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Intraspecific genetic diversity and coexistence in phytoplankton populations

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Abstract

The past two decades have seen a drastic increase in the availability and use of genetic techniques to study phytoplankton communities. As a result, it is now well documented that phytoplankton populations are genetically diverse, despite predominantly asexual reproduction and minute morphological variation. Genetic variation can lead to variation also in phenotype, and some traits vary more among genotypes than between species. Trait-based approaches tackle this by focusing on traits rather than on species. However, trait-based models often have difficulty predicting and explaining the huge trait-diversity among coexisting individuals competing for the same few resources. Thus, we ask the question: How do hundreds, if not thousands, of genotypes coexist in a highly competitive environment? In this review, we gather information on genetic and phenotypic variations in coexisting genotypes and elaborate on three mechanisms by which broad intraspecific genetic diversity may be possible: neutral mutations, environmental fluctuations, and trade-offs among traits. These have all been applied on an interspecies level, and we discuss their use also among coexisting genotypes. We find that genetic diversity to be almost exclusively studied in blooming species and that clonal diversity frequently measure above 0.95 (i.e., 95% of individuals sampled are genetically different). Genetic diversity seems stable throughout blooms, suggesting that competitive exclusion is low or that new genetic material is frequently being introduced into populations. Further, we find high intraspecific trait-variation in several key traits among coexisting strains but also that trait-variation is often neglected in studies on phytoplankton, making coexistence difficult to predict.

Phytoplankton diversity stabilizes ecosystems and generally determine the efficiency of many aquatic ecosystem processes such as primary production (Vallina et al. 2014), the transfer of energy through the trophic food web (Striebel et al. 2012), and carbon sequestration through the biological pump (Duffy and Stachowicz 2006; Tréguer et al. 2018). Since the seminal work of Hutchinson's "Paradox of the plankton" (1961), researchers have attempted to answer the question as to how phytoplankton communities maintain broad species diversity despite there being such few limiting

resources (Hardin 1960). There are now several mechanisms identified by which such diversity becomes possible, including environmental fluctuations (Hutchinson 1961), contemporaneous disequilibrium (Richerson et al. 1970), chaos (Huisman and Weissing 1999), phenotypic heterogeneity (Menden-Deuer et al. 2021), and trade-offs (Winter et al. 2010). These mechanisms have since been successfully implemented in models and theoretical considerations seeking to understand marine microbial community dynamics (Vallina et al. 2014; Acevedo-Trejos et al. 2018; Våge et al. 2018; Cadier et al. 2019; Dutkiewicz et al. 2020; Behrenfeld et al. 2021). Thus, the ultimate explanation for the paradox is likely not a single mechanism, but a combination of several and perhaps a paradox in itself (Roy and Chattopadhyay 2007; Wilson 2011; Record et al. 2014).

However, phytoplankton communities are diverse not only in terms of species, but also in terms of within-species variability. The past two decades have seen a drastic increase in the availability and use of genetic techniques to study phytoplankton populations (Rengefors et al. 2017; Rynearson et al. 2022). As a result, it is now well documented that phytoplankton populations are genetically diverse (de Vargas et al. 2015; Rengefors et al. 2017). Single-cell isolations from

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phytoplankton populations of various species have revealed high genetic and phenotypic diversity (Alpermann et al. 2010; Dia et al. 2014; Kashtan et al. 2014; Tammilehto et al. 2017), with blooms of some species estimated to contain thousands of genetically distinct lineages (Ryneckson and Armbrust 2005; Sassenhagen et al. 2022). Such broad genetic diversity may be essential to the evolutionary and adaptive ability of phytoplankton populations (Barrett and Schluter 2008; Godhe and Ryneckson 2017; Wolf et al. 2018; Ajani et al. 2021), but similar to the origins of Hutchinson's paradox we are still lacking an understanding of how it is maintained.

Genetic variation within a population may be maintained by at least three mechanisms: first, the genetic variation (i.e., the mutations) is neutral with no effect on the phenotype and, hence, the performance of the cells. Second, genetic variation leads to phenotypic (trait) variation and is maintained due to environmental fluctuations and the consequent lack of steady state in population sizes. Finally, genotypic variation leads to variation in several traits and is maintained through trade-offs between traits. That is, a genotype that performs above average in one trait (e.g., competitive ability) does this at the cost of a poorer performance with respect to another trait (e.g., defense), and two (or more) genotypes can therefore co-exist while competing for the same resource. This latter mechanism may in fact lead to very high genotypic variation within microbial populations (Thingstad and Lignell 1997; Winter et al. 2010).

While many studies have demonstrated that genetic variation is common within phytoplankton populations, there are only a few that have examined the potential phenotypic implications of genetic variation within a population. In this paper, we review information on intraspecific genetic and trait variations in coexisting phytoplankton strains. We have three distinct goals: first, we compile observations where genotypic diversity has been examined among coexisting strains; next, we explore to what extent genotypic variation leads to trait (phenotypic) variation; finally, we discuss how these strains can coexist.

