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THE SEASONAL SUCCESSION OF APPENDICULARIANS (TUNICATA: APPENDICULARIA) OFF PLYMOUTH

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Earlier descriptions showed that the community of appendicularians off the British coast was mainly composed of *Oikopleura dioica* (Appendicularia; Müller, 1846) and *Fritillaria borealis* (Appendicularia; Lohmann, 1896), rarely by *Oikopleura fusiformis* (Appendicularia; Fol, 1872) and *Fritillaria pellucida* (Appendicularia; Quoy & Gaimard, 1833) and exceptionally by *Oikopleura longicauda* (Appendicularia; Vogt, 1854). Based on weekly samples collected during 1989 at a single station off the coast of Plymouth, we describe the first complete seasonal cycle of appendicularians in this area. The results suggest that rather than being occasional visitors, *O. fusiformis*, *F pellucida* and *O. longicauda* are consistently present and abundant from mid to late summer. Moreover, the seasonal shifts in structure of the community of appendicularians in the area, as depicted by multivariate analysis, are consistent with those of the more southerly central Cantabrian coast (Spain). This suggests that they are viable populations rather than occasional expatriates from other areas.

Despite the growing number of ecological studies on appendicularians, the seasonal distribution of the species off the British coast is still poorly known. This is important, since the species distribution may largely determine the role of appendicularians in the pelagic ecosystem due to species-specific characteristics such as pore size of their filters, filtration rate or vertical distribution (Acuña, 1994 and references therein). According to Fraser (1981), appendicularian assemblages off the British coast are composed of *Oikopleura dioica* and *Fritillaria borealis* throughout the year. This author reports, however, on the unusual presence of *O. fusiformis* and *F. pellucida*, and on the exceptional presence of *O. longicauda*. During our routine collection for the BOFS (Biogeochemical Ocean Flux Study) experimental programme on appendicularians, we detected abundant populations of the warm-water species *O. longicauda* in the water column off Plymouth during the autumn months of recent years. This led us to analyse our weekly samples from 1989 to determine the patterns of seasonal succession. Here we report our findings and compare the seasonal succession of appendicularians off Plymouth with that of the more southerly central Cantabrian coast.

To describe the seasonal distribution of appendicularians we made use of the BOFS weekly sample collection, taken at station L4 (50°15′N 4°13′W; depth 51 m) from January to December 1989. Samples were obtained with oblique tows with 200-µm WP2 nets and fixed in 4% formalin in sea-water. At least a quarter of the sample volume was analysed for species identification and counting.

In close agreement with Fraser's (1981) description, the annual cycle of species abundance was characterized by the dominance of *O. dioica* and *F. borealis* throughout most of the year, the former being very abundant and frequent and the second more variable both in abundance and in presence (Figure 1). However, we also detected many *F. pellucida*, *O. fusiformis* and *O longicauda* during the summer and autumn months (Figure 1). The presence of *F pellucida* was

