Homage to Ramon Margalef; or, Why there is such pleasure in studying nature 45
(J. D. Ros & N. Prat, eds.). 1991. *Oecologia aquatica*, 10: 45-60

SIZE AS A FACTOR IN CENTRIC DIATOMS DISTRIBUTION: THE SPANISH RESERVOIRS AS AN EXAMPLE

SERGI SABATER

Departament d'Ecologia. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona. Spain.

Received: June 1990

SUMMARY

Centric diatoms are relatively abundant in the phytoplankton of Spanish reservoirs, and therefore they can be considered as indicative of the phytoplankton populations as a whole. Taxa distribution may often be related to some major environmental characteristics of the reservoirs. In the case of some species of the genus *Aulacoseira* (formerly belonging to *Melosira*), *A. distans*, *A. italica* and *A. subarctica* are confined to N-NW reservoirs, where there are waters of low mineral content, while *A. granulata* is more widespread, mainly preferring higher mineral content and/or nutrient richer waters. Among the smaller centrics, *Cyclotella comensis* and *C. radiosa* are the most frequent, but occur only in the hard-water reservoirs (East Spain, alkalinity > 1 meq l^{-1}). *C. radiosa* was located in northern reservoirs, while *C. comensis* preferred warmer waters. Other taxa had a more restricted distribution, but their presence was indicative of peculiar environmental conditions. For example, *Chaetoceros muelleri* is restricted to the phytoplankton of a meromictic, brackish water reservoir.

Some morphological observations of the cell valve (size, number of striae or areolae, number and disposition of fultoportulae) have been made with SEM on *C. comensis* and *C. radiosa* populations. The data come from a large number of reservoirs in the east of Spain, and were tentatively related to environmental variables of the reservoirs using statistical analyses. Cell diameter was revealed as the most directly related morphological character. Differences in size between populations of each species were consistent, as confirmed through an analysis of variance. Using the certainty that size has characteristic values in every population, its relationship with environmental variables has been explored using a stepwise regression analysis. Temperature is in fact a common factor affecting the size of organisms. Dependence on calcium content seems more unusual, and it may be considered as an accurate expression of the effect of ionic strength of the water on diatom cell size.

KEY WORDS: Phytoplankton, centric diatoms, reservoirs, cell size, environmental gradients.

INTRODUCTION

Certain notable biological manifestations may contribute to an understanding of the environmental factors which influence the composition and structure of phytoplankton assemblages. Among them, the distribution patterns of the assemblages themselves (or of some representative taxa) provide a general reflection of such relationship (HARRIS, 1986). Further, more detailed knowledge of certain environmental factors can be obtained by studying the responses of a single population. Morphological features of the population should be considered among others. The use of suitable techniques (e.g. SEM) can provide optimum sets of observations in some groups of organisms, such as centric diatoms. Although this perspective contemplates only a small part of the whole ecosystem, the particular response of these organisms should provide useful information on this subject.

The two assumptions outlined above undoubtedly offer a complementary vision of the influence of the environment on organisms. MARGALEF's outstanding paper (1969) surmised, from different taxa and populations of *Cyclotella* and *Melosira*, that variations in population size (taken as an expression of the morphological character of the population) were mainly related to certain environmental characteristics. He pointed to water salinity and water temperature as the factors most determinant in affecting size. The main objective of the present work is to test whether size (and certain related elements of the diatom valve) may be used as an appropriate indicator of environmental conditions in Spanish reservoirs. Phytoplankton assemblages in Spanish reservoirs have been grouped with respect to two major environmental factors (SABATER & NOLLA, in press). These were the ionic strength of the water and the trophic state of the reservoirs. In accordance with this, five groups of phytoplankton assemblages were outlined, ranging from slightly mineralized to hard water reservoirs, combined with the range from oligotrophic to eutrophic conditions. Centric diatoms are found in high numbers in each of these five groups, and their occurrence, relative abundance and morphology may be used as representative indices of the major environmental conditions defining the groups.

MATERIAL AND METHODS

The present study uses the observations performed on the phytoplankton samples collected at a depth of 5 m in a set of 104 reservoirs distributed all over Spain (SABATER & NOLLA, 1991). A HITACHI 2300 scanning electron microscope (SEM) was used to count the number of striae of small centrics, as well as in the observation of some potentially significant structures; fultoportulae (strutted processes), rimoportulae (labiate processes), areolae, granules and spines. The total number of striae per valve was counted instead of density of striae, in order to avoid statistical artifacts and consequent misinterpretation of results (THERIOT, 1988). Samples were not subjected to any previous oxidation treatment prior to observation with SEM.

Because not all the samples containing centric diatoms could be observed with SEM, results concerning distribution are sometimes necessarily incomplete. Diameter was measured with SEM when possible, but also with light microscopy (LM) in order to complete a statistically significant data set. For LM some drops of distilled-cleaned frustules were air-dried and mounted with Naphrax for observation at x1000. The number of specimens counted in each reservoir is given in Table II.

RESULTS

SOME TRENDS IN THE DISTRIBUTION OF CENTRIC DIATOMS IN PHYTOPLANKTON ASSEMBLAGES

The ease with which taxa of genus *Aulacoseira*, formerly a part of the genus *Melosira*, may be identified with the inverted microscope facilitates the accurate determination of their distribution in Spanish reservoirs. *A. distans*, *A. distans* var. *tenella*, *A. italica* and *A. subarctica* are confined to the central and western part of the northern half of the Iberian peninsula (Figs. 1; 1'-5). *A. granulata* is distributed in the rest of the peninsula, but is also found in certain reservoirs in the north, co-occurring with the former taxa. These are reservoirs of groups B and C (SABATER & NOLLA, 1991), that is to say of low ionic concentration but with a high proportion of eutrophic taxa in their phytoplankton assemblages. The dividing line between the *A. distans*-group (including *A. italica* and *A. subarctica*) and *A. granulata* corresponds approximately to the division between reservoirs with alkalinity lower or higher than 1 meq l^{-1}. A similar distribution for these taxa was already observed fifteen years ago (MARGALEF *et al.*, 1982).

Cyclotella comensis and *C. radiosa* (valid synonym for *C. comta* as shown by HÅKANSSON, 1988) are the most frequent taxa among the small centric diatoms of the phytoplankton in the reservoirs (Figs. 8-14; 15-19). Although their distribution (Fig. 2) may hide some gaps, it is noteworthy that they appeared only in reservoirs of groups D and E, which are of hard water. As may be observed from figure 2, both species are completely absent in the western reservoirs. As a usual trend, *Cyclotella comensis* is more frequent than *C. radiosa*. While *C. radiosa* has been found only in the north, *C. comensis* occupies all the area. However, *C. comensis* is not highly abundant when appearing together with *C. radiosa*. Difference in water temperature is the main factor influencing the relative distribution of *C. comensis* and *C. radiosa*. This is the only environmental variable to reach the level of significance required for an stepwise

