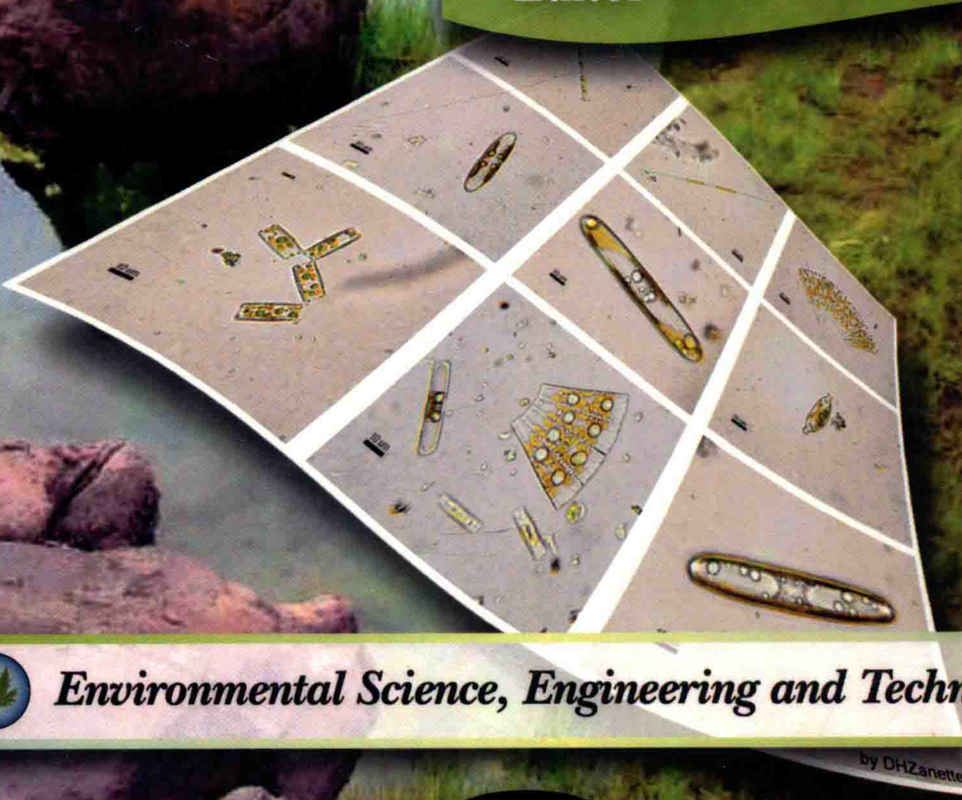
DIATOMS

Ecology and Life Cycle

James C. Compton
Editor



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DIATOMS: ECOLOGY AND LIFE CYCLE

JAMES C. COMPTON
EDITOR

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PREFACE

Diatoms are a major group of algae, and are one of the most common types of phytoplankton. Diatom communities are a popular tool for monitoring environmental conditions, past and present, and are commonly used in studies of water quality. This book presents topical research data in the study of diatoms, including the role of environmental factors in shaping diatom frustule; marine diatom communities; diatom classification methods; an analysis of the diatom flora of lakes, ponds and streams of the Kuril Islands; the ecological information of diatoms provides information on the reconstruction of palaeo-environments; and the regulatory influences of diatoms on benthic invertebrates.

Chapter 1 - Environment factors play an important role in driving morphological variations of diatom frustule. Adaptation to local physico-chemical changes translates into morphological plasticity, leading to structural variation of the valve toward the best solution in facing adverse conditions. Such phenotypic variations, that must be considered as an aspect of the gene expression within a species or population, mainly affect the cell size, the length:width ratio in pennate diatoms and the diameter in centrics, while always maintaining the normal outline of the valves; moreover, changes can involve pore openings and virgae, fibulae and anchorage structures.

In contrast, teratological forms, that can be induced by acute or chronic environmental stresses, do not have a genetic basis and are a consequence of alterations of the individual biochemical processes leading to valve formation. Diatom teratological forms usually have a deformed outline of the valve, a different striation pattern, loss of areolae and sometimes interruption of the raphe slit, all these modifications potentially altering cell movement and physiological mechanisms.

This chapter summarizes the results of the most important studies conducted on the morphological variability and teratological forms carried out from 1890 up to date, with the aim to provide a tentative attribution of the morphological variations to a series of environmental factors.

