

THE ECOLOGICAL IMPLICATIONS OF GROWTH FORMS IN EPIBENTHIC DIATOMS¹

Christiane Hudon²

Département de Biologie, Université Laval, Ste-Foy, Québec, Canada G1K 7P4

and

Pierre Legendre

Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succursale A, Montréal, Québec, Canada H3C 3J7

ABSTRACT

This paper evaluates the utilisation of space by epibenthic diatom cells, as a response to environmental variations. The aggregation pattern of five species of epibenthic diatoms was quantified and compared to provide evidence for the significance of cell motility as an adaptive mechanism for space occupation and monopoly. The epibenthic diatoms included (1) non-mobile colonial species forming either fan-shaped (*Synedra tabulata* (Ag.) Kz.) or arborescent (*Gomphonema kamtschaticum* var. *californicum* Grun.) colonies; (2) slow-moving (*Cocconeis costata* Greg. and *Amphora pusio* Cl.), and (3) fast-moving (*Navicula directa* (W. Sm.) Ra.) non-colonial species. The aggregation pattern of *S. tabulata* did not vary significantly among six different light intensities manipulated in nature. The major patterns of aggregation were identified using analysis of covariance and dummy-variable regression. Highly mobile *N. directa* are significantly less aggregated than the four other diatom species. Non-mobile and slow-moving species show a similar, highly aggregated pattern. The occurrence of two patterns of spatial dispersion indicates that growth forms bear far-ranging ecological implications with respect to colonization strategies, immigration, and possibly impact by grazers. An integrated model of growth form characteristics, biological properties, and ecological implications is presented for epibenthic diatoms.

Key index words: aggregation pattern; *Amphora*; analysis of covariance; *Cocconeis*; colonization strategy; diatoms; distribution; *Gomphonema*; *Navicula*; *Synedra*

Hutchinson (1975) defined growth forms as the set of adaptations developed by different taxa for a particular mode of life. These adaptations allow taxonomically unrelated species to use similar habitats, and to compete for a number of common resources. Among epibenthic diatoms, growth form can be defined using three characteristics combined in various ways: form, posture, and mobility (Hudon and Bourget 1983).

The diversity of growth forms found among living epibenthic diatoms was reported in early taxonomic records (Smith 1853, Van Heurck 1899). Charac-

teristics such as the formation of mucous tubes arranged in thallus were initially used as the basis for the definition of genus *Schizonema* (Greville 1827). This genus was abolished due to the high variability of the thalli and of the valve ornamentation, among species possessing the ability to produce tubes (Grunow 1880, Cleve 1894). Another example of the use of growth form to help delimit taxonomic units is the differentiation of genera *Fragilaria* and *Synedra* on the basis of their respective ability to form ribbon-like filaments or rosettes on a surface. Although the definition of these two genera is questioned (Lange-Bertalot 1980), the ecological significance of the distinction was convincingly argued by Round (1984) who presented comparative examples from other genera.

A growing number of studies deal with the architecture of epibenthic diatom communities (Patrick and Roberts 1979, Hoagland et al. 1982, Hoagland 1983, Hudon and Bourget 1981, 1983, Luttenton and Rada 1986, Steinman and McIntire 1986). The characteristic distribution pattern of different species was reported from observation of cells growing on agar (Lee et al. 1975), on plant material (Cattaneo 1978), on glass (Munteanu and Maly 1981), and on plastic substrates (Hudon and Bourget 1981). However, no quantitative study of the microdistribution of epibenthic diatoms has been conducted to evaluate the utilisation of space as a response to environmental variations.

Live observations of epibenthic diatoms led us to consider that growth forms in general, and mobility in particular, could influence the ecological success of a species. Growth forms and mobility should markedly affect space allocation and dominance during colonization of substrates by different species. One manifestation of the changes in space allocation is found in the small scale distribution of these algae, which leads us to expect the following results: (1) Species of epibenthic diatoms bearing different growth forms should exhibit different distribution patterns. (2) A species may alter its distribution pattern in response to environmental conditions.

Examples of distribution patterns and of the variances associated with given mean densities is given in Figure 1, for two hypothetical species of epibenthic diatoms possessing different types of mobility. Assuming the same immigration and growth rates,

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² Address for reprints and present address: Department of Fisheries and Oceans, Arctic Biological Station, 555 St-Pierre Blvd., Ste-Anne-de-Bellevue, Québec H9X 5R4, Canada.