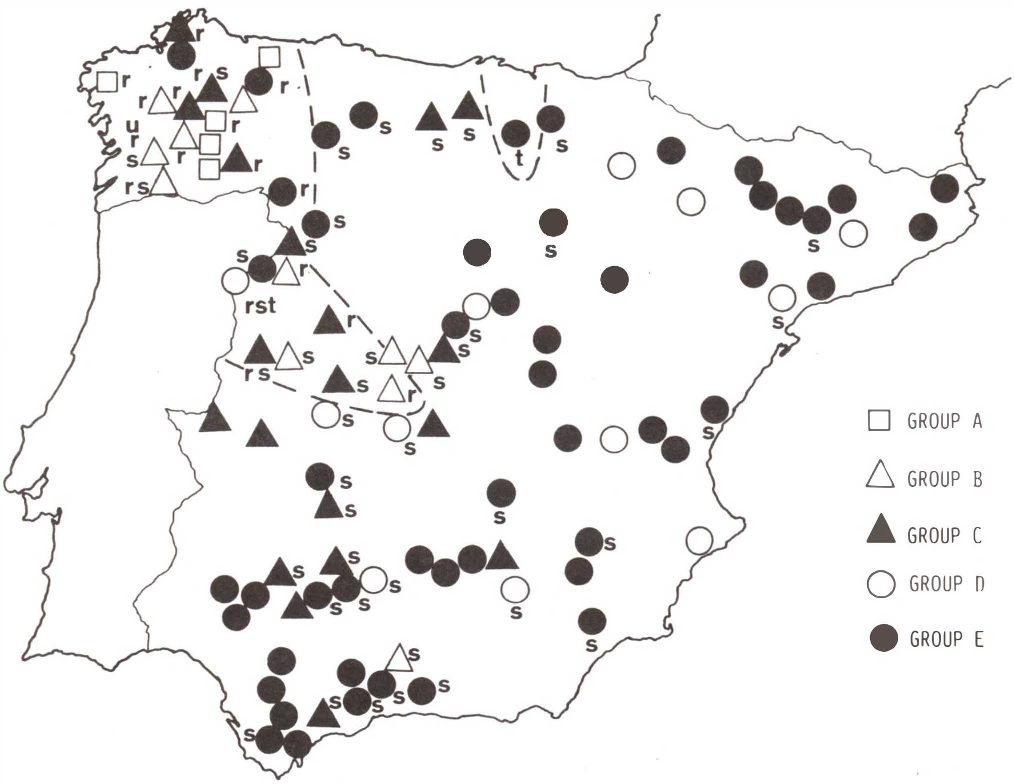


FIGURE 1. Distribution of *Aulacoseira* taxa in Spanish reservoirs: *A. distans* (Ehrenberg) Simonsen and its var. *tenella* (Nygaard) Ross (r); *A. granulata* (Ehrenberg) Simonsen (s); *A. italica* (Ehrenberg) Simonsen (t); *A. subarctica* (O. Müller) Haworth (syn. *A. italica* var. *subarctica* O. Müller) (u). Their presence is indicated with respect to the grouping of phytoplankton assemblages of SABATER & NOLLA (1991), that cluster the reservoirs from oligotrophic to eutrophic, either in those of slightly mineralized waters (A to C) or in those of hard waters (D and E). The broken line segregates the zone of occurrence of the *distans*-group from that of *A. granulata*.

regression analysis.

Cyclotella meneghiniana and *Stephanodiscus hantzschii* are found fairly frequently (Figs. 3; 20 and 23), but usually only in small numbers.

The distribution of other centric taxa of scarce appearance is shown in figure 3. *Chaetoceros muelleri* (Figs. 21-22) has been found only in a small saline reservoir, where water conductivity was about 5,700 μS cm^{-1} (ARMENGOL *et al.*, 1990). *Cyclotella stelligera* (figs. 27'-29) was limited to six reservoirs, always with a low number of individuals. *Cyclostephanos dubius* (Fig. 24), *Cyclotella atomus* (Figs. 6-7), *Stephanodiscus rotula* (Figs. 26-27) and *Thalassiosira pseudonana* (Figs. 29-32) may be considered as occasional in the phytoplankton of reservoirs, at least during the period of our study.

SIZE AND RELATED CHARACTERISTICS AS ECOLOGICAL INDICATORS

Some ecological questions arise from morphological considerations. Intriguing morphological variations are observable in nearly every one of the taxa quoted above. For instance, *Cyclotella stelligera* var. *pseudostelligera* has a remarkable variability concerning the degree of flatness and definition of its central area (see Figs. 27'-28). Such variability is not a special feature of the populations inhabiting the Spanish reservoirs. BELCHER *et al.* (1966) observed it in a population of an English

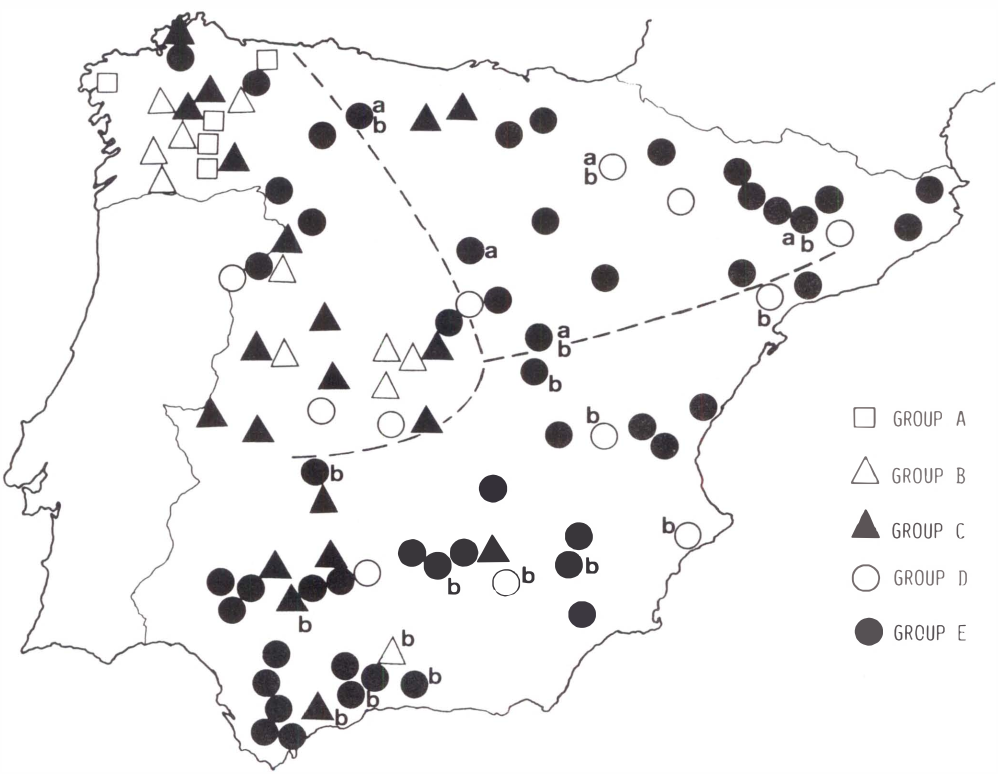


FIGURE. 2. Distribution of *Cyclotella radiosa* (Grunow) Lemmermann (a) and *Cyclotella comensis* Grunow (b) in the Spanish reservoirs. Their presence is indicated with respect to the grouping of phytoplankton assemblages of SABATER & NOLLA (1991) as explained in Fig. 1. The broken line indicates, at left the zone where both species are absent, and at right the zone where they inhabit together (upper) or where only *C. comensis* is found (lower).

pond, suggesting a relationship between sculpturing of the valves and availability of silica. HAWORTH & HURLEY (1986) have figured the heterovalvy of flat and ondulated valves in the same specimen, although they consider that prominency of one over the other may have some relation to phosphorus or silica during population growth. Moreover, complicating an accurate ecological interpretation, the segregation between forms of this taxon and others belonging to *Thalassiosira pseudonana* (Figs. 29-32) becomes sometimes quite difficult (e.g. in reservoir 91). Both taxa are inhabitants of eutrophic waters (KISS, 1984; SABATER & KLEE, 1990) and taxonomical boundaries between them are not sufficiently clear, at least when small specimens are considered (SABATER & KLEE, 1990).

