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Review

Molecular insights into the novel aspects of diatom biology

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Abstract. Diatoms are unicellular photosynthetic eukaryotes that are thought to contribute as much as 25% of global primary productivity. In spite of their ecological importance in the worlds oceans, very little information is available at the molecular level about the novel aspects of their biology. Recent advances, such as the development of gene transfer protocols, are now allowing the genetic dissection of diatom biology. Notable examples are advances in understanding the genetic basis for the silica-based bioinorganic pattern formation of their cell walls and for elucidating key aspects of diatom ecophysiology. The potentiation of current research will allow an evaluation of the use of diatoms to construct submicrometre-scale silicon structures for the nanotechnology industry and will reveal the molecular secrets underlying their ecological success.

Key words. Aequorin; Bacillariophyceae; *Cylindrotheca fusiformis*; diatoms; ecophysiology; endosymbiosis; fucoxanthin; frustule; frustulins; genetic transformation; heterokonts; marine algae; nanotechnology; pattern formation; *Phaeodactylum tricornutum*; phytoplankton; reporter genes; sex; silaffins; silica; silica deposition vesicle; Stramenopiles

Introduction

From the early days of microscopy diatoms have been a favourite group of organisms for biologists, due to their beautiful laceworklike cell walls, composed of amorphous silica (see example in fig. 1). These highly ordered structures were used as the basis for taxonomic classifications and for species identification. In parallel studies, the importance of diatoms in marine ecosystems and for global primary productivity was recognized. However, the underlying techniques of cellular and molecular biology, necessary for dissecting the biology of any organism, remained largely undeveloped. Also, the focus of much of the scientific community on the cornerstone model organisms such as yeast, *Drosophila melanogaster*, *Caenorhabditis elegans* and *Arabidopsis thaliana* resulted in diatom research being further marginalized away from the mainstream. But now, following the completion of large-scale genome sequencing programmes in the model organisms, attention is shifting towards less conventional organisms, with the hope of understanding novel processes, of dissecting molecular phylogenies, and for understanding organismal interactions with their environment. Consequently diatoms are now receiving renewed interest, most notably for understanding the molecular basis of their ecological success and for their potential applications in nanotechnology. This review summarizes our current understanding of some of the novel aspects of diatom biology and ecology.

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Diatom ecology

The world's oceans cover two-thirds of the earth's surface. As such they are an essential component of the global ecosystem. For example, approximately 50% of global primary productivity is derived from marine sources. Marine phytoplankton are at the bottom of ma-

rine food webs and thus determine the well-being (or not) of the whole marine ecosystem. We know very little about the biology of these organisms, partly because it has not yet been possible to establish representative model organisms for laboratory studies from the different algal groups.

Phytoplankton is comprised of photoautotrophic organisms from 12 taxonomic divisions spanning three Kingdoms [1]. It includes photosynthetic bacterioplankton such as prochlorophytes (e.g. *Prochlorococcus*) and cyanobacteria (e.g. the *Synechococcus* genus) [2], and eukaryotic microalgae such as heterokontophytes (brown algae), rhodophytes (red algae) and chlorophytes (green algae) [3]. Diatoms are a group of unicellular heterokonts.

Diatoms are the most important group of eukaryotic phytoplankton, responsible for close to 40% of marine primary productivity [1]. There are well over 250 genera of living diatoms, with perhaps as many as 100,000 species, making them the most diverse group of photosynthetic organisms after the angiosperms [3].

Diatom abundance is generally highest at the beginning of spring and in the autumn, when nutrients are not limiting and when light intensity and day length are optimal for diatom photosynthesis. More unusual adaptations have also evolved. For example, in nutrient-depleted conditions such as permanently stratified oligotrophic regions of the ocean, solitary or mat-forming diatoms (e.g. *Rhizosolenia*) can sometimes be successful [3]. This is thought to be due to vertical migration or through symbioses with nitrogen-fixing azotrophs. Diatoms are also an important component of phytoplankton in fresh waters.

In some regions of the oceans, the annual production of fixed carbon can be up to 2000 g m^{-2} (equivalent to a cereal or corn crop), e.g. in the Peruvian upwelling [3, 4]. Furthermore, algal blooms are often caused by diatoms. These blooms can sometimes be harmful, producing biofouling mucilage and/or toxins such as domoic acid (one of the causes of amnesic shellfish poisoning), which can have negative impacts on the local ecosystem, as well as on fishing and aquaculture activities.

