Multidimensional analysis of diatom morphologic and morphometric phenotypic variation and relation to niche[1]

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Abstract: There have been few past studies of relationships between phenotypic variation and population niche. In this study, phenotypic variation was separated into morphometric and morphologic variation which was related to niche for fourteen diatoms using canonical correspondence analysis (CCA). The degree of environmental influence was explored further via fuzzy coding of the variables and analyzed by a second CCA. Overall, the relationship between phenotypic variation and niche breadth varied on a dimension-by-dimension basis. Generally, morphometric characters of diatoms were influenced by genetic factors, while morphologic characters were environmentally influenced. CCA proved to be a useful method to depict relationships between phenotypic variation and niche.
Keywords: canonical correspondence analysis, diatoms, fuzzy coding, morphologic, morphometric, tolerance.

Résumé: À ce jour, il existe peu d'études portant sur les relations entre la variation phénotypique et la niche écologique des populations. Dans ce travail, la variation phénotypique de quatorze espèces de diatomées a été séparée en variations morphométrique et morphologique, lesquelles ont été associées à une niche particulière en utilisant l'analyse canonique des correspondances (ACC). Le degré d'influence de l'environnement a été étudié plus en détail grâce à un codage désordonné des variables puis à l'aide d'une deuxième ACC. Dans l'ensemble, le rapport entre la variation phénotypique et l'étendue de la niche variait selon une base dimensionnelle. De façon générale, les caractères morphométriques des diatomées étaient influencés par des facteurs génétiques, alors que les caractères morphologiques étaient plutôt influencés par des facteurs environnementaux. L'ACC est une méthode utile pour décrire les relations entre les variations phénotypiques et la niche écologique.
Mots-clés: analyse canonique des correspondances, diatomées, codage désordonné, morphologique, morphométrique, tolérance.

Introduction

Phenotypic variability is advantageous to an organism in an environment which changes temporally or spatially (Pianka, 1978). Organisms which have broader niches or ranges of tolerance to changing environmental conditions exhibit greater fitness, and therefore, higher adaptive ability (Pianka, 1978). Individuals which can utilize marginal resources have broader niches and have an advantage over those which cannot. In a population where phenotypic variability among individuals is great, population niche breadth may become broader as long as sufficient resources are available (Roughgarden, 1972). Alternatively, when there is little phenotypic variability and resources are scarce, the individuals' niches overlap greatly and may broaden in the process of resource utilization. Population niche breadth may also become broader (Soulé & Stewart, 1970). Increased between-phenotypic and within-phenotypic variability (Roughgarden, 1972) are the components which contribute to broadening population niche breadth.

Various hypotheses have been formulated and studies conducted on the relationship between phenotypic variability and niche breadth. A number of researchers have purported to prove the validity of the "Morphological Variation-Niche Breadth" hypothesis (Van Valen, 1965; Rothstein, 1973; Shugart & Blaylock, 1973; Babble & Selander, 1974; Steiner, 1977; Zangerl & Bazzaz, 1984). Others have

claimed to refute the hypothesis (Willson, 1969; Soulé & Stewart, 1970; Sabath, 1974; Ashton & Rowell, 1975; Beever, 1979). Some of these researchers and others indicate that an increase in phenotypic (or genotypic) variability of any type increases population niche breadth.

Prentice & Cramer (1990) used canonical correspondence analysis (CCA) to study phenotypic and genotypic variation in a perennial herb with respect to niche variation. They defined niche as a cross-section of species' response curves represented by species scores. Although species scores are optima (ter Braak, 1988) and tolerances represent niche breadth in CCA (ter Braak, 1990), their study showed that multidimensional analysis could be used to look at the relationship between phenotypic variation and niche.

One way to view the relationship between phenotypic variation and niche is to separate the roles of environmental and genetic influences on physiological processes. Physiological processes will occur at different rates under different environmental conditions (Pianka, 1978). An organism may change and adapt as its environment changes. Adaptation to the environment occurs genetically and by means of physiological flexibility (Pianka, 1978). Organisms which are adapted to their environment in a greater number of dimensions can tolerate greater changes than those which are not (Pianka, 1978). The resultant phenotypic variation reflects adaptation, and adaptation can be measured by breadth of tolerance.

The intent of this exploratory study is to examine the relationship between phenotypic variation and niche. This relationship will be examined on a multidimensional basis using CCA. To elucidate phenotypic variation, two categories will be created and delineated as morphologic and morphometric variation. In addition, the contribution of environmental and genetic factors to physiological processes affecting phenotypic variation will be explored. Measurements based on size (morphometric) *versus* measurements based on surface features (morphologic) may be useful in distinguishing the degree to which these influences are operating.

Methods

To implement this study, fourteen diatom species representing twelve genera served as models (Table I). These diatoms were chosen as they have been studied extensively, and there is a multitude of data available from the literature. In cases where information was sporadic for a particular species, or information was available for the genera only, data were pooled to represent at least two species from the genera. These genera/species were chosen to illustrate various possibilities which may be encountered in ecological analyses.

TABLE I. Species designation for species model used

Species designation	Species model
s1	*Stephanodiscus sp.* (very small species)
s2	*Aulacoseira italica*
s3	*Asterionella formosa*
s4	*Tabellaria flocculosa*
s5	*Rhizosolenia sp.* (freshwater)
s6	*Coscinodiscus cocinnus* and *C. granii*
s7	*Ditylum brightwelli*
s8	*Fragilaria crotonensis*
s9	*Nitzschia sp.*
s10	*Aulacoseira granulata*
s11	*Cyclotella meneghiniana*
s12	*Amphora sp.*
s13	*Surirella sp.*
s14	*Fragilaria capucina*

Each diatom was designated as follows: s1- species 1; s2- species 2; s3- species 3; s4- species 4; s5- species 5; s6- species 6; s7- species 7; s8- species 8; s9- species 9; s10- species 10; s11- species 11; s12- species 12; s13- species 13; s14- species 14. Species 6 and 7 would be considered brackish water forms. The remainder are typical freshwater forms.

