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# Evolution of Microalgae and Their Adaptations in Different Marine Ecosystems

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**Microalgae are unicellular eukaryotic organisms that are predominantly photosynthetic. They are found in a wide range of habitats, particularly marine ecosystems, and are responsible for a significant portion of the oceans biogeochemical cycling. Microalgae have a varied evolutionary history with genes derived from photosynthetic organisms, heterotrophic eukaryotes and bacteria. This has led to a wide range of adaptations, allowing them to thrive in a variety of conditions. Microalgae in coastal regions are adapted to turbulence, high nutrients and low light whilst open ocean microalgae have to contend with high irradiance and low nutrient concentrations. Polar microalgae are adapted to freezing temperatures, high nutrients and long periods of light and darkness. Microalgae genomes and transcriptomes uncover and interpret these adaptations, providing information on how microalgae have become a dominant force within marine ecosystems.**

## Introduction

The term microalgae is used to describe small unicellular eukaryotic algae, which live individually or associate in chains or colonies. Microalgae can be up to 1000 µm in size with the smallest at 0.95 µm (Courties *et al.*, 1994) and can be motile, either swimming with a flagella or gliding across surfaces or through sediments via a raphe. They occupy a diverse range of

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freshwater, marine and terrestrial habitats including extreme environments, such as snow, sea ice (psychrophiles), hot springs (thermophiles) and salt lakes (halophiles) (Rothschild and Mancinelli, 2001). Microalgae can be found in most habitats where water and sufficient light are available, however, the majority are found in the oceans (Figure 1) as part of the phytoplankton community, which includes both the eukaryotic microalgae and cyanobacteria. Together they are responsible for just over 45% of global primary production (Field *et al.*, 1998) substantially impacting the ocean's carbon fixation, oxygen production, nutrient cycling and food web. The majority of microalgae are photosynthetic, though they can be heterotrophic or mixotrophic, as a result, the majority can be found within the photic zone. A significant proportion of net production comes from temperate and polar frontal zones and in areas where nutrient rich water comes to the surface by upwelling (Field *et al.*, 1998).

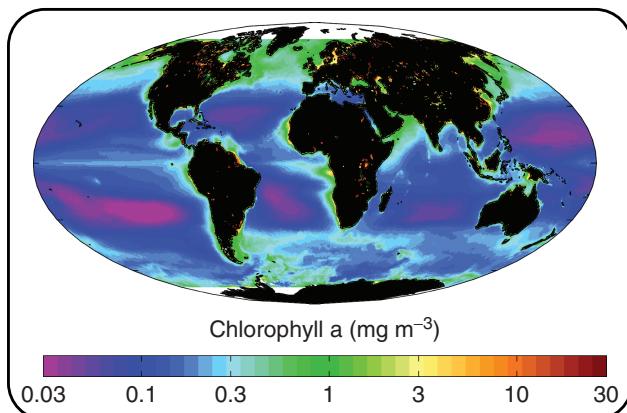
Microalgae play a large role in nutrient cycling, as they provide nutrients to other organisms through consumption and by sinking of organic matter. Sinking also transports carbon, fixed from atmospheric CO<sub>2</sub> to the oceans interior, and therefore microalgae are an important factor in CO<sub>2</sub> levels and climate change. These processes are especially transparent during algal blooms (Figure 2), where an excess of normally limiting nutrients such as nitrate and iron allows rapid and dense growth of often a single or a few species of microalgae (Boyd *et al.*, 2000). These blooms have been known to grow to an area the size of the United Kingdom, with some species responsible for these elevated densities producing toxins which are damaging to other organisms. Once the nutrients are depleted, the algal community sinks, cycling organic and inorganic products. Sinking of algal blooms highlights the geological contributions made by diatoms and coccolithophores, which produce intricate shells of silica and calcium carbonate, respectively. Blooms formed from these species result in diatomite and chalk deposits. Oil reserves are also linked to microalgal lipid deposition. **See also: Algal Calcification and Silification**

This review paper focuses on the adaptations of microalgae in different important marine ecosystems. Understanding this allows us to determine how these globally important organisms are able to thrive in their current environments and to predict the effect of global change on their biogeography. **See also: Biogeography of Marine Algae**

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**Figure 1** Average sea surface chlorophyll *a* concentration from 1998 to 2006. Chlorophyll *a* is used as an indicator of phytoplankton biomass.



