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Plankton species assemblages off southern Vancouver Island: Geographic pattern and temporal variability

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ABSTRACT

Multivariate classification and ordination methods are used to describe the patterns of zooplankton and phytoplankton community composition during four summer-period surveys of the continental shelf region off southern British Columbia. Sites identified by their species composition as being biologically similar form distinct clusters in species space and are also clustered geographically. Locations and shapes of the spatial clusters are stable over time and conform well with the patterns of bathymetry and physical circulation. However, the synoptic compositional ratios which define these spatial clusters change markedly between sampling periods and the regional composition pattern shows little association of a particular species assemblage with a particular location. This suggests that nonlocal succession coupled with advection are dominant in determining the local species composition.

1. Introduction

The spatial structure of plankton populations can be separated, both conceptually and in terms of applicable sampling and analysis methods, into two aspects—heterogeneity of total amount (biomass patchiness) and heterogeneity of kind (species composition). Studies of biomass patchiness have covered a more complete spectrum of contributing length scales (Denman and Mackas, 1978; Haury et al., 1978); the greater density of information is largely attributable to the comparative ease of obtaining continuous automated estimates of biomass. The biomass studies have demonstrated, particularly for coastal regions, intense coarse-to-mesoscale (roughly 10-200 km) horizontal patchiness of both phytoplankton and zooplankton, and frequent association of this patchiness with local features of the bathymetry and physical oceanography (e.g. Pingree et al., 1975; Walsh, 1977; Steele and Henderson, 1979; Herman et al., 1981).

The examination of compositional pattern has been less complete for both zooplankton and phytoplankton (see Haury et al., 1978 and Raymont, 1980, pp. 223-258 for general reviews). Studies of zooplankton variability at very large length

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scales (10^3-10^4 km) have shown distinct species assemblages which are coincident with the large scale pattern of currents and water masses (Fager and McGowan, 1963; McGowan, 1974). The range and sequential ordering of these assemblages are readily interpretable from presence/absence data, although measurements of the amount in each taxonomic category (interval-scaled data) may allow a superior discrimination between faunal zones (Fasham and Angel, 1975). Within their core geographic regions, the spatial and temporal uniformity of these species assemblages suggests (McGowan and Walker, 1979) a stable community actively structured and maintained by interactions between its members. In special circumstances, such as the warm and cold core rings associated with the Gulf Stream (Wiebe *et al.*, 1976) equally distinctive changes in species composition occur over much smaller spatial scales. However, the more typical pattern for separations smaller than about a thousand kilometers is a relative uniformity of species presence; changes in community composition occur primarily as shifts of dominance within a locally standard species list. Interval-scaled data and multivariate statistical methods are therefore almost essential to resolve the intra-community variability. A number of analyses using these tools (e.g. Colebrook, 1978; Gardner, 1979) have shown zooplankton dominance patterns which are correlated with hydrography over distances of order 10^2-10^3 km. Somewhat surprisingly, there have been few multivariate descriptions of zooplankton community pattern within the 1-100 km range despite the importance of this length scale in coastal zone biomass patchiness. Those which have been made (e.g. Cassie, 1960; Smith *et al.*, 1976; Magazda, 1979; Star and Mullin, 1981) have emphasized the shorter length scales within this range.

Studies of floristic composition have shown results similar in outline to those given above for the zooplankton, with a few important differences as noted by Raymont (1980). The first is that individual phytoplankton species tend to be much more cosmopolitan than do zooplankton species; their ranges are more extensive and their distributional boundaries less sharp. Second, the observed phytoplankton community associations tend to be broad groupings of species with similar environmental requirements, morphologies and physiological response rates. These groupings appear to correlate well with higher level taxonomic divisions, leading to the now familiar diatom-flagellate paradigm (Margalef, 1978). Third, (and contrasting with the relatively clear organization into ecological types) the within-type dominance hierarchy of individual species is highly labile in both time and space. This apparent instability of occurrence and rank of individual species has led to the recent assertion (Williams *et al.*, 1981) that phytoplankton species groups are essentially random associations rather than interacting and predictable "communities." Fourth, the statistical analysis of mesoscale species pattern has been more extensive than for the zooplankton (e.g. Estrada, 1978; Reid *et al.*, 1978; Blasco *et al.*, 1980).

Our recent studies of the continental shelf region of southern British Columbia, Canada have shown intense coarse-to-mesoscale pattern of physical, chemical, and

scalar biological variables (Mackas *et al.*, 1980; Denman *et al.*, 1981). In this paper we examine the following questions:

1. Do phytoplankton and zooplankton species data collected at spatial separation scales of 5-200 km show detectable structure in species space (the multidimensional space defined by abundance axes of the phytoplankton or zooplankton species)?
2. Does this biologically-defined pattern map coherently in geographic space?
3. Are the community resemblance patterns similar for phytoplankton and zooplankton; i.e., does similarity in faunistic structure imply similarity in flora?
4. Are the species patterns usefully correlated with and predictable from more basic oceanographic variables such as temperature, salinity, bathymetry and/or current pattern?

An accompanying paper (Mackas, in prep.) will examine the related issues of spatial autocorrelation of zooplankton and phytoplankton community structure and of comparison with the autocorrelation of total biomass.

2. Regional oceanography

The southern B.C. continental shelf is both wider and topographically more complex than neighboring coastal regions to the north and south. Figure 1 shows the area covered in this paper. The mean directional trends of both coastline and shelf break bend relatively sharply westward off Juan de Fuca Strait. The southern and widest portion of the shelf is deep (120-150 m) and is cut by a submarine canyon system (>250 m) which runs seaward from Juan de Fuca Strait. The offshore bathymetry shoals abruptly off the southeast corner of Barkley Sound forming a series of banks (70-100 m) and semi-enclosed basins (150-200 m). Further up the coast, the banks merge with the nearshore shallows and the shelf develops a smooth profile as it narrows gradually to the northwest.

Mean circulation is determined by an interaction of this bathymetry with seasonal wind pattern and the positive estuarine circulation in Juan de Fuca Strait (Tully, 1942; Freeland, pers. comm.). Late-spring through summer periods are characterized by a wind-driven northwest-to-southeast upper layer flow along the outer shelf, and a southeast-to-northwest coastal current emerging from the Strait. A persistent (through the summer) cyclonic gyre occupies the central portion of the shelf off Juan de Fuca Strait and is coupled laterally to the outer shelf and estuarine flows. During winter periods, average currents are from southeast to northwest over the entire region.

The shelf zone is characterized throughout the summer by very high levels of dissolved nutrients, primary productivity, and phytoplankton biomass (Mackas *et al.*, 1980; Denman *et al.*, 1981, 1982). We have frequently found healthy phytoplankton populations with chl. *a* concentrations as high as 10-50 mg m^{-3}.
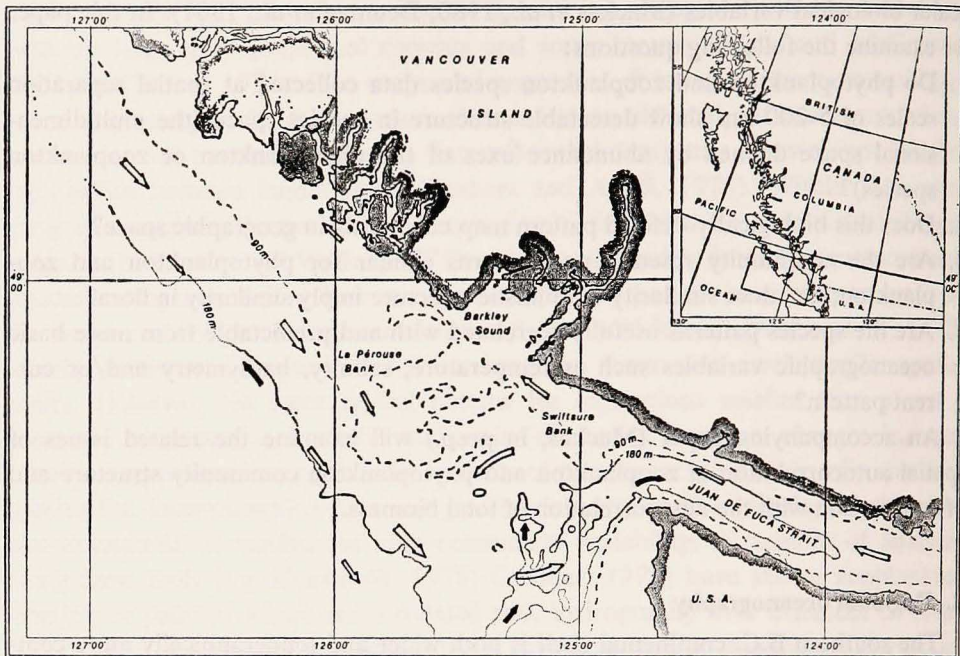
Figure 1. Map of the study area showing bathymetry and approximate summer circulation pattern. Solid arrows indicate near-bottom currents, open arrows show upper layer currents.