For each species, morphometric and morphologic characters were ranked based on data from the literature. Morphometric characters included surface to volume ratio (S/V) (Brzezinski, 1985; Smetacek, 1985; Pollingher, 1988; Reynolds, 1988; Turpin, 1988) and biovolume (Brzezinski, 1985; Conley, Kilham & Theriot, 1989) for all species. Length and width measurements (Patrick & Reimer, 1966; 1975) were ranked for pennates, and diameter (Gross, 1939a; b; Krammer & Lange-Bertalot, 1991; Edlund & Stoermer, 1993) was ranked for centrics. Morphologic characters included symmetry (bilateral or radial) (Patrick & Reimer, 1966; 1975; Krammer & Lange-Bertalot, 1986; 1988; Round, Crawford & Mann, 1990; Krammer &

Lange-Bertalot, 1991), presence of raphe (raphid/pseudo-raphid or araphid) (Patrick & Reimer, 1966; 1975), type of valve surface process (labiate, strutted, neither) (Round, Crawford & Mann, 1990), degree of silicification (weak, midway, or strong) (Round, Crawford & Mann, 1990), degree of undulation of valve surface (flat or undulate) (Round, Crawford & Mann, 1990), valve shape (approximate geometric form) (Round, Crawford & Mann, 1990), areolae pattern (radiate, undetermined, parallel striae, or divergent striae) (Patrick & Reimer, 1966, 1975; Round et al., 1990), density of areolae pattern (fine, midway, or coarse) (Round, Crawford & Mann, 1990), and colony formation (solitary or colonial) (Patrick & Reimer, 1966, 1975). Some characters of diatoms have been shown to exhibit an intra-phenotypic curvilinear relationship (Theriot, Håkansson & Stoermer, 1988). In this regard, CCA is the analytical tool of choice, since it is based on non-linear considerations (ter Braak, 1988).

The difference between an organism's environment and its niche is that niche is defined as the ways in which the organism uses its environment (Pianka, 1978). Niche is a fluid, dynamic structure which may change spatially and temporally as well as from dimension to dimension. Since diatoms require silica (Si), Si utilization and Si storage or content of the individual are important. Si concentration in the environment indicates availability. A diatom's biological response to Si in its environment is a function of what it "sees" (Maguire, 1973) or what it actually uses in its environment. Biological responses include growth rate and nutrient preference. A diatoms's niche response structure includes range of tolerance and refers to physiological and genetical adaptive processes (Maguire, 1973). The niche structure changes in response to environmental conditions as a pattern of biological responses.

For this study, the parameters used as biological responses with respect to niche were ranked based on data from the literature. The parameters used were growth rate-Si (rSi) (Tilman, 1981; Tilman, Kilham & Kilham, 1982; Sommer, 1988), growth rate-phosphorus (rP) (Tilman, 1981; Tilman, Kilman & Kilman, 1982), Si cell^{-1} (Conley, Kilham & Theriot, 1989), Si:P (Fairburn, Gibson & Foy, 1987; Sommer, 1988; Grover, 1989), pH tolerance (Gross, 1939a; b; Cholnoky, 1968; Lowe, 1974; Beaver, 1981), temperature tolerance (Lowe, 1974; Stoermer & Ladewski, 1976; Eppley, 1977; Tilman, Kilham & Kilham, 1982; Bienfang, Harrison & Quarmby, 1982), light intensity tolerance (Eppley, 1977; Tilman, Kilham & Kilham, 1982), and salinity tolerance (Gross, 1939a; b; Cholnoky, 1968; Lowe, 1974; Beaver, 1981). These parameters as optimal responses to environmental conditions will be referred to as niche variables.

CCA was used to depict relationships between morphometric and morphologic characters of diatoms and niche variables. Using the forward selection option, niche variables were chosen for inclusion in the analysis, provided they did not unduly influence the resultant ordination (ter Braak, 1990). For each niche variable, morphometric and morphologic characters were ranked as they occurred along each niche variable axis. These rankings were obtained by perpendiculars from character scores to each niche variable

axis and represented approximate weighted averages or optima for each morphometric or morphologic character. This specified the degree of influence of each niche variable from CCA. Niche variables were represented as arrows in the ordination. The closer a character was to the head of the arrow, the more greatly it was influenced by that niche variable. Interset correlation coefficients were examined to determine which constrained axis was correlated with which niche variable. A weighted correlation coefficient matrix was calculated to identify intracorrelation of niche variables.

Tolerances or niche breadths for each species were calculated from CCA as standard deviation of canonical scores. In this analysis, species were represented by sample scores, and sample heterogeneity represented tolerances. These tolerances represented niche structure with respect to species' biological responses rather than range of habitat. The broadness of niche refers to the degree of the species' biological ability to adapt to its environment. Tolerances were qualitatively examined on a dimension-by-dimension basis. Narrow niche breadth refers to approximately less than 0.5 tolerance or standard deviation units.

To further characterize the degree of environmental and genetic influence on phenotypic variation, a second CCA was performed. In this analysis, morphometric and morphologic characters as well as niche variables were ranked using fuzzy coding. Rather than using logical coding (0 or 1), fuzzy coding indicated variable values near a boundary but not completely within a given category. This coding reflected multiple, overlapping relationships. For example, centric diatoms will exhibit ranges of diameters. Therefore, coding for two or more diameter measurements would be used to cover this range.

Files were constructed with the same characters and niche variables. Each character or niche variable was subdivided into two to six categories (Tables IIa and b). Morphologic categories were qualitative. Morphometric categories were interval. Most niche variables also contained interval categories. The exceptions were light intensity tolerance, which was binary, and pH and salinity tolerances, which were spectra. All ranges were developed using numerous literature sources (Tables IIa and b).

Results

CCA ordination depicted variation in morphologic and morphometric characters with respect to niche variables (Figure 1). Only pH tolerance was omitted from the analysis because of high leverage (> 5) (ter Braak, 1990). Si cell^{-1}, rSi, rP, and light intensity tolerance had the longest arrows which signified the largest influences. This was substantiated by the interset correlation coefficients (Table III). The first constrained axis was correlated with Si cell^{-1}, the second with rP and rSi, the third with light intensity tolerance, and the fourth with light intensity tolerance and Si cell^{-1}.

