Review Paper

Grazing resistance in phytoplankton

Miquel Lürling

Abstract Phytoplankton is confronted with a variable assemblage of zooplankton grazers that create a strong selection pressure for traits that reduce mortality. Phytoplankton is, however, also challenged to remain suspended and to acquire sufficient resources for growth. Consequently, phytoplanktic organisms have evolved a variety of strategies to survive in a variable environment. An overview is presented of the various phytoplankton defense strategies, and costs and benefits of phytoplankton defenses with a zooming in on grazer-induced colony formation. The trade-off between phytoplankton competitive abilities and defenses against grazing favor adaptive trait changes—rapid evolution and phenotypic plasticity—that have the potential to influence population and community dynamics, as exemplified by controlled chemostat experiments. An interspecific defense–growth trade-off could explain seasonal shifts in the species composition of an in situ phytoplankton community yielding defense and growth rate as key traits of the phytoplankton. The importance of grazing and protection against grazing in shaping the phytoplankton community structure should not be underestimated. The trade-offs between nutrient acquisition, remaining suspended, and grazing resistance generate the dynamic phytoplankton community composition.

Keywords Adaptive trait · Algal defense · Anti-grazing response · Chemical defense · Induced defense · Morphology · Phenotypic plasticity · Rapid evolution · Trade-off

M. Lürling
Aquatic Ecology & Water Quality Management Group, Department of Environmental Sciences, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

M. Lürling (✉)
Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands
e-mail: miquel.lurling@wur.nl

Introduction

Phytoplankton can be defined as "the collective of photosynthetic microorganisms, adapted to live partly or continuously in open water" or "planktic photoautotrophs adapted for a life spent wholly or partly in quasi-suspension in open water, and whose powers of motility do not exceed turbulent entrainment" (Reynolds, 2006). The main challenge for photosynthetic plankton is to survive long enough to acquire sufficient energy and nutrients to build new biomass and to reproduce. Consequently, these organisms need to be

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regularly in the upper water strata to collect enough light energy and have a need to "maximize opportunities for suspension" (Reynolds, 2006). Phytoplankton cells also are in demand for nutrients that need to be concentrated from the surrounding water. Small-sized algae with a large surface-to-volume ratio have the most efficient uptake of dissolved nutrients and lowest sinking losses (Reynolds, 2006). Hence, small size might be beneficial for phytoplankton, yet sizes of phytoplankton can span over 9 orders of magnitude from 1 μm^3 in volume for pico-cyanobacteria to around 10^9 μm^3 for *Microcystis* colonies (Reynolds, 2006). Water column stability or frequency of its disturbance along with the availability of nutrients formed the basis for explaining large varieties in size and shapes, and seasonal variations in phytoplankton community composition (Reynolds, 1980, 1998). Three adaptive strategies are distinguished in freshwater phytoplankton: (1) high surface-to-volume colonist, small, fast-growing, (C) species; (2) large, low surface-to-volume, slow-growing, nutrient stress-tolerant (S) species; (3) light-harvesting, disturbance-tolerant ruderal (R) species (Reynolds, 1993; Smayda & Reynolds, 2001). Such classification suggests that "the physical structure of the environment, or of the availability of nutrients within it,… are, directly or indirectly, the most important variables likely to influence the general composition of the phytoplankton" (Reynolds, 1980). However, survival also means that phytoplankton is challenged to withstand grazing (Reynolds, 2012), which is one of the most important loss processes operating and one of the most powerful forces in phytoplankton selection (Smetacek, 2001).

Phytoplankton is confronted with an assemblage of protozoan and metazoan grazers (Lehman, 1988; Reynolds, 2006), exerting a grazing pressure that varies in time and space, and that can be a steering factor during several periods of the year (Sommer et al., 2012). Investment in adaptations to zooplankton attacks implies phytoplanktic "evolution is ruled by protection and not by competition" (Smetacek, 2001). Hence, grazing creates a strong selection pressure for traits that reduce mortality (Fig. 1). Inasmuch as these traits reduce zooplankton food intake, and therewith affect zooplankton growth and reproduction, they may have variable impacts on plankton dynamics, and, depending on magnitude, may also lead to trophic decoupling (Sommer et al., 2012).

Phytoplankton anti-grazing strategies

The various phytoplankton anti-grazing strategies can be grouped based on the type of defenses, such as morphological, physiological, and behavioral defenses (Pančić & Kiørboe, 2018). The review by Pančić & Kiørboe (2018) provides a detailed overview of the diverse defense mechanisms in phytoplankton. These authors emphasize the need for thorough research on costs and benefits (trade-offs) of the proposed defenses (Pančić & Kiørboe, 2018). Alternatively, phytoplankton defenses not necessarily need to be classified as phytoplankton traits (morphological, physiological, behavioral), but can also be grouped as strategies along the effects these traits exert on the phytoplankton–zooplankton interaction (Fig. 1). One strategy is to avoid ingestion, which can be achieved via adequate timing of recruitment from cysts (Hansson, 1996; Rengefors et al., 1998), migrating to regions with lower grazing pressure (Latta et al., 2009), changes in movements that result in lower encounter rates with grazers (Selander et al., 2011; Harvey & Menden-Deuer, 2012), growing to sizes beyond the ingestion capacity of most grazers (Lürling, 2003a), production of grazer deterrents (Xu & Kiørboe, 2018), or making thick silicate cell walls that provide protection against grazers that crush cells prior to ingestion (Pančić et al., 2019). Another strategy is to avoid digestion after being ingested (Fig. 1). Viable gut passage might be enabled by thickened cell walls (Van Donk et al., 1997), or embedment in mucous (DeMott et al., 2010). Strongly reducing grazing pressure by killing the most dangerous enemies is another highly effective strategy, particularly against generalist grazers, such as *Daphnia* (DeMott, 1999; Lürling, 2003b). Alternatively, if phytoplankton growth rate equals or exceeds the community filtration rate, the phytoplankton population will be maintained or may even expand (Reynolds, 1984, 2006). Hence, those species are able to tolerate the zooplankton community grazing pressure.