The high occurrence of *Cyclotella comensis* and *C. radiosa* in the Spanish reservoirs provides enough material for the study of their morphology in connection with ecological implications. *Cyclotella comensis* shows a high degree of morphological variability in the populations studied (Figs. 8-14). The three tripunctate cavities on the valve face which are predicted by Grunow's description of the taxon (KLING & HÅKANSSON, 1988) are difficult to observe in the Spanish populations. In fact, form, arrangement and number of cavities are variable from

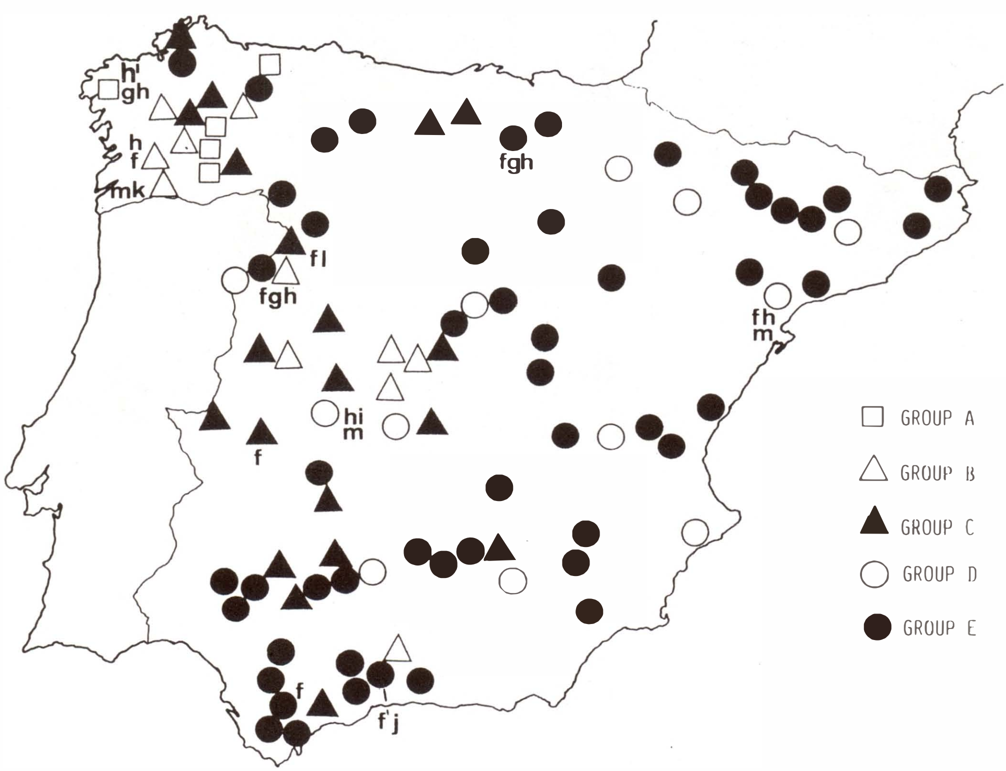
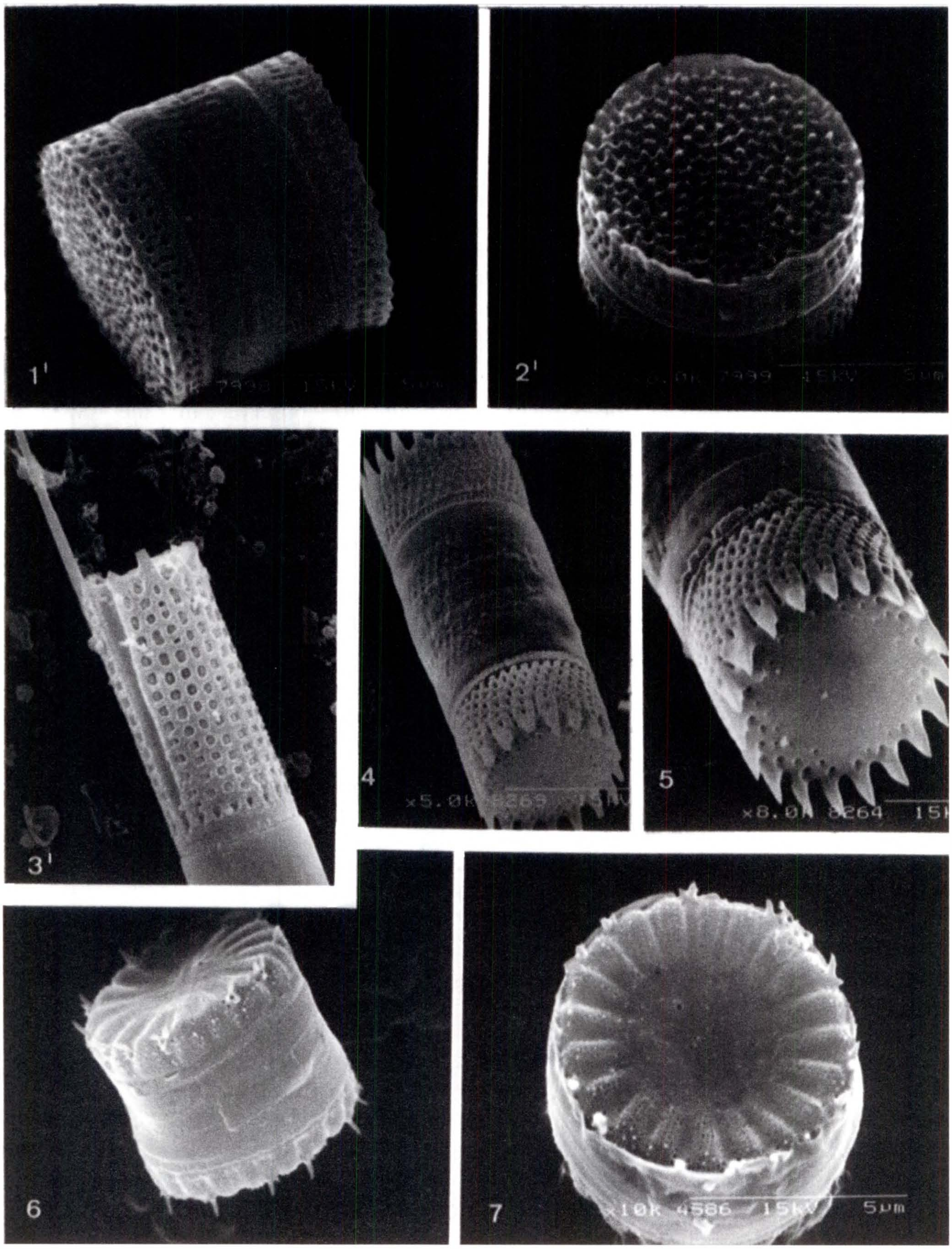
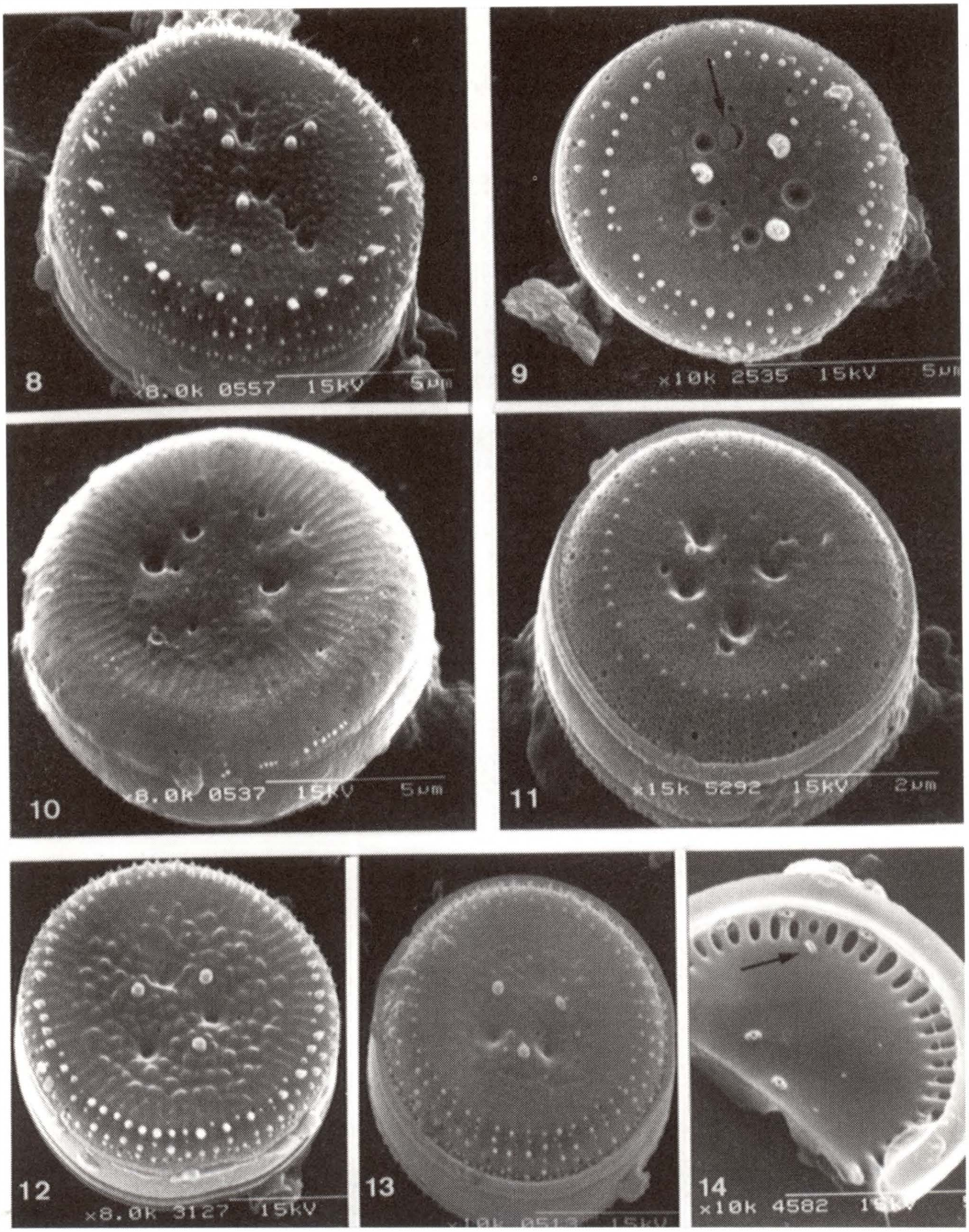