Overall, pennates were on the left, and centrics were on the right in the ordination diagram (Figure 1). Each character was ranked to determine degree of influence by each niche variable (Table IV). In terms of the morphologic characters, symmetry showed some degree of influence from all niche

TABLE IIa. Morphologic and morphometric characters, categories, and ordination codes for the second CCA based on: 1- Brzezinski, 1985; 2- Conley, Kilham & Theriot, 1989; 3- Edlund & Stoermer, 1993; 4- Gross, 1939a,b; 5- Holmes & Reimann, 1966; 6- Krammer & Lange-Bertalot, 1986; 7- Krammer & Lange-Bertalot, 1986; 8- Krammer & Lange-Bertalot, 1991; 9- Makoto, 1991; 10- Patrick & Reimer, 1966; 1975; 11- Reynolds, 1988; 12- Round, Crawford & Mann, 1990; 13- Smetacek, 1985; 14- Turpin, 1988

Morphologic/Morphometric Character	Categories	Ordination code	
Valve shape	disc	v1	
or geometry	ellipse	v2	
in a plane[12]	triangle	v3	
	trapezoid	v4	
	rectangle	v5	
Silicification[5,12]	weak	sil1	
	strong	sil2	
Valve areolae	radial	pu1	
pattern[10,12]	undetermined	pu2	
	parallel striae	pu3	
	divergent striae	pu4	
Type of process[12]	strutted	p1	
	labiate	p2	
	neither	p3	
Valve length (μ)[10]	< 25	l1	d1
or	26-50	l2	d2
Valve diameter (μ)[3,4,8]	51-75	l3	d3
	76-100	l4	d4
	> 100	l5	d
Valve width (μ)[10]	< 5	w1	
	> 5	w2	
Surface/Volume (μ^{-1})[1,9,11,13,14]	< 0.2	sv1	
	0.21-0.4	sv2	
	0.41-0.6	sv3	
	0.61-0.8	sv4	
	0.81-1.0	sv5	
	> 1.0	sv6	
Biovolume (μ^3)[1,2]	102	b1	
	103	b2	
	104	b3	
	105	b4	
	106	b5	
Symmetry [6,7,8,10]	radial	sy1	
	bilateral	sy2	
Raphe[10]	araphid	r1	
	raphid	r2	
Valve surface[12]	undulate	su1	
	flat	su2	
Colonial formation[10]	solitary	co1	
	stellate	co2	
	zig-zag	co3	
	row	co4	
Density of areolae	fine	den1	
pattern[12]	coarse	den2	

variables except Si cell^{-1}. That is, type of symmetry for a given diatom did not reflect the amount of Si cell^{-1}. Many morphometric characters showed practically no influence from niche variables. However, there were some noteworthy patterns. Width was least influenced by niche variables. Length was little influenced by Si cell^{-1}, but somewhat influenced by other niche variables. Diameter and biovolume were most influenced by Si cell^{-1} and somewhat influenced by salinity tolerance. S/V was strongly influenced by all except Si cell^{-1}.

For morphologic characters, presence of raphe was essentially not influenced by niche variables (Table IV).

TABLE IIb. Niche variables, categories, and ordination codes for second CCA based on: 1- Beaver, 1981; 2- Bienfang, Harrison & Quarmby, 1982; 3- Cholnoky, 1968; 4- Conley , Kilham & Theriot, 1989; 5- Eppley, 1977; 6- Fairburn, Gibson & Foy, 1987; 7- Gross, 1939a,b; 8- Grover, 1989; 9- Lowe, 1974; 10- Sommer, 1988; 11- Stoermer & Ladewski, 1976; 12- Tilman, 1981; 13- Tilman, Kilham & Kilham, 1982

Niche variable	Categories	Ordination code
Temperature (°C) Tolerance[2,5,9,11,13]	< 5	t1
	5.1-10	t2
	10.1-15	t3
	15.1-20	t4
	> 20	t5
Growth rate - Si (rSi)[10,12,13] or growth rate-P (rP)[12,13]	< 0.4	rsi1 rp1
	0.41-0.8	rsi2 rp2
	> 0.8	rsi3 rp3
Light intensity Tolerance[5,11]	low	li1
	high	li2
pH tolerance[1,3,7,9]	acidophilous	ph1
	indifferent	ph2
	alkaliphilous	ph3
	alkalibiontic	ph4
Salinity tolerance[1,3,7,9]	mesohalobous	sal1
	halophilous	sal2
	indifferent	sal3
	halophobous	sal4
	euryhalobous	sal5
Si cell^{-1} (pmol cell^{-1})[4]	< 1	c1
	1.1-10	c2
	10.1-20	c3
	> 20	c4
Si:P[6,8,10]	< 10	sip1
	> 10	sip2

TABLE III. Interset correlation coefficients from the first CCA. Values reported as 10^3

Niche variable	AX1	AX2	AX3	AX4
Temperature Tolerance	19	-256	-426	-123
rSi	-97	-656	-305	-85
rP	-348	-679	33	137
Light intensity tolerance	106	-442	604	-310
Salinity tolerance	163	-175	-359	-125
Si cell^{-1}	720	33	-202	239
Si:P	-332	-338	-447	-42

and salinity tolerances as well as Si cell^{-1}. Both rSi and rP were negatively correlated with Si cell^{-1}. Light intensity tolerance was negatively correlated with salinity tolerance and Si cell^{-1}. Si cell^{-1} was also negatively correlated with Si:P.

Species tolerances were calculated from CCA (Table VI). Tolerances for the first constrained axis or Si cell^{-1} represented range of ability to store available Si. For the rP-rSi or second constrained axis, tolerances were represented by reproduction or growth over a range of P and Si utilized. The third constrained axis represented light intensity tolerances. Tolerances for the fourth constrained axis were represented by a combination of light intensity tolerance and Si cell^{-1}.

