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Appendicularian assemblages in a shelf area and their relationship with temperature

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Abstract. The structure of the community of appendicularians was described by multivariate analyses throughout a seasonal cycle on the central Cantabrian coast. It is shown by correlation and principal components analysis that the appendicularian species may be arranged in a successional sequence in relative abundance that is closely coupled to a temperature gradient. This sequence starts with *Fritillaria borealis*, which exhibits highest relative abundance during January, being sequentially followed by *Oikopleura dioica*, *Fritillaria pellucida*, *Oikopleura fusiformis* and *Oikopleura longicauda*. This species numerically dominated the community from September to December. Sea surface temperature and the temperature at the depth of the chlorophyll maximum were both reliable predictors of the species composition of the community. However, only the latter provided an adequate explanation for the persistence of cryophilic communities in stratified oceanic environments and the dominance of thermophilic communities after the autumn mixing period. Under stratified conditions, surface temperatures are high (up to 21°C), but temperatures at the depth of the chlorophyll maximum are low (<15°C). These differences disappear after the autumn mixing, when the water column exhibits a uniform temperature profile (16°C). Critically, however, although there is a sharp decline in surface temperature, water at the depth of the chlorophyll maximum is warmer than during stratification. A simple conceptual model is proposed to account for these features and predictions are made regarding the vertical distribution of appendicularians during stratification. The relevance of non-anthropomorphic temperature measures, such as the temperature at the depth of the chlorophyll maximum, for other zooplankton groups is also discussed.

Introduction

Appendicularians are amongst the most abundant and ubiquitous non-crustacean mesozooplankton. They exhibit some uncommon biological properties, which explain the increased attention that has been devoted to this group during the last few decades. Their short generation time (e.g. Paffenhöfer, 1973; Alldredge and Madin, 1982) may cause significant increases in their population size (Seki, 1973). The ecological role of appendicularians is further enhanced by the fact that they are able to feed on extremely small particles, down to the submicrometric particle size range (Flood *et al.*, 1992). Therefore, in contrast to most copepods, they may also thrive on particle sizes corresponding to the 'microbial loop', a relevant trophic compartment in the dynamics of oligotrophic oceanic systems. This ability is due to the very fine meshes of their filtration mechanism (Flood, 1978; Deibel *et al.*, 1985; Deibel and Powell, 1987), a unique structure in the marine plankton. This mechanism, often called 'filter house', is continuously secreted and discarded (Fenaux, 1985) which suggests the appendicularians' role as sinks of organic carbon in pelagic ecosystems (Alldredge, 1976; Gorsky *et al.*, 1984). Appendicularians are also found in the diet of some larval fishes (Shelbourne, 1962; Keats *et al.*, 1987), which has led to the view that appendicularians are a trophic link between primary production and nekton.

Despite the large amount of information on their ecological role in pelagic ecosystems, the structure of communities of appendicularians remains to be properly assessed. The work of Fenaux (1961) was perhaps the first attempt to summarize the patterns of seasonal succession of appendicularians. He showed that the dominance of the different species in Villefranche (France) followed a well-defined sequence that started with *Fritillaria borealis* in January and was sequentially followed by *Fritillaria pellucida*, *Oikopleura dioica*, *Oikopleura fusiformis* and *Oikopleura longicauda*, which dominated the community from May to November. The interpretation of this pattern is difficult (Fenaux, 1961) and there have been no attempts to test the validity of this series in other geographical areas, or to propose possible causes.

In the central Cantabrian coast, the appendicularian fauna is similar to that of Villefranche. It corresponds to a transitional area in which there is a latitudinal substitution of the warm-water species *O.longicauda* by the temperate *O.fusiformis* from south to north (Fenaux, 1967). This area is characterized by alternate periods of winter mixing and summer stratification (Botas *et al.*, 1989b) typical of temperate seas. This simple hydrography is complicated by the frequent irruption of saline water bodies during the mixing period (Botas *et al.*, 1988) carrying allochthonous plankton populations within them (Fernández *et al.*, 1991) and also a persistent small-scale upwelling during the summer, probably favoured by the bottom topography (Botas *et al.*, 1990). These processes represent important sources of variability in plankton communities.

Our aim in this paper is to describe the seasonal changes of the structure of the community of appendicularians in the central Cantabrian coast by means of statistical multivariate methods. The species composition of this community is related to the physical and biological properties of the water column, and causal mechanisms for the patterns of organization of the appendicularian assemblages are proposed.

Method

Samples for the seasonal cycle were collected from 13 stations off Cape Peñas (north of Spain, Figure 1) on a total of nine cruises (COCACE cruises; Botas *et al.*, 1989a; Cabal *et al.*, 1990), made at almost monthly intervals in January, March, April, May, June, July, September, October and December during 1987.

The entire euphotic layer was sampled by vertical tows using a WP2 net with 200 μm pore size and 0.25 m^2 mouth area, at a speed of 1 m s^{-1}. The lower depth limit of the tow was the bottom at shallow stations and 200 m in deep oceanic stations. Samples were fixed in 4% formalin in sodium borate-buffered seawater. The entire sample was processed for the identification of appendicularians The abundance of species in each sample was expressed as individuals per square metre, instead of per cubic metre, in order to keep the estimate as close as possible to the raw count.