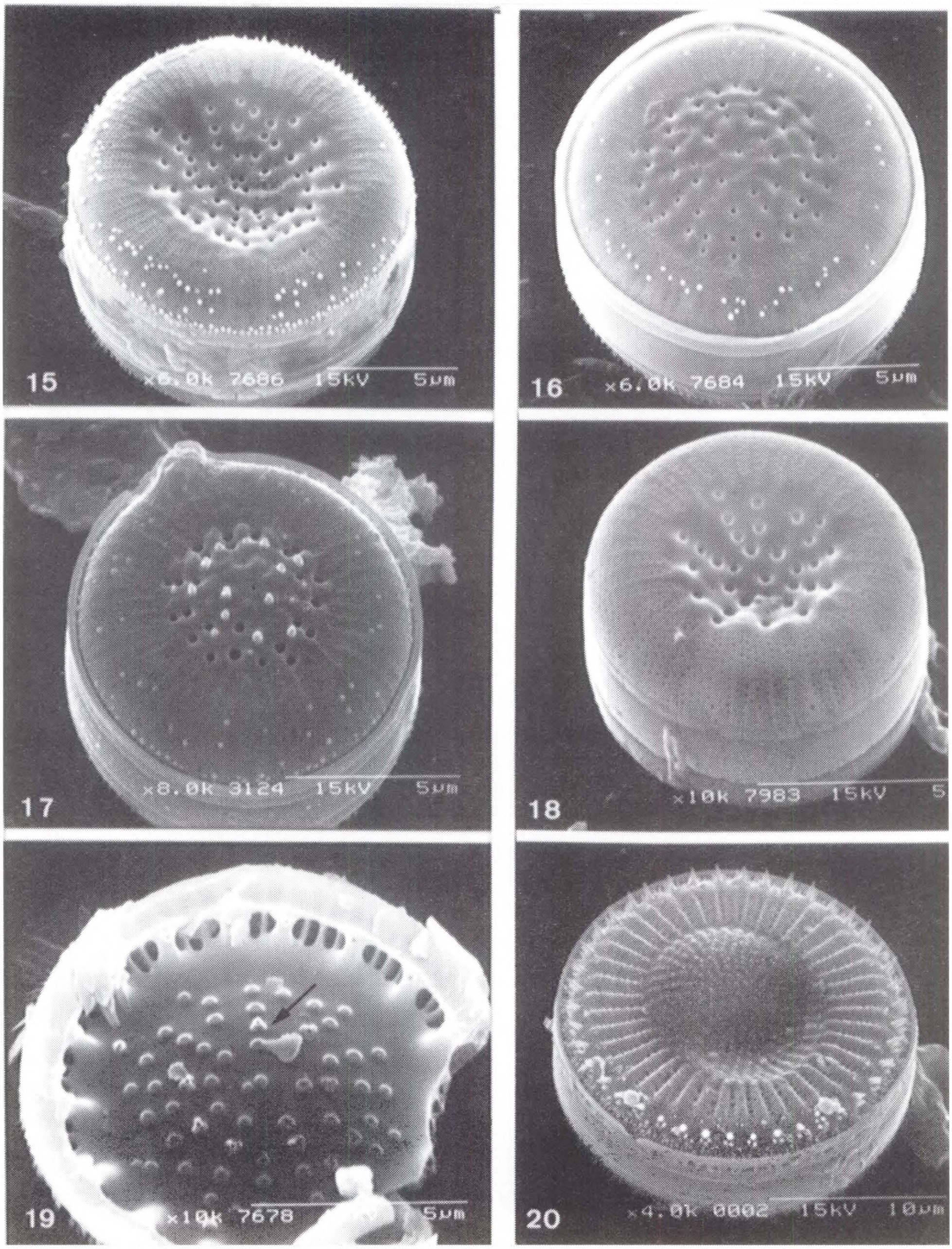
FIGURE 3. Occurrence of the less frequent centric diatoms in the Spanish reservoirs (grouping as explained in figure 1): *Cyclotella meneghiniana* Kützing (f); *Stephanodiscus hantzschii* Grunow (g); *Cyclotella stelligera* Cleve & Grunow (h) and its var. *pseudostelligera* (Hustedt) Haworth & Hurley (h'); *Cyclotella atomus* Hustedt (i); *Chaetoceros muelleri* Lemmermann (j); *Cyclostephanos dubius* (Fricke) Round (k); *Stephanodiscus rotula* (Kützing) Hendey (l); *Stephanodiscus minutulus* (Kützing) Cleve & Müller (m); *Thalassiosira pseudonana* Hasle & Heimdal (n).