**Figure 2** *Emiliania huxleyi* bloom off the coast of South West England.

## The Evolution of Microalgae

There are approximately 30 000 described species of phytoplankton and around 90% of these are eukaryotic (Table 1). In terms of species, diatoms account for the majority (>50%) of microalgae (Guiry and Guiry, 2015), however, numbers are estimated to be much higher than currently described (Guiry, 2012). The key to microalgae success is their evolution, which has enabled them to adapt to a myriad of different environments. In addition to the four major forces of evolution (mutation, selection, genetic drift and gene flow), evolution has been shaped by three additional evolutionary processes: endosymbiosis (Figure 3), vertical gene transfer and horizontal gene transfer (HGT). These three processes have significantly contributed to mosaic genomes characterised by a mix and match of genes from different organisms (Armbrust, 2009). Chlorophytes, glaucophytes and rhodophytes are the products of separate endosymbiotic events in which heterotrophic, single-celled,

eukaryotic hosts engulfed a cyanobacteria, eventually becoming membrane-bound organelles known as plastids (Falkowski *et al.*, 2004). Secondary endosymbiosis took place in new heterotrophic eukaryotes with green and red algae becoming plastids with additional membranes (Cavalier-Smith, 1999). This led to the evolution of two groups with green plastids: the euglenoids and chlorarachniophyte and four groups with red plastids: the cryptophytes, dinoflagellates, haptophytes (including coccolithophores) and heterokontophytes (including diatoms). There is also evidence of prior secondary endosymbiosis in the chromalveolates with a green alga, followed by gene transfer to the nucleus and plastid loss (Moustafa *et al.*, 2009). Some dinoflagellate members have undergone a tertiary endosymbiosis, whereby heterotrophic dinoflagellates have engulfed haptophytes or diatoms (Falkowski *et al.*, 2004). Algal genomes are made up of host, plastid and bacterial genes likely acquired by HGT (Bowler *et al.*, 2008; Raymond and Kim, 2012). The evolutionary origins of microalgae have most likely enabled them to adapt to a wide range of environmental conditions and habitats. See also: [Algae: Phylogeny and Evolution](#)

Arguably the most important aspect in microalgal evolution is endosymbiosis leading to gene transfer from an endosymbiont's nucleus, plastid and mitochondria to the host nucleus. Genes gained through endosymbiotic and HGT have shaped the metabolic pathways of microalgae that include haem (Oborník and Green, 2005), lipid (Chan *et al.*, 2013) and amino acid (Jiroutová *et al.*, 2007) biosynthesis. Fatty acid biosynthesis in diatoms is controlled by genes from green (prasinophytes) and red algal lineages and from the heterotrophic host (Chan *et al.*, 2013). The tryptophan biosynthesis pathway in diatoms also contains genes from the red algal symbiont and heterotrophic host as well as genes from bacterial origins. In *Phaeodactylum tricornutum*, this includes a gene fused to a sequence coding for a hypothetical protein of cyanobacterial origin (Jiroutová *et al.*, 2007). Genes from the primary endosymbiont and eukaryotic host are also found for haem biosynthesis in *Thalassiosira pseudonana* and *Cyanidioschyzon merolae* as well as a gene with possible mitochondrial origin (Oborník and Green, 2005).

