

Species dominance and niche breadth in "bloom" and "non-bloom" phytoplankton populations

Phytoplankton
Dominance
Niche breadth
Bloom

Phytoplankton
Prédominance
Amplitude de niche
Efflorescence

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ABSTRACT

This paper describes the quantitative relationships between phytoplankton abundance and species number, dominance and niche breadth during "bloom" and "non-bloom" stages in a coastal marine environment of the Eastern Mediterranean Sea. Analysis of the relative frequency distribution of the species breadth per sample showed each assemblage to be a mixture of species with narrow (< 3), moderate (4-8) and broad (> 8) niche breadth. Assemblages with higher (> 30) numbers of species tended to have a greater proportion (up to 25-30 %) of species with narrow breadth in relation to the samples with fewer taxa. In "bloom" assemblages, the total cell abundance increased above the concentration level of "non-bloom" assemblages (baseline population) by two-three class orders, 75.5-78.9 % of this increase being due to the first dominant species, 5.3-8.5 % to the second dominant and the remainder to all the other species. All dominant species exhibited moderate (5.91-7.94) breadth values. On the basis of the species niche breadth and their abundance the phytoplankton community-unit could be divided into certain levels or scales of hierarchy, *i. e.* a background population formed by broad breadth-low abundance species; a population with species demonstrating moderate breadth and high abundance (including dominants); and a population characterized by narrow breadth-low abundance (rare) species.

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RÉSUMÉ

Prédominance et amplitude de niche des espèces pendant l'«efflorescence» et la «non-efflorescence» des populations du phytoplancton

Cet article décrit les relations quantitatives entre l'abondance du phytoplancton (pendant les étapes de l'«efflorescence» et de la «non-efflorescence») et le nombre d'espèces, la prédominance et l'amplitude de niche dans le temps, dans les eaux côtières de la Méditerranée orientale. L'analyse de la distribution de la fréquence relative de l'amplitude de niche des espèces par échantillon montre que chacun d'eux est un mélange d'espèces ayant une amplitude de niche étroite (< 3), modérée (4-8) et large (> 8). Les échantillons les plus diversifiés tendent à avoir une proportion plus grande (jusqu'à 25-30 %) d'espèces d'amplitude de niche étroite par rapport aux échantillons ayant moins d'espèces. Dans les échantillons d'«efflorescence» l'abondance totale des cellules se trouve au-dessus du niveau de concentration des échantillons de «non-efflorescence» (ligne de base de la population) de deux ou trois ordres de grandeur ; 75,5-78,9 % de cette augmentation étant due à la première espèce dominante, 5,3-8,5 % à la seconde espèce dominante et le reste à toutes les autres espèces. Toutes les espèces dominantes montrent des amplitudes de niche modérées (5,91-7,94). En se basant sur les amplitudes de niche des espèces et leur abondance, l'unité de communauté du phytoplancton pourrait être scindée en certains niveaux ou ordres hiérarchiques :

a) une population de base, formée par des espèces ayant de larges amplitudes de niche mais peu abondantes ; b) une population avec des espèces d'amplitude de niche moyenne, mais abondantes (comprenant les espèces dominantes), enfin une population contenant des espèces d'amplitude de niche étroite et peu abondantes (incluant les espèces rares).

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INTRODUCTION

The phenomenon of rapid biomass increase (bloom) has historically been considered as one of the major quantitative properties of the phytoplanktonic life mode. The literature contains a large number of publications which make special reference to the biomass outbursts during the temporal development of the phytoplanktonic ecosystem (Morton and Lee, 1974; Reynolds and Walsby, 1975; Winter *et al.*, 1975; Niemi, 1979; Sournia *et al.*, 1987; Pearl, 1988; Cloern, 1991). Most of these investigations deal with the dynamic trends of blooms and/or nuisance blooms of certain phytoplanktonic species; analyses of the ecological aspects of algal blooms are relatively fewer (Smayda, 1980; Cosper *et al.*, 1989).

The dramatic biomass increase above the levels of the "non-bloom" baseline is due to the synergetic mechanisms of optimal physical and chemical conditions (Pearl, 1988) but might also be influenced by the community organization and the strategies of individual species (Maestrini and Graneli, 1991). The presence or absence of organisms, the degree of constancy in their concentrations, the "opportunistic", "rare" or "dominant" character of species and their niche breadth (McIntire and Overton, 1971) might all have a vital role in the bloom process of a phytoplanktonic community.