At least three enrichment mechanisms contribute to the dense phytoplankton growth. Seasonal wind and current patterns are conducive to episodic coastal up-welling, although probably of lower intensity than that observed further south (Denman *et al.*, 1981; Freeland and Denman, 1982). Estuarine discharge from Juan de Fuca Strait carries large nutrient concentrations brought to the surface by intense tidal mixing in the inner portions of the Strait (Herlinveaux and Tully, 1961; Mackas *et al.*, 1980). Third (and probably most important), interaction of the gyre mentioned above with a tributary of the Juan de Fuca submarine canyon causes transport onto the shelf of very nutrient-rich and oxygen-depleted water characteristic of the 350-450 m deep California Undercurrent (Freeland and Denman, 1982). Unlike the intermittent nutrient pulses provided by wind events, the latter two mechanisms maintain a persistent high level of enrichment throughout the mid-May to October period.

Zooplankton concentrations normally range from 1-10 g m^{-2} dryweight. We consistently observe an elongate zooplankton abundance maximum near the outer margin of the shelf. Fulton and Arai (1982) have noted a winter-spring maximum in the spatial distribution of macro-zooplankton along the same shelf-edge axis. Inshore maxima occasionally occur off Barkley Sound and at the mouth of Juan de Fuca Strait, while the mid-shelf region usually shows lower concentrations (Mackas

et al., 1980). Regionally averaged species composition and dominance hierarchy closely resemble that reported for the Oregon coast (Peterson and Miller, 1977).

3. Methods

a. Collection and identification. Data presented here were collected during four cruises (each of about 10-day duration) in July and August 1979 and June and August 1980. Zooplankton samples were obtained from 250 m or bottom-to-surface vertical hauls of a flow-metered 0.5 m diameter net fitted with 0.233 mm nylon mesh (dense phytoplankton populations prevented the use of a finer mesh). Formalin preserved samples were identified and counted (500 + individuals per sample, identification usually taken to species and developmental stage). A subsample of the preserved material was analyzed for dryweight, and the flowmeter reading was used to calculate abundance and biomass per square meter of sea surface.

Microplankton (phytoplankton plus microzooplankton) were collected as unfiltered water samples by bucket from the sea surface (underway samples) or by rosette sampler from the depth of the chlorophyll fluorescence maximum and were preserved with acid Lugol's solution. Settled subsamples were enumerated at 40× and 100× magnification. Because we were unsure of our ability to identify many of the microplankton to species level, we deliberately under-identified microplankton samples from the 1979 cruises. Many of the reported taxa (e.g., "small dinoflagellates," "microflagellates," "*Chaetoceros* spp.") are probably amalgamations of two or more species. The intent of this policy was both to prevent mis-identification, and to reduce the gradient in the apparent diversity that would accompany transition from large, morphologically distinctive phytoplankton (e.g., diatoms) to tiny and/or "difficult" forms (e.g., microflagellates). However, because the pooled taxa often formed a major fraction of the phytoplankton species assemblage, we also obtained an underestimate of the true intensity of between-site phytoplankton species variability. Samples from subsequent years are being analyzed in greater taxonomic detail and will be reported elsewhere. Full species lists and abundance estimates for the microplankton and zooplankton are reported in Hill *et al.* (1982a,b).

Background oceanographic data were collected using the vertical profiling system described by Denman *et al.* (1981). Continuous data (*T,S, in vivo* chlorophyll fluorescence) are archived as computer files at the Institute of Ocean Sciences, Sidney, B.C. Discrete data (water bottle samples for extracted chlorophyll, dissolved nutrients, oxygen, and point estimates of temperature and salinity transferred from the continuous data) are listed in Hill *et al.* (1982a,b). Primary productivity estimates were calculated from uptake of ^{14}C bicarbonate during two hour incubations at sea surface ambient temperature and under constant artificial illumination ("cool-white" fluorescent bulbs, approx. 50 Wm^{-2}). Production rates were normalized relative to biomass using the corresponding extracted chlorophyll measurements.

b. Reduction and analysis of species data. The goal of our analyses was to examine regional variation in relative dominance within the planktonic food web. Data reduction and analysis methods were selected to reflect this dominance pattern, and the contributions of the various species were weighted in approximate proportion to their local biomass. The raw data source for each cruise and sample type (microplankton and net zooplankton) consisted of abundance estimates A_{ij}, where i indexes over N sampling sites and j indexes over P taxonomic categories. The size of this data matrix was reduced by eliminating "very rare" taxa (operationally defined as those species which were absent at $\geqslant 80\%$ of the sampled sites for all cruises and which comprised $\leqslant 1\%$ of the total population at the sites where they were present). Zooplankton taxa were summed over developmental stage with the partial exception that "early juvenile" and "late juvenile-adult" categories were retained for *Pseudocalanus* sp., *Calanus marshallae*, and *Euphausia pacifica*. The reduced data matrices include those taxa which we consider to be both well identified and statistically well enumerated; species lists are given in Tables 1 and 2. "Stress" tests on the final reduced data matrix (Orloci, 1978) suggested that the between-site covariance structure would have been duplicated to about 95% accuracy using a considerably smaller species list (e.g., circa 10-12 zooplankton taxa).

We used the multiplicative coefficients listed in Tables 1 and 2 to give an approximate size scaling of the various taxa. The zooplankton coefficients are adapted and simplified from dryweight factors used in the Continuous Plankton Recorder surveys (R. Williams, pers. comm.). Phytoplankton coefficients reflect a five level nominal size classification. The size coefficients set the per unit abundance importance of each species for the subsequent analyses and reduce the otherwise strong tendency for domination of the results by a few numerically abundant but tiny species. The major features of the between-site resemblance (e.g. cluster membership, approximate ordination sequence) were normally reproduced using unweighted abundance data, suggesting that the results reported here are not heavily dependent on exact values of the size factors. The conventional geometric interpretation of the data matrix (Fig. 2) is that the elements of each row define coordinates of the respective sampling site in the positive sector of P-dimensional species space. The sampling site vector (= "quadrat vector," Orloci, 1978) connects the origin (abundance = biomass = 0 for all species) with this point. The direction of the vector describes the relative dominance of the various species, while the length is a measure of the total local biomass.

We used both ordination and classification analyses to characterize the distribution of sampling sites in the multidimensional space defined by the data matrix. Although the two approaches may eventually lead to similar interpretations of the data, they assume rather differing structures of between-site resemblance. Classification methods assume that the samples group naturally into a reduced number of swarms or clusters, with the members of each group sharing a characteristic and relatively

Table 1. Mean abundance (# per square meter), size-scaling coefficients, occurrence rates, and community dominance indices for zooplankton taxa included in the analyses. "Weighted % local population" is $1/N \sum_{i=1}^{N} (B_{ij} / \sum_{j=1}^{P} B_{ij})$, "weighted % all samples" is $(\sum_{i=1}^{N} B_{ij})/(\sum_{j=1}^{P} \sum_{i=1}^{N} B_{ij})$ where N is the total number of samples, P the number of taxa retained for analysis, and B_{ij} the estimated biomass (abundance multiplied by size coefficient) of species j in sample i.

Taxon	Mean abundance ($10^3\,m^{-2}$)	Relative size coeff.	Occur-rence rate (%)	Weighted % local population Mean	Max	Weighted % all samples
Calanus marshallae III-VI	8.80	1.40	100	23.4	79	24.1
Calanus marshallae I-II	2.00	0.31	91	1.6	10	1.2
Pseudocalanus sp. IV-VI	60.6	0.20	100	19.0	78	23.7
Pseudocalanus sp. I-III	14.2	0.08	96	2.2	15	2.2
Acartia longiremis	28.1	0.18	100	11.6	65	9.9
Oithona similis	12.7	0.14	98	3.5	18	3.5
Sagitta elegans	0.80	7.00	97	13.6	57	10.9
Metridia pacifica	2.87	0.55	93	2.7	26	3.1
Eucalanus bungii	0.18	4.00	88	1.4	16	1.4
Limacina	3.42	0.40	82	1.6	63	2.7
Euphausiid larvae	0.35	2.75	82	2.6	35	1.9
Amphipods	0.10	6.00	81	1.4	14	1.1
Medusae	0.18	5.00	78	1.8	52	1.7
Oithona spinirostris	1.20	0.20	78	0.5	12	0.5
Scolecithricella minor	0.48	0.30	74	0.3	2	0.3
Centropages abdominalis	0.63	0.50	70	1.0	10	0.6
Neocalanus cristatus	0.14	5.50	60	1.3	31	1.5
Eukrohnia hamata	0.17	6.00	56	2.0	20	2.0
Larvaceans	2.85	0.50	51	2.7	26	2.8
Paracalanus parvus	2.82	0.10	49	0.8	13	0.6
Neocalanus plumchrus	0.08	4.00	47	0.6	22	0.6
Euchaeta japonica	0.10	4.00	45	0.7	10	0.8
Euphausia pacifica	0.02	10.00	41	0.4	6	0.5
Cyclopoids (*Oncaea* + *Corycaeus* spp.)	0.17	0.10	37	0.0	1	0.0
Racovitzanus antarcticus	0.05	0.54	36	0.1	1	0.1
Clausocalanus spp.	0.39	0.31	26	0.3	7	0.2
Conchoecia sp.	0.12	0.50	26	0.1	2	0.1
Microcalanus sp.	0.29	0.08	26	0.0	<1	0.1
Thysanoessa spinifera	0.01	10.00	25	0.1	3	0.2
Mesocalanus tenuicornis	0.25	0.55	24	0.1	6	0.3
Gaidius + *Gaetanus* spp.	0.03	1.00	22	0.1	2	0.1
Tomopteris sp.	0.03	7.00	20	0.3	20	0.4
Pleurobrachia	0.06	5.50	17	1.0	13	0.7
Cladocerans (*Evadne* + *Podon* spp.)	1.58	0.10	17	0.6	12	0.3
Candacia spp.	0.02	1.40	16	0.0	2	0.0
Acartia clausi	0.30	0.18	15	0.2	<1	0.1
Tortanus discaudatus	0.02	0.40	14	0.0	<1	0.0
Lucicutia sp.	0.03	0.50	6	0.1	2	0.0