At each station a set of casts with 5 l Niskin bottles equipped with reversing thermometers was made at depths of 0, 10, 20, 30, 40 and 50 m, to obtain

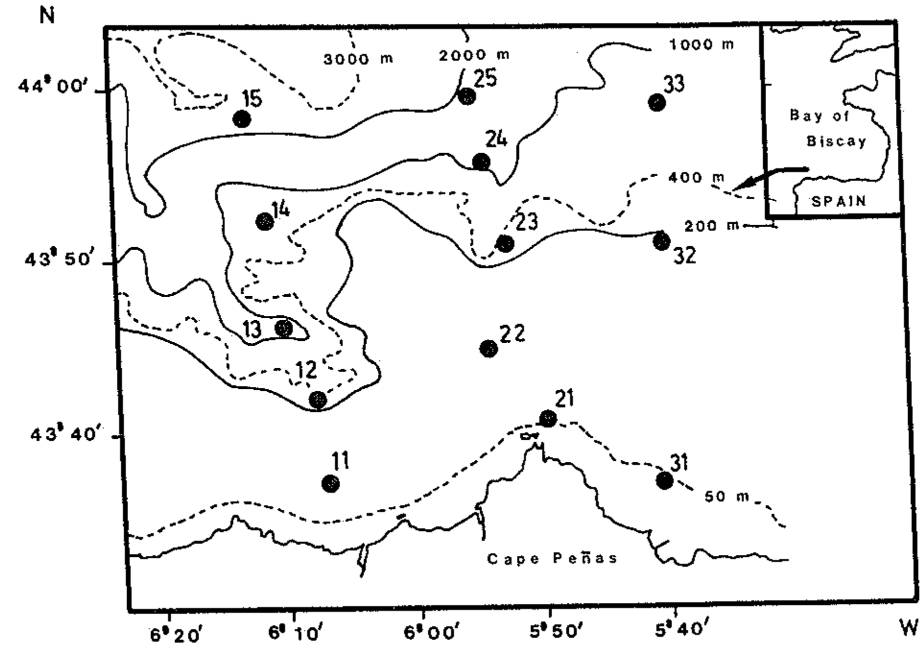

Fig. 1. Geographical location of the sampling stations (circles)

estimates of temperature, salinity and chlorophyll. Salinity was measured using a Watanabe inductometer Total chlorophyll was determined by fluorometry (Yentsch and Menzel, 1963; Holm-Hansen *et al.*, 1965) on particulate material collected on Whatman GF/C filters, which retained particles >0.8 μm (Hickel, 1984).

Two different measures of temperature were used in the analyses: surface temperature and temperature at the depth of the chlorophyll maximum. Given that bottle samples were taken at 10 m depth intervals, the best resolution in the determination of the depth of the chlorophyll maximum is to the nearest 10 m. Therefore, this temperature corresponds to the observed peak concentration of chlorophyll, but we will hereafter refer to it as temperature at the chlorophyll maximum. Averaged values of chlorophyll *a* and salinity from 0 to 50 m were also used as environmental descriptors. Although we have not measured productivity proper, chlorophyll *a* may be considered a good estimate of this variable since it explains a large proportion of production values in this area (Fernández and Bode, 1991).

Statistical analyses were performed on the log-transformed, centred and standardized species abundances (Legendre and Legendre, 1984a,b). Pearson's *r* product-moment correlation coefficient was used. Principal components analysis (PCA) was performed on the between-species correlation matrix. Cluster analysis was performed on the transformed species abundances by using squared Euclidean distance as a measure of dissimilarity. Agglomeration followed a criterion of minimal variance. In order to give an idea of distance from the coast, the stations have been arbitrarily divided into three groups: oceanic ('o', stations 14, 15, 24, 25 and 33), coastal ('c', stations 11, 21 and 31) and intermediate or shelf stations ('s', stations 12, 13, 22, 23 and 33).

Results

The hydrographic features of the central Cantabrian coast are those of a typical temperate sea. There is a period of mixing in the water column during the winter (from October to April), while summer stratification usually occurs between May and September (Figure 2). The process of stratification implies the development of a thermocline that progressively deepens during the summer, reaching its lowest depth in September, when it is located at ~30–40 m. This thermocline usually lies shallower in slope and coastal than in oceanic stations, a feature that is also reflected by their colder surface waters during summer. This feature is due to upwelling events, a process typical of this area (Botas *et al.*, 1989a,b). Coastal and on-shelf stations exhibit a surface layer of low salinities during summer, as a consequence of upwelling-induced offshore transport of neritic and estuarine waters, greatly influenced by freshwater effluents. This effect is more pronounced in coastal than in on-shelf stations (Figure 2).

Wide and shallow chlorophyll maxima are typical of mixing periods in this area. During summer, a well-defined subsurface chlorophyll maximum develops. This maximum tends to be deeper at oceanic stations and shallow at nearshore environments. At station 11, which was upwelled during most of the summer, this chlorophyll maximum appeared at the surface.

The greatest numbers of appendicularians (species pooled plus unidentified individuals) were recorded in April and the fewest in January (Figure 3). The largest abundances of each species were usually restricted to one or two months (except *O.longicauda*), but all species were present throughout the study period.

The between-species correlation matrix exhibits a highly organized gradient structure (Table I). When the species are arranged in order *O.longicauda*, *O.fusiformis*, *F.pellucida*, *O.dioica*, *F.borealis*, those cells that are closer to the diagonal exhibit higher correlation coefficients. Thus, the correlation between any two species is higher if they are closer in the sequence. This kind of correlation matrix is typical of a gradient structured community. Those species showing similar preferences for the intensity of the gradient exhibit similar abundance patterns. This is the case for *O.longicauda* and *O.fusiformis*, which exhibit high correlations, while the opposite occurs between *O.longicauda* and *F.borealis*, which exhibit a negative correlation.