For the Si cell^{-1} axis, narrow tolerance ranges were evident for species 10, 11, 13, and 14 (Table VI). For the rP-rSi axis, species 6, 7, and 8 had narrow tolerances. Species 4, 6, 7, 11, and 14 had narrow tolerance ranges with respect to light intensity axis. Many species had narrow ranges of tolerance with respect to the light intensity-Si cell^{-1} axis. These included species 2, 3, 4, 9, 10, and possibly species 5 and 7.

Overall, Si cell^{-1} and light intensity had the most influence (Table VI). The combination light intensity-Si cell^{-1} produced narrower tolerances for species 2, 3, 4, 5, 6, 7, 9, and 10 than Si cell^{-1} alone. When compared to light intensity alone, species 2, 3, 5, 7, 9, 10, and 13 had narrower niche breadths for the combination light intensity-Si cell^{-1}. Species 2, 3, 5, 7, 9, and 10 had broader niches to Si cell^{-1} and light intensity separately than the combination of the two niche variables.

For rP-rSi, species 4, 6, 7, 8, and 9 had narrower niche

Type of process showed a moderate influence as did areolae pattern. Except for Si cell^{-1} and salinity tolerance, little influence on degree of valve surface undulation was evident. Density of areolae pattern was mostly influenced by Si cell^{-1} and somewhat by other niche variables. Degree of silicification was influenced only slightly by niche variables.

Intracorrelation of niche variables was calculated as a weighted correlation coefficient matrix in CCA (Table V). Positive correlations with temperature tolerance were evident for rSi and rP. Both rSi and rP were positively correlated with light intensity tolerance and Si:P. Salinity tolerance was positively correlated with Si:P and Si cell^{-1}. Negative correlations with temperature tolerance were light intensity

TABLE IV. Ranking of morphologic/morphometric characters with respect to each niche variable for the first CCA

Si cell^{-1}	rSi & temperature tolerance	Light intensity tolerance	rP	Salinity tolerance
Diameter	S/V	S/V	symmetry	S/V
Valve surface	symmetry	symmetry	S/V	valve surface
Biovolume	valve shape	valve shape	valve shape	biovolume
Density of areolae	length	areolae pattern	length	diameter
Type of process	areolae pattern	length	areolae pattern	symmetry
Colonial formation	colonial formation	colonial formation	colonial formation	valve shape
S/V	type of process	biovolume	type of process	areolae pattern
Silicification	density of areola	type of process	density of areolae	length
Areolae pattern	biovolume	valve surface	silicification	colonial formation
Valve shape	valve surface	dentity of areolae	raphe	type of process
Length	silicification	diameter	biovolume	density of areolae
Width	diameter	silicification	valve surface	silicification
Symmetry	raphe	raphe	diameter	raphe
Raphe	width	width	width	width

360
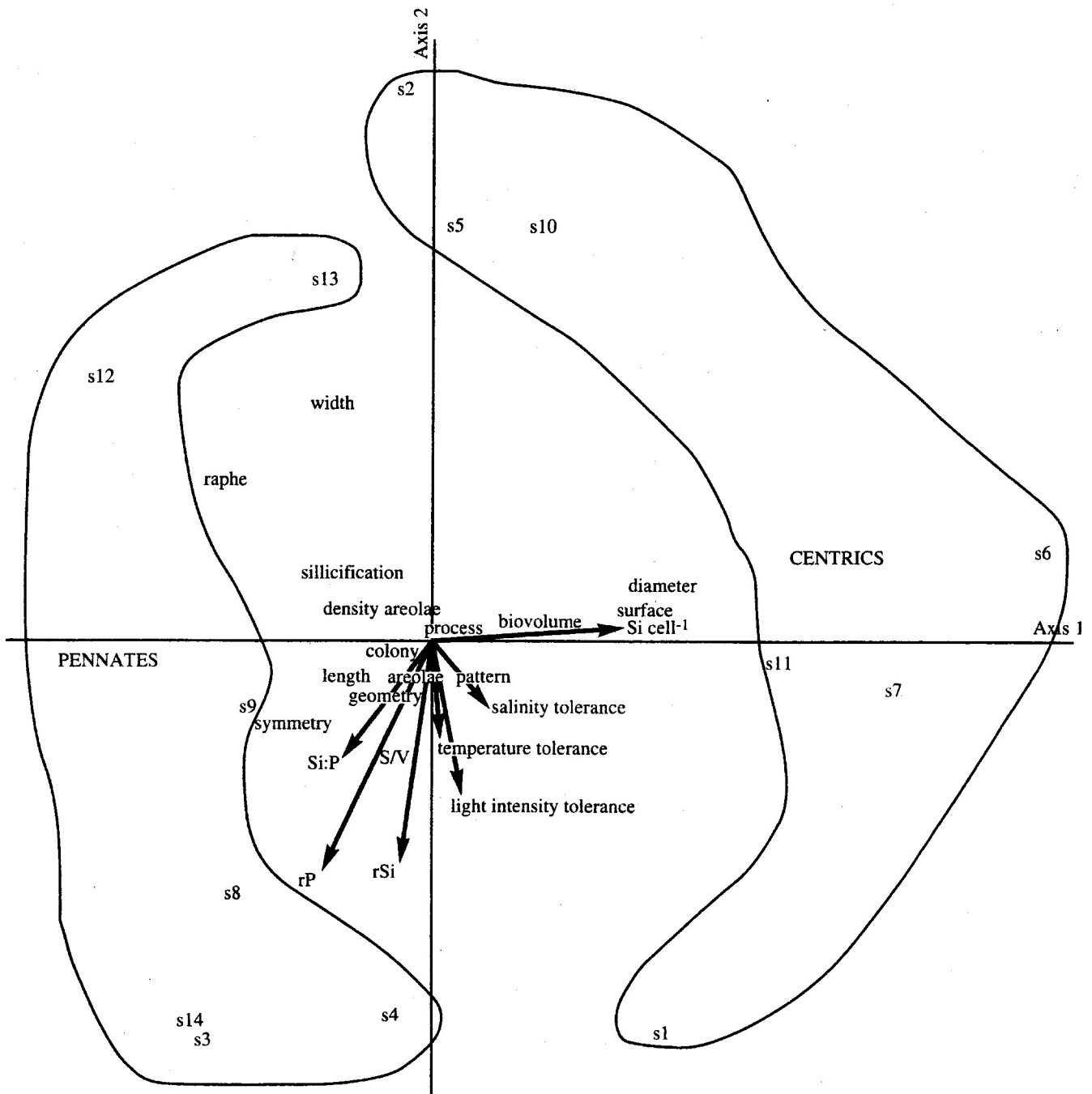
FIGURE 1. First CCA of all variables. Arrows signify niche variables. Pennates and centrics are circumscribed.

breadths compared to those for Si cell[-1]. Species 1, 6, 8, and 13 had narrower tolerances with respect to rP-rSi than to light intensity. When compared with the combination light intensity-Si cell[-1], narrower niche breadths for rP-rSi were exhibited by species 1, 6, 7, 8, 12, and 14.

