

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front

by J. Boucher,¹ F. Ibanez² and L. Prieur³

ABSTRACT

Results from five hydrographic and biological surveys at different seasons across the Ligurian Sea front, using horizontal continuous measurements and vertical profiles are presented. The vertical circulation across the front is described, and two divergences and one convergence are identified as permanent features from data. The key to find their location for each survey is given. The spatial patterns of 14 zooplankton taxa along the transect are established using variance analysis, principal component and correspondence analyses. The spatial distribution of each taxon is related to the physical structure, and the convection cells evidenced by the scheme appear as different biotopes. The daily variability of the spatial distributions is negligible compared to the annual variability. Distinctions are made between coastal species always inhabiting the peripheral (coastal zone) and others with distinct coastal, frontal and offshore distributions varying with the season. For the latter species the frontal zone is a preferential biotope during their seasonal growth period. Consequently the accumulation of organisms near the convergence cannot be created by only the dynamic causes. The role of biological processes in the observed distributions is discussed.

1. Introduction

The Ligurian Sea is the northeastern part of the Western Mediterranean Sea bounded by the French (Provence, Corsica) and Italian (Gulf of Genova) coasts. The general description of the physical structure and circulation was recently brought up to date by Bethoux and Prieur (1983). In this area, the permanent cyclonic circulation is well documented from numerous hydrocasts (Gostan, 1967, 1968; Stocchino and Testoni, 1977) and from monthly averaged values of areas 20×54 km where the hydrological parameters have been sampled from 1950 to 1973 (Nyffeler *et al.*, 1982). The Ligurian Current (Fig. 1) flows along the coast inside a strip about 30 km wide and 150 m deep with a yearly average transport of about 1.4×10^6 m³ s⁻¹ (Bethoux *et al.*, 1982).

1. Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER), Laboratoire Peches, Centre de Brest, BP 337, 29273 Brest Cedex, France.

2. Station Zoologique, BP 28, 06230F Villefranche Sur Mer, France.

3. Laboratoire de Physique et Chimie Marines, BP 08, 06230F, Villefranche Sur Mer, France.

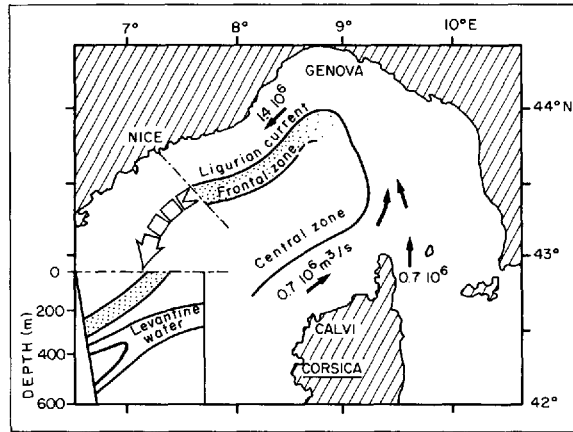


Figure 1. Schematic map of the circulation in the Ligurian Sea. Vertical distribution of water masses for the studied area is schematized in the lower left part of the figure.

From 1978 to 1980 the Pros III, Pros IV and Prolog cruises were made in late winter-early spring to observe the small-scale structure offshore Nice and Monaco. From horizontal surveys, a haline density front was always found. The surface front exhibits numerous meanders, but its main orientation is along shore. It separates the seaward central water mass from the inshore Ligurian Current. Three main hydrographic zones were defined in winter-spring (Prieur, 1979, 1981; Prieur *et al.*, 1981): (1) a coastal and peripheral zone, governed by the Ligurian Current; (2) a frontal zone identified by a rapid horizontal change of density which increases seaward; (3) an offshore central zone, where the surface density is high, close to that of the Levantine water, and stratification is weak.

The well-known Levantine water, high in salinity and temperature, flows slowly between the 400 and 600 m depth below the Ligurian Current in the same southwestward direction offshore from Nice. Thus, the surface frontal zone is the intersection at the surface of an inclined frontal layer which is about 300 m deep near the coast.

The relation between the physical structure and the spatial distribution of phyto- and zooplanktonic biomasses was also studied. The highest values of chlorophyll biomasses were localized in the marginal part of the central zone where the stability and nutrient-rich conditions should have enhanced the primary production (Prieur, 1981; Thévenot, 1981). In the same way, spatial patterns of zooplankton populations were related to the physical structure. These patterns can be explained for some populations (*Calanus helgolandicus*, *Euchirella rostrata*, *Pleuromamma gracilis*, *Cavolinia inflexa*) by an interaction between biological behavior and dynamic aspects of the environment (Boucher, 1984).

These results gave the first information on the spatial distribution of the planktonic populations in the Ligurian Sea, which is neither a continuum nor a random succession of patches. The frontal water masses appeared as particular biotope favoring the

development of some groups of organisms. However, these results were established in early spring, a season when the frontal structure is well formed in the surface layers, so the following questions remained unanswered: what is the evolution of the physical structure during the year and its impact on the spatial distribution of planktonic populations throughout their annual cycle? Are such distributions characteristic of the other planktonic populations inhabiting the area? The present study (the Pretrophos program) was planned in order to answer these questions.

As in the earlier studies, continuous records of the physical parameters and associated zooplankton populations were made along a transect crossing the frontal structure. But in addition, the records were duplicated within short time intervals (<5 h) and were made at different seasons to estimate both the reproducibility of the fine scale spatial distribution and its evolution throughout the year. The extraction of meaningful information from this considerable amount of data requires mathematical analyses to classify the variance sources and identify the connections between the physical and biological structures. The relations between these two structures vary with season and, therefore, a scheme of the frontal circulation, based on all the physical and biological data, is described and used as a physical framework for the interpretation of the observed changes in the spatial distributions of the zooplankton populations.

2. Survey method, instrumentation and data reduction

a. Strategy and data acquisition

Continuous measurements were made at the surface and along a NNW-SSE axis from the coast to 54 or 63 km offshore. The bathymetry of this axis varied from 300 to 2400 m. The whole of the Ligurian Current and the frontal structures were traversed on each transect. On each survey, two transects, one seaward and one shoreward, each of about six hours duration, were made aboard *N.O. Korotneff* in order to estimate the short temporal and spatial variations. A survey was made each month from June 1981 to late March 1982, to evaluate the seasonal variations of the physical and biological structures. Only the five surveys involving both physical and biological measurements (PBM) and zooplankton records (ZR) are reported here. The September, October and December 1981 surveys, without ZR, could only be considered in relation to the general results obtained by a complete data processing of the five other surveys (see Table 1). The July survey, shortened by bad weather, was not used.

The PBM included temperature (T), salinity (S), total scattering coefficient (b) and in vivo chlorophyll a fluorescence (F). Two instruments were towed together at the same constant depth (between 3 and 7 m) and speed (about 2.5 ms^{-1}): an *in situ* LPCM⁴ prototype probe measuring T , b and pressure P (as depth control), and a

4. LPCM: Laboratoire de Physique et Chimie Marines. Brevet ANVAR n° 79 175 35.

Table 1. Information on the surveys of program PRETROPHOS. Each line corresponds to one transect, seaward or return (first line of each data concerns the seaward). EC and EL columns give the distance (km) from the Cap Ferrat (near Nice) evaluated along a bearing of 123°. Local times for the beginning and end of the transects and their duration (min) are marked. The running numbers of samples are listed in the columns, for the end point inshore EC (1), the key points defined in the text, and the end point offshore EL successively. When EC were too far from the coast, the key point LC could not be found. The absolute mean speed of the ship was calculated from the positions of the end points and direction. The speed relative to the sea was maintained as close as possible to 2.5 ms⁻¹. At the bottom of the table the average running numbers of the key points were calculated.

Date	EC		EL		Duration (mn)	Speed (ms ⁻¹)	Running numbers of key points									
	Distance (km)	Time (L)	Distance (km)	Time (L)			EC	LC	PF	D1	C	FC	D2	EL		
10 Jun. 81	16.3	1249	63.2	1734	285	2.74	1	?	4	7	13	39	43	57		
10 Jun. 81	13.9	2314	64.8	1829	285	2.98	1	?	4	7	13	39	43	57		
3 Nov. 81	8.7	1025	50.0	1445	260	2.64	1	?	5	15	18	33	38	52		
3 Nov. 81	3.0	2110	46.3	1625	285	2.53	1	5	12	21	27	40	41	57		
12 Jan. 82	6.8	949	55.8	1554	365	2.20	1	4	12	19	34	51	57	73		
12 Jan. 82	0.1	2149	46.3	1704	285	2.70	1	4	21	24	29	38	43	57		
3 Mar. 82	3.4	1004	55.6	1544	340	2.54	1	9	18	26	31	42	47	68		
3 Mar. 82	0.5	2149	55.6	1604	345	2.66	1	9	19	27	32	43	47	69		
29 Mar. 82	3.7	923	55.6	1513	350	2.47	1	3	26	29	32	44	61	70		
												49	56			
29 Mar. 82	0.5	2113	55.6	1533	340	2.70	1	7	19	27	33	45	60	68		
												50	57			
						mean:	1	4	11	17	22	38	44	52		

CORA artesian well pump. The seawater was pumped at a flow rate of 1 l s⁻¹ via an opaque plastic hosing (1.9 cm internal diameter) into a 5 l debubbling tank and then split into three parts: (1) to a modified Guildline Autosol 8400 salinometer; (2) to a Turner Design model 10 fluorometer for the measurement of chlorophyll *a* fluorescence; (3) to an overflow pipe. The analog voltages for *T*, *S*, *F*, *b*, *P* were simultaneously sampled every 20s (i.e: one measurement for 50 m horizontal distance at 2.5 ms⁻¹). In the first second of each sequence, all the voltages were sampled ten times and converted in 12 digital bits. The 19 remaining seconds were used to calculate the means and to print, plot and record on the tape of the desktop computer and to await the next sequence.

The final resolution for *T*, *S*, *b*, *F*, *P* was 0.01°C, .005, 0.005 m⁻¹, 0.01 relative units and 0.05 m respectively. After calibration, the accuracy of the data was equivalent to about twice the resolution. The density of seawater ρ was calculated, using the Unesco (1981) formula, from *T* and *S*.

A high correlation was observed between *b* and *F* in the studied area (Fig. 2), except occasionally in the coastal zone (which may have contained terrigenous particles with

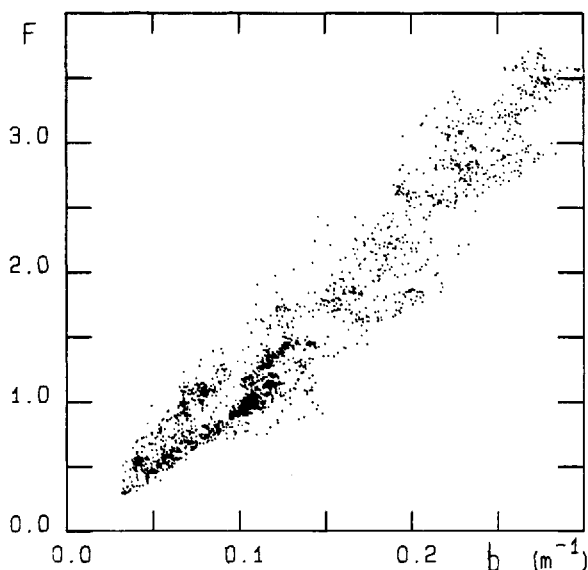


Figure 2. Scatter diagram of the fluorescence F (relative units) of chlorophyll a versus the light scattering coefficient b (m^{-1}). Data were obtained on the seaward and return transects on the 29th of March 1982. The value $F = 4$ corresponds to 1.4 mg m^{-3} of Chl a . The plot shows that either b or F can be used as an estimate of the algal biomass in the studied area.

a specific scattering different from that of biogenic particles and phytoplankton). Measurements of b are only sensitive to scattering by particles smaller than 20μ . Moreover, numerous data obtained in the same way from earlier cruises (PROLIG, PROS) also exhibited an approximate linear relation between chlorophyll a concentration and the total scattering coefficient. The relationship, which was valid for daytime sampling as well as for night-time was: $\text{Chl } a \text{ (mg m}^{-3}\text{)} = 4 b \text{ (m}^{-1}\text{)}$. No significant influence of daylight on phytoplankton fluorescence was observed using the described system. A further test of the validity of this relationship was made on March 29, 1982 using 21 samples of seawater analyzed for Chl a content by the spectrophotometric method (Lorenzen, 1967). The results suggest that the algal biomass can be estimated in terms of b or F . Absolute values in terms of chlorophyll a , not of fundamental interest here, may be found roughly by the above relationship or from Figure 2.

ZR were obtained simultaneously from the same depth as PBM with a Hai pump sampler. The animals were collected by a modified high speed Hai sampler. In addition an inboard peristaltic pump continuously delivers the animals from the net collector to the ship's deck. Each sample corresponds to five minutes of pumping (i.e. 770 m horizontal distance at 2.5 ms^{-1}). The sampling system was described by Boucher (1984). When appropriate, PBM were averaged over five minute intervals for comparison with the ZR.

On the day after the continuous surface measurements, six vertical profiles were taken at six stations, each nine kilometers apart, along the same transect. These stations have been visited every fifteen days since October, 1981 as part of the hydrographic survey program (PROS VI) of the Ligurian Current. The nearshore station was located 5.5 km from the coast. Each 0-800 m hydrocast, 40 minutes long, measured temperature and salinity using a high precision Guildline 8705 CTD probe and was followed by a 0-80 m profile of b and T by means of the LPCM probe. The vertical speed of probes, 0.6 m s^{-1} , was sufficiently high to prevent distortion of each profile by internal waves as shown by Mackas and Owen (1982). Possible distortion could exist in the comparison of the levels of b , T or S isolines. However, such a distortion should be limited. Other data, obtained in a fixed location by short time repeated casts in the same area, had shown that the amplitude of internal waves is less than 10 m in the upper layers of the Ligurian Sea. The sampling rates corresponded to a 1.5 m resolution for T and S after processing on HP 85 calculator and a 2.5 m resolution for b on HP 9825. The hand drawn isolines of T , S , b of each vertical section (e.g., Figs. 5, 6, 7) helped to understand and interpret the structure observed in the surface tow surveys. Dynamic calculations (not presented here) show that the Ligurian current was traversed totally by each survey and that the transect always ended within the central zone where the mean baroclinic flow is zero.

b. Zooplankton analysis

Counts of the organisms were made on aliquots ranging from $\frac{1}{2}$ to $\frac{1}{8}$ of the sample such that 500 to 1000 individuals were identified. The counts were all converted to number per m^3 . More than 60 taxonomic categories were identified in the 695 samples made during the 10 transects. Copepods were the most abundant organisms in the samples. Most of them were identified to species and for the dominant ones (according to frequency and numbers), adult and copepodite stages were separated. An exception was made for the genus *Clausocalanus* for which specific determination involves fine measurements of female seminal receptacle and basipodal spines. *Clausocalanus* were divided in three classes A, B and C according to decreasing size. The most frequent species were *C. farrani* and *C. lividus* for the class A, *C. furcatus* for class B and *C. paululus* for class C. The later includes also copepodite stages of the former classes. The number of samples per transect, major taxa and mean and standard deviation of their abundances, are summarized in the Appendix.

c. Mathematical treatment

The whole data base consists of a chronological series of 50 to 70 samples obtained from each of ten transects. The analysis of the data included two independent procedures.

