4.3 BATHYMETRIC DISTRIBUTION OF EPIPELON

4.3.1 Introduction

A cursory inspection of Loch Goil at a range of depths (0-40m) suggested that there are differences beween the physical environment on the bed of the loch in the shallow sublittoral zone compared with the deeper regions. The sea bed forms a shallow platform at 0-3m (Fig 17) and this is exposed to wave action, surface warming, and optimal light conditions. Beyond this is a slope; here as the water becomes cooler, light is progressively reduced and there is a transition from a coarse sand to finer muddy sediment. In addition, inspection indicated that the abundance of the epipelon varies with depth. Dense patches of epipelic algae discolour the sea bed in the shallows (approx. 0-12m) but are not evident at greater depths.

An assessment of the bathymetric distribution of the epipelic algae in relation to changes in physical and chemical parameters is essential to an understanding of the ecology of Loch Goil. In particular, because the loch is semi-fjordic, the subtidal region comprises most (96%) of the total area (Admiralty chart no. 3746, Edwards and Sharples, 1986). The bathymetry of Loch Goil has been documented (Admiralty chart no. 3746, Edwards and Sharples, 1986; Edwards *et al*, 1986; Mackay and Halcrow, 1976) but there is a paucity of biological data on the loch (Holt and Davies, 1991; CRPB unpublished data, MacDonald, 1927). In particular, there appears to be no information, in the literature, on the benthic micro-algal communities of Loch Goil or any other sea lochs in the Firth of Clyde. Norton and Milburn (1972) documented the depth distribution of marine macroalgae at eleven sites in Argyll from Oban to the Kyles of Bute. They found no macroalgae deeper than 36m and recorded the greatest variety of species in shallow water sheltered from excessive turbulence.

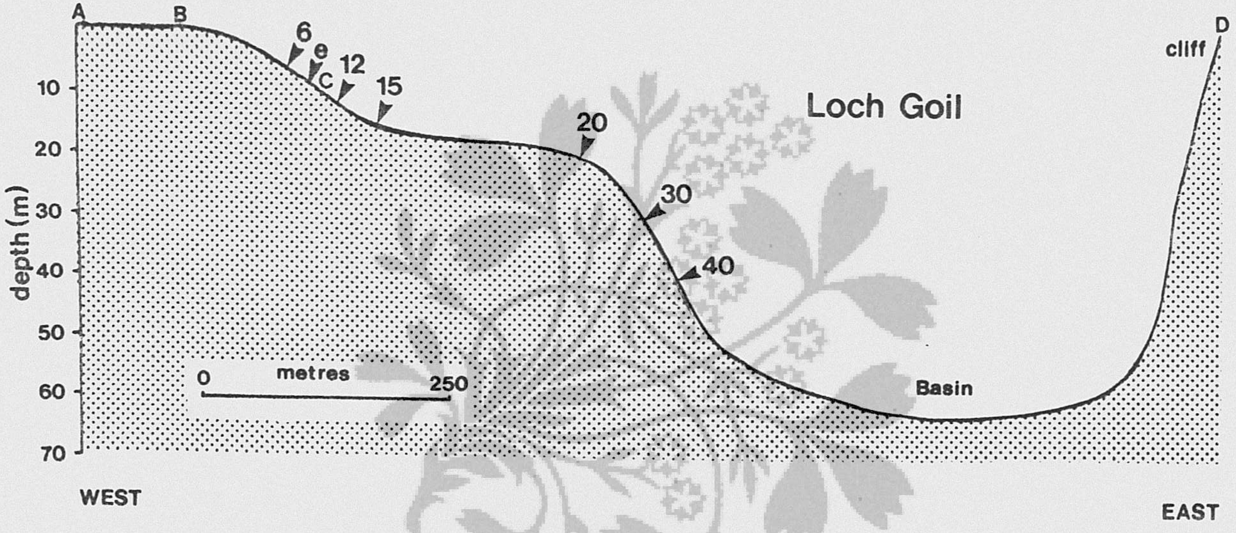


Fig. 17. Cross section of Loch Goil showing the location of the sample stations (6m, 12m, 15m, 20m, 30m, and 40m) along a bathymetric gradient (drawn from Admiralty chart no. 3746) . AB is the intertidal zone, A is at the position 56 07.73'N 04 54.45' W; B is the position of Chart Datum; C is the sample site used to monitor seasonal variation of the epipelon; D is at position 56 07.58'N 04 53.38'W.

