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Competition as a mechanism of adaptation to environmental stress in outdoor cultures of marine diatoms

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ABSTRACT: Effects were investigated of PO_4-P limitation and climate on natural assemblages of marine diatoms grown in outdoor semicontinuous cultures. The cultures were grown at 3 dilution rates (1.7; 0.851; 0.32 doublings d^{-1}) throughout the year. Temperature dependent maximum growth rate of cultures was predicted by the Eppley equation. Nutrient limitation measured as N : P and Si : P cellular ratios increased with decreasing dilution rate or increasing temperature in a manner analogous to that in single-species cultures studied by other workers. However, species dominance changed with changing nutrient stress. *Skeletonema costatum* was dominant at high dilution rates; it was replaced by *Chaetoceros* spp. and then *Cylindrotheca closterium* at lower dilution rates. *Thalassiosira* spp. co-existed with *S. costatum* or *Chaetoceros* spp. at low light intensities and temperatures. It is concluded that multi-species cultures adapt to nutrient stress by species replacement rather than physiological adaptation of a single species.

INTRODUCTION

Planktonic algae are known to respond to nutrient shortage through a variety of physiological adaptations. Changes in cellular content and ratio of nutrients, nutrient uptake rates and growth rates have been reported in nutrient limited cultures of phytoplankton (e.g. Droop, 1974). More recently, light and temperature have been shown to affect the physiological state of nutrient deficient algae (Yule Rhee and Gotham, 1981 a, b). Those studies have established that phytoplankton populations do not possess a constant metabolism; instead their cellular state can adapt to the prevailing nutrient environment.

Tilman (1977) and others have shown that multi-species cultures of phytoplankton respond to nutrient limitation by interspecific competition. This process can result in a single species displacing all other, less adapted competitors. In most competition studies, however, the species are chosen by the investigator, so it cannot be determined if other untested species would be even more adapted to the experimental conditions used. Harrison and Davis (1979) have avoided this problem by using natural communities in their studies on nitrogen and silica limitation. Their experiments presumably result in the most suitable naturally occurring species becoming dominant.

Combining the results of these physiological and population studies, nutrient stress can be seen to affect phytoplankton communities both at the cellular and population levels. This raises the question of the nature of the relation between species dominance and physiological state in natural communities. We investigated this problem by growing natural populations of marine diatoms outdoors under phosphorus limitation and by comparing the nutrient status of the cultures with their species composition.

MATERIALS AND METHODS

Culture conditions

All experiments were conducted at the Shellfish Research Laboratory, Carna, Ireland (53° 18′ N, 9° 50′ W). Solar radiation was calculated from sunshine hours (Vollenweider, 1974); it ranged from a daily average of 400 g cal cm^{-2} in June to 50 g cal cm^{-2} in December. Water temperature, measured at the laboratory inlet

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pipe, ranged from 5 °C in February to 19.5 °C in early September.

Algal cultures were grown in cyclindrical polyethylene plastic tanks, 1 m high and 1.3 m in diameter filled to 1000 l; the final experiment was performed in a 500 l tank. The culture medium consisted of unfiltered seawater pumped from a point 50 m offshore and enriched with 81.5 µg at l^{-1} NO_3-N, 70.5 µg at l^{-1} Si and 2.4 µg at l^{-1} PO_4-P (N : Si : P ratio of 34 : 29 : 1) added in the form of $NaNO_3$, $NaSiO_3 \cdot 5H_2O$ and NaH_2PO_4. This medium was considered to be P deficient relative to N or Si. Nutrient levels in the incoming seawater varied between 0.25 and 0.5 µg at l^{-1} P, 6.0 and 0.1 µg at l^{-1} N, and 10 and 2.0 µg at l^{-1} Si. Consequently, total enrichment was seldom more than 20 % higher than the intended enrichment. Salinity varied from 31 ‰ to 34 ‰ in the incoming seawater. The culture water was mixed by compressed air.

No algal inoculum was added to the cultures; instead, the natural phytoplankton was allowed to bloom. Once a population of 10^5 cells ml^{-1} was obtained, culture dilution commenced. Depending on the dilution rate, 30, 55 or 80 % of each culture was transferred every day to a clean tank. This fraction was made up to the original volume of 1000 l by the addition of more seawater. The remaining fraction of each culture was then discarded. The purpose of transferring the cultures to clean tanks was to prevent accumulation of detritus. Nutrient concentration was maintained by adding new nutrients in proportion to dilution rate. Cultures were grown for periods of 14 to 28 d with the exception of the final experiment which was maintained for 44 d (Table 1).