Table 2. Mean abundance (# per 0.1 ml), size-scaling coefficients, and community dominance indices (see Table 1) for the phytoplankton and microzooplankton taxa included in the analysis.

| Taxon	Mean abundance (0.1 ml)$^{-1}$	Relative size coeff.	Occurrence rate (%)	Weighted % local population Mean	Max	Weighted % all samples
Cryptomonads	32.5	0.2	100	8.1	33	3.0
Nannoflagellates	101.3	0.1	100	14.7	60	4.7
Unid. dinoflagellates	11.4	0.5	98	10.6	41	2.7
Zoociliates	3.0	2.0	94	9.2	43	2.8
Nitzschia + Cylindrotheca	16.5	2.0	92	17.3	92	15.4
Thalassiosira spp.	2.3	5.0	73	9.9	53	5.3
Chaetoceros spp.	7.7	2.0	61	8.3	58	7.2
Plectodinium sp.	0.3	5.0	52	2.1	23	0.7
Coccolithophorids	1.6	0.2	48	0.7	7	0.2
Rhizosolenia spp.	19.2	5.0	45	11.2	90	45.0
Skeletonema costatum	2.8	2.0	39	3.5	35	2.6
Peridinium sp.	0.3	5.0	32	0.6	9	0.8
Leptocylindricus danicus	3.3	5.0	32	4.2	85	7.7
Distephanus speculum	0.1	2.0	23	0.2	5	0.0
Thalassionema nitzschiodes	0.1	2.0	21	0.2	<1	0.1
Schroderella delicatula	0.3	5.0	15	0.5	8	0.7
Dactyliosolens sp.	0.4	5.0	15	0.3	4	1.0
Eutreptiella sp.	0.1	2.0	15	0.1	3	0.1
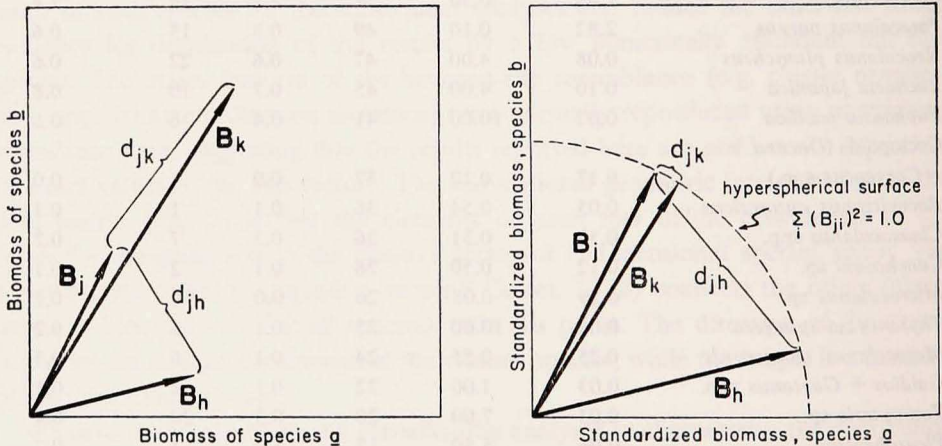
Figure 2. Geometric interpretation of "euclidean distance" dissimilarity metric for a two species (= two dimensional) community. Graph at left shows distance measure calculated from raw (non-normalized) data. Graph at right shows "chord length" distance resulting from normalization of site vectors B to constant length. The chord length measure ignores between-site differences in total abundance and emphasizes differences in species dominance hierarchy.

stable species occurrence and dominance hierarchy. Most methods assume approximate radial symmetry of the probability density within each cluster swarm, but permit substantial departures from linearity and normality in the overall (between cluster) pattern. Ordination methods allow a continuum of variability (samples do not need to form natural groups) and seek to identify a reduced number of axes onto which most of the inter-correlated species variability can be projected. However, they make the occasionally restrictive assumption that the pattern of species covariation is linear. More extensive discussions of multivariate methods are available in a number of reference books (e.g., Orloci, 1978; Pielou, 1969; Sneath and Sokal, 1973). A wide range of individual methods are available within each of the above categories. We selected among the less exotic for our use; however our choice was based on familiarity and apparent adequacy rather than any assessment of optimality.

We classified the sample sites by two different SAHN (sequential, agglomerative, hierarchic, nonoverlapping; Sneath and Sokal, 1973) clustering algorithms. Both use estimates of between-sample relatedness which are derived from a "squared euclidean distance" metric

$$d^2_{jk} = \sum (B_{ji} - B_{ki})^2$$

which is the summation over species of the squared differences in concentration between sampling sites j and k. If biomass estimates are used directly, this metric is sensitive both to between-station differences in total biomass (length of the sampling site vector) and to changes in composition (direction of the vector). Strong biomass patchiness (common in plankton ecosystems) will therefore obscure the pattern of changing species dominance. To isolate compositional patchiness from biomass patchiness we have selected an additional normalization procedure ("chord length" metric, Orloci, 1967, 1978) by which the site vectors are adjusted to unit length before the euclidean distance is calculated. This normalization projects the site vectors onto a hypersphere of unit radius (see Fig. 2); sampling sites differing in total amount but having the same relative composition will be interpreted as identical. An artificial feature of this transformation is that between-species correlations which are nonsignificant or weakly positive in the raw data can appear as negative correlations in the normalized data if the relative intensity of patchiness varies strongly between species. We therefore also routinely computed species correlation matrices from the nonstandardized data (see Orloci, 1978 for a good discussion of the transformations and distortions implicit in various common multivariate analysis protocols).

Results of the classification analyses are presented as dendrograms showing cluster membership at varying levels of within-cluster resemblance defined by the specific clustering method. Of the two algorithms selected, the "minimum variance" = "sums-of-squares" method (Orloci, 1967, 1978) forms groups in the sequence which

minimizes (at each step) the incremental change in the sum of squared distances of cluster members from their respective cluster centroids. The method is mildly "space dilating" (*sensu* Lance and Williams, 1967). It readily identifies "dense" or "tight" clusters but will tend to reject accretion to these tight clusters of "outlier" sites (sometimes resulting in formation of a group distinctive primarily for the large inter- and intra-cluster dissimilarity of its members).

"Centroid average linkage clustering" (Lance and Williams, 1967; Sneath and Sokal, 1973; Orloci, 1978) can operate on any similarity measure. We used two. The first is a simple transform of the chord length dissimilarity metric d^2_{jk}.

$$S_{jk} = \left(1 - \frac{d^2_{jk}}{2}\right)^{1/2}.$$

This method merges groups having the maximum similarity between their centroids, and is "space indifferent" (Lance and Williams, 1967).

As a check on the stability of classifications obtained from the chord length metric, we also applied the average-linkage algorithm using the "coefficient of proportional similarity" (Fasham and Angel, 1975) as our measure of relatedness. This is defined by

$$S'_{jk} = \frac{\Sigma x_{ji}\, x_{ki}}{(\Sigma x_{ji}^2\, \Sigma x_{ki}^2)^{1/2}}.$$

where x_{ji} is a log transform of the biomass estimate B_{ji} and the summations are over species. Two major differences from the chord length measure should be noted. First, sites with large biomass are weighted more heavily than sites with low biomass. Second, because of the log transformation, sites with identical composition ratios but different total amounts record as less than 100% similar.

Ordination of the samples was by principal components analysis. This method attempts to project the bulk of the total species variance (subject to strong covariance between species) onto a reduced number of statistically independent component axes. We performed a conventional R-mode analysis (Pielou, 1969; Orloci, 1978) on a species covariance matrix calculated from the normalized biomass data. Because scattergrams plotted against the first two-three component axes indicated strong clustering of the samples ("disjoint" structure, Orloci, 1978), we based most of our interpretation on the results of our classification analyses.