In a first step, within each transect, each spatial series was smoothed in order to reduce the noise of the log-transformed counts of organisms. Then PCA were made for

each of the ten transects to reduce the number of independent variables. The number of the retained components was fixed by their relative variance (the first two reached more than 90% of the total variance). In this reduced space the determination of groups of taxa was based on a semi-objective method described below. For each group a composite variable, named the pattern variable, was formed according to the cumulative abundance of the taxa which strongly contributed to definition of the group.

A grand PCA applied to the pattern variables of the ten transects allowed recognition of nine distinct new groups principally defined by the spatial distribution of the taxa, whereas the seasonal variation had a negligible influence.

The choice of PCA among other techniques is argued in the general discussion. The technique of smoothing and the method of determination of groups and pattern variables are described below.

A variance analysis of the coded distance of each of the nine groups to the coast indicated the relative importance of the source of the time-space variations.

In a second step, correspondence analysis was then performed to directly analyze the relationships between zooplankton abundances and hydrobiological structures. Simultaneous records of physical and biological parameters gave a reference which was independent of the geographical reference. The geographical position of the structures could shift between two records whereas the spatial distribution of populations would remain stable in relation to the dynamic structure. The records were segmented into six different physical zones. The ordination by the correspondence analysis of the biological variables allowed identification of the spatial distribution of the species, which showed seasonal variations related to the physical zones.

The precise description of the behavior of the different taxa showed complementary results with those of the first step of analysis (PCA).

Extraction of trends by smoothing techniques. The "high-low-mid-points" method was chosen for the smoothing of the zooplankton abundances (Ibanez, 1983; 1984). This technique, which is often graphically applied in economics, does not imply an *a priori* causal hypothesis such as is the case with approximations by a linear or polynomial model or by the moving average techniques. With the high-low-mid-points techniques, the trend is the locus of the points which are equidistant to the inferior and superior envelopes of the original curves (Fig. 3a). These two envelopes join the turning points which are values greater or less than their two neighbors. Such a technique conserves the low frequency below 0.2 cycles per sampling unit (Ibanez, 1983) such that periods smaller than five successive observations (25 min. or 3750 m of record in this work) are eliminated. In addition all the measurements are conserved.

A comparative study of the results of two principal component analyses (PCA) on the smoothed abundances and the original transformed data, gives the following main properties (Ibanez, 1983).

- (1) The means of smoothed data are less than means of the original data and the variances are more homogeneous.

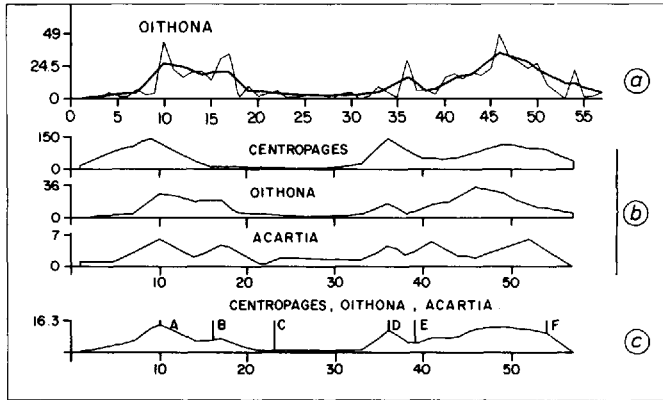


Figure 3. Survey on the 3rd of November 1981, return transect. The x axis represents distance from the coast scaled as the running number of the samples (1 sample is 750 m length). (a) comparison between original and smoothed abundance; (b) smoothed data relative to the three indicated taxa; (c) the pattern variable determined by PCA corresponding to these taxa showing similar trends. The Y units are the number of individuals by sample for a and b and the percentage which represents the sum of the individuals of the pattern variable in the total number of individuals inside the sample. The turning points of the survey graph for the plane of the first two components are marked from A to F. Most of them correspond to a change in the trend of this pattern variable.

(2) The correlations between variables are also higher.

(3) The total variance extracted by the first principal components increases.

The spatio-temporal contiguity of the observations is more emphasized in the first factorial plane of the smoothed data than of the original data.

Reduction of number of variables by PCA. The biological descriptors are defined as the set of abundances (50 to 70 samples) recorded on each outward or inward shiptrack for the same taxa. For instance, for the descriptor *Acartia*, the seaward record in November is distinct from *Acartia* collected during the inward record at the same time.

The principal component analysis (PCA) of the 695 observations with all the 98 identified descriptors could give a condensed representation of the data, but the number of items is so large that visualization of the proximities on the factorial planes would be very confusing.

The number of biological descriptors was reduced by grouping them according to similarities in the abundance gradients along each seaward or landward record, by PCA analysis.

PCA was made on the variance-covariance matrix in order to preserve the biomass differences, namely the seasonal variations. Only the first two principal axes were considered because their corresponding cumulated percentage of variance exceeded 92%.

Many authors presented very simple classification methods based on the elements of the first latent vectors: Chardy and Leguen (1971) defined groups by considering the signs of the elements for the first three axes; Lefkovitch (1976) used the same procedure for the cluster of objects (after Principal Coordinates Analysis), starting from the scores of the components; Cassie (1967), Cassie and Michael (1968), Margalef and Gonzalez-Bernaldez (1969) classified the species according to the principal component for which they have the largest absolute correlation value. Each of the primary groups can be subdivided according to the second important component and so on.

Taking into account only the first two axes, we used here a technique derived from the above principles: the latent vector matrix was rearranged in descending order of the elements of the first vector. At this step several groups were extracted considering the maximum values for the rows (species). Since for every PCA the variance of the first axes was repeatedly much larger than for the second, we then looked for an eventual obvious discontinuity in the ordered elements of the second vector. If there was an ambiguity, the groups were not subdivided or some species were considered as intermediates. This procedure is not an entirely objective method, but even a numerical classification method is based on some arbitrary concepts. The separation of groups was very easy here because the number of species did not exceed 12 for each transect.

These ten PCA led to a set of new descriptors called pattern variables, which were the cumulative abundances of the members of each taxon within each defined group. For instance, the landward record in November contained 12 biological descriptors and 52 samples. The PCA separated three groups which are the three pattern variables

PV13: *Oithona*, *Acartia*, *Centropages*

PV14: *Clausocalanus* A, B and C

PV15: *Temora*, *Candacia*, *Corycaeus*, *Euterpina*, Cladocerans, Chaetognaths.

In considering the trends of the biological descriptors, the abundance profiles of the descriptors within the same group were almost identical (Fig. 3b). Thus, only three cumulated pattern variables were retained instead of the twelve original descriptors (Fig. 3c).

An exhaustive presentation of the results of these ten PCA would lead to a very long development and is not reported in this paper. These individual PCA have been only used to define condensed new variables, the so-called pattern variables, which are listed in Table 2. A global PCA of these 39 pattern variables was then performed to give a general picture of the spatial distribution throughout the year.

3. Results

a. Physical and biological structures

The physical results (T , S , ρ) agree well with the conceptual scheme, discussed below, of the permanent physical and biological structures. Moreover, the physical

Table 2. The list of the types of organisms contained in the nine groups defined by the general PCA of covariance. The descriptors are the pattern variables themselves defined from the ten particular PCA of covariance of the smoothed abundances of organisms measured along the ten retained transects. Date, seaward transect (S) or return (R) and identification number of the variable patterns are given in the right-hand columns.

PCA groups	Pattern variables	Month	Record	Code	
Group 1	{ <i>Acartia</i> , <i>Euterpina</i> , <i>Oithona</i> <i>Corycaeus</i> , Cladocerans, Echinoderms, <i>Clauso. C.</i> }	April	R	39	
Group 2	<i>Clauso. B.</i> , <i>Clauso. c.</i>	November	S	11	
	Cladocerans	June	S	4	
	{ <i>Temora</i> , <i>Candacia</i> , <i>Corynaeus</i> Cladocerans, <i>Centropages</i> , Chetognaths }	November	S	12	
	{ <i>Temora</i> , <i>Candacia</i> , <i>Corycaeus</i> , Cladocerans, <i>Euterpina</i> , Chetognaths }	November	R	15	
	<i>Centropages</i>	January	S	18	
	{ <i>Acartia</i> , <i>Temora</i> , <i>Candacia</i> , <i>Corycaeus</i> }	January	S	20	
	{ <i>Corycaeus</i> , <i>Oithona</i> , <i>Clauso. B.</i> , <i>Calanus</i> }	January	R	22	
	{ <i>Acartia</i> , Echinoderms, <i>Centropages</i> <i>Clauso. A.</i> , <i>Clauso. C.</i> , <i>Acartia</i> }	January	R	23	
	Cladocerans, Echinoderms	March	S	24	
	Cladocerans, Echinoderms	March	S	29	
	{ <i>Acartia</i> , <i>Centropages</i> , Cladocerans Echinoderms }	March	R	33	
	<i>Euterpina</i> , <i>Corycaeus</i>	April	S	35	
	Group 3	<i>Clauso. C.</i>	March	R	30
	<i>Clauso. B.</i> , <i>Oithona</i>	March	R	31	
Group 4	<i>Centropages</i>	June	R	6	
Group 5	<i>Oithona</i> , <i>Acartia</i>	June	S	1	
	<i>Acartia</i> , Cladocerans	June	R	7	
	<i>Oithona</i> , <i>Clauso. A.</i>	November	S	9	
	<i>Oithona</i> , <i>Clauso. A.</i> , <i>Clauso B.</i>	January	S	19	
	<i>Temora</i> , <i>Candacia</i>	January	R	21	
	<i>Acartia</i> , <i>Oithona</i> , Echinoderms	April	S	36	
	{ <i>Centropages</i> , Cladocerans, <i>Clauso. A.</i> , <i>Clauso. B.</i> , <i>Clauso. C.</i> }	April	S	37	
	Group 6	<i>Acartia</i>	November	S	10
<i>Oithona</i> , <i>Centropages</i>	March	S	28		
Group 7	<i>Calanus</i>	January	S	16	
	<i>Clauso. A.</i>	March	S	25	
	<i>Clauso. B.</i>	March	S	26	
	<i>Clauso. C.</i> , <i>Calanus</i>	March	S	27	
	<i>Calanus</i> , <i>Centropages</i> , <i>Clauso. A.</i> , <i>B.</i>	April	R	38	

Table 2. (Continued)

PCA groups	Pattern variables	Month	Record	Code
Group 8	<i>Clauso. A., Clauso. B., Clauso. C.</i>	June	S	2
Group 9	<i>Centropages</i>	June	S	3
	<i>Oithona</i>	June	R	5
	<i>Clauso. A., Clauso. B., Clauso. C.</i>	June	R	8
	<i>Oithona, Acartia, Centropages</i>	November	R	13
	<i>Clauso. A., Clauso. B., Clauso. C.</i>	November	R	14
	<i>Clauso. C.</i>	January	S	17
	<i>Calanus, Clauso. A.</i>	March	R	32
<i>Calanus</i>	April	S	34	

structure provides a logical background to explain the spatial and seasonal variations of algal biomass (b , F). The scheme (Fig. 4) is based on the likely vertical circulation across the Ligurian current which flows along the coast. Several circulation cells are identified which are compatible near the surface with the observed density and biomass fields. Different key points are then defined and found for each survey to demarcate the physical zones which will be used for the interpretation of the zooplankton distributions.

The scheme and the method of choosing the key points are presented using, almost exclusively, the data from November 3rd, 1981 as an example for both brevity and clarity. Only the possible theoretical basis of the scheme is then evoked. A further interpretation of all the available physical, chemical and biological data from similar cruises will give more details using dynamic explanations not presented here.

The density field. The potential density field (Figs. 5 and 6) remains similar throughout the year though the absolute density may change (Fig. 4b). An onshore to offshore transect survey successively crosses the low density ρ_1 peripheral zone, the frontal one, and the high density ρ_2 zone. The mean horizontal density gradient $\rho_2 - \rho_1$ is high in the frontal zone and weak in the other two. The boundaries between the peripheral and frontal zones, so called PF, and the frontal central one, FC, are easily determined from the graph of ρ versus horizontal distance, x (Fig. 4a). However the graph of Figure 4a is diagrammatic. Occasionally the peripheral and central zones were not horizontally homogeneous in density; for example in June and November seaward transects. Slight gradients or local variations of density could occur. The ambiguity was clarified after considering the horizontal T - S diagram. Indeed, in such cases, the trend of the line corresponding to the transect was found to change inclination in reference to isopycnal lines. PF and FC were then set here, when density was sufficiently low (PF) or sufficiently high (FC). The distances from the coast of these two key points vary from day to day and with season. Typically, the width of the peripheral, frontal and central zones are 10 to 20, 1 to 20 and 60 to 110 km,

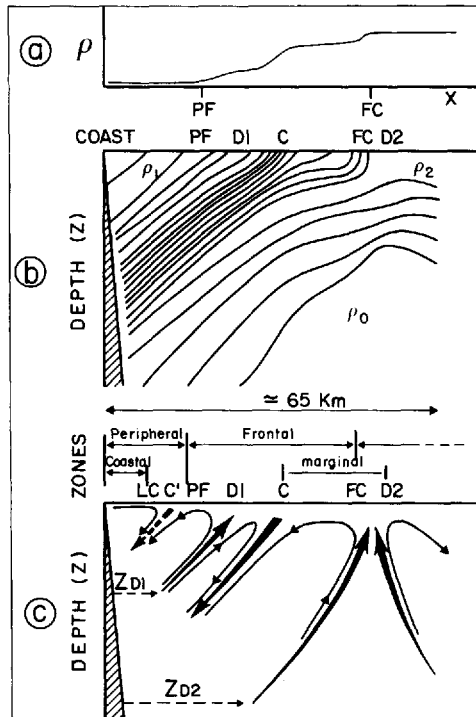


Figure 4. Schematic representation of the density field and circulation along a cross-frontal survey. (a) typical aspect of a horizontal profile of density at subsurface; (b) density field in a vertical section from the coast to offshore, with position of the key points and density ρ_1 , ρ_2 , ρ_0 ; (c) cross-frontal circulation showing the divergence and convergence lines (thick) and associated stream lines (thin). The names of the zones are indicated above (c). The peripheral zone stretched between the coast and the beginning of the horizontal density gradient. The frontal (PF-FC) and central (beyond FC) zones are encountered further seaward. From physical and biological data, the other key points LC, DI, C, D2 were found. They demarcate the convection cells and the spatial alternating of convergence and divergence which involve layers of various thickness. The coastal zone refers to the first cell near the coast, the marginal one (FC-C) to the cell inside which the seawater is upwelled from ZD2 by the deep divergence D2 and downwelled by the main convergence in the frontal zone. The typical values of density ρ_0 , ρ_1 , ρ_2 , the width of different zones and the depths ZD1, ZD2 are given in the text. Due to the conceptual nature of the scheme, no scale is marked here, excepted the overall length of the surveys.

respectively. The central zone extends to about 130 km from Nice. Beyond this zone, the SWNE current along the northern coast of Corsica is encountered (Bethoux and Prieur, 1983).