Experimental measurements

Water temperature was measured by max-min thermometer and the daily average was used in subsequent analysis. Water samples for nutrient analysis were filtered through glass-fibre filters and frozen. Nutrient analysis was carried out by the Central Marine Service Unit of University College, Galway. In Experiments 1 to 3, NH_4-N, NO_3-N, NO_2-N, PO_4-P and Si were determined; in subsequent experiments, total N and total P were also measured. The techniques used were those described in Strickland and Parsons (1972) for PO_4-P and NO_3-N; in Mullin and Riley (1955) for Si; in Bendschneider and Robinson (1952) for NO_2-N. Samples were photo-oxidized by UV light and then analysed for NO_3-N and PO_4-P in order to estimate total N and total P.

Cell counts were made by inverted microscope using samples preserved in Lugol's Iodine. Only species exceeding 10^4 cells ml^{-1} are considered in this paper.

Samples were taken from the experimental cultures every 2 to 3 d and from the inflowing seawater every 4 d. The seawater was not analysed in Experiments 1 to 3. An account of the natural phytoplankton in the coastal waters off the experimental site is given by Roden (in press).

Calculations

Culture dilution rate was calculated as doublings d^{-1}.

$$\text{Doublings } d^{-1} = \frac{\ln\left(\frac{1}{R}\right)}{\ln 2} \quad (1)$$

where R = proportion of culture transferred daily. A value of 30, 55 and 80 % transferred daily corresponds to daily dilution rates of 1.7, 0.86, and 0.32 doublings d^{-1} respectively.

Total cellular nutrient content was calculated as difference between total nutrient concentration (inoculum + enrichment) and medium nutrient concentration. Cellular ratios were then derived from calculated cellular content. In calculating cellular N, all forms of N (NO_3, NH_4, NO_2) were included.

Only data from cultures in near steady-state conditions, both in terms of external nutrient concentration and species composition, are considered in this paper. Consequently, data obtained during the initial period of species displacement are not included. The end of the species displacement period was arbitrarily set at the point when the ultimately dominant species reached 70 % of the total cell counts.

RESULTS

Outcome of competition

Fig. 1 shows the pattern of competition in 3 representative cultures. In Fig. 1a *Skeletonema costatum* Cleve is dominant throughout the experiment while the *Thalassiosira* group rapidly declines. In Fig. 1b an initial *Chaetoceros debile* Cleve bloom is replaced by *S. costatum*. In the final example, *S. costatum* is replaced by a *Chaetoceros* sp. while the *Thalassiosira* group maintains a nearly constant population, an example of apparent co-existence.

The results of all competition experiments are summarized in Table 1. Four recurrent species groups were encountered: (i) *Skeletonema costatum*; (ii) *Chaetoceros* sp., mainly *C. debile* and a small species-possibly *C. wighamii* Brightw; (iii) *Thalassiosira* group, mainly *T. rotula* Meunier and *T. gravida* Cleve but also *T. nordenskioldii* Cleve – a small *Thalassios-*

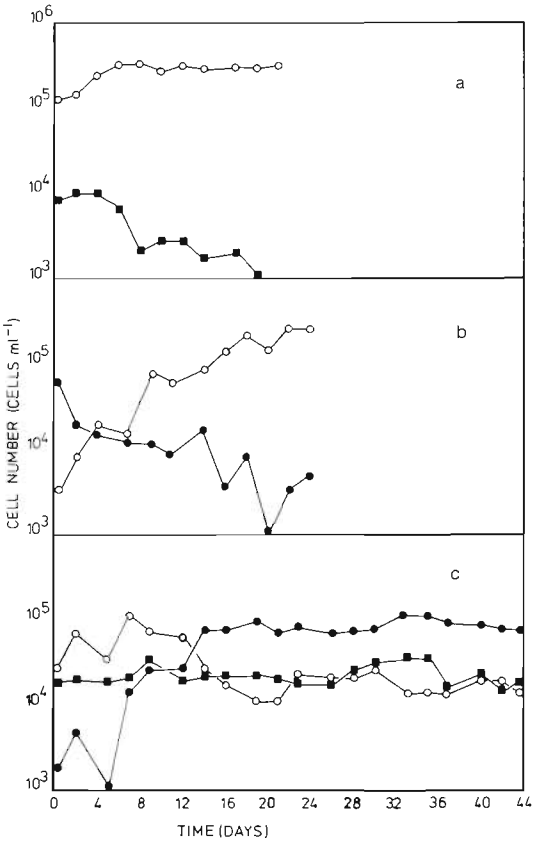

Fig. 1. Competition in 3 different diatom cultures. Experiment 12 (a), Experiment 18 (b) and Experiment 29 (c). See Table 1 for further details. Only species which exceeded 10^4 cells ml^{-1} on at least 1 occasion are shown. ○ *S. costatum*, ● *Chaetoceros* sp., ■ *Thalassiosira* sp.