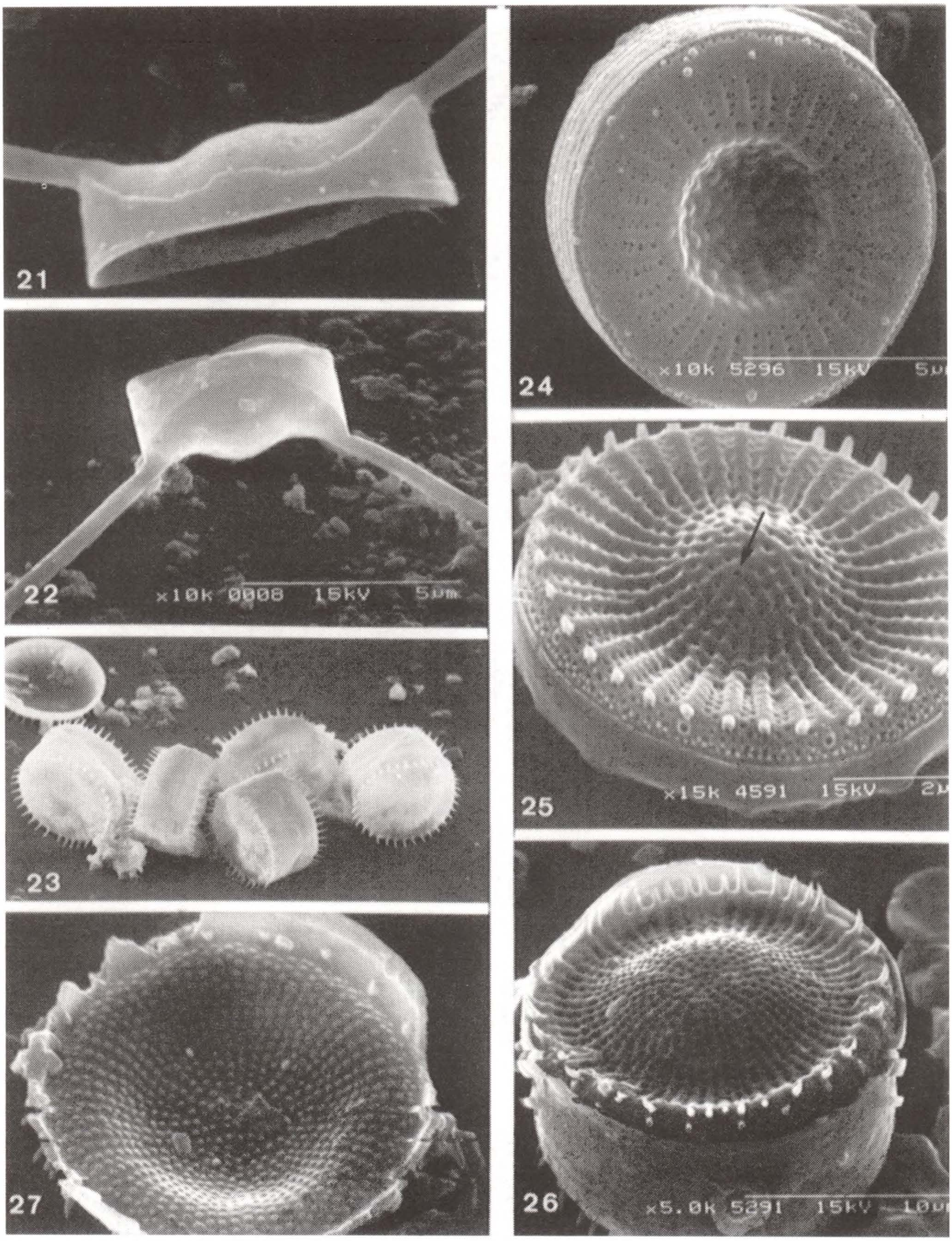
FIGURES 1'-2'. *Aulacoseira distans* var. *tenella*. Fig. 1', exterior view of a valve (x 3000, reservoir 16). Fig. 2', side view (x 4800, r99). Fig. 3'. *Aulacoseira granulata*. Exterior view of a limiting cell (x 2250, r35). Figs. 4-5. *Aulacoseira subarctica* (syn. *A. italica* var. *subarctica* O. Müller), two approximative views of a same filament. Fig. 5 shows the peripheric ring of areolae in the valve face (Fig. 4, x 3000; Fig. 5, x 4800; both from r97). Figs. 6-7. *Cyclotella atomus*. Fig. 6, side view (x 4800, r50). Fig. 7, valve view (x 6000, r50).



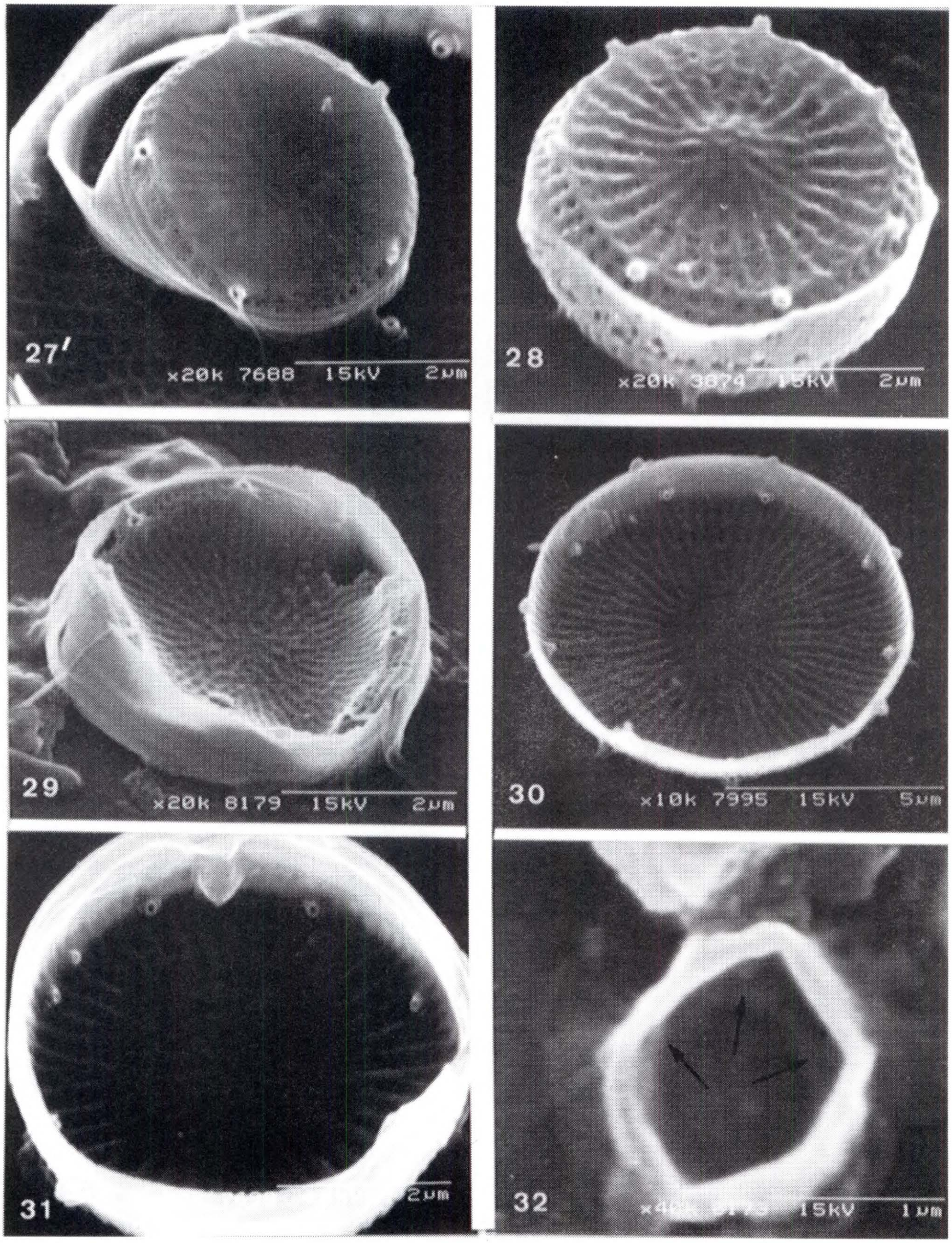
FIGURES 8-14. *Cyclotella comensis.* Figs. 8-13, exterior views of representative specimens covering the whole range of morphological variation. Figs 8 (x 4800, r73) and 9 (x 6000, r73), valves of verrucose surface, with granules on the face and spines on the rim of the valve; granules are variable with respect to their number and width. Note the crater-like cavities in fig. 9, one of them with a tapering flap of silica (arrowed). Fig. 10, an extreme example of specimen bearing a smooth valve face and without granules or spines (x 4880, r63). Fig. 11, valve bearing four cavities on its face (x 9000, r74). Fig. 12, valve showing a conspicuous verrucose face (x 4800, r94). Fig. 13, a specimen with a reduced central area (x 6000, r72). Fig. 14, interior view of a broken valve, showing two central fultoportulae, a rimoportula on a marginal position (arrowed), and some marginal fultoportulae, located every three to four costae (x 6000, r48).