Phytoplankton species are condemned to living with their enemies, yet not all species possess or express defenses against grazers. Many unicellular species lack any defenses and probably allocate savings from maintaining defenses to growth, which may be a most beneficial strategy in competitive environments (Acevedo-Trejos et al., 2018). Other
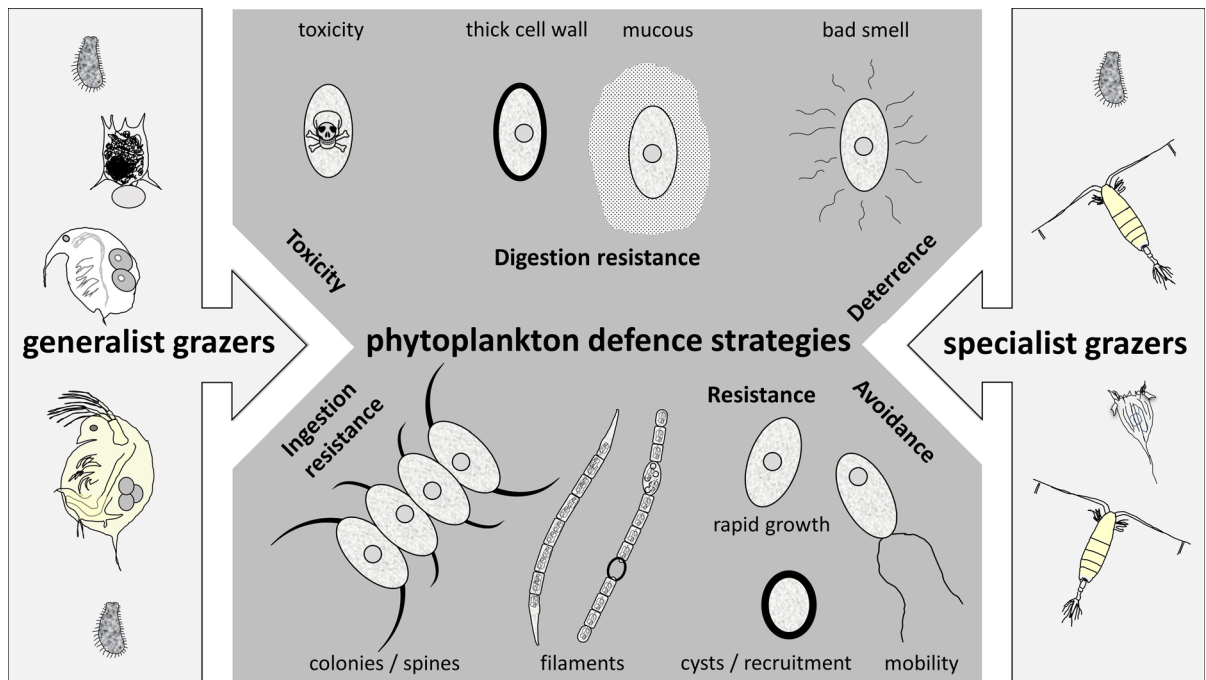
Fig. 1 Potential phytoplankton defenses against generalist and specialist zooplankton grazers. Defenses can be constitutive or inducible and include traits that reduce ingestion by zooplankton, reduce digestion, reduce the chance of encountering zooplankton, and even those that are directly detrimental to zooplankton

phytoplankton species may possess constitutive defenses, i.e., they are always expressed, or on an intraspecies–interindividual level, different clones with different traits may be favored depending on environmental factors. The intraspecific genetic diversity within a species allows a rapid adaptive trait change, in which grazing and competition may cause a quick change in the relative abundance of genotypes with different traits, such as competitive ability and defense against grazers (Yamamichi et al., 2011). For instance, exposure to rotifer grazers resulted in rapid evolution in the green alga *Chlorella vulgaris* Beijerinck that became less nutritious to the rotifers, but also less competitive in comparison with non-grazer exposed clones (Yoshida et al., 2003). The intraspecific genetic diversity is a prerequisite for rapid evolution, a fast, inheritable response (Yamamichi et al., 2011).

Another mechanism of rapid adaptation is inducible defenses, in which a single genotype produces different phenotypes in response to grazing. Induced defenses are typical expressions of phenotypic plasticity, the defenses will only be activated when needed. An overview of inducible defenses is given

in Van Donk et al. (2011). Inducible defenses are favored when the risk of mortality from grazing is variable and reliable cues are present, as defenses usually come with costs (Tollrian & Harvell, 1999; Pančić & Kiørboe, 2018).