Chapter 2 - Diatoms dominate the phytoplankton communities in the most productive oceanic areas, i.e., coastal ecosystems and geostrophic front. Consequently, their contribution to marine primary productivity at global scale is estimated to be 30% to 40%. Furthermore, this group forms the basis of the food web that characterizes these regions and sustains the most important fisheries on the planet. Recent studies indicate that the diatom genome diversity could be the secret of its success and dominance in the oceans as this genomic potential would explain its high response capacity to sudden environmental changes.

Accordingly, the high physiological plasticity of the diatoms has been demonstrated from laboratory studies. However, the studies demonstrating this acclimation capacity in natural assemblages are scarce. In the present report, diatom communities inhabiting the Alboran Sea (the westernmost basin in the Mediterranean) are characterized both taxonomically and physiologically by using data collected from different research surveys performed for the last 14 years. Four main type-communities dominated by diatoms were identified. The community 1 was co-dominated by Thalassiosira, Chaetoceros, Nitzschia, Thalassionema and Leptocylindrus. The community 2 was characterized by the dominance of Pseudo-nitzschia and Chaetoceros. The community 3 was clearly characterized by a high abundance of Leptocylindrus while the community 4 was dominated by Chaetoceros accompanied by Leptocylindrus and Pseudo-nitzschia. The analysis of the hydrological conditions indicates that the four communities grew at high nutrient concentrations. Besides, the communities 1 and 2 were isolated close to the lower limit of the mixed layer while the communities 3 and 4 grew in the surface layer, within the mixed layer. Consequently, the cells making up the communities 3 and 4 can be considered R-strategists. The physiological performance of the four communities was different. Thus, the differences in chlorophyll a specific absorption coefficients and primary productivity rates were significant statistically, especially between communities 3 and 4. These differences could be due partially to the higher S/V obtained for the community dominated by Leptocylindrus, which should improve its resource utilization rates per unit volume. However, these shape traits do not explain fully the photosynthetic performance of the two communities, suggesting that the differences could be a consequence of the taxonomical composition beyond the shape constraints.

Chapter 3 - The diatoms are very useful bio-indicators of the environment. They are an indicator of wide range of physico-chemical parameters, like the water quality and the trophic status parameters of the ecosystem. According to this, they can be classified into one class of a certain abiotic parameter. Without a domain expert knowledge, by using classical statistical approaches such as canonical correspondence analysis (CCA) and principal component analysis (PCA), it is possible to find a model for a diatom-indicator relationship with a certain degree of prediction accuracy. Although these techniques provide very useful insights into data, they are limited in terms of interpretability. By using classical decision trees, an obvious progress in a direction of interpretability is made. However, decision trees have several drawbacks, namely they are not resistant to over fitting and are not robust to data change, which is one of the essential properties of the ecological data.

In order to overcome these drawbacks, in this chapter, a novel method for diatom classification is proposed. The method induces pattern trees by using several evenly fuzzy membership functions. In this chapter, novel fuzzy membership functions are proposed by modifying some existing ones, in order to make more accurate models. An intensive study of the influence of the fuzzy membership functions and the number of membership functions used per attribute on the classification accuracy is made. The experiments show that some of the proposed fuzzy membership functions have outperformed the trapezoidal, triangular and Gaussian membership functions.

Since the ecological preferences of the known diatom organisms present the relation between the diatom and the indicators (certain trophic state or water quality class), the authors have transformed the physico-chemical parameters into water quality and trophic state classes. Then, pattern trees based on the water quality and trophic state classes are induced in the same manner.

The method is fully automated and produces model trees, which can be further transformed into rules. These rules are verified by the existing ecological preferences for the known diatoms in the literature, and add new knowledge about the unknown diatoms. Some of the obtained model trees will be presented and discussed in the chapter.

The proposed method is compared against several classification methods like C4.5, Boosted C4.5, Bagging C4.5, k-Nearest Neighbour and etc. The results show that the proposed method obtained high accuracy for diatom classification, maintain compact model structure, is resistance to over fitting, robust to data change and produces easily interpreted models.

