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FATTY-ACID ECOLOGY OF
PLANKTON COMMUNITIES

MASTER

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SUMMARY OF FINDINGS AND CONCLUSIONS

This research is based on the premise that clear correlates exist between fatty acid composition of marine communities and their ecological properties. After intensive, year-round sampling of macro- and micro-zooplankton in habitats ranging from coastal lagoon to offshore waters, we conclude the following:

- 1) Consistency of biochemical pattern is a direct correlate of productive organization in a plankton community;
- 2) The realm of biochemical space within which a zooplankton community operates is lessened by adverse environmental conditions of a physical nature. This realm of variation is also limited by structural problems of unknown origin that accompany diminished productive capacity.
- 3) Previously unknown fatty acid patterns -- revealed for the first time by advanced statistical methodologies -- disclose the status of a plankton community in its ever changing response to the environment. It follows that future, man-made changes should also be disclosed as departures from these fundamental cycles.
- 4) Plankton and benthos respond in different ways to seasonal change, but their patterns of fatty acid distribution are generally similar, which indicates a basis for comparison between, as well as within, major sectors of the marine biota. Longer chain length acids and increasing unsaturation are associated with ecological complexity. Patterns change most rapidly during species succession.
- 5) Discriminant function analysis of seasonal fatty acid patterns in zooplankton distributed along an environmental gradient produces a

classification that would seem to offer possibilities for world-wide application. Any localized departure from this chemical scale might indicate environmental abnormality, as well as the magnitude of biotic response possible and the biota's capacity for persistence.

6) From estuarine to offshore zooplankton assemblages, spatial heterogeneity expressed as the relation between linear distance and biochemical distance is a power curve in macro-zooplankton. Fatty acid composition changes rapidly with distance seaward from an estuary's inner end, leveling off beyond the headlands. In microzooplankton, composition changes in a linear manner with respect to distance.

7) Particulate domestic organic waste and detritus from marshes reinforce natural fatty acid patterns in the food of zooplankton.

8) Copepod species diversity is inversely related to the community's stability of fatty acid composition. The greater dynamical robustness of chemical pattern occurs in the prolific, yet simple, riverine habitat, suggesting that the stable domain of parameter space is likewise greater here than offshore.

9) Microzooplankton is more dynamically fragile than macrozooplankton.

10) A zooplankton sample can be accurately classified to habitat of origin, based upon constituent patterns of ten major fatty acids.

Zooplankton biomass and chlorophyll a concentrations over a two-summer period varied in relation to the relative amounts of a medium chain saturate and a long chain polyunsaturate, indicating an association with structure at the chemical level and production at the ecosystem level. Comparative stability estimates showed that fatty acid concentrations vary less than

zooplankton biomass. Thus comparisons drawn at the biochemical level are conservative as well as broadly applicable, transcending regionalized distributions of species populations.

11) Computerized measurements of size frequency distributions in copepods along an estuarine-offshore gradient, made in greater detail than has ever been possible before, revealed groupings consistent with those determined biochemically. Annual variation in these distributions may have considerable effect on the feeding of larval fishes and subsequent recruitment.

ENVIRONMENTAL GRADIENTS ON A COASTAL MEGALOPOLIS I:
BIOCHEMICAL CORRELATES OF SPATIAL HETEROGENEITY
IN ZOOPLANKTON COMMUNITIES

H. Perry Jeffries and Rose Lambert

International Council for the Exploration of the Sea
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Committee.)

Environmental gradients on a coastal megalopolis I:
Biochemical correlates of spatial
heterogeneity in zooplankton communities

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ABSTRACT

Distributions of organic constituents in marine communities should yield a worldwide classification scheme within which any localized phenomena would be immediately apparent. This idea was tested on the zooplankton along an environmental gradient extending from Rhode Island Sound, through Narragansett Bay and into its polluted tributary, the Providence River. On the basis of fatty acid composition, both the macro- and microzooplankton could be precisely classified to the habitat of origin. Biochemically the microzooplankton changed uniformly with respect to linear distance through the riverine, estuarine and offshore habitats. In macrozooplankton, the relation between biochemical change and linear distance from the river seaward was a power curve: sharply changing at first, becoming more nearly constant offshore. Particulate pollution in the river merely reinforced natural fatty acid sources in the zooplankton's food -- part of a pattern in which environmentally induced effects were expressed inshore, genetic influences offshore. In each habitat species diversity was inversely related to the community's stability of fatty acid composition. These estimates revealed greatest dynamical robustness in the prolific yet simple riverine zooplankton, suggesting that the stable domain of parameter space was likewise greater here than offshore. Despite its diversity, microzooplankton was more dynamically fragile than the macrozooplankton, in agreement with current theory on the stability of communities. We conclude that monomeric composition offers a basic rationale for characterizing the sensitivities of natural communities to environmental change.

INTRODUCTION

Horizontal gradients in the distribution of zooplankton communities are significant, for they reveal such natural processes as advective transport and indicate artificial complications due to pollution. Problems arise, however, when we try to express these gradients in any way more formal than tedious descriptions of species occurrences. Populations are distributed discontinuously in nature. Consequently data matrices are only 20% filled: zeroes occupy the remainder. It follows that when we apply multivariate techniques to examine how the variables interrelate, the result may be an artifact.

Fatty acids are ubiquitous monomers in nature, having special metabolic importance in marine organisms, an evolutionary consequence of life in a physically benign yet nutritionally sparse medium. Clear correlates relate a marine community's organic composition to its ever-changing ecological state. The fatty acid monomers comprising protoplasm vary quantitatively in relation to environmental and genetic influences, so we may logically compare ecological structure in one area with that in another, from data matrices that are by definition 100% filled.

Previous studies on biochemical correlates of ecological phenomena revealed the temporal aspect, e.g. seasonal succession and annual stability domains (Jeffries 1979, Jeffries and Lambert 1980). Here we examine spatial correlates along a sound-bay-river transect, when up to 60 mgd⁻¹ of raw city sewage was released into the river from a malfunctioning treatment plant (Oviatt 1980).

METHODS

Samples were taken biweekly during two summers (1979, 1980) along a six-station transect that extended 65 km from just east of Block Island in Rhode Island Sound, through Narragansett Bay and into the Providence River, immediately downstream from the aforementioned treatment plant (Fig. 1).

Two plankton samplers were used: for the zooplankton, an obliquely towed No. 6 mesh net (240 μ m aperture), 1/2-m in dia; for the microzooplankton, two concentrically mounted 1/2-m nets, Nos. 10 and 20 meshes, also towed obliquely, provided samples in the 73-153 μ m size range. Additional samples were taken in upper Pt. Judith Pond and in Green Hill Pond (Jeffries and Lambert 1980).

Following a brief rinse in distilled water, plankton samples

Fig. 1. Transect stations T₀ to T₅ in Block Island Sound, Narragansett Bay and the Providence River, RI. Secondary stations in upper Pt. Judith Pond (PJ) and Green Hill Pond (GH).

for biochemical analysis were immediately frozen in liquid nitrogen. Samples for species enumerations were preserved in formalin.

Upon esterification of freeze-dried plankton (Schultz and Quinn 1972), fatty acids were analyzed on packed columns (2m x 3.1 mm, 10% SP-2330 on Chromosorb W-AW, 100/120) in a Perkin-Elmer 900 gas chromatograph equipped with dual flame ionization detectors and controlled by a Sigma 1 data station.

Unless otherwise indicated, percents of total fatty acid

methyl esters were expressed as arcsin transforms in radians, which tended to insure multivariate normality. All results were maintained in SAS data files (Barr et al. 1976), from which the accompanying library was accessed, along with additional programs in the BMDP P-series (Dixon and Brown 1979).

RESULTS

Physical-chemical environment. Distributions of salinity, temperature and light penetration revealed a smooth habitat gradation extending from Block Island to the Providence River (Fig. 2). Biologically however, estuarine enrichment, most likely sewage in origin (Oviatt 1980) showed itself in the chlorophyll *a* distribution, which in the Providence River jumped 2-3 times over the next seaward station, only 11 km away.

Biomass distributions. Erratic spatial distributions of zooplankton contrasted with the smooth physical gradients described above. Moreover, the two sampling years differed; microzooplankton in the river was very much more plentiful the first year, a departure mirrored by Pt. Judith Pond but not by Green Hill Pond (Fig. 3). Macrozooplankton crop tended to be high in upper Narragansett Bay, becoming most abundant in the Providence River (T_5), much less abundant at the bay's mouth (T_2), then increasing toward the central sound (T_1). This central portion of the sound may have received deep influxes sweeping through the area from shelf waters. The only significant occurrence of the offshore distributed Calanus finmarchicus accompanied the minimum bottom temperature (10.8 C) and the maximum bottom salinity (32.75 o/oo) observed during this study.

Species distributions. Distributions of seven major copepod species, comprising at least 80% of the total individuals in the macrozooplankton, are shown in Fig. 4, along with diversity measures for total copepods. Although all eight major species extended throughout the entire habitat range, five were more common offshore or at the bay's mouth than within the bay proper. Total biomass increasing within the bay was clearly due to the Acartia species, particularly A. tonsa, the more oligohaline congenere (Jeffries 1962).

Minor copepod species (Parvocalanus crassirostris, Paracalanus parvus, Eurytemora herdmani, Calanus finmarchicus and Tortanus discaudatus) occurred at least once during the investigation at each station. Thus the diversity measures in Fig. 4 -- the averages of means for each of the two summers -- responded chiefly to the species evenness component of diversity, not number of species. In general the gradients from high

Fig. 2. Distributions of salinity, temperature, light penetration and chlorophyll a along a sound-bay-river transect. Summer 1979, 1980.

diversity offshore to low in the river were smooth, the only exception being at the mouth of the bay, an unstable transition area between coastal and estuarine habitats.

Fatty acid distributions. Stepwise discriminant function analysis (Dixon and Brown 1979) retained each of ten major fatty acid variables (> 2% of the total) as making significant contribution to the classification and ordered these variables by ANOVA F-ratios as shown in Table 1, with 18:0 first and 16:0 last. Both zooplankton fractions were the same in this respect.

Fig. 3. Distributions of standing crop in the macrozooplankton and microzooplankton from sound (T₀ - T₁) to polluted river (T₅), summer 1979, 1980.

Overall, however, the long-chain polyunsaturates (20:5 and 22:6, which characterize marine lipids), moved up in the microzooplankton rankings.

Mahalanobis distances, D^2 , (Barr et al., 1976), which here express biochemical separation of zooplankton at successive transect stations, bore close relation to the accompanying linear distances (km) separating these stations. From sound to river, the relation between biochemical and linear distances was a power curve in the macrozooplankton, rising slowly from offshore, then

Fig. 4. Distributions of the seven major copepod species along a transect, from Rhode Island Sound through Narragansett Bay and into the Providence River, summer averages 1979, 1980. Upper left: rarefaction, $E(S_n)$ (Hulbert 1971) and Gleason Index (G) (Margalef 1958). Upper right: Shannon Index (H') and Simpson Index, (S') (Pielou 1977).

rapidly within the bay. But in the microzooplankton, the two distance measures were linearly related throughout the observed range (Fig. 5).

The accompanying discriminant analysis produced surprisingly high correct classifications of plankton samples to station. Mistakes in classification occurred among adjacent stations (Table 1). Upon grouping stations as sound, bay and river, classification success was 90-100%, a remarkable result considering the ubiquity of fatty acid distributions. The

Table 1. Results of discriminant analyses classification to transect station, based on fatty acid composition of macro- and microzooplankton samples.