Costs and benefits of phytoplankton defenses

Phytoplankton species (or even clones within a species) have adopted various strategies of coping with the heterogeneity in their environment. In response to grazing, phytoplankton may possess no, induced, or constitutive defenses. Remaining small with a favorable surface-to-volume ratio allows fast growth and lowers sinking loss (Reynolds, 1984). In a competitive, mixed environment small phytoplankton species became dominant, whereas larger species were competitively excluded (Burson et al., 2018). However, undefended, nanoplanktic algae, i.e., algae between 2 and 30 µm in length, are a main food source for freshwater zooplankton (Sterner, 1989). There are countless experiments that underpin "the

fate of these algae is to be grazed" (Reynolds et al., 1982).

Growing to sizes above the ingestion capacity of zooplankton is an effective strategy to protect the cells against grazing (Lehman, 1988). Large size, forming colonies or elongated chains are widespread characteristics among numerous phytoplankton species. For instance, members of the genus *Microcystis* are among the most commonly found bloom-forming cyanobacteria (Harke et al., 2016) that are predominantly unicellular in the laboratory, but colonial in the field (Xiao et al., 2018). Several abiotic and biotic factors, including grazers, are involved in colony formation, which is mostly achieved through cell division, but in *Microcystis* colonies may additionally grow through cell adhesion (Xiao et al., 2017, 2018). The typical colonial morphology reduces zooplankton feeding rates (Fulton & Paerl, 1987, 1988). *Microcystis aeruginosa* (Kützing) Kützing colonies strongly depressed clearance rates in the flagellate *Ochromonas*, but at a tax of lower growth and higher sinking rates for colonies (Yang et al., 2009). Likewise, *Scenedesmus* colonies were far less grazed upon by zooplankton, but also had higher sinking rates than unicells (Lürling, 2003a). A trade-off between grazing loss and sinking loss in *Desmodesmus/Scenedesmus* has been found—larger, protected Scenedesmaceae had the lowest grazing loss, but the highest sinking loss (Verschoor et al., 2009). Metabolic costs that are associated with (induced) colony formation might be reflected in reduced growth of colonial populations (Zhu et al., 2016; Albini et al., 2019), particularly under resource limitation (Zhu et al., 2016). In diatoms, thick silicate cell walls provide protection against grazers that crush cells prior to ingestion (Pančić et al., 2019). Such thicker silicate cell walls may be induced in the presence of zooplankton grazers (Pondaven et al., 2007), but silica deposition decreased with increasing growth rates pointing to costs associated with the shell thickening (Pančić et al., 2019).

Also filamentous cyanobacteria may hamper ingestion by zooplankton when above critical concentrations (Gliwicz, 1990a, b). Filamentous cyanobacteria might further aggregate into big flakes in the presence of zooplankton (Lynch, 1980), or express thickening and shortening of filaments in the presence of *Daphnia*, its exudates or the kairomone sodium octyl sulfate that all reduce grazing loss (Cerbin et al., 2013;

Wejnerowski et al., 2018). Cells in filaments may also benefit from N_2 fixation in specialized cells. To date, costs of a filamentous morphology have not been assessed.

In contrast to an increase in size, also the opposite of becoming smaller and more defended can be an effective way of reducing grazing loss (Yoshida et al., 2004). *Chlorella vulgaris* grown with rotifer (*Brachionus*) grazers were heritably smaller, but competitively inferior relative to cells grown in the absence of rotifers (Yoshida et al., 2003). Food ingestion in *Brachionus* is steered by particle size, the feeding efficiency curve is bell shaped, which implies that feeding on algae either larger or smaller than the optimal size window will result in reduced feeding efficiency and lower rotifer population growth rates (Rothhaupt, 1990). Follow-up research on the study of Yoshida et al. (2003) revealed that the rotifers did not feed selectively on either the defended or undefended clone, but that the defended clone had far better gut passage survival than the more competitive, undefended clone of *C. vulgaris* (Meyer et al., 2006). Such resistance against digestion has also been observed in green algae with thickened cell walls (Van Donk et al., 1997). Green algae covered by mucilaginous sheaths are also defended against digestion and grazing promotes such digestion defenses at the cost of slower growth (DeMott & McKinney, 2015).

Whether phytoplankton cells may respond to grazers by forming colonies or becoming less colonial may depend on the most dominant grazer (Long et al., 2007). For instance, enhanced colony formation took place when *Phaeocystis* was exposed to chemical cues from the ciliate *Euplotes* sp., which consumes smaller particles, while colony suppression in *Phaeocystis* occurred when it was exposed to chemical signals from the copepod *Acartia tonsa* Dana that consumes larger particles (Long et al., 2007).

Copepod-induced breakup of chains in the chain-forming dinoflagellate *Alexandrium tamarense* (Lebour) Balech into single cells and reduced swimming speed allowed the dinoflagellates entering a "stealth mode" that lowered encounter rates with copepod grazers (Selander et al., 2011). Dinoflagellates may also produce a bioluminescence flash in response to copepods (Lindström et al., 2017), which leads to near complete rejection of dinoflagellates and with copepods that switch to alternative prey (Prevett et al., 2019). Despite these bioluminescent dinoflagellates

grow at one-third the rate of their competitors of equivalent size, their defense reduces losses to zooplankton grazers to such extent that they persist in the community (Prevett et al., 2019).