Inside the central zone, the deep density ρ_0 at depth z 200 m is always $1029.10 \text{ kg m}^{-3}$. The density difference $\rho_0 - \rho_2$ is typically 1 to 3 kg m^{-3} in summer and 0 to 0.15 kg m^{-3} in winter. The horizontal difference in density, $\rho_2 - \rho_1$, near the surface

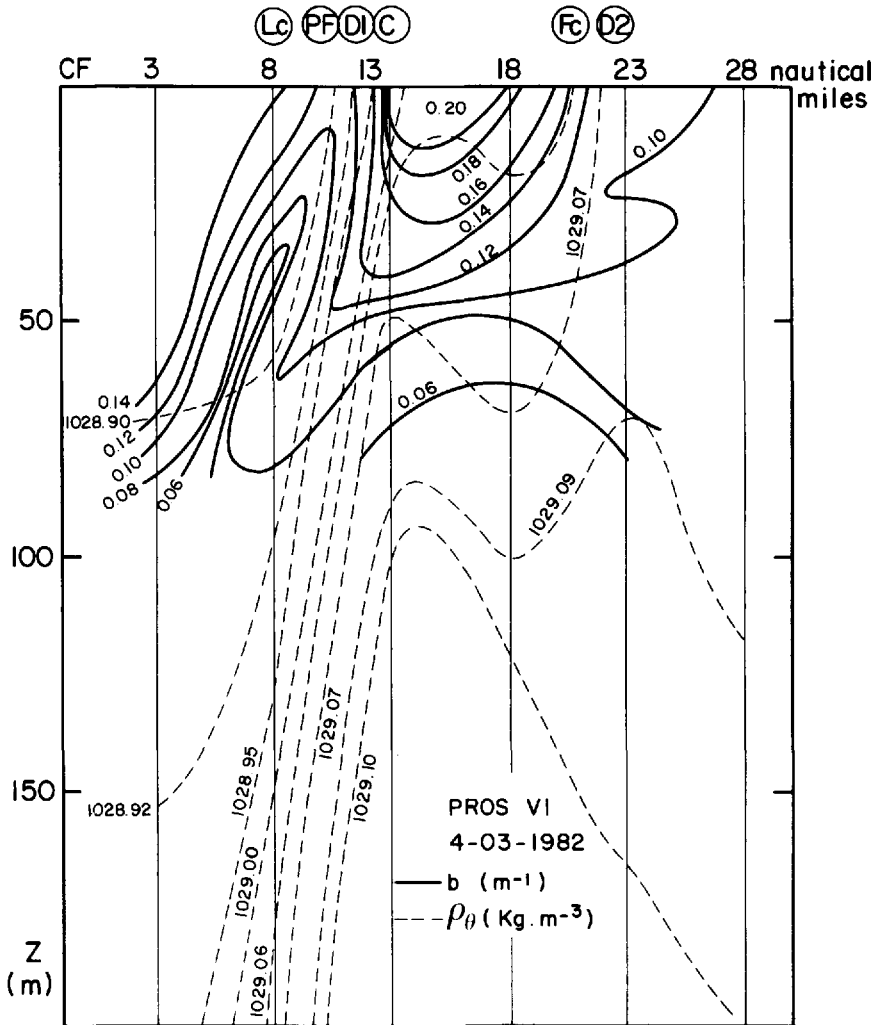


Figure 5. Vertical distributions of density (kg m^{-3} , broken lines) and scattering coefficient (m^{-1} , solid lines) for the 4th March 1982 (late winter). The downward movement of the biomass formed in the subsurface layer between the stations at 13 and 18 nautical miles from the coast is visible through the observed secondary maximum at depth 70 m, station at 18 miles from the coast. Note the very weak stratification beyond D2.

and across the front is larger in summer (.6 to 1) than in winter (.2 to .4). As the frontal zone is tilted with depth, the broadness of the coastal zone decreases with depth. The mean slope of the frontal isopycnal lines is lower in summer (0.3%) than in winter (1-2%). Such structure in the density field indicates the presence of a geostrophic current flowing southwestward along the coast. The current speed is as high as

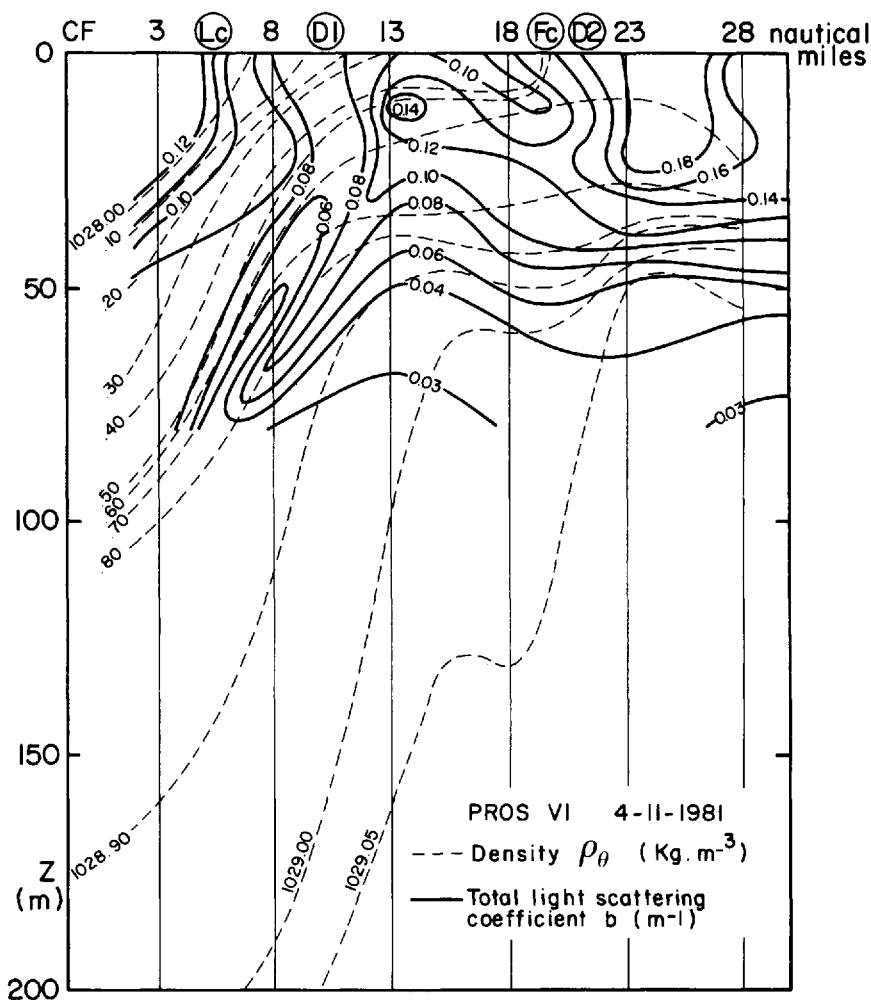


Figure 6. The same as Figure 5, for the 4th of November 1981. The downwelling of the biomass is along the isopycnal lines which are less horizontally inclined here. The maximum biomass is found beyond D2. The pycnocline is at a depth 50 m offshore, 100 m near the coast.

40 cm s^{-1} at the surface and decreases uniformly as depth increases (Bethoux and Prieur, 1983). Between 200 and 300 m, the current flows to about 5 cm s^{-1} and then decreases further to 2.5 cm s^{-1} in the Levantine water below. Inside the central zone the mean geostrophic current is zero for all depths.

The vertical circulation: scheme and other key points. Nonsimilar vertical distributions of T and S (Fig. 7), T - S diagrams (Fig. 8) and the heterogeneous horizontal and vertical algal biomass distributions when compared to the density field (Fig. 5 and 6) suggest a vertical circulation linked to the front and Ligurian geostrophic current.

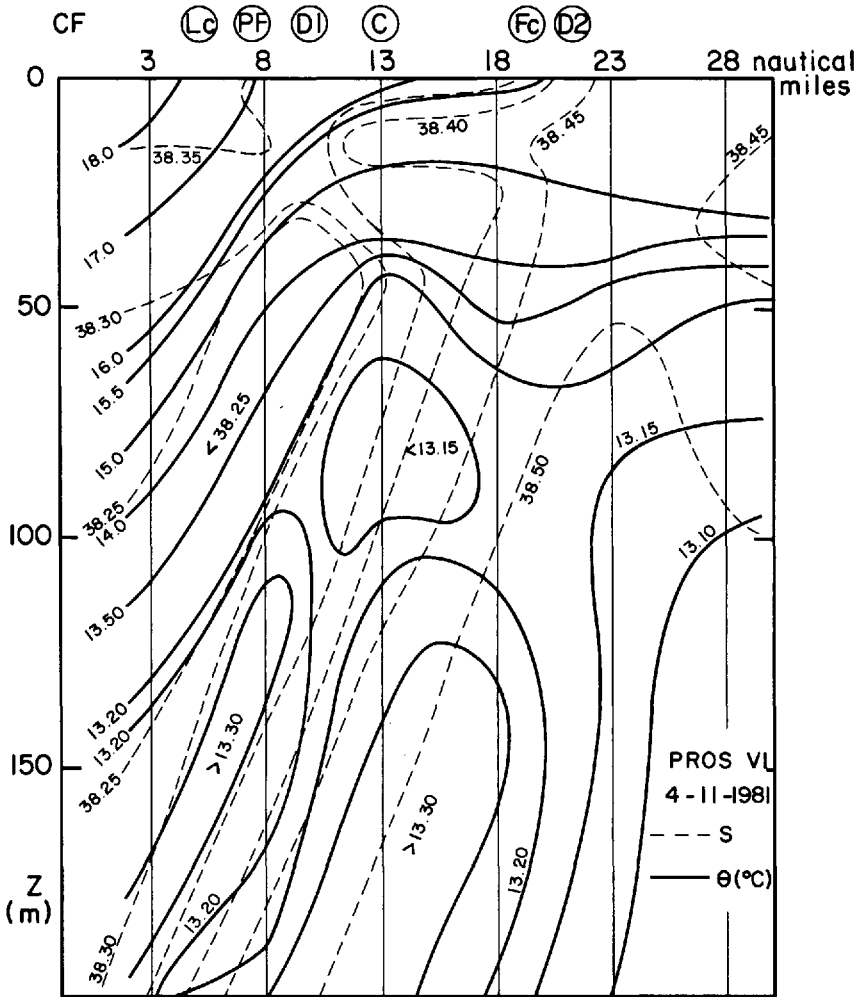


Figure 7. Vertical distribution of salinity (broken lines, practical scale) and potential temperature (solid line, °C) for the 4th November as in Figure 6. Only the upper layer (0–200 m) is presented here. The thermal gradient between 16–13.5°C is located in the area of the minimum in salinity (38.25). Conversely, below the pycnocline, there is a strong S gradient, but temperature is almost constant. This separation between the S and T gradient is also observed at the surface (Fig. 8) despite stratification. Only vertical (inclined) advection can explain such intersections of S and T isolines.

The almost permanent features exhibited by the vertical sections were a folding of the b isolines roughly along the isopycnals and a doming of the densest isopycnals in the deep central zone.

The doming is not apparent in surface (Fig. 6). However note the clear doming of the 38.50 S isoline at the station 23 miles from the coast (Fig. 7). In addition, in the 7 m deep horizontal transect, the absolute maximum of density (1028.63) and minimum of

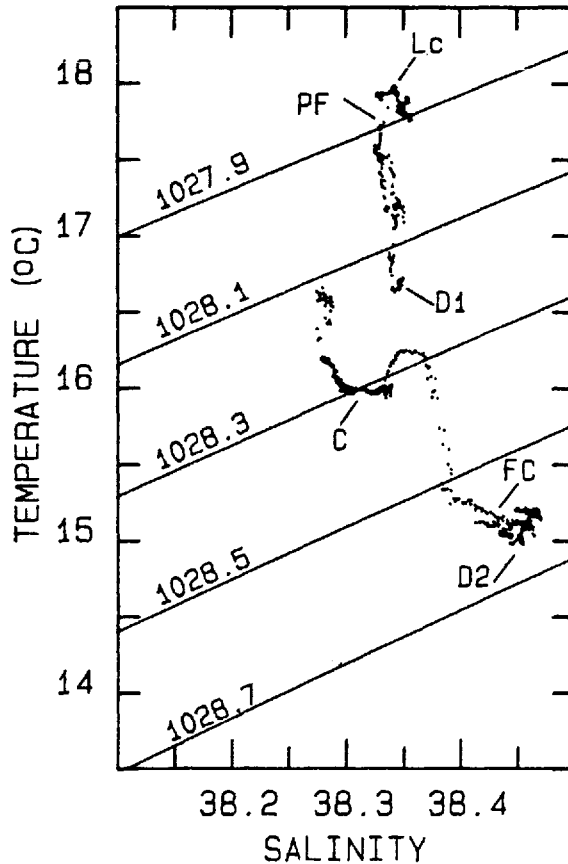


Figure 8. T - S diagram of the surface survey, return transect, on the 3rd of November 1981. One dot was plotted for every 50 m of the tow. The key points discussed in the text are marked near the corresponding dots.

temperature (14.99) were found near the same station. This location is marked D2 on the corresponding T - S diagram (Fig. 8). Offshore of this location, density and temperature were found to be almost horizontally homogeneous and close to 1028.60 and 15.20 respectively, values significantly different from the extrema. For the surveys other than the November return, which is the only one detailed here, water with high density and marked underlying T - S characteristics was also encountered in the central zone near the limit of the frontal zone. Accordingly it is thought that a deep divergence, named D2, brings underlying water to the surface near this limit.