This work describes the quantitative relationships between phytoplankton abundance (during "bloom" and "non-

bloom" stages) and species number, dominance and niche breadth in time (Pianka, 1973; May, 1974) in a marine phytoplanktonic community of the Eastern Mediterranean Sea. Species dominance is the most frequently assessed property in phytoplankton ecological studies, but where the species "niche" property is concerned, the information is scanty (McIntire and Overton, 1971; Karentz and McIntire, 1977; Harris *et al.*, 1983) and the "dominance" *versus* "niche" relationship has been investigated only in land plant communities (McNaughton and Wolf, 1970). The assessment of these properties and their relationships might provide a criterion for comparing phytoplankton assemblages and help in understanding the organization of community structure during and after a "bloom" event.

MATERIALS AND METHODS

Samples collected with a van Dorn water bottle from 1 m depth at a station (37° 55' N, 23° 35' E) in Saronicos Gulf during November-December 1987 at 1-7 day intervals (Tab. 1) were filtered on board and analysed for phosphates, nitrates, nitrites, silicates (Strickland and Parsons, 1968) and ammonia (Liddicoat *et al.*, 1976). Lugol-preserved subsamples were prepared for species identification and enumeration using an inverted microscope. Temperature and salinity were recorded for each sampling

Table 1

Physical and chemical parameters during the experimental period.

Sample No	Date (1987)	Temperature (°C)	Salinity	PO4	NH3	NO3 (µg-at/l ⁻¹)	NO2	SiO2
1	7/11	20.2	38.82	3.22	1.17	2.98	0.96	2.68
2	9/11	19.8	38.85	2.67	2.08	1.23	1.05	3.51
3	14/11	19.4	38.69	1.22	1.08	1.29	0.06	3.41
4	19/11	19.6	38.71	0.68	3.89	0.96	0.55	1.66
5	20/11	19.1	38.75	0.08	0.15	0.11	0.12	2.31
6	23/11	18.6	38.73	0.32	0.79	0.65	0.53	3.63
7	30/11	18.0	38.77	0.01	1.42	0.08	0.25	2.52
8	2/12	18.0	38.72	0.56	7.23	1.93	1.14	4.01
9	4/12	17.7	38.72	0.13	0.76	0.11	0.51	4.16
10	5/12	17.8	38.81	1.28	8.99	0.81	0.68	3.23
11	8/12	17.9	38.79	0.14	1.91	0.54	0.61	2.64
12	9/12	17.5	38.75	0.24	3.49	0.28	0.74	3.08
13	10/12	17.5	38.73	1.91	6.09	0.98	0.73	8.62
14	11/12	16.4	38.73	1.21	2.01	0.09	1.11	5.81
15	12/12	16.6	38.81	0.46	2.18	0.13	1.25	7.84
16	13/12	16.6	38.87	0.91	4.66	0.58	0.95	3.84
17	14/12	15.8	38.79	1.27	12.01	0.78	1.15	6.16
18	16/12	15.8	38.79	1.02	7.19	0.77	0.44	2.75

Table 2

Dominant species, relative dominance (Rel. Dom.), dominance index (D.I.) and number of taxa during the experimental period.