Fatty acids -- order of stepping										
	Step number									
Zooplankton component	1	2	3	4	5	6	7	8	9	10
Macro-	18:0	18:3	18:1	17:0	18:4	14:0	22:6	20:5	16:1	16:0
Micro-	18:0	20:5	18:1	18:3	18:4	22:6	17:0	16:1	14:0	16:0

Classification matrices for - zooplankton components

Zooplankton component	Station T	Percent correct	Number of cases classified as station						
			0	1	2	3	4	5	
Macro-	0	54.5	6	3	2	0	0	0	
	1	54.5	2	6	3	0	0	0	
	2	45.5	1	2	5	1	2	0	
	3	54.5	0	0	0	6	4	1	
	4	54.5	0	0	0	6	6	0	
	5	90.9	0	0	0	1	0	10	
Micro-	0	40.0	4	2	4	0	0	0	
	1	54.5	3	6	1	0	0	1	
	2	45.5	0	3	5	1	2	0	
	3	36.4	1	0	0	4	5	1	
	4	70.0	0	0	0	2	7	7	
	5	54.5	0	0	1	2	2	6	
			SOUND			BAY		RIVER	

associated classification functions for each station are listed in Table 2. An unknown would be classified to the station that gave the highest discriminant score.

In macrozooplankton, the 18:0 coefficients (Table 2) increase landward, whereas those for 22:6 increase seaward. These patterns seem to express dietary origins (environmental effects) in the first case, evolutionary origins (genetic effects) in the second. Taken together, the coefficients yield a linear additive transform (Green 1979) that must be fundamental to nature, but it is difficult for one to perceive because dimensionality exceeds constraints on visual representation. One solution is the derivation of a new linear compound with fewer variables than the original. These canonical variates maximize between group variation within the parent covariance matrix. The first canonical variate produces the largest ANOVA F among variables, and the second is orthogonal to the first (Cooley and Lohnes 1971, Oviatt et al., 1980). Station separations made from structure coefficients that correlate fatty acid variables with

Fig. 5. Linear distance (km) compared with biochemical distance (D^2) separating plankton communities along a sound-bay-river transect.

the canonical axes (Fig. 6) show clearly demarked arrangements of sound-bay-river station clusters. The macrozooplankton even subdivides into up-and-down-bay, but in agreement with species distributions, the bay's mouth ranges across biochemical character space from sound to up-bay. As indicated by diversity measures (Fig. 4), zooplankton at the bay's mouth is an intermediate between sound and bay, not just geographically and biologically, but biochemically as well. It is characterized by one influence then the other -- offshore or inshore -- depending upon tidal direction at sampling.

Table 2. Functions for classifying summer macro- and microzooplankton samples to transect station, from fatty acid composition (arcsin transformed percents in radians).

Zooplankton component	Fatty acid	Station T					
		0	1	2	3	4	5
Macro-	14:0	0.60	0.84	0.46	0.00	0.10	-0.10
	16:0	0.25	0.22	0.27	0.55	0.33	0.58
	16:1	5.37	5.36	4.85	4.63	4.24	3.91
	17:0	10.47	11.67	12.32	13.05	13.38	12.89
	18:0	0.06	-1.07	0.42	1.66	2.13	3.54
	18:1	1.45	1.77	0.95	-0.01	-0.09	-0.38
	18:3	14.49	14.39	14.22	15.11	14.69	15.95
	18:4	-0.74	-0.89	-0.15	0.15	0.38	0.28
	20:5	-0.21	-0.26	0.16	0.54	0.73	0.83
	22:6	4.02	4.08	3.58	3.51	3.25	2.93
	constant	-193.78	-194.77	-193.92	-214.57	-209.10	-224.06
Micro-	14:0	-0.09	0.05	0.09	0.23	0.08	0.72
	16:0	1.39	1.32	1.34	1.34	1.42	0.91
	16:1	8.78	8.47	8.68	8.37	8.44	8.07
	17:0	10.85	10.55	11.17	10.78	10.88	10.79
	18:0	5.45	5.58	6.12	7.36	7.47	7.88
	18:1	1.48	1.72	1.38	0.43	0.43	1.28
	18:3	9.58	9.18	9.82	10.06	9.96	10.20
	18:4	2.89	3.00	3.06	3.44	3.30	3.22
	20:5	6.07	6.00	6.34	6.22	6.34	6.52
	22:6	1.25	1.23	1.27	1.36	1.37	1.31
	constant	-298.44	-291.91	-316.73	-319.39	-322.88	-334.21

The ubiquity of fatty acids also allows us to compare stable relations along the transect in an objective manner. The natural logarithms of the determinants of fatty acid covariance matrices, both pooled for the entire transect and individually at each station, express variation during the observation period (Table 3). The macrozooplankton was less variable (more temporally stable) than the microzooplankton. Variability increased from sound to bay to river, the only anomaly being at the bay's mouth, a habitat that once again revealed its transitory character. In general, the greater the fatty acid variation, the lower the species diversity.

Fig. 6. Transect station groupings on the first two canonical axes of discriminant analysis, based upon fatty acid composition of macrozooplankton and microzooplankton. Clustering indicated for sound, bay and river stations.

Table 3. Stability estimates based on natural logarithms of the determinants of fatty acid covariance matrices.

Station	Natural log of the determinant of the covariance matrix	
	Macrozooplankton	Microzooplankton
T ₀ -T ₅ (pooled)	-5.74 ^a	-7.36 ^a
T ₀	-5.19 ^b	
T ₁	-6.25	
T ₂	-0.13	
T ₃	-5.95	
T ₄	-3.91	
T ₅	0.10	

^a arcsin transform of percent composition in radians

^b percent data T₀ - T₅

DISCUSSION

The rate of fatty acid change within a zooplankton community is closely related to linear distance along an environmental gradient. Biochemical change is more consistent than distributions of the separate populations in which it originates. Thus the biochemical gradient is an integral of populations, taking out ecological noise and parsimoniously reducing the remainder to a simple relation. The shape of this relation may change among size fractions (Fig. 5) or from one marine region to the next, but if it is produced by a coherent ecosystem -- one not altered by pollutants or other abnormality at some point -- the association is close indeed.

Linear additive functions, of which the discriminant analysis is one example, express interrelations among variable compounds in ways most useful for biological applications (Green 1979). Because the variables examined here are ubiquitous monomer's in life's processes (Morowitz 1968), the approach has certain advantages over species lists for comparative study of community structure. Thus from a broadened set of classification factors (Table 2) we may in the future be able to categorize plankton throughout the world's oceans. If a sample diverged

from its assigned group, perhaps in response to environmental abnormality or catastrophe, we would at least know the fact and be forewarned about the possibility of consequences elsewhere in the system, e. g. recruitment of fishes.

The first variable selected by the stepwise discriminant function was 18:0 (stearic acid), certainly not the most abundant component, averaging 2.6% at T_1 and 6.0% at T_5 in the macrozooplankton, and 3.5% to 5.5% in the microzooplankton, whereas 16:0, the last variable selected (and the most common), ranged overall from 13.8% to 21.4%. This 18:0 effect in estuarine zooplankton is regarded as nutritional in origin. Particulate organic matter, on which filter-feeding zooplankton subsist, is chiefly detritus, which in an estuary -- particularly at the inner end -- has two important sources: decaying vegetation, much of which comes from marshes, and sewage. Both sources are high in 18:0 (Jeffries 1972, Schultz and Quinn 1977), and their effects are focused at the estuary's turbid inner end, where small fishes filter or browse upon particulate organic matter in proportion to the availabilities of these dietary materials, as was shown by fatty acid analyses of gut contents in three species (Jeffries 1972, 1975).

Marine lipids are characterized by long-chain fatty acids. Although an explanation is not apparent for amounts in excess of those needed for maintaining membrane permeability and protoplasmic viscosity, the pattern exhibited by 22:6 seems to be a generalized indicator of genetic origins at the transect's marine end. By ranking the coefficients in Table 3 for each fatty acid along the transect, we find the following:

marine influence - 14:0, 16:1, 18:1, 22:6
 estuarine influence - 16:0, 18:0, 18:4, 20:5

Upon these quantitatively expressed influences rests the characterization scheme for spatial heterogeneity. Acartia tonsa, by far the major macrozooplankton constituent, is estuarine and marine in the distributional scheme for neritic copepods (Jeffries 1967). Because its population distribution extends throughout an estuary's reaches, then into the ocean, and the 18:0 effect is strongest at the inner end of the range, the cause seems to be environmental. All detritus regardless of origin is high in 18:0 and low in 22:6; so is raw sewage flowing into the river end of the estuary. Thus particulate wastes merely reinforce a natural pattern in the foods of filter feeders. Added to the detritus effect is a pollution reinforced nutrient availability, which supports high chlorophyll a levels (Fig. 2). The result is a rich habitat for zooplankton, where abundances far exceed (at least for the summer months) those at

down-bay and offshore areas.

Fatty acid patterns within natural communities may reveal for practical purposes a correlate to the notion of a stable domain in parameter space. Within this phase space, mapped from the interactions of all populations with each other and with environmental variables (May 1975), a community survives. Beyond the domain's limits the equations describe a collapsing system. Theoretically at least, for theory defies empirical demonstration in natural zooplankton, a comparatively simple, low diversity system should have a large stable domain relative to that of a complex one, opposite to the previously held idea that "diversity generates stability." Mathematical simulations indicate that a simple system should yield a large stable domain, one that is dynamically robust; a complex system on the other hand, is dynamically fragile within a smaller stable domain. This theory appears to be borne out by our results. Thus we propose that a community's monomeric composition provides testable behavior of the stable domain concept.

Indications of useful correspondences between chemical and ecological behaviors were demonstrated in plankton and fouling communities (Jeffries 1979). Temporal change was shown by sample trajectories in a statistical space defined by fatty acid variables. Here we use, more simply, the natural logarithm of the determinant of the fatty acid covariance matrix. The stable domain thereby approximated for comparative purposes is smaller in the microzooplankton, which has more species, both holo- and mero-planktonic, than in the macrozooplankton. Also the fatty acid analog of the stable domain is smaller in the more complex community of the sound than it is in the comparatively simple but prolific Acartia tonsa dominated system in the river's enriched habitat. Dynamical robustness in the latter area remains intact during the summer, throughout swings in taxonomic composition due to heavy predation by the ctenophore Mnemiopsis leidyi, until the limits are reached during autumnal cooling, and the community is replaced by a winter-spring species group, an absolute change that is accompanied by major relative changes at the biochemical level. Thus, estimates of stability, involving most likely resilience and elasticity, are to be found in fatty acid covariance matrices.

Correlates between organic composition and ecological phenomena may allow us to express spatial heterogeneity of zooplankton throughout the world's oceans. Moreover, the momentary condition within a particular plankton community -- how it is responding to the immediate environment -- could also emerge. Continued research in this area is aimed at further calibration of biochemical scales. These linear additive

functions should provide simple scores that express the robustness of plankton and perhaps its productive capacity as well. As these relations become better known we would know whether a gradient on megalopolis had an enriching effect, or if it were deleterious to natural distributions.

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BIOCHEMICAL CORRELATES OF STRUCTURE AND
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Abstract: Fatty acid composition of zooplankton revealed specific responses to habitat type along a transect extending from Rhode Island Sound to the inner reaches of Narragansett Bay. A medium chain saturate (palmitic acid) characterized riverine plankton -- a direct effect of the populations feeding upon particles rich in natural detritus and raw sewage. A long chain polyunsaturate (docosahexaenoic acid) denoted affinities in tissue composition more genetically determined than environmentally based. A discriminant function based on these two acids clearly separated estuarine from offshore zooplankton. In a broader context, however, zooplankton seemed to produce higher levels of 18:0 and less 22:6 in the eastern than in the western North Atlantic. Zooplankton biomass and chlorophyll a concentrations over two summers varied in relation to the same two acids, indicating an association between structure at the chemical level and function at the ecosystem level. System's stability--its propensity to change consistently in degree, amount or concentration--increased in the order of physical environment, planktonic community and biochemical composition. Thus, not only are fatty acids ubiquitous in nature and especially important energetically in zooplankton, but they are also most conservative dynamically, which means that they serve well in comparative study, whether it is intended for monitoring a segment of nature or for analysis of an entire system.