Table 1. List of experiments. Experiments 1 to 3 and 12 to 28 are grouped as summer experiments and Experiments 4 to 11 and 29 are treated as winter experiments (Fig. 4 to 8). Species dominance is indicated as S = *Skeletonema costatum*, Cd = *Chaetoceros debile*, μC = small *Chaetoceros (C. wighamii)*; P = *Cylindrotheca closterium* and pennate diatoms; Tr = *Thalassiosira rotula*, Tg = *T. gravida*, μT = small *Thalassiosira* − culture washed out; + culture collapsed

Experiment No.	Dilution rate	Temperature (°C)	Dominant species	Experimental period
1	0.45	12–17	Cd	May 1980
2	0.2	14–17	P	July 1980
3	0.7	14–17	S	July 1980
4	0.45	4–10	S	Nov/Dec 1980
5	0.45	4–10	S	Nov/Dec 1980
6	0.7	4–10	−	Nov/Dec 1980
7	0.7	4–10	−	Nov/Dec 1980
8	0.45	5–10	S/Tg/Tr/μT	Feb 1981
9	0.45	5–10	S/Tg/Tr/μT	Feb 1981
10	0.7	5–10	−	Feb 1981
11	0.7	5–10	−	Feb 1981
12	0.45	6–11	S	Mar/Apr 1981
13	0.45	6–11	S	Mar/Apr 1981
14	0.7	6–11	−	Mar/Apr 1981
15	0.7	6–11	−	Mar/Apr 1981
16	0.45	12–14	+	May 1981
17	0.45	12–14	S	May 1981
18	0.7	12–14	S	May 1981
19	0.7	12–14	S	May 1981
21	0.45	13.5–17.5	Cd/μC	Jul 1981
22	0.45	13.5–17.5	Cd/μC	Jul 1981
23	0.7	13.5–17.5	+	Jul 1981
24	0.7	13.5–17.5	+	Jul 1981
25	0.45	14–19	Cd	Sep 1981
26	0.45	14–19	Cd	Sep 1981
27	0.7	14–19	S	Sep 1981
28	0.7	14–19	S	Sep 1981
29	0.2	5–10.5	μC/Tr/Tg	Nov/Dec 1982

ira sp. – and *Porosira glacialis* Jorg; (iv) a mixture of *Cylindrotheca closterium* (Ehrenb.) Reiman and Lewin and other pennate diatoms. The first 2 groups occurred alone or in combination with the *Thalassiosira* group. This group was only found in combination with the *Skeletonema* or *Chaetoceros* groups, within the *Chaetoceros* group *C. debile* appeared to displace the small species in summer but was not found in winter. Within the *Thalassiosira* group no significant species displacement was noted even in Experiment 29 which lasted for 44 d.

Fig. 2 illustrates species dominance as a function of dilution rate and water temperature. No growth is possible when low water temperatures are combined with high dilution rates. At higher temperatures or reduced dilution rates, cultures dominated by *Skeletonema costatum* or a *S. costatum/Thalassiosira* group mixture occur. At still higher temperatures or at lower dilution rates, *Chaetoceros* sp. or a *Chaetoceros/Thalassiosira* mixture appears, and eventually *Cylindrotheca closterium* and pennate diatoms dominate.

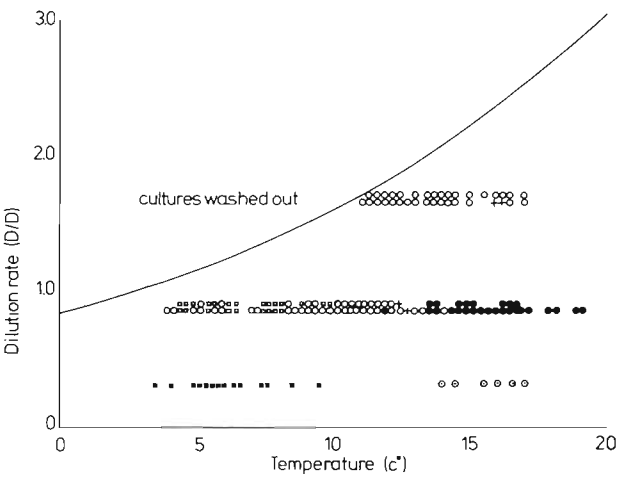

Fig. 2. Species dominance as a function of temperature and dilution rate. Each symbol represents a single count. Equation 2 is shown as a solid line. ○ *S. costatum*, ● *Chaetoceros* sp., ⊙ *C. closterium* dominated group, □ *Skeletonema/Thalassiosira* sp., ■ *Chaetoceros* sp./*Thalassiosira* sp. + unstable mixtures

In 3 experiments (Table 1) unstable algal blooms occurred which were subject to periodic collapses; as these cultures did not reach equilibrium they are not considered further in this report.

