate Si (Thamdrup and Hildebrand, 2008). Those binding components are probably controlled within 5–10 minutes after intracellular Si-pools drop. The model diatom Thalassiosira pseudonana can sustain growth for three cell cycles without P addition, but ceases growing within 2 hours of silicate depletion (Parlow et al., 1984). Furthermore, the timing of Si-depletion has an impact on how fast diatom cells stop and re-start growth. Diatoms of different species will experience a prolongation of their reproductive cycle (Brezezinski et al., 1990; Martin-Jézéquel et al., 2000), or even programmed cell death (Wang et al., 2017), under Si-limiting conditions. This strong dependence of diatoms upon silicate generates striking ecological effects. For example, damming of the Danube River led to a 3-fold decrease of Si flux (Cociasu et al., 1996), leading to a subsequent loss of diatoms from Black Sea surface waters (Humborg et al., 1997). In any case, fluctuating or artificially lowered Si inputs in all aquatic systems will affect diatom blooms with subsequent effects on food webs. Lower Si content in diatoms makes them more prone to grazing (Liu et al., 2016).

Furthermore, the increase of atmospheric CO₂ and lowered availability of Si in some waters may promote an increase of toxicity in Pseudo-nitzschia fraudulenta (Tatters et al., 2012). Interestingly, the artificial addition of silicate can shift phytoplankton compositions from flagellates towards diatoms, albeit without increasing biogenic sedimentation rates, in the form of Chl a, in mesocosms (Svensen et al., 2001). These results can be explained by onset of an additional Fe limitation, where Fe-deplete and Si-replete conditions will lead to thick-shelled diatoms (Assmy et al., 2013), through prolonged Si-incorporation during Fe growth limitation (Wilken et al., 2011). However, those cells will mostly sink as empty silicate shells, without promoting much C-transfer into deeper waters (Assmy et al., 2013). The management option of controlling biogenic flows through forced species compositional changes may therefore depend upon co-limitations for other nutrients. Further work is thus needed to evaluate the feasibility of manipulating the Si cycle to prevent harmful blooms, or to manage food webs.

**Interactions of cell size with acclimation**

Biovolume is not a fixed taxonomic trait but can rather change within phytoplankton taxa (Peter and Sommer, 2015; Bernstein et al., 2016; Weisse et al., 2016), either at single-cell level, or as a colony, thereby altering buoyancy control (Gemmel et al., 2016). Cell size regulation can depend upon temperature, light, salinity, nutrient availability or grazer occurrence (Staehr et al., 2002; Buma et al., 2006; Staehr and Birkeland, 2006; Bernstein et al., 2016; Ayache et al., 2020; Lürling, 2020). Temperature is assumed to act directly on cell size, as increasing temperatures increase resource demands and solubility of CO₂ in water decreases (Atkinson et al., 2003).

Increasing temperatures may also increase growth rates of some taxa, thereby favouring small, fast-growing cells (Staehr and Birkeland, 2006). However, under optimized laboratory conditions, with no resource limitation, biovolume can increase at increasing temperatures (Thompson et al., 1992). In contrast, high irradiance can increase cell size, with an increase of C content per cell in diatoms (Buma et al., 2006), prasinophytes, chlorophytes (Staehr et al., 2002) and cyanobacteria (Bernstein et al., 2016). With increasing temperature and possibly light (through stratification) in the future, phytoplankton blooms may grow even faster in conjunction with higher available nutrients, thereby destabilizing and replacing current macrophyte-dominated systems.

Occurrence of grazers can promote cell size change (Lürling, 2020) within taxa or at the community level, towards either cells grown larger than digestible size (Lürling, 2003) or smaller towards passage through predator ingestion systems (Yoshida et al., 2004). It is still debated how grazing will shape phytoplankton communities of the future, towards larger or smaller cells (reviewed in Sommer et al., 2017), and trends will likely differ across systems.
Intraspecific interactions, with displacement of genotypes, can be recurrent seasonal successional replacements, with genotypes sequentially dominating, in contrast to genotype losses or replacements under sustained new environmental regimes (Fig. 3). Changing nutrients, light and temperature can act as bottlenecks, with only a sub-selection of genotypes surviving. Intraspecific genotype replacement has been found in planktonic cyanobacteria (Wilson et al., 2006), diatoms (Godhe and Rynearson, 2017), green algae (Narwani et al., 2015) and benthic red algae (Urzi et al., 2003). Intraspecific replacements depend on the capacity of each genotype to cope with environmental changes through phenotypic plasticity (Callahan et al., 2008) and their role within the ecosystem, whether C (competition) or S (survival) strategists based on either r or K selection (Reynolds, 2012). Indeed, a variety of genotypes can occur within an ecosystem without dominating it, as the metabolic acclimations or viral susceptibilities of each genotype may only allow net growth up to limitations imposed by environmental or biotic factors. Replacements of one genotype with a congener may have an ecological impact equivalent to loss of the taxon completely (Des Roches et al., 2018) so losses of intraspecific variations may indirectly shape communities through, e.g. trophic cascades.