Data collection

We collected data on clonal diversity (i.e., the number of distinct genotypes divided by the number of clones isolated) and intraspecific trait variation using Web of Science or Google Scholar searches. Data on clonal diversity were acquired from past compilations (Godhe and Ryneckson 2017) and by searching using the terms “phytoplankton clonal diversity” or “phytoplankton genetic diversity.” To find publications on intraspecific trait variation, we used combinations of the terms “phytoplankton,” “intraspecific variation,” and “intraspecific trait variation.” A coefficient of variation (CV, %) was calculated for trait values among strains from the same population. We excluded one CV that was based on a negative mean. For both clonal and trait diversities, we included only strains that

were coexisting at the time of isolation, and we thus excluded studies where strains originated from different geographical locations or were isolated from different populations, from sediments, or where this information was not available. We chose not to include studies that had used strains that had been acquired from culture collections with the exception of Brand et al. (1981), where strains were used within a reasonable time after isolation. Clonal diversity and trait data values were extracted from the text, tables, or complementary data files, digitized from graphs, or acquired directly from the authors.

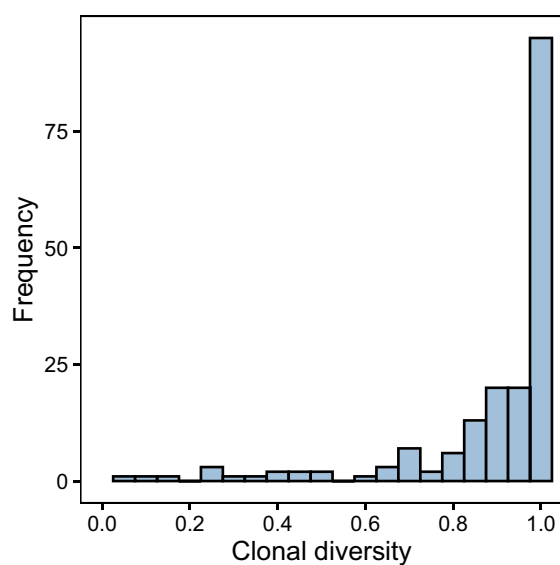
Genetic diversity of phytoplankton populations

We found 14 studies that reported clonal diversity and that fit our criteria of isolates (i.e., strains) originating from the same population and sampling occasion (Table 1). These 14 studies include between 2 and 11 isolates from different phytoplankton populations. The number of isolates genotyped from each population or sample did not influence clonal diversity (Supporting Information Fig. S1); thus, we did not exclude populations that included only a few strains.

Apparent from the collected data is that genetic diversity is almost exclusively studied in blooming species. During blooming, phytoplankton mainly reproduce asexually. Coupled with low morphological (i.e., shape and overall cell structure) variation among individuals of the same species and the fact that blooms are often dominated by one or few taxa, low genetic diversity may be expected. On the contrary, almost all studies reported intermediate to high clonal diversity, that is, between 0.42 and 1.00 (Table 1; Fig. 1), with the majority (105 out of 181 samples or populations) reporting clonal diversity > 0.95 (Fig. 1). The sole exception of such clonal diversity is found during an autumn bloom of the diatom *Pseudo-nitzschia multistrata* in the Gulf of Naples in 2013. Here, Ruggiero et al. (2018) found clonal diversity as low as 0.06 during a single sampling occasion, and 0.18 throughout the entire bloom. High clonal diversity is found in both freshwater and marine environments and across several groups of phytoplankton (Table 1). How well these data represent the actual in situ population from which they are isolated is difficult to answer. Generally, individual cells or colonies are isolated via pipette, and cultures (strains) are established from these isolates. A common issue is that there can be high variability in the fraction of isolates that survive and can actually be cultured, with anything from 0% to 100% of isolates surviving the process (e.g., Wilson et al. 2005; Tammilehto et al. 2017). Hence, a form of selection occurs, and genetic (and phenotypic) variation may end up lost. In the 14 studies compiled for Table 1, we found no statistical relationship between clonal diversity and isolate survival in the studies that reported survival for the individual sampling dates (Supporting Information Fig. S1), and thus we decided not to exclude any data based on this.

Table 1. Clonal diversity within phytoplankton populations.

Environment	Group	Species	Clonal diversity	Isolates genotyped	Reference
Freshwater	Ochrophyte	<i>Gonyostmum semen</i>	1.00	4–20	Lebret et al. (2012)
Freshwater	Cyanobacteria	<i>Microcystis aeruginosa</i>	0.42–1.00	2–12	Wilson et al. (2006)
Marine	Diatom	<i>Ditylum brightwellii</i>	0.96	24	Rynearson and Armbrust (2000)
Marine	Diatom	<i>D. brightwellii</i>	0.87–1.00	20–76	Rynearson and Armbrust (2005)
Marine	Diatom	<i>D. brightwellii</i>	0.82–1.00	2–51	Rynearson et al. (2006)
Marine	Diatom	<i>Pseudo-nitzschia multistrata</i>	0.46–1.00	7–57	Tesson et al. (2014)
Marine	Diatom	<i>P. multistrata</i>	0.06–1.00	2–61	Ruggiero et al. (2018)
Marine	Diatom	<i>Pseudo-nitzschia pungens</i>	0.89–1.00	3–50	Casteleyn et al. (2009)
Marine	Diatom	<i>Thalassiosira gravida</i>	0.91–1.00	20–116	Chen and Rynearson (2016)
Marine	Diatom	<i>Thalassiosira rotula</i>	0.98–1.00	8–96	Whittaker and Rynearson (2017)
Marine	Dinoflagellate	<i>Alexandrium fundyense</i>	0.83–0.92	12–42	Erdner et al. (2011)
Marine	Dinoflagellate	<i>A. fundyense</i>	0.47–0.97	17–77	Richlen et al. (2012)
Marine	Dinoflagellate	<i>Alexandrium minutum</i>	1.00	9–40	Dia et al. (2014)
Marine	Dinoflagellate	<i>Alexandrium tamarense</i>	1.00	77	Alpermann et al. (2010)

**Fig. 1.** Frequency distribution of clonal diversity within 181 samples or populations of phytoplankton. Data from various sources (see Table 1).

