Review

Evolution of Phytoplankton as Estimated from Genetic Diversity

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Abstract: Phytoplankton are photosynthetic, single-celled organisms producing almost half of all oxygen on Earth and play a central role as prey for higher organisms, making them irreplaceable in the marine food web. As Global Change proceeds, imposing rapidly intensifying selection pressures, phytoplankton are forced to undergo evolution, local extinction, or redistribution, with potentially cascading effects throughout the marine ecosystem. Recent results from the field of population genetics display high levels of standing genetic diversity in natural phytoplankton populations, providing ample 'evolutionary options' and implying high adaptive potential to changing conditions. This potential for adaptive evolution is realized in several studies of experimental evolution, even though most of these studies investigate the evolution of only single strains. This, however, shows that phytoplankton not only evolve from standing genetic diversity, but also rely on de novo mutations. Recent global sampling campaigns show that the immense intraspecific diversity of phytoplankton in the marine ecosystem has been significantly underestimated, meaning we are only studying a minor portion of the relevant variability in the context of Global Change and evolution. An increased understanding of genomic diversity is primarily hampered by the low number of ecologically representative reference genomes of eukaryotic phytoplankton and the functional annotation of these. However, emerging technologies relying on metagenome and transcriptome data may offer a more realistic understanding of phytoplankton diversity.

Keywords: phytoplankton; evolution; genetic diversity; population genetics; metagenomics

1. Introduction

Primary production, the build-up of organic carbon, is considered the most valuable process in the global ocean, largely enabling life on Earth, as we know it. The major part of the marine food web depends on the inherent energy produced in this process by single-celled, photosynthetic pro- and eukaryotes, or so-called phytoplankton [1]. Eukaryotic phytoplankton, which are the main focus of this review, evolved 1.5 billion years ago and have been shaped by past evolutionary history and climate change ever since [2]. Three principal phytoplankton clades dominating the oceans today, dinoflagellates, coccolithophores, and diatoms increased in ecological relevance during the Mesozoic Era (251 to 65 mya). Phytoplankton has subsequently undergone significant adaptive radiation leading to an immense species diversity in today's marine, freshwater, and terrestrial ecosystems [3]. It is estimated that diatoms alone, which account for 25% of primary production on Earth, may consist of 100,000 different species [4]. As a consequence of past climatic variations, such as ~7 °C warmer temperatures during the middle Miocene (~16 mya), followed by ocean cooling 14.7 mya, many species groups have evolved wide environmental tolerances and occur as cosmopolites in today's ocean [5]. In the face of continued global warming, that has a rate an order of magnitude greater than the last glacial-to-interglacial period [6], this key planktonic realm is subjected to rapidly increased selection pressure, inevitably forcing phytoplankton species to undergo evolution, local extinction, or redistribution, posing cascading effects throughout the marine ecosystem [7–10]. As a consequence of anthropogenic

activity and Global Change, also many other properties of the oceanic environment are changing rapidly. These include, for example, light, nutrients, oxygen, and CO_2 [11,12]. In this context, and because phytoplankton are critical to the diversity of the marine biosphere in general [13], it is of central importance to understand the prerequisites of evolution in marine phytoplankton.

The relationship between genetic diversity and evolution has been reviewed in a population genetic framework previously by Rengefors et al. (2017) [14]. The purpose of this review is to focus on evolution and genetic diversity of marine phytoplankton that is relevant in the context of ongoing environmental change and include findings from experimental studies looking into the past and the future. I also focus on how we can make use of emerging approaches related to high throughput sequencing (HTS) to investigate the vast diversity within and between phytoplankton genomes. As this is a rapidly growing field, and it has partly been reviewed recently by others, I limit the scope of this review to mainly focus on results published during the last five years. When an organism undergoes an evolutionary change, making it more suitable to its environment, we often refer to the term adaptive evolution. In general, adaptive evolution is shaped by the interaction of population genomics, natural selection, and underlying biochemical constraints [15]. Thus, HTS data in combination with population genetic theory and targeted phenotyping experiments hold great potential for providing a more realistic understanding of evolution in phytoplankton as estimated from genetic diversity.