The most distinctive characteristic of diatoms is their siliceous cell wall that resembles a glass (or more accurately quartz) box. Ecologically the diatom requirement for silica means that they are a critical component of global biogeochemical silica cycling [1]. The fossil deposits from past geological periods are now used as diatomaceous earth, which is used in filters, deodorants and decoloring agents, and as an abrasive in toothpaste, amongst other things. Furthermore, the invention of dynamite was made possible by adsorbing nitroglycerin onto diatomite.

Basic features of diatom biology

Diatoms are within the class *Bacillariophyceae* in the Heterokont division. Their most well known characteristic is the presence of a unique type of cell wall (known as frustule), which is constructed from two halves of amorphous polymerized silica taking the form of a box with an overlapping lid [3]. The inner frustule is known as the hypotheca, and the outer one is denoted the epitheca. The frustules typically comprise beautiful highly ordered laceworklike silica structures (fig. 1). Diatom cell walls can therefore be regarded as a paradigm for the controlled production of nanostructured silica, and their ceramic manufacturing capabilities go well beyond current human capabilities, both in terms of miniaturization and complexity (see later). The ecological role of the silica frustule is not yet understood. It has been suggested that it may form a robust first line of defence against grazers [5].

There are two major diatom groups, the centric diatoms and the pennate diatoms, which are distinguished from each other on the basis of differences in cell wall structure [3]. A pennate diatom is elongated and bilaterally symmetrical in face view, whereas centric diatoms are radially symmetrical and often resemble a petri dish. In both cases, the silica cell walls are ornamented with species-specific patterns and structures, which has made identification and taxonomic classification over the last century straightforward.

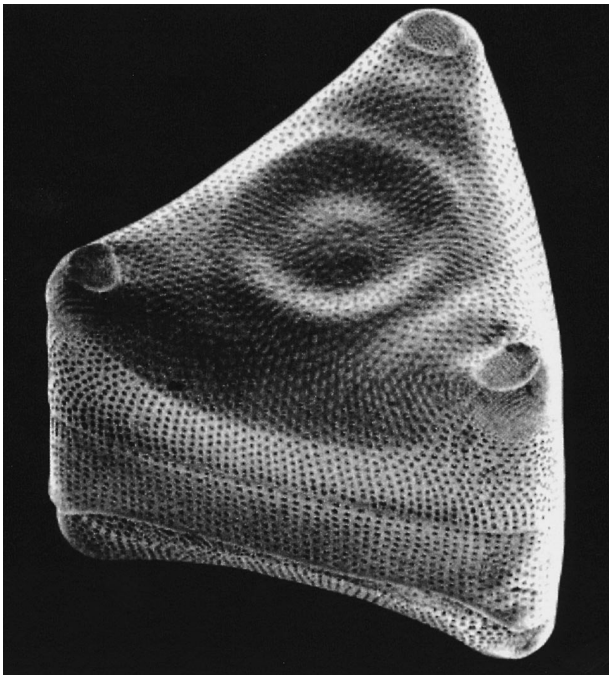

Figure 1. Life in a glass box. Scanning electron micrograph of *Lampriscus (Triceratium) shabdoltianum* Grev. (×760). Photograph courtesy of Masahiko Idei, Bunkyo University Women's College, Kanagawa, Japan.

Like other photosynthetic eukaryotes, the photosynthetic apparatus of diatoms is housed within plastids inside the cell. Plastids are likely to have arisen from the engulfment of a photosynthetic bacterium such as a cyanobacteria by a unicellular eukaryotic heterotroph at least 1.5 billion years ago [3, 6, 7]. But whereas the plastids of green algae and higher plants are surrounded by two membranes, diatom plastids have four membranes. It is therefore believed that diatoms and related algae arose following a secondary endosymbiotic event in which a eukaryotic alga was engulfed by a second eukaryotic phagocyte [8, 9]. In such a scenario the inner two membranes would represent the membranes that normally surround the chloroplast, whereas the third membrane (as counted from the inside) is derived from the endosymbiont's plasma membrane, and the outer membrane is continuous with the endoplasmic reticulum of the host cell. These different plastid structures reflect the very different phylogenetic histories of green algae and diatoms [3, 9–11].