"e" is the location of the "experimental area" and 9m station used to study the seasonality of the epipelon.

The extent to which the shallow water epipelic community extends into the deep (50-93m) water basin of the Loch Goil is unknown, with little relevant literature from anywhere in Britain or elsewhere. A number of studies have investigated the effect of depth on the epipelic algal community in fresh water lakes (Round, 1961; Roberts and Boylen, 1988, Stevenson *et al*, 1985; Stevenson and Stoermer, 1981; Gruendling, 1971; Kingston *et al*, 1983; Stevenson *et al*, 1985) and marine habitats (Bodeanu, 1964, 1968, 1971; Manea and Skolka, 1961; Sundbäck, 1986; Smyth, 1955; Plant-Cuny, 1969, 1973). These studies indicate that bathymetric zonation of species and algal density is a common feature of the sublittoral epipelon although there appears to be no common pattern to the species that inhabit a particular depth or light regime. These changes with depth are attributed, primarily, to variations in the amount and spectral composition of light reaching the sediment. According to Round (1981):

> "other factors such as wave "other factors sediment, grazing etc., undoubtedly interact with light in determining the distribtiion (...of species, biomass and photosynthesis of epipelon) under various depths of water."

The effects of light intensity on benthic micro algae has been investigated extensively in field and laboratory studies, which are reviewed by Admiraal (1984) and Colijn and van Buurt (1975).

Smyth (1955) investigated the depth distribution of epipelic algae in Loch Sween (Argyll), but only as a minor part of a broader ecological investigation of the benthic diatoms of Loch Sween. Smyth used glass slides laid on the surface of the mud from 1-20m depth, at 40m depth and in Loch Fyne at 110m. Between 1-10m there was no evidence that depth affected the composition of the diatom flora and differences recorded from 20m were attributed to:

> "unusually unfavourable conditions in the mud....that reduced light intensity"

The major species between 1-20m depth included: *Amphora coffeaeformis*, *A. laevis*, *A. macilenta*, *A. marina*, *Cocconeis scutellum*, *Navicula bahusiensis*, *N. pygmaea* and *Nitzschia closterium*. However, Smyth did record a marked difference between the epipelic diatom community in the shallow subtidal region (1-20m) and the deeper water community (40m). At 40m in Loch Sween and at 110m in Loch Fyne small individuals of *Cocconeis scutellum* were observed. In addition a single specimen of *Navicula pygmaea* was recorded at 40m in Loch Sween. Although Smyth recorded these algae from deep water sediments his samples were only qualitative. He also confirmed that only some of the diatoms had healthy chloroplasts and did not succeed in demonstrating that the algae were alive at these depths. Smyth attempted to confirm his observations from slides, by examining core samples. Cores taken at Millport in April 1948 at depths of 20, 40 and 60 fathoms showed there to be only empty frustules of *Navicula abrupta*. An estimate of epipelic abundance made from two core samples taken in Loch Sween showed there to be 1 and 5 x 10^8 cell m^{-2} at 40m depth. The presence of *Cocconeis scutellum* in deep water sediment is confirmed by Mare, 1942 who recorded this specis in abundance at 72m depth in the English Channel.

Sundbäck (1986) studied the epipelon from 5-20m depth in a shallow inlet of the heavily eutrophic Kattegat. From laboratory experiments and field observations Sündback showed that light-saturated photosynthesis occurred down to 10m during April-Sept. and that primary productivity was greatest at 14-16m depth. Benthic microalgae were shown to be limited by both light and nutrients and that microalgal actively influences nutrient fluxes and oxygen conditions at the sediment/water interface.

Plante-Cuny (1973) investigated the bathymetric distribution (5-38m) of diatoms living in tropical marine sands off the NW coast of Madagascar. He found that mean cell sizes of epipelic diatom populations increased as sediment particle size decreased and as depth increased. The distribution of sediment with depth was linked to a hydrodynamic gradient.

This study of the bathymetric distribution of epipelon in Loch Goil is particularly interesting as it represents the first quantitative investigation of its kind in a sea water loch. The unusual epipelic community of Loch Goil (see Appendix 1) and the unique hydrodynamical characteristics of sea lochs in general (compared with fresh water lakes or coastal and oceanic marine waters) reduces the relevance of the literature in predicting the pattern of depth distribution in this habitat.