Nutrient status of the cultures

The maximum temperature dependent dilution rate of the cultures appears to coincide with the predicted temperature dependent maximal algal division rate predicted by Equation 2:

$$\mu mc = 0.851\ (1.066)^T \qquad (2)$$

where μmc = culture maximum division rate; T (C°) = water temperature. This equation was proposed by Eppley (1972) and is indicated in Fig. 2 and 3.

Fig. 3 shows external Si concentrations as a function of dilution rate and temperature. Si concentration

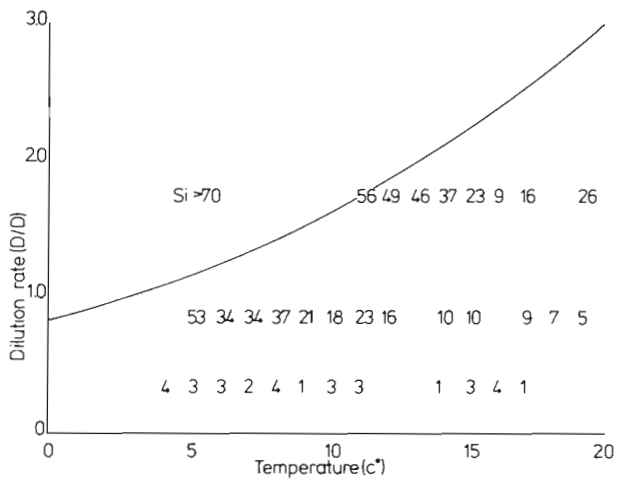

Fig. 3. Average external silica levels in µg at l^{-1} as a function of temperature and dilution rate. Equation 2 plotted as solid line

increases with increasing dilution rate or decreasing temperature; it approaches the initial medium concentration of 70.5 µg at l^{-1} near the washout point. Fig. 3 illustrates only average Si concentrations, hence the variability of the data cannot be displayed. This problem is overcome by combining dilution rate and temperature in a single factor, the community relative growth rate $\mu/\mu mc$, defined as

$$\mu/\mu mc = D/0.851\ (1.066)^T \qquad (3)$$

where D = culture dilution rate.

Fig. 4 shows external Si as a function of $\mu/\mu mc$. Si increases with increasing relative growth rate, but the data suggest that at a given $\mu/\mu mc$ concentrations are higher in winter than in summer. (See Table 1 for

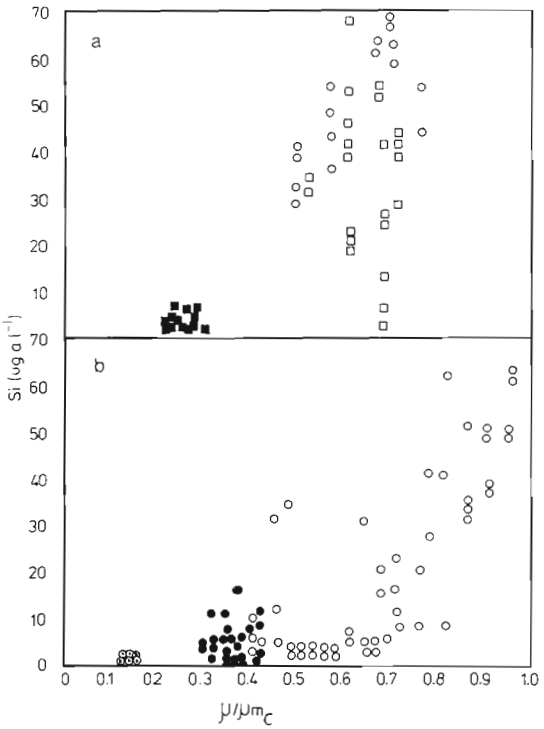

Fig. 4. External silica plotted against community relative growth rate ($\mu/\mu mc$). (a) winter data; (b) summer data. Species dominance shown by symbols used in Fig. 2

summer/winter division of the experiments). Data points are scattered, perhaps due to Si levels reflecting the fluctuating light and temperature climate.

NO_3-N and PO_4-P levels are plotted against $\mu/\mu mc$ in Fig. 5 and 6; external N distributions closely resemble Si levels, but PO_4-P levels are generally low at all levels of $\mu/\mu mc$ both in summer and winter, with the exception of some data from Experiments 4 and 5.

Phytoplankton nutrient content can be calculated as the difference between total added nutrient concentration and medium nutrient concentration. From these data phytoplankton nutrient ratio can be derived. These are shown in Fig. 7 and 8 as a function of $\mu/\mu mc$. Both the N : P and Si : P ratios increase with decreasing $\mu/\mu mc$; they are equal or exceed the initial medium ratios of N : Si : P = 34 : 29 : 1 when $\mu/\mu mc < 0.3$. When $\mu/\mu mc = 1.0$, the N : P ratio lies between 10 : 1 and 20 : 1, and the Si : P ratio ranges from 4 : 1 to 12 : 1.