The dinoflagellate *Alexandrium minutum* Halim responded to polar lipids excreted from copepods with up to a 20-fold increase in the production of saxitoxins that intoxicate copepods (Selander et al., 2015). Although one would expect elevated metabolic costs involved in toxin production, up to date such costs have not been detected (e.g., Tillmann et al., 2009). Possibly, costs will only show up under less nutrient-enriched conditions (Pančić & Kiørboe, 2018). Chemical defenses, such as use of deterrents or toxicity, are also found in cyanobacteria (DeMott & Moxter, 1991). For instance, *Microcystis* strains produce numerous compounds that are detrimental to zooplankton, among them a class of heptapeptides—microcystins. Some studies reported that exposure to zooplankton or to cell extracts and microcystins elevated the microcystin content in remaining cells (Jang et al., 2003, 2007; Schatz et al., 2007). These microcystins are toxic to zooplankton and cues related to it can be used by selectively feeding zooplankton to avoid ingestion (Ger et al., 2016), which caused those grazers to switch to alternative non-toxic prey therewith alleviating competition for *Microcystis* (Ger et al., 2019). Comparison between a microcystin producing wild-type and a microcystin-free mutant strain of *M. aeruginosa* indicated metabolic costs associated with the production of this cyanobacterial toxin (Briand et al., 2012). Dinoflagellates and cyanobacteria generally have lower growth rates than their competitors. They show a widespread ability to respond adaptively to grazers or grazing-associated cues, whereas their mobility (dinoflagellates) or buoyancy control (cyanobacteria) prevent them sinking out of the euphotic zone. Clearly, these organisms have adopted strategies to cope with the major phytoplankton loss processes operating—grazing and sedimentation (Reynolds, 1984; Smetacek, 2001).

From the above it becomes evident that there is a clear trade-off between the costs and benefits of defenses. Those defenses can always be present, or activated only when needed. For example, the colonial green alga *Desmodesmus quadricauda* (Turpin) Brébisson was classified as permanently defended (Verschoor et al., 2007), whereas *Desmodesmus subspicatus* (Chodat) E. Hegewald & A.W.F. Schmidt showed an inducible defense, i.e., it formed colonies when confronted with a grazer, but otherwise remained unicellular (Hessen & Van Donk, 1993). This grazer–*Desmodesmus/Scenedesmus* interaction is perhaps the best studied model system on inducible defenses in phytoplankton.

Grazer-induced colony formation

Hessen & Van Donk (1993) discovered that when they exposed unicellular *D. subspicatus* (at that time *Scenedesmus subspicatus*) to water in which the grazer *Daphnia* had been present, or to one live *Daphnia*, the algae rapidly formed colonies within 48 h. *Desmodesmus subspicatus* increased in size from 8×5 μm (length × width) in unicells to 40×6 μm in 8-celled colonies, with more and rigid spines. Confronted with a high proportion of 8-celled *D. subspicatus* colonies, grazing of a 1.75 mm *Daphnia* was reduced by 75% reflecting an increased grazing resistance of the colonies (Hessen & Van Donk, 1993). Research in the decade following upon this discovery yielded more insight in the spread of the response among members of the family Scenedesmaceae, on costs (higher sedimentation rate) and benefits (lower grazing mortality), and further underpinned induced colony formation is an adaptive response to zooplankton grazers caused by a chemical cue (Lürling, 2003a).