By pursuing the interpretation of results in terms of vertical circulation, the fold could be generated by a local system of divergence (D1) and convergence (C). Indeed water deeper than 70 m was almost devoid of particles (low b), but at the station 8 miles from the coast low b isopleths were locally uplifted by almost 30 m (Figs. 5 and

6). Beneath, the relatively high values of b , in reference to the depth, may have been advected down from the adjacent surface biomass found between the station 13 and 18 miles. The 7 m depth horizontal transects on March 3 and November 3 confirmed the patterns of b interpolated by eye from the vertical profiles; particularly the low b area between the stations at 8 and 13 miles.

Note that such a folded pattern is not detected on the T or S fields as represented by Figure 7. However the T - S diagram for the station at 8 nautical miles off the coast exhibits between 50 and 200 m some interleaving layers which were not drawn with details on this figure, and which could correspond to quasi-isopycnal advections. Due to the spacing interval and the handdrawn interpolation between stations, the minimum of salinity at 38.25 does not appear near the surface on Figure 6, but appears clearly (Fig. 8) on the T - S diagram of the horizontal continuous measurements. A local maximum of density, marked D1, appears also on this diagram. We think that the center of the convection cell D1-C was occupied by the less salty water, which originated from the previous winter. So the upward tongue-like aspect of this water which is observed and maintained throughout the year could be explained by a vertical circulation around the tongue.

The authors are fully aware that the preceding arguments from the interpretation of the Pretrophos data are not actual proof of vertical or isopycnal advections. However, similar folds and doming were observed in March 1980 and May 1982, and also in concurrent oxygen and nitrate measurements. Inside the downward part of the fold, nutrients were low as they had been consumed by phytoplankton and oxygen high; and inside the upward part, above the deepest maximum of biomass, oxygen was as low and nutrients as high as in subjacent waters below 100 m near the coast. If isopycnal advection is not retained, it would be difficult to explain why, in a stratified field, the high nutrient content of a well illuminated zone in the water column is less utilized than 30 m below where illumination is poor. In this area the 1% light level is generally found between 40 and 60 m depth (Prieur, 1973). Again in March 1980, a narrow band only 1 km broad with very high nutrient content and oxygen undersaturated water was found on the surface along the front and close to the limit of the frontal zone. No doubt can be retained on the deep origin of the water encountered there. These peculiar distributions are well explained by the quasi-isopycnal advections. As already announced, this will be detailed in a further paper.

Given the isopycnal slope (0.3% to 1.5%) and the proximity of D1 and C in depth near the fold (about 30 m), given the small horizontal dimension in surface of the divergence D2, only very close stations (3 to 10 km apart) and vertical and horizontal PBM could show the existence of such inclined advections. This may explain why such a scheme of vertical circulation near a front has not yet been described.

For each of the ten transects under study, the key points D1, D2, C were chosen by examining the corresponding Figures 5 to 8, with the horizontal distributions of T , S and density. From vertical sections, the b fold gave a first indication on the isopycnals concerned with D1 and C. Then T - S diagrams and vertical sections of T and S led to

fix D1 on the horizontal transects where a local maximum of density or marked underlying water properties was encountered. The convergence C was fixed in the transect at the corresponding horizontal gradient of salinity or density found in the lower part of the fold. On the T - S diagram (Fig. 8) C was put at the beginning of the horizontal part of the transect line. Finally D1 was chosen near the absolute maximum of density where the absolute maximum of S or minimum of T , depending on the season, was encountered. Divergences points were not systematically chosen at the local maximum of density which could be nonsignificant, but could be shifted where the underlying water properties were most marked. That was made on the basis that a divergence is not necessarily marked by a doming of isopycnals in the inclined field of density (Bennett, 1986) if diapycnal flow is assumed weak.

This scheme is concerned with the vertical circulation only in the surface layer. The deep closures of the circulation cells are not precise through lack of information from any tracer, biological or otherwise. The estimation of the depth of the origin (ZD1 and ZD2) of the upwelled waters by divergences may be made supposing that the advection lines are close to the isopycnals. Typically ZD1 and ZD2 are 50 m and 100-200 m in summer, and 100-200 m and 500-800 m in winter. The origin depth is of great biological interest because nutrients, which enhance algal growth rates, can be advected into the well-lit layer from depth, but only if the source is sufficiently deep (e.g., > 150 m). Moreover, some stratification, inhibiting deep and quick convection, is required to allow algal growth as a result of nutrient enrichment. Thus, the location of the biomass maximum is dependent on the intensities of the two processes: enrichment by the divergences, and stratification beside the divergences (Legendre, 1981). Accordingly, favorable locations are found in different parts of the explored transects. The biomass maximum is found in the continuous surface records between D1 and C in early winter, inside the so-called marginal zone between C and D2 in spring when the value of Chl a is 5 mg m^{-3} , and beyond D2 (e.g., November 1981) in the summer and fall when the stratification is high and the isopycnal slope is weakest. No more detail about the distribution of algal biomass is given here. This brief presentation has been made to point out that the maximum food of grazers is linked closely, though with seasonal and spatial variability, to the physical structure as defined, not in terms of temperature and salinity, but by unknown vertical advection speed and stratification.

A peculiar zone is noted in Figure 4 close to the coast where the light scattering coefficient b is sometimes high. This zone is called the coastal zone as it is influenced by rivers and coastal discharge. Its offspring limit LC is determined from the horizontal distributions of b and sometimes T and S or ρ , when the river discharges are occurring. A possible convergence C' should close the convection cell from D1 to the coast.

In fact the key point D1, D2 and C are neither points nor alongshore lines, but are alongshore bands of variable width. Finally, five zones are identified from PBM and used to interpret ZR with respect to the cross frontal component u of the current, which is one order of magnitude less than the alongshore component v of the Ligurian current

and is taken as positive seawards. These zones are coast-LC ($u > 0$), LC-D1 ($u < 0$), D1-C ($u > 0$), C-D2 ($u < 0$) and the D2-end of transect and beyond into the central zone.

Discussion of the scheme. Such a scheme of vertical circulation is a rather crude image of the actual structure. The vertical circulation is not strictly two dimensional. Moreover, meanders of the front exist (Prieur, 1981) and at times are visible by satellite imagery (Crepon *et al.*, 1982). Thus, in one transect the marginal zone C-D2 may be totally or partially crossed more than once which explains why two points C and two points FC were found in March 29, 1981 (Table 1). Clearly the scheme has to be considered as a vertical section across a complex three-dimensional structure, not necessarily a plane section but possibly a broken section. The scheme is thought here as a heuristic simplification of the actual vertical circulation to study the possible influence of the physical structure and the associated field of the phytoplankton biomass on the distribution of zooplankton.

Without giving the theoretical foundations, we recall that the cross frontal, vertical circulations have already been studied by some authors for fronts that are buoyancy driven (Kao, 1980; Tang, 1982, 1983). They treated the problem in a semigeostrophic approximation, taking into account the vertical or lateral friction in the frontal zone. Divergences and convergences should be caused by Ekman layers near the front which induce a vertical ageostrophic circulation in a similar way to a coastal upwelling. Both the Kao and Tang models predict a convergence inside the frontal zone, especially the former, and one divergence inside the central zone near the front (Tang) or inside the peripheral zone (Kao). But neither could predict both divergences identified by our measurements. However, in a three dimensional numerical model, James (1984) found that the existence of one or two cells of vertical circulation in the front of the Norwegian coastal current crucially depends on assumptions of vertical variations of eddy viscosity and buoyancy diffusivity. These authors found vertical velocities of between 8 and 80 m per day. Since the doubling time of algae is typically one day, such vertical circulation can enhance production by influx of nutrients into the photic zone, and also downwell a fraction of the biomass formed in the surface layer. The interpretation of the fold of the b isolines in terms of inclined advections is thus plausible, even though b is not a conservative property.

In other respects, the high winter slope of the inclined isopycnals and the meanders of the front are compatible with dynamic instabilities. The barotropic or baroclinic nature of these instabilities is not yet well known though more information exists on the baroclinic mode (Gascard, 1978; Crepon *et al.*, 1982). In each case instability drives vertical advections which are discontinuous in time and space. On the other hand Ekman layers should be continuous along the front, although possibly variable in thickness (Woods *et al.*, 1977; Woods, 1980). In the present state-of-the-art and to the best of our knowledge, several dynamic processes should be studied to explain definitively the scheme established from numerous multiparametric measurements.

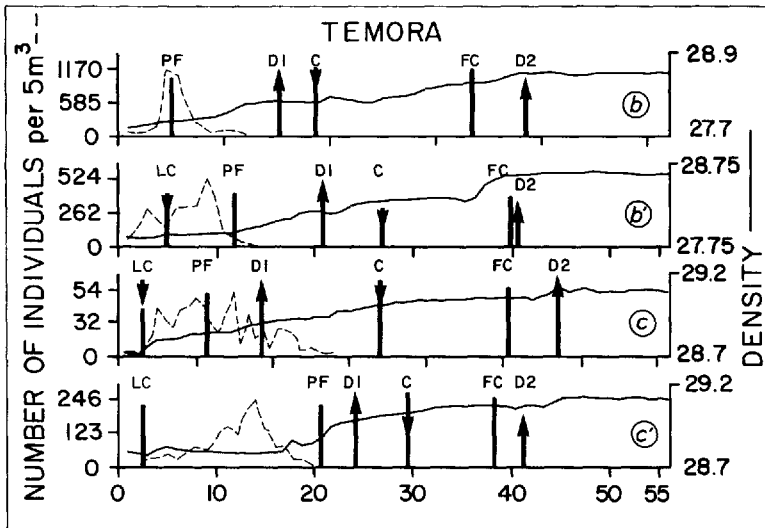


Figure 9. Variations of abundance (dotted line) for *Temora stylifera* according to the variations of density (continuous line) along the transect (running number of successive samples of about 750 m length each). The key points of the physical structure (see text and Table 1) are indicated by vertical bars or arrows. *b* is for the November seaward transect, *b'* for November return, *c* and *c'* for January seaward and return. *Temora stylifera* was absent in all samples of the other transect records.

b. Biology

Faunistic aspects and spatial distributions. Some copepod species such as *Neocalanus gracilis*, *Nannocalanus minor*, *Eucalanus* spp., *Euchaeta* spp., *Pleuromamma abdominalis* and *P. robusta* show an increase in their mean abundances between seaward and return records (from zero values to some ten individuals per m^3 , see the Appendix). At the time these species were present in the area, they were only sampled at night during the return record. Night and day variations of abundances are explained by diurnal vertical migrations which are well known behavior for such species (Mazza, 1963, 1968; Hure *et al.*, 1974). Other taxa as Pteropods (*Cavolinia inflexa*) and Euphausiids (Furcilia and adult stages) also show increasing abundances by a factor of two at night. All such taxa were not considered for the multivariate analysis.

Finally, 14 taxa were selected according to their mean abundances ($>10 \text{ ind } m^{-3}$), their frequent occurrence (presence in more than 1/3 of the total records) and the absence of evident diurnal vertical migration. These included: *Calanus helgolandicus* (adults and juveniles), *Clausocalanus* classes A, B and C, *Temora stylifera*, *Centropages typicus* (adults and juveniles), *Candacia* spp., *Acartia clausi* (adults), *Euterpina acutifrons*, *Oithona* spp., *Corycaeus* spp., Cladocerans, Echinoderm larvae and Chaetognaths.

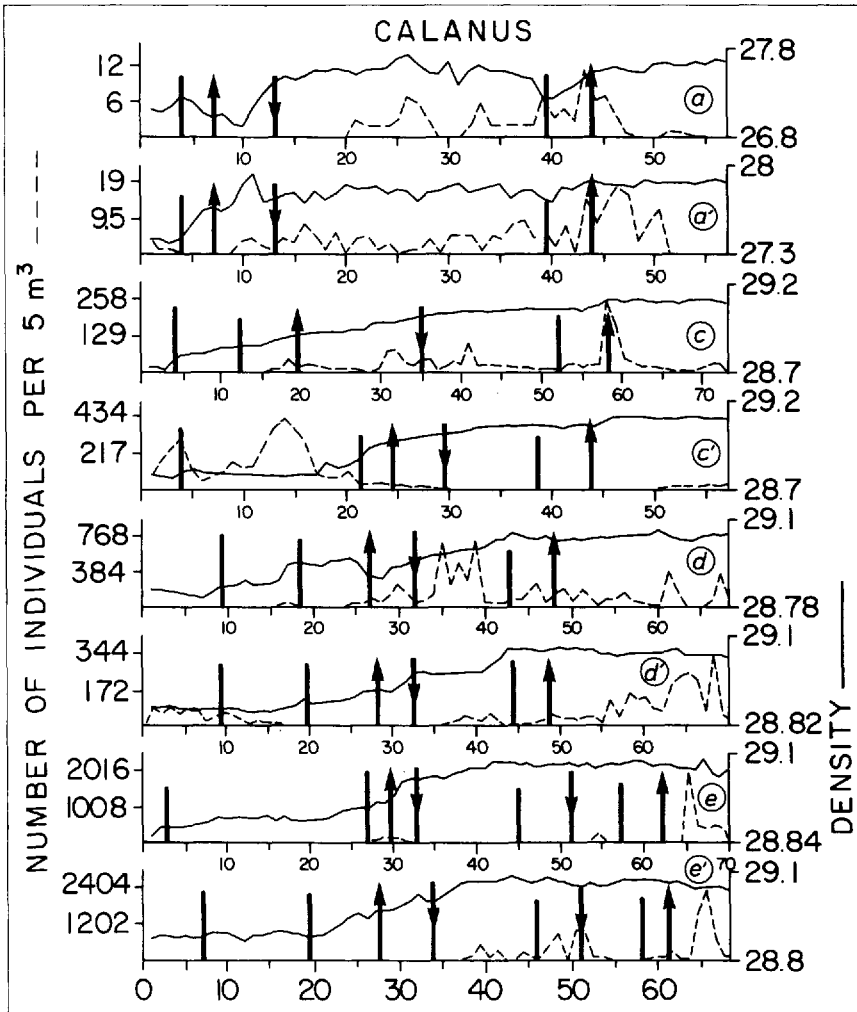


Figure 10. Same as Figure 9 but for *Calanus helgolandicus*. The dates of each record, 10th of June (1981), November 3rd (1981), January 10th (1982), March 3rd and March 30th (1982) are identified by the letters a to e successively without " " for the seaward record and with it for the return. *Calanus helgolandicus* was absent in November.