The brown colour of diatoms is due to the characteristic presence of the carotenoid fucoxanthin, which is utilized together with chlorophyll *a* and *c* for photosynthetic light harvesting. These pigments are bound within the light-harvesting antenna complexes by fucoxanthin, chlorophyll *a/c*-binding proteins (FCPs), which are homologous to the chlorophyll *a/b*-binding proteins (CABs) of green algae and higher plants. The FCPs are integral membrane proteins localized on the thylakoid membranes within the plastid, and their primary function is to capture and target light energy to chlorophyll *a* within the photosynthetic reaction centres [12].

Several *FCP* genes have been cloned from diatoms, e.g., two *FCP* gene clusters have been isolated from *Phaeodactylum tricornutum*, containing, respectively, four and two individual *FCP* genes [13, 14]. The 5′ and 3′ regulatory sequences of these genes are the most commonly utilized sequences for the generation of chimeric genes for diatom transformation (see later).

As would be expected, *FCP* genes are generally inducible by light. They have therefore been used to perform action spectra to determine the active wavelengths of light for mediating photoregulated gene expression in diatoms. These studies have revealed that *Thalassiosira weissflogii* is likely to utilize cryptochrome and rhodopsin photoreceptors, and surprisingly also phytochrome-like receptors, because gene expression was found to be responsive to low fluence red- and far red-light pulses [15]. The molecular nature of diatom photoreceptors awaits their definitive isolation and cloning.

Like the CABs of higher plants, diatom FCPs are nuclear encoded. However, although FCPs are functionally and structurally homologous to higher plant CABs, the transport mechanisms that target them to the diatom plastid are very different, due to the fact that diatom plastids are enclosed within four membranes. It has been found that the N-terminal translocation sequences of immature FCPs are in fact bipartite. One of these is likely to be utilized for translocation through the outer membrane, whereas the other (a more conventional plastid transit peptide) is necessary for transport through the inner two membranes [16]. The former sequence resembles an endoplasmatic reticulum signal peptide and, indeed, is capable of mediating cotranslational import and processing by microsomal membranes. The process has been more thoroughly studied for a related presequence from the γ subunit of the plastid ATP synthase from the centric diatom *Odontella sinensis* [17]. However, it is not yet clear how proteins traverse the second (as counted from the outside) membrane, which is thought to be derived from the plasma membrane of the algal endosymbiont (discussed in [17]).

Studies to date indicate that the functioning of diatom photosynthesis is highly similar to other photosynthetic eukaryotes and that they contain the usual complement of proteins involved in photosynthetic reactions. A few of the genes encoding some of these components have been described (e.g. [14]). One anomaly is that both the small and large subunits of ribulose 1,5-bisphosphate carboxylase/oxygenase (RUBISCO) are plastid-encoded in diatoms, whereas in green algae and higher plants the small subunit (RBCS) is nuclear encoded. Also, the primary structure of diatom ATP synthase genes are more similar to cyanobacteria than green algae and higher plants [18], which highlights the different phylogenetic histories of green and brown algae.

One highly significant observation that has recently been made is that diatoms appear to be capable of C_4 photosynthesis [19]. This is a specialized form of photosynthesis restricted to a few land plants such as sugar cane and maize which allows a more efficient utilization of available CO_2. In these plants, C_4 metabolism is restricted to one cell type, whereas RUBISCO-mediated carbon fixation is spatially separated in another. The report by Reinfelder and colleagues [19] is the first description of C_4 photosynthesis in a marine microalga (*Thalassiosira weissflogii*), and the data suggest that C_4 carbon metabolism may be confined to the cytoplasm, away from the RUBISCO-dependent reactions within the plastid. If shown to be a universal feature of diatoms, C_4 photosynthesis may be one explanation for their ecological success in the world's oceans, in that it provides a means of storing carbon for use in less favourable conditions. Furthermore, study of the process in unicellular diatoms promises to reveal strategies in which yields could be improved in crop plants through genetic manipulation.