PCA analysis extracted two components that explained 68% of the variance in the data space. The first component accounts for 45% of the total variance. It is a combination of the abundances of all the species except *F.borealis* (Table II). Therefore, it separates periods according to the total abundance of appendicularians, reaching the highest average values during late spring and summer (Figure 4). The second component accounts for 23% of the variance. It is a linear combination of all the species abundances whose loading coefficients may

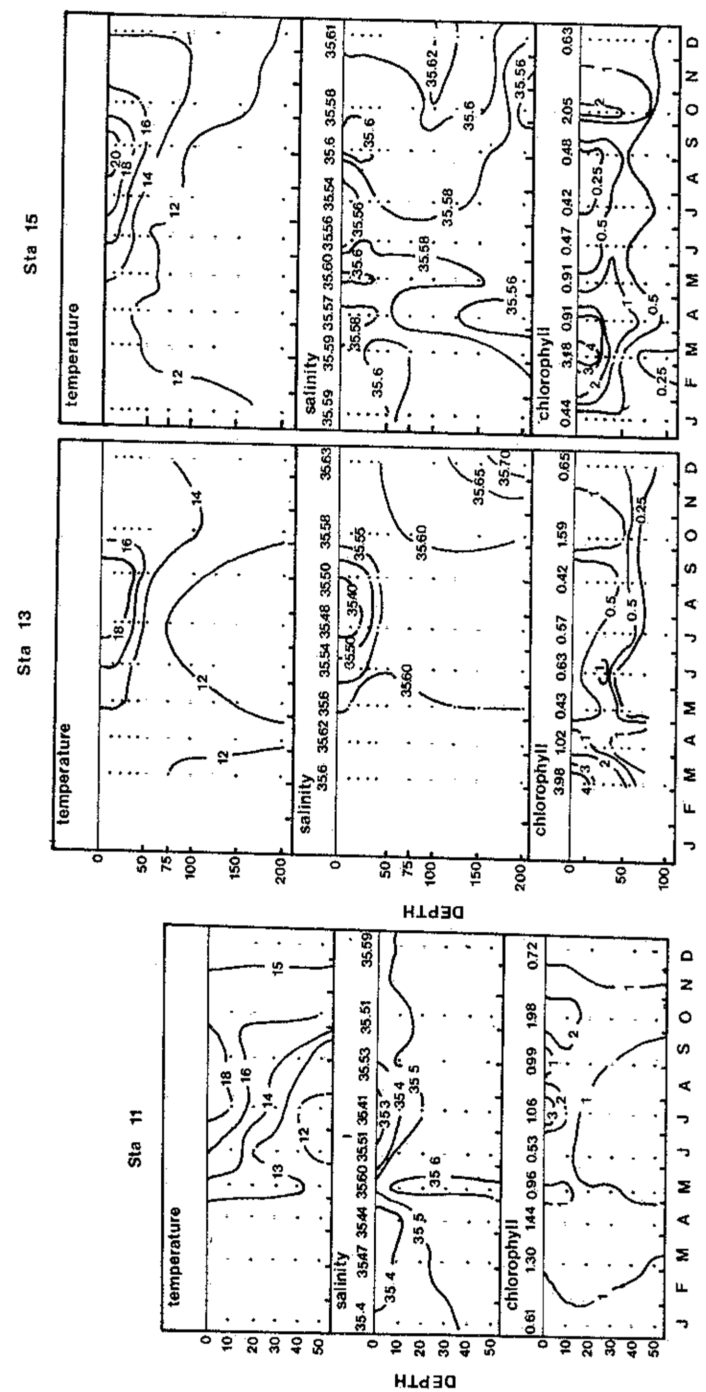

Fig. 2. Annual variation of the environmental descriptors at different depths in station 11 (**left**), representative of a coastal station, station 15 (**right**), representative of an oceanic station and station 13, representative of an on-shelf station of the COCACE cruises. Numbers in the upper row of the salinity and chlorophyll diagrams represent averaged values of these variables for each profile.

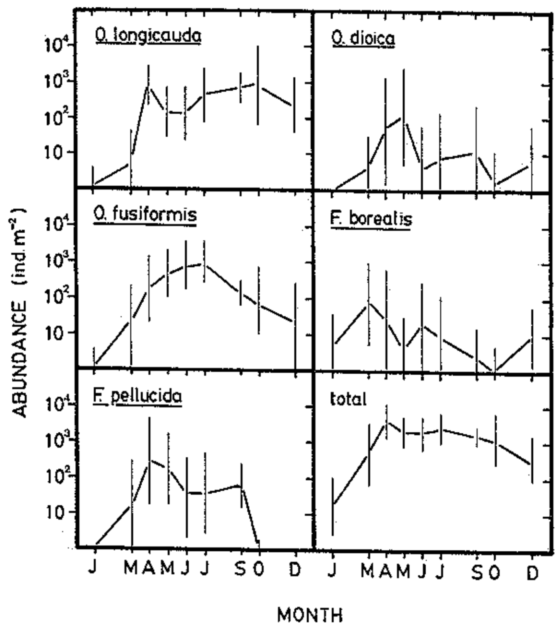

Fig. 3. Seasonal abundance of the different species and total abundance of appendicularians (log scale). Dots indicate mean values Vertical lines indicate standard errors.