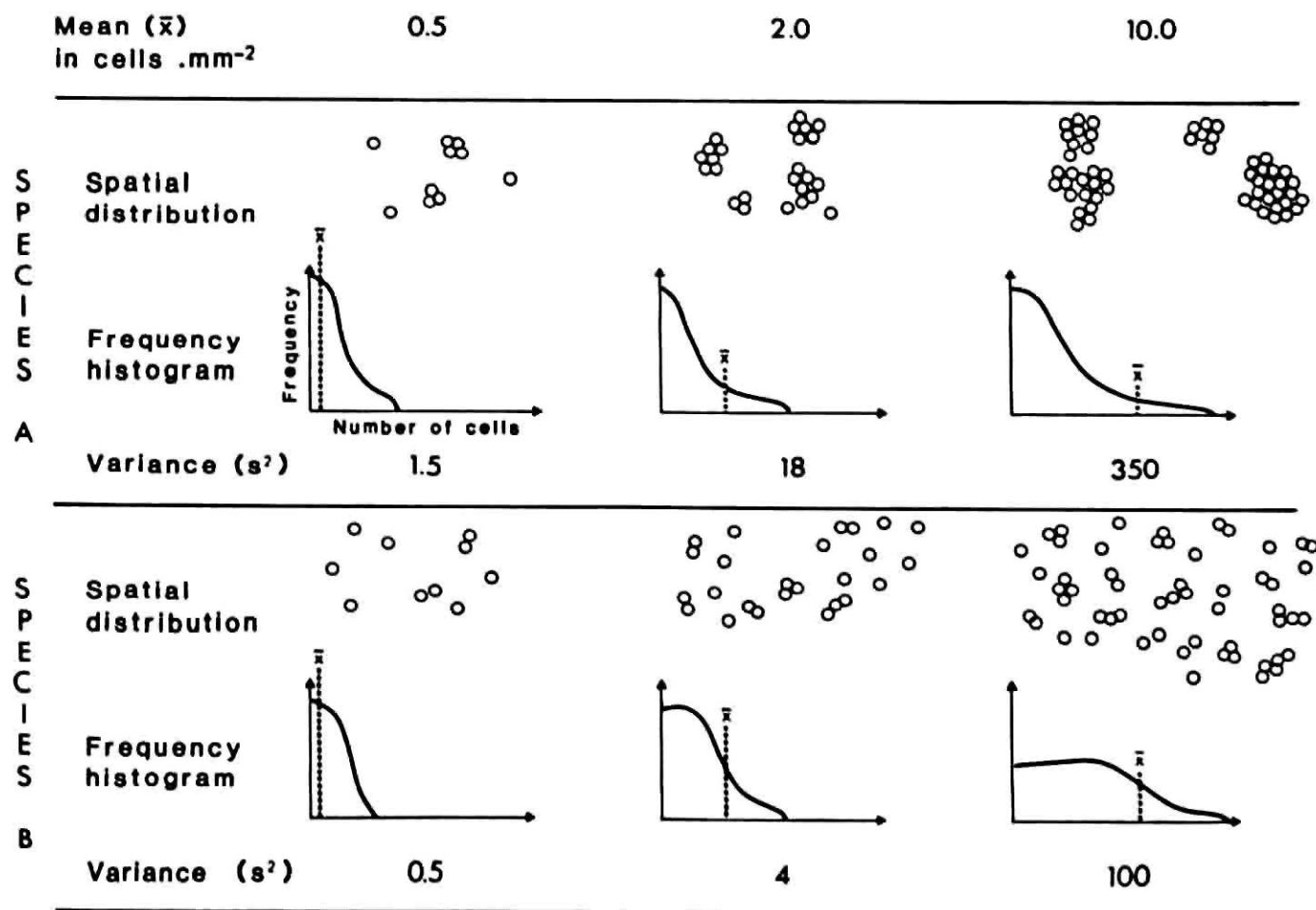


FIG. 1. Examples of distribution patterns that could be observed for two epibenthic diatom species of different mobility, over an increase in mean density.

the immobile species (A) should produce a small number of very dense clumps, hence a very highly aggregated pattern. On the other hand, the highly mobile species (B) should be more dispersed and form a larger number of small, scattered clumps.

Our aim is to examine the ecological implications of different growth forms among epibenthic diatom species. We first describe different growth forms of epibenthic diatoms from observations and measurements on living cells. Five species bearing different growth forms are used to compare the distribution patterns resulting from their varying ability to move on the surface. We then go on to examine a common (ubiquitous) species, *Synedra tabulata*, to determine whether its distribution pattern varies under different light intensities. Finally, we summarize the ecological implications associated with different growth forms and discuss the physiological adaptations related to particular morphologies.