For each taxon, abundances were plotted with respect to the physical features: density averaged on five minutes and dynamic structures (divergences, convergences, etc.) as identified before (see Section 3b). Such diagrams were made for each of the 10 records in which the taxon was represented. The analysis of diagrams reveals seasonal differences of abundances for each species and, for them all, a patchy distribution along the transect (Figs. 9, 10 and 11). The spatial scales (normal to the coast) of the patch range from 4 to 7 km. *Temora stylifera* (Fig. 9) is an example of a coastal

species. This species was only abundant during autumn and early winter (November-January). Its distribution is bounded by the first divergence D1 and is only found beyond this boundary in one transect, but with very low abundances ($<5 \text{ ind. m}^{-3}$). In November and January the highest abundances were recorded at the boundary PF of the peripheral and frontal zones. This spatial distribution was conserved in March despite the low abundances observed at this time.

In comparison, *Calanus helgolandicus* was frequently observed in the offshore part of the records (Fig. 10). The highest abundances (450 ind m^{-3}) were localized in the marginal and central zones near the deep divergence D2. The spatial pattern of this species is not as strictly conserved during the year as that reported for *T. stylifera*. Some individuals were sampled in the peripheral zone in winter; e.g., up to 80 ind m^{-3} in January and 15 ind m^{-3} in March. But such samples contained only a small part of the total population.

The spatial distribution of *Acartia clausi* (Fig. 11) is more variable with season. For most of the records, peaks of abundance are observed at the beginning of the frontal zone up to the first divergence D1. That is particularly evident in spring (March-April) where the highest abundances are observed. Nevertheless, other patches are also found at the end of the frontal zone near the deep divergence D2.

Thus, it is clear that the patchy distribution of these populations and their relation with the physical structure can be described from such plots. Such analysis quickly becomes tedious with increasing number of records and taxa, and more importantly it is too subjective and allows the introduction of personal bias in the interpretation. For these reasons alternative mathematical analyses were designed to allow general and unbiased treatment of the data. The treatments were designed according to the following guidelines: (1) definition of spatial patterns, (2) classification of the variance sources such as time-space scales of observations (day and monthly variations), (3) investigation of the relationships between physical and biological spatial structures.

The general patterns of spatial distribution of the zooplankton populations. The 98 descriptors (smoothed abundances for each taxa and time of record) are reduced to 39 pattern variables by the ten particular PCA performed on each record (see section 2c). The general PCA diagonalizes the variance-covariance matrix of these pattern variables. The extracted total variance by the two first components exceeds 90%, so that the identification of groups is easy. The correlations between the pattern variables and the two first components are summarized in Figure 12 (axis 1 : 78.7%; axis 2 : 11.5% of the total variance). Nine distinct groups are defined. The partition of the original descriptors between these nine groups is described in Table 2. A new pattern variable is associated with each of the groups. Its variation along a transect summarizes the distribution of the mean abundance of the whole group of included taxa. Changes in the spatial distribution between the groups is the dominant feature of the PCA and the groups are numbered from 1 to 9 according to the offshore extent of their

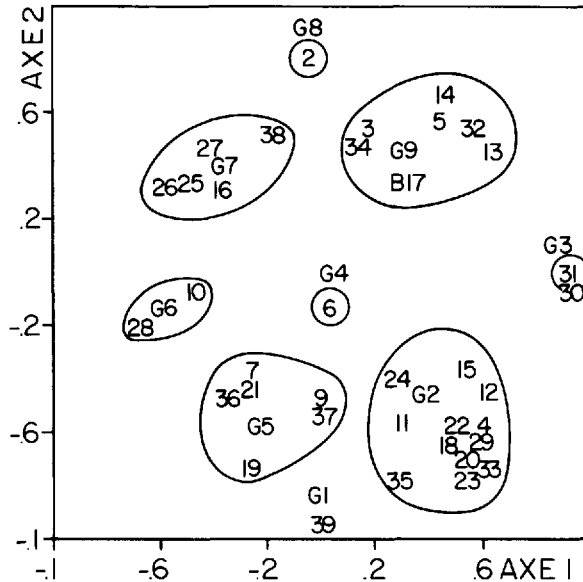


Figure 12. Results of the general principal component analysis (PCA), in terms of the positions of the 39 pattern variable (PV) axe relative to the first two principal components. Only the end points of the axes are represented. The numerical code of PV is detailed in Table 2. The nine groups (G1 to G9) are defined in the text.

highest abundance (Fig. 13). The first axis separates the groups with highest abundances at the ends (nearshore or offshore) of the transect, such as the G3 group, from those with highest abundances in the middle (e.g. G6). The second axis divides the groups according to their nearshore (G1, G2 and G5) or offshore (G7, G8 and G9) localization. The group G4, which is constituted by only one descriptor (*Centropages typicus* June, return record), is located near the origins of the axes. This descriptor shows three abundance peaks, one at the beginning, one in the middle and one at the end of the transect. Figure 13 exhibits the typical spatial pattern of the variables. For instance, the profile of *Acartia* for the November seaward transect (Fig. 11) most resembles the pattern of group 6. Effectively Table 2 indicates that *Acartia* belonged to this group at that time.

Each pattern variable defines the actual spatial distribution of species at one date, rather than for a mixture of several transects.

According to these results, the groups are principally defined by the spatial distribution patterns of the taxa, whereas the seasonal variations of these patterns have a negligible influence on this ordination.

Ordination of the observations, relationship with physical structure. The global PCA on the covariance matrix orders the 52 observations common to the ten records

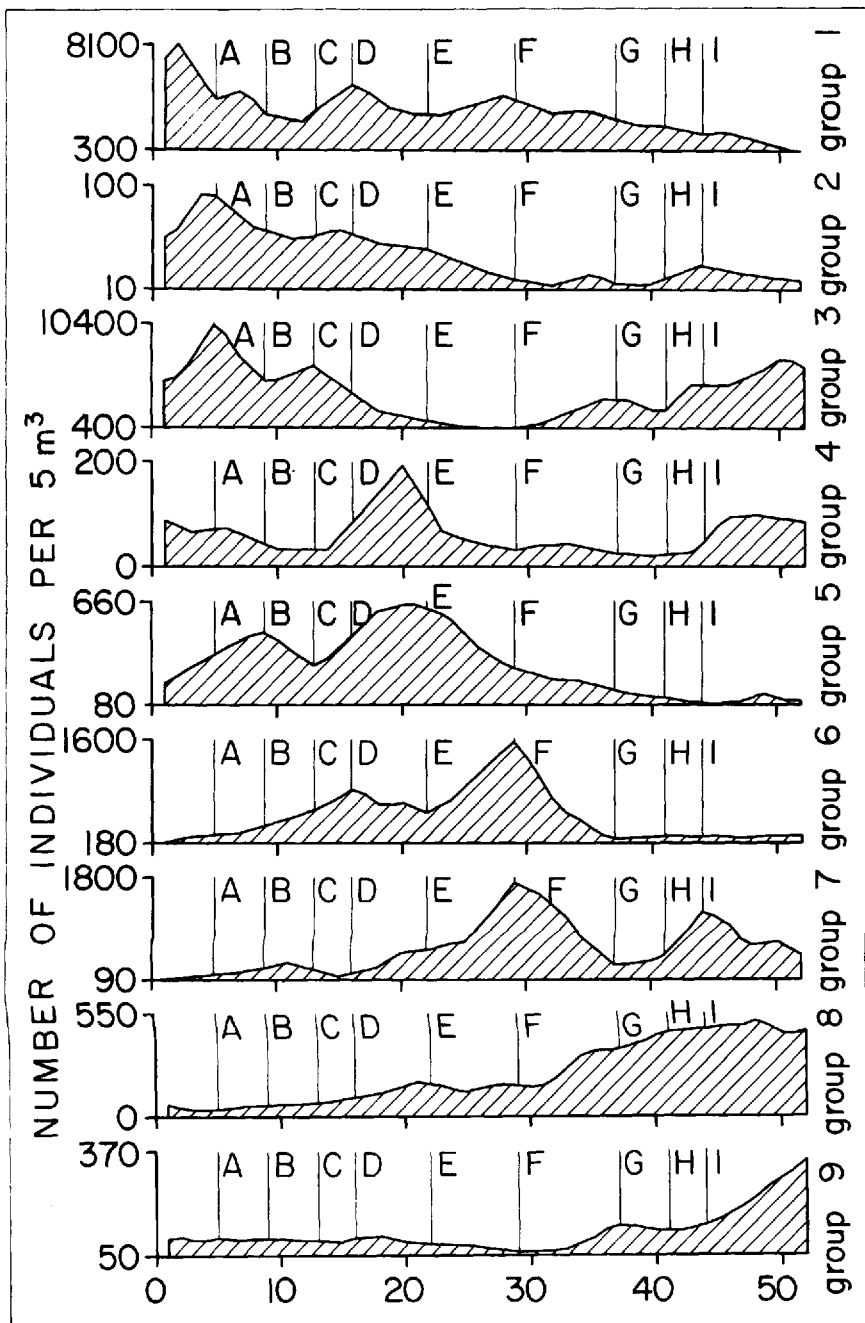


Figure 13. Distributions along the transect (x axis) of the cumulated smoothed abundances of the species constituting the nine groups (G1 to G9) defined by the general PCA. They are numbered from 1 to 9 according to the spatial pattern drifting from the coast to the offshore. Letters A to I correspond to the turning points of the graph of the 52 observations in Figure 14. For example A corresponds to the turning point encountered at the observation numbered 5. On this figure the abundance maximum of group 3 is logically seen at this number, since this group is strongly correlated with the first axis (Fig. 12).

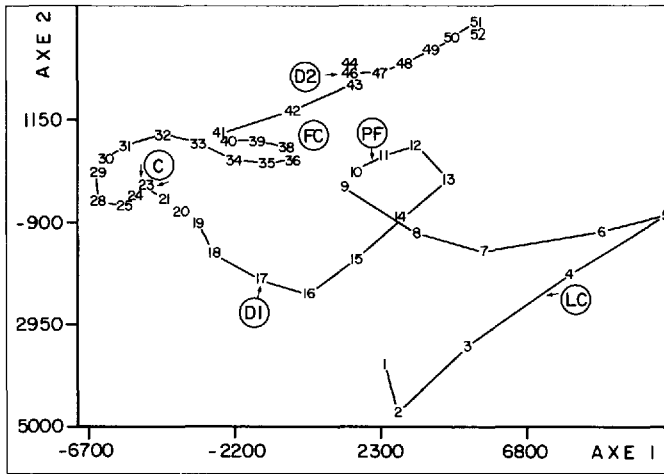


Figure 14. Projection of the end points of the 52 observation vectors in the first two principal axes as defined using the general PCA of the zooplankton data for five surveys. The mean location of the key points as deduced independently from physical and biological data are also marked.

(Fig. 14). In the plane defined by the two first principal components, the succession of the zooplankton observations roughly draws an inverted letter Z characterized by four main inflexion areas (points 5, 8 to 14, 28 to 30, 36 to 42) and minor ones (points 16 and 17, 23, 43 to 46).

These turning points of the biological structure correspond to changes in physical structure independently defined (Section 3b) from the temperature, salinity, density and fluorescence parameters. A rough estimate allows the location of physical limits by their spatial references in terms of the running number of samples (see Table 1) and the calculation of their arithmetic mean for the year. The coincidence of the average position of the physical discontinuities with the turning points defined by the PCA analysis of the faunistic observations is shown in Figure 14. Each dynamic zone defined in Section 3a, which corresponds to one convection cell of the physical pattern, contains one turning point of Z. The points 2, 5, 29 and 51 are inside the dynamic zones; onshore-LC, LC-D1, C-D2 and D2-EL respectively. The zone D1-C does not contain any turning point, but the maximum of abundance of the group 4 (Fig. 13). The absolute value of this maximum is too weak to induce a turning point through the PCA and the minor inflexions of the Z (points 8-14, 36-42 and 16, 22, 43-46) correspond to the boundaries of the main physical zones (PF, FC) and those of the dynamic zones (D1, C, D2) respectively. Given the biological significance of the turning points; i.e., maximum or minimum abundances of the pattern variables, the changes in the faunistic assemblages along the transect are coincident with the locations of the convection cells.

Table 3. The group number in which each of the 14 taxa was found, which depends on season (month) and transect (seaward or return). The arithmetic mean of lines and columns are given in the right-hand column and bottom line respectively. Zeros are excluded from the averaging.

	Jun.		Nov.		Jan.		Mar.		Apr.		Σ/n
	S	R	S	R	S	R	S	R	S	R	
<i>Euterpina</i>	0	0	0	2	0	0	0	0	2	1	1.7
<i>Corycaeus</i>	0	0	2	2	2	2	0	0	2	1	1.8
Chaetognatha	0	0	2	2	0	0	0	0	0	0	2.0
L. Echinoder.	0	0	0	0	0	2	2	2	5	1	2.4
Cladocera	2	5	2	2	0	0	2	2	5	1	2.6
<i>Temora</i>	0	0	2	2	2	5	0	0	0	0	2.7
<i>Candacia</i>	0	0	2	2	2	5	0	0	0	0	2.7
<i>Acartia</i>	5	5	6	9	2	2	2	2	5	1	3.9
<i>Centropages</i>	9	4	2	9	2	2	6	2	5	7	4.8
<i>Oithona</i>	5	9	5	9	5	2	6	3	5	1	5.0
<i>Clausoc. C</i>	8	9	2	9	9	2	7	3	5	1	5.5
<i>Clausoc. B</i>	8	9	2	9	5	2	7	3	5	7	5.7
<i>Clausoc. A</i>	8	9	5	9	5	2	7	9	5	7	6.8
<i>Calanus</i>	0	0	0	0	7	2	7	9	9	7	6.8
Σ/n	6.4	7.1	3.0	5.8	4.3	2.3	5.1	3.9	4.8	3.2	

In the issue of PCA, the taxa are classified according to their spatial distribution of abundances and the obtained patterns are related to the hydrobiological structures. In such an analysis seasonal changes appear as exchange of taxa between spatial groups between seasons. However, the influence or importance of these variations are not easily estimated or interpreted.

A variance analysis was performed to test the possible spatial distributional changes with time.