Table I. Between-species correlation matrix

	O.longicauda	*O.fusiformis*	*F.pellucida*	*O.dioica*	*F.borealis*
O.longicauda	1.00	0.62 ***	0.33 **	0.29 **	−0.26 **
O.fusiformis	0.62 ***	1.00	0.45 ***	0.43 ***	0.14
F.pellucida	0.33 ***	0.45 ***	1.00	0.38 ***	0.08
O.dioica	0.29 **	0.43 ***	0.38 ***	1.00	−0.02
F.borealis	−0.26 **	0.14	0.08	−0.02	1.00

*$P < 0.05$
**$P < 0.01$
***$P < 0.001$.

Table II. Loading coefficients of each species on the components extracted by PCA analysis

	Component 1	Component 2
O.longicauda	0.76	−0.40
O.fusiformis	0.85	0.13
F.pellucida	0.71	0.23
O.dioica	0.68	0.06
F.borealis	−0.29	0.95

be arranged in a similar series (Table II) to that obtained by correlation analysis. Therefore, this component may be interpreted as the result of a gradient from samples with a high proportion of *F.borealis* to samples with a high proportion of *O.longicauda*. The average value of this component decreases progressively from March to October (Figure 4).

The projection of the scores of each sample onto the plane defined by the principal components (Figure 5) shows that the swarm of points may be interpreted as a circular structure with three branches oriented to the right of the diagram. These branches are characterized by high variability in the first component, but low variability in the second.

Cluster analysis divided the bulk of samples into six groups. Apart from group 1, which corresponds to winter samples, and group 6, which corresponds to the October mixing period, there was not a clear correspondence between seasons and cluster groups (Figure 5). Cluster group 2 is composed by coastal (stations 11, 21 and 31), oceanic (stations 14, 15, 24, 25, 32 and 33) and on-shelf stations (stations 12, 13, 22 and 23) sampled during the beginning of the spring, but it also contains several samples taken at oceanic stations during summer. Also, group 3 is composed of coastal and on-shelf samples taken during late spring, and on-shelf samples taken during summer, while group 4 is composed of samples taken at upwelled coastal stations during summer. Finally, group 5 is formed mainly of summer on-shelf and oceanic samples, especially those taken during September.

This result suggests that there are no clear seasonal trends in the composition of cluster groups. However, the results of PCA and cluster analysis are coherent in that both suggest the same groupings (Figure 5), which indicates that there is

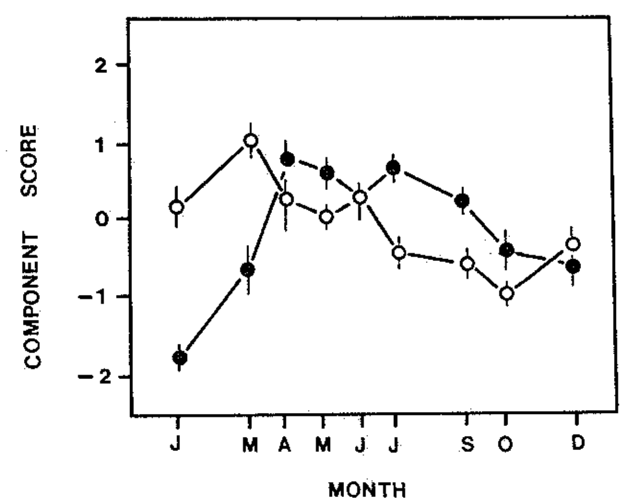

Fig. 4. Annual variation of the scores of the principal components extracted by PCA analysis. Solid circles indicate the averaged monthly score of component 1 (abundance). Open circles indicate the averaged monthly score of component 2 (position in the species sequence) Vertical lines indicate standard errors