Chapter 4 - An analysis of diatoms of the fresh-water bodies (lakes, streams, hot springs) in islands of the North (Shiashkotan, Kharimkotan, Onekotan, Simushir, Matua), Middle (Ketoi, Rasshua) and South (Kunaschir, Iturup, Shikotan, Zelenyy, Tanfilyeva and Iuriy) Kuriles was carried out. In the water bodes studied, more than 500 taxons of diatoms were identified. The peculiarities of forming the diatoms associations in the multitype water bodies were considered and it was shown that the abundance of diatoms, their species composition and ecological structure of complexes were first of all related to local conditions of water bodies differing in the water structure, depth, mineralization, alkalinity and temperature.

Chapter 5 - Ecological information about diatoms is useful for reconstruction of palaeo-environments influenced by marine transgression and regression. Each diatom has a different habitat, especially regarding salinity. In the coastal region, salinity changes occur controlled by marine transgression and regression. And, these salinity changes cause changes of diatom assemblages. If diatoms are in the sediments deposited under the influence of marine transgression and regression, reconstruction of palaeo-environmental changes based on ecological information of diatoms can be done.

The authors analyzed diatom assemblages from sediment cores from the Nobi Plain, central Japan. Five diatom assemblage zones were identified: (1) at the beginning of the Holocene, freshwater species were dominant; (2) then, marine and brackish-marine species increased, indicating transgression; (3) in the middle Holocene, proportions of marine and brackish-marine species became almost constant, with marine species dominant; (4) marine species began to be replaced by freshwater species, indicating marine regression as a result of delta progradation; and (5) freshwater species again became dominant.

These diatom assemblages correlate with previously defined lithological units: zone 1 and 2 with fluvial to coastal plain deposits, zone 3 with inner bay or prodelta deposits, zone 4 mainly with delta front slope deposits, and zone 5 with delta front platform deposits and delta plain and flood plain deposits. And, the percentage of marine diatom species is almost positively correlated with electrical conductivity (EC—which is considered to be a proxy of salinity, although there are the effects of compaction and grain size distribution), especially in inner bay deposits.

In summary, if there are many diatoms in sediments with good storage condition, the authors can directly reconstruct salinity with high accuracy. Thus, the ecology of diatoms is useful for reconstruction of palaeo-environmental changes, especially those controlled by marine transgression and regression.

Chapter 6 - Diatoms play several ecological roles in the marine benthos as well as in the plankton. Some diatoms have a deterrent power against grazers as they produce toxic aldehydes and other compounds able to reduce the viability of planktonic copepod embryos. Correspondingly, diatoms of the genus Cocconeis and in particular C. scutellum parva and C.

neothumensis, are able to selectively destroy the androgenic gland (AG) and the testis of the shrimp Hippolyte inermis, so determining its early sex reversal, in the field and in the laboratory. These effects are due to a specific apoptogenic activity affecting the shrimp's AG in a very narrow temporal window. Extracts of these diatoms also trigger the quick apoptosis of selected cancer cells. The still unknown active compound might have, therefore, interesting biotechnological applications. In addition, it was demonstrated that among the wound-activated compounds characterizing several benthic diatoms, also a large set of volatile organic compounds (VOC) exists. VOCs produced by Cocconeis spp. after wounding influence the behaviour of several benthic invertebrates, acting as a repellent or attractant according to the life strategy of individual species. In this chapter the authors review our knowledge about the "regulatory" influences of diatom metabolites on benthic invertebrates, discussing their role as both physiologic modulators and infochemicals.

Chapter 7 - Benthic diatom assemblages were studied to highlight their response to different nutrient concentrations. Three sublittoral sites of the Gulf of Trieste (Italy) were investigated: St. C1 (a marine sanctuary), St. AA1 (subjected to river flows) and St. Duct (nearby an underwater sewage duct). Nutrients were analysed in the overlying water. Benthic diatom abundance was estimated by microscopic analyses. Diversity indices were calculated and k-dominance curves were applied to abundance data. A cluster analysis on species was performed. Principal component analysis was computed on species abundance, nutrients and samplings. Fuzzy set theory was applied to obtain the degrees of membership between each species and each nutrient. St. Duct was characterised by ammonium (NH4+) and phosphate (PO43¯) enrichment. The highest richness and diversity were obtained at St. C1, whereas St. Duct was characterised by the highest dominance. Navicula and Nitzschia were the most abundant genera at all the investigated stations. Paralia sulcata was the most abundant benthic species at St. C1 and St. AA1 (8.2% and 20.0%, respectively), while at St. Duct Navicula directa was dominant (51% of the total abundance). The dendrogram separated five groups; one of these comprised only one species, i.e. the tychopelagic Cylindrotheca closterium. The fuzzy sets revealed a phosphate loving group which included, among others, N. directa, Thalassiosira eccentrica, Entomoneis alata and Nitzschia panduriformis. The highly silicified P. sulcata showed the highest degree of membership with silicate, while the majority of Nitzschia species showed the highest ones with nitrite. C. closterium did not show high degree of membership with any of the nutrients, seeming to prefer oligotrophic conditions. In nutrient enrichment conditions, total abundance was high, but an enhanced dominance of a single species occurred, leading to a decrease in diversity. In oligotrophic conditions, when diatoms were limited by more than one nutrient, thus not providing a competitive advantage to any single species, high diversity was maintained. This study suggests that not only macrobenthos but also marine benthic diatoms can be useful indicators of nutrient enrichment, representing a potential and innovative tool in biomonitoring.