Temporal variation in bloom diversity

One could imagine that blooms are most diverse in their early phase when cell densities are low and there is less competition for space and resources. As the bloom progresses, theory predicts that the most fit genotype should become dominant and hence that the genetic diversity decreases. On the contrary, genetic diversity seems stable throughout blooms. In a bloom of the ochrophyte *Gonyostmum semen* in a southern Swedish lake, Lebret et al. (2012) even found that genetic diversity increased during the ~ 5-month long blooming event. This could be due to constant reseeding of cysts or resting spores from sediments (Lebret et al. 2012). Indeed, studies of isolates from sediments have found them as

genetically diverse as the pelagic population (Godhe and Härnström 2010; Jerney et al. 2022). Thus, if intense competition in the pelagic is constantly leaving strains outcompeted, the introduction of new genetic material from the deep could maintain genetic diversity. Biotic and abiotic barriers can separate genetically distinct populations (Casteleyn et al. 2010; Dia et al. 2014; Godhe et al. 2016), even at the same geographical location (Rynearson et al. 2006), but gene flow between populations is known to occur (Godhe et al. 2013, 2016). Chen and Rynearson (2016) found four co-existing populations of the diatom *Thalassiosira gravida* during a spring bloom in the North Atlantic. They suggested that this could, among other things, be due to ocean current transport from other regions.

Available field data support the notion of some sort of genotypic succession throughout and between blooms of the same species. Thus, Rynearson and Armbrust (2005) sampled only 11% of 607 clonal lineages more than once over 11 sampling occasions throughout a bloom of the diatom *Ditylum brightwellii* in Pudget Sound, Washington, and only 4% were sampled three or more times.

Phenotypic diversity among coexisting phytoplankton strains

Studies have now shown that populations of phytoplankton are distinctly different not only in their genotypes, but also in their physiology. As such, the genetic difference found within phytoplankton populations may also result in phenotypic differences, despite being subjected to the same environmental conditions. Larry E. Brand (e.g., Brand 1981, 1985; Brand et al. 1981) pioneered such experiments, often using a multitude of strains isolated from the same locations. In experiments with isolates from populations of the diatom *D. brightwellii*, Rynearson and Armbrust (2004) suggested that

strain specific growth-rate differences within two populations were likely due to genetic differences rather than morphological (i.e., cell size), and found that no isolate consistently grew slower or faster at all three different levels of light. Similar phenotypic variation among coexisting strains have been demonstrated in other diatoms (Ajani et al. 2021; Olesen et al. 2022) and other types of bloom-forming phytoplankton, such as dinoflagellates (Calbet et al. 2011; Brandenburg et al. 2018) and cyanobacteria (Wilson et al. 2005; Willis et al. 2016). Thus, despite belonging to the same species and population, different strains may vary in their properties, and this may influence the dynamics of ecosystems.

One way of documenting phenotypic diversity is to quantify how different genotypes may vary in their expression of traits, and genotypic diversity has been found to be closely associated with differences also in phenotype (Rynearson and Armbrust 2004; Gsell et al. 2012). A trait is a measurable feature of an organism that largely governs how it interacts with its environment (McGill et al. 2006). Trait-based approaches were initially used in terrestrial ecology, but has in the past two decades been applied more frequently to describe also aquatic ecosystems (Litchman et al. 2007, 2013; Kiørboe et al. 2018; Beukhof et al. 2019). In phytoplankton, the key traits (i.e., the traits that explain most of an organism's fitness) are cell size, growth, resource acquisition, and defense (Litchman and Klausmeier 2008; Kiørboe et al. 2018). These data are now available for a multitude of phytoplankton species (e.g., Edwards et al. 2012; Marañón 2015; Pančić and Kiørboe 2018), but we are still lacking in how these traits may vary within species despite the important role of intraspecific variation in community ecology (Vellend 2006; Bolnick et al. 2011; Violle et al. 2012). Trait-based approaches tackle trait variation by focusing on traits rather than on species but still have difficulties predicting and explaining the huge trait-diversity among coexisting individuals competing for the same limiting resources. Thus, phytoplankton traits are often analyzed in terms of species mean values, despite the apparent issues in doing so (Ives et al. 2007; Xiao et al. 2017; Fontana et al. 2018). Recent analyses have shown that intraspecific variation has considerable effects on ecosystem dynamics (Siefert 2015; Hart et al. 2016; Des Roches et al. 2017), and particularly so for primary producers (Raffard et al. 2019). Populations with high intraspecific diversity are generally more robust to disturbance and global change (Mimura et al. 2017). Variations in traits within a species can affect reproductive success, resource acquisition, and interactions with other species, all of which influence the structure and function of ecosystems. However, many such analyses and subsequent theoretical considerations for primary producers often have their roots in terrestrial plant data (Hughes et al. 2008; Raffard et al. 2019), although intraspecific variation in phytoplankton are now starting to get similar recognition (Godhe and Rynearson 2017; Menden-Deuer et al. 2021; Litchman 2022). Thus, if we are to fully understand the impact intraspecific

variation in phytoplankton, whether from an evolutionary or an ecosystem viewpoint, we need first to increase our efforts in documenting it.