Diversity-dependent niche width

The focus on a few selected genotypes as model organisms, including Synechocystis PCC6803 or T. pseudonana CCMP1335, may therefore be misleading when describing the wider physiological capacities of phytoplankton assemblages based upon phylogenetic composition (Kemp and Villareal, 2018) or broad shared traits, such as morphology. Gross morphology is not only a weak trait for phylogenetic relatedness (Alexandrou et al., 2015; Albrecht et al., 2017), but also a weak predictor of competitive advantage (Narwani et al., 2015). Furthermore, describing phytoplankton taxa only by a particular mean trait value for an entire taxon may lead to an underestimation of the overall taxon physiological performance by up to one order of magnitude (Malerba et al., 2016). Phytoplankton diversity changes sharply along gradients of, e.g. light (Urbach et al., 1998) or ion composition (Laamanen et al., 2002). Diversity is also likely driven by ecosystem perturbation rates, so that under stable conditions a specialist clade can dominate (Fuller et al., 2003), whereas under constantly changing conditions, as in estuaries, higher diversity can persist (Chen et al., 2006).

One prominent example for strong niche specialization is Prochlorococcus (Dufresne et al., 2005), which constitutes, together with Synechococcus, 30–55% of carbon biomass of picophytoplankton in the oceans (Buitenhuis et al., 2012). There are multiple Prochlorococcus ecotypes, with genome sizes varying from 1.6 to 2.6 Mb (Kettler et al., 2007). These genotypes cannot replace each other in their respective niches. For example, MED4 as part of the HL-clade is adapted to high light and high O2 concentrations, whereas MIT9313 exploits low light (Rocap et al., 2003). Closely related Prochlorococcus or Synechococcus genotypes (based on 16S rRNA) can differ in their genetic capacities for N and P uptake and utilization (Moore et al., 2005; Martiny et al., 2009a, 2009b), based on their encoded capacities to produce phosphatases, N or P uptake systems. Analogously, populations of the diatom Ditylum brightwellii differ between sampling locations in microsatellite allele distributions, but not in their 18S rDNA pattern (Rynearson and Armburst, 2004).

Effects on restoration

Analogous differences in genotype-specific responses occur in other groups including the chlorophytes Ostreococcus (Six et al., 2012) and Haematococcus (Allewaert et al., 2017), the cyanobacteria Microcystis (Wilson et al., 2006), the dinoflagellate Alexandrium catenella (Jauzein et al., 2010) and the diatom Thalassiosira hyalina (Wolf et al., 2018). For Ostreococcus one genotype might dominate under higher irradiances and elevated N inputs, whereas another genotype grows better under lower light and lower N concentrations (Six et al., 2012). Two genotypes of the toxic dinoflagellate A. catenella showed different requirements for P, with regulation of uptake rate dependent on C:P ratios within cells (Jauzein et al., 2010).

Such differences in P requirements can lead to bloom formations from genotypes needing less P, for example after nutrient inputs into a system have been lowered. Strongly lowering P favoured the occurrences of Planktothrix HABs in Lake Zurich (Posch et al., 2012), whereas a non-toxic Planktothrix strain probably dominated during preceding eutrophic conditions (Ostermaier et al., 2012). A similar high intraspecific variability was found across 32 isolates of Microcystis aeruginosa from 12 lakes based on an increase of population growth rate with colony biovolume (Wilson et al., 2005). Five isolated genotypes of M. aeruginosa and Raphidiopsis raciborskii (Guedes et al., 2019) showed either significantly different growth rates or different PSI efficiency at early stationary phases upon P depletion. However,
pooling the effects within a species evened out the effects of each intra-species genotype, leading to no overall competitive advantage of one taxon over the other during P limitation. Thus, conserved phylogeny may not explain realized niches in phytoplankton, especially not when considering lateral gene transfer (Dufresne et al., 2008) or sexual reproduction (Reusch and Boyd, 2013). From a management and conservation perspective, this intraspecific diversity is challenging, as widely applied morphological resolved data sets may not catch the actual trend of species and their respective physiological capacities during restoration. With the drop in cost of sequencing it is therefore useful to assess several genotypes per population to define potential and realized niches within a system. Information on community composition and presumed exploitative strategies will help decision makers to formulate individual options per ecosystem.