## Adaptations in Different Marine Ecosystems

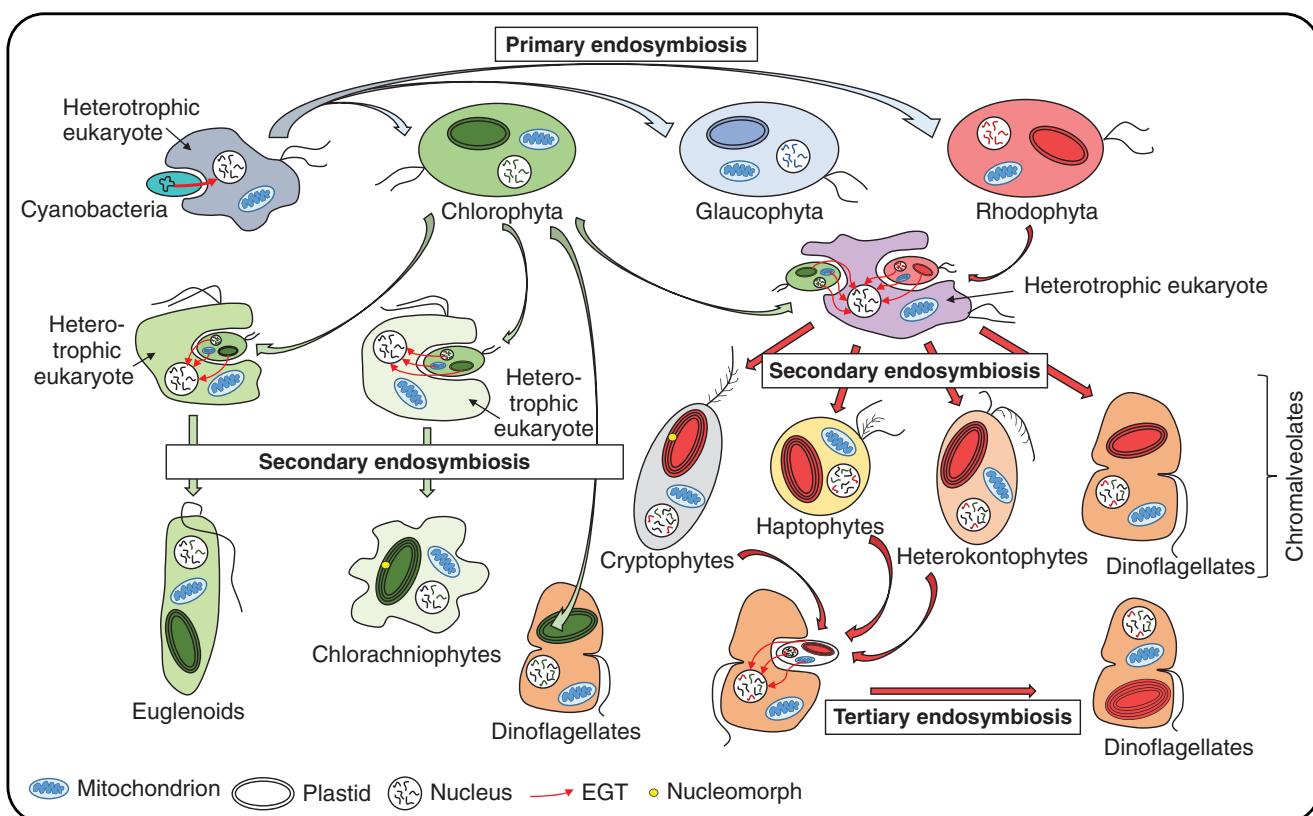
### Coastal and estuarine regions

Coastal and estuarine regions are characterised by high and fluctuating nutrient levels, turbulence and light conditions which can be both low and variable (Figure 4). Turbulent conditions result in sediment suspension maintaining high nutrient concentrations in the water column (Smetacek, 1985). Diatoms and prasinophytes dominate these regions (Rodrigues *et al.*, 2014) and are adapted to use a 'velocity strategy' for nitrate (Litchman *et al.*, 2007) and phosphate (Kwon *et al.*, 2013) acquisition, characterised by high maximum uptake rates and high growth rates (Litchman *et al.*, 2007). High uptake and lower growth rates allow some diatoms to store nutrients in large vacuoles during high nutrient pulses (Litchman *et al.*, 2007), allowing

**Table 1** Number of described microalgae species

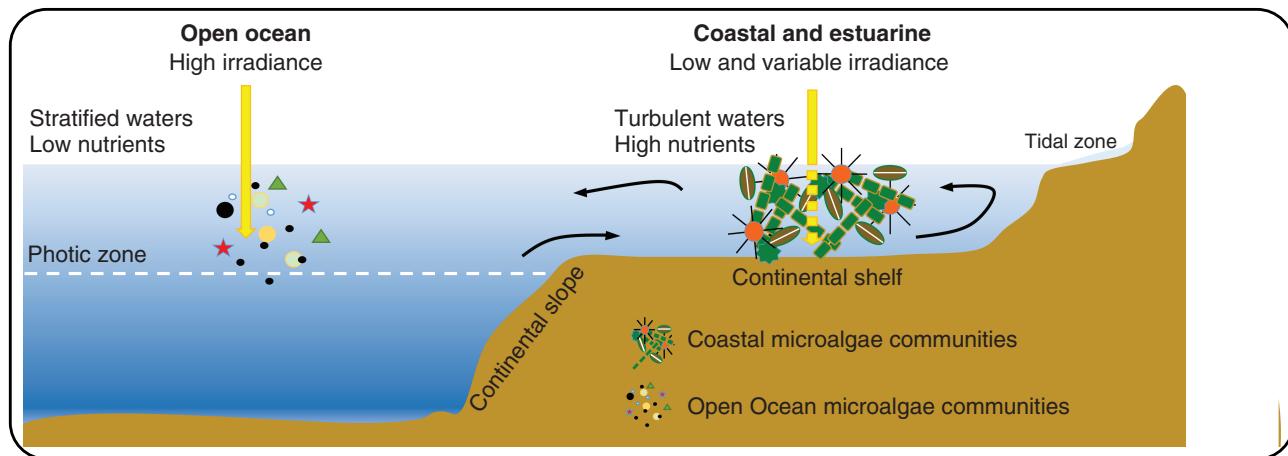
| Marine groups of microalgae         | Level  | Number of species |
|-------------------------------------|--------|-------------------|
| Bacillariophyta                     | Phylum | 13 426            |
| Chlorarachniophyceae                | Class  | 14                |
| Chlorophyta                         | Phylum | 4500 <sup>a</sup> |
| Cryptophyta                         | Phylum | 194               |
| Dinophyta                           | Phylum | 3308              |
| Euglenozoa                          | Phylum | 1323              |
| Glaucophyta                         | Phylum | 20                |
| Haptophyta                          | Phylum | 626               |
| Rhodophyta                          | Phylum | 600 <sup>a</sup>  |
| Heterokonts besides Bacillariophyta | Phylum | 1670              |