DISCUSSION

Validity of the data

Indoor phytoplankton cultures can be grown in fully controlled environments. Hence variability in experimental data ought to be explicable in terms of experi-

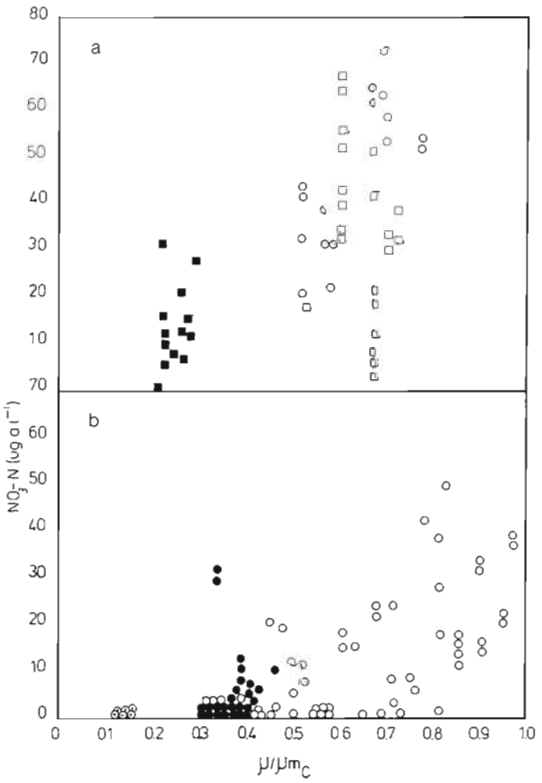

Fig. 5. External NO_3-N plotted against community relative growth rate. See Fig. 4 for details

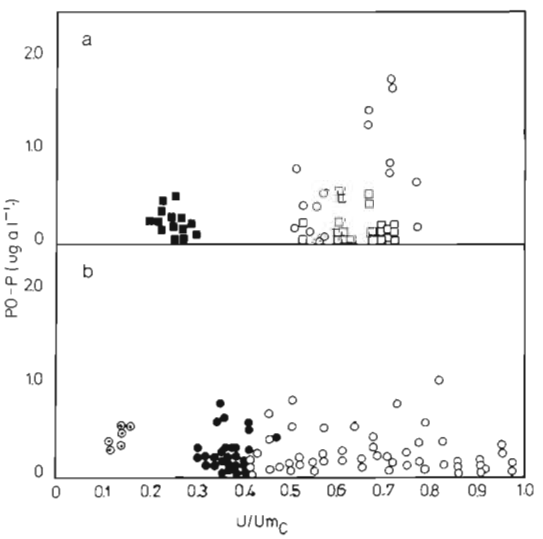

Fig. 6. External PO_4-P plotted against community relative growth rate. See Fig. 4 for details

mental treatment. This cannot be achieved in outdoor conditions. In this study it is assumed that the semi-continuous cultures were growing in approximately P limited steady-state conditions. While this assumption

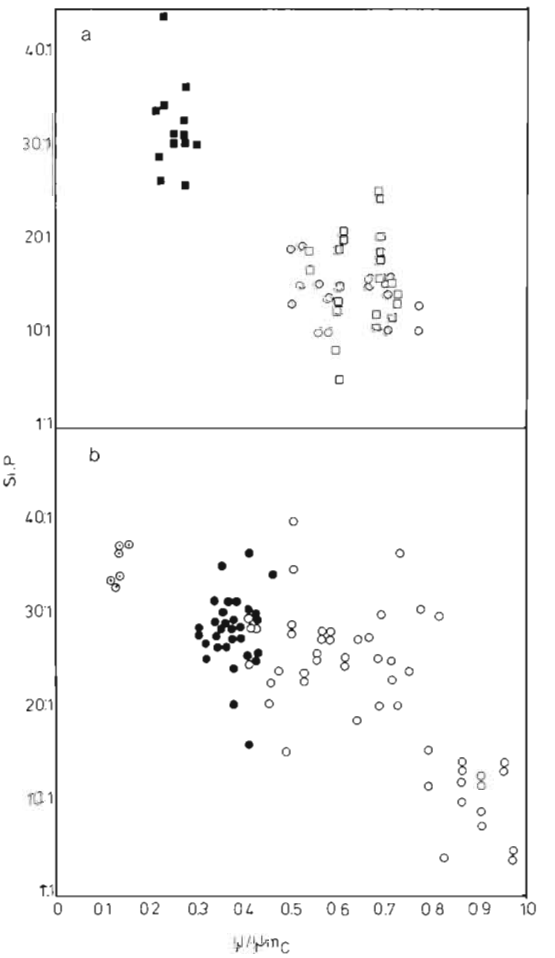

Fig. 7. Cellular Si : P ratios plotted against community relative growth rate. See Fig. 4 for details

is generally true, fluctuations in light and temperature were correlated with changes in cell number. To this extent the cultures were not in a true steady state.