**Resistance and resilience**

A question for future studies will be why a nuisance taxon does not rise to dominance earlier during eutrophication. It is likely that the pre-eutrophication community itself showed resilience through genotype diversity, thereby resisting apparent succession. For example, disturbance through application of precipitating agents to control P (Barçante et al., 2020) applies a pulse stress of nutrient withdrawal. Pulse-wise re-supply can then favour the fastest growing taxon, or intraspecific competitor (Klappenbach et al., 2000), which rises to dominate a pulse-disturbed community. This exploitation of pulsed habitats can be positive for natural ecosystems experiencing disturbance, but also negative if such buffering capacities must be overcome to alter community composition towards a desired goal. In the case of a Baltic lagoon system, this stabilizes a perennial, morphotypically homogeneous but intraspecifically diverse phytoplankton assemblage (Schiewer, 2007; Albrecht et al., 2017), by its exploitation of a pulse-wise nutrient supply for growth (Berthold and Schumann, 2020).

Instead of such a pulse-disturbance, a press-disturbance with sustained, strong lowering of nutrient inputs may suppress species rapidly exploiting pulsed nutrient supplies. Slow-growing species (low RNA/DNA ratio) make better use of systems with limiting nutrient concentrations, as they maximize resource use (Lee et al., 2009). This strategy leads to an overall resource-limited ecosystem that is more resistant against press disturbance (Shade et al., 2012). From the phytoplankton perspective, reducing nutrient inflows is a stress factor that is perceived as either press or pulse disturbance. Management actions need to consider not only the amplitude but also the frequency of restoration measures to overcome such variable community responses to resource limitation. Furthermore, half a century is sufficient to select for newly adapted strains during pre- and post-eutrophication, as seen from cyst revival experiments (Girault et al., 2021) so there is no short return to a pre-disturbance array of genotypes.

Diversity can stabilize sub-populations of genotypes within and across habitat boundaries (Kremp et al., 2016; Godhe and Rynearson, 2017). Multi-genotype populations of the Arctic diatom *T. hyalina* were able to buffer potential deviations from today’s temperature and pCO₂ concentrations, through intraspecific selection for the best adapted among the genotypes (Wolf et al., 2018, 2019). This genotype variation was identified as a driver of evolutionary and ecological success of diatoms, despite global change (reviewed in Godhe and Rynearson, 2017). Thus, genotype niches are smaller than the respective population niche, which leads to a population niche depending on both: local intraspecific diversity and the actual habitat (Fig. 3). Such population diversity has so far been described for freshwater and marine habitats (Tesson et al., 2014; Van Den Wyngaert et al., 2015). The rate of acclimation vs. adaptation in intraspecific diversity develops over several hundreds of generations to, for example temperature increase (Aragonuren-Gassis et al., 2019). With human management of inputs, the increase/decrease of key elements can shift the genotypic composition of a population, within similar morphotypes. For example, *Synechococcus* and *Synechocystis* share a similar phenotype, but show completely different transcriptional responses, when facing different abiotic conditions (Billis et al., 2014). Such genetically diverse phytoplankton communities may contain several taxa with complementary response traits that have the potential for rapid compensatory growth after pulsed disturbance (Yachi and Loreau, 1999; Shade et al., 2012).

**Conclusions and Prospects**

Phytoplanktons thrive in all aquatic ecosystems worldwide, but human impacts shift the occurrences and frequencies of taxa. The management of aquatic systems needs to consider not only nutrient inputs and balances, but also the microdiversity of phytoplankton. Phytoplankton responses are not fixed but depend upon the genetic diversity that underlies physiological diversity, which in turn drives the functional diversity within an ecosystem. Unravelling the hidden diversity and ranges of physiological responses, on an intrataxa as well as intertaxa level is a next step towards understanding phytoplankton succession. However, all these patterns depend on knowledge from the bottom (nutrients, light, temperature) and the top (higher trophic levels). For that, long-term monitoring data sets continue to be necessary, to inform and define the needed ecophysiological and genetic studies.

**A Baltic case study**

A prediction into the future is difficult, yet some systems, as for example the Baltic Sea, can be used as models (Reusch et al., 2018) due to above-average temperature increase and a long history of monitored eutrophication, with its densely inhabited catchment area and low water exchange with the Atlantic Ocean. Policy interventions to control and reverse
eutrophication are now well advanced in the Baltic region, temporally overlapping with surface water warming in recent decades (HELCOM, 2014).