Sample No	Dominant species	Rel. Dom. (%)	D.I. (%)	Taxa No	Sample No	Dominant species	Rel. Dom. (%)	D.I. (%)	Taxa No
(1)	<i>Skeletonema costatum</i>	50.4	57.8	30	(10)	<i>Hemiaulus sinensis</i>	57.0	65.6	24
	<i>Chaetoceros decipiens</i>	7.4				<i>Chaetoceros curvisetus</i>	8.6		
(2)	<i>Skeletonema costatum</i>	77.5	86.0	35	(11)	<i>Hemiaulus sinensis</i>	76.0	83.3	29
	<i>Leptocylindrus danicus</i>	8.5				<i>Phaeocystis pouchetii</i>	7.3		
(3)	<i>Skeletonema costatum</i>	55.7	74.6	36	(12)	<i>Hemiaulus sinensis</i>	37.3	45.7	30
	<i>Leptocylindrus danicus</i>	18.9				<i>Chaetoceros affine</i>	8.4		
(4)	<i>Phaeocystis pouchetii</i>	26.5	38.0	35	(13)	<i>Phaeocystis pouchetii</i>	16.1	32.2	29
	<i>Skeletonema costatum</i>	11.5				<i>Hemiaulus sinensis</i>	16.1		
(5)	<i>Thalassionema nitzschioides</i>	19.3	30.3	32	(14)	<i>Phaeocystis pouchetii</i>	78.9	84.2	26
	<i>Phaeocystis pouchetii</i>	11.0				<i>Chaetoceros socialis</i>	5.3		
(6)	<i>Leptocylindrus danicus</i>	18.5	31.7	31	(15)	<i>Phaeocystis pouchetii</i>	39.2	48.6	29
	<i>Lithodesmium undulatum</i>	13.2				<i>Leptocylindrus danicus</i>	9.4		
(7)	<i>Phaeocystis pouchetii</i>	15.9	28.2	26	(16)	<i>Phaeocystis pouchetii</i>	71.5	77.5	29
	<i>Chaetoceros affine</i>	12.3				<i>Leptocylindrus danicus</i>	6.0		
(8)	<i>Hemiaulus sinensis</i>	51.3	64.9	26	(17)	<i>Eucampia zodiacus</i>	12.3	21.3	28
	<i>Phaeocystis pouchetii</i>	13.6				<i>Shroederella delicatula</i>	9.0		
(9)	<i>Phaeocystis pouchetii</i>	35.0	58.2	25	(18)	<i>Phaeocystis pouchetii</i>	50.2	53.5	31
	<i>Hemiaulus sinensis</i>	23.2				<i>Chaetoceros socialis</i>	3.3		

day. Univariate methods were performed on species abundance data as follows:

1) Species dominance (D) after the index described by McNaughton (1967)

$$D = 100 (N_1 + N_2)/N$$

which is equal to the percentage of the two most abundant species (N_1 and N_2) to the total number of individuals.

2) Species niche breadth (in time) was measured (McIntire and Overton, 1971) by the expression:

$$B_i = \exp \left[- \sum_{r=1}^q (n_{ir}/N_i) \log_e (n_{ir}/N_i) \right]$$

where n_{ir} is the number of individuals of the i -th taxon found in the r -th sample and N_i the summation of individuals of the " i -th taxon found at all q - samples. The magnitude of B_i is an indication of the taxon's ability to do equally well in the samples under consideration and its value can range from 1 to q .

3) Frequency distribution analyses of niche breadth data were made by using the program *Statgraphics*.

RESULTS

During the experimental period sea-water temperature dropped from 20.2°C to 15.8°C but salinity did not show any considerable fluctuations, and ranged from 38.69 to 38.87 (Tab. 1). The nutrient concentrations exhibited continuous pulses ranging as follows: P-PO₄, 0.01-3.22 µg-at/l⁻¹; N-NH₃, 0.15-12.01 µg-at/l⁻¹; N-NO₃, 0.08-2.98 µg-at/l⁻¹; N-N-NO₂, 0.06-1.25 µg-at/l⁻¹; Si-SiO₂, 1.66-8.62 µg-at/l⁻¹. The nutrient levels indicate the eutrophic character of the water in this area (Ignatiades *et al.*, 1992).

Records of algal cell concentrations showed (Fig. 1) the development of three distinct blooms during the experimen-

tal period. The first peak (sample No. 2) was recorded on the second sampling day and levelled up to 3.9×10^5 cells.l⁻¹; the second peak (sample No. 11, 2.0×10^5 cells.l⁻¹) developed 32 days after the first peak; and the third peak (sample no 14, 2.5×10^5 cells.l⁻¹) occurred three days after the second peak. The cell concentrations of "bloom" samples exhibited a significant increase (range: 1.5×10^5 - 3.9×10^5 cells.l⁻¹) above the baseline cell concentration (3.5×10^4 : mean cells.l⁻¹ concentration of all samples excepting the "bloom" samples).

Dominant species, dominance index, the relative dominance between the two dominant species in each sampling day as well as the number of taxa are given in Table 2. It may be seen that the samples associated with phytoplankton blooms (samples Nos. 2, 11 and 14) have higher values of species dominance (86.0, 83.3 and 84.2 % respectively) in relation to the "baseline" cell concentration samples. *Skeletonema costatum* (relative dominance 77.5 %) with *Leptocylindrus danicus* (relative dominance 8.5 % dominated during the first bloom; *Hemiaulus sinensis* (relative dominance 76.0 %) with *Phaeocystis pouchetii* (relative dominance 7.3 %) during the second bloom; and *Phaeocystis pouchetii* (relative dominance 78.9 %) with