Intraspecific variation in the expression of traits has been found in several types and species of phytoplankton, but many, if not most, have focused on strains that originate from different geographical locations, were isolated at different times, or were acquired from culture collections where similar growth conditions over time may influence trait expression (Berge et al. 2012). Cultures that are kept in stable and similar conditions may lose intraspecific differences and cause changes in the expression of certain traits (Lakeman et al. 2009). Although these changes can be minimized (e.g., through cryopreservation), there are a multitude of examples of how phytoplankton changes over time in culture. For example, cultures may over time lose mixotrophy ability (Blossom and Hansen 2021), phototaxis (Moldrup et al. 2013), change morphology (Willis et al. 2022), or possibly evolve different competitive abilities depending on the conditions to which they are exposed (Bernhardt et al. 2020). Berge et al. (2012) found that strains of the dinoflagellate *Heterocapsa triquetra* that had been kept in culture for more than 10 yr grew slower and had higher tolerance to pH compared to strains that had been in culture for less than 10 yr. Lack of exposure to predation may also influence traits. Thus, Lindström et al. (2017) found that a dinoflagellate (*Lingulodinium polyedra*) had lost its bioluminescent capabilities after years in culture. Its ability to flash, however, was restored after exposure to predatory copepod cues. Martins et al. (2004) found that a clonal isolate of the dinoflagellate *Alexandrium lusitanicum* had lost its ability to produce toxins. Interestingly, a subculture of the same isolate sent to another laboratory still produced the toxins. These changes are of course also possible in self-isolated cultures (as we compare in this paper), but we find that most studies (for where this information is available) quantify traits within a year of isolation (see Supporting Information Appendices A1–A7). The main focus and use of many studies comparing traits among strains are rather how these are adapted to their specific locations (Sjöqvist et al. 2015; Sildever et al. 2016; Sefbom et al. 2022), their invasive capabilities (Thomas and Litchman 2016), how these environments may have influenced their evolution (Lakeman et al. 2009; Bernhardt et al. 2020), or how they may be affected by a changing climate (Kremp et al. 2012; Ribeiro et al. 2013; Matson et al. 2016; Wolf et al. 2018; Bishop et al. 2022), and not how strains coexist. Consequently, studies exemplifying trait-variation among coexisting strains originating from the same population or bloom are dramatically fewer.

In our search of the literature, we found 22 studies that fit our selection criteria for trait diversity among coexisting strains of the same species (Fig. 2). Of these, 18 were from marine ecosystems and four from freshwater. The majority (11) had quantified only 1 trait (Fig. 2a), and on average only 2.68 traits were quantified. The 22 studies included isolates from 58 different populations (Fig. 2b).

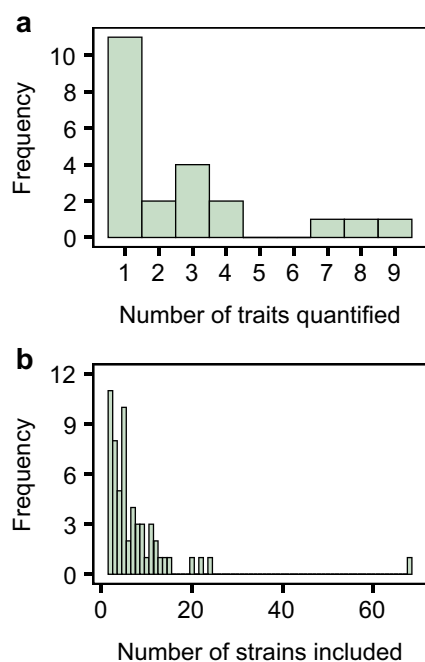


Fig. 2. Frequency distributions of the number of traits quantified in the 22 studies that fit our selection criteria (**a**), and the number of strains included from each population in these studies (**b**).

The average number of strains included from each separate population was 7.6 (Fig. 2b). More than half of the sampled populations included five strains or less. Growth rate was the most quantified trait (18 studies), followed by cellular toxin content (9), and cell size (6).

Among the 58 populations studied we found widespread variation among traits that closely relate to phytoplankton fitness (Fig. 3), that is, growth, cell size, resource acquisition, and defense (i.e., toxicity, colony size). Growth rate was the trait with the lowest average variation within populations (i.e., among coexisting strains), $24.6\% \pm 34.7\%$ (mean \pm SD, $n = 122$, Supporting Information Appendix A1), but also had the largest range (CV between 1% and 220%) (Fig. 3a). Cell size varied slightly more, $32.7\% \pm 24.0\%$ ($n = 16$, Supporting Information Appendix A2). Toxicity had among the highest variation, $59.1\% \pm 38.9\%$ and $81.7\% \pm 32.5\%$ for intracellular ($n = 14$, Supporting Information Appendix A3) and extracellular ($n = 8$, Supporting Information Appendix A4) toxicities, respectively (Fig. 3c). We also found moderate to high variation also in other key traits, such as nutrient affinity ($43.1\% \pm 20.8\%$, $n = 3$, Supporting Information Appendix A5), nutrient uptake rate ($57.8\% \pm 19.2\%$, $n = 9$, Supporting Information Appendix A6), and colony size ($30.9\% \pm 20.5\%$, $n = 7$, Supporting Information Appendix A7), although data for these traits were scarcer (Fig. 3d–f). Sample size did not significantly influence CV positively or negatively (linear regression, $R^2 = 0.0002$, $p = 0.97$; Supporting Information Fig. S2).