Introduction

Structural comparisons between natural communities are made difficult by the units that are commonly used -- the species present and their abundances. This problem is especially acute when we compare populations distributed across the continental shelf. Any attempted ordination runs afoul of divergences in numbers and kinds of species. Recently, however, close correspondences between organic composition and ecological properties in plankton and benthos have been demonstrated (Jeffries 1979, Jeffries and Lambert 1980). This approach to comparative study is based upon statistical properties of fatty acid patterns within organisms.

Fatty acids comprise a lipid class that is especially important in plankton. Temporal variation among the major fatty acids produces a message of sorts, which although noisy, reveals processes vital to a community's survival as a definable entity in nature. Thus during seasonal succession the pattern changes quickly, responding first to environmental influences, then to genetic change as species representation shifts among biogeographic groups.

In this paper, biochemical correlates of zooplankton distribution are considered in a spatial context--along an inshore-offshore gradient. The component populations may be classified as either true estuarine, estuarine and marine, or stenohaline marine (Jeffries 1967). The extent to which these categories are reflected in biochemical patterning of the entire zooplankton appears sufficiently close to permit a broad-scale system of comparison.

Methods

Zooplankton was sampled biweekly for two summers (1979-1980) along a six-station transect extending from Rhode Island Sound, through Narragansett Bay, and into its polluted tributary, the Providence River (Fig. 1). A No. 6 mesh net (240 μ aperture), 4-m dia having a General Oceanics meter mounted off-center in its mouth was towed obliquely for 5-10 min periods. A surface water sample was filtered at the same time for fluorimetric determination of chlorophyll a. The filter and plankton samples were frozen immediately in liquid nitrogen and later held at -20 C in a vacuum desiccator.

Fatty acids extracted from freeze-dried zooplankton were analyzed as their methyl esters (Schultz and Quinn 1972) by gas chromatography on packed columns (2 m x 3.1 mm, SP-2330 on Chromosorb W-AW, 100/120). Only the major fatty acids (>2% of the total) are reported here. These analyses are believed to be precise within $\pm 2\%$ of stated values, based upon repeated analyses of duplicate extracts. For statistical analysis, percents of total fatty acid methyl esters were transformed to their arc sin equivalents.

Results

Environmental properties at the mid-sound and river stations are shown in Table 1; mean distributions of the 10 major fatty acids in zooplankton are compared in Table 2. Chlorophyll a was much higher in the river than offshore, a response to organic pollutants (Oviatt 1980). Zooplankton in the river responded to enrichment, with standing crops ranging up to 372.6 mg dry wt m^{-3} (Fig. 1), but the mean value was statistically the same in the

river as offshore, a result of heavy predation by the ctenophore Mnemiopsis leidyii during mid-summer.

Principal components analysis (Dixon and Brown 1979) on the entire fatty acid data set (11 observations at each of six stations) produced the eigenvectors corresponding to the first four eigenvalues given in Table 3. Grouping fatty acids by their patterns of ranking first and second (sign disregarded) within the eigenvector matrix yielded the following five groups:

<u>Group</u>	<u>Component fatty acids</u>
I	14:0, 16:1, 17:0, 18:0
II	16:0
III	18:1
IV	18:4, 20:5
V	22:6

The tendency for these variables to cluster, though weakly defined, is due chiefly to both chain length and unsaturation; quantitatively, these properties in a trophic system are abetted at the herbivore level and reversed in detritus formation (Jeffries 1972).

Linear additive transforms (Green 1979) calculated from the first and second eigenvectors are shown in Fig. 2. Although principal components analysis is not really intended for classification (Maxwell 1977), grouping is evident for the sound, bay and river stations. Thus, macrozooplankton produced distinctive patterns of monomeric composition in response to habitat type. Microzooplankton in the 73-153 μ size range, collected by towing two concentrically-mounted nets (Nos. 10 and 20) at the surface, is shown for comparison. Copepod nauplii, larval benthos and diatoms comprised this fraction. Sound stations were broadly superimposed on the bay and river with no separation being evident.

For comparative purposes, fatty acid matrices reduced to their major components are still complex. We can simplify the situation further to include only 18:0, a saturated member of the shorter-chain length, chiefly saturated components (group I) and 22:6, the longest and most unsaturated component (group VI). For a comparison of the spatial limits within which the system behaves only the mid-sound (T_1) and river (T_s) stations need to be considered. (Station T_0 , although farthest offshore, is so close to Block Island, for logistical purposes, that T_1 is a better representative of conditions in the Sound.) In this form, comparison is made by discriminant analysis on a pooled covariance matrix.

In Davis' (1973) notation, the discriminant index, R_0 , is the midpoint between two centers of distributions, which in this case are stations. Then, for arc sin transformed data expressed in degrees:

$$\begin{aligned} R_0 &= \lambda_1 \psi_1 + \lambda_2 \psi_2 \\ &= -0.846 (11.505) - 0.005 (22.6) \end{aligned}$$

$$R_0 = -9.84$$

λ_1 and λ_2 are the respective coefficients for 18:0 and 22:6, and

ψ_1 and ψ_2 are the corresponding group means.

Fig. 3 shows the average position of each station in relation to R_0 . To broaden the comparison, mean summer locations for macrozooplankton in two Spanish estuaries -- Ria de Arosa and Ria de Muros et Noya, adjacent bays on the Atlantic Coast of northern Spain (Tenore and Gonzalez 1975, Tenore et al. 1981) -- are indicated on the Rhode Island discriminate function. Although the Spanish samples have greater species diversity than the zooplankton in estuaries bordering the Western North Atlantic, they do fall on the estuarine

side of R_0 . Also indicated are locations on the discriminant function for samples from: Placentia Bay, Newfoundland, chiefly Temora longicornis (Ackman and Hooper 1970); Villefranche Bay in the Mediterranean, average of three samples (Goutx and Saliot 1980); the North Sea, outside the Wadden Sea, average of six copepod species (Kattner et al. 1981). Location is set on this particular function chiefly by the 18:0 concentration; 22:6 is included as a representative of the long chain polyunsaturated component. Discriminatory capacity probably would be increased with other fatty acids included, e.g. 16:0, the next lower homologue in the saturated series.

Ecological stability can be estimated from sequences of increases and decreases at various organizational levels (Patten 1961). For each variable there is a matrix of transition probabilities: stability is simply the determinant of the matrix. These determinants are then averaged at each ecosystem level, giving an estimate of change and recovery -- resistance and resilience -- ranging from -1.0 (least stable) to 1.0 (most stable).

Stability at three levels is considered here: temperature and salinity at the environmental level; zooplankton biomass and chlorophyll a at the community level; and 18:0 and 22:6 at the chemical level. Stability is lowest, at the environmental level, greater at the planktonic (community) level and greatest at the chemical level (Table 4). It follows that comparisons drawn at chemical level are the most conservative, but they are based on metabolic processes dynamically tuned to environmental properties.

The estimate for offshore environmental stability is anomalously lower than inshore, which arises from logistical constraints on sampling.

Integrated values over the water column would show, of course, greater stability offshore than inshore and merit more refined calculation (Patten 1962), but the physical environment's rank as least stable among the three levels would probably remain the same.

Discussion

Although much maligned, species diversity indices remain as one of the few quantitative measures available for comparisons of community structure. In their application to zooplankton, however, we run across a problem in trying to decide what to call an ecologically meaningful group. For example, the copepodite I stage of Acartia tonsa differs greatly in environmental requirements from its adult stage, perhaps more so than the adults of some so-occurring species. Diversity becomes increasingly confounded when samples include naupliar stages and fish larvae, groups that are difficult taxonomically, as well as ever changing in relation to their surroundings.

Biochemical correlates of community structure provide a logically sound basis for continuous ordination along an environmental gradient, a task so complex by traditional methods that it is infrequently attempted today. Not only are fatty acids ubiquitous in nature but their ecological behavior is conservative compared to the environmental and organismic levels of ecosystem organization. Thus, we can separate, categorize and classify communities on a chemical scale, in a manner analogous to the comparative anatomist's arrangements of increasing structural complexity and functional dependencies on an evolutionary scale.

The ordination shown in Fig. 3 is derived from biochemical distances separating estuarine and coastal zooplankton. It is calibrated with respect to mean distances during summer conditions in Rhode Island. Superimposed on this scale are positions for the North Sea and the Mediterranean; they tend strongly toward the estuarine end of the scale. The European data from which these R values were calculated (Kattner et al. 1981, Table 1; Goutx and Saliot 1980, Table IV) indicate higher 18:0 and lower 22:6 levels than the corresponding Rhode Island values given in Table 1. Also at the high or estuarine end of the R scale are the two Spanish rias. Back in the Western North Atlantic, a Newfoundland copepod population (Ackman and Hooper 1970) is clearly in the offshore sector of the ordination, even though 22:6 is 10% lower than in Rhode Island, perhaps because concentrations of this particular polyunsaturate decrease in cooler waters (Jeffries 1970).

The cause underlying this ordination may be nutritional. Compared to living phytoplankton, the detrital foods of filter-feeding zooplankton are rich in 18:0 and low in long-chain polyunsaturates (Jeffries 1972, Schultz and Quinn 1977). Thus, as the proportion of detritus to total particulate matter increases inshore, so does the nutritional intake of 18:0 by zooplankton. An additional 18:0 input is sewage: the source is usually most noticeable well within an estuary--downstream from a malfunctioning sewage treatment plant, as is the case in the Providence River. Because fatty acid distributions in the diet are passed on partially intact to consumers, we expect that tissue 18:0 concentrations also would be highest where the detrital load is heaviest (Jeffries 1972). The polyunsaturate,

however, is synthesized internally from C₁₈₋₂₀ unsaturates in the diet. A canonical correlation (Cooley and Lohnes 1971) substantiates this point. Macrozooplankton biomass and chlorophyll a on one side are significantly associated with macrozooplankton 18:0 and 22:6 concentrations on the other. As a result of food chain enrichment, the Providence River's organic wastes show up in a luxuriant plankton crop. But in European zooplankton, a strong 18:0 effect in open waters suggests that food web dynamics may differ quantitatively from the North American condition. Only further sampling will tell.

To cross levels of natural organization, this approach draws upon stability estimates. Stabilities at the organismic and biochemical levels do not appear to differ appreciably at the sound and river stations. This similarity of response to habitat type is important because the river was receiving up to 60 mgd ($227,100 \text{ m}^3 \text{ day}^{-1}$) of raw sewage from the City of Providence during both summers investigated. Consistent with these stability estimates, neither the macrozooplankton, microzooplankton nor chlorophyll a concentrations gave indication of adverse effect. Rather, organic enrichment apparently provided additional food and stimulated plankton growth, until predation by the ctenophore Mnemiopsis leidyi drastically reduced zooplankton crops in late summer.

Once a community has been cast on a biochemical ordination, a single number replaces all the complexity in a data matrix that could include the entire suite of major fatty acid variables numbering 10 or more. Perhaps this is an answer to Pielou's (1972) question: "...can any single number--a descriptive statistic, coefficient, or index--be envisaged that would measure the amount of structure, or the degree of 'structuredness,' of an ecological community?" In the future, biochemical scales

would be calibrated with respect to areas or regions dictated by the particular application. Even now, however, the result raises important questions on the comparative aspects of food web dynamics in the North Atlantic.