<sup>a</sup>Approximate numbers are used for chlorophyta and rhodophyta owing to large numbers of macroalgae within these groups. Based on data from AlgaeBase (<http://www.algaebase.org>).

**Figure 3** Evolution of algae according to primary, secondary and tertiary endosymbiotic events. EGT, endosymbiotic gene transfer.

them to thrive at fluctuating nutrient levels. Nitrate transporters are highly expressed in the diatom *Skeletonema costatum* under nitrate-available and nitrogen-limiting conditions (Hildebrand and Dahlin, 2000), suggesting that diatoms take up nitrate when it is both plentiful and scarce. Coastal diatoms, *S. costatum* and *Cylindrotheca fusiformis*, are adapted to maximise uptake of ammonium over nitrate as it is less costly to assimilate. This is accomplished by downregulating nitrate transporter genes in the presence of ammonium and increasing ammonium transporters in nitrogen-limiting conditions (Hildebrand and Dahlin,

2000; Hildebrand, 2005; Liu *et al.*, 2013). Coastal and estuarine microalgae can uptake and use a variety of essential nutrients from their surroundings, including nitrate, ammonium, phosphate, sulfate, silicate and iron. Genes for transport of organic nutrients such as amino acids and purines (Armbrust *et al.*, 2004; Bowler *et al.*, 2008; Worden *et al.*, 2009) may help provide nitrogen during oscillating nutrient levels, whilst genes for a complete urea cycle, thought to originate from the host of secondary endosymbiosis, may allow rapid recovery after nitrogen deprivation (Allen *et al.*, 2011). A major limiting factor for



**Figure 4** Major differences between nutrient, light and turbulence in marine coastal and open-ocean ecosystems.

growth in some coastal regions is iron concentration (Hutchins and Bruland, 1998). Microalgae have adapted mechanisms for uptake and storage of iron at low levels, as well as reducing iron requirements. Allen *et al.* (2008) looked at transcript levels in the pennate diatom *P. tricornutum* under low iron conditions. A marked decrease in mechanisms that rely on iron-dependent enzymes such as photosynthesis and respiration was shown. In response to these decreases *P. tricornutum* reduced carbon flux to respiratory processes and increased polysaccharide breakdown to release sugars. Iron-requiring and -independent antioxidants were down- and upregulated, respectively allowing reactive oxygen species (ROS) formed by the Fe-limited photosynthetic components to be scavenged. To reduce the production of ROS, excess electrons were channelled to mitochondrial alternative oxidase and dissipated by upregulation of genes to increase non-photochemical quenching (NPQ) capacity. Downregulation in nitrate assimilation genes was compensated by recycling proteins. Bacterial-like ferrichrome-binding proteins and a suite of iron-sensitive genes have been found in *P. tricornutum* but not in *T. pseudonana*, which requires much higher iron concentrations to survive (Allen *et al.*, 2008). Although some genes such as ferric reductases (Allen *et al.*, 2008) are shared, *T. pseudonana* appears to display different iron-associated genes under iron-limitation compared to *P. tricornutum*, including a ferroxidase, metal transporters and two iron permeases (Kustka *et al.*, 2007). This highlights the role that different genes play in adaptation to different conditions.