Species showed coherent patterns of variation from dimension to dimension. Species 1 and 12 had similar niche breadths for the first three constrained axes and broader tolerances for the combination light intensity-Si cell[-1]. Species 2, 3, 5, and 9 had similar tolerances for all except narrower niche breadth for light intensity-Si cell[-1]. Broader tolerance for the first constrained axis represented species 6,

7, and 8. However, species 6 and 8 had broader tolerances with respect to the fourth constrained axis, unlike species 7. In contrast to species 6 and 8, species 10 and 13 had broader niche breadths with respect to rP-rSi and light intensity than the first and fourth constrained axes. Species 11 and 14 had similar niche breadths for the second and fourth constrained axes with narrower tolerances for the first and third constrained axes. Only species 4 had broader niche breadth with respect to Si cell[-1] and rP-rSi and narrower tolerance to light intensity and the combination light intensity-Si cell[-1].

In the second CCA ordination, variation of the fuzzy-coded or discretized data were depicted (Figure 2). Some of

TABLE V. Weighted correlation matrix of niche variables from the first CCA. Bold values indicate important associations

Temperature tolerance	1.0000						
rSi	**.4076**	1.0000					
rP	**.2541**	.3253	1.0000				
Light intensity tolerance	**-.0457**	**.2307**	**.1065**	1.0000			
Salinity tolerance	**-.3541**	.0256	.026	**-.1575**	1.0000		
Si cell⁻¹	**-.1820**	**-.1297**	**-.3651**	**-.2627**	**.4008**	1.0000	
Si:P	.1620	**.5266**	**.1752**	-.0010	**.2551**	**-.2355**	1.0000
	temperature tolerance	rSI	RP	light intensity tolerance	salinity tolerance	Si cell⁻¹	Si:P

the niche variables were omitted for having negligible influence (ter Braak, 1988) or high leverage (ter Braak, 1990). Those niche variables were Si:P (sip1 and sip2), slight to indifferent salinity tolerances (sal2 and sal3), and low temperature and 10-20°C tolerance (t1, t3, and t4).

Interset correlation coefficients determined the association of niche variables to canonical axes (Table VII). The first constrained axis was correlated with highest temperature tolerance (t5), mid rSi (rsi2), and largest amount of Si cell⁻¹ (c4). Fast rSi (rsi3), pH tolerance of 7 or greater (ph2 and ph3), tolerance for brackish water (sal1), and smallest amount of Si cell⁻¹ (c1) were correlated with the second constrained axis. Low temperature tolerance (t2) and small amounts of Si cell⁻¹ (c2) were associated with the third canonical axis. The fourth constrained axis was correlated with highest temperature tolerance (t5), light intensity tolerance (li1 and li2), and broad salinity tolerance (sal5).

Variation in the discretized data of morphometric and morphologic characters showed definite patterns (Figure 2). A gradient was evident along the first constrained axis with pennates on the left, and centrics on the right. The pennate morphologic characters of raphe/pseudoraphe, flat surface, labiate process, and striae also were projected on the left side of the ordination. Similarly, on the right side, araphid, undulate surface, strutted process, and radial/undetermined areolae were identified with centrics. Type of process had a microgradient with the second constrained axis. No process was associated with species 5 in the upper right quadrant, and strutted process occurred in the lower right quadrant of the ordination.

In addition, there was a very general gradient of two morphometric characters (Figure 2). Larger S/V and smaller

biovolume were on the left, and smaller S/V and larger biovolume were on the right in the ordination. However, within S/V and biovolume, microgradients were evident and aligned with the second constrained axis. On the left side of the ordination, larger S/V and smaller biovolume were associated with the upper quadrant, while smaller S/V and larger biovolume were associated with the lower quadrant. A smaller S/V and larger biovolume near the upper right quadrant graded into a larger S/V and smaller biovolume just below.

On the second constrained axis, two morphological characters had gradients (Figure 2). Weak silicification and fine striae/areolae were associated with the upper part of the ordination. Strong silicification and coarse striae/areolae were associated with the lower part.

Morphometric characters also showed particular gradients (Figure 2). Long (length), narrow (width) pennates were associated with the upper left quadrant of the ordination while short (length), wide (width) pennates were associated with the lower left quadrant. In general, for centrics, larger diameter was associated with the upper right quadrant, and smaller diameter was associated with the lower right quadrant of the ordination. However, two divergent microgradients were evident with respect to diameter. Smaller diameter near the first constrained axis graded to larger diameter in the upper right quadrant for one microgradient.