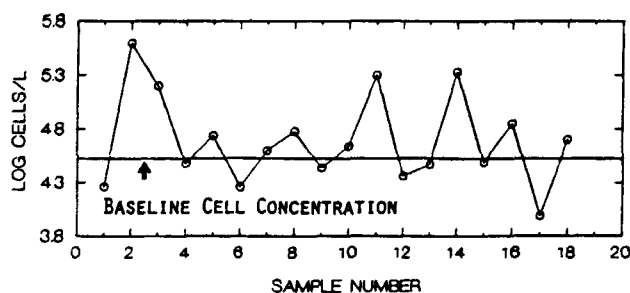


Figure 1

Phytoplankton concentrations of the three recorded "blooms" (samples 2, 11, 14) in relation to the baseline cell concentration (mean cell concentration of all samples excepting the "bloom" samples).

Chaetoceros socialis (relative dominance 5.3 %) during the third bloom. It is obvious that of the two species sharing dominance in the "bloom" samples, one is the major and the second the subordinate contributor to the value of the dominance index as defined by McNaughton (1967). The same relationship existed between the dominant species of most "baseline" samples with the exception of samples 5, 6, 7 and 13, where the two dominant species shared almost equally in percentage the value of the dominance index. A list of the identified eighty-eight species and their niche breadth in time is given in Table 3. It is of interest to note that fifty species had narrow (< 3) niche breadths, and thirteen species broad breadths (> 8), whereas the dominant species associated with "bloom" conditions exhibited moderate breadth values (*Skeletonema costatum*: 5.91; *Hemiaulus sinensis*: 6.86; *Phaeocystis pouchetii*: 7.49).

An example of the occurrence of selected species representing each scale of the niche breadth in sequential sampling order is given in Figure 2. It is seen that the species with broad breadth (> 9) i. e. *Rhizosolenia fragilissima*, *Eucampia zoodiacus*, *Centrodinium pavillardii*, *Ceratium pentagonum* and *Prorocentrum micans* were present almost continuously in the phytoplankton community with low concentrations (10^2 - 10^3 cells.l⁻¹); these species might be characterized as constituting the background population of the community. Chosen as examples of the species with moderate breadth were the dominant species *Phaeocystis pouchetii*, *Hemiaulus sinensis* and *Skeletonema costatum*, which exhibited an exponential growth up to 10^5 - 10^6 cells.l⁻¹ but each at a different time during the experimental period. All species having moderate niche breadth showed a degree of better growth in certain samples. Finally, representatives of narrow breadth

Table 3

List of identified species and their niche breadth in time.