FIGURES 15-19. *Cyclotella radiosa.* Figs. 15 and 16, lacunate and scutate valves of specimens with a wide central area; note the two kinds of pores radially arranged; some larger (fultoportulae), other small (loculi; both at x 3600, r94). Figs. 17 and 18, scutate and lacunate valves with narrow central area and wider larger pores (x 4800, r8; x 6000, r3). Fig. 19, interior view of a valve showing in its central part the two kinds of pores; the loculi with their domed criba, and the central fultoportulae (arrowed), bearing each one three struts (x 6000, r94). Fig. 20. *Cyclotella meneghiniana.* Exterior view of a typically undulated valve (x 2400, r103).



FIGURES 21-22. *Chaetoceros muelleri*. Girdle view of valves showing the outer surface and the emergence of setae (Fig. 21, x 9000; Fig. 22, x 6000; both from r103). Fig. 23. Group of *Stephanodiscus hantzschii* (x 1500, r15). Fig. 24. *Cyclostephanos dubius*. Exterior view of a valve with scattered spines (x 6000, r20). Fig. 25. *Stephanodiscus minutulus*. Exterior view; the external opening of the central fultoportula is arrowed (x 9000, r50). Figs. 26-27. *Stephanodiscus rotula*. Exterior and interior views, showing the central fultoportulae distinctive of this species (x 3600, x 3000; both from r26).



FIGURES 27'-28. *Cyclotella stelligera* var. *pseudostelligera.* Fig. 27'. External view of a valve of *C. stelligera* var. *pseudostelligera* (form *woltereck* Hustedt) placed over a *Stephanodiscus*; note the smoothness of the surface (x 1200, r91). Fig. 28. Undulated form of *Cyclotella stelligera* var. *pseudostelligera.* Figs. 29-32. *Thalassiosira pseudonana.* Fig. 29. External view of a sculptured valve (x 1200, r15). Figs. 30-31. Interior views; note that the central fultoportulae have two struts (x 6000, r29; x 12000, r91). Fig. 32, very small forms (1.6 mm Ø), tentatively identified as specimens of *Thalassiosira pseudonana*, of a weakly silicified structure; arrowed there are three marginal fultoportulae.

TABLE I. Regression functions which express the dependence of some rotational elements of the diatom valve against diameter in *Cyclotella comensis* and *Cyclotella radiosa.*

a) *Cyclotella comensis*

COSTAE = 8.42 DIAMETER $^{0.84}$	r^2 = 0.910, p< 0.001, n = 18 (reservoir 74)
COSTAE = 8.23 DIAMETER $^{0.86}$	r^2 = 0.874, p< 0.001, n = 12 (reservoir 72)
COSTAE = 5.76 DIAMETER $^{1.08}$	r^2 = 0.976, p< 0.001, n = 12 (reservoir 78)
COSTAE = 9.6 DIAMETER $^{0.77}$	r^2 = 0.774, p< 0.001, n = 23 (reservoir 73)

b) *Cyclotella radiosa*

COSTAE = 10.9 DIAMETER $^{0.64}$	r^2 = 0.980, p< 0.001, n = 5 (reservoir 8)
DIAMETER CENTRAL AREA = 0.33 DIAMETER$^{1.17}$	r^2 = 0.976, p< 0.001, n = 33 (reservoirs 3, 8, 31, 94)
NUMBER AREOLAE = 3.84 DIAMETER $^{0.95}$	r^2 = 0.343, p< 0.001, n = 32 (reservoirs 3, 8, 31, 94)

population to population, but a rather high variation appears in any given one. In some cases morphology of cavities is peculiar (Fig. 9), but this seems to be more closely related to the process of cellular division and cell wall morphogenesis than to environmental causes (SCHMID, 1985). Moreover, marginal fultoportulae are arranged irregularly, even in the same occurring valve, varying from two to five costae (Fig. 14). Variability of these characters is very high, and no stable quantitative pattern has been established.

Number and dimensions of granules - and of spines too - on the central and/or marginal part of the valve face in *C. comensis* are also variable. The occurrence of granules seems to follow a more-or-less stable pattern, because they appear in some populations, but not in others. A possible relationship between the appearance of granules and changes in salinity has been suggested by A.M. Schmid (personal communication). Studies of specific cultures with populations bearing granules or not may lead to an understanding of such regularity.

Variability of morphological characteristics was also noteworthy in populations of *Cyclotella radiosa* (Figs. 15-19). The width of the central area, the number and diameter of the areolae covering the valve face, and the presence or absence of granules follow divergent patterns from reservoir to reservoir. The marginal fultoportulae are usually arranged irregularly, from two to five costae, but then diverge from the classical description (HÅKANSSON, 1988).

The ecological interest of all these structures is sometimes difficult to establish, often because it is hard to count them in a statistically significant number. On the other hand, it is easier to measure the number of costae and the diameter, which facilitates the search for a pattern.

The dependence of some rotational elements of the valve with respect to the diameter was investigated. A linear and positive regression against diameter is expected, as has been summarized by THERIOT (1988). In the case of the total number of costae, the significance is not so high in *C. comensis* and in *C. radiosa*. The exponential functions obtained with the respective logarithmically transformed values had an r^2 of 0.769 in the former, but only of 0.25 in the latter (Figs. 33 and 34). Slopes of the regression lines ranged from 0.77 to 1.08 for *Cyclotella comensis* (Table I); with *C. radiosa* the relation was not significant in a high number of reservoirs (Table I).

This supports the statement of MARGALEF (1983) that the density of any given element is related to a dimension of the valve following an exponential function with a slope of 0.66. One possible consequence of such an empirical assumption is that morphological characteristics of the valve are not completely dependent on (nor completely independent of) cell size.

This might be true of the number of striae, although interpretation is rather complex. Ecologically, variation of number of striae has been related to changes in, for instance, water temperature (KACZMARSKA & FRYXELL, 1986) or water salinity (GEISSLER, 1982; MAKAROVA, 1982). But in these cases size, when considered (cf. MAKAROVA, 1982), also appears to be affected by the same environmental factor.

Additionally, in those characteristics for which slope will move significantly from the stated value, a different ecological interpretation may be made. For instance, in *C. radiosa* the regression of the central area diameter against size has a slope of 1.2 while, for the number of areolae, the slope is 0.95. This may suggest a close dependence of such associated structures on valve size, and it therefore has no real independent significance.

In order to examine any relationship between size and environment, the variations in diameter in *C. comensis* and *C. radiosa* populations were analyzed among certain reservoirs (Table II), with two objectives: first, to determine whether there were consistent differences in size among populations; second, if so, to relate them to certain environmental parameters.