More recent research elucidated the chemical nature of the cues involved, which were identified as aliphatic sulfates and sulfamates (Yasumoto et al., 2005, 2006, 2008a, b). These so-called kairomones show strong structural similarity with synthetic anionic surfactants. Two commercially available anionic surfactants (sodium dodecyl sulfate and FFD-6) evoked a similar formation of colonies in *Scenedesmus* as the natural cues (Lürling, 2012). The morphological response occurred at concentrations far below those that inhibited growth, a traditional endpoint in ecotoxicology, and drastically reduced the clearance rate of *Daphnia* (Lürling et al., 2011). Such distortion of the adaptive response by pollutants may have consequences for population dynamics of both species in the interaction, but could also be spread out in the ecosystem through numerous biological interactions (Hanazato, 1999).
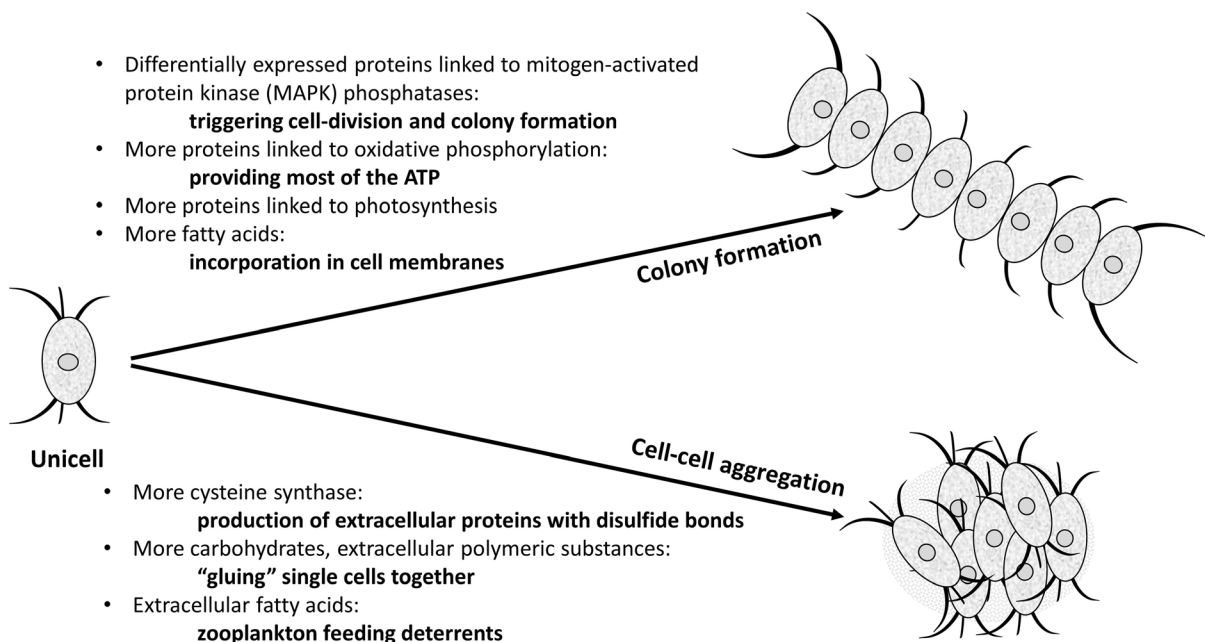
The molecular processes behind the response of *D. subspicatus* to produce colonies and form aggregates as an adaptive response to *Daphnia* cues have been unraveled recently (Roccuzzo et al., 2020). These authors identified a role of the mitogen-activated protein kinase (MAPK) phosphatases signaling pathway in the response of *D. subspicatus* to *Daphnia* infochemicals. MAPK is triggering cell division and colony formation (Fig. 2). Investments into fatty acid metabolism were also needed for colony formation. Cell–cell adhesion was stimulated by the export of carbohydrates and proteins with disulfide bonds in the extracellular polymeric substances matrix, which also contained fatty acids, a known class of feeding deterrents (Roccuzzo et al., 2020; Fig. 2).

Meanwhile, colony formation in response to zooplankton has been observed in several freshwater green algae, such as *Actinastrum*, *Chlamydomonas*, *Chlorella*, *Coelastrum*, *Desmodesmus*, and *Scenedesmus* (Boraas et al., 1998; Van Donk et al., 1999; Yasumoto et al., 2000; Lürling, 2003a; Fisher et al., 2016), but also in the cyanobacteria *Microcystis* (e.g., Yang & Kong, 2012) and *Aphanizomenon* (Lynch, 1980), and in the marine haptophyte *Phaeocystis* (Jakobsen & Tang, 2002; Tang et al., 2008). Hence, induced colony formation seems widespread in

phytoplankton. As indicated before, a change in morphological appearance, such as unicellular or colonial, may be a result of both phenotypic plasticity or rapid evolution. For instance, the colonial appearance of *C. vulgaris* in presence of the phagotrophic flagellate predator *Ochromonas* (Boraas et al., 1998) or when exposed to the rotifer *Brachionus*, was caused by rapid evolution. Intriguing is that certain species, such as the green alga *Chlamydomonas reinhardtii* P.A. Dangeard, may form either inducible defensive colonies (palmelloids) against rotifer grazing (Lürling & Beekman, 2006), or heritable constitutive palmelloids (Becks et al., 2010). Both rapid evolution and phenotypic plasticity occur because of the trade-off between phytoplankton competitive abilities and defenses against grazing. Those adaptive trait changes in prey organisms have the potential to influence population and community dynamics.

Consequences of phytoplankton defenses for population and community dynamics

In a scenario where grazers and undefended algae are co-cultured, strong population fluctuations will occur. First, due to high phytoplankton growth rates,


Fig. 2 Overview of the molecular processes in two anti-grazer defense responses: colony formation and cell–cell adhesion: in the green alga *Desmodesmus subspicatus* (cf. Roccuzzo et al., 2020)

phytoplankton biomass will strongly increase, but as they are heavily preyed upon, it will be followed by a strong increase in the grazer leading to high grazer densities and low phytoplankton biomass (Fig. 3A). Generally, grazer (predator) oscillations lag behind phytoplankton (prey) oscillations by a quarter of the period (Cortez, 2011). A fixed defense in phytoplankton may reduce the oscillations, or when the phytoplankton cells become virtually inedible, the grazer population may collapse (Fig. 3B). In case of fast, inducible defenses, theory predicts that they promote stability in the phytoplankton–grazer system (Fig. 3C; Cortez, 2011). In contrast, rapid evolution, or quickly evolving traits can desynchronize cycles and increase the lag between the phytoplankton and grazer

oscillations (Fig. 3D; Cortez, 2011). Indeed, all such patterns have been observed in experiments (Yoshida et al., 2003, 2004, 2007; Verschoor et al., 2004; Lürling et al., 2005; Lürling & Beekman, 2006; Meyer et al., 2006; Van der Stap et al., 2006, 2009; Becks et al., 2010; Kasada et al., 2014).