Relative importance of the sources of the time space variations. The classification of the taxa into the groups defined by the general PCA is summarized in Table 3. The data submitted to variance analysis correspond to the group numbers into which, for each transect, each of the 14 taxa were placed by the preceding PCA ordination. Groups were numbered consecutively according to the distance to the coast of the highest abundance of their contained data. Thus the numeration represents the spatial relationship of each group to the shore.

The mean for each line gives an index of the localization of the maximum abundance along the transect through the year. The coastal species (*Euterpina*, *Corycaeus* spp., Chaetognaths, echinoderm larvae, cladocerans) have mean values less than those for taxa with offshore distributions (*Oithona* spp., *Clausocalanus* A., *Calanus helgolandicus*). *Acartia clausi* and *Centropages typicus* are located between these two groups.

Table 4. Analysis of variance with three sources of variation. The number of degrees of freedom, the results of test F with significant threshold are listed.

Source of variation	Degrees of freedom	F -Test	Probability level
Total	129		
Taxa	12	17.97	**
Seaward – Return	1	0.28	
Seasons	4	3.39	*
Taxa \times Seasons	48	5.07	**
Taxa \times S – R	12	3.59	**
Seasons \times S – R	4	8.66	**
Residual	48		

**variations are significantly different at the 1% level.

*variations are significantly different at the 5% level.

Coastal species are absent or rare in fall and winter whereas offshore taxa are found closer to the neritic area at this time.

The results of a variance analysis on this coding are summarized in Table 4 (ANOVA with three variation sources: among taxa, among seasonal transects and among outward and return records).

The spatial distributions of the populations along the transect vary significantly with taxa and season but the variations between outward and return records are not significantly different on a yearly scale: e.g., the general trend of each biological descriptor was similar for both the seaward and return transects.

In addition the first interactions among the three variation sources are all significant. Thus:

- (1) the spatial distribution patterns vary from one season to another but not in the same way for all the taxa;
- (2) the differences between outward and return distributions are significant for taxa and season;
- (3) for all the taxa considered together, the heterogeneity differs importantly between the daily and yearly scales.

In conclusion, the principal results of this ANOVA are the unsteady relationships between taxa on all time scales, the significant variations of the spatial distribution patterns according to the seasons and the negligible daily variations in spatial distribution in comparison to the variability over the whole year.

c. Relations between plankton and physical structure: seasonal variations

In order to define more precisely both the relations between spatial structure of the planktonic communities and the physical structure and their seasonal changes, an inertia analysis (principal component analysis of the correspondences) was chosen which allowed simultaneous treatment of these two types of information.

Table 5. Number of samples contained in each physical zone retained from the scheme of cross-frontal circulation. Each physical zone is identified as (PF,D1(which indicates that the sample at PF is included and the sample at D1 is excluded from the sums listed in that column.

	(EC-PF((PF-D1((D1-C((C-FC((FC-D2((D2-EL)
June	6	7	11	52	8	35
November	15	19	9	28	6	22
January	31	10	20	26	11	32
March	35	16	10	22	9	45
April	43	11	9	38	18	21

The transect was segmented in six hydrodynamic zones. The peripheral zone was retained instead of the coastal zone (onshore-LC) because of the lack of physical knowledge about the coastal convergence C' and the similarity of samples in this area. The marginal zone C-D2 was divided into two zones respectively, neighboring the convergence (C-FC) and the deep divergence (FC-D2). The partition emphasizes the role of the divergence as a boundary between the marginal zone and the remainder of the central zone. The original abundances of the taxa were separated in series corresponding to each dynamic zone for each record. According to the results of variance analysis (about the negligible daily variations), the outward and return abundances were averaged to obtain estimates of the abundance in each hydrodynamical zone and season. The six physical zones so defined and the number of relevant samples for each season are summarized in Table 5. For example, in June six samples were made in the peripheral zone during outward (3) and return (3) records; the mean abundance for each taxon in this zone is the sum of the abundances of each sample divided by 6. Fourteen times 5 biological variables should have been obtained, but, due to the absence of some taxa during entire transects (Table 3), only 50 variables could be considered.

The ordination of the 50 biological variables for the six physical zones is shown in Figures 15 and 16 (axis 1: 66.7%; axis 2: 18%; axis 3: 7.9% of the total variance). The second axis separates the coastal and peripheral zone EC-PF from the marginal zone (C-FC, FC-D2). The first axis separates the central zone FC-D2 from the part of the frontal zone that is shoreward of the first convergence PF-D1 and D1-C (Fig. 15). The third axis separates the two zones bounded by the deeper divergence, i.e. the part FC-D2 of the marginal zone and the central zone D2-EL (Fig. 16).

The marginal zone corresponds to a well defined group in the three dimensional draft. This group is more similar to the group representing the remainder of the frontal zone shoreward of C than to the part of central one beyond the D2 divergence. The latter zone D2-EL appears isolated from the whole track. The first D1 divergence appears as a weaker boundary than the C convergence and the boundary PF of the peripheral and frontal zones.

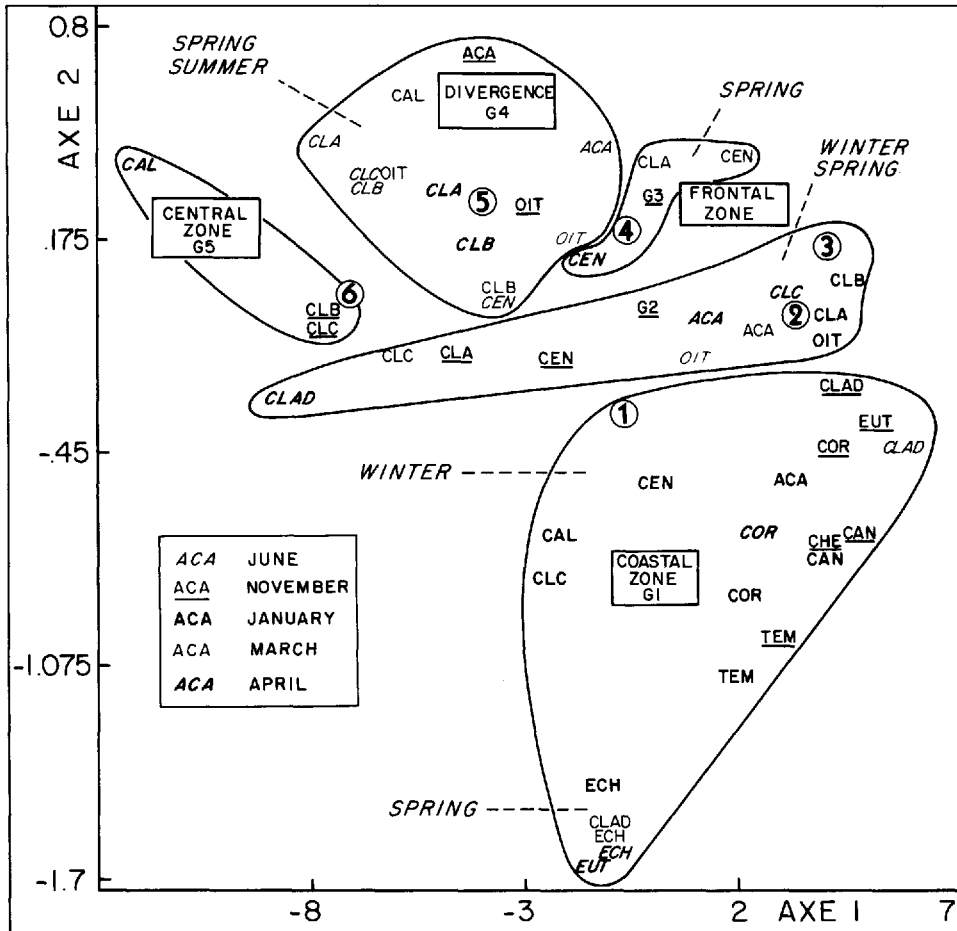


Figure 15. Results of the factorial correspondence analysis. Projection of the 50 zooplankton descriptors and the six physical zones (numbered 1 to 6 from the coast to offshore, from left to right in Table 5) in the first factorial plane (axis 2 versus 1). The attributed name of each physical zone is superimposed inside rectangles on the corresponding group of descriptors. The date key is marked on the diagram for *Acartia* as an example. CAL: *Calanus helgolandicus*; CLA, CLB, CLC: *Clausocalanus* A, B, or C; TEM: *Temora stylifera*; CEN: *Centropages typicus*; CAN: *Candacia* spp.; ACA: *Acartia clausi*; EUT: *Euterpina acutifrons*; OIT: *Oithona* spp.; COR: *Corycaeus* spp.; CLAD: Cladocerans; ECH: Echinoderm larvae.

According to this analysis, the zooplanktonic populations are divided into five distinct groups: (1) the so-called coastal populations found in the peripheral zone; the frontal populations divided into two sets dependent on whether they are distributed (2) around the D1 divergence from PF to C or (3) in the marginal part of this frontal zone C-FC; (4) the marginal populations found inside the D2 divergence FC-D2; (5) the central populations outside D2. Despite the continuity of the cross frontal water

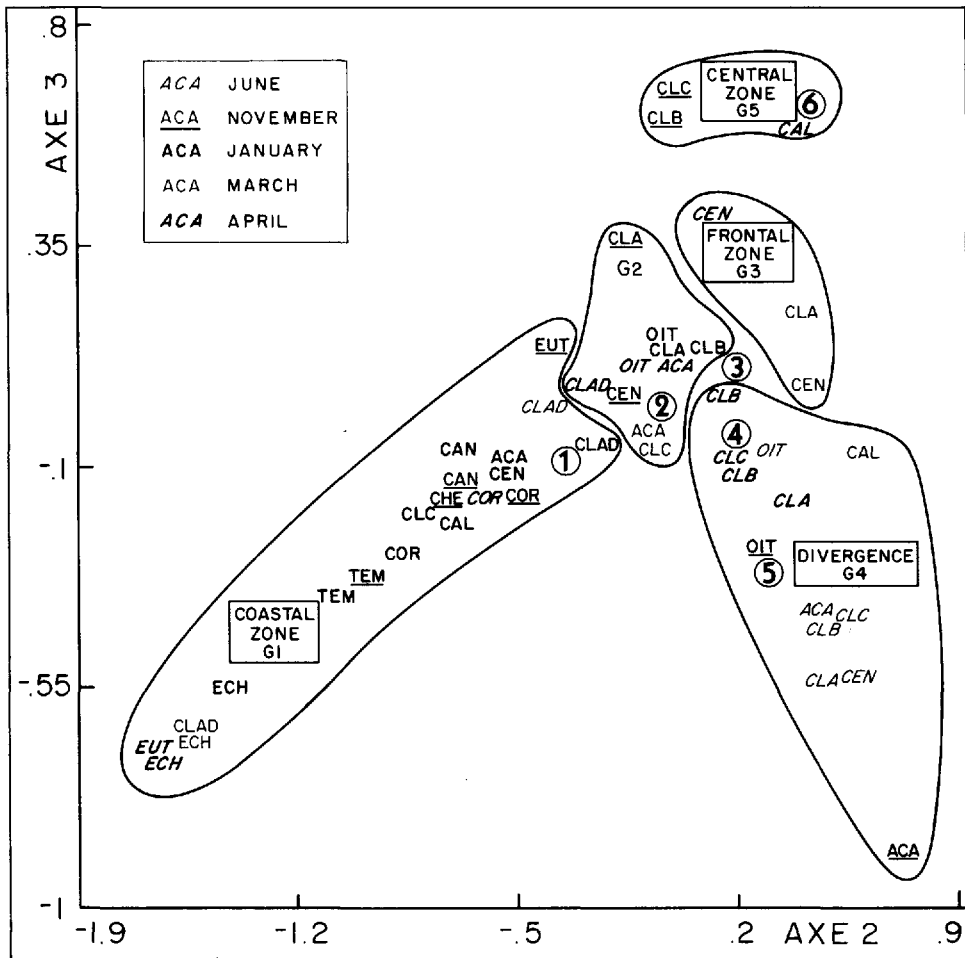


Figure 16. Same as Figure 15, but in the second factorial plane (axis 3 versus 2).

circulation in the marginal zone, the division of this area into two subzones is conserved as a result of the observed populations.

The five groups defined by the correspondence analysis are numbered G1 to G5. The G1 group consists of all strictly coastal taxa (echinoderm larvae, chaetognaths, cladocerans, *Temora stylifera*, *Candacia* spp., *Euterpina acutifrons* and *Corycaeus* spp.). In winter some taxa with spring or fall offshore distributions are represented in this group: *Calanus helgolandicus*, *Clausocalanus*, *Centropages typicus* and *Acartia clausi*. In the factorial planes the G1 points formed a "stretched cloud." The taxa with the highest abundances in spring are found at the extremities of the axes. The rare and winter taxa are closer to the origin. The G2 group corresponding to the frontal zone PF-C is more homogeneous. The component populations *A. clausi*, *Oithona* spp., and

Clausocalanus C are more or less close to the peripheral and central zones depending on the season. This zone does not appear as an exclusive biotope.

The G3 group occurs between the convergence and the boundary of the frontal and central zone C-FC. This group is spatially more coherent. It is defined by the association in spring of *C. typicus* and *Clausocalanus A*.

The G4 group corresponding to the deep divergence zone FC-D2 contains most of the populations mentioned above but only in spring and summer. Only *A. clausi* and *Oithona* spp., ubiquitous species, were observed in fall in this zone.

The final group G5 distributed on the offshore side of the divergence D2 is characterized by *Clausocalanus B* and *C* in winter and *Calanus helgolandicus* in spring. The deep divergence appears as an impassable boundary for the migrating taxa such as *A. clausi*, *C. typicus* and *Oithona* spp.

This analysis allowed the definition of the spatial distribution of all the analyzed taxa and their movements throughout the year. With the exclusion of the coastal species, all the populations showed a seasonal variation in the position of their bulk of abundance with relation to the physical zones.

In summary, there are three main physical regions from a biological point of view: the peripheral zone bounded by the frontal zone, the frontal-marginal zone bounded by the deep divergence and, to seaward, the central zone. For the zooplankton populations there are two main groups depending on whether they occur mainly in the same physical region (coastal populations) or vary from one region to another.