Adaptive evolution is underpinned by genetic changes in populations and may be characterized as the movement of a population towards a phenotype that best fits the present environment [16]. The tendency of adaptive evolution to occur is partly dependent on the level of genetic diversity the population harbors, either as standing variability or as new variability arising from mutations or recombination. For clarity, acclimation and evolutionary adaptation are two different, but related, processes. During acclimation, individual strains of phytoplankton display changed gene expression giving rise to short-term changes in the phenotype. This is called phenotypic plasticity and is common in phytoplankton inhabiting environmentally variable habitats [17]. When novel mutations are selected for and their relative allele frequency in a population increases, or when selection is acting on pre-existing genetic diversity (genotypic variability), evolutionary adaptation may occur [18,19]. However, not all evolution is adaptive in the sense that it is helpful for the organism. Evolution may also be neutral as a simple consequence of random genetic drift. Genetic drift refers to the change in the frequency of alleles in a population due to random sampling of organisms [20]. In the context of phytoplankton, this means that the alleles in a population are a sample of those in the 'parents', and that chance has a role in determining whether a given genetic variant survives and reproduces. In this way, genetic drift may cause genetic variants to disappear from populations and thus reduce genetic variation. On the 'other side of the coin', evolution may also be maladaptive, meaning a trait becomes more harmful than helpful for the organism as it evolves in a specific direction [17]. Sometimes the process of maladaptation may lead to 'evolutionary traps' as seen in seabirds ingesting floating plastics that mimic food items [21,22].

When predicting the ecological response of species to future environmental change, the role of adaptation has often been neglected, or included only indirectly [23,24]. For example, models predicting future species distributions of phytoplankton either build on occurrence data across environmental gradients, or on experimentally produced reaction norms of single genotypes, the latter falsely representing the phenotype of an entire species [25]. Thus, the significance of evolutionary potential as estimated from genetic diversity is not quantified in most contemporary studies [26]. At the same time, a current shift in methodology from genetic markers and single-gene approaches to genome-wide studies are helping us to identify variation in specific genes that is under selection from Global Change. This helps us to see evolution in marine phytoplankton in a new light.

2. Experimental Studies of Genetic Diversity and Evolution

Evolution and adaptation potential in phytoplankton have, in many cases, been studied using a "forward-in-time" method, i.e., experimental evolution [27]. The field of experimental evolution, defined here as the study of evolutionary changes occurring in experimental populations as a consequence of conditions imposed by the experimenter [28], has significantly increased our understanding of the adaptation potential and plasticity in microorganisms [26,29] and is believed to increase the understanding further, also more specifically for phytoplankton [25,30]. The main challenge within this field is that the observations are often based on "domesticated" study organisms, not necessarily mirroring how evolutionary processes would occur in the natural environment. Another limitation is the lack of any species interactions in monospecific experiments, which may drastically affect evolutionary potential [31]. However, the strength and value of these types of observations are that they can address the evolutionary and mechanistic processes in a controlled environment, teaching us about the inherent potential in nature.

The field of experimental evolution has shown us that phytoplankton can undergo rapid evolution (referring to evolution on shorter timescales than Global Change) to environmental change, such as temperature and CO_2. Many studies have focused on model species, such as *Emiliania huxleyi* [32–34], *Thalassiosira pseudonana* [35,36], and *Chlamydomonas reinhardtii* [37] to quantify evolution in response to currently relevant selection regimes. The two most commonly studied selection pressures are thermal stress and ocean acidification. In Table 1, I highlight some examples of adaptive evolution in response to these environmental variables and provide information on evolution in traits or functions identified by the authors. When examining the relationship between evolution and genetic diversity in phytoplankton, it is evident that when populations adapt to a change, it will occur through a combination of selection acting on existing standing genetic variation within the species, as well as de novo mutations. This is especially well documented in a few papers where adaptation has been studied simultaneously at different levels of genetic diversity as the 'starting material'. For example, Lohbeck et al., 2012 [32] where adaption to increased CO_2 levels was observed separately, in both single- and multi-strain populations. With such an approach it is valid to conclude that adaptation can occur both through positive selection on de novo mutations (in single strain approach) and via sorting of multiple genotypes representing standing genetic diversity. It is, however, still commonplace to use only a single strain for adaptation assays making it difficult to evaluate the relative contribution of de novo mutations vs. standing genetic diversity to adaptive potential in phytoplankton. The examples shown in Table 1 mostly used single strains as starting material and support the role of de novo mutations in phytoplankton adaptation. These results do not exclude adaptive evolution from selection on standing genetic diversity as an important factor in natural populations. Intuitively, adaptive evolution from standing genetic diversity is even highly likely given the huge population sizes and genetic diversity levels observed in most phytoplankton species.