Means of coexistence within phytoplankton populations

From the above, it is clear that phytoplankton populations exhibit large intraspecific variation on both a genetic and phenotypic level. Understanding the mechanisms that allow for such coexistence to take place is crucial for predicting ecosystem stability and function (Litchman et al. 2007; Kiørboe et al. 2018). In this section, we will explore three mechanisms by which this may be possible: (i) neutral mutations, (ii) environmental fluctuations, and (iii) trade-offs between key traits. All of these have previously been applied on an interspecific level, and we will discuss their application also within populations. Since intraspecific trait-variation may be as large as (or even larger than) interspecies trait-variation, it is likely that the same mechanisms constraining species diversity applies also within species.

Neutral mutations

Mutations that result in phenotypic changes may be subjected to either positive or negative selection, depending on the selective pressures acting on the cell. As such, mutations that come with a fitness advantage are more likely to be accrued in the population and vice versa. However, a mutation that is not subject to natural selection is considered neutral and neither help nor harm an individual's fitness (Kimura 1983). Thus, neutral mutations can lead to the development of subpopulations (i.e., different strains within a larger population) that differ slightly in their genetic makeup, but that do not differ significantly in their fitness. Different strains can accumulate these mutations over time without advantages or disadvantages in survival and reproduction. The accumulated mutations can serve as a smorgasbord of genetic material for evolution to act upon should environmental conditions, and thus selection pressure, change (Rengefors et al. 2017). Thus, neutral mutations may become non-neutral, and the ultimate effect of a mutation on cell fitness is therefore context dependent. Our data compilation suggests that genetic variation between genotypes may become manifested in phenotypic variation. Rarely, however, do studies quantify both genetic and phenotypic variations, thus, the relationship between the two remains cryptic except in few cases (Rynerason and Armbrust 2004; Gsell et al. 2012). This relationship may perhaps be assessed as genomic resources improve (e.g., Postel et al. 2020), instead of relying on neutral markers (e.g., microsatellites)—so far almost exclusively used to determine genetic diversity—that do not provide information on functional diversity and thus what genes are under selection. This has been an issue also in phytoplankton studies focusing on local adaptation (Rengefors et al. 2017) or the effects of global change (Sjöqvist 2022). In a population of thousands of clonal lineages or more (Rynerason and Armbrust 2004), we, however, find it likely that most mutations have none or negligible

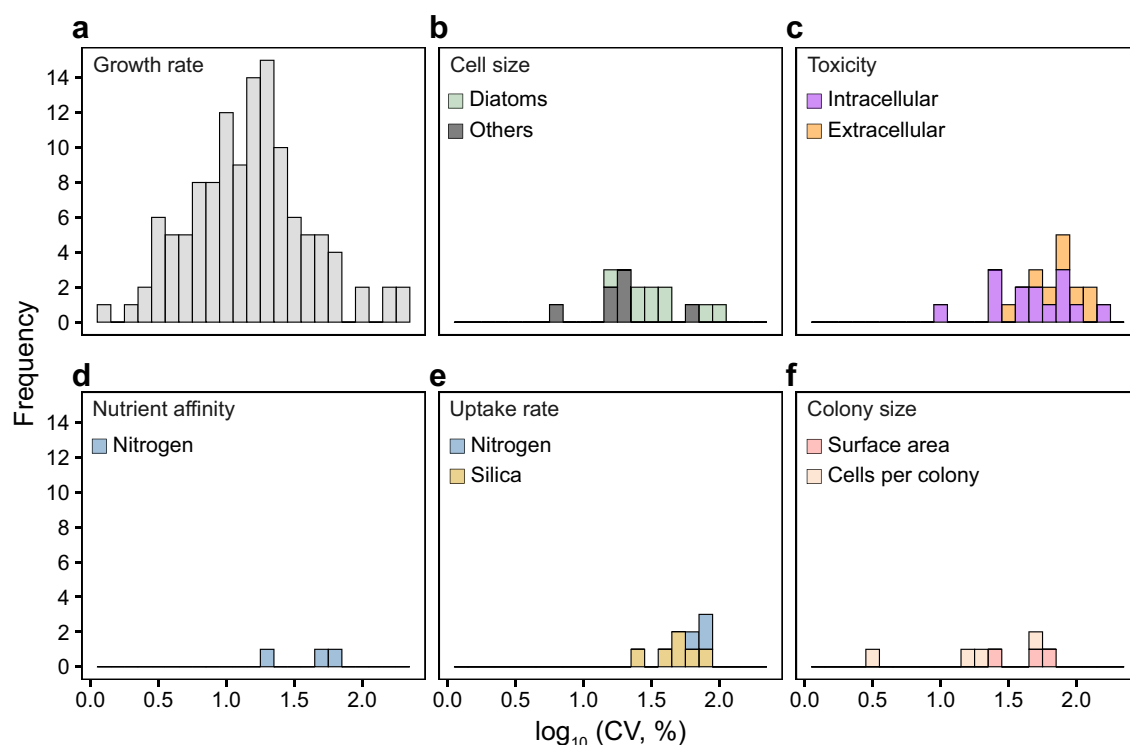


Fig. 3. Frequency distributions for intraspecific trait variation (presented as CV in %) among six traits that strongly correlate to cell fitness. Growth rates include measurements taken on the same population (set of strains) at different environmental factors, that is, temperature, light, and pH.

trait implications, thus, allowing co-existence between genetically different but physiologically identical strains.