SPECIES	BREADTH	SPECIES	BREADTH
1. <i>Prorocentrum oblongum</i> Schiller	1.00	45. <i>Trichodesmium</i> sp.	2.58
2. <i>Calcidiscus leptoporus</i> (Mur.& Black.) Loeb.& Tap.	1.00	46. <i>Ceratium tripos</i> (Mull.) Nitzsche	2.82
3. <i>Protoperidinium globulus</i> (Stein) Balech	1.00	47. <i>Bacteriastrum elegans</i> Pavillard	2.82
4. <i>Chaetoceros concavicornis</i> Mangin	1.00	48. <i>Ceratium massiliense</i> (Gour.) Jorgensen	2.99
5. <i>Rhizosolenia acuminata</i> (H.Per.) Gran	1.00	49. <i>Dinophysis lenticula</i> Pavillard	2.99
6. <i>Dictyocha speculum</i> Ehrenberg	1.00	50. <i>Dictyocha octonaria</i> Ehrenberg	2.99
7. <i>Odontella mobiliensis</i> (Bail.) Grunow	1.00	51. <i>Chaetoceros socialis</i> Lauder	3.16
8. <i>Chaetoceros borealis</i> Bailey	1.00	52. <i>Chaetoceros atlanticus</i> Cleve	3.25
9. <i>Emiliania huxleyi</i> (Loh.) Hay & Mohler	1.00	53. <i>Prorocentrum balticum</i> (Lohm.) Loeblich	3.36
10. <i>Ornithoceros magnificus</i> Stein	1.00	54. <i>Thalassiothrix mediterranea</i> Pavillard	4.34
11. <i>Ceratium candelabrum</i> (Ehr.) Stein	1.00	55. <i>Protoperidinium granii</i> (Osten.) Balech	4.45
12. <i>Ceratium macroceros</i> (Ehr.) Cleve	1.00	56. <i>Navicula pennata</i> Schmidt	4.55
13. <i>Protoperidinium diabolus</i> (Clev.) Balech	1.00	57. <i>Chaetoceros danicus</i> Cleve	4.74
14. <i>Michaelsarsia elegans</i> Gran	1.00	58. <i>Guinardia blavyana</i> Peragallo	4.82
15. <i>Chilomonas marina</i> (Braar.) Halldal	1.00	59. <i>Lithodesmium undulatum</i> Ehrenberg	4.99
16. <i>Synedra hennedyana</i> Gregory	1.00	60. <i>Eutreptia</i> sp.	5.21
17. <i>Chaetoceros lauderi</i> Ralfs	1.00	61. <i>Nitzschia pungens</i> Grunow	5.27
18. <i>Rhizosolenia imbricata</i> Brightwell	1.00	62. <i>Ceratium furca</i> (Ehr.) Clap. & Lachmann	5.34
19. <i>Chaetoceros eibonii</i> (Grun.) Meun. ex Van Heu	1.00	63. <i>Acanthoica</i> sp.	5.74
20. <i>Protoperidinium leonis</i> (Pav.) Balech	1.00	64. <i>Chaetoceros decipiens</i> Cleve	5.87
21. <i>Asterionella japonica</i> Clev.& Moller ex Gran	1.00	65. <i>Skeletonema costatum</i> (Grev.) Cleve	5.91
22. <i>Chaetoceros pendulus</i> Karsten	1.00	66. <i>Pleurosigma normanii</i> Wm. Smith	6.46
23. <i>Melosira moniliformis</i> (Mull.) Agardth	1.00	67. <i>Dictyocha fibula</i> Ehrenberg	6.58
24. <i>Ceratium fusus</i> (Ehr.) Dujardin	1.00	68. <i>Leptocylindrus danicus</i> Gran	6.84
25. <i>Rhizosolenia robusta</i> (Nor.) ex Pritchard	1.00	69. <i>Hemiaulus sinensis</i> Greville	6.86
26. <i>Oxytoxum scolopax</i> Stein	1.43	70. <i>Chaetoceros diversus</i> Cleve	7.23
27. <i>Pronoctiluca spinifera</i> (Loh.) Schiller	1.43	71. <i>Thalassionema nitzschioides</i> Hustedt	7.29
28. <i>Lauderia borealis</i> Cleve	1.54	72. <i>Phaeocystis pouchetii</i> (Har.) Lagerheim	7.49
29. <i>Alexandrium tamarense</i> (Leb.) Balech	1.65	73. <i>Chaetoceros affine</i> Lauder	7.58
30. <i>Dactyliosolen mediterraneum</i> Peragallo	1.71	74. <i>Thalassiosira rotula</i> Meunier	7.72
31. <i>Chaetoceros convolutus</i> Castracane	1.88	75. <i>Shroederella delicatula</i> (Per.) Pavill.	7.93
32. <i>Streptotheca tamesis</i> Shrubsole	1.89	76. <i>Bacteriastrum hyalinum</i> Lauder	8.19
33. <i>Chaetoceros compressus</i> Lauder	1.89	77. <i>Rhizosolenia alata</i> Brightwell	8.26
34. <i>Coccolithus pelagicus</i> (Wall.) Schiller	1.91	78. <i>Nitzschia closterium</i> W. Smith	8.32
35. <i>Bacteriastrum delicatulum</i> Cleve	1.93	79. <i>Odontella sinensis</i> (Grev.) Grunow	8.70
36. <i>Thalassiothrix frauenfeldii</i> Grunow	1.95	80. <i>Prorocentrum micans</i> Ehrenberg	8.99
37. <i>Prorocentrum marinum</i> (Cienk.) Loeblich III	1.98	81. <i>Rhizosolenia stouterfothii</i> Peragallo	9.26
38. <i>Coscinodiscus</i> sp.	2.00	82. <i>Ceratium pentagonum</i> Gourret	9.75
39. <i>Chaetoceros densus</i> Cleve	2.00	83. <i>Gymnodinium breve</i> Davis	10.13
40. <i>Protoperidinium bipes</i> (Pauls.) Balech	2.01	84. <i>Centrodinium pavillardii</i> Taylor	10.82
41. <i>Phalacroma pulchellum</i> Lebour	2.14	85. <i>Chaetoceros didymus</i> Ehrenberg	11.42
42. <i>Scrippsiella trochoidea</i> (Stein) Loeblich III	2.29	86. <i>Eucampia zoodiacus</i> Ehrenberg	11.45
43. <i>Oxytoxum constrictum</i> (Stein) Butschli	2.51	87. <i>Chaetoceros curvisetus</i> Cleve	12.31
44. <i>Chaetoceros peruvianus</i> Brightwell	2.58	88. <i>Rhizosolenia fragilissima</i> Bergon	12.72