The examples were included here because they also provided some functional explanation for the observed adaptation. For example, increased photosynthetic capacity, as a consequence of downregulated respiration in higher temperatures [26,37] was identified as an evolving function in green algae. Altered thermal reaction norms, which were observed to evolve in diatoms [35,38] may initially sound oversimplified and self-evident when examining adaptation to thermal stress. However, this can mean slightly different things for different species. An altered thermal reaction norm in some species can mean shifting the critical thermal minimum and maximum, with no shift in the optimal temperature (T_{opt}). This enables higher growth rates (μmax) at higher temperatures, but lower growth capacity in the lowest end of the thermal spectrum. In contrast, other species may adapt by increasing their μmax under warmer conditions and shifting their T_{opt} [38].

Results emerging from studies within the field of experimental evolution show that phytoplankton species are likely to adapt all the time also in natural conditions. However, experimental evolution on its own may have little to do with factual processes taking place

in the natural environment, making clear-cut predictions about adaptation and ecological effects in relation to environmental change extremely challenging [27]. In order to design appropriate studies within the field of experimental evolution, we also need to identify the relevant selective pressures caused by climate change.

Table 1. Examples of studies from the field of experimental evolution showing adaptive evolution in phytoplankton as a response to increased temperature or CO_2.

Selection Pressure	Species	Diversity Level	Generations/Time	Evolved Traits/Functions	Reference
Temperature	*Chlorella vulgaris*	1	100	Downregulation of respiration	[26]
	C. reinhardtii	8–10	10 years	Increased photosynthetic capacity and reduced susceptibility to photoinhibition	[37]
	T. pseudonana	1	300	Transcriptional regulation, oxidative stress, redox homeostasis	[36]
	T. pseudonana	1	350	Altered thermal reaction norm	[35]
	Chaetoceros sp., *Thalassiosira* sp., *Synedra* sp.	1	200–600	Altered thermal reaction norm	[38]
CO_2	*E. huxleyi*	1/6	500	Increased calcification	[32]
	Ostreococcus tauri	16	400	Reduced cell size and C:N ratio	[39]
	E. huxleyi	1	500	pH regulation	[33]
	Gephyrocapsa oceanica	1	1000	Reduced growth rates, enhanced POC, PON, decrease in PIC:POC ratio	[40]

The relatively young field of resurrection ecology offers a "backward-in-time" approach and can be defined as the revival and study of long-dormant organisms via hatching of dormant life stages. This enables the direct quantification of phenotypes over temporal scales exceeding the average human lifespan [41,42]. Many phytoplankton species form dormant resting stages that sediment at the sea floor after vegetative growth is ceased in the water column. This also means that only a small proportion of the total species diversity can be observed at any time in the water column [43], which has significantly hampered any analyses of diversity in marine phytoplankton. Seed banks of phytoplankton are considered archives of evolutionary history and have provided unique insights into past genetic changes in relation to environmental change [44–46]. Most previous studies conducted with resurrected phytoplankton [44,47,48] have used neutral genetic markers, such as microsatellite loci, for the quantification of genetic diversity and correlation to environmental change. For improving the understanding of adaptation processes in phytoplankton from the natural environment, documenting evolution from these hidden historic archives at the seafloor is a useful approach and has not been used to its full potential considering the latest molecular tools and approaches. In order to advance the field of resurrection ecology focused on phytoplankton, and for investigating the relationship between genetic diversity and evolution, applying re-sequencing of genomes of resurrected isolates from temporal series acquired from geologically dated sediment cores seem promising. We have very restricted knowledge about the genetic diversity of organisms buried in coastal sediments even though it has a high potential for the study of adaptation to environmental change. As seen above, rapid adaptation to singular environmental changes has been inferred for several phytoplankton species in experimental evolution studies. However, natural populations may experience a multitude of selection pressures simultaneously, which is complicated to simulate in experiments. By resurrection of millennia-old, pre-Anthropocene dormant resting stages of phytoplankton [49,50] and subsequent experimental work, we may be offered several advantages compared to studies of experimental

evolution. Resurrected strains from temporal series across times of environmental change may be re-sequenced and analyzed for signatures of adaptation to documented changes in a region. This provides a more realistic understanding of the relationship between diversity and evolution as evolution that actually occurred can be quantified from natural populations. However, this requires access to reference genomes for ecologically relevant species, which is still lagging behind regarding eukaryotic phytoplankton.