We estimated local diversity of the plankton community using the information index

$$H' = -\Sigma\, p_i \log_e p_i$$

where p_i are the estimated fractions of the local biomass contributed by each taxon and the summation is over the truncated list of species used in the cluster and ordination analyses. The "species evenness" component of diversity was calculated using

$$J' = H' (\log_e T)^{-1}$$

where T is the number of taxa from the truncated list found in the sample. Both estimates are biased low due to the truncation of the species list imposed by limited sample size (Pielou, 1969) and by our data reduction protocol. However, we felt that the less biased Brillouin index (Pielou, 1969) which is calculated from integer count data would be excessively weighted by the numerical dominance of the small taxa.

Congruence of the within-cruise dissimilarity patterns of zooplankton and microplankton (do stations with similar phytoplankton assemblages also have similar zooplankton assemblages?) were tested for statistical significance using the Mantel test (Sokal, 1979). This method computes the summed products of corresponding elements of two $N \times N$ resemblance matrices (euclidean distances for our application) and compares this observed cross-product with its expected value and variance under random permutation of the site labelling for one of the matrices. Results are expressed as standard deviates from the expected value, and are tested using the Student's "t" distribution.

4. Results and discussion

a. Intensity of community heterogeneity. The between site variability of the zooplankton community consisted primarily of dominance shifts within a regionally cosmopolitan species list. Table 1 gives frequency of occurrence (% of sampling stations at which the species was found) and two indices of community dominance.

Two features should be noted. One is the general correlation between occurrence rate and position in the biomass dominance hierarchy (Spearman rank correlations with "local" and "all sample" dominance are 0.86 and 0.84 respectively). Species with occurrence rates below 50% were rare where they occurred (species-averaged maximum percent local dominance 6.5%; mean percent dominance 0.3%); and occurrence rates for these species may have been underestimated due to small sample size. The bulk of the zooplankton community is made up of taxa present at all or nearly all of the sampling sites (e.g., species present in >75% of the samples comprise >85% of the total population analyzed). The only significant exceptions to the above pattern are *Oikopleura* and *Pleurobrachia* (which occurred sporadically but which sometimes formed a major fraction of the population at the sites where they were present), a few widely distributed copepods with uniformly low abundance (*Scolecithricella, Microcalanus, Corycaeus* and *Oncaea*), and species whose vertical migration pattern restricted their occurrence to deep water (*Neocalanus* spp. and adult euphausiids).

The second point is that, with the exceptions of the lumped amphipod category and a possible *Pseudocalanus* species complex, the zooplankton are identified with
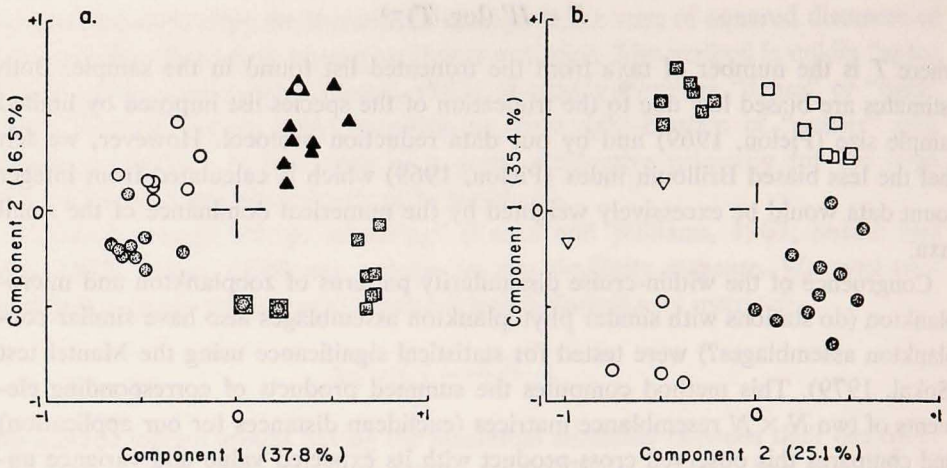
Figure 3. Principal component ordination of phytoplankton (a) and zooplankton (b) samples, August 1979. Values in parentheses indicate the percentage of total variance in the normalized data which projects onto (is accounted for by) each component axis. Symbols mark individual samples; their coding corresponds to cluster membership from the classification analyses. Double symbols in (a) show sites where classification by sums-of-squares (inner) and ALS average linkage (outer) algorithms gave differing results. See text and Figure 12 for species dominance patterns corresponding to the various symbols.

sufficient taxonomic resolution to prevent significant underestimation of the dissimilarity metric.

In contrast, the phytoplankton/microzooplankton data show greater between-site variability at the presence/absence level, despite their coarser taxonomic classification (Table 2). Taxa present at 75% of the sites accounted for less than 30% of the total population analyzed. In addition, the apparently most cosmopolitan taxa (cryptomonads, microflagellates, small dinoflagellates, ciliates, *Nitzschia* spp., *Thalassiosira* spp., and *Chaetoceros* spp.) were those that were most severely lumped at the identification stage.

The above patterns are reflected in differing structures of the dissimilarity matrices for the two data types. Mean (± standard error) between-site dissimilarity ($\overline{d^2}$) for the photoplankton/microzooplankton is 1.19 ± .08, corresponding to a mean angular separation of 62.4° out of a possible 90°. For the net zooplankton $\overline{d^2} = 0.78$ ± .04 (corresponding to a mean angular separation of 49.6°). These results match those previously reported for much larger separation length scales in that the zooplankton show more spatial uniformity in both species presence and dominance hierarchy than do the phytoplankton.

b. Community pattern in species space. The standardized data from both microplankton and net zooplankton were typically distributed in species space as several
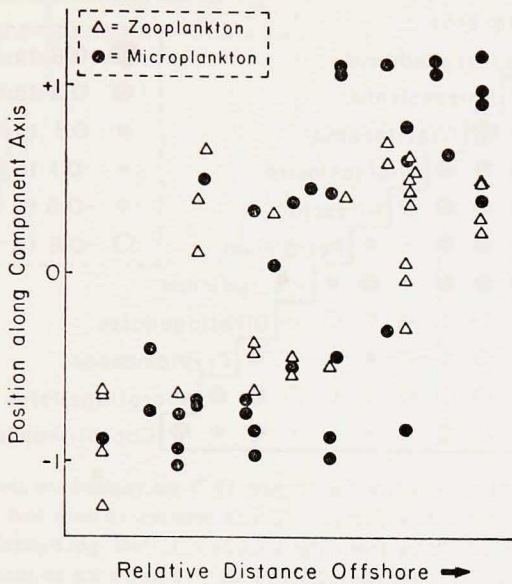
Figure 4. Comparison of "onshore-offshore" principal component score (component 1 for phytoplankton, component 2 for zooplankton) with relative position in cross-shelf station line (fraction of distance from innermost to outermost station in the line). Correlation is approximately 0.7 for both phytoplankton and zooplankton samples; some of the scatter is attributable to the steplike transitions in the compositional pattern.

disjoint swarms rather than as a single continuous cloud (Fig. 3). This result suggests at least temporarily distinct species associations rather than either purely random variation or a smooth gradient of community composition, and encouraged our primary reliance on classification rather than ordination of the data. However, most features of the data structure were detectable by both methods.

Scattergrams of a typical set of principal component station scores are shown in Figure 3a-b (note the relatively disjoint clusters). One of the dominant (by projected fraction of total variance) ordination axes could be interpreted as an onshore-off-shore gradient (Fig. 4), and typically had one or more swarms of points at either end. We have plotted this onshore-offshore component as the horizontal axes in Figure 3 (the left end of each figure contains the more seaward samples). For the two phytoplankton data sets (July and August 1979), the cross-shelf gradient was consistently defined by a shift in community composition from predominately diatoms (on the shelf) to predominantly flagellates (offshore). The nature and extent of this dominance shift differed slightly between the two sampling periods. Samples from the July cruise had higher absolute abundances of both flagellates and diatoms shoreward of the shelf break and inter-species correlation coefficients were positive or indistinguishable from zero for nearly all taxa. The dominance shift was due to
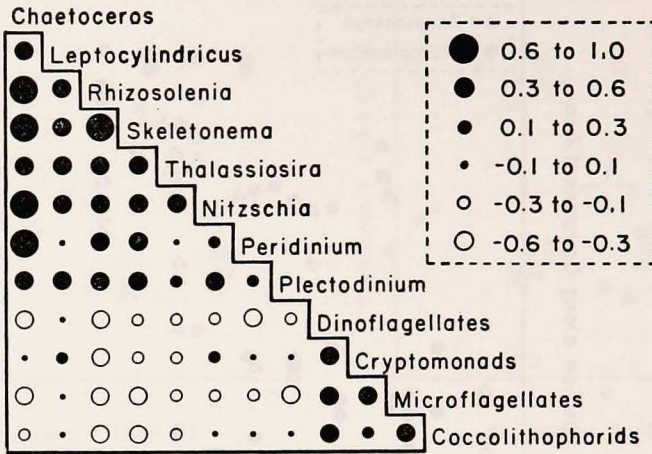
Figure 5. Species correlation matrix for August 1979 microplankton samples, calculated prior to biomass normalization. Negative correlations between diatom and flagellate taxa suggest partial exclusion of flagellates from the continental shelf phytoplankton, unlike our July 1979 data which showed greater abundance of all taxa inside the continental shelf break.

the dramatic gradient in diatom abundance and was largely imposed by the vector standardization procedure. In contrast, the August data suggest a genuine displacement of the flagellates from the shelf zone, as indicated by the frequent and relatively strong negative correlations between diatom and flagellate taxa (Fig. 5).