To compare far and wide, throughout the world's oceans, all we need is an expanded set of discriminant coefficients and stability estimates. Perhaps there is an aspect of nature's uniformity, as well as its diversity, to be found here. If so, we should be able to measure with ease the various responses of marine assemblages to controlling factors and state what conditions are expected and what are not. Requirements for studying biochemical correlates are modest compared to those involved in functional models, a factor that may encourage others to explore these emergent phenomena.

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Table 1. Environmental properties of Rhode Island Sound and Providence River, summer 1979, 1980.

Property	Station	
	Sound	River
Surface temperature °C		
$\bar{X}$	18.0	23.2
range	14.4- 22.0	17.6- 27.8
Surface salinity ‰		
$\bar{X}$	31.8	23.3
range	31.0- 32.4	20.9- 27.7
Chlorophyll <u>a</u> $\mu\text{g l}^{-1}$		
$\bar{X}$	0.8	26.6
range	0.2- 1.8	3.0- 61.4
Zooplankton mg m^{-3}		
$\bar{X}$	116.8	110.7
range	7.1-232.3	0.2-372.6

Table 2. Fatty acid composition of summer zooplankton in Rhode Island Sound and Providence River, percent of total fatty acid methyl esters, standard errors in parentheses.

Fatty acid	Station	
	Sound	River
14:0 ^a	5.8 (1.2)	5.6 (0.6)
16:0	13.8 (1.4)	21.4 (1.2)
16:1	6.6 (1.0)	4.9 (0.3)
17:0	1.0 (0.1)	1.7 (0.2)
18:0	2.6 (0.4)	6.0 (0.6)
18:1	8.0 (0.9)	7.6 (1.0)
18:3	2.7 (0.3)	2.9 (0.3)
18:4	4.5 (0.7)	4.0 (0.7)
20:5	13.7 (1.3)	14.4 (1.2)
22:6	15.6 (1.6)	14.3 (1.4)
Other ^b	26.2	17.2

^ashort hand notation for number of n-carbon atoms:number of double bonds;

^bless than 2%.

Table 3. Eigenvectors corresponding to the first four eigenvalues (principal components). For each fatty acid the largest eigenvector is underlined with a solid line, the second with a broken line (sign disregarded). Arc sin transforms expressed in radians.

Fatty acid	Eigenvalue			
	1	2	3	4
14:0	<u>0.36</u>	<u>0.41</u>	0.13	0.12
16:0	<u>0.34</u>	0.00	0.22	<u>-0.40</u>
16:1	<u>0.35</u>	<u>0.53</u>	-0.03	0.14
17:0	<u>0.35</u>	<u>-0.43</u>	-0.17	-0.17
18:0	<u>0.42</u>	<u>-0.30</u>	-0.10	-0.25
18:1	0.00	<u>0.15</u>	0.02	<u>-0.70</u>
18:3	<u>-0.39</u>	0.07	0.00	<u>-0.31</u>
18:4	<u>-0.28</u>	0.15	<u>0.57</u>	-0.25
20:5	<u>0.30</u>	0.07	<u>0.48</u>	0.08
22:6	0.01	<u>-0.47</u>	<u>0.57</u>	0.23

Table 4. Comparative stability estimates; summer conditions.

Ecosystem level	Station	
	Sound	River
Environmental	-0.27	-0.19
Organismic	-0.05	-0.03
Chemical	0.07	0.05

FIGURE LEGENDS

Fig. 1. Station locations in the Rhode Island Sound-Narragansett Bay area.

Zooplankton standing crop, mg dry wt m^{-3} $\pm$ standard error of the mean, summer 1979 and 1980.

Fig. 2. Station groupings of zooplankton on the first two principal components, as sound (T_0-T_2), bay (T_3-T_4) and river (T_5); based on distributions of 10 major fatty acids. Microzooplankton (73-153 μm) and macrozooplankton ($>240 \mu$) over two summers in the Rhode Island Sound-Narragansett Bay area.

Fig. 3. Ordination of North Atlantic zooplankton on a biochemical scale derived from 18:0 and 22:6 concentrations (percent of total fatty acid methyl esters, arc sin transformation in degrees) for Rhode Island Sound and the Providence River. Positions for the rias de Arosa and Muros et Noya in northern Spain were calculated from concurrently obtained samples ($>240 \mu$) representing areas of mussel aquaculture (stations 10 and 7 respectively), the middle of the Arosa (7) and the mouth of the Muros (2). Mussel culture is most intense at Sta. 10 in Ria de Arosa.

Fig. 1

FIG. 2

Fig. 3

BIOCHEMICAL CORRELATES OF COMPLEXITY AND CHANGE IN
PLANKTON COMMUNITIES

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International Council for the Exploration of the Sea
C. M. 1980/L:68 Biological Oceanography Committee

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Biochemical correlates of complexity and
change in plankton communities

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ABSTRACT

Zooplankton and microzooplankton were sampled monthly for two years in three coastal habitats ranging from relatively benign to physically severe. In addition to traditional species enumerations, we analyzed plankton samples for component fatty acids and expressed the ensuing patterns of biochemical variation as statistical trajectories in time. Biochemical behavior of these entire communities was not directly related to species diversity or habitat stability.

Consistency of biochemical pattern was, however, a direct correlate of productive organization in the three plankton communities. Because fatty acid patterns change in relation to environmental control, a practical method appears possible for predicting the fate of species groups in nature.

INTRODUCTION

Studies on planktonic and benthic communities have shown that the changes taking place in species assemblages can be portrayed and characterized by a statistical representation of the organisms' component fatty acids. Thus for any traditional property that a community expresses, there is also a biochemical correlate that is readily determined and objectively standardized (Jeffries 1979). To develop this paradigm further -- for purposes of eventual application to environmental management -- we hypothesize that fatty acid patterns are less variable in planktonic communities supported by physically benign conditions than they are in situations that fluctuate widely without pattern. If this hypothesis is true, we should in time be able to make predictions on the biotic integrity of any marine area.

Fatty acids have been selected because their structure is flexible, allowing modifications that are environmentally induced, perhaps to a degree that for marine organisms is unique. Moreover, storage of nutritional reserve is a common problem facing marine organisms. The strategy developed by many planktonic species seems to rely on modification and selective utilization of the all-important lipid fraction, rather than depot storage in specialized organs. It follows that fatty acid levels should to some extent reveal the ecological status of plankton communities.

METHODS

Three coastal areas representing a gradient of increasing physical severity -- Block Island Sound, Narragansett Bay and Green Hill Pond, Rhode Island (Fig. 1) -- were sampled monthly over an annual cycle. Macrozooplankton was collected with a No. 6 mesh net (243 μ aperture), 1/2-m dia. equipped with a flow meter and towed obliquely through the water column; phytoplankton-microzooplankton was sampled with a surface pump that discharged through concentrically mounted No. 10 (153 μ) and No. 20 mesh nets (73 μ), the latter fraction being retained for analysis.

Figure 1. Study areas in Green Hill Pond (inset A)
Block Island Sound (*) and Narragansett Bay (+).

Samples for biochemical analyses were drained, rinsed briefly with distilled water, immediately frozen in liquid nitrogen and then freeze-dried; samples for species enumerations were preserved in formalin. Other observations included temperature, salinity, light penetration and chlorophyll *a*.

Fatty acids were analyzed as methyl esters (Schultz and Quinn 1972) on packed columns (2 m x 3.1 mm, 10% SP-2330, Chromosorb W-AW, 100/120) in a Perkin-Elmer 900 gas chromatograph equipped with dual flame ionization detectors and interfaced with a Sigma 1 data system.

RESULTS

Physical environment. Temperature and salinity varied the most in Green Hill Pond, less in Narragansett Bay and least in Block Island Sound (Fig. 2).

Figure 2. Salinity (S ‰) and temperature (T °C) in three contrasting environments: Block Island Sound (BIS), Narragansett Bay (NB) and Green Hill Pond (GHP), from September 1978 through September 1979.

A similar trend was evident in light extinction (Fig. 3), which increased markedly from Block Island Sound (40 m) to the shallower waters of Narragansett Bay (20 m) and then into the even shallower Green Hill Pond (2 m), where the Secchi disc was usually visible on the bottom.

Ecological distributions. Distributions of standing crop in the phytoplankton-microzooplankton and in the macrozooplankton are shown in Fig. 4. In Green Hill Pond, the macrozooplankton decreased during the colder months when the

Figure 3. Extinction coefficient (K') in Block Island Sound and Narragansett Bay. 1978-79.

pond froze and thawed periodically. The spring phytoplankton bloom stimulated zooplankton growth, and by mid-summer the zooplankton biomass reached a maximum among the three areas compared.

In Narragansett Bay, the winter zooplankton community was dominated by Acartia clausi. Contrary to expectation, no phytoplankton bloom occurred during the spring. Thus, zooplankton declined into summer; Acartia tonsa did not become established in its usual abundance, presumably due to the absence of a spring diatom bloom.

In Block Island Sound, the macrozooplankton tracked the phytoplankton-microzooplankton biomass until spring when zooplankton increased significantly. Production appeared closely linked to phytoplankton-microzooplankton abundance, which became depressed through grazing. As the summer progressed, an increase in ctenophores (Mnemiopsis leidyi) led to a reduction in zooplankton biomass and a consequent reduction in predation on the phytoplankton-microzooplankton, which responded with increased abundance. The decrease in zooplankton biomass in the late summer in Green Hill Pond may also be attributed to ctenophore predation.

Table 1 gives the coefficient variations for the macrozooplankton and phytoplankton-microzooplankton biomass distributions in the three areas. For the macrozooplankton, relative variation was greatest in Green Hill Pond; this was a significant result in the development of our general hypothesis because the Pond was physically the most variable of the three habitats compared. Although not expected, minimum variation was found in Narragansett Bay, but this is in agreement with biochemical patterns discussed later. In

Figure 4. Standing crop (mg m⁻³ dry wt.) in Green Hill Pond, Narragansett Bay and Block Island Sound. Phytoplankton-microzooplankton (#20) and macrozooplankton (#6).

Table 1. Relative variation in biomass over an annual cycle, expressed as coefficient of variation.^{a,b}

	Macrozooplankton	Phytoplankton-microzooplankton
Block Island Sound	103.1	97.9
Narragansett Bay	60.7	93.4
Green Hill Pond	140.8	74.2

^a(standard deviation/mean) x 100;

^bIt is assumed that values for biomass are normally distributed.

the phytoplankton-microzooplankton, Green Hill Pond biomass varied least due to continuous contribution to this shallow area of larval stages during the spring-fall.

Accompanying distributions of total numerical densities are given in Fig. 5. Compared with the Pond, the range of densities was smaller in Narragansett Bay ($1,900-16,902 \text{ m}^{-3}$) and the pattern was less symmetrical. The seasonal low occurred in September, coinciding with the annual invasion of the carnivorous ctenophore, *Mnemiopsis leidyi*. Winter levels in the Bay were maintained by the northern copepod *Acartia clausi*, in contrast to the disjunctive distribution of this copepod population in Green Hill Pond, where severe environmental conditions during the winter delayed development of the boreal component until April.

Figure 5. Seasonal abundance, no. individuals m^{-3} , in the macrozooplankton (No. 6 fraction) and phytoplankton-microzooplankton (No. 20 fraction) of three habitats.

Block Island Sound had the smallest range in zooplankton densities ($490-15,072 \text{ m}^{-3}$) but it also had the lowest average density. Neither *Acartia clausi* nor its summer-fall replacement, *A. tonsa*, attained densities reaching those that occurred in the Bay, although the annual cycles were similar in both locales. A one-month lag in the appearance of *A. tonsa* in Block Island Sound probably resulted from temperature-salinity interactions involved in successions (Jeffries 1962). Never, however, did a coherent assemblage of

populations rise and fall, as is typical for temperate coastal waters. Rather, the Sound communities seemed to be more of a transient assortment, more opportunistic than truly indigenous in comparison with Narragansett Bay, an interesting anomaly considering the Sound's greater physical stability.