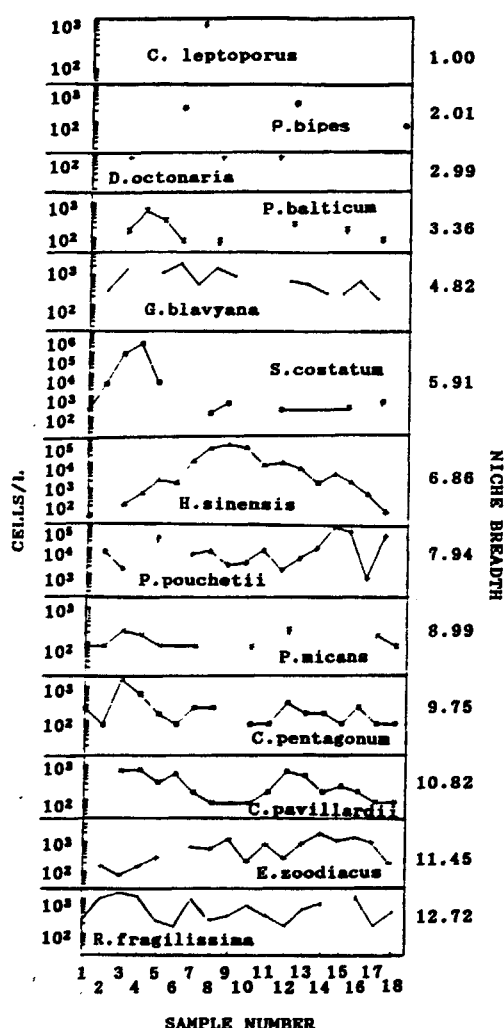


Figure 2

Occurrence of selected species representing each scale of niche breadth (1 through 12.72) in relation to their cell concentration in sequential sampling order.

(*Guinardia blavyana*, *Prorocentrum balticum*, *Dictyocha fibula*, *Peridinium minusculum*, *Calcidinius leptoporus*) as well as all species belonging in this category showed low (10^2 - 10^3 cells.l⁻¹) sporadic growth.

The pattern of the breadth frequency distribution (Fig. 3) showed a great departure from normality in all samples. Analysis of the relative frequency distribution of the species breadth per sample (Fig. 3, superimposed curves) showed that assemblages with higher (> 30) number of species (samples 2 to 6 and 18) had a tendency to have a greater proportion (up to 25-30 %) of species with narrower breadth (< 3) in relation to the samples with fewer taxa. On the other hand, the species with broad niche breadth (> 8) ranged between 10-20 % in most samples. A significant (at the 0.01 level) negative relationship between mean niche breadth of the taxa occurring in a particular sample and the number of species occurring in that sample is shown in Figure 4.

DISCUSSION

A species' specialization in the community, the share of the community resources that it utilizes and its particular way

of relating to other species and to intracommunity conditions of environment, space, and time is termed its "niche" (Whittaker, 1965). Variational aspects of the niche (temporal or spatial) have been well documented for land animal (Pianka, 1973) and plant (McNaughton and Wolf, 1970) populations. As far as the phytoplanktonic communities are concerned, Venrick (1982) argued the occurrence of niche diversification whereas others (Levandowsky, 1972; Smayda, 1980; Harris, 1986) recognized the existence of such diversification and McIntire and Overton (1977) calculated the niche breadth in time and space of littoral diatoms in the Yaquina Estuary, Oregon.

The present investigation evaluated the extent to which each species was active in successive assemblages of a marine phytoplankton community by estimating its niche breadth in time (Tab. 3), and further evaluated the relationship of the species' niche breadth to its maximum contribution in the community, expressed as dominance and/or bloom.