TABLE VI. Species tolerances for each axis from the first CCA

Species model	Tolerance AX1	Tolerance AX2	Tolerance AX3	Tolerance AX4
s1	0.9	1.1	1.4	2.0
s2	0.8	1.2	1.2	0.4
s3	1.0	1.1	1.1	0.5
s4	1.0	0.8	0.4	0.5
s5	0.9	1.1	1.0	0.6
s6	1.3	0.1	0.4	0.8
s7	1.4	0.4	0.1	0.6
s8	1.0	0.4	0.8	1.6
s9	1.0	0.8	0.7	0.4
s10	0.5	1.3	1.2	0.2
s11	0.4	0.9	0.3	0.7
s12	1.0	1.3	1.3	1.5
s13	0.4	1.0	1.7	0.8
s14	0.2	0.9	0.2	1.0

TABLE VII. Interset correlation coefficients from the second CCA. Values reported as 103. See Table IIb for references to ordination codes

Ordination code	AX1	AX2	AX3	AX4
t2	-245	-250	-321	-15
t5	546	-117	-69	-599
rsi1	287	-109	85	-287
rsi2	-646	476	111	-115
rsi3	251	-369	81	-166
rp1	-324	-49	-21	-122
rp2	-154	228	205	-281
rp3	-319	79	-32	-58
li1	279	293	343	685
li2	-279	-293	-343	-685
ph1	-324	-49	-21	-122
ph2	-32	-410	-212	-113
ph3	55	403	120	336
ph4	287	-109	85	-287
sal1	-147	-432	-312	126
sal4	-324	-49	-21	-122
sal5	457	133	-141	-582
c1	-425	-316	-187	70
c2	-63	100	422	306
c3	-324	-49	-21	-122
c4	588	190	-335	-399
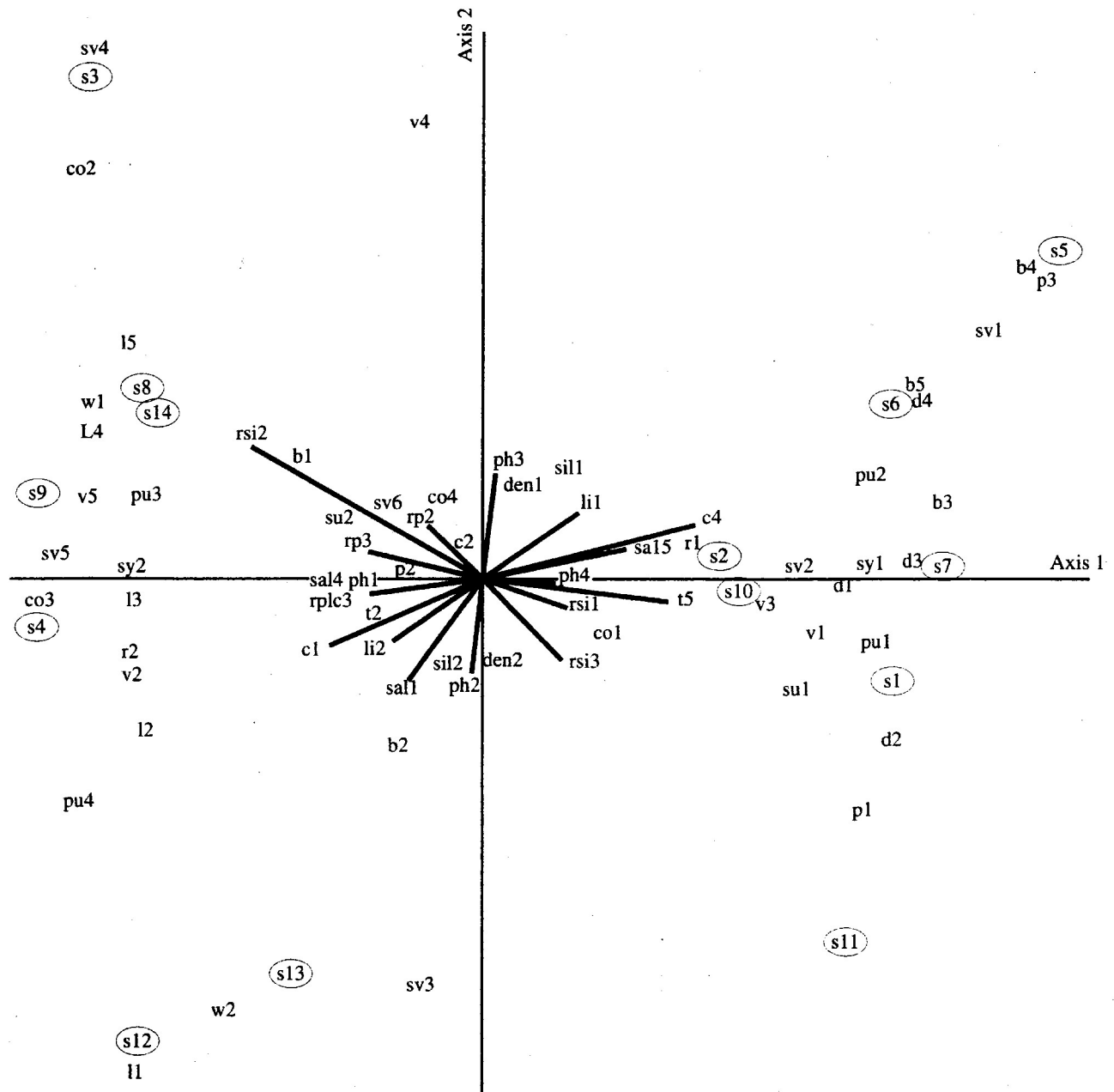
FIGURE 2. Second CCA of discretized variables. Arrows signify niche variables. Species are circumscribed. For key to ordination codes, see Tables IIa and b.

The other had smaller diameter near the first constrained axis and larger diameter in the lower right quadrant.

Two morphologic characters were species-specific (Figure 2). Valve shape or geometry and colony formation were depicted as point references for particular species rather than forming gradients.

Intracorrelation of the discretized niche variables was calculated as a weighted correlation coefficient matrix (Table VIII). Positive correlation coefficients of 0.5 or greater revealed a number of associations. Tolerance for brackish water (sal1) and low temperature (t2) were correlated. Fast rSi (rsi3) and broad salinity tolerance were correlated with high temperature tolerance (t5). Slow rSi

(rsi1) was associated with alkaline water tolerance (ph4) and the highest amount of Si cell^{-1} (c4). Mid rSi (rsi2) and mid rP (rp2) were associated with each other. Slight acidic water tolerance (ph1), freshwater tolerance only (sal4), and a higher amount of Si cell^{-1} (c3) were correlated with each other, and all variables were correlated with slow rP (rp1). Smallest amount of Si cell^{-1} (c1) was associated with fast rP (rp3). Small amount of Si cell^{-1} (c2) was correlated with slight alkaline water tolerance (ph3). Fully alkaline water tolerance (ph4) was associated with the highest amount of Si cell^{-1} (c4).