For purposes of comparison between environmental and biochemical patterns, Table 2 summarizes physical and biological characteristics of the three areas.

Table 2. Summary of relative variation in three habitats.

	Relative variation annually		
	Least	→	Most
Physical environment	Sound	Bay	Pond
Macrozooplankton			
biomass	Bay	Sound	Pond
total numbers m ⁻³	Bay	Sound	Pond
Microzooplankton			
biomass	Pond	Bay	Sound

Biochemical trajectories.

Zooplankton samples taken over an annual cycle can be cast in a statistical space defined by the organisms' component fatty acids. Thus for plankton sampled monthly and analyzed for ten fatty acids we would have 12 sample points in 10-dimensional space. By correspondence analysis, dimensionality is reduced to two or three principal axes, from which the community's trajectory in time is drawn. Correspondence analysis also shows the opposite relation: arrangement of variables in sample space. The nearness of variables to sample points is an expression of their relative affinity (Jeffries 1979).

In Fig. 6, annual sample domains on the first two axes of correspondence analysis are compared. They have been simplified to solid lines that mark general limits over the annual cycle. Narragansett Bay had the largest sample domain in fatty acid space. Although not shown, change occurred consistently here, not erratically as the Sound, or in the Pond, the most unpredictable of the three habitats. Comparatively small sample domains for the Sound and Pond indicated that their macrozooplankton assemblages were spatially lacking in a biochemical sense. In a temporal sense so were their respective species assortments, particularly in the unstable Pond habitat, where the boreal (winter) component was all but lacking. As shown in Fig. 6, the Pond's sample domain was in the summer-fall portion of biochemical space. So was its plankton production, led by the characteristic summer copepod, Acartia tonsa. A rich complement of species occurred in the Sound, but crops were low and erratically produced. Population dynamics indicated that the area supported admixtures from inner and outer coastal areas rather than a definable fauna fully functioning on its own. The Sound's sample domain only extended

weakly into both periods, the winter-spring and summer-fall seasons, a biochemical correlate of the inconsistent and poor development of the boreal as well as temperate species components.

Next, the positions of fatty acid variables in relation to sample domains revealed, as has been observed before (Jeffries 1979), that the monounsaturated 16 and 18 carbon fatty acids (16:1 and 18:1), characterized the winter-spring plankton, whereas the 14-18 carbon saturates (14:0 and 18:0) along with the long-chain polyunsaturate 22:6, typified summer-fall assemblages. Change occurred around the pivotal position of 20:5.

Annual trajectories in the phytoplankton-microzooplankton were more erratic in these chiefly meroplanktonic assemblages than in the holoplankton. Again this suggests that consistency of biochemical pattern is a direct correlate of productive organization in plankton communities.

CHEMICAL DOMAINS OF ZOOPLANKTON COMMUNITIES IN THREE MARINE HABITATS.

MICROZOOPLANKTON

MACROZOOPLANKTON

Figure 6. Correspondence analysis of fatty acids in plankton samples taken monthly in sound, bay and pond habitats; diagrammatic representation of sample domains on first two principal axes, showing relative areas; also indicated are locations of fatty acid variables (no. n-carbon atoms:no. double bonds) in relation to sample domains.

DISCUSSION

We proposed that there exists a direct relation between stability of annual fatty acid patterns in planktonic communities and environmental predictability of the habitat in which they were produced. Contrary to expectation, Block Island Sound zooplankton varied more than Narragansett Bay in terms of consistent replacement patterns between zoogeographic components. But spatial domains in the plankton behaved accordingly: biochemical trajectory and robustness of pattern in the Bay exceeded that in the Sound. A consistent relation between a seemingly well modulated biochemical signal during species replacement and maintenance of plankton production was made clear in Narragansett Bay's annual cycle of plankton production. Both ecologically and biochemically, Green Hill Pond's zooplankton behaved with anticipated irregularity, while Block Island Sound may have experienced another "atypical year" (Jeffries 1970). (Data from the second year of this study, although presently incomplete, indicate a far more robust and coherent fatty acid domain than do the previous year's results.)

As environmental assessment now stands, we look for abnormalities. But what is normal? For most of the oceans we do not know because traditional enumerations and flux measurements are difficult to make or equivocal in interpretation. Current paradigms simply do not provide a workable rationale for rapid environmental assessment. "There is no way of determining thresholds for the myriad of substances that can be developed...no way of monitoring the substances...and little basis for belief that thresholds for effects on natural ecosystems exist," (Woodwell 1974). What we must seek are measures that reveal dynamically the integrity of natural systems. When a synoptic expression of structure tells us that integrity has been threatened, then is the time to measure function.

We propose that all natural systems generate over time a decipherable biochemical message. This message expresses the biota's status -- as it interacts with the ever-changing environment -- disclosing its success in doing so by way of variations in monomeric composition. Any deviation or loss of integrity on the part of the biota should be revealed immediately as homeostatic mechanisms respond at a low organizational level, perhaps before species replacement or changes in abundance respond at higher levels. The integral of all this -- the integrity of a community, or what we accept as being normal -- is patterned by a planktonic community's annual cycle of biochemical change. For other systems, a period of time may be required before the biota develops a stable limit cycle, but the principles are the same. Thus in the monomeric composition of nature we find a way to compare and evaluate widely different species assemblages, while also being able to make an instantaneous determination of a particular system's integrity as a fully functioning entity in nature.

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ENVIRONMENTAL GRADIENTS ON A COASTAL MEGALOPOLIS II:
SIZE FREQUENCY DISTRIBUTIONS IN ZOOPLANKTON

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International Council for the Exploration of the Sea
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Environmental gradients on a coastal megalopolis II:
Size frequency distributions in zooplankton

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ABSTRACT

Size structure of zooplankton communities along a transect from Block Island, through Narragansett Bay and into the Providence River, Rhode Island was determined with a computerized image analyzer. This technique for the characterization of plankton communities without recourse to species counts processed samples 5 times faster than traditional methods. During the summer of 1979 three distinct copepod communities occurred along the transect, characterizing the sound, bay, and coastal pond habitats. In 1980 much of this pattern had broken down. Comparison of the size frequency data with species counts showed that this was due in part to the absence of Centropages typicus in the Rhode Island Sound stations.

INTRODUCTION

The study of marine food chains has been limited by the time and expense required for the counting and identification of plankton samples (Parsons 1969). However, for certain types of study (e.g. ecosystem modeling, and fisheries management), an exact knowledge of the plankton species distributions is unnecessary. Rather, the analysis can be based on size frequency distributions (Parsons 1969; Parsons and LeBrasseur 1973).

Several attempts have been made to use electronic measuring devices on zooplankton samples. Coulter counters are difficult to use on large, irregularly shaped animals, but Maddux and Kanwisher (1965), and Boyd and Johnson (1969) modified the basic technology for in situ zooplankton counts. Other approaches have included holography (Knox 1966), and light-beam interruption counting (Mitson 1963, Davis and Paulik 1965, Cooke et al. 1970, Fulton 1972).

Our approach to this problem has been to modify a commercial image analyzer, originally designed for the study of metal crystals. This system will not only count and measure animals, but it also allows the operator to classify animals into predetermined groups. The results are transmitted to a computer for analysis. We have used this system to analyze spatial and temporal gradients in the community structure of the copepods in the Narragansett Bay, Rhode Island estuary.

METHODS

Samples were collected biweekly during the summers of 1979 and 1980, from oblique tows taken with a 0.5 m, No. 6 mesh net (240 μ m aperture). Stations were located along a transect from the Providence River to Block Island (Fig. 1). (For a more complete description of the sampling program see Jeffries and Lambert, 1981.) Portions of formalin preserved samples were stained overnight in an aqueous solution of methylene blue. The stained animals were distributed in counting chambers, and their length and group classification were determined and recorded with a modified Bauch and Lomb Omnicon image analyzer. Each animal was singled out on the instrument's monitoring screen with a light pen. When the pen was pressed to the screen, the longest dimension of the digitized image was recorded (see also Jeffries et al. 1980, Berman et al. 1981). The operator then entered a group number, classifying the animal as a copepod, cladoceran, chaetognath, fish egg, or other. Antennae and spines were not included in the measurement of the animals. A minimum of 300

Fig. 1. Transect station used in this study: T₀ = Block Island (BI), T₁ = Rhode Island Sound (RIS), T₂ = Whale Rock (WR), T₃ = Wickford (WICK), T₄ = Rocky Point (RP), T₅ = Providence River (PR) and T_p = Point Judith Pond (PJP).

animals per sample were measured. Data were transmitted from the image analyzer to the University of Rhode Island's computer center for analysis by SAS (Helwig and Council 1979) and BMDP (Dixon and Brown 1977).

RESULTS AND DISCUSSION

Because changes in one group tend to be masked by unrelated changes in other groups, the analyses discussed here are limited to the copepods. A mean size for each station during each year of the survey was determined and tested for significant difference by analysis of variance (Table 1). For both years

Table 1. Analysis of variance of copepod body length vs. station for the Narragansett Bay / Rhode Island Sound transect.

<u>1979</u>					
<u>SOURCE</u>	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>PR > F</u>
Station	6	6.36	1.06	23.71	0.0001
Error	6143	274.48	0.04		
Total	6149	280.84			

<u>1980</u>					
<u>SOURCE</u>	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>PR > F</u>
Station	6	7.80	1.30	41.76	0.0001
Error	7360	229.17	0.03		
Total	7366	236.98			

Table 2. The mean length (mm), and number of copepods measured at each station. Stations grouped together had no significant difference in size spectrum.

<u>1979</u>		
<u>STATION</u>	<u>MEAN</u>	<u>N</u>
RIS	.658	660
BI	.653	591
WR	.594	931
PR	.585	923
RP	.584	800
WICK	.581	1052
PJP	.561	1193

stations had a highly significant effect on the copepod size ($p < .0001$). Duncan's multiple range test (Steele and Torrie, 1960) revealed the pattern of the effect. In 1979 there were 3

distinct groups of copepods (Table 2). The largest animals were in the two Rhode Island Sound stations. Copepods in Narragansett Bay stations had similar sizes. Point Judith Pond, with the smallest copepods, grouped with neither the bay nor the sound.

The species counts on these samples reflect the above groupings according to size (Fig. 2). The sound stations were

Fig. 2. The species composition of the copepod communities at each station in 1979, showing the dominance of the 4 genera listed.

characterized by *Centropages typicus*, *Pseudocalanus minutus*, and *Oithona* spp. With the exception of the transitional Whale Rock station at the mouth of the bay, Narragansett Bay stations were all dominated by *Acartia* spp. Although the Point Judith Pond community was also a virtual *Acartia* monoculture, the significant difference between the size of these animals and those from the bay (Table 2) suggests a different population or age structure existed at this station.

This pattern of distinct communities (size groups) in each habitat -- sound, bay, and pond -- changed abruptly the following

summer (Table 3). In 1980 there were 5 distinct groups of copepods and they bore only a weak relationship to the geography

Table 3. The mean length (mm), and number of copepods measured at each station. Stations grouped together had no significant difference in size spectrum.

<u>1980</u>		
<u>STATION</u>	<u>MEAN</u>	<u>N</u>
PR	.603	1029
RIS	.571	762
WR	.566	1274
WICK	.548	1274
UPJP	.527	1193
RP	.524	1026
BI	.498	1114

of the transect. The copepods from the Block Island station were the smallest sampled, and the station grouped by itself rather than with the other Rhode Island Sound station. This is indicative of the greatly reduced role of Centropages typicus in the Block Island community in 1980 (Fig. 3). The Rhode Island Sound and Whale Rock stations still showed a separate copepod community, one dominated by Pseudocalanus minutus and Oithona spp. as opposed to the Acartia spp. dominated bay stations.