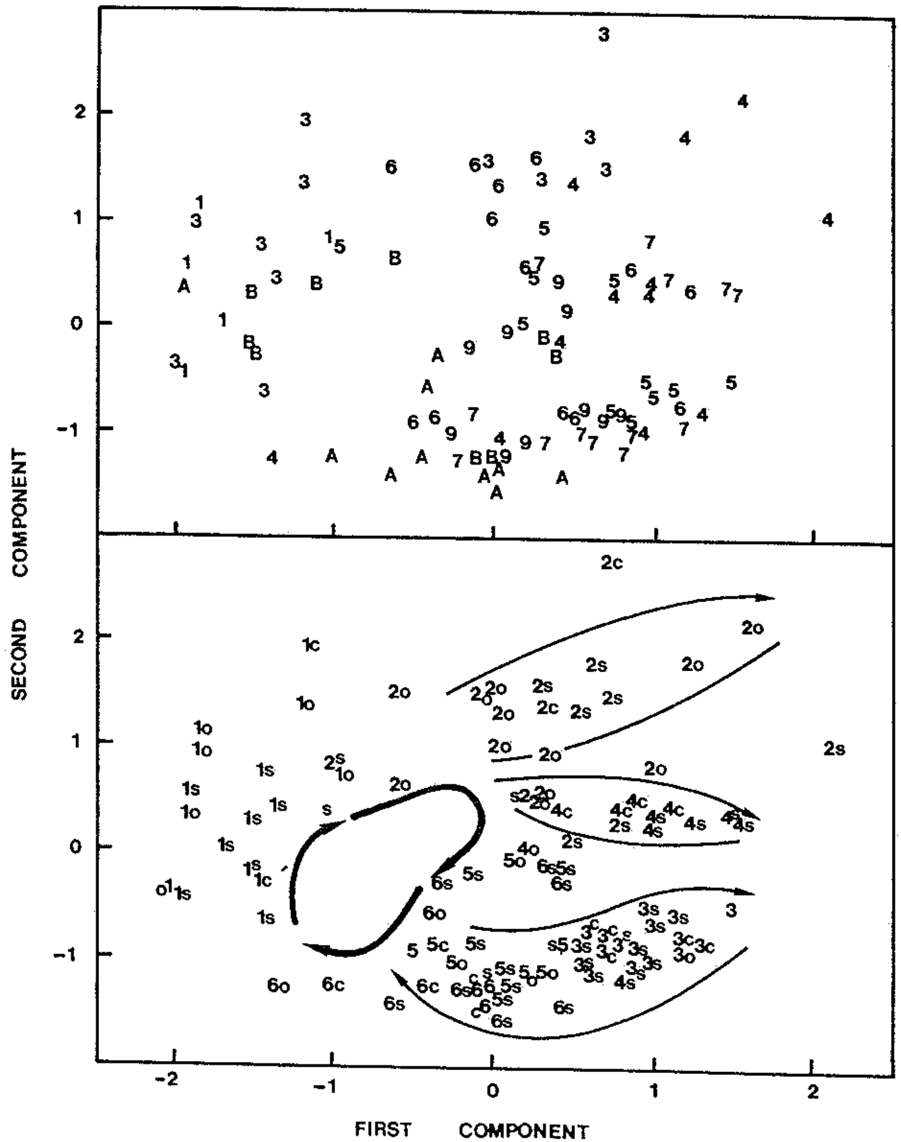

Fig. 5. Upper panel: projection of sample scores on the plane defined by the two components extracted by PCA analysis. Codes indicate 1 = January, 3 = March, 4 = April, 5 = May, 6 = June, 7 = July, 9 = September, A = October, B = December. **Lower panel**: the same figure, but sample codes correspond to cluster groups 1–6. Letters o, c and s indicate oceanic stations 14, 15, 24, 25 and 33 (o), coastal stations 11, 21 and 31 (c), and slope stations 12, 13, 22, 23 and 32 (s). See the text for an explanation of the thick line (main circle) and the thin lines (branches).

an underlying structure in the data. The main circle in Figure 5 is composed by groups 1, 2, 5 and 6, while groups 2, 3 and 4 are responsible for the three branches oriented to the right of the diagram.

In general terms, it may be seen that the abundance of *F.borealis* decreases from group 1 to 6, while the tendency is inverse for *O.longicauda* (Table III). The rest of the species show the highest abundances in intermediate groups. There is no clear trend for the average values of chlorophyll nor for salinity between groups. It may be seen that group 5, which exhibits the highest surface temperatures, does not correspond with the highest temperatures at the depth of the chlorophyll maximum. Moreover, there is an increase in mean surface temperature from group 1 to group 2, but this increase is not noticeable for the temperature at the depth of the chlorophyll maximum. Group 6, characterized by intermediate surface temperatures, exhibits the highest temperatures at the depth of the chlorophyll maximum.

The correlations of the species abundances with temperature parameters (Table IV) suggest that the species sequences obtained by correlation and PCA analyses are consistent with a gradient of temperature. However, there is no reason to prefer either surface temperature or temperature at the depth of the chlorophyll maximum as environmental descriptors for the community of appendicularians. The correlations between species abundances and both salinity and chlorophyll were generally low.

Oikopleura longicauda, *O.fusiformis*, *F.pellucida* and *F.borealis* exhibited a tendency for larger numbers of individuals (note the log scale) at 15–16, 13–14, 13–14 and 12–13°C, respectively, whereas *O.dioica* presented larger abundances at 13–14 and 16–17°C (Figure 6). No pattern was found for the total abundance of appendicularians.

Figure 7 represents the relationship between surface temperature (ST) and temperature at the depth of the chlorophyll maximum (TC). As TC cannot exceed ST, the swarm of points is limited by a straight line with a 45° slope. It is clear that, as summer progressed, the difference between ST and TC increased, whereas during mixing periods (winter and autumn) both temperatures were similar (Figure 7). Both temperatures were low during the spring (left angle in the swarm of points) and high during the autumn (coincides with group 6 samples in the diagram). Low-temperature spring waters are represented by cluster groups 1 and 2. The usual stratification sequence, with an increase in the difference between ST and TC during the summer, is more marked at oceanic stations, and is represented by groups 2 and 5 which tend to occupy the lower portion of the swarm of points. In oceanic stations there is also a slight increase of TC with increasing ST, but at a lower rate. Unusual summer samples, in which TC and ST are similar (Figure 7), correspond to coastal stations (mainly groups 3 and 4). Finally, group 6 samples show roughly similar ST and TC.

During mixing periods neither temperature measure offers a very distinct spatial distribution (Figure 8). Homogeneity is the main horizontal feature and the distributions of groups cannot be clearly associated to any onshore–offshore gradient. During summer TC distributions offer a quite distinct picture, with a marked tendency for lower temperatures at offshore stations, contrasting with

Table III. Means and standard errors (in parentheses) of the abundances of each species and the total number of appendicularians, and of the environmental descriptors in groups 1–6. Total abundance of appendicularians includes unidentified individuals