Only two negative correlations greater than 0.5 were calculated which produced self-evident results (Table VIII).

TABLE VIII. Weighted correlation matrix of niche variables from the second CCA

	t2	t5	rsi1	rsi2	rsi3	rp1	rp2	rp3	li1	li2	ph1	ph2	ph3	ph4	sal1	sal4	sal5	c1	c2	c3	c4
t2	1.0000																				
t5	-.2690	1.0000																			
rsi1	.1828	-.1382	1.0000																		
rsi2	-.1493	-.3307	-.1763	1.0000																	
rsi3	-.1434	.5331	-.0737	-.1763	1.0000																
rp1	-.1497	-.1443	-.0769	.4363	-.0769	1.0000															
rp2	-.0395	-.0279	.3622	.5277	.3622	-.2123	1.0000														
rp3	.1908	-.1443	-.0769	-.1841	-.0769	-.0803	-.2123	1.0000													
li1	-.3296	-.3176	-.1693	-.0429	-.1693	-.1768	.1226	.1768	1.0000												
li2	.3296	.3176	.1693	.0429	.1693	.1768	-.1226	-.1768	-1.0000	1.0000											
ph1	-.1497	-.1443	-.0769	.4363	-.0769	1.0000	-.2123	-.0803	-.1768	.1768	1.0000										
ph2	-.0593	.1455	-.1417	-.3390	-.1417	-.1479	-.3911	-.1479	-.2022	.2022	-.1479	1.0000									
ph3	.0275	.0669	-.4551	.0845	.1992	-.4751	.2053	.2080	.3658	-.3658	-.4751	-.5661	1.0000								
ph4	.1828	-.1382	1.0000	-.1763	-.0737	-.0769	.3622	-.0769	-.1693	.1693	-.0769	-.1417	-.4551	1.0000							
sal1	.8720	-.1443	-.0769	-.1841	-.0769	-.0803	-.2123	-.0803	-.1768	.1768	-.0803	.0810	.0372	-.0769	1.0000						
sal4	-.1497	-.1443	-.0769	.4363	-.0769	1.0000	-.2123	-.0803	-.1768	.1768	1.0000	-.1479	-.4751	-.0769	-.0769	1.0000					
sal5	-.2107	.7834	-.1082	-.2590	-.1082	-.1130	-.2989	-.1130	-.2488	.2488	-.1130	.2751	-.0678	-.1082	-.1082	-.1130	1.0000				
c1	.0303	-.2128	-.1134	-.2714	-.1134	-.1184	-.3131	.6781	-.2607	.2607	-.1184	.4570	-.1970	-.1134	-.1134	-.1184	-.1667	1.0000			
c2	.1371	-.0590	-.3227	.2725	.2598	-.3370	.4104	-.3370	.3513	-.3513	-.3370	-.3728	.6878	-.3227	-.3227	-.3370	-.2602	-.4969	1.0000		
c3	-.1497	-.1443	-.0769	.4363	-.0769	1.0000	-.2123	-.0803	-.1768	.1768	1.0000	-.1479	-.4751	-.0769	-.0769	1.0000	-.1130	-.1184	-.3370	1.0000	
c4	-.1450	.3219	.5294	-.2310	-.1862	.1792	-.1370	-.1944	-.1258	.1258	.1792	.0804	-.4959	.5294	-.1944	.1792	.5150	-.2866	-.6457	.1792	1.0000

Indifferent (ph2) and slightly alkaline water tolerance (ph3) were negatively associated. Highest amount of Si cell^{-1} and small amount of Si cell^{-1} were also negatively correlated.

Discussion

Niche breadth for each species varied from dimension to dimension (Table VI). Qualitatively, over four dimensions, species 1, 2, 3, 5, 8, 12, and 13 had the broadest niches. They would comprise the within-phenotype component of population niche breadth. The remaining species would comprise the between-phenotype component. On an overall multidimensional basis, there was a similar contribution from each component.

For each dimension considered separately, a different view emerged (Table VI). For each of the first three dimensions, only three to four species had narrow niche breadths, which suggested that population niche breadth was dominated by the within-phenotype component. For the fourth dimension, there were as many species representative of the within-phenotype component as there was of the between-phenotype component. This dimension mirrored overall multidimensional population niche breadth.

From both CCA ordinations (Figures 1 and 2), morphometric and morphologic character variability showed some distinct separations in terms of relationship to niche variables. Only those niche variables common to both CCA's will be discussed. Generally, two-dimensional morphometric characters were not influenced by niche variables, and therefore, not influenced by environmental factors (Table IV). Cell reduction via division governs measures such as length and width for pennates (Round, Crawford & Mann, 1990) and diameter for centrics (Geissler, 1986; Round, Crawford & Mann, 1990).

The influence of Si depended on the way Si was represented in the analysis. Diameter was essentially not influenced by rSi and Si:P, and rSi was positively correlated with Si:P (Table V). Si:P has been found to be correlated with diameter-independent variation such as areolae pattern, type of process, and areolar density (Theriot & Stoermer, 1984). Most morphologic characters were influenced by Si:P (Table IV). Physiological process with genetic influence may be viewed as one way to characterize rSi and Si:P, if Si:P is considered to represent Si availability (Theriot & Stoermer, 1984). Theriot (1987) determined that higher Si:P produced heavily silicified *Stephanodiscus* cells. He also determined that silicification was not influenced by environment or growth. Degree of silicification in two *Stephanodiscus* species was suggested to have a genetic basis. The present study corroborates this since degree of silicification is little influenced by rSi or rP (Table IV).