An additional feature of the phytoplankton data was the tendency of the diatom-dominated samples to have low within-sample (and large between-sample) diversity. For example, the samples forming the cluster at the lower right of Figure 3a consisted of an intense and nearly monospecific bloom of *Nitzschia* sp. (average diversity $\bar{H}' = 1.15$, average evenness $\bar{J}' = 0.48$). A similar but even more monospecific outer-shelf bloom of *Rhizosolenia setigera* occurred during the July cruise. The stations forming the group at the upper right of Figure 3a were more diverse in their internal composition (average diversity $\bar{H}' = 1.48$, average evenness $\bar{J}' = 0.64$) but were again heavily dominated by blooms of *Chaetoceros* and *Leptocylindricus*. Despite constraint by low taxonomic resolution to a limited number of identified taxa, the flagellate dominated samples had the highest overall diversity $\bar{H}' = 1.58$) and showed much greater evenness ($\bar{J}' = 0.84$).

Although the zooplankton data also had a disjoint structure and also showed a cross-shelf compositional gradient (Fig. 3b), their within and between-cluster taxonomic pattern could not be as readily generalized. There was large between-cruise variation in the geographic location of the individual species assemblages and in the details of their species composition, and relatively little consistency in the geographic pattern of zooplankton diversity (however, the most oceanic samples again appeared to be most diverse).
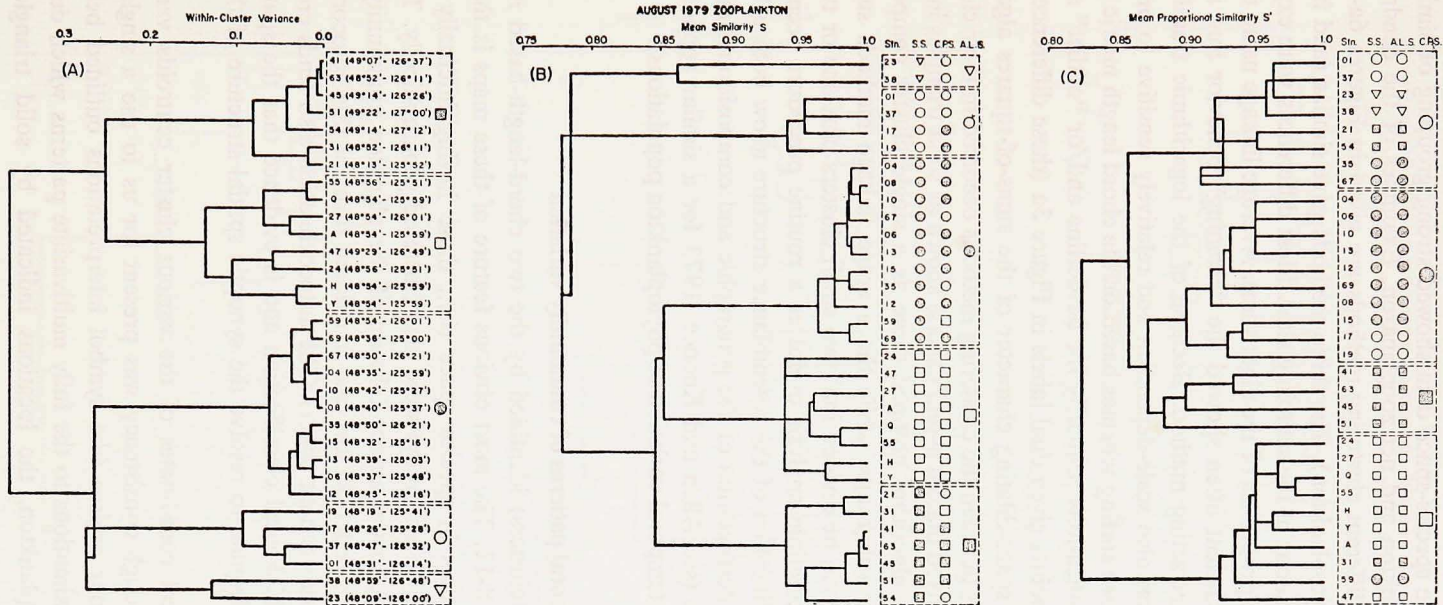
Figure 6. Classification of the August 1979 zooplankton samples by three clustering methods. Decreasing within-cluster resemblance is shown by increasing cumulative branch length from the dendrogram tips. Different clustering methods define resemblance and compute cluster membership by different rules (see text). (a) is sums-of-squares (S.S.) algorithm; clustering level is mean squared distance of members from the cluster centroid. Average-linkage methods (b-c) measure the average similarity between cluster members. (b) (A.L.S.) uses the chord length similarity measure while (c) (C.P.S.) uses the coefficient of proportional similarity. Symbols at right of dendrograms indicate our interpretation of dominant cluster groups; see text and Figure 12 for biological composition.

Cluster analysis of the species-space data showed strong grouping of similar stations for both microplankton and net zooplankton. Examples of the dendrograms produced by the three different clustering methods are given in Figures 6a-c (zooplankton) and 7a-c (phytoplankton). The three methods gave similar (and in many cases identical) classifications of the sampling sites. Most differences were explicable in terms of the expected properties of the algorithms. Average linkage using the proportional similarity coefficient often showed the "chaining" behavior that is characteristic of a space-contracting method. Because of the logarithmic transform of the data, this method was also scale-dependent and relatively sensitive to presence-absence variation. The two sorting schemes based on the chord length metric showed internally differing classifications primarily for borderline and/or "outlier" samples such as the three data points given dual labels in Figure 3a (these differences probably resulted from the space-dilating character of the sums-of-squares algorithm). The strongest differences between the clustering methods occurred in their classification of the inner-shelf mixed diatom assemblage(s) shown as solid triangles in Figure 7. The sums-of-squares algorithm grouped these as a single cluster composed of two relatively dissimilar subgroups, while the average linkage methods suggested that this assemblage should be divided into two small clusters plus one or two outliers. We consider the multiple analysis useful as a routine procedure because the differing rules for simplification of the resemblance structure allow both a broader and a more thorough interpretation of the geographic and compositional ranges of the species assemblages (see Allen and Koonce, 1973 for a similar application of multiple analyses to the temporal variation of phytoplankton populations).

5. Geographic and temporal patterns of community variation

The sample groups (clusters) identified by the two chord-length-based methods are mapped in Figures 8-11. The most obvious feature of these maps is that samples which formed clusters in species space (i.e., those having internally similar species lists and dominance hierarchy) were also clustered geographically. This observation suggests strong spatial autocorrelation of the plankton community structure over length scales of order 50 km (the functional form of this autocorrelation will be considered in a subsequent paper). The autocorrelation also lends credibility to the "reality" of the biological classification and is evidence that the spatial grid of our sampling was adequate to resolve the synoptic spatial structure of the community composition.