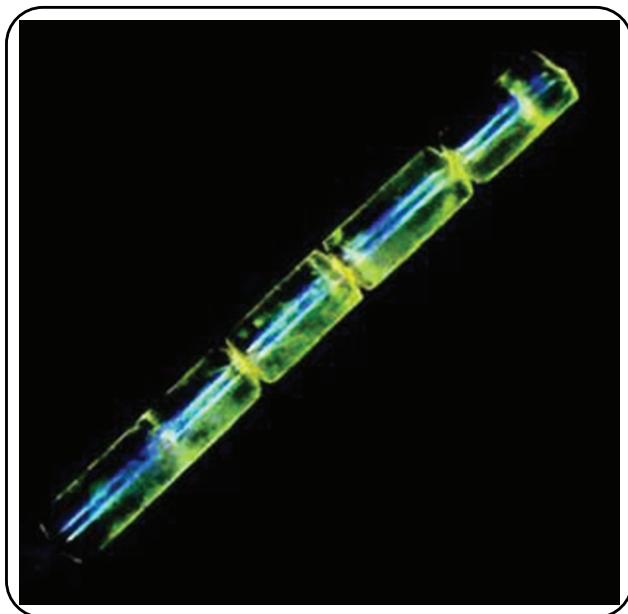
Suspension of sediment, organic matter and cells by turbulence along with tidal changes and scattering of light can create low and variable light conditions (Depauw *et al.*, 2012). Microalgae are able to acclimate to low light conditions by increasing the concentration of their photosynthetic pigments (Rodrigues *et al.*, 2014; Ezequiel *et al.*, 2015). Whilst this increases photosynthetic efficiency, it also increases excess light energy under high irradiance, leading to photoinhibition and production of ROS which can damage the cell (Goss and Lepetit, 2015). It is therefore important to have an effective mechanism to dispel excess photons. This role is normally carried out by NPQ. The role of NPQ has been recently reviewed for several plant and algal groups by Goss

and Lepetit (2015). Diatoms use an NPQ system that converts diadinoxanthin (Dd) to diatoxanthin (Dt) in the presence of a proton gradient induced by high light. The Dd-Dt xanthophyll cycle is beneficial in coastal regions as it responds faster to high light than the VAZ (violaxanthin, antheraxanthin and zeaxanthin) cycle found in algae such as the chlorophytes. Components of the Dd-Dt cycle are more soluble within the thylakoid membrane, meaning they can occur at higher concentrations. Several genes for LHCX proteins, linked to modulation of NPQ under high and fluctuating light conditions (Goss and Lepetit, 2015), have been found in diatoms (Armbrust *et al.*, 2004; Bowler *et al.*, 2008). Some microalgae are also able to use motility to avoid photodamage and maximise light harvesting (Ezequiel *et al.*, 2015). Genes with homology to photoreceptors have been found in diatoms (Armbrust *et al.*, 2004), which may mean that some microalgae are able to detect their position in the water column relative to light levels.

The silica frustule may also play a role in the adaptation and dominance of diatoms in coastal systems. Drag on frustules spines may help cells to spin in the water, increasing nutrient uptake by microturbulence (Smetacek, 1985). For chain-forming microalgae (Figure 5) in turbulent conditions, stiffer chains were modelled to have higher nutrient uptake per cell, indicating a potential advantage for silicified diatom chains (Musielak *et al.*, 2009). Adaptations such as the formation of gaps between cells reduce the impact of lower nutrient diffusion per cell seen for chains, whilst taking advantage of higher nutrient transport seen in chains during turbulent conditions (Pahlow *et al.*, 1997). The shape of the frustule may also give some diatoms an advantage, with elongated cells, such as pennate diatoms, modelled to have a greater diffusive nutrient supply (Pahlow *et al.*, 1997). The silica frustule may also act to focus light into the cell (De Stefano *et al.*, 2007), benefiting diatoms in low light conditions. **See also: Diatoms**

## Open oceans and oligotrophic waters

The open ocean is characterised by stratified waters, low nutrients and high irradiance (Figure 4). It homes a range of microalgae



**Figure 5** *Melosira* sp. chain illustrating the advantages of a silica frustule: rigidity in microalgae chains can increase nutrient uptake in turbulent conditions. Images of diatoms collected during the Tara Oceans expedition 2009–2012. Courtesy of Christian Sardet and Chris Bowler.