	Group G1	G2	G3	G4	G5	G6
O longicauda	8 (4)	542 (218)	901 (219)	1046 (478)	1235 (295)	2163 (675)
O fusiformis	2 (1)	1711 (570)	1137 (369)	1107 (289)	234 (65)	308 (89)
F pellucida	13 (13)	908 (367)	982 (443)	375 (130)	133 (87)	0 (0)
O dioica	13 (13)	408 (277)	645 (183)	1632 (821)	2 (1)	41 (17)
F borealis	74 (55)	663 (216)	0 (0)	34 (7)	3 (2)	6 (3)
Total appendicularians	265 (107)	5130 (1133)	4086 (743)	4387 (1192)	1990 (375)	2666 (754)
Surface temperature	13 0 (0.25)	14 9 (0 55)	16.4 (0 65)	16 8 (0.64)	17.9 (0 80)	15.7 (0 47)
Temperature at depth of Chl maximum	12.9 (0 24)	13 1 (0.18)	14 5 (0 36)	15 7 (0 55)	14 6 (0 31)	15 7 (0.44)
Salinity	35.55 (0 018)	35 55 (0 013)	35 52 (0.021)	35.52 (0 024)	35 54 (0.013)	35 49 (0.51)
Chlorophyll *a*	1 27 (0.27)	0 83 (0.09)	0 88 (0.11)	0.76 (0.08)	0.70 (0.09)	1.35 (0.15)

Table IV. Correlation coefficients between abundance of species and environmental descriptors

	Surface temperature	Temperature at depth of Chl maximum	Salinity	Chlorophyll
O.longicauda	0.51 ***	0.49 ***	−0.19	−0.15
O.fusiformis	0.45 ***	0.27 **	−0.02	−0.21 *
F.pellucida	0.12	−0.06	0.00	−0.21 *
O.dioica	−0.02	0.15	−0.19	0.02
F.borealis	−0.24 **	−0.37 ***	0.13	−0.07

*$P < 0.05$.
**$P < 0.01$
***$P < 0.001$

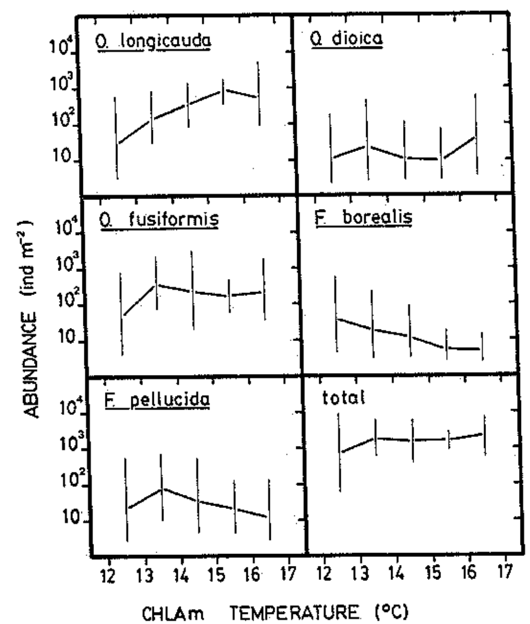

Fig. 6. Diagrams showing the relationship between temperature at the depth of the chlorophyll maximum (*X*-axis) and abundance of each species and total of appendicularians (*Y*-axis, log scale) Data for each temperature interval are presented as mean ±SD

high temperatures at coastal stations (Figure 8). Temperatures are even higher at the centre of the upwelling, located at station 11 in June and July, and at station 21 in September. Another interesting feature is the high degree of variability of this measure during summer months. While the range of variation of ST in the study area during summer is <1°C, TC varies by up to 4°C. During