Environmental fluctuations

The competitive exclusion principle states that, at steady state, the species (or as in our case, strain) with the best competitive ability will outcompete others (Hardin 1960; Litchman et al. 2007). It has recently been demonstrated that phenotypic heterogeneity (i.e., phenotypic variation that is not genetically based) on its own promotes co-existence in microbes (Menden-Deuer et al. 2021). Also, in reality phytoplankton communities are very seldom, if ever, at steady state: when environmental changes occur on time scales that are shorter than the population time scale, strains with different environmental adaptations to, for example, temperature (Pančić et al. 2015; Bishop et al. 2022), nutrient resources (Thessen et al. 2009), pH (Pančić et al. 2015), and light (Rynerason and Armbrust 2004) may temporarily coexist (Descamps-Julien and Gonzalez 2005). Environmental fluctuations and incomplete mixing can create temporal or spatial variations in temperature and resources, allowing coexistence through niche partitioning or patchiness (Hutchinson 1961; Richerson et al. 1970; Bracco et al. 2000). In addition, stochastic events like storms and nutrient pulses can disrupt the competitive hierarchy. In the plankton, environmental conditions change on scales from daily, throughout a bloom, to seasonally (Cloern 1996; Tiselius et al. 2016; Brandenburg et al. 2017).

This likely has implications not only for coexistence but also governs the bloom and seasonal succession of strains, although this has rarely been examined in detail. Gallagher (1982) found differences in growth rate, cellular chlorophyll *a* (Chl *a*), and carbon uptake among summer and winter populations of *Skeletonema marinoi* isolated in Narragansett Bay (Rhode Island), and suggested a cyclic form of natural selection influenced by seasonal variation to be the cause of the succession between these populations (Gallagher 1980). Rynerason et al. (2006) found that the transition between two genetically different populations of the diatom *D. brightwellii* in northwestern United States was associated with changes in solar irradiance and available silicic acid.

In addition to resources and temperature, variations in predator field may also matter. Grazers not only influence phytoplankton succession on a seasonal scale (Mariani et al. 2013), but also likely throughout a bloom since strains may vary in their response to grazers (Olesen et al. 2022). Thus, at the start of a diatom-dominated spring bloom in temperate ecosystems, the strains with high growth rates should initially dominate the biomass. As the bloom progresses, the abundance of fast-growing micrograzers increases (Tiselius and Kuylenstierna 1996) and the strains with the highest chance of success will be those forming long chains that prevent ingestion from smaller, size-limited grazers (Ryderheim et al. 2022). Toward the end of the bloom, larger grazers such

as copepods increase in numbers, and chain formation becomes obsolete (Ryderheim et al. 2022). Thus, the strains responding by breaking up chains (Bergkvist et al. 2012), increasing their stickiness, and sinking out of the photic zone away from grazing pressure will secure a large seed population for the next growth opportunity (Grønning and Kiørboe 2022). In a summer bloom of dinoflagellates, the dynamics will work differently. Here, defense may be needed for bloom initiation since grazer biomass is initially high.

Environmental fluctuations and disturbances have frequently been used as an explanation for phytoplankton composition, coexistence, and biodiversity (Hutchinson 1961; Levins 1979; Litchman and Klausmeier 2001), and likely apply also on an intraspecific level given how different strains may exhibit variation in their competitive traits and growth optima similar to, or even larger than, between species (Brand et al. 1981; Ryneerson and Armbrust 2004; Pančić et al. 2015; Bishop et al. 2022). In fact, some of the higher CVs recorded for growth rate are due to differences in thermal niche and some strains reaching zero or negative growth at different temperatures (Brand et al. 1981; Bishop et al. 2022; Supporting Information Appendix A1). However, obvious from our data collection is that studies often disregard this completely (i.e., only comparing growth at one or too few temperatures) or test too narrow a range of growth conditions for growth optima models to be accurately constructed (Collins et al. 2022). This may in fact mask potential variation, whether higher or lower, compared to if traits are quantified across numerous temperatures (Fig. 4). In addition, such growth performance curves may further vary if additional drivers (e.g., nutrients) are included (Litchman and Thomas 2023).

Trade-offs among key traits

Trade-offs may allow co-existence between species and strains (Tilman 1990, 2000). Often, trade-offs are tied to cell size (Andersen and Visser 2023). For example, smaller phytoplankton cells generally have higher specific affinities for nutrients, but at