Chapter 8 - Paleoclimatologists advocate learning from the past to know the natural and anthropogenically induced climatic shifts that occurred in the history of the Earth, and to estimate future changes in ecological systems related to the projected range of temperature increases. Framed within this context, current rates of global warming are unprecedented based on the last 10,000 years of paleoclimatological evidence. Diatom analysis has played a major role in the reconstruction of these past climate changes, bringing evidences of water and air temperature fluctuations, as well as of climatically driven variations in water chemistry variables. Most of these evidences came from North American and European records, while the number of studies in South America has been considerably lower. Hence, many questions regarding the natural climatic cycles and the strength of human induced changes remain unanswered for vast regions of South America. In Central Argentina, the occurrence of many shallow lakes with sedimentary records encompassing the last 10,000 years, as well as outcropping alluvial sequences of Late Pleistocene and Holocene origin, provide good opportunities for studying these topics. Moreover, the diverse ranges of temperature and precipitation that characterize this region would allow studying the patterns of distribution of modern diatom assemblages against climatically driven environmental variables, as well as to assess the potential application of these modern datasets to the quantitative reconstruction of past climates. In this chapter, the authors analyze the problems and potentialities regarding to the application of the modern diatom data to assess past climate changes in central Argentina. The main objective is to identify particular lines of research that need to be addressed in order to allow precise quantitative reconstructions of Holocene climatic changes in this region.

Chapter 9 - Diatoms are an important and often dominant component of the microalgal assemblages in estuarine and shallow coastal environments. Given their ubiquity and strong relationship with the physical and chemical characteristics of their environment, they have been used to reconstruct paleoenvironmental changes in coastal settings worldwide. The quality of the inferences relies upon a deep knowledge on the relationship of modern diatom species and their ecological requirements, as well as on the taphonomic constrains that can be affecting their preservation in sediments. In Argentina, information on estuarine diatom ecology is scattered and fragmentary. Studies on estuarine diatoms from the 20th century have been mostly restricted to taxonomic descriptions of discrete assemblages. Given the lack of detailed studies on the distribution of modern diatoms in local estuarine environments and their relationship with the prevailing environmental conditions, most paleoenvironmental reconstructions were based on the ecological requirements of European diatoms. However, studies on diatom distribution along estuarine gradients from Argentina have increased in recent years, constituting a potential source of data for paleoecologists. In this chapter, the literature on modern estuarine diatoms from Argentina is revised in order to synthesize the available ecological information and to detect possible modern analogues for Quaternary diatom assemblages. The main objective is to build bridges between ecology and paleoecology, and to discuss the reaches and limitations of the different approaches to diatom-based paleoenvironmental reconstructions. Further studies exploring the relationship between estuarine diatom distribution and environmental characteristics are necessary in order to increase the precision of paleoenvironmental inferences in the region and to generate new hypothesis for further study.

Chapter 10 - Biological processes, structures, functions and materials provide powerful inspiration for novel approaches in architecture. In this chapter, a variety of biological systems are introduced: Bacillus subtilis, the green alga Euglena gracilis, diatoms and red blood cells. Subsequently results of bionanotechnological research performed (by physicists) on these systems are presented. In the next step, the systems and the results are discussed with an architect, resulting in a multitude of ideas, possible approaches, experiments and projects. Such interdisciplinary access corroborates the power of collaboration across established fields in modern science and technology.