3. Recent Population Genetic Studies Indicate Vast Diversity

As a consequence of mainly asexual reproduction, large population sizes and seemingly vast dispersal potential, marine phytoplankton populations were traditionally assumed to consist of one or only very few clonal lineages at any point of place and time [51]. However, population genetic studies using neutral genetic markers have repeatedly shown us that this is not the case (reviewed in [14]). Clonal diversity, which is available for evolution as a source of standing genetic diversity, is comparably high in phytoplankton species. Phytoplankton populations investigated using genetic markers actually display extremely low proportions of identical multi-locus genotypes (MLGs) in natural conditions [25], with a few exceptions [52,53]. Population genetic studies are continuously providing new evidence from natural populations supporting the understanding of vast genetic diversity in phytoplankton species [54–60]. These types of studies show us that populations can be genetically structured over small and large geographic areas and over temporal scales and that genetic diversity may function as a proxy for a species' adaptive potential [61–63]. Subsequently, it is likely to be the reason for why phytoplankton survive in highly variable environments. On the other hand, high standing diversity may slow down evolution through clonal interference [64], something that has been hypothesized also from studies on natural populations [60]. The same study applied traditional microsatellite markers and Restriction-site DNA (RAD) sequencing for the study of genetic diversity in the marine dinoflagellate *Alexandrium ostenfeldii* in bloom vs. seed bank populations. The results suggested that a strong benthic–pelagic coupling, combined with frequent sexual reproduction, prevent the dominance of single clonal lineages. Population genetic studies of phytoplankton have, and probably will, significantly increase our understanding of genetic diversity and evolution of phytoplankton. In addition, recently developed approaches such as the PoolSeq barcoding [65] utilizing genetic markers without the need of single cell isolation and cultivation, entail the potential to improve our ability to follow intraspecific dynamics over space and time in natural populations. However, neutral markers are inherently restricted in the sense that they cannot provide knowledge about functional genes under selection. This is why utilizing population genomic approaches may be an important addition in the study of evolution and intra-species diversity in marine phytoplankton. In some cases, genomic data have offered a more realistic understanding of intraspecific diversity as shown for the ubiquitous unicellular marine phytoplankton species *E. huxleyi*. Resequencing of geographically separated genomes in this species contains surprisingly limited variability, likely because the range of population sizes exceeds the range of genetic diversity by many orders of magnitude [66].

Towards Population Genomics of Phytoplankton

Metabarcoding studies targeting the ribosomal RNA (rRNA) 16S and 18S genes in environmental DNA (eDNA) surveys has significantly increased our understanding of marine phytoplankton diversity in the recent decade [67,68]. However, the evolutionary significance of the discovered taxonomic and functional variability is still largely unknown. The rRNA genes are appropriate for community level investigations but generally do not provide sufficient genetic resolution to reveal intraspecific diversity patterns. Species with identical 16S or 18S rRNA sequences may have highly divergent genomes and phenotypes [69–72]. Even though not numerous yet, studies with a genome-wide approach are steadily increasing. These are believed to aid in a better understanding of how selection affects patterns of variation, and in identifying what genes are involved when phytoplank-

ton evolve to new conditions. These technologies have shown that phytoplankton adapt genomically to contrasting nutrient conditions [73–75] by gene gain and loss. This is information that is out of reach in traditional population genetics. Genome-wide approaches utilizing eDNA include metagenomics [76,77] and metatranscriptomics [78]. Other approaches, requiring laboratory isolation or sorting of cells, such as single-cell genomics [79] have revealed previously underestimated functional diversity and unknown interactions in uncultivated protists [80,81].

These technologies emerging in the field of phytoplankton population genomics are facilitated by approaches primarily developed for studying prokaryotic diversity [82,83] and comparative microbiome studies [84]. On one hand, studies utilize eDNA in combination with reference genomes of cultivated organisms, such as [85] for studying genome adaptation across the seascape. This approach is based on shotgun sequencing of eDNA, where resulting sequence reads are aligned to a previously established reference genome. The complete genome sequences created for *Prochlorococcus* and *Synechococcus* [86] have, for instance, been utilized in this way for investigating how genomic adaptation regulates phosphate uptake [76]. The genomic content in these organisms was significantly altered in reciprocal transplant experiments carried out in the nutrient-rich Labrador Sea in the NE Atlantic and the ultra-oligotrophic Sargasso Sea in the S Atlantic. Interestingly, these two phytoplankton lineages seem to adapt their genomes rapidly in terms of the frequency of P acquisition genes, which can be directly linked to shifts in nutrient uptake rates between two contrasting regions. When such metagenome data is collected across vast geographical areas and integrated with trait-based modeling (as in [87]) it can even be used to predict regional conditions in terms of elemental composition of marine plankton communities. This means that the study of genomic variation and adaptation can reveal regions with nutritional challenges (for example iron, N, P limitation) in the global marine ecosystem [85]. Hence, the value of sequence-based, comparative population genomic approaches is that they can provide us with more functional understanding than before. However, for eukaryotic phytoplankton this is still hampered by a lack of relevant gene annotations. Recent comparative studies with a genome-wide scope are also in line with population genetic studies and conform to early work on full genome sequencing of phytoplankton [88–90]. Namely, it is increasingly clear that phytoplankton are characterized by considerable sequence variation between homologous chromosomes, likely translating into high levels of intra-species variation in natural populations and a high potential for adaptive evolution.