For the first zooplankton group the peripheral zone is an exclusive biotope; the first D1 divergence is an impossible boundary for the populations of *E. acutifrons*, *Corycaeus* spp., *T. stylifera*, *Candacia* spp., cladocerans, chaetognaths and echinoderm larvae. For the second group of populations, the frontal zone appears as their biotope in spring, the time of their highest annual abundance. At this time the group can be split into two parts, one restricted to the nearshore part of the frontal zone (inside the D1 divergence: *Clausocalanus C*, *A. clausi*, *C. typicus*) and the second in the marginal part of the frontal zone (*Clausocalanus A* and *B*, *C. helgolandicus*, *Oithona* spp.). In the other seasons, the occurrence of these populations along the transect (radial) corresponds to the part of the frontal zone which they inhabited in spring (e.g., the peripheral zone for *A. clausi* and *C. typicus*, D2 divergence and central zone for *C. helgolandicus*, *Clausocalanus A* and *B* and *Oithona* spp.). Only *Clausocalanus C* were observed in all the physical regions throughout the year. It is not surprising, because this taxa is a composite one, including small species and copepodite stages of larger clausocalanidae species.

4. Discussion and conclusion

a. The aim of mathematical treatment

Comments on PCA technique. Among the wide range of multivariate techniques, principal component analysis (PCA) was chosen, though it is restricted to the linear

covariation of the variables (Gauch *et al.*, 1977), because of its simplicity and stability. Indeed, PCA gives quite similar results for the ordination of zooplankton counts when different mathematical transformations are performed, the logarithmic form being the best model for a single transformation of all the variables (Ibanez, 1971).

Theoretically, inertia methods are not appropriate to the analysis of stochastic processes (in time and/or space) if the successive observations are correlated. However, since Cassie (1967), many authors have used PCA in order to define the interactions between variables and to ordinate samples. As contiguity in time (and space) is not taken in account by PCA, often the groups in the factorial space gather stations very distant in time and space unless the plankton community structure presents a very strong spatio-temporal autocorrelation (Mackas, 1984). The nonconformity between ecological clustering in species space and in geographical space allows neither a clear identification of the discontinuities of the series nor the detection of sequences corresponding to particular properties of the ecosystem. Several authors have proposed clustering methods with the contiguity constraint (time contiguity; Gordon (1973), Ibanez (1981, 1982, 1984), Legendre *et al.* (1985); space contiguity; Leftkovitch (1978), Lebart (1978)). A simple technique for extraction of the general trend of each variable was employed here (Ibanez, 1984). By smoothing, high frequency noise introduced by sampling and counting variability is eliminated and the autocorrelation of the successive observations are reinforced. In the factorial space, instead of a blurred cloud of sample points, a continuous succession according to the time sequence is obtained.

Different questions arise from the set of PCA used to reduce the number of variables involved in year-round analysis. First, the determination of pattern variables, was based on a semi-objective method. Indeed this procedure limits the validity of further interpretations; but no classification technique can be considered independent of some arbitrary decisions.

Secondly, because the groups were defined by their spatial distribution, seasonal variations were difficult to interpret. A coding of the spatial group according to their distance to the shore permitted the variance analysis. This led to emphasis of the significance of the seasonal variations. One of the first positive result was that plankton distribution did not differ significantly among daily replicate records in comparison to seasonal variations throughout the year. This test of reproducibility of the records for small time duration was important (Ibanez, 1976) considering that effects of vertical distribution were neglected by discrete horizontal sampling. Note that such daily stability has already been mentioned (for March) in relation to the spatial structures of zooplankton (Boucher, 1984), phytoplankton (Thévenot, 1981) and physical field (Prieur, 1983).

Thirdly, nonlinear relationships between variables are not taken into account by the PCA model. Thus the particular shape of the line joining the observations after the grand PCA, could reflect an artificial structure. However in this case, considering the number of turning points actually corresponding to physical changes, only an

improbable coincident set of artifacts could explain such pattern. Nevertheless a second independent analysis was performed in order to characterize these relationships. The precise description of the seasonal and spatial pattern of the different taxa by the correspondence analysis showed complementary and not contradictory results in connection to those obtained by the PCA treatment.

b. Origin of the defined spatial pattern

Role of the dynamic features. For each season, zooplankton populations are segregated precisely according to the discontinuities of their environment. Statistically, zooplankton populations can be grouped into communities defined by their spatial distribution in relation to the physical structures. The limits of distributions of these communities are well defined by the vertical movements of water (divergences D1 and D2, convergence C). Nevertheless, these dynamic structures are not always impassable boundaries for the populations. Seasonal variations are also superimposed on this scheme. All the analyzed populations inhabit a territory defined by a particular physical zone; but most of them (except the strict coastal species) are not restricted to the same water mass all year long. For these species, their environment (i.e., water mass) changes with the considered phases of their biological cycle. For example *C. typicus* and *A. clausi* are coastal species in fall and winter; inhabit the frontal zone (neighboring the first divergence D1 for *A. clausi*) in spring, their annual peak abundance period; and are found near the deep divergence D2 in summer. *Oithona* spp. and *Clausocalanus* A and B exhibit their highest spring abundances in the deep divergence and marginal zones, respectively. These latter species are never encountered in the peripheral (coastal) zone.

The spatial patterns of the populations change according to species and season despite the fact that the general physical structure of the Ligurian front is conserved. The vertical cross-frontal circulation is permanent, but varies in intensity, throughout the year. The inclined advections are probably weakest in summer and autumn and strongest in winter, depending on whether the stratification and related slopes of the isopycnals are high or low respectively. Their intensities are intermediate in spring. If the accumulation of zooplankton was only dependent on hydrodynamic features (e.g., convergence speed), the maxima of abundances along a survey would always be observed inside the frontal zone, especially in winter. In actual fact, these maxima are found there only for some species and in spring, the season of their maximum growth and that of maximum algal biomass. Furthermore a species exhibits changes in its response to the seasons, despite the conservation of dynamical factors throughout the year. In addition, all species do not exhibit the same abundance distribution although their morphological characteristics and swimming capabilities are similar. In particular, as mentioned for the area studied here (Boucher, 1984), this second set of data confirms that copepods with similar morphology (e.g., *Centropages typicus* and *Temora stylifera*) do not respond in the same manner to the same dynamical

environment. For these reasons hydrodynamical features are insufficient to explain the observed distributions. Other ecological requirements and behavior are involved.

Biological processes at the yearly scale. The strict coastal species (echinoderm larvae, chetognaths, cladocerans, *Euterpina acutifrons*, *Candacia* spp., *Corycaeus* spp., and *Temora stylifera*) never occur beyond the first divergence (D1) whereas *Acartia clausi* and *Centropages typicus* are encountered throughout the area studied. The annual peak of density of all these species appears in the same season as observed in the Bay of Villefranche (Seguin, 1981); Although, relative to the Bay of Villefranche, strict coastal species are less abundant along the transect and the *Acartia-Centropages* group, localized in spring in the frontal zone is more abundant. Less strict ecological requirements could explain survival of the later group when entrained away from the coastal system, allowing them to multiply when they encountered seasonally favorable conditions far from shore.

In contrast, the role of seasonal vertical migrations is obvious in the variations observed for the other taxa.

Calanus helgolandicus adults appear in January (1 to 15 ind m⁻³). In spring, cohorts with dominant C4 and C5 are localized in the frontal area. This biomass (up to 500 ind m⁻³) disappears in May (unpublished results from 1982 TROPHOS II cruise) and June when a few adults (1–4 ind m⁻³) have an offshore distribution (Boucher, 1984). The summer population migrates to a deeper area. A vertical distribution between 600–1500 m was observed in May, June and October in the Adriatic Sea whereas a bimodal distribution with an additional 0–200 m population was observed in February, March and April (Scotto di Carlo *et al.*, 1984). This shallower distribution was also observed, in late winter-early summer only in different neritic areas of the western Mediterranean Sea (Vives, 1963, 1966; Vucetic 1966, 1967; Gaudy, 1972). Such a seasonal migration is known for the Pacific and Atlantic closely related species *Calanus marshallae*, *C. glacialis*, *C. finmarchicus*, *Calanoides carinatus* as well as *C. helgolandicus* (Longhurst, 1967; Marshall and Orr, 1972; Binet and de Sainte Claire, 1975). It is a life strategy to exploit seasonal production (spring bloom, upwelling. . .) and to ensure survival during unfavorable seasons. The onset and end of the overwintering stage are determined by exogeneous factors: temperature, and food availability and quality (Binet and de Sainte Claire, 1975) but also endogeneous factors (Tande, 1982; Hirche, 1983; Bamsted and Ervik, 1984). For the Mediterranean form, such endogeneous factors are also necessary for the onset of both the late winter up-migration (deep environment without light and temperature cycle) and the early summer down-migrations. In this sense, we add several involved questions to those proposed by Peterson *et al.* (1979) in their consideration of the role of life history adaptations in zonation patterns observed in the Oregon upwelling zone.

The other offshore taxa (*Clausocalanus* A and B) and, to lesser extent, *Oithona* (not found offshore in summer) have seasonal spatial patterns similar to *C. helgolandicus*.

They are encountered throughout the area all the year round but in lower density. Their annual peak abundance occurs in summer: in the marginal zone for the two former taxa and in the frontal zone for the latter. Seasonal vertical migrations of sibling species have been analysed in the Tyrrhenian Sea (Hure *et al.*, 1980). They are weaker migrants than *C. helgolandicus* with shallower (about 100 m deep) fall and winter distributions. Their occurrence at a low density outside the production season could correspond to upwelling in the surface layer of a portion of the deeper populations. For these species as for *C. helgolandicus* the role of exogeneous and endogeneous factors in the seasonal vertical migrations is an unresolved question.

Calanus helgolandicus adults do not increase significantly in spring and their distribution, not analyzed here, is different of these of the later developmental stages (Boucher, 1984; Ibanez and Boucher, 1987). These observations are consistent with the zonation observed for *C. marshallae* in the Oregon upwelling zone, as determined by differences in the depth distribution and behavior (Peterson *et al.*, 1979). In the case of the Ligurian marine front, active swimming to maintain a depth localization by interacting with neighboring convergent and divergent circulation cells could compensate cross-frontal drift, as discussed by Boucher (1984). This scheme, but at a larger spatial scale, is similar to the model of the distribution of active swimmers in Langmuir cells (Stavn, 1971, in Mackas *et al.*, 1985). The differences in species patterns in the frontal zone are consistent with such an interpretation.

Further improvement of this scheme and an extension to the other populations requires more observations on the vertical distribution at both daily and annual scales. Nevertheless it appears that hydrodynamic processes can favor or inhibit the spatial distributions of individuals. In both cases, observed maintenance of distributions with or despite dynamic dispersion involved active behavioral processes determined by physiological status.

The analyzed results emphasize strong relationships between zooplanktonic spatial patterns and dynamic features. They remain ambiguous, (in the sense of Legendre and Demers, 1984), however, because one of the causative agents, the behavior, is deduced rather than observed. Nevertheless they illustrate the complex interaction of different time and space scales and the cross-interactions between physiological processes, behavior and hydrodynamics. Spatial scales are defined according to hydrodynamic features. Time scales should be defined according to species life cycles or according to cycles other than calendar dates.

Biological significance of the frontal area. At the seasonal scale, all species, except the strict coastal ones which exhibited seasonal peaks, were found to inhabit the frontal zone in this period of their annual cycle. In this manner the frontal zone appears as a nursery area where species are localized in their spawning growing phase. Constant or increasing abundances between early and late March considered with regard to the generation time of 3 to 4 weeks at these temperatures, as well as the presence of

	JUNE			NOVEMBER			JANUARY			EARLY MARCH			LATE APRIL			n:68
	S	m	R	S	m	R	S	m	R	S	m	R	S	m	R	
<i>Callinanus helgolandicus</i> C6	1.7	2.5	3.9	4.3	23.2	38.4	75.0	106.7	104.7	151.5	48.9	67.5	71.2	259.2	180.1	407.5
<i>Callinanus helgolandicus</i> C1									39.7	39.9	18.4	14.0	26.9	52.2	12.7	25.9
<i>Callinanus helgolandicus</i> C2									57.2	55.8	20.5	24.0	30.3	22.2	26.7	36.2
<i>Callinanus helgolandicus</i> C3									63.1	56.3	35.5	40.2	94.7	59.1	33.4	40.6
<i>Callinanus helgolandicus</i> C4									112.5	124.1	54.2	77.9	51.6	203.8	84.1	61.0
<i>Callinanus helgolandicus</i> C5										2.8	4.6	4.6				407.0
<i>Naupacalanus glacialis</i>								5.4	7.6							
<i>Naupacalanus glacialis</i>								14.8	24.9							
<i>Eucalanus</i> spp.								10.9	15.6							
<i>Callinectes</i> spp.										3.2	6.0					
<i>Clusocalanus</i> A	44.5	52.2	55.5	38.4	20.1	14.6	101.7	88.5	38.5	35.0	14.4	18.1	427.0	462.4	339.2	327.9
<i>Clusocalanus</i> B	321.6	245.7	225.7	151.0	37.9	32.5	209.8	254.6	253.1	227.3	90.8	80.7	910.2	1447.7	1321.5	1307.8
<i>Clusocalanus</i> C	376.4	256.3	356.6	239.9	12.0	12.5	43.6	61.6	48.5	72.8	482.2	560.1	1566.8	1768.2	6600.9	4856.5
<i>Eucalanus</i> spp.																7.2
<i>Eucalanus</i> spp.																28.4
<i>Scolecithricella</i> spp.																
<i>Temora stylifera</i>																
<i>Petromma</i> spp.																
<i>Centropages</i> spp.																
<i>Centropages typicus</i> Ad.	36.5	38.8	68.7	54.1	49.2	52.7	54.3	55.6	6.7	7.2	7.6	13.8	272.9	352.1	68.6	40.1
<i>Lucicutia</i> spp.									4.0	6.8			180.3	222.1	50.9	33.3
<i>Lucicutia</i> spp.																
<i>Heterorhabdus</i> spp.																
<i>Canthacia</i> spp. Ad. juv.																
<i>Acopetes</i> cf. <i>Acopetes</i>	48.5	44.3	55.5	45.6	11.4	13.5	2.2	2.9	1.6	3.9	1.6	2.4	248.8	230.7	216.2	291.8
<i>Euterpina aculeifrons</i>																
<i>Diithona</i> spp.	929.3	463.7	524.1	318.8	13.1	14.2	11.3	11.9	55.4	56.8	38.6	49.9	1546.5	1272.3	414.6	342.7
<i>Clypeosoma</i> sp.																
<i>Oncaea</i> spp.																
<i>Sapphirina</i> spp.																
<i>Conyctus</i> spp.																
<i>Siphonophora</i>	2.7	2.8	0.7	1.3												
<i>Cladocerans</i>	15.5	33.1	18.8	37.6	26.8	58.8	13.6	29.6								
<i>Ostracoda</i>					2.0	4.8										
<i>Euphausiids</i> ad. juv.					2.9	6.3	4.4	4.4	4.4	5.8	6.4					
<i>Crustacean</i> larvae					39.4	43.7	55.3	70.5	1.1	3.5	9.3	9.1	59.0	54.6	32.3	68.3
<i>Pteropoda</i>													10.1	15.2	12.4	15.6
<i>Chaetognath</i> larvae																
<i>Amphipods</i>	0.5	0.9	1.7	2.3	2.6	5.5	2.2	4.0								
<i>Appendicularians</i>	1.4	7.2	4.5	14.9												
<i>Thalassera</i>																
<i>Echinoderm</i> larvae																
Eggs																
<i>Nauplius</i>																
<i>Acantharians</i>					15.6	21.1	21.2	45.9	9.7	16.5	7.3	5.5	14.5	11.9	15.0	13.1

APPENDIX Mean abundance (m), standard deviation (σ) of the 44 numbered taxa for each seaward (S) or return (R) records (n is the number of samples) at successive months during 1981 and 1982. The + symbol indicates an observed presence of specimen with very low abundance.

copepodite 4 and 5 cohorts for *Calanus helgolandicus*, are consistent with this hypothesis. In such areas trophic conditions are particularly favorable for planktonic filter feeders. The frontal zone was adjacent to the absolute maximum of phytoplankton biomass (in terms of fluorescence F), where nutrients and stability conditions should activate primary production. In this Ligurian marine front, the phytoplanktonic features and therefore, the available food for zooplankton, are highly variable over distances of a few kilometers (Thévenot, 1981; Prieur and Tiberti, 1984). But no exact co-occurrence of phytoplankton and zooplankton peaks was found. Nevertheless in establishing such a relationship, other factors such as grazing pressure and quality of the primary production in terms of age and nature of phytoplankters should be taken into account (Herman *et al.*, 1981). The physiological requirements of individuals should also be considered (see Longhurst, 1981, for a review of this question). Such a study would have to include too many parameters of food and grazer characteristics to be included here.