the same time may experience increased predation pressure (Edwards et al. 2012; Pančić and Kiørboe 2018). Motile and flagellated protists may use their motility and flagella to enhance nutrient uptake, but generate fluid disturbances leading to increased mortality risk (Nielsen and Kiørboe 2021). Thus, the “currency” of trade-offs often manifests as growth and mortality rates (Kiørboe et al. 2018). As such, the perhaps most prominent trade-off in ecology is that between growth and avoiding predation, that is, defense (Kiørboe et al. 2018; Pančić and Kiørboe 2018). Predation is the major source of mortality for phytoplankton (Calbet and Landry 2004; Suttle 2007), and phytoplankton utilize a wide variety of strategies to negate this. The identification and quantification of defense trade-offs in phytoplankton have received increasing attention in recent years (e.g., Wang et al. 2015; Zhu et al. 2016; Kapsetaki and West 2019; Ryderheim et al. 2021; Olesen et al. 2022). While established growth-defense trade-offs are scarce (Pančić and Kiørboe 2018), theory predicts that defense must come at a cost, particularly because many, if not most, phytoplankton defenses are inducible (Van Donk et al. 2011; Selander et al. 2019). Thus, evolutionary theory predicts that inducible defenses will evolve only if costs are associated with the defense (Karban 2011). The fact that defenses often are inducible adds complexity when looking for trade-offs. Thus, some defense trade-offs may not be apparent unless phytoplankton are exposed to the threat of predation (Lundholm et al. 2018; Olesen et al. 2022).

There are just a few examples of trade-offs within species, possibly because it has been examined only in few cases. Trade-offs stemming from intraspecific differences in nutrient kinetics and cell size may allow for coexistence of large and small cells also within the same species (Ward et al. 2014). Intraspecific differences in cell size may be significant, suggesting that such trade-offs should be prominent (Fig. 3b). In our trait-data compilation, traits related to defense, that is, size, toxicity, and colony size, are some of the most variable within populations (Fig. 3). Olesen et al. (2022) exposed eight

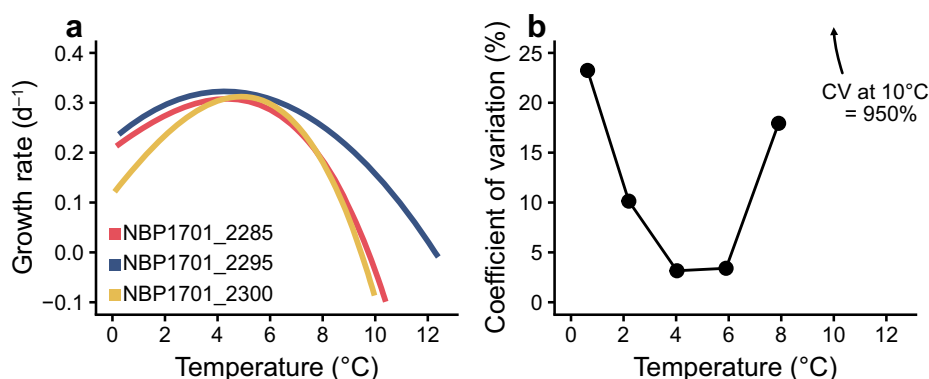


Fig. 4. Temperature performance curves (TPC) for three strains of the diatom *Actinocyclus curvatulus* isolated from the same location in the Ross Sea in Antarctica (a), and CV among strains in growth rate at six temperatures (b). Intraspecific variation in temperature dependencies may be hidden if only comparing growth at one or two temperatures compared to including more measurements over a larger temperature range. Data from Bishop et al. (2022). CVs were calculated from differences between TPCs and not the original data.