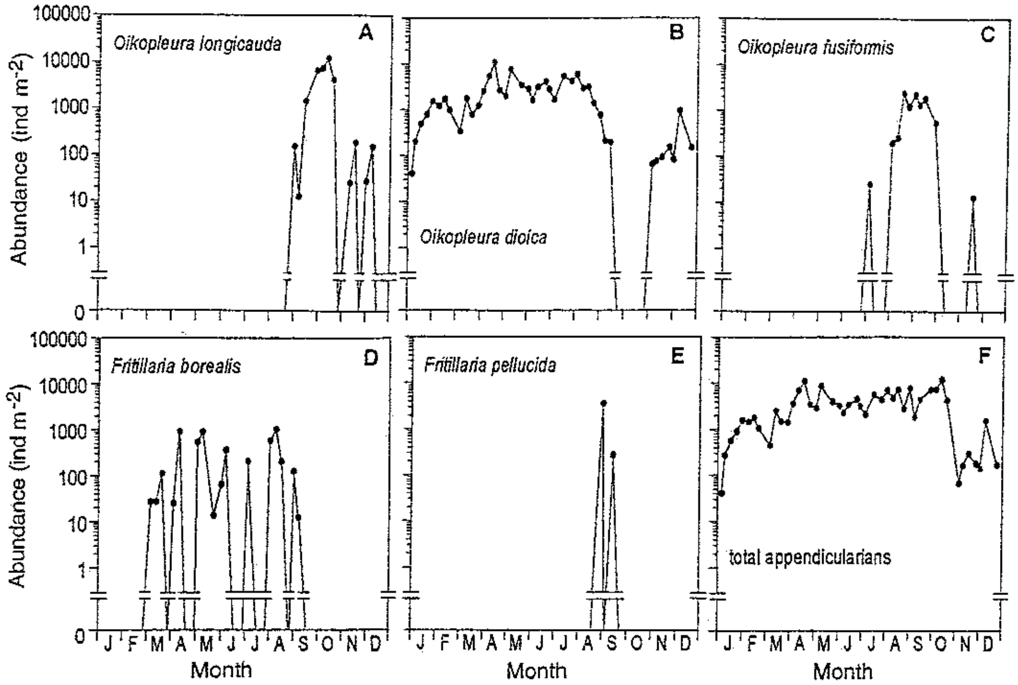

Figure 1 The annual variation of the abundance of each species and of the total number of appendicularians (plus unidentified individuals) at station L4.

restricted to August and September. *Oikopleura fusiformis* appeared in July and disappeared from samples by November, and *O. longicauda* appeared at station L4 in August, and was present until December, showing peak densities between August and September (Figure 1). Both the species composition of the community, and their seasonal succession resemble those described off Villefranche-sur-Mer, French Mediterranean coast (Fenaux, 1961), or on the central Cantabrian coast, northern Spain (Acuña & Anadón, 1992), with a certain delay in the time of appearance of the species.

Many species of oceanic or south-westerly distribution are brought to the Devon coast by unusual weather conditions and water movements (Southward et al., 1988; Maddock et al., 1989). If the presence of these warm-water appendicularians is a consequence of an occasional process of advective population transport, the structure of the whole community should follow an erratic pattern of variation through the year. It is difficult to define 'erratic' here, since there are no previous records to compare with. However, it is possible to compare the structure of the community as observed at station L4 with that of a different but close area.

To do this, we have made use of the same set of data that Acuña & Anadón (1992) used to describe the seasonal cycle of abundance of appendicularians in the central Cantabrian coast (CCC). This data set corresponds to samples taken with 200-μm WP2 vertical tows with an almost monthly periodicity, from January to December 1986, at 13 stations between 6°20'W and 5°40'W and 44°00'N and 43°30'N. The samples were fixed and processed in the same way as the L4 samples.

A Principal Components Analysis (PCA, Legendre & Legendre, 1984a,b) performed on the CCC data set (samples by species matrix, data log-transformed, centred and standardized), yielded two principal components that explain 45 and 23% of the variance, respectively (Acuña & Anadón, 1992). All species have positive loading coefficients on the first component, except *F. borealis* (Table 1). This component may therefore be interpreted as total abundance of appendicularians.

Table 1. *Loading coefficients of each species on the components extracted by PCA from the CCC data set (from Acuña & Anadón, 1992).*

	Component 1	Component 2
Oikopleura longicauda	0.76	-0.40
Oikopleura fusiformis	0.85	0.13
Fritillaria pellucida	0.71	0.23
Oikopleura dioica	0.68	0.06
Fritillaria borealis	-0.29	0.95

According to their loading coefficients on the second component, the species may be arranged along the series *O. longicauda, O. dioica, O. fusiformis, F. pellucida* and *F. borealis*, from lower to higher (more positive) coefficients (Table 1). This series shows a strong correlation with temperature (Acuña & Anadón, 1992), the exception being *O. dioica*, which is found closer inshore. Therefore positive scores mean dominance of warm water species, and negative scores dominance of cold water species. When plotted on the plane of the first two components, the scores of the CCC samples form a circular structure (Figure 2) with the seasonal succession of samples moving clockwise. An oceanic station circles closer to the centre of the structure, while a coastal station circles further from the centre. Scores of the winter samples are located to the left of the swarm of points.