including coccolithophores, prasinophytes, dinoflagellates and pelagophytes (Litchman *et al.*, 2007; Rodrigues *et al.*, 2014). Affinity strategists such as coccolithophores have low half saturation constants, which allow them to compete for nutrients at low concentrations (Litchman *et al.*, 2007). The important pelagic coccolithophore *Emiliania huxleyi* has a high affinity for phosphate but not nitrate (Riegman *et al.*, 2000), giving it an advantage in phosphate-limiting conditions. When comparing genes between prasinophytes, an oligotrophic *Micromonas* sp. was found to encode a higher number of transporters from a larger range of protein families than a high-nutrient sourced *Ostreococcus*. This may reflect the need to optimise nutrient uptake in low nutrient conditions (Worden *et al.*, 2009). The number of phosphate transporters also varied between *E. huxleyi* strains, suggesting differences in uptake capability within the same species (Read *et al.*, 2013). Low uptake rates for nitrate in *E. huxleyi* may be assuaged by the ability to uptake a variety of nitrogen forms including nitrate, nitrite, urea and ammonium (Read *et al.*, 2013). The importance of ammonium as a nitrogen source can be seen in the high number of ammonium transporter genes found in this species (Read *et al.*, 2013).

Adaptations such as mixotrophy may supplement nutrient uptake or allow species with less capacity to compete for nutrients such as dinoflagellates (Litchman *et al.*, 2007) to survive. Interactions with bacteria may also provide vitamins (see Biological Interactions).

Many microalgae in open oceans need to cope with low iron concentrations. Production of several enzymes, which use zinc, copper, manganese and nickel instead of iron, helps to reduce iron demands, whilst iron transporters and binding proteins optimise acquisition (Read *et al.*, 2013; Worden *et al.*, 2009). A reduction in photosystem I complexes reduces the demand

for iron in the oceanic diatom *Thalassiosira oceanica*. This has led to the loss of rapid NPQ under variable light conditions, but as this species thrives under continuous light, it seems that iron requirement exerts higher selective pressure (Strzepek and Harrison, 2004). Acclimation to high light levels in open waters involves a reduction in photosynthetic pigments such as fucoxanthin chlorophyll *a-c*-binding protein (FCP) seen in *E. huxleyi* (McKew *et al.*, 2013). Removal of excess energy by NPQ through an increase in xanthophyll, Dd (McKew *et al.*, 2013) and photoprotection-linked LHC Lhc<sub>z</sub> proteins (McKew *et al.*, 2013; Read *et al.*, 2013) is also important. Adaptations to protect cells from ROS produced under high light include production of antioxidants that can be utilised under iron-limiting conditions such as Cu or Zn superoxide dismutase (Worden *et al.*, 2009; Read *et al.*, 2013) and production of proteins for repair of photosystem II. See also: **Genomics of Algae**

## Marine polar systems

Microalgae in marine polar systems are subjected to a variety of extreme conditions: cold temperatures, high irradiance during summer and total darkness during winter. Additionally, freezing of surface waters leads to high salt and oxygen concentrations and limited gas exchange in sea ice (Mock and Thomas, 2008). In the Southern Ocean, nutrient levels are high owing to upwelling and strong vertical mixing. This leads to high nitrate, phosphate and silica concentrations although iron tends to be limiting. Iron limitation is less pronounced in the Arctic Ocean owing to river run-off (Mock and Thomas, 2008). Pennate diatoms dominate the polar oceans (e.g. *Fragilariopsis*, *Navicula*), haptophytes and dinoflagellates also occur (Mock and Thomas, 2008), suggesting that chromalveolates are particularly well adapted to environmental conditions of polar marine ecosystems.

It is important to maintain photosynthetic efficiency, whilst minimising damage during long periods of irradiance. As seen with microalgae in warmer conditions, *Fragilariopsis cylindrus* responds to high irradiance by increasing NPQ and reducing proteins involved in light harvesting. This is accomplished by upregulating genes linked with energy dissipation such as high-light FCPs along with downregulating other light-harvesting genes (Mock and Hoch, 2005). LHC<sub>x</sub> proteins are a component of the FCP complex involved in light harvesting (Goss and Lepetit, 2015) and are also capable of binding xanthophyll pigments associated with NPQ (Lyon and Mock, 2014). An increase in LHC<sub>x</sub> proteins during high light conditions, and a greater number of LHC<sub>x</sub> genes in *F. cylindrus* compared to temperate diatoms, suggests that LHC<sub>x</sub> proteins play a role in adaptation to both high light and lower temperatures. Another adaptation to high light levels including ultraviolet irradiance is the presence of antioxidants that are able to scavenge ROS. An increase in antioxidants can be seen in response to high light in *F. cylindrus* (Mock and Hoch, 2005). The ability to repair proteins damaged by light-related processes is also important in these conditions, which may explain the presence of multiple peptidase genes in *F. cylindrus* (Mock and Valentin, 2004). Adaptations to low light levels under freezing conditions include upregulation of FCP genes (Mock and Valentin, 2004), leading to an increase in photosynthetic pigments and light-harvesting ability (McKew *et al.*,

2013). The combined presence of both high light and extreme cold imposes more stress on polar microalgae, which explains upregulation of stress response genes under these conditions (Mock and Valentin, 2004). Polar microalgae also experience long periods of darkness. Adaptations such as the ability to accumulate and use storage molecules including lipids, glucan and starch and enter hibernating states can aid survival without photosynthesis (Lyon and Mock, 2014).