As far as is known, vegetative diatom cells are diploid. Diatom cell division normally proceeds through asexual mitotic divisions. However, because vegetative cellular growth is normally restricted by the rigid siliceous cell walls, the two daughter cells are initially formed inside

the parent cell. One sibling cell is therefore identical in size to the parent cell in that its epitheca is derived from it, whereas the other daughter cell is smaller because its epitheca is derived from the hypotheca of the parent cell [13]. Consequently, mitotically dividing diatom populations decrease in mean size over time. In the majority of species, size restoration occurs through sexual reproduction followed by auxospore formation once a critical size threshold has been reached (typically 30–40% of the maximum size), below which mitotic cell division is no longer possible [20].

Even after 150 years of microscopic observations, knowledge of diatom sex is only fragmentary. The main reasons for this are because diatom sexuality is limited to brief periods (minutes or hours) which may occur less than once a year in some species and which involve only a small number of vegetative cells in a population. This is presumably a reflection of the fact that sex in a unicellular organism has considerably more risks than in a complex multicellular organism.

Sexual reproduction in diatoms takes many forms [21]. In centric diatoms sex appears to be universally oogamous, with the production of haploid sperm and eggs. Within the pennate diatoms there is much more variety, including anisogamy, isogamy, automixis and apomixis. Several in-depth reviews are available on the topic (e.g. [3, 21, 22]). Sex is often induced when vegetative cells are exposed to unfavourable growth conditions [20]. In the centric diatom *T. weissflogii* sexual reproduction can be induced by a sudden change in the ambient light regime [23]. Armbrust exploited this phenomenon to identify genes that were induced during the onset of sexual reproduction [24]. Three of the genes identified (*SIG1*, *SIG2*, *SIG3*) encode proteins with a series of common features. All have putative amino-terminal signal sequences, suggesting that they are secreted, and all contain a cysteine-rich domain originally identified in human epithelial growth factor (EGF) and which is also present in a family of extracellular matrix glycoproteins known as tenascins. Tenascins promote cell-cell interactions during animal development by promoting cell adhesion. It is therefore possible that the SIG polypeptides are involved in sperm-egg recognition.

Silica deposition

To date, the process that has been best studied in diatoms is that of silica cell wall formation, most notably by electron microscopic observations from the laboratory of Ben Volcani (recently deceased) and Jeremy Pickett-Heaps (e.g. [25]). During cell division, two new silica valves are produced back-to-back, one inside each daughter cell. These valves are formed by the controlled precipitation of silica within a specialized membrane vesicle called the silica deposition vesicle (SDV). Because it has not yet been possible to isolate SDVs, knowledge of its composition is still only rudimentary. However, it has recently been discovered that one of the first events of the silica deposition process within the SDV is the formation of nanoscale spheres [26]. This is mediated within diatom cell walls by a combination of polyamines together with modified peptides known as silaffins, that contain covalently modified lysine-lysine repeat elements. The covalent modifications are oligo-*N*-methyl-propylamine units, a modification that has not been found in any other biological system. The silaffins and polyamines can even promote silica precipitation in vitro, generating a network of nanospheres with diameters between 100 and 1000 nm, depending on the molecules used [26].

Silaffins bind the silica scaffold of diatom cell walls extremely tightly and can only be removed following complete solubilization of silica with anhydrous hydrogen fluoride. *Cylindrotheca fusiformis* contains two major types of silaffins, denoted silaffin-1A (4 kDa) and silaffin-1B (8 kDa). Both are proteolytically derived from a single gene denoted *SIL1*.

Hydrogen fluoride-extractable material also contains another fraction of high molecular mass, denoted HEP200 (200-kDa hydrogen fluoride-extractable protein). Immunolocalization experiments revealed that HEP200 was specifically localized to a subset of silica strips that may correspond to the region in which the epitheca overlaps the hypotheca in intact *Cylindrotheca fusiformis* cell walls [27].

A small gene family encodes HEP200-like proteins which are localized together in the *C. fusiformis* genome, much like the *FCP* gene clusters in *Phaeodactylum tricornutum* [13]. All encode proteins with characteristic repeat domains, so have been denoted HEP proteins.