In experiments in which an undefended strain of *D. subspicatus* was co-cultured with the rotifer *Brachionus calyciflorus* Pallas, strong populations fluctuations occurred, but those fluctuations were absent in co-cultures with either inducible defended *Scenedesmus obliquus* (Turpin) Kützing or permanently defended *Desmodesmus quadricauda* (Van der Stap et al., 2006). The rotifer went extinct in all replicates with large permanently defended *D. quadricauda*
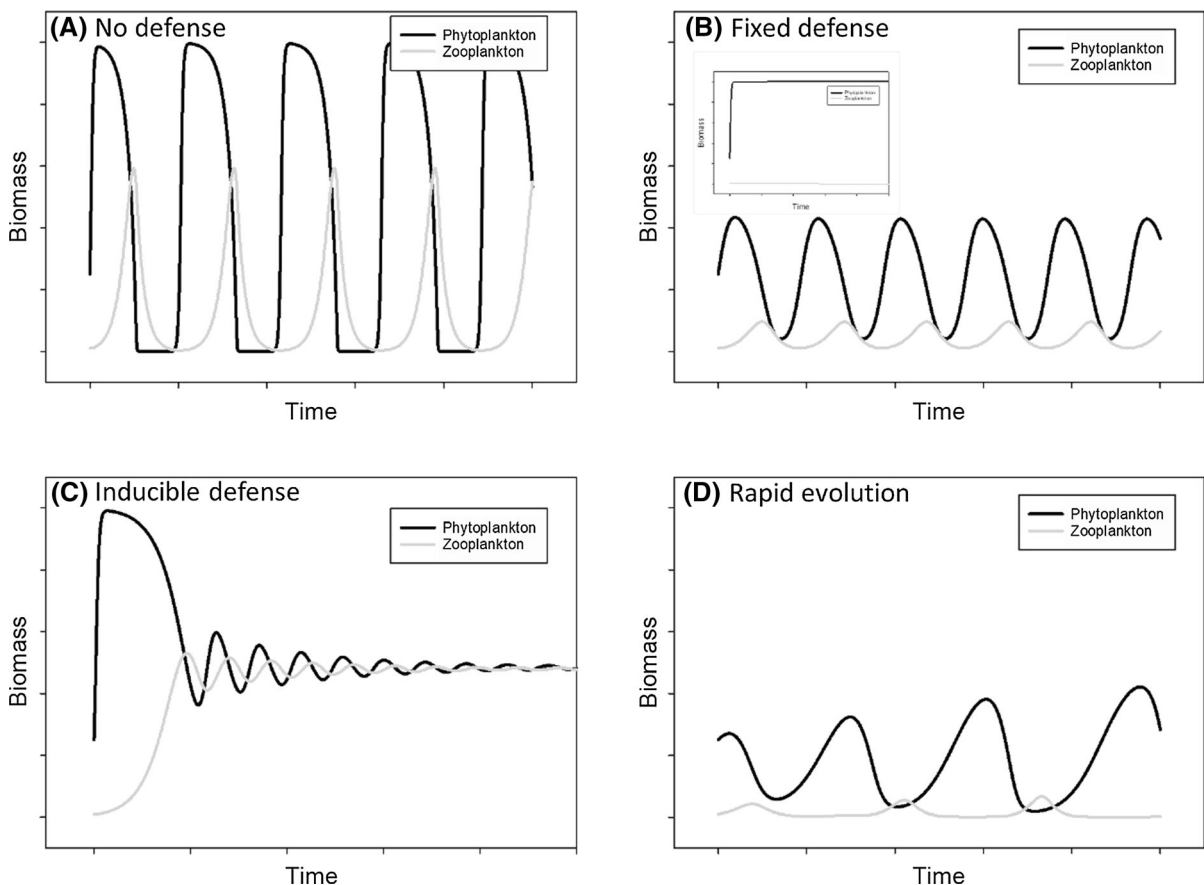
Fig. 3 Theoretical predator–prey cycles in co-cultures of a grazer (for instance the rotifer *Brachionus*) with undefended phytoplankton (e.g., *Selenastrum capricornutum* Printz; Panel **A**), with permanent defended phytoplankton (e.g., *Desmodesmus quadricauda*; Panel **B**)—the inset reflects a condition with completely inedible phytoplankton causing extinction of

the grazer, with inducible defended phytoplankton (e.g., *Scenedesmus obliquus*, *Chlamydomonas reinhardtii*; Panel **C**), and rapidly evolving phytoplankton (e.g., *Chlorella vulgaris*, *Chlamydomonas reinhardtii*; Panel **D**). Based on chemostat studies and modeling studies (see text)