Although the biological coordinates of the various cluster centroids varied between time periods, enough consistency was present for us to use a single set of symbols covering all four cruises (the symbol interpretations outlined below are highly simplified approximations to the fully multivariate patterns which define the clusters). For the zooplankton, the locations indicated by solid triangles were
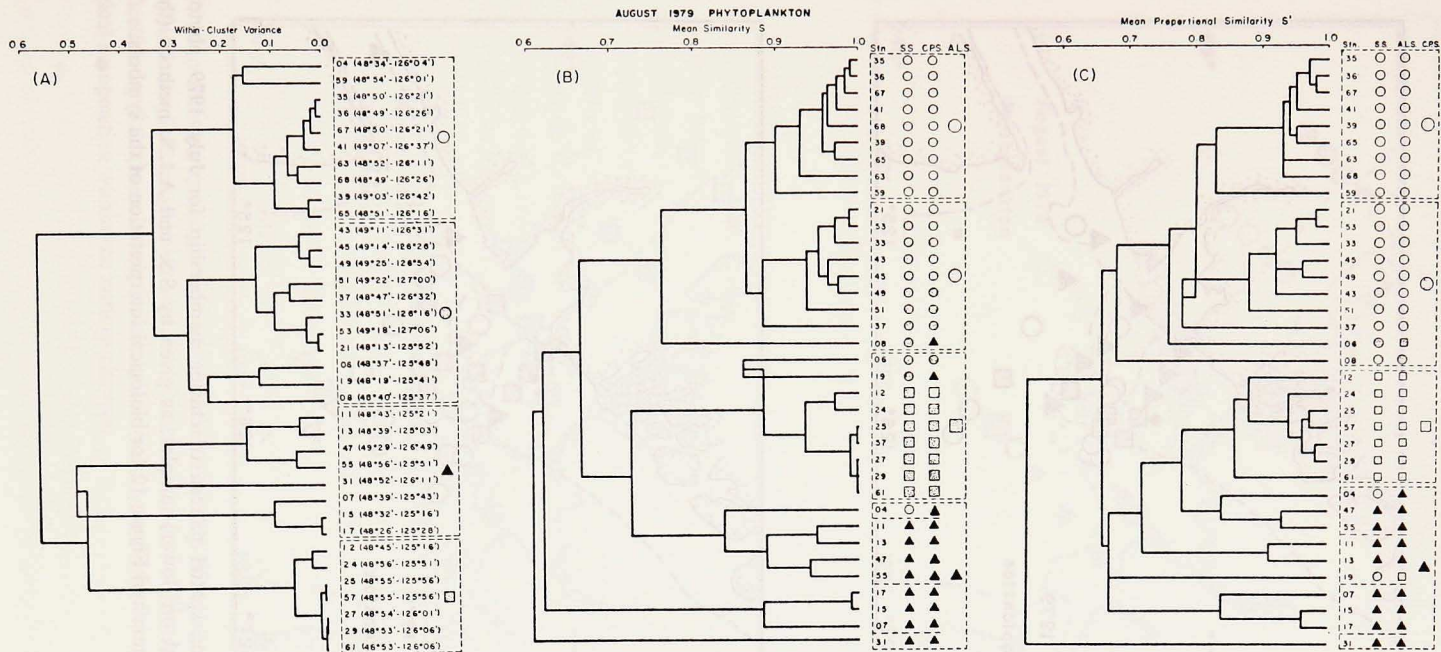
Figure 7. Classification of August 1979 microplankton samples by three clustering methods. (a) shows results of sums-of-squares algorithm, (b) is average linkage of the chord-length similarity index, and (c) is average linkage of the coefficient of proportional similarity (see text for definitions). Symbols at right of dendrograms indicate our interpretation of dominant cluster groups and extent of agreement between methods. See text for compositional patterns corresponding to the symbols.
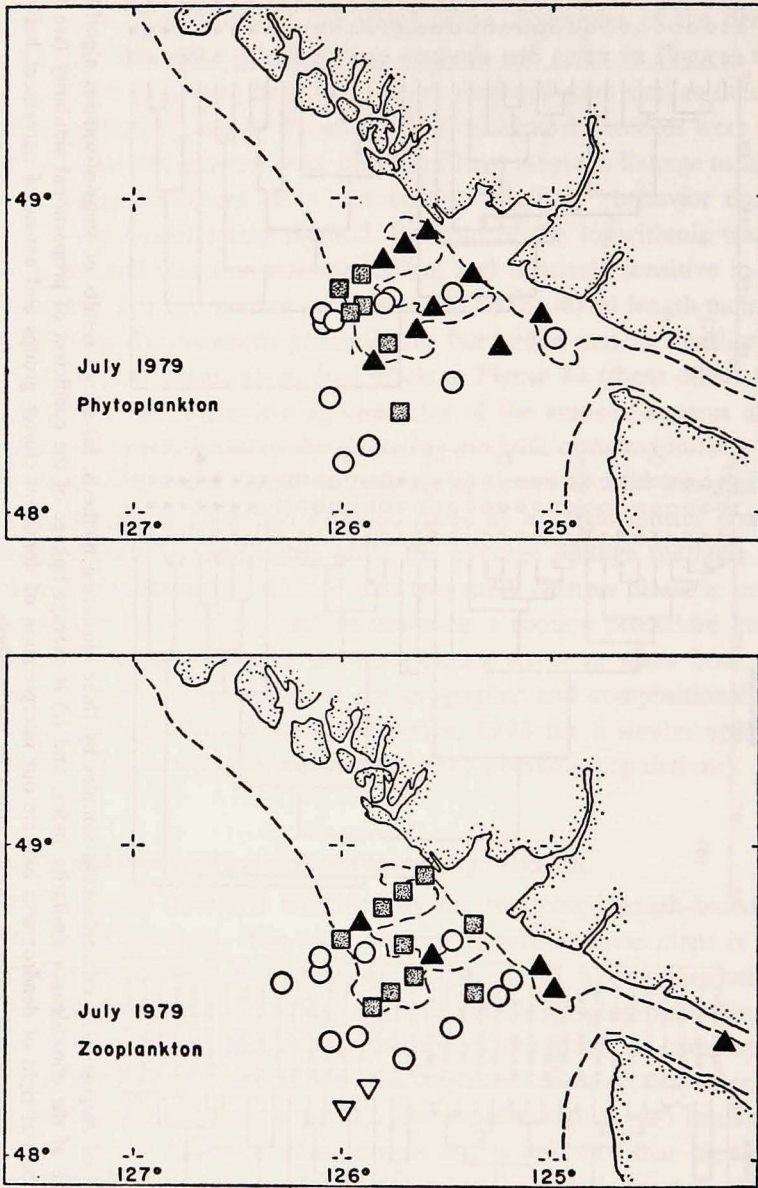
Figure 8. Map showing spatial pattern of cluster membership for July 1979 phytoplankton (upper) and zooplankton (lower) samples, as given by S.S. and A.L.S. methods (the results were identical). See text and Figure 12 for biological interpretation of the symbols.
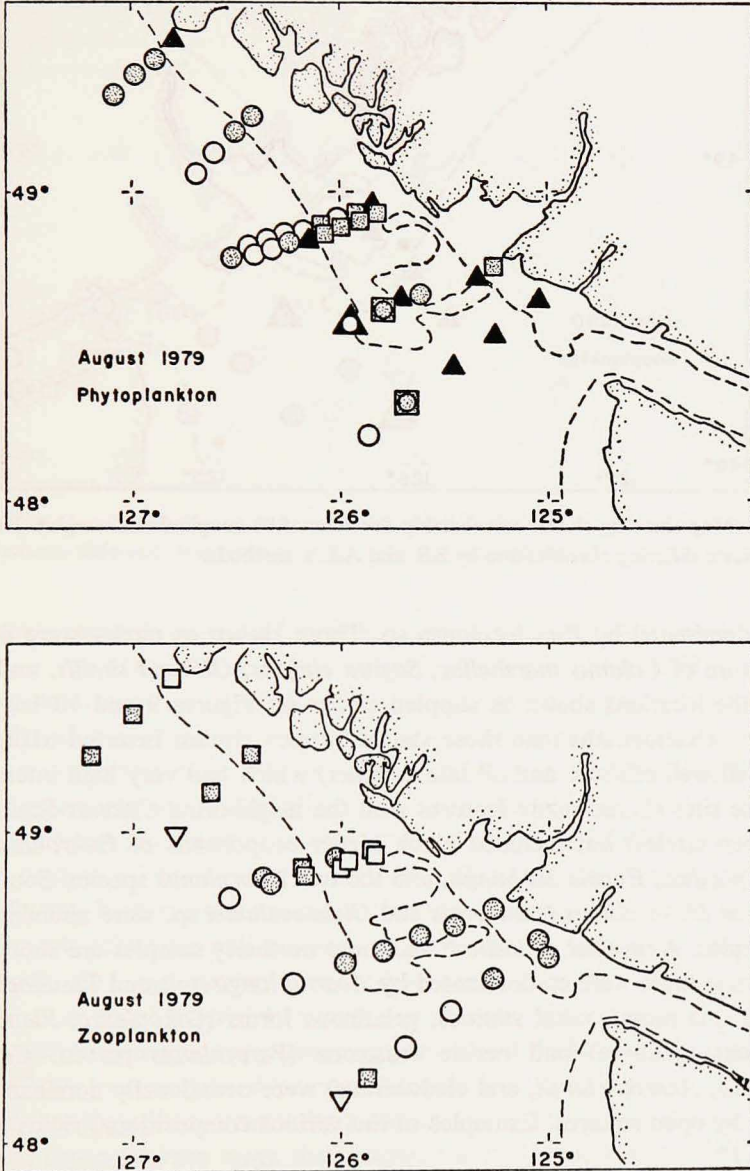
Figure 9. Map showing spatial pattern of cluster membership for August 1979 phytoplankton (upper) and zooplankton (lower) samples. Double symbols in Figures 9-11 show differing classification by S.S. (inner symbol) and A.L.S. (outer) methods. See text and Figure 12 for biological composition within the various clusters.
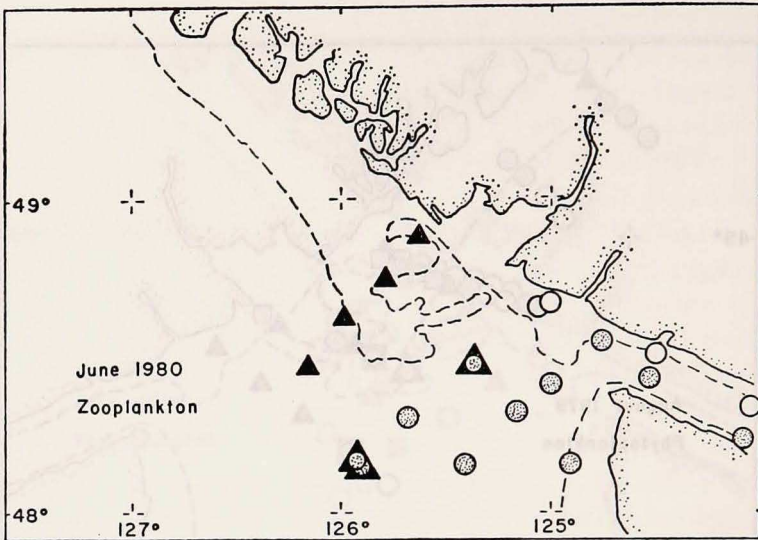
Figure 10. Map showing cluster membership for June 1980 zooplankton samples. Double symbols indicate differing classification by S.S. and A.L.S. methods.