CONTENTS

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Chapter 1

THE ROLE OF ENVIRONMENTAL FACTORS IN SHAPING DIATOM FRUSTULE: MORPHOLOGICAL PLASTICITY AND TERATOLOGICAL FORMS

Elisa Falasco** and Guido Badino
DBAU, University of Turin, via Accademia Albertina 13,
I-10123 Turin, Italy

ABSTRACT

Environment factors play an important role in driving morphological variations of diatom frustule. Adaptation to local physico-chemical changes translates into morphological plasticity, leading to structural variation of the valve toward the best solution in facing adverse conditions. Such phenotypic variations, that must be considered as an aspect of the gene expression within a species or population, mainly affect the cell size, the length:width ratio in pennate diatoms and the diameter in centrics, while always maintaining the normal outline of the valves; moreover, changes can involve pore openings and virgae, fibulae and anchorage structures.

In contrast, teratological forms, that can be induced by acute or chronic environmental stresses, do not have a genetic basis and are a consequence of alterations of the individual biochemical processes leading to valve formation. Diatom teratological forms usually have a deformed outline of the valve, a different striation pattern, loss of areolae and sometimes interruption of the raphe slit, all these modifications potentially altering cell movement and physiological mechanisms.

This chapter summarizes the results of the most important studies conducted on the morphological variability and teratological forms carried out from 1890 up to date, with the aim to provide a tentative attribution of the morphological variations to a series of environmental factors.

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* Author for correspondence: Elisa Falasco
E-mail elisa.falasco@unito.it
phone number: +39 0116704520
fax number: +39 0116704508

1. Introduction

Natural frustule size decrease, during the vegetative stage of diatom cell division, can be often accompanied by considerable alterations of the outline shape, number and pattern of striae and areolae (Ross & Mann, 1986). Theriot & Stoermer (1984), for example, highlighted the dependence of many structural characters such as the number of total spines, the total fascicles and the total central struttured processes of *Stephanodiscus rotula* valves with their diameter.

Beside this, intraspecific variability within diatom populations could be also considered a clear response to environmental conditions. Even though silica cell wall is generally preserved and faithfully reproduced through the generations, frustule morphology can be mould by environment in different ways, leading to the production of polymorphic and teratological forms.

Over the years, this wide range of morphological variants sometimes lead to confusion in literature. Several teratological forms have been identified as "new" species (McLaughlin, 1988), and new taxa have been confused with abnormal forms. This is the case of *Hannaea (Ceratoneis) arcus* initially considered a teratomorphosis of the genus *Fragilaria* (Round *et al.*, 1990; Krammer & Lange-Bertalot, 1991; Schmid, 1997) and *Centronella reicheltii* defined as a teratological form of *Fragilaria crotonensis*, appearing as a result of an error during initial valve formation (Schmid, 1985; 1997). On the other hands, frustule variability can be expressed with different extents, from the simple cell size reduction to heterovalvate conditions or tripolarity. In these latter cases, the record of unusual population in single samples could lead to the description of different species, since the gradual intraspecific changes caused by an environmental gradient can be missed.

Anyway, polymorphic and teratological forms seem to have different ecological meaning, the first being generally the expression of natural environmental variations, the second being more related to a toxic contamination or an environmental stress. Considering the increasing interest for the diatom communities in the freshwater ecosystem assessment, it is important to clarify how it is possible to distinguish between teratological forms and naturally polymorphic ones. Both teratology and polymorphism lead to unusual cell forms. But, while morphological variation due to phenotypic plasticity leads to the improvement of the phenotypic features in response to natural environmental changes, teratological alteration of cells leads to abnormal morpho-physiological characteristics that often must be considered non-adaptive. Teratologies lead to deformed frustules, potentially affecting cell movement and physiological mechanisms.

This chapter includes and summarizes some of the most important published research concerning the relationship between environmental stress and diatom morphological variations. The aim of this work is i) to clarify the role of some environmental factors in moulding diatom cell morphology, both in adaptive (polymorphisms) and non-adaptive (teratological forms) terms, ii) to propose a list of morphological features useful to discern between these two typologies.

2. Morphological Variability of Frustule

According to Cox (2006), diatom frustule characters are not constant within a species, as normally assumed for practical identification purposes: a significant phenotypic variation often occurs in natural populations and is regulated by ecological factors.

Changes in the frequency of different variants within a population should be considered an adaptive response to spatial and temporal variation of environmental factors. Thus local populations and species enhance their ability to face adverse habitat changes, as a condition of their survival.