(Van der Stap et al., 2006). In chemostat systems with undefended *Desmodesmus bicellularis* (Chodat) S.S. An, T. Friedl & E. Hegewald and rotifer *Brachionus calyciflorus* strong population fluctuations that spanned several orders of magnitude were observed, while these were strongly dampened when *Brachionus* was co-cultured with the inducible defended *S. obliquus* (Verschoor et al., 2004). The stabilization also occurred when the experiment was run with tritrophic food chains including the predator *Asplanchna* (Verschoor et al., 2004). Stabilization of intrinsic oscillations was also observed in other *Brachionus–Scenedesmus* systems, where the induced defense in *S. obliquus* resulted in more algal biomass and reduced zooplankton growth (Lürling et al., 2005). A similar result was obtained with the green alga *Chlamydomonas reinhardtii* that formed defensive palmelloid colonies in the presence of rotifers (Lürling & Beekman, 2006; Becks et al., 2010). In chemostats with permanently defended *Desmodesmus quadricauda*, the rotifer densities remained very low regardless dilution rate, while these were much higher when grown with inducible defended *Scenedesmus obliquus* (Van der Stap et al., 2009). In those systems, the phytoplankton–rotifer dynamics did not follow expected limit cycles and phase shift between phytoplankton and rotifer oscillations (Van der Stap et al., 2009). The latter might point towards 'cryptic cycles' that may occur when phytoplankton cells vary genetically for defense traits, which are effective, but not costly (Yoshida et al., 2007).

Single-clone cultures of *Chlorella vulgaris* (without genetic variability) grown together with *Brachionus* produced typical short-cycle oscillations with quarter-period phase lags, whereas multi-clonal *C. vulgaris* (with genetic variability) produced long cycles with phytoplankton and rotifer densities nearly out of phase, as theoretically predicted (Yoshida et al., 2003). *C. vulgaris* cultivated together with rotifers became heritably smaller and competitively inferior relative to *C. vulgaris* grown in the absence of rotifers. Hence, there was a trade-off between grazing resistance and competitive ability among the *C. vulgaris* clones (Yoshida et al., 2003). Meyer et al. (2006) further elaborated on this using the clonal pair UTEX265 (defense) and UTEX396 (undefended) that possessed a trade-off between competitive ability and resistance to grazing. Using an allele-specific quantitative PCR technique these authors showed that the

superior competitor UTEX396 dominated initially, but as rotifer densities increased, the grazing-resistant clone UTEX265 became dominant. These two clones have a relatively "cheap defense" trade-off, which means that the defense is effective, but the loss in competitive capacity, expressed in growth rate, is relatively small (Kasada et al., 2014). In contrast, the clones UTEX1809 (undefended) and UTEX1811 (defended) have a relatively "costly defense" trade-off, which means the defense is not very effective despite a strong reduction in growth rate (Kasada et al., 2014). When mixtures of these two pairs of clones were co-cultured with *Brachionus*, the relatively high cost of a weak defense favored the undefended clone in the UTEX1809/1811 pair, whereas the defended clone became dominant, or both clones coexisted, for the cheap defense trade-off pair UTEX265/396 (Kasada et al., 2014). Based on the trade-offs between phytoplankton growth and defense against grazing, Yamamichi & Miner (2015) illustrated in a mathematical model that adaptive evolution of the prey may rescue the predator from extinction.

Despite results from chemostats and models may be difficult to extrapolate to aquatic ecosystems, because most natural planktic systems are not steady state systems (Harris, 1986), they are powerful to yield insight in mechanisms that may steer population dynamics and species interactions and can be used to evaluate observed patterns. In temperate freshwater lakes, a typical sequence of events may be noted, as exemplified from Lake Gødstrup (Denmark) that showed a spring bloom of diatoms was grazed down effectively by *Daphnia* where after grazing-resistant *Aphanizomenon* flourished until summer storms introduced nutrients that promoted fast-growing, small-sized cryptomonads (Jacobsen & Simonsen, 1993). Likewise, in Lake Constance (Germany) highly repetitive annual patterns of fast-growing, edible phytoplankton in spring is followed by strong grazing pressure and subsequent promotion of defended phytoplankton (Ehrlich & Gaedke, 2020; Ehrlich et al., 2020). The sequence of events is summarized in the PEG model, which reflects biomass patterns of phyto- and zooplankton, but does not zoom in on species replacements (Sommer et al., 2012). Evidently, mixing, competition, grazing by protists and metazoan zooplankton, and parasitism will have an impact on phytoplankton species composition and on the genetic composition of species.

In the example of Lake Constance, the spring dominance of fast-growing, well-edible phytoplankton species was possible because the grazer community was forced towards small-bodied protist grazers (mostly ciliates) that were controlled by small carnivores (cyclopoid copepods). When large-bodied grazers (*Daphnia*) appeared the edible phytoplankton community was grazed down rapidly favoring grazing-resistant phytoplankton species, while the carnivore community shifted towards larger carnivorous cladocerans reducing the grazers (Ehrlich & Gaedke, 2020). This study demonstrated that the trait dynamics were 'primarily endogenously driven by competition and trophic interactions' (Ehrlich & Gaedke, 2020). It underpins that the CSR model, which is based on the physical structure of the environment (Reynolds, 1993; Smayda & Reynolds, 2001), should be extended with grazing pressure (Fig. 4).
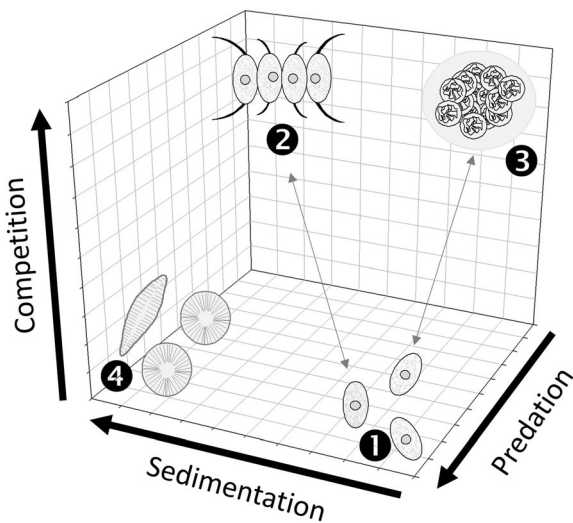
Fig. 4 Three selection forces operating on phytoplankton in the pelagic. Predation is generally largest on small-sized phytoplankton. Sedimentation is usually highest for large cells, colonies, and aggregates that have no buoyancy control, and small cells that have rather high specific mass (diatoms). Competition is mostly strongest on larger cells and colonies that have a less favorable surface-to-volume ratio, and thus lower growth rates. Consequently, small-celled, fast-growing cells suffer most from predation (1) but have in general low sinking loss, and because of favorable surface-to-volume ratio generally experiences less competition (4). Diatoms can only prevail in a mixed water column (4). Large, sometimes armored cells or colonies have lower growth rates, experience higher sinking rates, but are protected against grazing (2). Some of the slow-growing colonies or filaments possess the capacity of buoyancy control. The gray arrows indicate potential phenotypic plasticity