MATERIALS AND METHODS

Sampling of epibenthic diatoms was carried out at Pointe Mitis, Québec (68°00' W, 48°40' N), on the south shore of the St. Lawrence Estuary. Black plastic panels and glass slides attached to

plywood panels were immersed at constant depths of 1 and 5 m from the surface. Some panels were shaded with mosquito net screen so as to modify light intensity while keeping other variables constant. This produced four treatments with different percentage of ambient light intensities. Two other sets of panels were immersed in Baie des Sables (1 m below mean low water level), and in Pointe Mitis (5 m below mean low water level). These panels were located on the bottom, which subjected them to semi-diurnal tides of amplitudes up to 2 m, further increasing the variability of light conditions (Table 1).

Observations of living epibenthic diatoms settled on the glass slides were done by light microscopy. For these observations, two small plastic rings (6 mm diam. $\times$ 1 mm thickness) delimiting a 30 mm² surface were glued to each slide using silicone sealant, so that water could be retained in the rings during observation. Species growth forms, measurements of cell velocity and immigration rates were determined at low magnification ($\times$ 125) and low field illumination, within 2 h of collection. It was not possible to evaluate if these procedures altered cell activity although no obvious change was observed with increasing field illumination. Cell velocity was evaluated using an ocular micrometer and a stopwatch, by measuring the distance travelled by the cells on rectilinear segments of trajectory. Cell immigration was evaluated as the percentage of cells of each species, found on slides immersed for 24 h.

The distribution patterns of epibenthic diatoms were determined using replicate scanning electron microscope (SEM) observations on 4-cm² samples punched out of the black plastic

TABLE 1. Description of the immersion conditions used for comparisons of growth conditions (*Synedra tabulata*) or of growth forms (five species together).

Station	Depth (m)	Tidal influence	Light (% of surface intensity)	<i>Synedra tabulata</i> number of samples	Other species* number of samples
(1) Mitis	1	no	15-30	10	—
(2) Mitis	5	no	1-5	5	—
(3) Mitis	1	no	10-20*	6	—
(4) Mitis	5-1	no	3-15 ^{a,b}	7	—
(5) Baie des Sables	1	yes	10-30	7	—
(6) Mitis	5	yes	1-5	11	71
Total				46	+ 71 = 117

* Panels shaded with mosquito screen.

^b Panel transferred from deep to shallow water after one month.

* *Amphora pusio*, *Cocconeis costata*, *Gomphonema kamschaticum*, *Navicula directa*.

panels. Samples were collected weekly over an immersion period of up to three months, so as to observe a range of densities for each species (Table 2). Each sample was fixed in phosphate buffered (pH 7.2) glutaraldehyde for 2 h and transferred to a graded series of ethanol solutions (25%, 50%, 75%) for dehydration. Prior to SEM observation, the samples were transferred to absolute ethanol and air dried. The samples were then glued to aluminum stubs and coated with gold-palladium (Garland et al. 1979).

Replicate counts of the number of cells of each species present on 500× SEM fields (40 000 µm²) were made to evaluate the mean density ($\bar{x}$) and variance (s^2). This magnification was chosen because it could contain a large number of diatom cells while still permitting simultaneous identification of common species. In a preliminary sampling, 30 random SEM fields were first observed to determine the number of additional fields necessary to keep the standard error of the mean below 20% (Elliott 1977). In 90% of the cases, the observed frequency distribution was not significantly different from the expected frequencies of the negative binomial distribution (Pearson's χ^2 statistic, $P > 0.05$). The negative binomial distribution model was selected for its generally good performance to describe aggregation in biological populations (Taylor et al. 1979). The mean ($\bar{x}$) and the variance (s^2) were recorded for each diatom species that was sufficiently represented on each of the 4-cm² samples, and were analysed as the initial data set.

The immersion conditions used for comparisons of growth conditions (for *Synedra tabulata*) or of growth forms (five species together) are described in Table 1. The spatial distribution of *Synedra tabulata* growing under different growth conditions was compared using 46 samples from 6 stations (Table 1). *Synedra tabulata* was the only species for which the number of samples from different locations was sufficiently large to allow examining

the effect of different growth conditions on its spatial distribution. The samples used to compare the distribution of diatom species bearing different growth forms were taken from the same station (Table 1, Table 2).