Acknowledgments. We wish to thank J. D. Gaffet for her technical assistance in counting the organisms and S. Gros for the diagrams. We also thank the crew and officers of *N. O. Korotneff* for their able assistance during the Pretrophos and Pros VI cruises, and F. Louis and D. Tailliez for the maintenance of the electronics and their participation at sea. Gratitude is extended to C. Brownlee and G. Mitchelson for readings and commenting on the manuscript. The research was supported by CNRS (LA 353, ERA 228, GRECO 034) and CNEXO under Grant 62 625 and Project 111 121.

REFERENCES

- Bamstedt, U. and A. Ervik. 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda calanoida) overwintering on the west coast of Norway. *J. Plankton Res.*, 6, 843-858.
- Bennett, S. L. 1986. The relationship between vertical, diapycnal and isopycnal velocity and mixing in the ocean general circulation. *J. Phys. Oceanogr.*, 16, 1, 167-174.
- Bethoux, J. P., L. Prieur and F. Nyffeler. 1982. The water circulation in the NW Mediterranean Sea, its relations with wind and atmospheric pressure, in *Hydrodynamics of Semi-enclosed Seas*, J. C. Nihoul, ed, Elsevier, 129-142.
- Bethoux, J. P. and L. Prieur. 1983. Hydrologie et circulation en Méditerranée Nord-Occidentale. *Pétroles et Techniques*, ISSN 0152-5425, 299, 25-34.
- Binet, D. and E. Suisse de Sainte Claire. 1975. Le copépode planctonique *Calanoides carinatus*: répartition et cycle biologique au large de la côte d'Ivoire. *Cah. ORSTOM, ser. Oceanogr.*, 13, 15-30.
- Boucher, J. 1982. Peuplement de copépodes des upwellings côtiers Nord-Ouest africains. II-Maintien de la localisation spatiale. *Oceanol. Acta*, 5, 199-207.
- 1984. Localization of zooplankton populations in the Ligurian marine front: role of ontogenic migration. *Deep Sea Res.*, 29, 953-965.
- Cassie, M. 1967. Principal component analysis of the zooplankton of Lake Maggiore. *Mem. Inst. Ital. Idrobiol.*, 21, 129-144.
- Cassie, R. M. and A. D. Michael. 1968. Fauna and sediments of an intertidal mud flat: a multivariate analysis. *J. Exp. Mar. Biol. Ecol.*, 2, 1-23.

- Chardy, P. and J. C. Leguen. 1971. Essai d'analyse multivariée d'une série de chalutages au Congo. Cah. ORSTOM. sér. Océanogr., 9, 97-106.
- Crepon, M., L. Wald and J. M. Monget. 1982. Low frequency waves in the Ligurian Sea during December 1977. J. Geophys. Res., 87, 595-600.
- Gascard J. C. 1978. Mediterranean deep water formation, baroclinic instability, and oceanic eddies. Oceanologica Acta, 1, 315-330.
- Gauch, H. G., R. H. Whittaker and T. R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. J. Ecol., 65, 157-174.
- Gaudy, R. 1972. Contribution à la connaissance du cycle biologique de copépodes du golfe de Marseille. 2: Etude du cycle biologique de quelques espèces caractéristiques. Tethys, 4, 175-292.
- Gordon, A. D. 1973. Classification in the presence of constraints. Biometrics, 29, 821-827.
- Gostan, J. 1967. Etude du courant géostrophique entre Villefranche sur Mer et Calvi. Cah. Oceanogr., 19, 329-345.
- Contribution à l'étude hydrologique du Bassin Liguro-Provençal entre la Riviera et la Corse. Thèse Doct. Etat. Fac. Sci. Paris, 206 pp.
- Herman, A. W., D. D. Sameoto and R. A. Longhurst. 1981. Vertical and horizontal distribution patterns of copepods near the shelf break south of Nova Scotia. Can. J. Fish. Aquatic Sci., 38, 1065-1076.
- Hirche, H. J. 1983. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. Mar. Biol., 11, 291-297.
- Hure, J. and B. Scotto di Carlo. 1974. New patterns of diurnal vertical migration of some deep water copepods in the Tyrrhenian and Adriatic Sea. Mar. Biol., 28, 179-184.
- Hure, J., A. Ianora and B. Scotto di Carlo. 1980. Spatial and temporal distribution of copepod communities in the Adriatic Sea. J. Plankton Res., 2, 295-316.
- Ibanez, F. 1971. Effet des transformations des données dans l'analyse factorielle en écologie planctonique. Cah. Océanogr., 23, 336-349.
- 1976. Contribution à l'analyse mathématique des événements en écologie planctonique. Bull. Inst. Oceanogr. Monaco, 72, 1-96.
- 1981. Immediate detection of heterogeneities in continuous oceanographic recordings. Application to time series analysis of changes in the Bay of Villefranche-sur-mer. Limnol. Oceanogr., 26, 336-349.
- 1982. Sur une nouvelle application de la théorie de l'information à la description des séries chronologiques planctoniques. J. Plankton Res., 4, 619-632.
- 1983. Optimisation de la représentation des séries chronologiques planctoniques multivariées. Rapp. Comm. Int. Mer Médit., 28, 113-115.
- 1984. Sur la segmentation des séries chronologiques planctoniques multivariées. Oceanologica Acta, 7, 481-491.
- Ibanez, F. and J. Boucher 1987. Anisotropie des populations zooplanctoniques dans la zone frontale de la mer Ligure. Oceanologica Acta (in press).
- James, I. D. 1984. A three dimensional numerical shelf-sea front model with variable eddy viscosity and diffusivity. Continental shelf Res., 3, 60-98.
- Kao, T. W. 1980. The dynamics of oceanic fronts. Part I: The Gulf Stream. J. Phys. Oceanogr., 10, 483-490.
- Lebart, L. 1978. Programme d'agrégation avec contraintes (C. A. H. contiguïté). Cah. Annal. Données, 3, 275-287.
- Lefkovich, L. P.: 1976. Hierarchical clustering from principal coordinates: an efficient method for small to very large number of objects. Math. Biosci., 31, 154-174.

- 1978. Cluster generation and grouping using mathematical programming. *Math. Biosci.*, *41*, 91–110.
- Legendre, L. 1981. Hydrodynamic control of marine phytoplankton production: the paradox of stability, in *Ecohydrodynamics*, J. C. Nihoul, ed, Elsevier, Amsterdam, 191–207.
- Legendre, L. and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.*, *41*, 2–19.
- Legendre, P., S. Dallot and L. Legendre. 1985. Succession of species within a community chronological clustering, with applications to marine and freshwater zooplankton. *Am. Nat.*, *125*, 257–288.
- Longhurst, A. R. 1967. Vertical distribution of zooplankton in relation to the Eastern Pacific oxygen minimum. *Deep Sea Res.*, *14*, 51–63.
- 1981. Significance of spatial variability, in *Analysis of Marine Ecosystems*, A. R. Longhurst, ed, Academic Press, 415–441.
- Lorenzen, C. 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnol. Oceanogr.*, *12*, 343–346.
- Mackas, D. L. 1984. Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. *Limnol. Oceanogr.*, *29*, 451–471.
- Mackas, D. L., K. L. Denman and M. R. Abott. 1985. Plankton patchiness: biology in the physical vernacular. *Bull. of Mar. Sci.*, *37*, 652–674.
- Mackas, D. L. and R. W. Owen. 1982. Temporal and spatial resolution of pump sampling systems. *Deep Sea Res.*, *29*, 883–892.
- Margalef, R. and F. Gonzalez-Bernaldez. 1969. Grupos de especies asociadas en el fitoplancton del mar Caribe. *Inv. Pesq.*, *33*, 287–312.
- Marshall, S. M. and A. R. Orr. 1972. *The Biology of a Marine Copepod*. Springer Verlag, Berlin, 195 pp.
- Mazza, J. 1963. Copépodes des côtes orientales de Corse. *Rapp. Comm. int. Mer Médit.*, *17*, (2), 563–572.
- 1968. Données sur la répartition verticale des copépodes de la surface aux eaux profondes en Méditerranée Occidentale. *Rapp. Comm. int. Mer Médit.*, *19*, (3), 501–503.
- Nyffeler, F., J. Raillard and L. Prieur. 1980. Le bassin LiguroProvençal, étude statistique des données hydrologiques 1950–1973. *Rapp. Sci. Tech. CNEXO*, *42*, 163 pp.
- Peterson, W. T., C. B. Miller and A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep-Sea Res.*, *26*, 467–494.
- Prieur, L. 1973. Interpretation d'une zone de forte turbidité sur la radiale Nice Calvi. *Rapp. comm. int. mer Médit.*, *22*, 59–61.
- 1979. Structures hydrologiques, chimiques et biologiques dans le Bassin LiguroProvençal. *Rapp. comm. int. Mer Médit.*, *25–26*, (7), 75–76.
- Hétérogénéité spatio-temporelle dans le Bassin LiguroProvençal. *Rapp. Comm. int. Mer Médit.*, *27*, (6), 177–179.
- 1983. Bilan des opérations en Mer Ligure. *Compte rendu d'activités 1980–1983 du GRECO 34 du CNRS*, 37–61. (Unpublished document).
- Prieur, L., J. P. Bethoux, M. Albuissou, L. Wald and J. M. Monget. 1981. A comparison between infra-red satellite images and sea truth measurements. in *Oceanography from Space*, J. F. Gower, ed, Plenum Press, *13*, 159–167.
- Prieur, L. and M. Tiberti. 1985. Identification et échelle des processus physiques et biologiques responsables de l'hétérogénéité spatiale près du front de Mer Ligure. *Rapp. Comm. int. Mer Médit.*, *29*, (3), 35–36.
- Scotto di Carlo, B., A. Ianora, E. Fresi and J. Hure. 1984. Vertical zonation patterns for

- Mediterranean copepods from the surface to 3000 m at a fixed station in the Tyrrhenian Sea. *J. Plank. Res.*, **6**, 1031–1056.
- Seguin, G. 1981. Dynamique des copepodes pélagiques en rade de Villefranche sur Mer à partir de prélèvements quotidiens (année 1972). *Oceanologica Acta*, **4**, 405–414.
- Stavn, R. H. 1971. The horizontal-vertical distribution hypothesis Langmuir circulation and *Daphnia* distribution. *Limnol. Oceanogr.*, **16**, 453–466.
- Stocchino, C. and A. Testoni. 1977. Nuove osservazioni sulla circolazione delle correnti nel Mar Ligure, Istituto Idrografico della Marina F. C., *1076*, 40 pp.
- Tande, K. S. 1982. Ecological investigations on the zooplankton community of Baljsforden, Northern Norway: generation cycles and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in copepod *Calanus finmarchicus*. *J. Exp. Mar. Biol. Ecol.*, **62**, 129–142.
- Tang, C. L. 1982. A model for frontal upwelling, in *Hydrodynamics of Semi-Enclosed Seas*, J. C. Nihoul, ed, Elsevier, Amsterdam, 329–348.
- 1983. Cross front mixing and frontal upwelling in a controlled quasi-permanent density front in the Gulf of the Saint-Lawrence. *J. Phys. Oceanogr.* **13**, 1468–1481.
- Thévenot, A. 1981. Relations entre la chlorophylle et l'hydrographie en Mer Ligure. Analyse mathématique des séries enregistrées en continu à la surface. Thèse 3ème cycle, Univ. P. et M. Curie, Paris, 100 pp.
- Unesco. 1981. Tenth report of the joint panel on oceanographic tables and standards, Sidney BC Canada, 1–5th, 1980, Unesco tech. papers in Marine Science, **36**, 23 pp.
- Vives, F. 1963. Sur les copépodes pélagiques (Calanoida) de Méditerranée Occidentale. *Rapp. Comm. int. Mer Médit.*, **17**, 175–292.
- 1966. Zooplankton neritico de las Aguas de Castellon (Méditerranée Occidentale). *Invest. Pesq.* **30**, 49–166.
- Vucetic, T. 1966. On the biology of *Calanus helgolandicus* (Claus) from the Veliko jezero. I. Mljet. *Acta Adriatica*, **6**, 91 pp.
- 1967. Zooplankton investigations in the sea water lakes "Malo jezero" and "Veliko jezero" on the Island of Mljet (1952–1954). *Acta Adriatica*, **6**, 51 pp.
- Woods, J. D. 1980. Do waves limit turbulent diffusion in the ocean? *Nature, London*, **288**, 219–224.
- Woods, J. D., R. L. Wiley and M. G. Briscoe. 1977. Vertical circulation at fronts in the upper ocean. A voyage of Discovery, M. Angel, ed., *Deep-Sea Res.*, **24** (Suppl.), 253–275.