Both the Point Judith Pond and the Providence River stations grouped differently in 1980 than in 1979. This was due to the fact that copepods from all other stations were significantly

Fig. 3. The species composition of the copepod communities at each station in 1980, showing the dominance of the 4 genera listed.

smaller in 1980 than in 1979 (T test, $p < .01$). The Point Judith Pond animals did not vary significantly in size from one year to the next, whereas the Providence River copepods were actually larger in 1980 ($T = 2.17$, $N = 1950$, $p < .025$). The reason for the smaller size structure of the Bay community in 1980 can not be assessed, although it may be related to an altered environment arising from the drought of 1980 (Fig. 4).

Size structure of the copepod communities in Narragansett Bay and Rhode Island Sound is complex and subject to great variation from one year to the next. Our method of community assessment detects such changes without recourse to time and labor intensive manual plankton counts. One operator was able to make all of the measurements for this study (21,839 animals, of which 13,517 were copepods) in approximately 1/5 the time that it took to do the species counts. Although loss of specific information is inherent in the technique, we feel that the type of data collected should be broadly useful, especially in

Fig. 4. The means and range of major environmental parameters at each station for the 2 summers samples.

ecological modelling and fisheries management. Increases in speed and efficiency of sample processing meet demands that until now have resulted in bottlenecks or gaps in coverage.

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BIOCHEMICAL CORRELATES OF SEASONAL CHANGE IN MARINE COMMUNITIES

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Orians (1975) and May (1975) presented simple graphs to summarize complicated ideas on the stability of natural systems: Orians showed arrangements of "stable points in a phase space"; May mapped out the "stable region of parameter space" for simple and complex systems. Their diagrams have considerable heuristic value, even though the axes, labeled only as dimensions 1 and 2 or as α and β , refer to no specific measurement or property. As May (p. 165) stated the problem: "How, in natural systems, can we measure the size of the stable domain ... How quantify dynamical fragility or robustness?"

The problem is one of approach and associated measurement. Deriving a mathematical landscape mapped from growth and interaction parameters seems technologically impractical for a major marine community. In this paper, fatty acid patterns from entire communities are compared with the rise and fall of seasonal species groups. The relations appear sufficiently clear for application of chemical pattern to stability theory.

Ecologically useful signals are probably generated by several chemical groups. Fatty acids have been selected because they are ubiquitous monomers, abundantly represented throughout the plant and animal kingdoms—to an extent in marine representatives that ultimately bears on the very nature of life, response and adaptation in their everchanging surroundings.

Fatty acids are quickly determined by precise, objectively standardized instruments. The common monomers are always present, which facilitates multivariate analysis, whereas absences usually occupy 80% or more of taxonomic species data matrices.

Because stability (constancy) depends on adaptive characteristics (Orians 1975), we expect that the system's overall monomeric composition should respond in a corresponding manner within limits that are homeostatically defined for seasonally recurrent species groups. Each fatty acid analysis thereby represents an integral of community state, its distributional qualities having been brought together by homogenization and selective extraction.

The biochemical signal emerging from an entire community is obviously the sum of many signals from individual species, their developmental stages, and everchanging physiological states. A community's signal may shift greatly or change little in response to a major change in structure; yet we know almost nothing about such

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patterns in seasonally recurrent situations, let alone those that are stressed by environmental abnormalities.

I wish to establish here that despite inherent limitations a clear chemical trajectory does exist in the plankton and fouling communities of temperate estuaries. The basic pattern is laid down at the primary producer level, and it is elaborated within trophic webs. The result is a generally similar pattern for different communities in the same ecosystem.

Estuarine communities retain their chemical identity in a dynamic sense—by way of chain lengthening and unsaturation processes that arise differentially in seasonally defined species groups: a winter-spring component with boreal affinities followed by a more southern, summer-fall group. Replacement of one biogeographic group by the other is virtually complete in plankton, because the controlling seasons are longer than the species' life cycles. Among larger benthic species—those with life cycles a year or more in length—habitat partitioning is more spatial than temporal (Jeffries 1966). The biochemical correlate is also a matter of degree in the way a community responds to change.

The chemical trajectory accompanying a single annual cycle represents only one turn through a community's stable domain. With each successional phase, physiological limits come through as quick changes on the overall pattern of statistical relations between component fatty acids. Only one annual cycle in each of three assemblages is presented here, but when the means and variances have been established by repeated observation over several years, chemical ecology might be applied to management situations in which the cumulative effects of synergistic stressors must be recognized before adverse biological responses become irreversible. More importantly, if chemical pattern and ecological structure turn out to be strong correlates, another way should be opened for "confronting theoretical ideas about stable domains with real world observations ..." (May 1975, p. 165).

METHODS

Fouling Community

Eleven glass plates measuring 25.4 cm on a side were suspended vertically in a rack floating $\frac{1}{2}$ m beneath the surface of lower Narragansett Bay, Rhode Island (41°29'30" N, 71°25'9" W). Two experiments were run, the first from April 7 to October 15, 1971, the second from November 8, 1971, to January 25, 1972. At 3–6 wk intervals, consecutively numbered plates were removed: Plates 1–8 comprised experiment 1, plates 10 and 11 experiment 2. Plate 9 was immersed on May 20 and removed September 3.

Upon removal of individual plates, species abundances were assessed without delay so that chemical patterns would be preserved in natural state. All the material on a plate was scraped free, freeze-dried, and stored in a desiccator at -20°C for fatty acid analyses by flame-ionization gas chromatography (Jeffries 1972). Lipid extracts obtained by the Bligh and Dyer (1959) method were methylated by procedures of Luddy et al. (1960, 1968). From these samples, up to 35 free and combined fatty acids were separated on packed columns (17% diethylene glycol

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succinate on Chromosorb W (HP) 100/120 mesh). Identification was based on comparison of retention time with that of a standard and from log retention time, relative to methyl stearate, as a function of number of carbon atoms: number of double bonds (Ackman 1969).

Plankton

Samples were taken in Narragansett Bay (41°33'50" N, 71°24'15" W) at monthly intervals indicated in table 1. Phytoplankton-microzooplankton was sampled qualitatively with a no. 20 mesh net (nominal aperture 0.076 mm) towed at the surface; zooplankton was sampled quantitatively by stepped oblique tows with a no. 2 mesh net (0.366 mm aperture). The fine net retained diatoms, nauplii and copepodite stages I-III for the most part. Although these organisms represented several ecological subgroups within the plankton, they were in a size range that formed a diet of the larger and chiefly omnivorous zooplankton taken by the coarse net.

Samples were drained immediately, refrigerated and freeze dried. Lipid extracts were saponified with KOH, and, as above, the recovered fatty acids were methylated in boron trifluoride-methanol and analyzed by gas chromatography. Further detail was given in my first attempt to express chemical states of marine communities (Jeffries 1969, 1970).

Precision

Chromatographic peak areas were determined planimetrically and electronically; concentration of each fatty acid was expressed as a percentage of total peak area. Standard errors for repeated analyses on the same extract and for multiple extracts of the same sample indicated that the major components (> 10% of the total) were precisely estimated within $\pm 7\%$ of the mean. From each data set, 10 common (usually the most common) fatty acids were selected for multivariate analyses.

STATISTICAL ANALYSIS

Correspondence Analysis

Correspondence analysis reduces dimensionality in complex matrices and groups overall variability into smaller sets that are mathematical functions of the whole (Benzecri 1970; Estrada 1972; Ibanez and Seguin 1972; David et al. 1974; Chardy et al. 1976; and Gauch et al. 1977). A unique feature of correspondence analysis is simultaneous representation of p -dimensional variable space and N -dimensional sample space.

Thus the distribution of 10 fatty acids in 12 samples taken at monthly intervals may be regarded as a cloud of 10 fatty-acid points in 12-dimensional sample space. Alternatively we may view the annual pattern as a cloud of 12 sample points in 10-dimensional chemical space. Planes are found in both parameter spaces best accounting for the total observed variation. Simultaneous projection of sample and fatty acid points on the first two principal axes yields a simple graph in which the

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sample points may be compared with the fatty acid variables chiefly responsible for a trend, departure, or cluster. As more axes are computed, the variation accounted for statistically is increased, but no more than three axes are required for a variety of ecological applications (Malmgren et al. 1978).

Results from a correspondence analysis (e.g., fig. 2) are interpreted in a convenient sequence: (1) Similar processes produce clusters of sample points, (2) a group of variable points indicates correlation within the set, (3) variable points close to a sample cluster characterize that cluster. The idea of an annual sample pattern is introduced in this paper. The pattern itself is a line connecting consecutive sample points in fatty acid space. Positions of fatty acid variables in relation to sample pattern further characterize changes taking place.

The chief benefit of correspondence analysis, apart from the ready associations that may be drawn between samples and variables, is freedom from limiting assumptions. Chardy et al. (1976) applied six multivariate methods to 30 benthic samples taken in silted sands on the North Gascony Continental Shelf and compared the results given by each method with respect to "influence capable of affecting structures," (p. 203) e.g., species abundances, multiple absences, sampling intensity and profile. Only correspondence analysis was unaffected by all influences. Malmgren et al. (1978) noted applications to infauna, fossil foraminifera, zooplankton, and a fouling community considered further here.

An occasionally overlooked requirement in multivariate analysis is independence among samples and variables, which is clearly not the case in ecological application. Correspondence analysis is distribution free, "each variable point is the center of gravity of the sample point weighted by the relative importance for that variable," and the contribution of each variable to the factor is a form of "correlation coefficient between that factor and each variable" (David et al. 1974, p. 135).

Biochemical Dominance

The biochemical dominance index is an easily calculated expression of departure from equal representation among n components:

$$D_m = \frac{1}{n} \left[\frac{100}{a_t} \sum_{i=1}^n (n-i+1)a_i - \frac{100}{n} \sum_{i=1}^n i \right],$$

where a_i represents the amount of the i th constituent in the ranked sequence $a_i \geq a_{i+1}$, $i = 1, 2, \dots, n$, and where $a_t = a_1 + a_2 + \dots + a_n$ is their total (Jeffries and Alzara 1970). The more evenly represented the n components are, the higher the index. Thus D_m is directly related to the equitability or evenness component (Peet 1974) of species diversity.

RESULTS

Fouling Community

Seasonal progressions of major taxa, biomass, chemical dominance, and four important fatty acids are shown conventionally in figure 1.

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FIG. 1.—Seasonal progressions of fouling communities on plates submerged in Narragansett Bay, R.I. Top, successions of major taxonomic groups and species on plates 1-8 (Apr.-Oct.) and plates 10-11 (Nov.-Jan.). Center, biomass (g) and biochemical dominance, D_{m10} , among 10 fatty acids given in figure 2. Lower, relative changes of four fatty acids; shorthand notation for normal carbon chain length: no. of double bonds.

Plate 1 in the spring-fall series was removed 43 days after immersion. Early colonization consisted of vorticellids, microflagellates, and colonial diatoms, an assemblage so taxonomically diverse that identification and enumeration were not feasible. Colonial hydroids (*Tubularia* sp., *Obelia* sp.) soon formed a heavy mat that engulfed the plant assemblage (plate 2, removed early June, day 56), but decay set in (plate 3, late June, day 78), making available a rich substrate for the feeding and shelter of an active, but short-lived, amphipod-polychaete group (plate 4, mid July, day 99). During the 3 wk between plates 3 and 4, the fouling community changed

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abruptly. Populations died and others arose in quick succession, yet biomass increased exponentially throughout the period. The next stage, beginning with plate 5 (late July, day 113), was a slower growing, longer lived and taxonomically simpler group (mussel-barnacle-limpet: *Mytilus edulis*, *Balanus eburneus*, *Crepidula* spp.). The descending portion of the bell-shaped biomass curve (fig. 1) may have been an artifact due to mussels and limpets falling to the bottom as spatial relations became established on the plates.