Another group of unrelated proteins has been localized to *C. fusiformis* cell walls. These are calcium-binding glycoproteins known as frustulins [28, 29], which are much more loosely associated and can be extracted from diatom cell walls with EDTA. To date, five different types of frustulins have been described, based on their different molecular weights: α-frustulin (75 kDa), β-frustulin (105 kDa), δ-frustulin (200 kDa), ε-frustulin (35 kDa) and γ-frustulin (140 kDa). All contain characteristic acidic cysteine-rich domains (ACR domains). The function of this domain is not yet known [29]. Immunological studies have demonstrated that, unlike HEP200, the frustulins are localized ubiquitously over the exterior of the diatom cell wall [27], although it is possible that individual frustulins have specific localization profiles.

Each of the frustulin, HEP and silaffin protein families are synthesized as precursor forms which contain amino-terminal presequences. The most N-terminal sequences resemble typical signal sequences required for cotranslational import of proteins into the endoplasmatic reticu-

lum, whereas the subsequent sequence seems to represent a new type of targeting sequence. It has been speculated that this may serve as the targeting sequence to direct these proteins from the Golgi apparatus to the SDV [29]. Such a model implies that the SDV and the Golgi apparatus are connected via transport vesicles, something which has not yet been demonstrated. It is also not known how silica is directed into the SDV.

The species-specific patterns of silica nanofabrication indicate that there is a considerable genetic basis underlying pattern formation. The groundbreaking work of Kröger and colleagues [26–29] has revealed clues about how different patterns could be formed by different batteries of frustulins, HEPs and silaffins, but we are still a long way from understanding the underlying mechanisms. It is likely that many other cell wall components await identification. Clearly, dissection of the genetic-based mechanisms of bioinorganic pattern formation by which diatoms can transform soluble silica into sturdy intricate structures at ambient temperatures and pressures could eventually allow materials scientists to generate nano- and micrometre-scale silica-based structures that could be used in molecular computers and for ceramic-based microfiltration, microsieve and microcapture devices [30–32].

In one study from the group of Ben Volcani [33] silicon-responsive complementary DNAs (cDNAs) were isolated from *C. fusiformis*. Some of these were subsequently identified as silicon transporters (SITs) [34, 35] specifically able to transport silica tetrahydroxide, the most abundant form of soluble silica in the oceans. *SIT* gene expression is induced at the onset of cell division, demonstrating the dynamic control of silica metabolism in diatoms.

Genetic transformation

A major bottleneck for exploring the molecular and cellular biology of diatoms was for many years the absence of a protocol for genetic transformation. This was finally resolved in 1995, with a report on the successful generation of transgenic lines of *Cyclotella cryptica* and *Navicula saprophila* [36]. Similar approaches were subsequently used to transform *P. tricornutum* [37, 38] and *C. fusiformis* [39]. These systems are based on helium-accelerated particle bombardment of exogenous DNA followed by selection of transfected cells using antibiotics. In all cases, it was important to use diatom-derived regulatory sequences to control transgene expression, most commonly derived from *FCP* genes.

The systems are most advanced for the pennate diatom *P. tricornutum*. A range of antibiotic resistance genes can be used to select for transgenic clones, including kanamycin, phleomycin, nourseothricin and puromycin, and plasmids containing nonselectable genes can be cotransformed with these selectable markers at an efficiency of around 60%, even though transformation efficiencies are low, on the order of 10^{-6} per microgram of plasmid DNA. The plasmid DNA is integrated randomly into the genome in one or a few copies by illegitimate recombination, and is stable without selection pressure [38].

The generation of transgenic organisms is an essential tool for dissecting basic biological processes. In diatoms, transgenic technologies hold the promise of revealing the fundamental mechanisms of protein targeting, e.g. to the plastids and to the silica deposition vesicles and frustules, of understanding mitotic and meiotic cell division, and for studying diatom interactions with their environment.

Because genetic transformation is such a recent development in diatoms, and because only a handful of groups are utilizing the technology, progress is painfully slow, and most efforts are still at the level of establishment of the rudimentary technologies. Such technologies include the use of reporter genes to study gene regulation and protein targeting, such as chloramphenicol acetyl transferase [37], luciferase [38], β-glucuronidase (GUS) [38, 40] and green fluorescent protein (GFP) [40] (figs. 2, 3). The next few years will witness the use of these reporter genes to elucidate novel aspects of diatom cell biology. A recent report also detailed the use of transgenic diatoms containing the calcium-sensitive photoprotein aequorin to study diatom perception of environmental stimuli [41] (see later).