While PO_4-P was intended to be the limiting nutrient, at no stage was P completely removed from the medium. However, Droop (1974) also detected PO_4-P concentrations of 0 to 0.3 μg at l^{-1} in P limited chemostat cultures of *Pavlova (Monochrysis) lutheri*. It is possible that marine phytoplankton cannot fully utilise dissolved PO_4-P.

Ideally, each culture should have been maintained until 1 species had displaced all others. This was impossible as climatic changes overtook the process of competition if experiments were too prolonged. So it is possible that some species might never be completely excluded but instead might grow indefinitely as a very small proportion of the combined population. But here we assume that with the exception of *Thalassiosira* all species become dominant or are washed out.

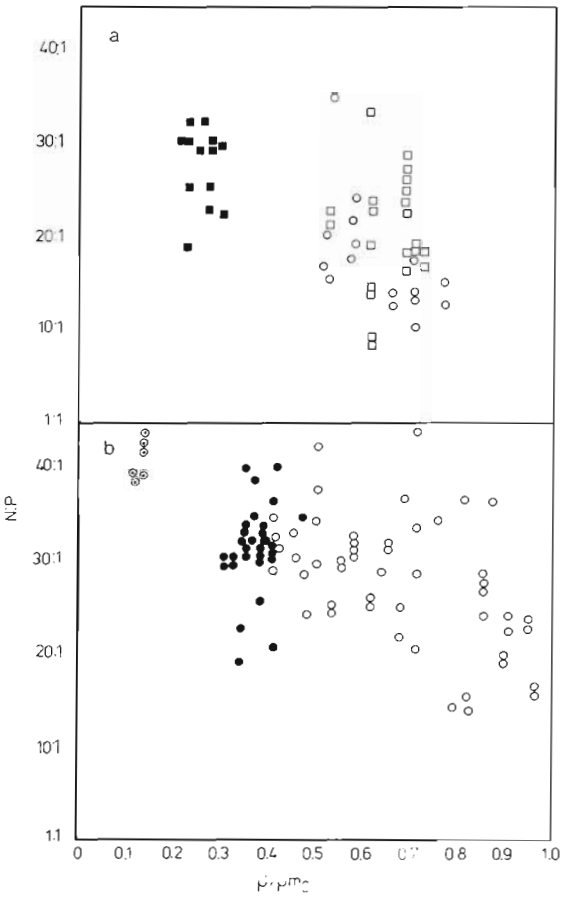

Fig. 8. Cellular N : P ratios plotted against community relative growth rate. See Fig. 4 for details

Physiological response to nutrient limitation

An initial problem in the study of multi-species cultures is the definition of a community maximum growth rate which is independent of the fluctuating populations of the component species. The successful prediction of the washout point of our cultures by the equation proposed by Eppley (1972) offers a solution to this problem (see Equation 2). His equation is an empirical description of the relation between maximal phytoplankton division rate and temperature. The equation was derived from a survey of published growth rates of numerous species, many of which divided more slowly than the equation predicted but none grew faster.

If a maximal division rate can be defined, it is possible to express the dilution rate of any culture as a fraction of the maximum, the relative growth rate of a culture. But as Eppley's equation incorporates a temperature term, relative growth rate is temperature dependent when defined as in Eq. 3:

$$\mu/\mu mc = D/0.851\ (1.066)^T \qquad (3)$$

A decrease in dilution rate or an increase in temperature reduces relative growth rate. In Fig. 3 external Si concentrations decline as temperature increases or dilution rate decreases. Fig. 4 to 8 show that external NO_3-N also increases with increasing $\mu/\mu mc$ while internal limiting to non-limiting nutrient ratios are inversely proportional to this factor.