Both objectives start from the discussion of cell size reduction. The idea that the cells undergo a progressive reduction of size during vegetative reproduction has been widespread since the classic work of PFITZER (1871). Although GEITLER (1932) justified that auxospore formation would be a way for recovering size, BETHGE (1925) showed that auxospore formation had no direct implication for the size spectrum of a given population. Anyway, if such a reduction exists, it does not happen as a regular process (PATRICK, 1966). In certain unialgal diatom cultures lasting several years no decrease in size of the species occurred (WIEDLING, 1948; MARGALEF, 1969). Therefore, the assumption of size reduction cannot be taken as a rule. MARGALEF (1969) hypothesized that the average diameter of a given population of *Cyclotella* or *Melosira* would be an expression of environmental properties, more than the result of the sexual cycle. Recently, size variation has been used as a palaeolimnological indicator of past conditions (STOERMER *et al*., 1989), or as indicative of the trophic state

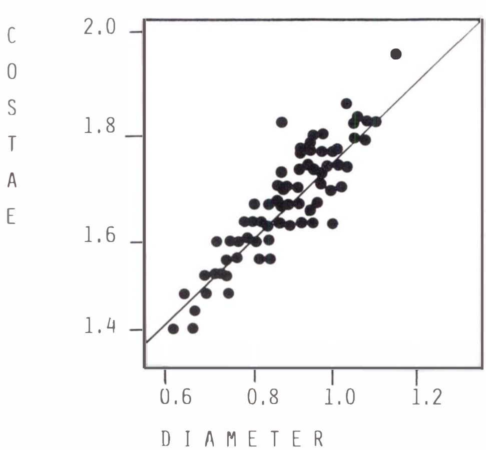


FIGURE 33. Regression function describing relationship of number of costae with respect to diameter (log transformed values) in *Cyclotella comensis* (Costae = 9.28 diameter$^{0.79}$; $r^2 = 0.769$, $p < 0.001$, $n = 97$).

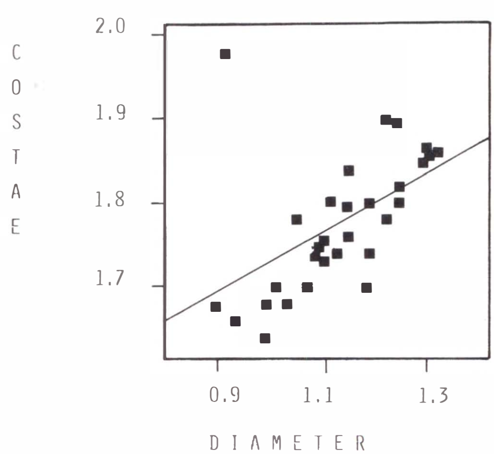


FIGURE 34. Regression function describing relationship of number of costae with respect to diameter (log transformed values) in *Cyclotella radiosa* (Costae = 22.5 diameter$^{0.38}$; $r^2 = 0.25$, $p < 0.004$, $n = 30$).

TABLE II. Means and coefficients of variation of some morphometric characters in *Cyclotella radiosa* and *Cyclotella comensis* populations.

a) *Cyclotella radiosa*

RESERVOIR	DIAMETER	NUMBER OF COSTAE	NUMBER OF AREOLAE	DIAMETER OF CENTRAL AREA	FREQUENCY
3	8.88 (0.25)	59.7(0.23)	38.7 (0.54)	5.5 (0.23)	73
94	14.44 (0.19)	63.4 (0.12)	54.1 (0.15)	8.3 (0.22)	24
8	12.39 (0.18)	59.4 (0.15)	43.0 (0.24)	6.5 (0.23)	59
31	11.27 (0.19)	44.5 (0.05)	27.3 (0.14)	4.5 (0.10)	54

b) *Cyclotella comensis*

RESERVOIR	DIAMETER	NUMBER OF COSTAE	FREQUENCY
3	6.8 (0.27)	56.3 (0.2)	10
73	9.4 (0.34)	46.8 (0.27)	98
74	7.47 (0.22)	47.1 (0.24)	68
72	8.9 (0.19)	53.8 (0.15)	62
78	8.1 (0.14)	53.3 (0.18)	62
94	10.3 (0.15)	52.5 (0.13)	23
8	9.8 (0.27)	39 (0.1)	12
63	8.49 (0.14)	53.0 (0.14)	11

in lakes (THERIOT *et al.*, 1988). However, the complexity of such a question is obvious (cf. LEWIS, 1984; ROUND *et al.*, 1990). As has been summarized by GEISSLER (1982) through studies on *Stephanodiscus hantzschii*, size may be related either to the process of division or to ecological conditions. The environment would act by selecting a given morphotype, or conversely, a phenogenic response of the population would follow the environmental change (MARGALEF, 1969). In any case, we may use size as an indicator of environmental conditions, but we should be aware that other implications may be involved. In nature, differences of time scale between the generation period of a given species and the changes of environmental conditions are important. Otherwise, genetic variation is high. Therefore, when working with natural populations, the difficulty of obtaining reliable results increases.

Size distribution of frequencies did not follow a continuous pattern in every local population, but showed discrete peaks. This is shown by three different populations of *Cyclotella radiosa* (Fig. 35), which discourages the idea of the existence of a continuous growth linked to an auxosporulation cycle for those populations. Consequently, differences in size among populations (Table II) were found to be consistent both in *Cyclotella comensis* and in *C. radiosa*, as is shown with an analysis of variance ($p < 0.00001$ in the two sets of data).

In addition, in three reservoirs where both *Cyclotella* coincided, a representative number of valve diameters were counted. In spite of the low number of replicates, a covariance in size of the two *Cyclotella* was also found to be significant by another

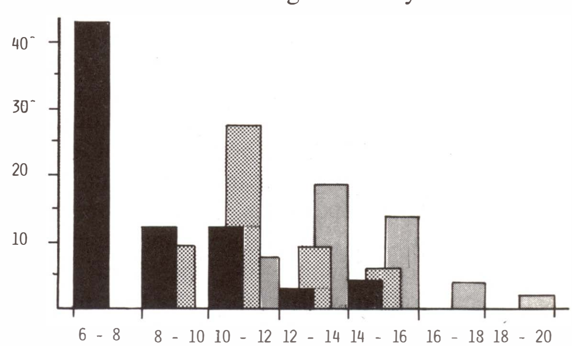


FIGURE 35. Distribution of *Cyclotella radiosa* valve diameter (x axis represents every 2 mm categories; y axis represents the number of valves examined) in three different populations: r3 (black), r8 (dotted), r94 (shaded).

anova ($p < 0.1$). This may be taken as a test of the value of the diameter as an indicator of the environmental variation affecting the two species populations. In the words of MARGALEF (1969), "correlation between changes of size in species that live in association should be one of the best criteria of significance when size is used as an ecological indicator".

Significance of the variance analysis was also high when other characters of the diatoms valve were considered: diameter of the central area ($p < 0.003$) and number of areolae ($p < 0.09$) in *C. radiosa*, number of areolae ($p < 0.003$) and total number of costae ($p < 0.009$) in *C. comensis*.

Using the fact that size has characteristic values in every population, its relationship with environmental conditions has been explored through stepwise regression analysis. In a first, exploratory analysis only water temperature, depth of the photosynthetic layer, conductivity, nitrogen as PON and planktonic chlorophyll-a were considered. These variables were selected because they are major descriptors of physico-chemical and biological properties of the reservoir. Transformed log values were used for all the variables involved in the analysis. The following expression is obtained when both *Cyclotella* populations are considered as a whole:

$$\log \text{diameter} = 2.31 - 0.53 \log \text{temperature} - 0.29 \log \text{conductivity} \quad (1)$$

Hence, water temperature and water mineral content (as indicated by conductivity) may tentatively be pointed out as the major factors affecting size in the *Cyclotella* populations. Furthermore, in order to clarify the relative importance of some contributors of the total ion concentration with respect to the diatom variation of size a new stepwise analysis was carried out. Log-transformed values of total alkalinity, silicate (as total silicates and as reactive soluble silicate), calcium, carbonate, bicarbonate, and sulphate concentrations, were added to the previous variables. In this case, size of both *Cyclotella* populations was significantly dependent on temperature and calcium content in the reservoirs:

$$\log \text{diameter} = 2.43 - 0.78 \log \text{temperature} - 0.16 \log \text{calcium} \quad (2)$$

Similar expressions are obtained when populations of the two species are considered in particular. While temperature has been found to affect size of organisms elsewhere (MARGALEF, 1974), calcium is highlighted among other components of water mineral content as influencing size. Although the abundance of this element in the eastern Spanish reservoirs is striking, the relative abundance of some other ions (e.g. sulphates) is also high there (ARMENGOL *et al.*, in press a). Neither silicates, which are important components of the diatom cell wall, are revealed as affecting size. The relationship expressed by the stepwise regression allows us to hypothesize some possible physiological implications of calcium concentration with respect to the valve size. However, only detailed observations with cultures would bring a more complete response to this assumption.