To determine whether the pattern of seasonal succession at station L4 is or is not similar to that of a CCC station, we calculated the scores of each 1989 L4 sample using the loading coefficients calculated from the CCC data set. Then the position of each L4 sample was plotted on the plane of components (Figure 2). There are some characteristics that differentiate the swarms of L4 and CCC points. One of them is a conspicuous line of L4 points located on the centre of the diagram, which corresponds to those L4 samples in which only *O. dioica* was present, a situation that rarely happens in CCC coastal waters. Winter CCC samples usually contain low numbers of fritillarids

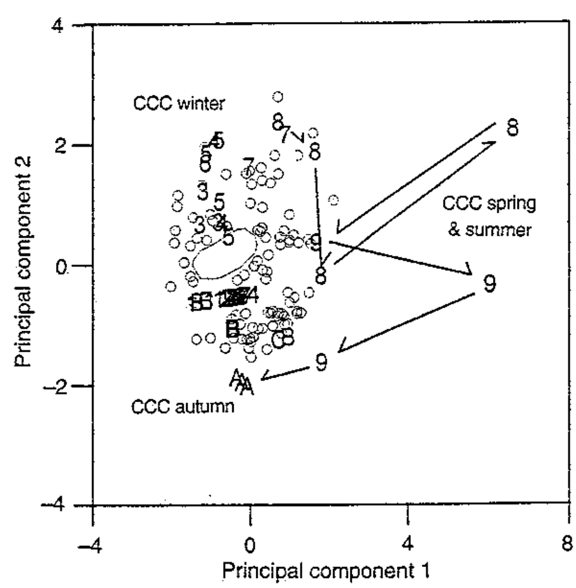

Figure 2. Projection of the scores of the samples on the plane of the first two components extracted by PCA from the CCC data set. ○ indicate CCC samples. The thin circular line in the centre of the diagram indicates the centre of rotation of CCC samples round the seasonal cycle. Letters and symbols indicate consecutive samples taken at station L4 in 1989 during the months of: 1, January; 2, February; 3, March; 4, April; 5, May; 6, June; 7, July; 8, August; 9, September; A, October; B, November; C, December. The thick arrows connect these sample points by consecutive sampling dates.

and some *O. longicauda* and *O fusiformis*, but rarely *O dioica* We find *O. dioica* to be associated with nearshore habitats, both in the CCC and off the Devon coast (personal observation). None of the CCC coastal stations was close enough to the shore to present significant numbers of this species. There is also a difference in the total abundance of appendicularians between summer CCC and L4 samples. The L4 points corresponding to summer–autumn months (August to November) exhibit higher scores on the first principal component than summer–autumn CCC samples, which means that appendicularians are more abundant at station L4 during these months.

Despite these differences, the temporal succession of scores of the L4 samples on the plane of CCC principal components is not erratic (Figure 2). The L4 winter samples in which only *O. dioica* and *F. borealis* were present occupy the upper left portion of the diagram (Figure 2), in a similar position to that of the CCC winter samples. The temporal succession of the scores of the remaining L4 samples, from August to December, smoothly followed the seasonal succession of a CCC coastal station, circling clockwise on the components' plane (Figure 2). This result indicates that there is a coherence in structure between both data sets, which suggests that summer and autumn populations of *F pellucida, O. fusiformis* and *O. longicauda* at station L4 are viable populations rather than occasional expatriates.

Long-term changes in the ecosystem using indicator species have been generally linked to climatic variations (Southward et al., 1988; Maddock et al., 1989). The presence of warm-water appendicularians at station L4 might be the result of an exceptionally warm year. Peak surface temperatures at station L4 reached ~21°C in 1989 (personal observation), close to the highest observed surface temperatures in the CCC during 1986 (Acuña & Anadón, 1992). However, to establish it formally one should examine longer time records of appendicularians and compare them with the physical–biological structure of the water column.

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