strongly dominated by *Pseudocalanus* sp. Those shown as circles were dominated by a mixture of *Calanus marshallae, Sagitta elegans, Oithona similis,* and *Pseudocalanus*; the locations shown as stippled circles on Figures 9 and 10 had substantially fewer chaetognaths than those shown in open circles. Inverted triangles mark stations (all well offshore and all late summer) which had very high internal diversity. These sites shared many features with the neighboring *Calanus-Sagitta* assemblage (open circles) but included much higher proportions of *Eukrohnia hamata, Metridia pacifica, Eucalanus bungii,* and the two *Neocalanus* species. Southern species such as *Mesocalanus tenuicornis* and *Clausocalanus* sp. were abundant only in these samples. A number of inshore and more northerly samples are shown as stippled squares; these were co-dominated by *Acartia longiremis* and *Pseudocalanus* sp. Finally, at the most coastal stations, gelatinous forms (*Oikopleura, Pleurobrachia,* and various medusae) and neritic crustacea (*Paracalanus parvus, Centropages abdominalis, Acartia clausii,* and cladocerans) were occasionally dominant, and are indicated by open squares. Examples of the various compositional ratios are shown in Figure 12.

Our labelling of the two phytoplankton data sets (Figs. 8 and 9) is simpler but less precise. We distinguish pure flagellate assemblages (open circles), flagellate-dominated sites with minor amounts of diatoms (stippled circles), an inshore mixed diatom assemblage (triangles) and a nearly monospecific outer-shelf diatom flora (stippled squares) which was dominated by *Rhizosolenia setigera* in July 1979 and by *Nitzschia* sp. in August. Most of the observed large variability in photosynthetic
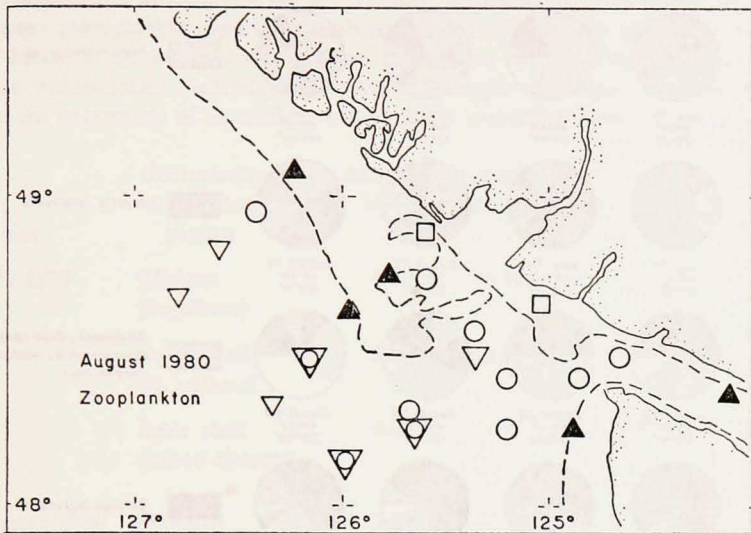
Figure 11. Map showing cluster membership for August 1980 zooplankton samples. Double symbols indicate differing classification by S.S. and A.L.S. methods.

carbon fixation rate was correlated with variation in phytoplankton biomass (range 1-65 mg C $m^{-3}h^{-1}$ for the July and August 1979 samples; $r^2 \sim 0.88$ for each of the two linear regressions of photosynthetic rate on chlorophyll concentration). Neither cruise showed significant dependence of assimilation number (mg C (mg chl a)$^{-1}h^{-1}$; equivalent to individual slope estimates for the photosynthesis vs. chlorophyll regression) on chlorophyll or nitrate concentration.

However, it is interesting to note that a portion of the variability in assimilation number is attributable to between-community differences in specific growth rate (Table 3). During both cruises, the highest average assimilation number was found in the offshore flagellate assemblage, and the lowest in the dense outer shelf diatom bloom. Despite the large overlap in individual assimilation number estimates, the null hypothesis of equal population means was rejected at the ten percent level for eleven out of fifteen pairwise comparisons (paired t-test). Differences were significant at the one percent level or better for seven of these.

Temporal stability of the community pattern was low. It is clear from both zooplankton and phytoplankton maps that, except for the general diatom-to-flagellate sequence discussed previously, no single species or species assemblage was consistently dominant within a given geographic subregion. The prevailing picture is of compositional patches which are coherent over time scales of 1-10 days (the duration of a single sampling survey) and over space scales of about 50 km but which exhibit large compositional shifts when measured over longer time intervals. This result contrasts strongly with observations from the Oregon coast 400 km to the
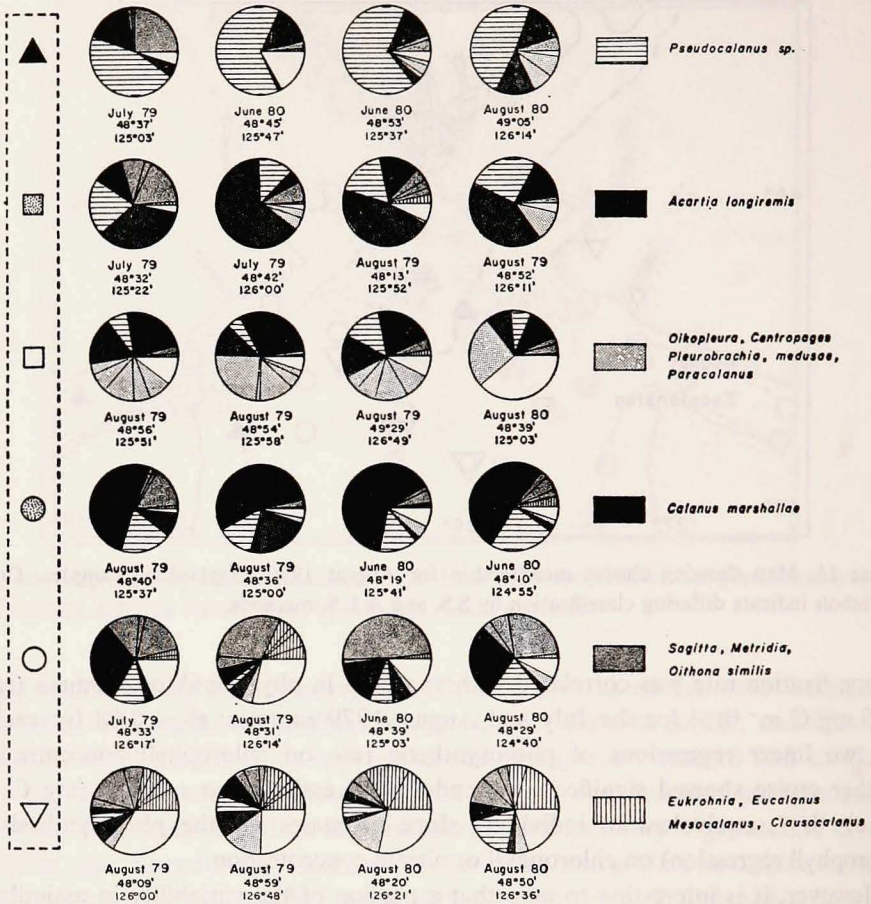
Figure 12. Piegraphs showing representative zooplankton compositional pattern (fraction of local estimated biomass) for the cluster types identified by the classification analyses. See text for further characterization of the species pattern.

south which suggested a highly stable cross-shelf gradient of dominance structure for essentially the same species found in our region (Peterson *et al.*, 1979).