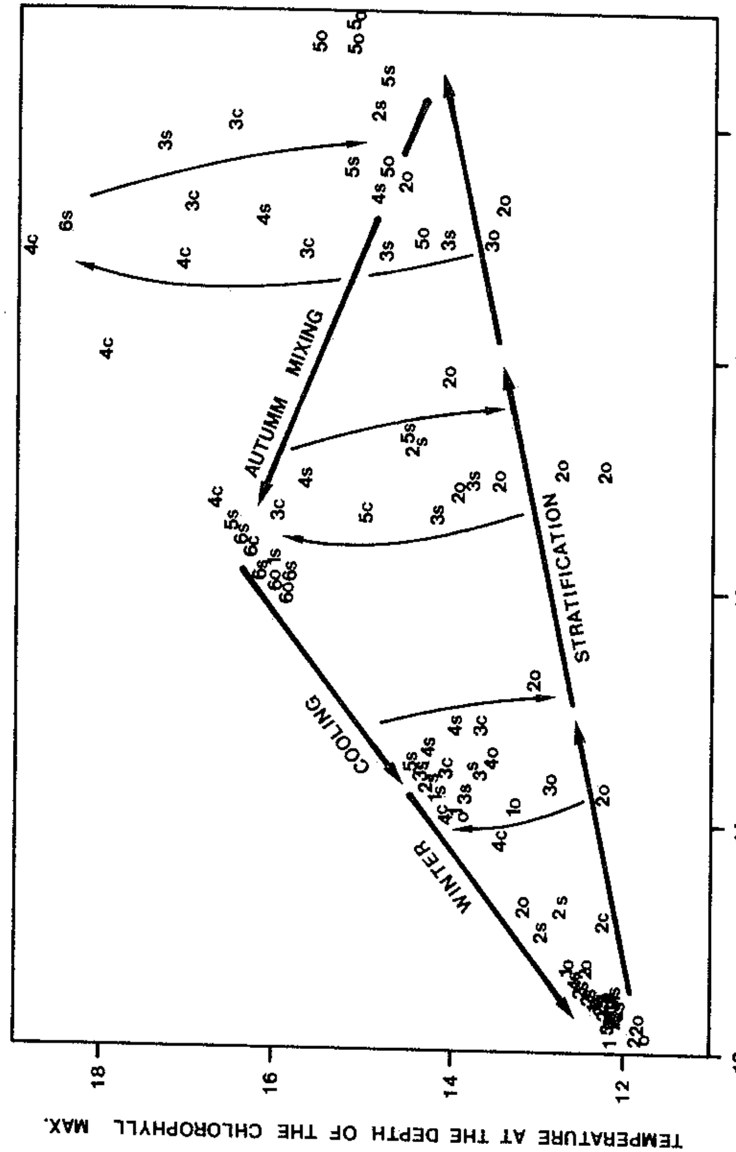

Fig. 7. The relationship between temperature at the depth of the chlorophyll maximum and surface temperature at all the stations sampled. Numbers represent cluster group codes (1–6). The letters o, c and s indicate oceanic stations 14, 15, 24, 25 and 33 (o), coastal stations 11, 21 and 31 (c), and slope stations 12, 13, 22, 23 and 32 (s). The lines on the diagram represent the same sequence of events as the lines in Figure 5. The thick lines indicate the seasonal cycle in an unperturbed station, whereas the thin lines represent episodic mixing events during the stratification period that lead to an increased temperature at the depth of the chlorophyll maximum See Discussion for more details

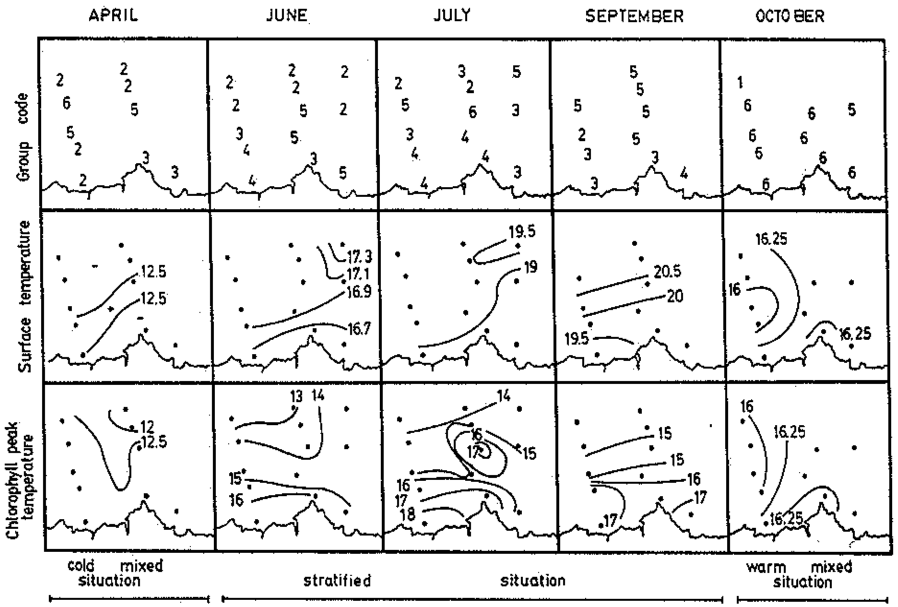

Fig. 8. Spatial distribution of cluster group codes (first row), surface temperature (second row) and temperature at the depth of the chlorophyll maximum (third row), during April (cold, mixed situation; first column), June, July and September (stratified situation; second, third and fourth columns), and October (warm mixed situation; fifth column)

the summer months, group 2 is progressively substituted by group 5 samples at oceanic stations until this group becomes dominant during September and group 6 in October (Figure 8).

Discussion

It has been shown in this study that the community of appendicularians in the central Cantabrian coast exhibited an annual succession in the relative abundance of species This seasonal succession was similar to that found in Villefranche (Fenaux, 1967) and shifted progressively along the series *F.borealis*, *O.dioica*, *F.pellucida*, *O.fusiformis* and *O.longicauda* from January to December. The gradient structure of the community, clearly exemplified by the matrix of correlations, was coupled to variations in temperature. In terms of statistical significance, both ST and TC were reliable predictors of the structure of the community. ST, however, led to some qualitative inconsistencies in the interpretation of space and time distributions of the community.

The first inconsistency was group 2 samples, characterized by the abundance of cold-water species. This group contained samples taken during the spring, when the water column exhibited low ST. However, this group also contained samples taken at summer oceanic stations, characterized by the highest ST. The second inconsistency was related to group 6, which contained samples dominated by the warm-water species *O.longicauda*, with the other species in low abundance These samples were taken after the autumn mixing period, when ST showed a drastic decrease. In contrast, TC seems to account for these patterns of distribution.

These features may be explained by taking into account the ecological characteristics of appendicularians. First, appendicularians exhibit a low metabolic regulation (Gorsky and Palazzoli, 1984; Gorsky *et al.*, 1987) which suggests that they are highly sensitive to water temperature. Also, they seem to be unable to perform systematic diel migrations (Longhurst, 1985; e.g. Palma, 1986). This implies that they are not able to distribute the time spent at each temperature (depth) to maximize fitness (McLaren, 1963). Binet (1976) suggested that the vertical distribution of appendicularians might be related not only to temperature, but also to the depth of the maximum productivity. We expect maximum productivity to be allocated at or near the chlorophyll maximum, except in situations with a very deep thermocline (Longhurst and Harrison, 1989). Therefore, we hypothesize that the abundance of appendicularians in a given season or location depends on primary production, while the patterns of relative abundance depend on the temperature at which that production occurs. Therefore, the community will be dominated by the species whose optimum physiological temperature is closest to TC.