A significant obstacle for sequence-based studies that aim for comparative analyses is the lack of relevant reference sequences when it comes to eukaryotic phytoplankton. The situation is significantly better for marine prokaryotic phytoplankton [91]. Studies with a pure re-sequencing or re-mapping approach of –omics data are still limited by the low number of established reference genomes available for ecologically relevant eukaryotic phytoplankton. Free-living planktonic phytoplankton with full genome sequences include the dinoflagellate *Polarella glacialis* [92], the pelagophyte *Aureococcus anophagefferens* [93], Cryptophytes, such as *Chroomonas mesostigmatica* [94], *Cryptomonas paramecium* [95], *Guillardia theta* [96] (nucleomorph genome), the eustigmatophyte *Nannochloropsis gaditana* [97], the coccolithophorid *Emiliana huxleyi* [98], and the diatoms *Fragilariopsis cylindricus* [99], *Phaeodactylum tricornutum* [89], *Pseudo-nitzschia multiseries* [100], *P. multistriata* [101], *Thalassiosira pseudonana* [88], *T. oceanica* [90], and *Skeletonema marinoi* [102]. In addition, initiatives such as the Marine Microbial Eukaryotic Transcriptome Sequencing Project (MMETSP) [103], providing over 650 assembled and functionally annotated transcriptomes (396 unique strains assigned to 210 distinct genera) was an important addition and facilitates comparative studies of intra-species diversity and evolution [104]. However, as most of the included taxa in MMETSP represent cultivated strains, the immense diversity of uncultivated phytoplankton remains out of reach.

4. Environmental Genomics Target Uncultivated Eukaryotic Phytoplankton without Previous Reference Genomes

The circumglobal Tara Ocean expedition (2009–2012) revealed that >90% of the most abundant eukaryotic protists in the marine environment do not match any known species, and most of them are represented by lineages without any cultivated representatives [105]. This seriously complicates the assessment of how variable selection pressures are structuring genomic variability in natural populations of species that may have a much more important ecological role in the global ocean than what was previously appreciated [106,107]. Recent studies adopting a metagenomic approach show that such previously undescribed genomic diversity can be targeted by the reconstruction of metagenome-assembled genomes (MAGs) [108–110]. This is similar to previous work applied on samples from, e.g., the brackish Baltic Sea using eDNA for the reconstruction of prokaryotic MAGs [111]. Other recent studies have focused on developing much needed bioinformatic pipelines for quantification of intra-species genomic variability from metagenomic data [82,112–114] and have largely highlighted the importance of adaptive divergence as a structuring mechanism in the evolution of uncultivated bacterioplankton. Eukaryotic MAGs are of lower quality compared to re-sequenced genomes of cultivated isolates, but they offer genome-wide information about the diversity of phytoplankton from natural ecosystems. One challenge is that eukaryotic genomes are much more complex than those of prokaryotes, which means we cannot expect to use only the same tools for exploring the eukaryotic diversity. The ecological context of eukaryotic protists is also significantly different from that of bacteria, meaning that using only the genome data of eukaryotes cannot produce the same insights about, e.g., ecological functioning as it does in prokaryotes [115]. However, more in-depth analyses of the population genomic diversity and differentiation in eukaryotic MAGs may provide novel insights into what environmental drivers are dictating the evolution and metapopulation structure also in uncultivated eukaryotes.

5. Conclusions

In this mini-review, I discussed how marine phytoplankton have evolved and are evolving to continuously changing environmental conditions. I examined standing genetic variation and de novo mutations as assessed from experimental studies and investigations in natural populations. Recent population genetic studies support the understanding of high genetic diversity in marine phytoplankton, facilitating a high adaptive potential in the face of rapidly changing selection pressures. The field of resurrection ecology, i.e., the revival of up to millennia-old resting stages of diatoms offer new possibilities for investigating diversity and evolution in this organism group. Additionally, the emerging approaches utilizing metagenome and transcriptome data covered here are revolutionizing the study of genomic variation and evolution in phytoplankton. The reconstruction of MAGs has already provided novel insights in marine prokaryotic phytoplankton. This may be especially relevant for the study of many eukaryotic species that we are currently not able to cultivate in laboratory conditions.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The author declares no conflict of interest. The funder had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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