Analysis of the entire set of species recorded in this investigation showed (Tab. 3) that species with narrow breadth (rare species) were the most numerous, comprising 57 % of the algal community; they had low growth rate (abundance: 10^2 - 10^3 cells.l⁻¹), and a fast rate of succession (present in one-two samples). Species with broad breadth were fewer (14 % of all species) in number, had low abundance (equivalent to that of the narrow-breadth species) and a low rate of succession, being recorded in nearly all samples (baseline population). The most successful species as far as abundance is concerned (10^3 - 10^6 cells.l⁻¹) proved to be those with moderate breadth, comprising 29 % of all species; they were recorded in most samples, but had their best growth in a few samples and in this category belonged to the dominant species. Thus, the functional role of a species in the community is a sequence of its niche as was demonstrated by Hurlbert (1981). Diversification in species niche breadth could be mainly attributed to the fact that each species has its own genetic, physiological and life cycle characteristics as well as its own relationships with the physical environment and interactions with other species (Smayda, 1980).

Further investigation on the species recorded in each of the 18 assemblages showed each assemblage to be a mixture of species with narrow (< 3), moderate (4-8) and broad (> 8) niche breadth in time, whereas the proportions of species belonging to each breadth category differed among assemblages (Fig. 3). Thus, assemblages with many taxa tended to have a greater proportion of species with narrower breadth than those with fewer taxa (Fig. 4); these results are in agreement with the data published by McIntire and Overton (1971). McArthur and Levins (1967) developed the theoretical basis for relationships between niche breadth and number of competing species and defined also an inverse trend between them.

The results of this investigation demonstrated that in each "bloom" assemblage (Fig. 1, samples 2, 11, 14) the total cell abundance increased above the concentration level of "non-bloom" assemblages (baseline populations) by two-three class orders; and that 75.5-78.9 % of this increase was due to the first dominant species, 5.3-8.5 % to the