According to this conceptual model, cryophilic species (group 2) dominated the community during spring, since this season was characterized by the conjunction of high phytoplankton biomass with low temperatures (Figure 7). These species also dominated in summer oceanic stations, where subsurface chlorophyll maxima were usually associated with low temperatures (Figure 7). Mixing and upwelling processes, characteristic of coastal waters in this area (Botas *et al.*, 1990), interrupted the process of deepening of the subsurface chlorophyll maximum, thereby enhancing the temperature at which this chlorophyll maximum appeared. A consequence of this is that these environments became more suitable for thermophilic species. Also, coastal upwelling processes involved the coexistence of species well separated within the gradient because of mixing processes between layers of different temperature. As a result, heterogeneous communities (the branches formed by groups 3 and 4 in Figures 5 and 7) appeared at coastal and shelf stations. As summer progressed, TC increased slightly in oceanic stations (Figure 7), and thermophilic (group 5) species became dominant in the community.

During the autumn bloom, mixing in the water column had occurred after a situation of the highest heat content (Botas *et al.*, 1989b) The chlorophyll maximum was associated with high temperatures and, therefore, the thermophilic species *O.longicauda* completely dominated the community (group 6) (Figure 7). Later in the seasonal cycle, TC progressively decreased as a consequence of the progressive loss of heat in the water column, but it did not fall below 14°C until December. This explains the persistence of *O.longicauda* up to this month. All these features are in agreement with those described by Fenaux (1961, 1967) and suggest that these relationships may not be peculiar to the seasonal cycle on the central Cantabrian coast, but a feature common to other temperate seas.

According to the above proposed ecological constraints, some patterns might also be expected in the vertical distribution of appendicularians. During mixing periods, the vertical distribution of appendicularians might be homogeneous whenever there is enough turbulence to disperse the populations. During stratification, the largest total numbers of appendicularians may be expected at the depth of the chlorophyll maximum, but the maximal relative abundance for each species should be located at the depth at which there is the optimal temperature for this species. Taking into account the successional sequence, it may be expected that a similar series will develop in the relative abundance of species on a vertical scale. This vertical sequence will progressively shift downwards as a consequence of the process of stratification. The result is that the successional series of species will become a vertical gradient of the relative abundance during the stratification period, and consequently cold-water species will be found deeper than warm-water species. To our knowledge, Fenaux (1968a,b) reports the only available information on the species vertical distribution of appendicularians. He showed that fritillarids prefer deeper waters than oikopleurids (mainly *O.longicauda* and *O.fusiformis*). These findings are in agreement with the predictions of the model. However, he did not find any difference between the vertical distributions of *O.longicauda* and *O.fusiformis*. This is probably because he used presence–absence data instead of abundances. Also, his tows covered prefixed depth intervals, regardless of the physical structure of the water column, and the samples were collected over a long time period. Based on data obtained during subsequent cruises, we have seen that *O.fusiformis* and *F.pellucida* are consistently associated with cold deep water (J.L.Acuña, unpublished data). These results, and their implications for the mesoscale distributions of appendicularians, will be presented elsewhere. Phenomena of seasonal vertical differentiation between boreal and temperate species are not new amongst other taxa (e.g. Williams, 1985).

There are some physiological bases for the existence of a unimodal numerical response of appendicularians to temperature. A negative correlation between the size of mature *O.dioica* and temperature, and a positive relationship between size and fecundity, have been described (Paffenhöfer, 1975). Generation time is also inversely related to temperature. According to McLaren (1963), a higher temperature will lead to a shortened generation time and lower fecundity for different zooplankters. The result of such conflicting relationships is that appendicularian species exhibit a maximum reproduction rate at an intermediate temperature and, consequently, a unimodal response of population size to temperature. At least in *O.dioica* and *O.longicauda*, these optimum temperatures may be expected to be different since they exhibit differences in the parameters of their metabolic equations (Gorsky and Palazzoli, 1984; Gorsky *et al.*, 1987). Indirect evidence for unimodality in the numerical response of population abundance to temperature has also been reported by Essenberg (1922).

In this study, we have shown the inadequacy of ST to explain some of the seasonal and spatial patterns in appendicularian communities. It is clear that the use of purely physical measures, such as ST, disregards important biological features of the water column that may be of great relevance to plankton populations. This is important since most studies dealing with zooplankton ecology utilize physical measures at fixed depths, which implies an anthropomorphic rather than a biological criterion. Mapping of physical parameters at the level of significant biological phenomena, such as the chlorophyll maximum, may lead to a very different view of the same environment. The recent theoretical arguments of Aksnes and Giske (1990) also suggest that the biological constraints proposed herein for appendicularians may also be imposed on many copepods with non-fixed generation times. Thus, it may be expected that biological-derived temperature measures will be of greater interest in the study of these animals than measures taken at fixed depths. An example of this kind of biological approach is that of Ohman (1983), who found that seasonal changes in temperature at the depth of the chlorophyll maximum approximate changes in temperature at the median daytime depth of a *Pseudocalanus* population. Later, Ohman (1986) used temperature at the depth of the chlorophyll maximum to estimate temperature-dependent survivorship and mortality rates for this population.

We could not find any significant correlation between field estimates of the abundance of consumers and producers. A delay in the response of the community of appendicularians to pulses of phytoplankton biomass might be the cause of this lack of correlation. Although temperature may help to explain patterns of species composition, there are no measurable parameters allowing us to predict the absolute abundance of appendicularians. Knowledge of these factors will improve our predictions. A detailed description of the vertical distribution of appendicularians and producers, at time scales appropriate to their generation time, is still required.

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