The mean number of cells of each species per microscope field ($\bar{x}$) found on the samples, and the estimated variance (s^2) were used to analyse the distribution pattern resulting from different growth conditions or different growth forms. The data was log-transformed (base 10) to linearize the relationship (Taylor 1961). The regression lines of the transformed values of the variance ($\log s^2$) on the mean ($\log \bar{x}$) for each data subset were compared with respect to their slope (b) and intercept (a), which are two ways of quantifying aggregation (Elliott 1977). The slopes and 95% confidence intervals were calculated with a Model II regression technique (reduced major axis; Kermack and Haldane 1950), which allows for error on both the X and Y axes (Sokal and Rohlf 1981). When slopes are not significantly different among species or growth conditions, the intercepts of the regressions can be compared using an analysis of covariance (ANCOVA). In addition to linearity (obtained by log-transformation) and homogeneity of slopes, the assumptions of ANCOVA include the homogeneity of the subset variances, and normality of the errors. These conditions were verified on the transformed data using Bartlett's (Sokal and Rohlf 1981) and Kolmogorov-Smirnov's (Lilliefors 1967) tests, respectively. Since ANCOVA is a Model I technique, results were double-checked with a multiple linear regression using the species or the growth forms as dummy variables.

RESULTS

Epibenthic diatoms can adopt either a solitary or a colonial form. Cells can have a prostrate or erect posture on the surface, or occur within the community cell matrix, without direct link to the surface. The capability and type of movements, as well as speed, can be measured on live cells. Combinations of these three basic characteristics define the various growth forms (Table 2). Solitary cells were often mobile, being either slow and prostrate on the substrate (*Cocconeis*, *Amphora*), or swift and capable of complex movements within the community matrix (*Nitzschia*, *Navicula*). Colonial forms comprised non-mobile as well as mobile species. Presented in increasing degree of erectness, we observe fan or rosette-shaped colonies adherent to the surface by one apex (*Synedra*) (Fig. 2A); ramified arborescent forms (*Licnophora*, *Gomphonema*, *Rhoicosphenia*); finally, linear chains (*Fragilaria*, *Melosira*, *Biddulphia*, *Rhabdonema*).

Presence or absence of movement, and measurement of speed, showed the range of "behaviours"

TABLE 2. Description of the growth form characteristics observed on the five species of diatoms. Mobility is given as: mean (standard deviation).

Species	Form	Posture	Mobility (µm s ⁻¹)	Immigration (%)	Number of samples	Range of mean density values ($\bar{x}$) used for ANCOVA
<i>Navicula directa</i>	solitary	matrix	12.4 (2.4)	33.57	17	0.8-23.7
<i>Amphora pusio</i>	solitary	prostrate	7.5 (1.4)	<1	6	1.3-6.9
<i>Cocconeis costata</i>	solitary	prostrate	3.3 (0.4)	<1-9	29	1.1-22.9
<i>Synedra tabulata</i>	colonial	upright	no	13-29	46	1.7-106.4
<i>Gomphonema kamschaticum</i>	colonial	upright	no?	1-3	19	0.6-24.1
Total					117	