Si cell^{-1} was highly influential on diameter (Table IV). This parameter varies with cell size and on an intraspecies basis (Taylor, 1985; Conley, Kilham & Theriot, 1989). Si cell^{-1} also varies during cell division and in conjunction with light, temperature, nutrient limitation, growth rate, and salinity (Conley, Kilham & Theriot, 1989). Generally, Si cell^{-1} was negatively correlated with growth rate and Si:P (Table V). However, growth rate is a function of Si cell^{-1}

when Si is limiting (Paasche, 1973a). Paasche (1973a) found that fast growth rate with respect to Si, when an ample supply of Si is present, produced heavily silicified valves. In the present study, strongly silicified diatoms were generally associated with fastest growth rate with respect to Si (Figure 2).

Slow rSi and rP were associated with Si cell[-1] (Table VIII). This seems to be contradictory to Paasche's (1973a) findings. Again, interpretation of results depends on the way in which Si is expressed and used in analysis. Degree of silicification as a morphologic character was not greatly influenced by Si cell[-1], a niche variable (Table IV). In diatoms, allocation of Si to different valve features varies (Theriot, 1987).

In general, marine diatoms have less Si cell[-1] than freshwater diatoms. This may have a genetic basis (Conley, Kilham & Theriot, 1989; Kociolek & Stoermer, 1989) or may result from other factors such as salinity (Conley, Kilman & Theriot, 1989). Salinity did have an influence on diameter (Table IV). McMillan & Johansen (1988) found that at lower salinity, Thalassiosira decipiens had smaller valve diameter. The influence of salinity on diameter is also complicated by the inter-relation between salinity and degree of silicification, a morphologic character (Table IV). One study showed salinity with respect to silicification adversely affected Surirella (Schmid, 1979). A number of other studies have shown that at high salinity, degree of silicification is less than that for low salinities (Paasche, Johansson & Evensen, 1975; Hasle & Evensen, 1976; Tuchman, Theriot & Stoermer, 1984). In addition, low to high salinity conditions produced a shift from Cyclotella meneghiniana to C. cryptica type morphology, respectively (Schultz, 1971). Moreover, under similar conditions, C. meneghiniana exhibited genetic variability implying changes in silicification (Tuchman, Theriot & Stoermer, 1984). Paasche, Johansson & Evensen (1975) found that growth rate was independent of salinity in the 1 to 10‰ range. These results agree with this study in that practically no correlation was found between salinity and rSi and rP (Tables V and VIII).

The three-dimensional morphometric characters, S/V and biovolume, were influenced differently. Biovolume was related to niche variables in a way similar to diameter (Table IV). In contrast, S/V was the most influenced by all niche variables except Si cell[-1] (Table IV). Generally, larger S/V cells were associated with small Si cell[-1] in the lower quadrant of the second CCA ordination (Figure 2). Paasche (1973b) found that thin, delicate-structured valves with large S/V of valve Si were likely to undergo Si dissolution and subsequent reutilization adding to Si supply. In this case, Si cell[-1] would represent Si uptake (Paasche, 1973b), and Si:P would indicate Si availability. S/V was highly influenced by Si:P in the present study (Table IV).

Light intensity and rSi exhibited an inter-related positive effect (Table V). In cultures of Coscinodiscus, low growth rates with low light intensities produced increases in Si cell[-1] (Taylor, 1985). Generally, low light intensity, slow rSi, and high Si cell[-1] were associated with the first constrained axis in the second CCA ordination (Figure 2). S/V was highly influenced by rSi and rP as well as light intensity (Table IV).

These environmental influences have been found to affect S/V (Reynolds, 1989).

Si cell[-1] was negatively correlated with light intensity (Table V). Paasche (1980) found that light intensity may enhance or adversely affect Si cell[-1] depending on the diatom species. Moed (1973) determined that an increase in light intensity produced decreased silicification in Asterionella formosa cultures. In addition, Happey-Wood & Hughes (1980) found that Asterionella exhibited genetic variability, since clones produced different physiological responses to similar environmental conditions.

Light intensity was influential on most morphologic characters (Table IV). Antoine & Benson-Evans (1986) found that for Fragilaria (among other diatoms) increased light intensity and temperature produced disruption in the pattern of Si deposition.

Temperature was also interconnected with the effects of growth rate and light intensity (Table IV). Both rSi and rP were positively correlated with temperature (Table V). The influence of rSi, rP, and temperature was almost identical with respect to morphometric and morphologic characters. Temperature is dependent on light intensity, and these two factors affect nutrient availability (Stoermer & Ladewski, 1976). Increased temperature increased maximum growth rates for Stephanodiscus hantzschii, Asterionella formosa, and Fragilaria crotonensis (van Donk & Kilham, 1990). A similar result was found in the present study with fast growth rate at high temperature (Table VIII). Length and S/V were markedly influenced by temperature (Table IV). Bellinger (1977) found a similar result as increased temperature produced an increase in length and decrease in S/V for Asterionella formosa.

From the inter-relations developed in this study, a model was devised to summarize the general direction of influences on phenotypic variation (Figure 3) Environmental factors affecting physiological processes will mostly produce morphologic variation. Genetic influences will produce mostly morphometric variation. Environment will influence morphometric variation to a lesser degree. Similarily, genetics will influence morphologic variation to a lesser degree.
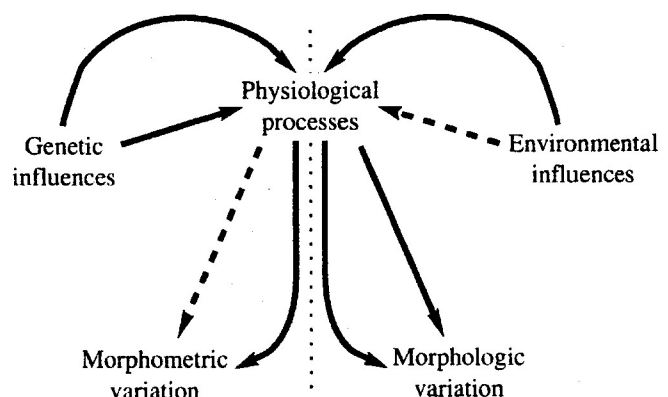

FIGURE 3. Model of the generalized direction of influences on phenotypic variation. Solid arrows of heaviest type represent greatest influence; dashed arrows represent lesser influence.

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