In a quantitative sense, chemical progression accompanied seasonal succession. Biochemical dominance, D_m (fig. 1), among the 10 fatty acids listed in table 2 decreased at the outset and then recovered in the taxonomically less diverse, but more stable, mussel-dominated group.

Individual fatty acids varied more than their dominance pattern. For example, 22:6 (shorthand notation for normal carbon chain length: number of double bonds) increased with time, paralleling the community's exponential growth phase, whereas both 16-carbon acids shown in figure 1 decreased, the monounsaturate (16:1, palmitoleic acid) dropping faster than the saturate (16:0, palmitic acid). Chemical progression during the 56 days between plate 1 (algae) and plate 4 (amphipods-polychaetes) was large and fast: Medium-chain acids (14-18 carbon atoms) decreased 18.7%, whereas the long-chain, chiefly polyunsaturated acids increased 18.3%.

Lumping fatty acids into long- and medium-chain groups may cause one to lose sight of the whole. It is desirable to consider all samples in relation to all component variables, and for such purposes correspondence analysis is helpful.

The first three axes of correspondence analysis shown in figure 2 cumulatively account for 91% of the total variation in all 11 sample plates. Asterisks represent each fatty acid in sample space. The heavy line connecting plates 1-8 in chronological order of removal is the sample pattern in fatty acid space. The pattern's major trend is from left to right on the first axis. We should expect such simplicity in a community represented chemically—a smooth progression that corresponds to a continuum of species populations.

The pattern was interrupted midway on the first axis by a spiral downwards on the second and third axes. This spiral coincided with a rapid series of changes in community structure: The hydroid mat decayed (plate 3) and supported a diverse polychaete-amphipod assemblage (plate 4) for a brief period. Within this spiral must lie the biochemically stable domain of the polychaete-amphipod phase. The community recovered with the advent of a mussel-dominated group (plate 5) and a return to the left-right sample pattern.

Positions of individual fatty acid variables in relation to sample pattern showed the major trend of chemical progression (fig. 2). Fatty acids quantitatively richer in the plant-dominated early community (14:0, 16:1) clustered to the left on the first axis, whereas to the right longer chain polyunsaturates (18:3, 22:6) characterized later development in the animal assemblage. Chemical progression from spring through fall was longer chain length and more unsaturation—a correlate to the increasing complexity of community development.

The long-chain saturate 22:0 rose from 3.9% in plate 1 to 7.8% in plate 3, when the hydroid mat began to decay, and then it fell below 3.0% during collapse and subsequent recovery in the *Mytilus* stage. These are high concentrations for 22:0 (R.

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FIG. 2.—Correspondence analysis of fatty acid pattern in fouling communities. Each filled circle represents the position of a sample plate in three-dimensional fatty acid space. The heavy line connecting plates 1-8 is the sample pattern for the spring-fall period (experiment 1, fig. 1). The broken line to plate 9 shows how the pattern may swing back to the winter condition represented by plates 10 and 11 (experiment 2). Asterisks show the affinity of each fatty acid variable to the sample pattern.

G. Ackman, personal communication), so identification should be regarded as tentative. If it is correct, saturated homologues may denote impending change. The sample pattern's swing backward at plate 9 was signaled by 20:0 increasing from 1.0% to 7.6%, while 18:0 increased from 3.6% to 6.2%.

The fall-winter samples (plates 10 and 11, experiment 2) suggested that the annual pattern was circular. These samples fell near the spring trajectory of experiment 1, despite clear taxonomic differences (fig. 1). Plate 9, which also developed an advanced mussel-dominated community in a comparatively short period, indicated a likely trajectory for the return swing.

The central position of 20:5 on all axes indicated that it was a locus around which change occurred, a uniqueness possibly owing to the major role of long-chain polyunsaturates in marine organisms (Gunstone 1967). Why marine organisms elongate 18:3 and 18:4 to 20:5 is a mystery, perhaps related to the packing of phospholipids in membranes. Accumulation of 20:5 may exceed need, and a small amount is changed to 22:6, especially in depot fats (oils) of fishes (R. G. Ackman, personal communication). The 20:5 acid also holds a pivotal position in sample space within two planktonic communities considered next.

Plankton

Seasonal characteristics of the Narragansett Bay plankton are shown in table 1. All pertinent data on fatty acid composition are listed in table 2.

Species abundance and production in Narragansett Bay are strongly controlled by temperature (Pratt 1959; Jeffries 1970, 1972), which increases from 0° C in February to over 20° C in August (table 1). Because Bay salinity is high (30-32.5‰) and

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comparatively free from unpredictable variations (table 1), seasonal progressions of species populations are well defined in the nontidal drift that slowly moves seaward (Jeffries and Johnson 1973; Smayda 1976). Tidal influxes seed the Bay's community, but most production is indigenous. Thus the winter-spring plankton has boreal characteristics, whereas affinities of the summer-fall plankton are temperate and tropical.

Chlorophyll a concentrations (table 1) peaked during the winter and fall diatom blooms typical of coastal waters in the Western North Atlantic. Flagellates became increasingly prevalent during summer (Pratt 1959). Nevertheless the pigment ratio D_{430}/D_{665} varied little (table 1). At its extremes pigment diversity corresponded inversely to chlorophyll concentrations: The minimum (2.1) occurred in January, when chlorophyll a reached $27.8 \mu\text{g/L}$; the maximum (3.7) occurred in April, when chlorophyll a fell to the annual minimum, $1.1 \mu\text{g/L}$. In general then, pigment diversity increased with maturity and flagellate preponderance, behaving in a manner similar to that described by Margalef (1968).

Relative amounts of phytoplankton and microzooplankton in the fine mesh (no. 20 net) samples varied seasonally. During spring and early summer (table 1), when copepod nauplii were abundant and many plant cells were too small to be retained by the net, lipid and nitrogen contents each exceeded 9%. In the winter-spring bloom, however, the fine-mesh net samples contained mostly diatoms, and nitrogen content fell below 5%.

The zooplankton usually responded within 1 mo to pulses in primary production, but the biggest increase (106.2 mg/m^3) occurred in July, a recovery from near elimination due to predation by the white jellyfish, *Aurelia aurita* (table 1). Succession from *Acartia clausi*, the winter-spring dominant copepod to *Acartia tonsa*, its summer-fall replacement, was nearly complete by April (Jeffries 1962).

Correspondence analysis is shown schematically in figure 3. The heavy line is the trajectory of consecutive samples in each sample set; dashes indicate periods of species succession. Only the key fatty acid variables associated with change are plotted. The total observed variation accounted for by the first two axes is 80.7% in the phytoplankton-microzooplankton and 61.6% in the zooplankton; the third axes bring the totals to 88.8% and 77.7%.

Seasonalities and pattern were better defined at the monomeric level than they were by pigment ratios and proximate analyses. Changes occurred especially fast during species succession, which occurred midway on the first chemical axis.

Both assemblages produced loop-like annual patterns with 20:5 centrally located, but their details differed. The phytoplankton-microzooplankton had two complete subloops in fatty acid space, the larger loop corresponding to winter species (boreal or North Temperate, diatom), the other to the summer group (South Temperate, flagellates). In zooplankton, the winter (*Acartia clausi*) and summer (*Acartia tonsa*) groups also separated chemically on the first axis, but here the pattern folded back upon itself in a U-shaped manner, forming a half loop for each biogeographic group. By inference, each loop was part of a stable domain in fatty acid space. The zooplankton's comparatively erratic sample pattern may have reflected resource depletion. Diatom blooms in Narragansett Bay are controlled by copepod grazing (Pratt 1965; Martin 1965).

TABLE I

PHYSICAL CONDITIONS; CHLOROPHYLL *a*; ABSORBENCY RATIO; ACETONE EXTRACT OF FILTERED BAY WATER; PROXIMATE ANALYSES OF PLANKTON;
DOMINANT SPECIES; SAMPLE PROJECTIONS OF FIRST THREE CORRESPONDENCE AXES, PHYTOPLANKTON-MICROZOOPLANKTON AND ZOOPLANKTON
(Narragansett Bay, West Passage, 1965-1966)

PROPERTY	SAMPLES												
	Oct. 6	Nov. 3	Dec. 1	Dec. 29	Jan. 26	Feb. 23	Mar. 23	Apr. 20	May 18	June 22	July 20	Aug. 17	Sept. 28
Surface temp. °C	13.9	10.4	6.4	3.0	0	1.0	5.4	6.4	11.8	17.4	19.0	20.6	17.0
Surface salinity ‰	31.9	31.9	31.5	31.3	30.5	30.2	29.4	30.4	30.4	30.6	...	...	...
Chlorophyll <i>a</i> µg/L	16.9	3.8	4.9	23.0	27.8	11.6	7.1	1.1	4.5	8.0	7.1	5.0	...
D ₄₃₀ /D ₆₆₅	2.6	2.4	2.8	2.2	2.1	2.4	2.4	3.7	3.2	2.7	2.5	...	...
Total zooplankton mg/m ³	19.1	80.4	6.6	49.7	51.9	25.6	22.8	51.3	5.6	...*	106.2	91.7	14.8
Total lipids % dry wt.													
phytoplankton	4.7	6.5	...	9.9	...	...	...	16.0	13.7	12.5	10.7	5.6	4.0
zooplankton	11.9	10.4	12.3	14.3	17.5	15.9	25.9	17.3	12.9	9	10.8	9.7	10.9
Total nitrogen % dry wt.													
phytoplankton	3.3	5.1	...	4.4	4.1	4.6	1.6	9.8	9.8	9.6	...	...	...
zooplankton	8.6	11.1	11.1	10.8	10.2	10.4	9.8	10.6	10.4	9.8	...	...	...
<i>Acartia clausi</i> No./m ³	4	ND†	2,869	2,139	1,536	814	672	59	2,243	...*	ND	...	...
<i>Acartia tonsa</i> No./m ³	923	1,875	ND	ND	ND	ND	ND	152	43	...*	1,314	...	...
Correspondence analysis sample projections													
Phytoplankton													
1st axis	.026	.248	...	-.190	-.427	-.484	-.363	.028	.329	.284	.607	-.166	...
2d axis	-.139	.132	...	.164	-.129	.248	-.099	.241	-.142	.011	.014	-.391	...
3d axis	.092	.035	...	-.150	.059	-.138	.029	.266	-.051	-.149	-.025	-.002	...
Zooplankton													
1st axis	-.248	-.118	-.070	-.057	.518	.470	.276	.275	-.337	-.180	-.176	-.102	-.229
2d axis	-.136	-.171	-.235	-.236	-.077	-.081	.186	.193	.239	.308	-.080	.178	-.119
3d axis	-.104	-.054	.199	.068	-.155	-.309	.273	.239	-.194	-.083	.072	-.047	.082

* *Aurelia aurita* dominated.

† ND = not detectable.