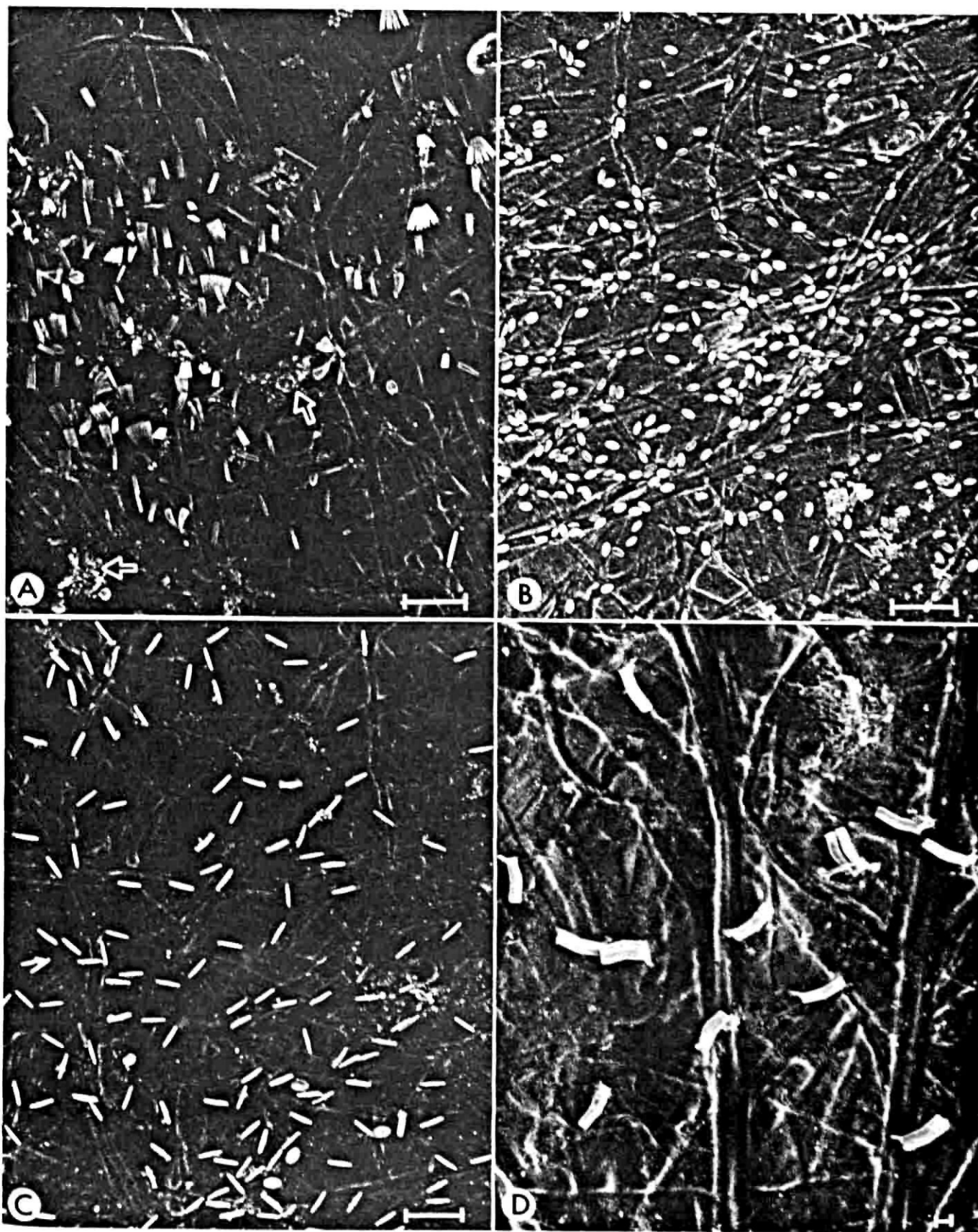


FIG. 2A-D Four different growth forms. (A) Fan or rosette-shaped colonies (*Synedra tabulata*). Arrows show the presence of detritus among cells. Scale bar equals 100 μm . (B) Slow-moving *Amphora pusio* cells, showing a tendency to remain inside the cracks of the substrate. Scale bar equals 100 μm . (C) Swift-moving *Navicula directa* moving freely over the substrate. Scale bar equals 100 μm . (D) Clump of *Achnanthes pseudogroenlandica*, with cells bearing a short peduncle; cells are located 1-2 cell lengths from one another. Scale bar equals 10 μm .

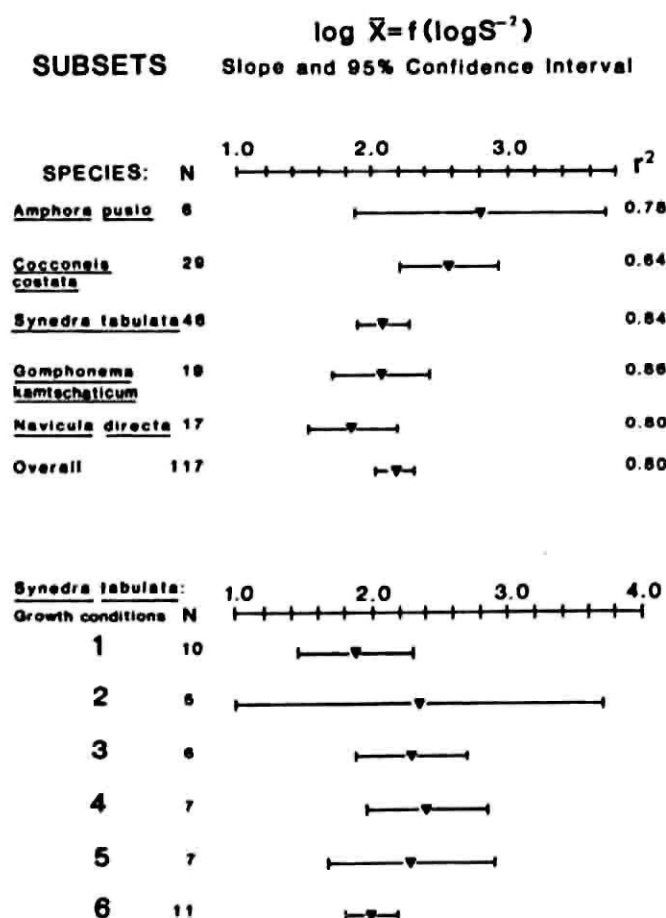


FIG. 3. Comparison of slopes and of 95% confidence intervals for the five species of epibenthic diatoms (upper panel) and for the six growth conditions for *Synedra tabulata* (lower panel).

encountered among epibenthic diatoms. Mobile species associated with the substrate exhibited repetitious movements, slowly gliding, stopping, and reversing their direction every few minutes. Movements of this type did not exceed $8 \mu\text{m}\cdot\text{s}^{-1}$, and the net displacement produced by the reversing motion was small. *Cocconeis* and *Amphora* were commonly observed moving in such fashion; some *Navicula* species also exhibited this type of movement (Fig. 2B).