In the Baltic Sea the seasonal Chl-maximum has already shifted from a diatom bloom in spring towards the cyanobacteria bloom in summer within four decades (Kahru et al., 2016). This increase, extension and shift of dominant blooming taxa is permitted by non-limiting nutrients in spring (Fisher et al., 1992; Pastuszak et al., 2003) earlier onset of a high cumulative amount of incoming shortwave irradiance through altered cloudiness patterns (Kahru et al., 2016) or by altered hydrological flows into the system through either heavy rainfall (Mallin et al., 1993) or exchange with the open sea (Trombetta et al., 2019). More broadly, water temperature also acts through complex interactions with the abiotic environment and other trophic levels. Water temperature regulates turn-over times of nutrients within the water column, by altering re-mineralization within the sediment and water column and through altering nutrient transport rates throughout the water column by increased stratification (Behrenfeld et al., 2006; Ryckzewski and Dunne, 2010; Kraemer et al., 2015; Kemp and Villedal, 2018). For example, increasing water temperatures increase oxygen consumption by sediments, lowering the redox poise of sediments and therefore mediating nutrient release, particularly phosphate, which can (re)fuel primary production (Cowan and Boynton, 1996; Spears et al., 2008).

This increased nutrient background will further shape phytoplankton succession by favouring growth strategies depending on frequency or spatial distribution of nutrients. A regulated drop in external nutrient supply can lead to a compositional change towards taxa that are able to control their buoyancy and take nutrients up from the thermocline, as described for lakes and the Baltic Sea (Nausch et al., 2012; Posch et al., 2012). However, non-point sources from the coast may still influence the Baltic Proper through large-scale eddy-mediated transport of plankton and nutrients (Vortmeyer-Kley et al., 2019).

The Baltic Sea and its tributaries show resistance to reversion of past eutrophication, with current dominance by a large diversity of previously unrecognized smaller phytoplankters in the Baltic and its coastal basins (Hugerth et al., 2015; Albrecht et al., 2017; Celepli et al., 2017). These small phytoplankters are possibly favoured by lowered, pulsewise nutrient releases and increasing temperatures. In lagoon systems of the Baltic Sea, with negligible nutrient input from the suboxic waters/sediments, phytoplankton grows adjacent to the wetland, but not in the centre of the water body (Berthold et al., 2018). In such shallow waters, nutrient runoff from land (Karstens et al., 2016) and from fluctuating redox conditions within the wetland (Karstens et al., 2015), can deliver P pulse wise to the phytoplankton, which is not light limited in the shallow waters.

The combination of increasing temperature and decreasing nutrients in input-managed systems can lower the overall biovolume of phytoplankton communities (Peter and Sommer, 2013), potentially leading to dominance of smaller cells in future warmer aquatic ecosystems (Daullsnes et al., 2009; Sommer et al., 2017). As mentioned above, small cell diameter can be an adaptation to low light (Vincent, 2000), particularly in conjunction with low nutrients that place a premium upon light capture per invested elemental resource (Finkel, 2007). Cell size strongly influences nutrient uptake (Finkel et al., 2004) and cell quotas for key elements (Finkel et al., 2010a). Establishment of a phytoplankton community dominated by small cells may therefore pre-empt the re-establishment of larger phytoplankters, or macrophytes, through shading and through rapid re-uptake of recycled nutrients. Systems with such increasing dominance by picophytoplankton have been described for freshwater, brackish and shelf sea areas (Schiewer, 2007; Callieri, 2008; Schmidt et al., 2020), when nutrients and light become limiting to other groups.

In contrast, large cyanobacteria tend to dominate, when the overall turbidity, temperature and TP concentration is high (Scheffer et al., 1997; Håkanson et al., 2007; Schwaderer et al., 2011). Thin filaments of larger cyanobacteria capture light in turbid waters as well as the same biovolume of small cells (Kirk, 1976). Larger colonies alter microscale oxygen environments, favouring N fixation (Ploug, 2008; Stal, 2017), but even single filaments of Trichodesmus can show higher N fixation rates than colonies (Eichner et al., 2019). There may be other advantages of colony formation besides N fixation. Thus, the postulated dominance of small cells may not become a universal pattern. Ecosystems will eventually change with the food webs adapting to the prevailing composition of primary producers (Motwani and Gorokhova, 2013; Liénart et al., 2021), thereby affecting higher ecosystem services. If a shift towards toxic blooms or picophytoplankton dominance alters ecosystem services, managing systems towards new or renewed communities requires predictive understanding of how these phytoplankton communities persist in exploiting post-eutrophied systems (Table 1). And, on a cautionary note, multiple nuisance taxa may well replace each other before some desired ecosystem state is reached.

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