Pseudocalanus sp. provides a good example of the temporal variability in our data. In July 1979 *Pseudocalanus* was a major member of the zooplankton assemblage at all sites (~20% of the total zooplankton sampled) and strongly dominated (45-57%) the samples collected in and near the mouth of Juan de Fuca Strait (Fig. 8). One month later (August 1979, Fig. 9), its abundance had sharply decreased throughout the southeastern half of the study area (averaging 7.5% of the local total) and, although present in reasonably high concentrations, it was subdominant to *Acartia longiremis* at the more northerly locations. By June 1980 (Fig. 10), *Pseudocalanus* had regained its status as a major component of the zooplankton

Table 3. Variability in productivity per unit biomass (estimated as assimilation number) within and between phytoplankton species assemblages as identified by the sums-of-squares classification. "Mean" is the within-cluster average assimilation number, "standard deviation" measures the within-cluster variability of individual sample estimates, and "standard error" estimates the uncertainty of an assumed within-cluster population mean.

| Cruise | Community dominance pattern | Assimilation number (mg C (mg chl a)$^{-1}$hr^{-1}) | | | |
		Mean X	Std. dev. s_x	Std. error $s_{\bar{x}}$	d.f.
July 1979	Offshore (flagellates)	4.78	1.08	0.27	15
	Outer shelf (*R. setigera*)	3.36	0.87	0.25	11
	Inner shelf (mixed diatoms)	4.58	0.93	0.19	23
August 1979	Offshore (flagellates)	5.68	1.24	0.26	21
	Outer shelf (*Nitzschia* sp.)	4.03	1.00	0.33	8
	Inner shelf (mixed diatoms)	4.79	0.80	0.23	10

community throughout the study area (38%); however its highest abundance and percent local dominance occurred on La Perouse Bank and along the shelf break (24-79%). August 1980 samples (Fig. 11) again showed large amounts of *Pseudocalanus* along the outer margin of La Perouse Bank (as in June 1980) plus a separate center of dominance associated with Juan de Fuca Strait (as in July 1979). The distribution patterns for the other dominant species (*Calanus, Acartia, Sagitta*) showed a similar degree of drift between sampling periods.

Despite the between-cruise variability in regional composition (the "colors" of the community map), there is considerable consistency in the number and location of the geographic subregions that were delineated. For example, we consistently found a strong alongshore compositional gradient centered near the southeast margin of the shelf banks (marked by a dominance shift from *Acartia* to *Calanus* in July and August 1979, and from *Pseudocalanus* to *Calanus* in June and August 1980). Both phytoplankton and zooplankton also showed cross-shelf compositional gradients (roughly perpendicular to the above) which ran from northwest to southeast along the shelf break. The phytoplankton data (e.g., July 1979) are particularly suggestive that patches overlying this region of sloping bottom topography can be quite distinct from both their inshore and their offshore neighbors. Influence of the outflow from Juan de Fuca Strait is suggested by the July 1979 and June 1980

zooplankton data. And, finally, most of the community maps (particularly July 1979 and August 1980) show a curling of the offshore communities around the southern edge of La Perouse Bank into the deeper shelf water and basins west of the mouth of Juan de Fuca Strait and immediately south and west of Barkley Sound. All of these distributions are consistent with the summer pattern of average circulation described by Freeland (pers. comm.) which we summarized in Figure 1—namely a strong northwest to southeast flow following the outer margin of the shelf, an estuarine circulation in and immediately northwest of Juan de Fuca Strait, and a cyclonic gyre centered over the shelf at the north end of the Juan de Fuca submarine canyon system.

We interpret the temporal variability of the community pattern and its approximate spatial correlation with the flow pattern as strong evidence for advective control of local species compositions—relative dominance at a given site and time period is probably determined largely by the recent success of the various species in the three "upstream" regions (northern B.C. shelf, Georgia Strait/Juan de Fuca system, and deep California Undercurrent). Current speeds are adequate to cause large advective displacements of plankton patches; the outer shelf alongshore current averages 10-20 km day^{-1} over the upper 75 (Freeland, pers. comm.), and the estuarine discharge from Juan de Fuca Strait is of similar magnitude (Huggett *et al.*, 1976; Cannon, 1978). Deeper circulation is probably dominated by intrusive flow of California Undercurrent water up the Juan de Fuca submarine canyon system (Freeland and Denman, 1982); this transport appears to peak in April-May at a volume flux of order 10^9 m^3 day^{-1} (sufficient to replace the bottom 50-100 m layer south of the banks within a time interval of 1 month).

Alongshore flows of comparable or greater magnitude have been measured in other eastern boundary current regions such as Oregon, Peru and Northwestern Africa (Smith, 1981). Advective effects can be responsible for large alongshore biomass flux in these regions (Blackburn, 1979). However, alongshore continuity of the community dominance pattern in these regions is either observed (Peterson *et al.*, 1979) or assumed in the sampling design (Peterson and Miller, 1977; Blackburn, 1979; Smith *et al.*, 1981). Short time scale (1-15 days) variations in zooplankton composition have been interpreted (e.g. Smith *et al.*, 1981; Peterson *et al.*, 1979) as wobble in the cross-shelf position of faunal boundaries due to time variation in the onshore-offshore component of flow (in turn driven by the event cycle of local wind forcing).

The between-cruise variability we find in zooplankton community pattern is at best only partially attributable to time variable wind forcing. Seasonally-averaged Bakun upwelling indices at 48N 125W imply weak to moderate cross-shelf Ekman transport in both 1979 and 1980 (23.3 and 33.6 respectively; Freeland and Denman, 1982 using daily data provided by A. Bakun). Short term averages (mean ± standard deviation for ~20 day periods prior to and including the cruises) were −2 ±

49 for 28 June-12 July 1979, 9 ± 14 for 15-30 August 1979, 57 ± 62 for 28 May-8 June 1980, and 58 ± 31 for 18 July-8 August 1980. Note that July and August 1979 had similar wind conditions, as did June and August 1980. However, relatively marked differences are apparent in the corresponding zooplankton distribution (Fig. 8 vs. Fig. 9 and Fig. 10 vs. Fig. 11). In addition, a significant fraction of the between-cruise variability occurred as compositional shifts within the alongshore pattern, rather than as regionally coherent shoreward or seaward displacement of the cross-shelf gradients.

The main features of the interannual variability were greater average abundances of *Pseudocalanus, Calanus marshallae* and *Eukrohnia hamata* in 1980, and greater abundance of *Acartia longiremis* in 1979 (the year with weaker upwelling-favorable winds). These patterns are inconsistent with the Oregon coast (44°40′N) observations of Peterson and Miller (1977) which primarily identified a reduced dominance by their "neritic" species (*Pseudocalanus, Centropages, Acartia clausi, Paracalanus* and cladocerans) in weak upwelling years. Much of the B.C. variability occurred in those species (*Calanus, A. longiremis*) that in the Oregon system were weakly coupled to the average upwelling intensity, and as many of the neritic species contradicted the Oregon pattern (*Centropages, A. clausi,* cladocerans) as supported it (*Pseudocalanus* and possibly *Paracalanus*).

Additional evidence for advective control of local compositional structure can be found in a within and between-cruise comparison of phytoplankton and zooplankton communities. Absence of systematic temporal covariance of pattern would suggest that there is little structuring of one trophic level by the other. Note (Figs. 8-9) that in July 1979, diatoms co-occurred with *Pseudocalanus* and *Acartia longiremis* and flagellates with *Calanus, Metridia,* etc. while in August this spatial association pattern was almost perfectly reversed.

In the absence of biologically-forced congruence of the phytoplankton and zooplankton community patterns, we interpret synoptic spatial covariance as evidence for probable shared physical control, (advection and diffusion by the same system of currents and eddies). We consider the phytoplankton and zooplankton community patterns to be congruent if within a single sampling period their station-to-station dissimilarity geometries (distances in independently-defined species space) are similar; i.e., if on average sites with similar phytoplankton composition have similar zooplankton and those with dissimilar phytoplankton have dissimilar zooplankton. Inspection of the cluster maps suggests that this congruence is present; however, its significance can be tested more rigorously by means of the Mantel test (Sokal, 1979). We found that the phytoplankton and zooplankton patterns were similar for both 1979 data sets (July $p \sim 0.01$, August $p \sim 0.10$). A portion of this shared pattern is attributable to the spatial autocorrelation (similarity of neighboring sites) in both patterns. However, spatial autocorrelation of the phytoplankton was restricted to relatively short separation scales (Mackas, in prep.) while the congruence of phyto-

plankton and zooplankton appeared to hold more generally over the entire study area.

Peterson *et al.* (1979) suggested that the cross-shelf pattern of zooplankton composition is maintained off Oregon by a favorable interaction of life history and vertical distribution preferences with the normal range of the summer circulation pattern. If this is true, the atypical (vs. the Washington-Oregon-California coast) topography and circulation pattern off Juan de Fuca Strait may select against retention of zooplankton biomass and temporal stability of community pattern.

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