Co-evolution of zooplankton grazers to sizes that would allow them to ingest even the largest phytoplankton cells, colonies, and aggregates is strongly constrained as zooplankton themselves are on the menu of visually hunting predators (Lass & Spaak, 2003; Sommer et al., 2012). Even short-term fish predation events may lead to longer-term reduction in large-bodied grazers (Ersoy et al., 2019). Visually, hunting fish may induce several defenses in zooplankton too, such as *Daphnia* becoming smaller (Lass & Spaak, 2003), where smaller animals also have a lower maximum size of particles they can ingest (Burns, 1968).

Concluding remarks

In the pelagic arena, grazing is one of the most important losses of phytoplankton biomass and thus a very strong selection force for traits that lower grazing losses (Sterner, 1989). It is not surprising that various constitutive or inducible defense strategies in phytoplankton have evolved—avoiding ingestion, avoiding digestion, deterring grazers or even killing zooplankton (Fig. 1). However, cells are also challenged to remain suspended and to cope with competitors. There is ample evidence that the conflicting allometries of selection pressures (Lehman, 1988)—competition that favors small, fast-growing cells with high nutrient uptake and low sinking losses, and grazing that favors large, or defended, slower growing organisms with higher sinking loss—drive the size and shape diversity of phytoplankton (Acevedo-Trejos et al., 2018). It is the whole suite of environmental factors that constrains survival and growth of phytoplankton and confronts cells with trade-offs in how to respond to the constraints (Tilman, 1990).

These trade-offs form the basis for different strategies, which are adopted by representatives of all taxonomic groups. Small size, competitively superior phytoplankton of less than 2 μm is, for example, found in diatoms (e.g., *Discostella*, *Cyclotella*), in green algae (*Choricystis*, *Pseudodictyosphaerium*), in cyanobacteria (*Prochlorococcus*, *Synechococcus*), but these groups also include very large, grazing-resistant phytoplankton of more than 1 mm in size (diatom *Ethmodiscus*, green alga *Volvox*, cyanobacterium *Microcystis*). These morphologies determine how the organisms cope with nutrient acquisition,

sinking and grazing, which formed the basis for the functional group concept (Reynolds et al., 2002). In addition to being very different and avoiding competition, being sufficiently similar has also been proposed as a feasible strategy (Scheffer & van Nes, 2006), which finds support in the outcome of a recent competition experiment (Burson et al., 2018).

Based on traits, Ehrlich et al. (2020) clustered 199 different phytoplankton species in Lake Constance into 36 dominant morphotypes and found a clear trade-off between defense and growth rate. Using 21 years of measurements in Lake Constance, a concave defense–growth trade-off was found, in which seasonally increasing grazing pressure shifted the phytoplankton community to higher defense levels at the cost of lower growth rates (Ehrlich et al., 2020). Hence, these authors showed that defense and growth rate represent key traits of the phytoplankton in Lake Constance with changes that were fast enough to prevent competitive exclusion. Using an interspecific defense–growth trade-off, Ehrlich et al. (2020) increased the understanding of seasonal shifts in the species composition of the phytoplankton community. Not only insight in species replacements, but also in genetic shifts within species is needed. While the defense–growth trade-off might be helpful in understanding the development of a cyanobacterial bloom in response to grazing pressure, it will not elucidate whether the bloom will be dominated by toxic or non-toxic genotypes. Future research could be directed into intraspecific, genotype variability along the trade-off curve between competitive ability and defense against grazers.

Resuming, in the pelagic one could imagine adaptive trade-offs between nutrient acquisition (competition), remaining suspended (sedimentation) and grazing resistance (predation) that generate the dynamic phytoplankton composition (Fig. 4). In that view, phytoplankton communities not only "...should be regarded not as the menu, but as the unserved portion of the meal" (Reynolds, 1980), but, besides unserved, also as the mostly inedible left-overs of the meal. Grazing resistance in phytoplankton seems a widespread phenomenon and a key trait in shaping phytoplankton community diversity and species replacements.

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