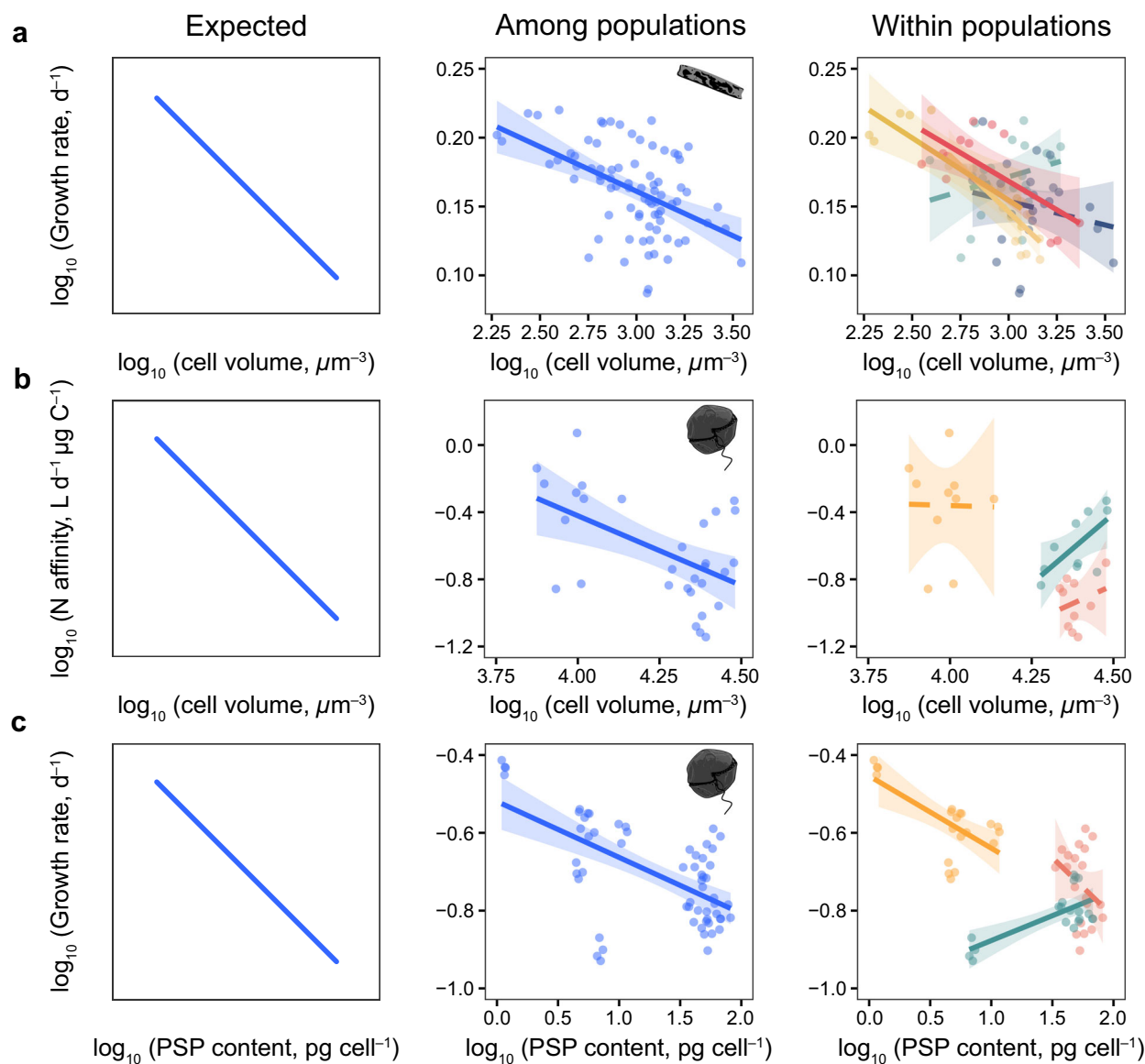


Fig. 5. Expectations vs. reality in phytoplankton trait relationships. Growth rate as a function of cell volume in the diatom *Leptocylindrus danicus* (a) from Ajani et al. (2021). Specific affinity for nitrogen as a function of cell volume for the dinoflagellate *Alexandrium ostenfeldii* (b) from Brandenburg et al. (2018). Affinity was estimated as $V_{\max}/K_{1/2}$. Growth rate as a function of cellular paralytic shellfish toxin (PSP) content in *A. ostenfeldii* (c) from Brandenburg et al. (2018). Solid and dashed lines indicate significant ($p < 0.05$) and nonsignificant ($p > 0.05$) regression fits, respectively. The different colors indicate different populations.

strains of the toxin-producing diatom *Pseudo-nitzschia seriata* to chemical cues from copepod grazers. The eight strains had very different levels of toxicity, but they all responded by increasing their toxin production. The more toxic cells were more frequently rejected by copepods; however, this led to a reduction in population growth rate (i.e., a cost). The absolute cost was similar among the eight strains, suggesting that other trade-offs or properties would be required to explain coexistence.

The experimental data generated by Ajani et al. (2021) and Brandenburg et al. (2018) allow further exploring of within-species trait relationships. These studies quantify a

larger number of traits than usual in six and three populations of the diatom *Leptocylindrus danicus* and the dinoflagellate *Alexandrium ostenfeldii*, respectively. Two out of the *A. ostenfeldii* populations were sampled from the same location but during different years, that is, we do not consider that these strains coexist. In addition, each population contains data from more than three strains. As an example, we explore how population growth rate varies with three traits related to fitness (cell size, affinity for nitrogen, and toxicity). Based on species-level empirical data and theoretical considerations they are all expected to have negative relationships (Marañón 2015;

Blossom et al. 2019; Andersen and Visser 2023). In accordance with expectations, all three negative correlations are found at the species level (i.e., among populations) (Fig. 5). However, certain trade-offs that are observed at the species level dissipate within populations or even exhibit opposite patterns (i.e., positive rather than negative relationships). Thus, trade-offs that emerge between and within species may not be universal.

The world is not enough—How many strains should we include in our studies?

The above has documented very large genetic diversity in phytoplankton populations, and data suggest that phenotypic variation may also be significant, but studies examining the latter in coexisting strains are rather scarce. Even fewer studies have explored trade-offs between traits within populations. Within population trait variation and associated trade-offs is a substrate for evolution and hence for the possibility of phytoplankton populations adaptation, for example, to climate change. To gain an understanding of intraspecific trait variation and associated trade-offs in phytoplankton, studies will have to include more strains and quantify more traits. These strains should originate from the same time and location, preferably be characterized genetically (Rynerason and Armbrust 2004; Gsell et al. 2012), and be used within a reasonable time from isolation. While we realize this a big task, a good start would be to include strains that are on the opposite ends of a trait-space, rather than selecting them randomly (Violle et al. 2012). Growth rate is a relatively easy trait to measure, and studies could aim to include strains that are on the opposite ends of this trait-space, for example, one fast-growing and one slow-growing strains and then compare how these may differ in their other traits, particularly those related to grazing resistance and how the expression of defense may differ among strains. So-called “single-cell approaches” may be of particular interest, for example, as a tool to allow high-throughput sequencing and analysis of gene expression (Ku and Seb e-Pedr os 2019; Rosenwasser et al. 2019). After all, the trait-based approach considers interactions among individuals, and not species. Just as species-level traits shaped our understanding of species coexistence, exploring the complexities of intraspecific trait variation promises to unveil a new dimension of ecological dynamics and challenges in the ever-so-evolving study of phytoplankton communities.

Data availability statement

Collected data are publicly available through Figshare (10.6084/m9.figshare.24230065).

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Conflict of Interest

None declared.

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