Figure 2. GUS activity in transgenic cells of *P. tricornutum*. The enzyme activity has been visualized by a histological staining procedure, revealed as a blue colour, as previously described [38].

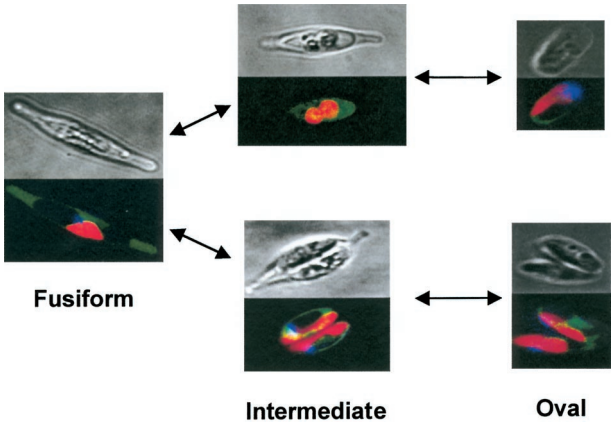

Figure 3. Morphotype transformation in *P. tricornutum*. Cells expressing a chimeric gene containing *GFP* were observed by fluorescence microscopy. The GFP-derived green fluorescence allows better visualization of the changes occurring in the cytosolic compartment during morphotype cell shape changes in this species of diatom. The images show transformations of oval and fusiform cells. Chlorophyll is shown in red, and the nucleus is shown in blue. *P. tricornutum* is an atypical diatom in that it is able to change shape. Normally, the rigid siliceous diatom shell prevents such phenomena. However, the frustules of *P. tricornutum* cells are only weakly silicified, thus permitting changes in cell shape [25]. These morphotype changes are not thought to be important for the *P. tricornutum* life cycle, although in benthic habitats (attached to a surface rather than free living, i.e. planktonic), *P. tricornutum* cells tend to display an oval morphotype, whereas in planktonic conditions the cells tend to be fusiform. Photographs by Oxana Malakhova.

There is currently only one report in which diatom metabolism was significantly modified by genetic engineering [39]. In this work, a frustulin gene from *Navicula pelliculosa* was expressed in *C. fusiformis* and shown to be correctly targeted to the cell wall. However, it was not shown whether this resulted in any modifications in cell wall architecture. In the same report a *Chlorella* glucose transporter gene was expressed in *C. fusiformis*, and transgenic cells were able to take up glucose.

In addition to the future exploitation of reporter gene-based technologies to explore diatom biology, the adaptation of genetic transformation protocols to other diatom species is also important. To date, almost all studies have been performed on 'lab rat' diatom species such as *P. tricornutum* and *C. fusiformis*, neither of which possesses highly ornamented cell walls nor has significant ecological importance (although *C. fusiformis* is closely related to *Cylindrotheca closterium*, which does have these characteristics). Furthermore, although *T. weissflogii* could be transiently transfected with a *GUS* reporter gene [38], the only centric species that can be stably transformed at this moment is *Cyclotella cryptica* [36]. Work in our laboratory has demonstrated that current transformation protocols are not effective in other diatom species (e.g. *Thalassiosira rotula*, *Ditylum brightwelli*, *Odontella sinensis*) [S. Scala and C. Bowler, unpublished observations], so major investments are likely to be necessary to develop transformation systems for ecologically relevant diatom species.

It is also important that other technologies be established, e.g. for inactivating gene expression. The best way to generate organisms with a specific knockout in a gene of interest is by homologous recombination. Such methods are straightforward in organisms such as yeast, moss and mice, although not in higher plants. Unfortunately, the limited information available suggests that homologous recombinaton of transgenes is unlikely in diatoms [38]. However, alternative techniques are available in other organisms, such as antisense and sense suppression, and RNA interference [42] (collectively known as posttranscriptional gene silencing) [43]. Due to the universality of the basic cellular mechanisms involved, there is a good likelihood that these approaches will also be effective in diatoms.