Research on the nutrient physiology of single-species phytoplankton cultures has demonstrated that non-limiting nutrient absorbtion increases with a decline in relative growth rate (Rhee, 1974; Tilman and Kilham, 1976). Goldman et al. (1979) report that in certain species of marine algae, the ratio of limiting to non-limiting nutrient decreases as $\mu/\mu m$ increases. When $\mu/\mu m = 1$, the N : P ratio was about 16 : 1, a value which coincides with our data (Fig. 6 to 8). Harrison et al. (1977) report values of 12 to 8 : 1 and 6.7 to 3.8 : 1 for cellular N : P and Si : P ratio in nutrient sufficient cultures of *Skeletonema costatum, Chaetoceros debile* and *Thalassiosira gravida.*

Rhee and Gotham (1981a) found that either an increase in temperature or decrease in dilution rate had a similar effect on nutrient limitation in cultures of *Asterionella* or *Scenedesmus.* These reports reveal that the behaviour of single-species cultures is comparable to the behaviour of the mixed cultures described in this paper. But as community relative growth rate was defined without reference to species composition it follows that nutrient limitation in these mixed cultures can be analysed independently of species composition.

In outdoor cultures, light as well as temperature varies; consequently community maximum division rates are not just temperature dependent. In the temperate climate experienced at Carna light and temperature co-vary (O'Mahony, 1982) as a result it is difficult to separate light and temperature effects. The problem is made more difficult if one applies the findings of Rhee and Gotham (1981b) on light nutrient interactions; they found that light and temperature had very similar effects on nutrient limitation. Therefore to some extent Equation 2 is an inaccurate estimate of μmc. In Fig. 4 to 8, nutrient limitation measured as luxury consumption of N and Si or increased cellular N : P and Si : P ratios, appears more severe in summer than in winter at a given $\mu/\mu mc$. A possible explanation is that increased light intensity in summer increases nutrient limitation. Harrison and Davis (1979) report that decreasing light intensity in low-dilution-rate cultures, had an effect similar to increasing dilution rate: a reduction in nutrient competition. Therefore a more accurate expression of $\mu/\mu mc$ should incorporate light intensity.

$$\mu/\mu mc = D/f\ (I, T) \qquad (4)$$

where I = light intensity.

However, it is unclear if this modification would greatly affect the presentation of our results and would require accurate estimates of light intensity and knowledge of light/temperature interactions.

Competitive response to nutrient limitation

In contrast to continuous variation of the physiological measurements made in this study, species composition changes abruptly; *Skeletonema costatum* is dominant when $\mu/\mu mc > 0.5$ but is replaced by *Chaetoceros* sp. and *Cylindrotheca closterium* once $\mu/\mu mc$ falls below 0.4. There is an obvious correlation between species composition and the degree of community nutrient limitation; *S. costatum* is dominant when limitation is not severe, N : P and Si : P ratios are low, and luxury consumption of N and Si small; *C. closterium* is dominant when these conditions are reversed. A similar sequence of species was found by Harrison and Davis (1979) working with NH_4-limited natural populations and by other workers undertaking indoor experiments (see Harrison and Davis for references).

In theory, if a species is competitively superior in a nutrient-limited continuous culture it will eventually displace all other species (Tilman, 1977). It follows that in assessing the result of mixed-culture experiments more weight should be given to a species' ability to displace other species than to absolute cell numbers at a given time. Our results indicate that the shift from *Skeletonema costatum* to *Chaetoceros* sp. competitive dominance is sharply defined and reflects a shift in nutrient uptake ability as portrayed in the competition models of many authors, for example Tilman (1977) or Stewart and Levin (1973). The *Thalassiosira* group, however, appears to co-exist with both *Chaetoceros* sp. and *S. costatum* even when these species are themselves competing (Fig. 1).

Possibly, the *Thalassiosira* group, which only occurs in winter, is adapted to nutrient competition in the dark; it is favoured by the 17 h long night which occurs at Lat 53° N in winter. Thus the *Thalassiosira* group has a niche separate from *Chaetoceros* and *Skeletonema*, which compete best in daylight. Both Conway and Harrison (1977) and Mickelson et al. (1979) concluded that *T. gravida* was a poor competitor against *S. costatum* or *Chaetoceros* sp. under continuous illumination.

Tilman (1977) demonstrated that co-existence occurred if each species was limited by a separate nutrient. At very low $\mu/\mu mc$, luxury consumption effectively removes not only P but N and Si from the medium, so it cannot be stated that any one nutrient is most limiting nor does it follow that every species absorbs these nutrients in similar proportions. Quite conceivably, different species are limited by different nutrients; the inability of *Cylindrotheca closterium* to displace other pennate diatoms by the end of Experiment 2 might be explained by this assumption.

Dominant species in nutrient-limited environments

Comparison of the physiological and population responses to decreasing $\mu/\mu mc$ shows that while the algal cultures as a whole exhibit signs of increasing nutrient limitation, certain species are only dominant at low values of $\mu/\mu mc$. It follows that such species are dominant only under sub-optimal conditions or alternatively, these species are adapted to grow best in a nutrient-limited environment.