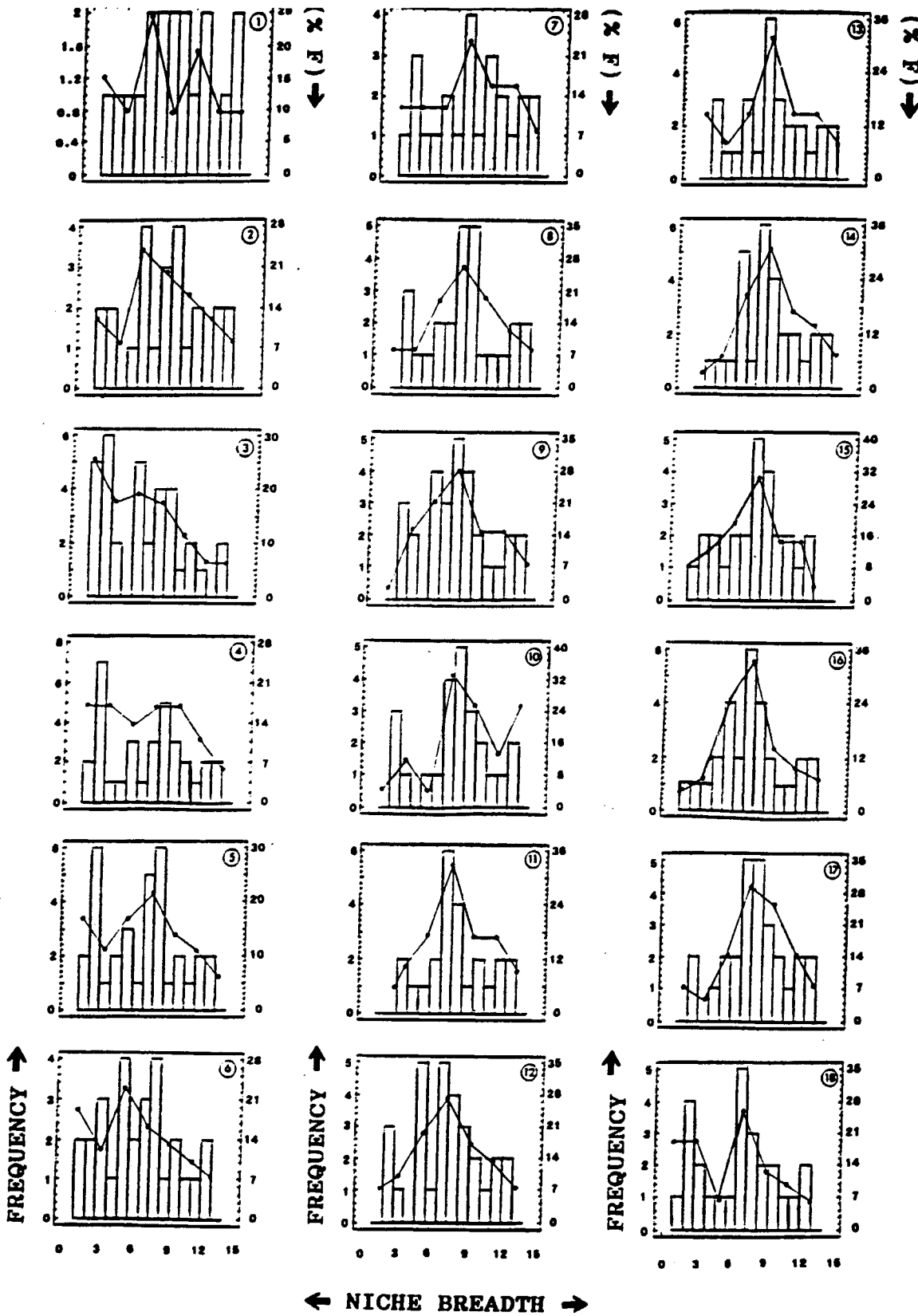


Figure 3
 Frequency distribution (bars) and relative frequency (curve superimposed, F %) of the species niche breadth in each sample.

second dominant, and the rest to all the other species in the assemblage (Tab. 2). All the bloom-forming first-dominant species (*Skeletonema costatum*: sample 2, *Hemiaulus sinensis*: sample 11, *Phaeocystis pouchetii*: sample 14) belonged to the moderate-breadth category. These data are in accordance with the results of McIntire and Overton (1971) but at variance with McNaughton and Wolf's (1970)

conclusion that dominant species have broader niches than subordinate species, a theory that has also been criticized by McIntire and Overton (1971).

The dominant species *Skeletonema costatum*, *Hemiaulus sinensis* and *Phaeocystis pouchetii* had a distinct temporal partitioning in their maximum growth defined as "bloom", but were also first or second dominants in several prece-

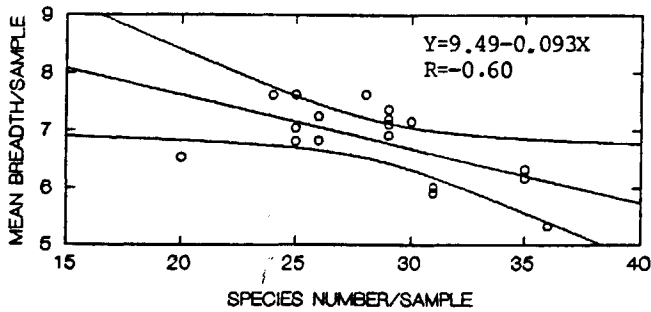


Figure 4

Regression line expressing the relationship between the mean niche breadth per sample and the species number per sample.

ding and following non-bloom assemblages (Tab. 2), sharing and possibly competing for food resources. Petersen (1975) and Tilman (1977) have shown that niche diversification can allow competitive coexistence on the basis of differential nutrient uptake kinetics. Changes in the competitive advantage of each species might also be associated with the frequency of changes of the environmental variables (Grenney *et al.*, 1973). The sharp boundaries between "bloom" assemblages (Fig. 1) might be attributed to the competitive displacement among dominants (Austin,

1985) and/or to their strong consumption by zooplankters (Frost, 1980) or sinking (Smayda, 1970).

On the basis of the species niche breadth and their abundance, the phytoplankton community-unit could be divided into certain levels or scales of hierarchy, *i.e.* into a baseline or background population comprising broad breadth-low abundance species; a population of moderate breadth-high abundance (including dominant) species; and a population of narrow breadth-low abundance (rare) species (Fig. 1, 2). Whittaker (1965) developed a similar hierarchical model of the organization of plant communities based on species abundance and niche relationships. It must be noted that the hierarchical organization presented in this work characterized a phytoplankton community proliferating in eutrophic waters (Tab.1); the phytoplankton structure in oligotrophic waters should thus be a subject of future study.

It is evident from the preceding discussion that ecological niche is a useful device for describing concisely the patterns and limits of organisms (Colwell and Fuentes, 1975) and the relative importance of competition (Austin, 1985), and that together with dominance, the "niche breadth" variable is a good measure of the species' importance in the community (McNaughton and Wolf, 1970). Thus, this variable should be considered as a fundamental estimator of the community organization of phytoplankton.

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