Membranes surrounding the cell and organelles in microalgae need to be kept fluid during cold temperatures. Fluidity can be maintained by increasing concentration of polyunsaturated fatty acids (PUFA) (Lyon and Mock, 2014), seen by an upregulation of genes involved in fatty acid production under freezing conditions (Mock and Thomas, 2008).

Genes for ice-binding proteins (IBPs) have been found in diatoms, haptophytes and prasinophytes adapted to polar environments (Raymond and Kim, 2012). *F. cylindrus* responds to freezing temperatures by upregulating IBPs genes (Mock and Thomas, 2008). Presence of IBPs leads to ice-pitting activity and formation of smaller ice pockets (Raymond and Kim, 2012). This keeps the immediate environment surrounding microalgae as a liquid state, allowing import and export of molecules between the cell and surrounding water. Interestingly, IBP genes in the Raymond and Kim (2012) study showed homology to bacterial genes, suggesting that they were acquired by HGT. The acquisition of genes such as IBP may be a key component in the colonisation of sea-ice by microalgae.

It is important for microalgae to have sufficient access to nutrients and carbon whether they are limited by entrapment in sea-ice or freely available. It has been shown that enzymes involved in uptake of nitrate, ammonium and carbon in ice diatoms have evolved to be active at very low temperatures, whilst others such as nitrate reductase have been found to work best at slightly higher temperatures but are less sensitive to temperature changes (Priscu *et al.*, 1989). Enzymes such as ribulose-1,6-bisphosphate carboxylase (RUBISCO) involved in carbon fixation (Devos *et al.*, 1998) or ribosomal proteins for translation (Toseland *et al.*, 2013) make up for a decrease in activity in cold environment by increasing concentration.

Polar microalgae produce a range of osmoprotectants that protect cells by reducing the intracellular freezing point, an adaptation essential for sea-ice microalgae, which have to contend with high salinity and freezing temperatures. These include betaine, DMSP, sugars, polyols and amino acids (Lyon and Mock, 2014). Genes for proline synthesis, an important osmolyte, have been found in *F. cylindrus* salt shock EST libraries (Krell, 2006). In the same study, several abundant ion-transporters including antiporters were found, allowing *F. cylindrus* to maintain cellular homeostasis in high salt concentrations by passing ions both in and out of the cell (Krell, 2006).

Whilst some genes involved in adaptation can be linked to specific mechanisms and conditions, others may be harder to immediately identify. Many of the genes upregulated in transcription libraries or found after genome sequencing have no homology to known proteins (Mock *et al.*, 2006; Hwang *et al.*, 2008). Some genes such as putative transcription factors or those involved in protein editing show differential regulation (Hwang *et al.*, 2008), but further work is needed to determine their targets. As

mentioned earlier, several proteins display an increase or decrease in concentration in relation to conditions such as the cold, salinity and irradiance. Transcriptional and translational regulations underline these changes, and as such adaptations in gene regulatory networks are likely to be important in polar microalgae.

## Biological Interactions

Associations between microalgae and other organisms occur across marine ecosystems and shape microalgae evolution through both direct and indirect interactions.

Several reports detailing interactions between microalgae and bacteria show an exchange of products (reviewed by Natrah *et al.*, 2014), including organic compounds (e.g. sugars), inorganic nutrients (e.g. nitrogen and iron) and vitamins (e.g. B12 and biotin). This may be enhanced by attachment of bacteria to algal cells (Amin *et al.*, 2012). Bacterial products have the potential to impact microalgae evolution by selective pressure. A good example of this is dependence on cobalamin (vitamin B12) produced exclusively by bacteria. Microalgae contain two forms of methionine synthase: METH, which is B12 dependent and METE which is B12 independent, but thought to produce methionine at lower efficiencies (Helliwell *et al.*, 2011). Loss of METE has occurred independently on several occasions in a range of microalgae, likely due to downregulation of METE in the presence of B12 leading to a possible mechanism for loss in B12-rich environments (Helliwell *et al.*, 2011). The B12-dependent coccolithophore *E. huxleyi* was able to grow in media without B12, possibly due to close interactions seen with bacteria (Helliwell *et al.*, 2011). Interactions with bacteria provide the opportunity for HGT, which likely explains the large number of bacterial genes found in several microalgae (Armbrust *et al.*, 2004; Bowler *et al.*, 2008). Chances for HGT may be increased by algae themselves, by stimulating the release of transformable plasmid DNA in bacteria (Matsui *et al.*, 2003).