Apart from the influence I assume that some physico-chemical factors may exert on the size of a diatom population, some other factors can not be disregarded. MANN (1988) suggests that selection of a given population size in the pennate diatom *Nitzschia sigmoidea* would be related to the action of parasites. Predation, which would appear to affect larger cell classes more than small ones, may also potentially affect the size of a population. Therefore, it will be interesting to compare such outlined dependence on the populations of the reservoirs with other sets of data elsewhere where conditions or/and species are different.

ACKNOWLEDGEMENTS

This work has been sponsored by the CAICYT of the Ministry of Education and Science (project number PB85-0166). My gratitude to Rolf Klee (Munich), A.M. Schmid (Salzburg) and E.Y. Haworth (Windermere) for their comments on different aspects of centric diatoms. The Microscopical Service of the University of Barcelona provided their facilities and technical help. Dr. Ramon Margalef has contributed with his personal learning and papers to the ideas which I have tried to express in this study.

REFERENCES

ARMENGOL, J., RIERA, J.L., MORGUí, J.A. in press. Major ionic composition in the Spanish reservoirs. *Ver. Internat. Verein. Limnol.*, 24.

ARMENGOL, J., CATALAN, J., GABELLONE, N., JAUME, D., DE MANUEL, J., MARTÍ, E., MORGUÍ, J.A., NOLLA, J., PEÑUELAS, J., REAL, M., RIERA, J.L., SABATER, F., SABATER, S. & TOJA, J. 1990. A comparative limnological study of the Guadalhorce reservoirs system (Málaga, SE Spain). *Scientia Gerundensis.*, 16(2): 27-41

BELCHER, J.H., SWALE, E.M.F. & HERON, J. 1966. Ecological and morphological observations on a population of *Cyclotella pseudostelligera* Hustedt. *J. Ecol.*, 54: 335- 340.

BETHGE, H. 1925. *Melosira* und ihre Planktonbegleiter. *Pflanzenforschung*, 3: 1-80.

GEISSLER, V. 1982. Experimentelle Untersuchungen zur Variabilität der Schalenmerkmale bei einigen zentrischen Süsswasser Diatomeen. *Nova Hedwigia Beih.*, 73: 211-247.

GEITLER, L. 1932. Der Formwechsel der Pennaten Diatomeen (Kieselalgen). *Arch. Protistenk*, 78: 1-226.

HÅKANSSON, H. 1988. A study of species belonging to the *Cyclotella bodanica/comta* complex (Bacillariophyceae). In: *Proc. 9th. Internat. Diatom Symp.* (F. Round, ed.): 329-354. Biopress. Bristol. Koeltz. Koenigstein.

HARRIS, G.P. 1986. *Phytoplankton ecology*. Chapman & Hall. New York.

HAWORTH, E.Y. & HURLEY, M.A. 1986. Comparison of the stelligeroid taxa of the centric diatom genus *Cyclotella*. In: *Proc. 8th. Internat. Diatom Symp.* (D.G. Mann, ed.): 43-57. Koeltz. Koenigstein.

KACZMARSKA, I. & FRYXELL, G.A. 1986. The diatom genus *Nitzschia*; morphological variation of some small bicapitate species in the Gulf Stream Warm Core rings. In: *Proc. 8th. Internat. Diatom Symp.* (D.G. Mann. ed.): 237-252. Koeltz. Koenigstein.

KISS, K.T. 1984. Occurrence of *Thalassiosira pseudonana* Hasle et Heimdal (Bacillariophyceae) in some rivers in Hungary. *Acta Bot. Hungarica*, 30 (3-4): 277-287.

KLING, H. & HÅKANSSON, H. 1988. A light and electron microscope study of *Cyclotella* species (Bacillariophyceae) from Central and Northern Canadian lakes. *Diatom Res.*, 3(1): 55-82.

LEWIS, W.M. 1984. The diatom sex clock and its evolutionary significance. *Amer. Nat.*, 123: 73-80.

MAKAROVA, I.V. 1982. Principles of the systematics of *Thalassiosira* Cleve and the significance of its taxonomic characters. In: *Proc. 6th. Internat Diatom Symp.* (R. Ross, ed.): 1-12. Koeltz. Koenigstein.

MANN, D.G. 1988. Why didn't Lund see sex in *Asterionella*? A discussion of the diatom cycle in nature. In: *Algae and the aquatic environment* (F.E. Round, ed.): 384-412. Biopress. Bristol.

MARGALEF, R. 1969. Size of centric diatoms as an ecological indicator. *Mitt. Internat. Verein. Limnol.*, 17: 202-210.

MARGALEF, R. 1974. *Ecología*. Omega. Barcelona.

MARGALEF, R. 1983. *Limnología*. Omega. Barcelona.

MARGALEF, R., PLANAS, D., ARMENGOL, J., VIDAL, A., PRAT, N., GUISET, A., TOJA, J. & ESTRADA, M. 1976. *Limnología de los embalses españoles*. Dirección General de Obras Hidraúlicas. Ministerio de Obras Públicas. Madrid.

MARGALEF, R., MIR, M. & ESTRADA, M. 1982. Phytoplankton composition and distribution as an expression of properties of reservoirs. *Can. Wat. Res. J.*, 6: 26-50.

PATRICK, R. 1966. *The diatoms of the United States*. Acad. Natural Sciences of Philadelphia.

PFITZER, E. 1871. Untersuchungen über Bau und Entwicklung der Bacillariaceen (Diatomaceen). In: *Botanische Abhandlungen aus dem Gebiet der Morphologie un Physiologie*. Bonn

ROUND, F.E., CRAWFORD, R.M. & MANN, D.G. 1990. *The diatoms: Biology and morphology of the genera*. Cambridge University Press. Cambridge.

PLANAS, D. 1975. Distribution and productivity of the phytoplankton in Spanish reservoirs. *Ver. Internat. Verein. Limnol.*, 19: 1860-1870.

RIERA, J.L., MARTÍ, E. & MORGUÍ, J.A. in press. Changes in the trophic state of the Spanish reservoirs during the last fifteen years. *Ver. Internat. Verein. Limnol.*, 24.

SABATER, S. & KLEE, R. 1990. Observaciones sobre diatomeas centrales del fitoplancton del río Ebro, con especial interés en algunas pequeñas *Cyclotella*. *Diatom Res.*, 5 (1): 141-154

SABATER, S. & NOLLA, J. 1991. Distributional patterns of phytoplankton in Spanish reservoirs: first results and comparison after fifteen years. *Ver. Internat. Verein. Limnol.*, 24: 1371-1375

SCHMID, A.M. 1985. Valve morphogenesis in diatoms. In: *Schalen in Natur und Technik* (K. Bach & B. Burkhardt, eds.): 300-316. Mitt. Instituts für leichte Flächentragwerke, 28.

STOERMER, E.F., EMMERT, G. & SCHELSKE, C.L. 1989. Morphological variation of *Stephanodiscus niagarae* Ehr. (Bacillariophyta) in a Lake Ontario sediment core. *J. Paleolimnology*, 2: 227-236.

THERIOT, E. 1988. An empirically based model in rotational elements in centric diatoms with comments on ratios in phycology. *J. Phycol.*, 24: 400-407.

THERIOT, E., HÅKANSSON, H. & STOERMER, E.F. 1988. Morphometric analysis of *Stephanodiscus alpinus* (Bacillariophyceae) and its morphology as an indicator of lake trophic status. *Phycologia*, 27 (4): 485-493.

WIEDLING, S. 1948. Beitrage zur Kenntnis der vegetativen Vermehrung der Diatomeen. *Botanika Notiser*, 1948 (3): 322-354.