Species moving freely within the community showed both a higher speed and greater variety of movements. For those cells, the presence of a slime trail and the direct contact with the substratum usually associated with diatom locomotion were not always observed. Solitary cells could execute wide gyrations and complex rotations along their long axes. When the tip of the valve occasionally touched the surface, it could serve as a gyrating point. Linear displacement was more important than for the previous group as the measured speed was over $10 \mu\text{m}\cdot\text{s}^{-1}$. In this group were members of the *Nitzschia* and *Navicula* genera (Fig. 2C). It is noteworthy that different types of movement could be observed among species of the same genus.

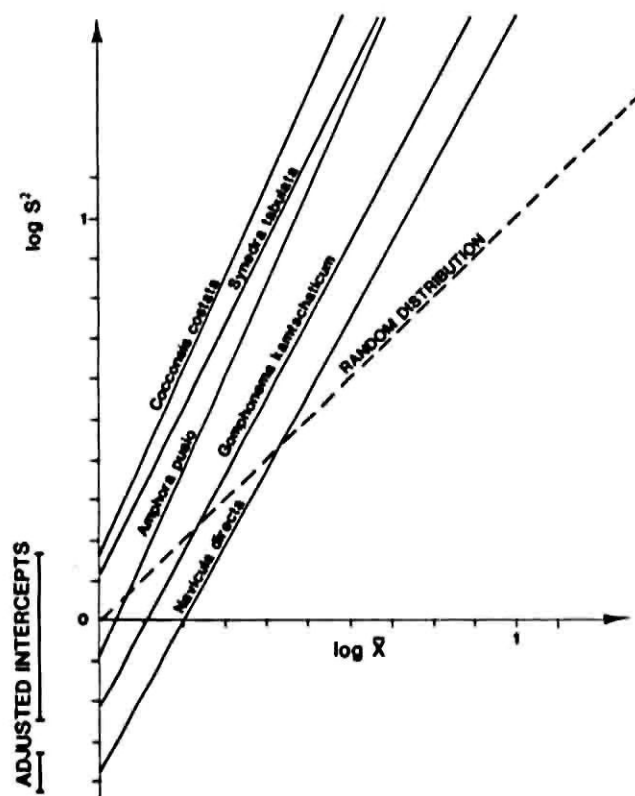


FIG. 4. Regression lines of log-variances over log-means, for the five species of epibenthic diatoms. The interruption of the line next to "adjusted intercepts" indicates a significant difference between the species. Intercepts are adjusted for the regression lines as a result of analysis of covariance.

Cells of raphe-bearing genera such as *Achnanthes*, *Rhoicosphenia* and *Gomphonema* should possess the ability to move (Halfen 1979), but were not observed doing so in this study. These types were always found bearing a mucous stalk located some distance from neighbouring cells. The structure of the monospecific clump suggested that a short migration (1–2 cell lengths) had taken place from the originating cell (Fig. 2D).

Navicula spp. was the fastest settling group, representing from 33 to 57% of all cells found after 24 h of immersion (Table 2). Intermediate settlement rates were achieved by *Synedra tabulata* (13–29%), *Cocconeis costata* (<1–9%), *Gomphonema kamtschaticum* (1–3%), and *Amphora pusio* (<1%) had low immigration rates on glass slides.

For all species, observed frequency distributions obtained from cell counts on the substrate agreed with the binomial negative distribution. Agreement with this theoretical distribution indicated that the organisms were strongly aggregated and occurred initially in patches interspersed on the otherwise bare surface; this coincides with visual qualitative observations during colonization reported in a previous paper (Hudon and Bourget 1981).