Interactions with the environment

The ecological success of diatoms suggests that they must be highly adaptable to changing environmental situations and that they must have sophisticated sensing systems that activate responses to it. These aspects have traditionally been difficult to study. But in a watershed article Miralto et al. [44] recently reported that diatoms synthesize specific aldehyde molecules that can arrest mitosis during egg development of their principal grazers, the copepods. Such a 'birth-control pill' suggests a mechanism whereby diatom populations can influence their local environment by controlling the population size of the zooplankton that eat them. These molecules also display antimitotic activity in diatoms themselves [45]. In addition to being defined as 'defence molecules', these aldehydes may therefore have a 'signaling' role for the control of diatom population size, e.g. by acting as a suicide trigger for bloom termination. Such a proposal is a radical alternative to the traditional dogmas about bloom decline based on nutrient depletion.

Although this is the first example of a putative signaling molecule in a marine phytoplankton, it is likely to be just the first of many hundreds that will be discovered in future years. The traditional view that diatoms and other phytoplankton are passive components of marine ecosystems is wrong, and the oceans are likely to be a heterogeneous soup of different signals that are perceived by sophisticated sensing mechanisms to control organismal adaptive responses.

The importance of molecular sensing of environmental signals has been further supported by studies of calcium-dependent signal transduction in *P. tricornutum* responding to environmental signals such as light, nutrients and pollutants [41]. In this work, we utilized transgenic diatom

cells expressing the calcium-sensitive photoprotein aequorin. Based on the premise that calcium is a second messenger in the vast majority of cellular responses to external signals in other eukaryotes, we measured changes in intracellular calcium in diatom cells exposed to a range of different ecologically relevant stimuli. Most notably, this work revealed that diatoms possess sensing mechanisms for perceiving changes in turbulence and osmotic stress.

Furthermore, the existence of exquisitely sensitive calcium-dependent signaling mechanisms induced by iron but not other nutrients was demonstrated. Iron appears to be the critical nutrient regulating phytoplankton abundance in many regions of the oceans (see [1] and references therein). This study therefore demonstrates the power of transgenic technologies to elucidate fundamental aspects of diatom ecology.

Signaling in an ecological context can also be inferred from studies of iron uptake mechanisms in algal communities [46]. In this work it was demonstrated that different algae can utilize different complexed forms of iron, e. g. cyanobacteria can transport Fe-complexed siderophores, whereas diatoms utilize preferentially iron complexed in porphyrins. Because siderophores are important molecules in cyanobacterial metabolism, as are porphyrins in diatom metabolism, such specifically differentiated uptake mechanisms can clearly provide selective advantages for one cell type over another.

Although it is possible that these molecules remain in the boundary layer around each cell, it is more likely that they are freely diffusible. Consequently, it would make little sense for one cell to use this strategy unless its neighbours within the community also did the same thing. It is therefore plausible that these molecules are used for quorum sensing and that the individual cells within the population are able to act together for the collective well-being of the community by sharing the available resources.

Concluding remarks

The arrival of the new millenium has brought a paradigm shift in biological research. No longer are we confined to the study of single genes and single isolated phenomena, as was the case for the last 30 years or so. The completion of several genome projects and the sheer volume of sequence data available in the public databases now allows the study of several thousand genes at a time as well as the possibility to finely dissect highly complex processes at the whole genome level.

In the year 2001 where does diatom research stand? Perhaps up until now the most significant success stories have been the realization of the importance of diatoms for aquatic and marine ecosystems and in a convincing theory of their phylogenetic origins [3, 9–11]. But their unique origins and ecological success intuitively infer that they possess many novel cellular characteristics. Unfortunately, many of the molecular secrets of diatoms still await discovery. In this regard it is incredible that public databases of DNA sequences currently contain less than 50 accessions for nuclear-encoded protein coding sequences from diatoms.

In summary, although diatom research has made some important advances in recent years, it is clear that radical measures are required to make diatoms accessible to the enormously powerful genomic and postgenomic research platforms that are now available for better-studied organisms. Given the novelty and potential applicability of certain aspects of diatom ecology and cell biology, this is surprising. However, now that a range of molecular technologies are in place it is to be hoped that more researchers will be attracted to this field so that progress can be accelerated.

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