Dinoflagellates of the *Symbiodinium* genus are well known for their symbiosis with a range of cnidarians, in particular corals. Leggat *et al.* (2007) identified genes for ammonium and sulfate transporters, possibly associated with the transfer of inorganic nutrients from coral to dinoflagellate. A sugar permease was also identified which may provide the host with sugars, a common role within the coral-*Symbiodinium* symbiosis. A high number of antioxidants genes have been found within symbiotic *Symbiodinium* sp. which may be an adaptation to reduce the impact of ROS species, produced by photosynthesis, on the host (Bayer *et al.*, 2012). Amongst the antioxidants found was a bacterial nickel-type SOD containing an ubiquitin domain, suggesting that the gene may be a fusion from eukaryotic and prokaryotic lineages.

The presence of signal transduction pathways linked to cell surface receptors in a cultured *Symbiodinium* sp. may enable them to sense and explore the environment (Voolstra *et al.* 2009), which could be useful in host colonisation. An important consideration in microalgae within a symbiotic relationship is the coevolution between microalgae and host. Voolstra *et al.* (2009) found three species-specific genes (out of 115) in a colonising *Symbiodinium* not associated with other dinoflagellates. The highest dN/dS ratio,

an indicator of selective pressure, was found in one of these genes, indicating positive selection. It has been speculated that this may be necessary to coevolve with the host or to compete with other symbionts (Voolstra *et al.*, 2009). **See also: Algal Symbioses**

Several groups of algae are able to source nutrients from bacteria by phagotrophy. This includes haptophytes, cryptophytes, chlorophytes and dinoflagellates (Unrein *et al.*, 2014). The haptophyte *Prymnesium parvum* preys on bacteria and ciliates to complement its photosynthetic capabilities (Liu *et al.*, 2015). Genes to process fatty acids were upregulated in the presence of both types of prey, suggesting that *P. parvum* was able to use organic carbon acquired from both. Nitrogen, however, was primarily sourced from ciliates and iron from bacteria. In ciliate-associated cultures, genes for inorganic nitrogen uptake and processing were downregulated, whilst glutamine synthetase was downregulated and glutamate dehydrogenase was upregulated. This suggests that amino acids from ciliate prey are being used as a nitrogen source. In the presence of bacteria, genes for iron uptake were downregulated.

Whilst some interactions are beneficial, others can be harmful, leading to the evolution of defence mechanisms. Polyunsaturated aldehydes (PUA) are produced by several diatoms to reduce fitness in copepod grazers when mechanically disrupted (Pohnert *et al.*, 2002). Genes involved in PUA production include phospholipase and lipoxygenase (Amin *et al.*, 2012). The ability to use PUAs to reduce grazing depends not just on the species but the strain as well. One strain of *Thalassiosira rotula* was able to reduce the fitness of copepods, whilst the other was not (Pohnert *et al.*, 2002), demonstrating that different adaptations can be found within the same species. Dimethylsulfoniopropionate (DMSP), an organosulfur compound, is produced by several algal groups and may act to deter grazers. DMSP has other functions, so selective pressure may be influenced by factors other than predation. Mechanical defences such as the ability to produce a silica frustule in diatoms deter grazers (Hamm *et al.*, 2003) and antimicrobial compounds protect against pathogenic bacteria (Amin *et al.*, 2012).

Being able to sense either synergistic, pathogenic, competitive or predatory organisms may be highly advantageous. Very little is known regarding the ability of algae to sense other life forms, however, putative GAF domains have been found in *T. pseudonana* and *P. tricornutum*, which may bind acyl homoserine lactones associated with bacterial sensing (Amin *et al.*, 2012).

## Concluding Remarks

There are many adaptations found within marine microalgae, which enable them to survive in a variety of marine habitats. Differences in essential processes such as photosynthesis, NPQ and nutrient acquisition as well as acquisition of specialist genes allow microalgae to cope with a range of conditions. Their diversity and abundance has a far-reaching impact on ocean ecosystems including carbon cycling, primary production, geochemical deposits and as a food source. Microalgae have acquired their mosaic gene pool from photosynthetic organisms, heterotrophic eukaryotes and bacteria, giving them a unique range of abilities.

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