The slope of the regression of the variance on the mean (in log) provided an indication of the rate of

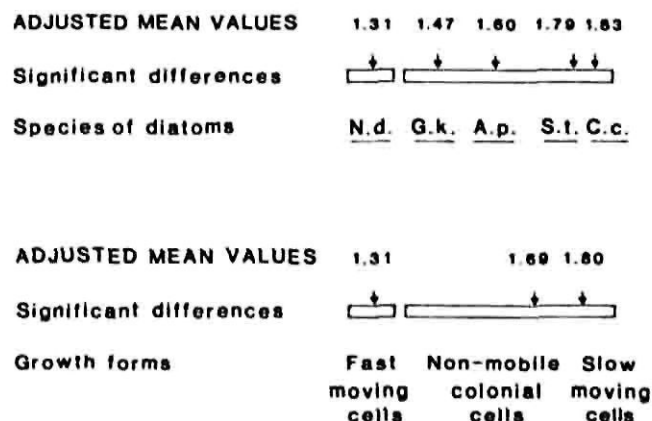


FIG. 5. Results of the *a posteriori* tests of comparisons of means. Upper panel: between species (abbreviations of species names: see Table 2). Lower panel: between growth forms.

increase of aggregation with density. The slope of the regression tended to be larger for solitary, slow-moving species (*Amphora pusio* and *Cocconeis costata*), indicating that aggregation tends to increase faster with density for these two species than for mobile or colonial species. This difference was particularly marked for the species located at the ends of the range (*Cocconeis costata* and *Navicula directa*), for which the confidence intervals of the slopes did not overlap at the 95% level (Fig. 3). However, this difference was marginal and disappeared at the 99% confidence level, which authorizes the use of the analysis of covariance (ANCOVA); this analysis will serve to interpret the differences in intercepts among the five species under study.

In the context of this study, the intercepts of the regression lines of the variance over the mean (in log) can be used as an index of aggregation for each species (Downing 1979, Taylor 1980). Differences in the intercepts should then indicate which of the five species of diatoms was the most efficient surface invader. Comparison of the intercepts using ANCOVA showed that very highly significant differences ($P \leq 0.001$) existed among intercepts. *A posteriori* comparisons showed this to be due to a single difference, between *Navicula directa* and the four other species (Fig. 4, Fig. 5, upper panel). The difference remained when species were re-grouped on the basis of their mobility (Fig. 5, lower panel). This result was confirmed by a multiple linear regression with dummy variables. On the other hand, no difference in aggregation was found among growing conditions for *Synedra tabulata*, showing that the physical arrangement of multiplying cells remained constant regardless of the light regime.

DISCUSSION

The ecological significance of growth forms is best shown by the great plasticity of the physical arrangement of cells in space, which lessened the importance of this factor in recent taxonomic studies of diatoms (Patrick and Reimer 1966). Relations be-

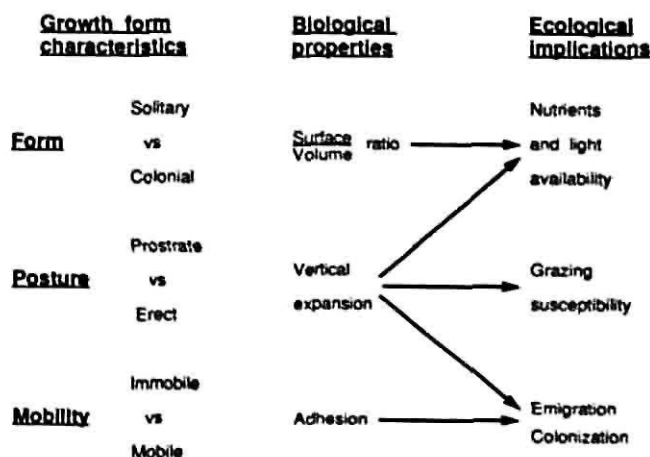


FIG. 6. Relationships between growth form characteristics, the biological properties they induce, and their ecological implications.

tween growth forms and ecology were discussed for phytoplanktonic algae (Margalef 1978, Sournia 1981) as well as for macroalgae (Littler and Littler 1980). This approach allows the integration of morphology, ecological interactions (competition, predation), and physiological functions (primary productivity and respiration) and the elaboration of a model describing the ecological implications of growth forms of epibenthic diatoms.

Epibenthic diatom populations offer many advantages for the quantitative study of changes occurring in the distribution of organisms as a response to changes in their environment. Contrary to studies dealing with macroscopic organisms, a large number of replicate quadrats can be processed quickly to obtain estimations of mean density and its associated variance within a pre-selected level of precision. Short generation time also allows easy manipulation and observation of a wide range of densities. The epibenthic diatom community thus represents an ideal material for studying the implications of the different growth forms with respect to space utilisation, under different environmental conditions.

The aggregated distribution of epibenthic diatoms can be explained by the rapid division of cells that immigrated from the outside medium and settled on the experimental surfaces. If uniform microhabitat conditions prevail, migrant cells should settle at random and their successive divisions should produce randomly distributed clones. If local microhabitats are found on the surface, due to obstacles (detritus, other cells) to water flow, the presence of microeddies will enhance the probability of settlement of cells in their immediate neighbourhood (Stevenson 1981), and consequently increase the aggregation of cells. An example of this phenomenon is observed in Figure 2A, in which cells of other diatom species and detritus are found within a clump of *Synedra tabulata* growing on an otherwise bare surface.