Morphological variability of diatoms has been studied in relation to different environmental constraints since the 1960s, especially in planktonic populations. The high variability of the limnological environment combined with the ease of sampling helped to expand our knowledge on the relationship between phenotypic features of planktonic species and environmental changes. It seems that size variability strategy (surface/volume ratio and greater linear axial dimension (GLAD)) is the strongest driving force shaping phytoplanktonic populations under variable environmental conditions (Morabito *et al.*, 2007). Temperature and light intensity (during summer and autumn) and nutrient availability (during winter and spring) are some of the environmental variables influencing morphometric features in phytoplanktonic communities, leading to the increase in the cell size as far as the environmental conditions become more and more favourable. Morphological plasticity mainly concerns the length:width ratio in pennate diatoms and the diameter in centrics, while always maintaining the normal outline of the valves; moreover, changes can involve pore openings and virgae, the number of fibulae in 10 μm and anchorage structures. It has been demonstrated that clones of a given size are able to increase the silicification process, producing thicker frustules, if they grow at high temperatures (Durbin, 1977). In the same way, gross phosphorous loading could have influenced silica availability in Lake Ontario, becoming consequentely the responsible of different morphotypes of *Melosira islandica*. The wall cell thickhness was indeed, directly correlated to the increase of phosphorous loading and silica limitation (Stoermer *et al.*, 1985).

2.1. Frustule Size Reduction

More frequently a morphological variation of frustule is a transient response to an acute or chronical alteration of one or more environmental factors of a diatom population. The extent of phenotypic plasticity of wall morphology in diatoms varies in different species as a consequence of different environmental factors. Significant variation in outline and ornamentation of frustule was observed both in pennate and in centric diatoms (Håkansson & Chepurnov, 1999).

The most common expression of phenotypic plasticity is probably the cell size reduction: it is well known that the diatom valves undergo a significant reduction of size during the period between two auxosporulation events. Such phenomenon can be also induced or increased by physical and chemical factors and it is considered, by some diatomists, as a possibly adaptive but transient response of a diatom population to an environmental stress. In fact, from a theoretical point of view, large and long-lived organisms are more sensitive to stress than small, short-lived and fast-reproducing ones: then, systems under stress would be dominated by smaller organisms with faster metabolism and flux rates (Granetti, 1968a; Peters, 1983; Odum, 1985; Rapport *et al.*, 1986; Kinross *et al.*; 1993).

A variety of environmental factors can induce changes in frustule size.

2.1.1. Ph, Light and Moisture Content of Air

Charles *et al.* (1990) related the proportions of the longest forms (≥ 45 μm) and the shortest ones (< 45 μm) in a population of *Asterionella ralfsii* var *americana* to changes of pH or dissolved organic carbon concentration.

Smaller cells can achieve a higher nutrient flux per unit of volume (Smith & Kalff, 1981) and they have a higher photosynthetic efficiency (Geider *et al.*, 1986); moreover, they are better adapted to poorly illuminated environments (O'Farrell *et al.*, 2007). Low light conditions in autumn lead to cell diameter reduction in *Stephanodiscus neoastraea* (Jewson, 1992).

Several studies have shown a positive correlation between aerophilous diatom valve length and the moisture content of their habitat: smaller forms are more adaptive since they seem to survive longer in drought conditions than larger ones (Petersen, 1915; Kolbe, 1932; Lund, 1945; Hayek & Hulbary, 1956; Round, 1957; Van de Vijver & Beyens, 1997).

2.1.2. Nutrient and Si Limiting Conditions

Nutrient and Si limiting conditions can also induce the development of smaller cells: the length of *Stephanodiscus minutulus* significantly decreased in N-limited waters (Lynn *et al.*, 2000). Manoylov & Stevenson (2002) showed that the length of *Cymbella excisa* was significantly greater with N than with P or NP enrichment; moreover, dorsal striae counts in 10 μm were significantly greater with NP treatment than with N enrichment or in the controls.

However, the response of valve size to nutrient can be opposite; for example, in the centric diatoms *Aulacoseira ambigua* and *A. distans* var. *alpigena*, the valves tend to be smaller, in terms of diameter and height, in nutrient rich water (Turkia & Lepistö, 1999).