TABLE 2

FATTY ACID CONCENTRATIONS IN PHYTOPLANKTON-MICROZOOPLANKTON (P) AND ZOOPLANKTON (Z) AS PERCENT OF TOTAL FATTY-ACID METHYL ESTERS;
PROJECTION OF VARIABLES ON THE FIRST THREE PRINCIPAL AXES OF CORRESPONDENCE ANALYSIS FOR THE PHYTOPLANKTON-MICROZOOPLANKTON
AND ZOOPLANKTON

PROPERTY		VARIABLES*										
		14:0	16:0	16:1	18:0	18:1	18:4	20:1	20:5	22:1	22:6	Total
% total fatty acids												
Oct 6	P	15.5	23.4	10.2	4.1	8.1	5.0	3.6	11.8	.1	8.9	90.7
	Z	5.3	25.9	4.3	5.3	7.0	4.0	1.6	14.8	.1	24.7	94.0
Nov 3	P	5.1	23.2	8.3	3.5	8.3	6.8	6.0	14.7	2.6	12.9	92.4
	Z	5.0	26.7	8.5	4.6	6.2	7.7	4.3	13.5	.1	15.5	93.1
Dec 1	Z	6.1	20.7	6.3	3.0	7.8	9.4	10.7	14.9	.1	13.1	92.1
Dec 29	P	12.9	13.4	16.1	.1	8.5	5.8	3.3	14.8	3.8	6.6	85.3
	Z	5.7	19.4	4.8	2.4	8.7	8.7	3.5	18.0	.1	13.9	85.2
Jan 26	P	17.3	12.4	22.0	6.2	9.8	3.1	4.5	9.5	2.6	1.8	89.2
	Z	9.3	13.0	18.2	1.8	13.5	4.2	2.2	18.3	.1	6.4	87.0
Feb 23	P	11.2	10.0	23.7	.1	10.4	4.2	3.0	15.3	3.9	1.3	82.1
	Z	12.8	15.9	18.7	2.8	9.4	2.7	2.1	15.2	.1	6.8	86.5
Mar 23	P	14.8	14.1	16.9	3.9	9.3	4.9	2.3	13.1	.1	1.1	80.5
	Z	4.7	13.1	12.1	2.6	19.2	5.6	5.8	12.7	3.7	12.9	92.4
Apr. 20	P	7.3	18.6	12.0	3.5	17.2	5.1	5.9	10.3	3.4	11.2	94.5
	Z	6.3	12.8	12.3	2.5	16.9	5.5	5.6	12.9	4.4	13.4	92.6

May 18	P	14.6	16.9	5.0	5.4	4.7	7.2	3.5	9.4	3.6	17.3	87.6
	Z	6.1	18.3	5.8	16.0	6.0	6.8	3.6	10.1	1.7	16.8	91.2
June 22	P	8.0	21.1	8.8	4.1	3.0	9.6	5.8	13.9	3.0	12.8	90.1
	Z	4.9	30.0	5.9	10.8	9.0	2.8	4.2	14.6	4.0	7.2	93.4
July 20	P	3.2	20.9	2.5	6.0	4.0	9.0	5.0	13.7	1.9	19.9	86.1
	Z	5.3	27.5	4.5	4.8	10.6	6.7	5.7	7.2	.1	10.6	83.0
Aug 17	P	14.8	11.6	13.1	6.6	3.4	4.2	2.8	7.1	.1	5.1	68.8
	Z	4.8	22.6	6.4	7.7	11.9	2.4	2.7	11.9	2.0	14.4	86.8
Sept 28	Z	5.2	23.0	3.2	4.9	6.5	9.7	4.1	14.3	1.4	14.9	87.2
Correspondence analysis variable projections												
Phytoplankton												
	1st axis	-.285	.184	-.510	.168	-.249	.258	.150	-.013	.019	.645	
	2d axis	-.271	-.014	.025	-.463	.255	.008	.088	.112	.420	.010	
	3d axis	-.033	.050	-.060	.159	.283	-.141	.066	-.122	-.207	-.006	
Zooplankton												
	1st axis	.233	-.203	.563	-.461	.267	-.145	-.051	.094	.091	-.208	
	2d axis	-.099	-.043	.032	.417	.155	-.234	-.074	-.093	.977	-.070	
	3d axis	-.213	-.049	-.161	-.299	.187	.202	.367	-.037	.461	.042	

* Shorthand notation for no. C atoms : no. double bonds.

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PHYTOPLANKTON - Microzooplankton

FIG. 3.—Schematic representation of sample pattern in phytoplankton-microzooplankton (upper) and zooplankton (lower) on the first two principal axes of correspondence analysis (details in tables 1 and 2). Note that the overall pattern is elliptical. Positions of selected fatty acid variables are shown by the filled circles.

The important point was the similarity of pattern in two planktonic assemblages. Significant summer variables were 16:0, 18:0, and 22:6. Winter plankton was characterized by 14:0, 16:1, and 18:1. This general arrangement also resembled the fouling community's annual distribution (fig. 2).

Thus the ratio 16:1/16:0 is a sensitive indicator of ecological change; values decrease sharply during spring succession and rise in fall or winter (Jeffries 1970). These dynamics originate in phytoplankton, and they are passed to zooplankton and benthos, where effects may be amplified as the trophic web responds to the same seasonal factors that initiate metabolic restructuring and then species progression at the primary producer level.

DISCUSSION

Four notions of chemical stability in the benthos are shown schematically in figure 4. They are based on Oriens' (1975, p. 142) "graphic representations of some concepts of stability." The fouling community's annual trajectory (fig. 4A, simplified from fig. 2) is an open ellipse, upon which loop-like departures that accompany major reorganization (e.g., hydroid decay) are superimposed. Distance between consecutive monthly samples is a chemically defined measure of species progression, whereas distance between annually separated points may represent ecological succession.

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FIG. 4.—Hypothetical sample trajectories in chemical space for benthic community development and associated stable relations.

I speculate that a fouling community's annual trajectory would tighten in later years to a comparatively stable cycle (fig. 4B). Most of the biomass in this phase is molluscan, and the species have comparatively long life cycles. Consequently we would expect a less robust trajectory than that produced in the rapidly changing plant-hyroid-amphipod-polychaete sequence, which characterizes initial colonization.

Each year seasonally adventitious forms would appear in a well developed fouling community and expand the trajectory beyond that due to the persistent molluscs alone. Also, the phytoplankton's seasonally variable chemical signal (fig. 3) would be imprinted on the food chain. But if the community continued to progress, in the

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absence of heavy predation by fishes, toward increasingly constant species-area relations on the plate, each annual loop and its displacement might become smaller than before and then converge to a stable cycle (fig. 4C).

Several trajectories may lead to the same stable cycle (trajectory stability, fig. 4C): Path 2 is established from the spring-summer experiment; path 3 is inferred from the fall-winter experiment; and path 1 is imagined. The outcome of a fouling experiment may depend on when the plate is immersed (Robert Hillman, personal communication; Sutherland 1974). Path 4 is such a case, leading to a different stable cycle.

If fouling experiments were run for several years under conditions chronically and acutely stressed, a statistical limit could be placed on the annual cycle. This limit of chemical integrity is indicated in figure 4D by the dashed line. If it is exceeded, the annual species aggregate becomes something else, perhaps after reverting to an early chemical state, from which a new trajectory would be established, conceivably progressing to the original stable cycle. Within the limit of integrity lie the limits on seasonally recurrent groups, best exemplified by the winter-spring and summer-fall components of the plankton. Their growth and replacement are part of the usual order of events, and each is encompassed by the whole.

A large enclosed area means that the community is dynamically robust; a small domain indicates dynamical fragility (May 1975). If dynamical robustness is related to the vagaries and range of sample pattern, plankton would appear less dynamically stable than the benthos, chemically as well as taxonomically.

We should be able to establish by repeated observation alone the statistical limit of chemical integrity for selected planktonic communities. Because chemical pattern is homeostatically regulated within a species group, any significant departure from the norm should precede structural and perhaps even functional change in the community itself. Application of this predictive capability may be possible after further comparisons have been made in communities adapted to various environmental ranges.

The limit of chemical integrity is believed to define, at least for empirical purposes, a correlate to the stable domain proposed by Orians (1975) and May (1975). Instead of mathematical landscapes derived from interaction coefficients—a seemingly impossible practical goal—we may wish to consider chemical patterns. The idea is traceable to Margalef (1961, p. 128): "An animal population could be simplified also to the form of a mixture of selected easily analyzable, chemical compounds." What he called noise and channel width in an ecological message may be found in the means and variances of chemical patterns. Determining these statistics is a logical next step in the study of biochemical correlates to ecological structure.

SUMMARY

Plankton and benthos respond in different ways to seasonal change, but their patterns of fatty acid distribution are similar. The general trend of chemical progression is toward longer chain lengths and increasing unsaturation. Thus, as a temperate community matures and becomes more complex, so does its fatty acid composition. Chemical progression is most rapid during succession from winter-spring to summer-fall species groups, a period of reorganization among characteristic fatty

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acid sets. Increasing amounts of saturated acids seem to disclose a change in community structure, whereas an important polyunsaturate forms a locus around which these progressions take place.

Structural change within a community can be portrayed in a space defined by its fatty acid variables. The patterns formed here were oval over an annual cycle. An embellishment on the benthic pattern corresponded to collapse in a pioneer stage and subsequent reorganization at a higher taxonomic level. In general however, benthos had a less robust trajectory in fatty acid space than plankton.

Biochemical sample patterns are believed to bear sufficient correspondence to the stable domain of parameter space (Orians 1975, May 1975) for convenient testing of stability theories. Because they are based on ubiquitous monomers, these patterns also permit fundamental comparisons between natural communities in various states and conditions.

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OTHER PROGRESS

1. Nutritional studies.

As part of a cooperative study, relations between food quality and population growth are being studied in experimental situations. This work, in conjunction with Dr. Kenneth Tenore, Skidaway Institute of Oceanography, on cultures of the polychaete Capitella capitata has suggested an enormous influence of bacterial activity on the qualitative nature of fatty acids in various food sources. This effect is seen by comparison of fatty acid patterns in foods that are added to the experimental populations, both in the presence and absence of actively growing Capitella. Thus, the role of bacterial metabolism in detrital food chains may not be the long-argued enhancement of protein and carbohydrate content, but rather the key process is in production of essential metabolites.

2. Studies on positional isomers.

In addition to routine gas chromatographic analysis of total fatty acids on packed columns, each sample is also analyzed on a high performance capillary column having the ability to separate positional isomers and branch-chain forms. We expect that this detailed information will yield increased resolution on the distributional schemes and response patterns observed so far.

3. Hydrocarbon analysis.

Methods for preserving zooplankton prior to extraction and purification of hydrocarbon analysis have been worked out and tested extensively for contaminants and other artifacts. A separate analyzer with a non-

polar glass capillary column has been reserved for these analyses and tested for performance.

4. Cooperative investigations on Spanish rias.

In cooperation with the Instituto Español de Oceanografía, zooplankton samples have been taken at approximately monthly intervals at stations in the Ria de Arosa and the Ria de Muros et Noya. About 1/3 of these samples were analyzed by Jose Cabanas-Lopez of the Instituto's La Coruña laboratory during a visit to the USA for experience on analytical procedures and computerized statistical routines. His results indicated a unique pattern of sample trajectory localized in the mussel aquaculture area of the Ria de Arosa. So heavy is the growth of mussels in this estuary, that its very nature is now dominated by the mussel population's feeding and contribution to detrital load.

5. Cape Cod Bay transect.

A feasibility study on analyzing additional coastal transects, in a manner similar to that of the Rhode Island Sound-Narragansett Bay study, was attempted with great success across Cape Cod Bay, from off Provincetown to Boston Harbor at Logan Airport. By using a high speed boat and relying on shore facilities, we were able to conduct sampling operations at less than 10% the cost of current charges for boat-time on a larger vessel. Preliminary sample examination indicates that comparison with the Narragansett Bay transect that terminates at Providence will be most interesting. Indeed, this operation has worked out so well that we propose applying it to the apex of the New York Bight. Ideally, this study should also include a transect across the Georgia shelf, where materials in river outflow control and characterize the entire trophic system.