In turn, each growth form characteristic might be expected to bear certain biological properties, with ecological implications that might influence the success of each species (Fig. 6). These elements pertain to three categories: nutrients and light availability, susceptibility to grazing, and emigration and colonization rates.

Our results showed that four species, two of them colonial and non-mobile (*Synedra tabulata* and *Gomphonema kamtschaticum*), and two solitary and slow-moving (*Amphora pusio* and *Cocconeis costata*), were characterized by a similar, highly aggregated pattern. This suggests that the characteristic form (colonial or solitary) does not bear an overwhelming influence on species distribution patterns. However, the characteristic form affects the surface-to-volume ratio (S/V) of the cells. Previous studies carried out on phytoplankton (Sournia 1981) showed that the increase in size generated by the colonial form decreased S/V, therefore allowing lower light absorption and nutrient assimilation than for small solitary cells. The higher relative efficiency of small cells might partially explain their higher representation among solitary slow-moving diatoms.

The similarity that we observed between distributions of slow-moving and of immobile species also indicates that the capacity to move a little gives but a small advantage over immobile species in terms of surface monopoly strategy. However, moving a little can be useful for individual cells to invade cracks of the surface (as shown in Figure 2B), or to emerge from under an obstacle to reach light; it certainly facilitates clonal expansion. This result also suggests that the growth rate of cells within a clone is centrifugal, showing an increase from the center towards the edges, because there is room for expansion only at the edge of the clone. In colonial species, expansion away from the surface might be the alternative solution, allowing cell spacing and avoiding overcrowding. It has been proposed that vertical expansion improves light and nutrient availability but makes the uppermost layer of cells vulnerable to sloughing-off by currents (Hoagland 1983, Hudon and Bourget 1983, Luttenton and Rada 1986, Steinman and McIntire 1986) and by grazing (Hudon 1983).

With respect to grazing, the apparent selectivity or avoidance of grazers towards particular species of diatoms was shown to be related to diatom availability, which was in turn related to their posture on the surface. A wide variety of grazers, from ciliates to tadpoles, were reported to "select" arborescent and filamentous colonial diatoms over small, prostrate species (see the review by Hudon 1983). High aggregation may also result in an all-or-nothing impact under a randomly occurring grazing pressure or local disturbances. On the other hand, highly dispersed species will have a high probability of experiencing minor losses under all conditions. A frequent "cropping" of the dispersed population

may reduce the chances of overcrowding and of accumulation of excretory products, thus stimulating cell division.

Alternatively, the low adhesion of highly mobile cells (see the review by Harper 1977) and their easy resuspension in the water as free-floating forms may contribute to their early colonization of freshly immersed surfaces (Patrick 1967). This opportunistic strategy is supported by the high percentage of occurrence of *Navicula* cells on new glass slides after 24 h immersion, and could represent a positive trade-off against their physical vulnerability.

From results of previous studies and from our observations, it appears that not all combinations of form, posture and mobility are found in nature, presumably because some of these combinations cumulate more cost than benefit. Solitary prostrate cells are often mobile, possibly to alleviate the disadvantages of smothering. It is notable that species likely to be smothered or living in low light environments have developed physiological adaptations to compensate the effects of their growth form. Frequently buried epipsammic forms possess a strong tolerance to darkness and anoxia (Moss 1977) whereas most mud-dwelling forms, capable of fast migration back to the surface of the mud (Harper 1977), do not tolerate those conditions (Moss 1977).

On the other hand, colonial non-mobile forms are seldom prostrate on the surface. This could result from the positive phototropism of the growing filament (Dennison 1979), making the cells grow away from the surface and thus maintaining their erect posture. In this study, the aggregation of a non-mobile colonial species did not respond to changes in the environment (*Synedra tabulata*). This indicates that cells may adapt physiologically to their light environment before undergoing changes in their physical organisation on a surface. The physiological adaptations of cells during an increase in density was shown for the filamentous species *Tabellaria flocculosa*. Filaments of this species had different photosynthetic capacity and pigment ratio whether they were sampled close to the rock on which they were attached or near the apex of the filament (Hudon et al. 1987). Other mechanisms may contribute to the vertical expansion of colonial forms, such as water movement or the entrapment of oxygen bubbles within the mucous matrix of the colony (C. Hudon, pers. obs.). For tube-dwelling species, the immobile stance of the tube itself could be compensated by the mobility of the individual cell within it. Furthermore, the capability of this group to survive and colonize new surfaces as solitary individuals or as a colony provides additional ecological flexibility.

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