Frustule size reduction of *A. ralfsii* var. *americana* could also be due to Si limitation in the presence of high aluminum concentration in the water column (Gensemer, 1990). Culture tests have shown that different-length forms into the same diatom population can be experimentally induced, especially under Si limitation. Limiting Si concentrations in the external environment resulted in reduced levels of silicification (Paasche, 1975; Davis, 1976; Harrison *et al.*, 1977a; Brzezinski *et al.*, 1990). Since the division rate is maintained near maximum even under low Si conditions (Paasche, 1973a; Brzezinski *et al.*, 1990; Nelson & Dortch, 1996), silicic acid uptake is diminished to a greater extent than growth, leading to less silica deposition during the cell cycle (Paasche, 1973a; Olsen & Paasche, 1986). As a consequence, Si-limited cells present thinner frustules (Håkansson & Chepurnov, 1999) and diminished or absent siliceous spines (Paasche, 1975; Davis, 1976; Harrison *et al.*, 1977b; Brzezinski *et al.*, 1990). Indeed, Kling (1993) hypothesized that a rapid cell-size reduction of *Asterionella formosa* could be an adaptive response to Si limitation, whereby cellular requirements for frustule formation are minimized.

Eutrophic conditions besides low Si availability can also induce a size reduction of valves, as demonstrated by Klee & Schmidt (1987) in *Tabellaria flocculosa,* by Jewson (1992) in *Stephanodiscus neoastraea* and by Stoermer *et al.* (1989) in *S. niagarae.*

2.1.3. Heavy Metals

Several studies have evidenced a significant correlation between valve size reduction and heavy metal contamination of water. In *Nitzschia closterium*, for example, heavy metal contamination leads to competition for nutrients required for reproduction and moreover to a decrease of thiol intracellular level, thus to a reduction of metal immobilization capacity of cells (Perrein-Ettajani *et al.*, 1999). Therefore, the smaller cells become dominant into the population (Joux-Arab *et al.*, 2000), because the growth processes are inhibited due to i) changes in the photosynthetic activity (Overnell, 1976; Stauber & Florence, 1987; Paulsson *et al.*, 2000), ii) loss of cellular components following alteration of the plasma membrane (Overnell, 1975), iii) inhibition of nutrient uptake (Harrison *et al.* 1977a; Rueter *et al.* 1981) and interference in enzymatic activities (Fisher *et al.*, 1981; Husaini & Rai 1991) or iv) inhibition of protein synthesis (Lage *et al.*, 1994). The final result is the reduction of cell size (Cattaneo *et al.*, 1998). Morin (2006) found a positive relation between Zn and Cd contamination and size reduction of *Gomphonema parvulum* and *Nitzschia palea.* Cattaneo *et al.* (1998; 2004) also recorded valve length reduction in *Achnanthidium minutissimum* associated with acute Cu and Zn pollution in the water column. Size reduction in *Navicula pygmaea, N. monoculata, N. seminulum, N. minima* and *Achnanthes minutissima* are also induced by mercury contamination (Peres *et al.*, 1995).

2.1.4. Artificial Growth Conditions

Locker (1950) demonstrated that several taxa, such as *Achnanthes microcephala, Fragilaria capucina, Navicula seminulum, Nitzschia frustulum* var. *perminuta* and *Synedra ulna* var. *danica*, present size reduction when grown in artificial conditions. This could be due to one or few nutrient limitation. Håkansson & Chepurnov (1999) observed that the valves of *Cyclotella meneghiniana* were only more lightly silicified when the monoclonal cultures became rather dense and suggested that this could be due to silica limitation.

2.2. Frustule Outline Variability

Another evident form of phenotypic plasticity is the one involving cell outline. For example, *Phaeodactylum tricornutum* is a pleiomorphic diatom existing in three different forms. The morphotypes usually found in nature are fusiform and triradiate, typically planktonic and partially lacking of silicified structures on the cell wall. On the other hand, an oval morphotype exists; this is a benthic form, occasionally observed in culture collections and characterized by a silicized raphe. In this case, such morphotype expression seems to be independent from the genotype, but could be defined as a manifestation of morphogenetic mechanisms induced and regulated by external factors (Tesson *et al.*, 2009). Environmental features, such as non optimal culture conditions, can be the cause of this ecophenotype production. Indeed, fusiform morphotype dominates in natural environments or under optimal culture conditions. Oval cells can be produced maintaining fusiform and triradiate strains under unfavourable culture conditions: i.e. nutrient depleted media, solid media instead of liquid one and suboptimal temperatures and salinity (De Martino *et al.*, 2007; Tesson *et al.*, 2009).