Ketchum (1939) reports that the exponential growth rate of *Cylindrotheca closterium* in nutrient-sufficient conditions at about 20 °C (room temperature) is 1.0 divisions d^{-1}, but at 20 °C μmc calculated from Eq. 2 is 3.0 divisions d^{-1}. That means, *C. closterium* could only grow up to 0.32 μmc. This parallels our finding that *C. closterium* is only prominent when $\mu/\mu mc < 0.2$ and suggests that this species would be washed out at higher dilution rates. Similarly, *Skeletonema costatum*, which was dominant at $\mu/\mu mc > 0.5$, is reported to have a division rate which equals or exceeds μmc (Smayda, 1976). Myklestad (1974) found that *S. costatum* had a nutrient-sufficient growth rate of 1.5 to 1.75 divisions d^{-1} at 13.0 C° while *Chaetoceros debile* and *Thalassiosira gravida* had growth rates of 1.2 to 1.5 and 0.75 to 1.0 divisions d^{-1} respectively. Expressed in terms of μmc, *S. costatum* has a division rate of 0.89 μmc; *C. debile*, of 0.76 μmc; and *T. gravida*, of 0.51 μmc. Our results (Fig. 4 to 8) show that as $\mu/\mu mc$ decreases *S. costatum* is replaced by *Chaetoceros* sp. which in turn is replaced by *C. closterium*.

While it is established that the ratio of non-limiting to limiting nutrient increases with increasing nutrient limitation (Goldman et al., 1979), Myklestad (1977) has shown that this ratio varies from species to species. He showed that *Skeletonema costatum* had a lower N : P ratio than *Chaetoceros affine* even during nutrient-sufficient growth at all medium N : P ratios tested. He concluded that *C. affine* was only P limited when the internal N : P ratio exceeded 32 : 1 if calculated on the basis of subsistence quota, though lower estimates of 17 or 20 : 1 were obtained on the basis of cell number or carbohydrate production. *S. costatum* appeared to be phosphorus limited once the cellular N : P ratio exceeded 12 : 1 using all 3 methods of estimation. When applied to the present study, these results suggest that *Chaetoceros* species which are dominant when the community N : P ratio is 30–35 : 1 are no more

P limited than *S. costatum* which is dominant when the community N : P ratio is less than 30 : 1.

In terms of both maximum growth rate and internal nutrient ratio, the dominant species encountered in this study display similar values whether growing in monoculture or mixed culture. One can conclude that these species are only dominant when community values resemble species-specific values.

This conclusion contradicts the hypothesis of Goldman et al. (1979) who proposed that phytoplankton growing in non-limiting conditions had an N : P ratio of 16 : 1. They furthermore suggested that as most natural marine phytoplankton populations had an N : P ratio of 16 : 1 their growth was not nutrient limited. This proposal adequately describes the behaviour of *Skeletonema costatum* in our cultures, but hardly explains the occurrence of *Chaetoceros* sp. which appears to occur only during community nutrient limitation when cellular N : P ratios exceed 30 : 1. Our results suggest that species which are dominant when $\mu/\mu mc$ is low have an increased capacity for luxury consumption. Consequently, as $\mu/\mu mc$ decreases, internal N : P ratios will increasingly reflect the external or medium values. Thus the observation of Goldman et al. (1979) that natural populations had an N : P ratio of 16 : 1 could be explained either as a case of nutrient sufficiency or in terms of efficient consumption causing the cellular ratio to reflect the external seawater ratio of 16 : 1 N : P (Redfield ratio).

CONCLUSIONS

Droop (1974) speculated that it might be possible to apply mathematical models based on single-species cultures to describe mixed cultures and species successions. The results of this study suggest that his idea is not unreasonable. Nutrient limitation in our cultures can be described in terms of changing nutrient ratios and relative growth rates much as in single species cultures without the necessity of referring to species composition.

Species composition is not random, however. In our cultures, adaptation to nutrient stress was achieved by species replacement rather than by modification of the physiology of a single universal species. Quantities such as growth rate or N : P ratio which appear to be very plastic in monocultures are seen to be more constant and species specific in natural assemblages. Apparently, competition ensures that species are not severely stressed but are replaced by other more adapted species once conditions become unfavourable.

However, all the dominant species encountered in the study were diatoms even though dinoflagellates and other groups are often abundant in nearby coastal waters (Roden, in press). This suggests that the type of nutrient enrichment is very important in determining species dominance. A given enrichment (e.g. organic or inorganic nutrients) allows a certain suite of species to grow; dominance within this group is determined by the rate of nutrient supply and the light and temperature climate. It is probable that species in such a group have very similar physiological characteristics. Small differences in the size of growth or uptake rates have allowed individual species within the group to evolve strategies suited to different nutrient supply rates as suggested by Guillard and Kilham (1977).

However, neither the factors which may control the number of species within such a group, nor the ecological requirements of each group are as yet described or understood.

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