Therefore, the objectives of this study were (1) to estimate the abundance and biomass of the epipelon along a gradient of depth, (2) describe the bathymetric distribution of epipelic species, (3) describe the temporal variation of this bathymetric distribution, recorded in the summer of two consecutive years, (4) determine whether epipelic algae inhabit the deep water basin of Loch Goil to a depth of 40m and (5) attempt to relate the changes in the epipelon to light penetration, sediment type, and to the gradient of physical and chemical parameters.

4.3.2 Methods

4.3.2.1 Sampling methods

Replicate sediment samples (9 x 15.2 cm^2) were collected by hand at depths of between 6m and 40m in June 1989 and July 1990. Sampling was by a team of four divers operating from an inflatable boat. Fig. 17. shows the location of the sample sites along a transect which extended approx. 500m from the western shore at 56^{o} 07.69'N, 04^{o} 54.33'W (Admiralty chart no. 3746). The relocation of the sample stations was achieved using an echo-sounder and sextant.

Samples of interstitial water were collected at the sediment/water interface using a polypropylene syringe (50ml) and the concentration of dissolved oxygen (DO), salinity and temperature were measured (see 3.4). An attempt to measure the light attenuation with depth was made using a portable monitoring unit (see 3.4.1.2). However, in both 1989 and 1990 this proved unsuccessful due to technical difficulties with the apparatus and insensitivity of the probe to light intensity at depths greater than 6m. However, having observed the levels of light over the whole depth profile I can confirm that no discernible light penetrates to depths greater than approx. 30m depth. Therefore, a conservative estimate would be that 30m to 40m depth represents the lower limit of the euphotic zone within Loch Goil.

4.3.2.2 Laboratory methods

Epipelic algae were harvested from the samples using the standard extraction method (see 3.2). Living cells (intact chloroplasts) were counted and an estimate made of epipelic algal abundance, chlorophyll-a and composition of species (see 3.3).

Sediment particle size analysis was carried out on the samples following the extraction of epipelic algae (see 3.4.6) and the data characterized by calculating the mode, median, mean and sorting statistic (McManus, 1988).

4.3.2.3 Data analyses

Multivariate statistical analyses (Dendrogram, Twinspan and Decorana) were used to compare the epipelic species abundance data recorded from the different depths, and provide quantitative estimates of dissimilarity between sample communities (see 3.5.1). Spearman Rank correlation analysis was used to analyse relationships between scores from the first two ordination axes (Decorana), epipelic density and environmental variable values. These analyses were then used as a descriptive tool to discern basic patterns of distribution and to test the null hypothesis (H_O): "there are no differences in the epipelon along a bathymetric gradient in Loch Goil". The use of multivariate and rank correlation analyses on a large and complex data set, is simlar to the analysis methodology used by Blanc *et al* (1972) for the study of marine phytoplankton.

Graphs are used to compare community data recorded in 1989 with that recorded in 1990 and to relate changes in the epipelon in both years to the gradient of physical and chemical parameters.

4.3.2.4 Sampling and analysis of the phytoplankton

A composite sample of phytoplankton was collected from a vertical column ($1.13cm^2$) of water to a depth of 8.2m. This was achieved by means of a length of plastic hose (internal diameter 12mm) which was weighted at one end and hung over the side of the stationary boat. The top of the hose was then blocked and the weighted end retrieved by means of a line. The sample (1l) was transferred to a container and preserved with Lugol's Iodine. In the laboratory the phytoplankton was allowed to precipitate in the dark for approx. 12hrs. The precipitate was then mixed and an aliquot (4 drops) removed for qualitative analysis of the phytoplankton community.

4.3.3 Results

4.3.3.1 Epipelic Abundance and Biomass

The epipelon showed a dramatic decrease in abundance and chlorophyll-a (biomass) with increasing depth in both 1989 and 1990 (Fig 18).

In June 1989 the abundance of epipelon was negatively correlated ($P=<0.050$) with depth and decreased in a linear fashion with increasing depth. The maximum standing crop (277.84×10^6 cells m^{-2}) was recorded at the shallowest station (6m), decreasing to 1.45×10^6 cells m^{-2} at a depth of 30m. No algae (numbers or chlorophyll-a) were found at the deepest station (-40m) by the standard

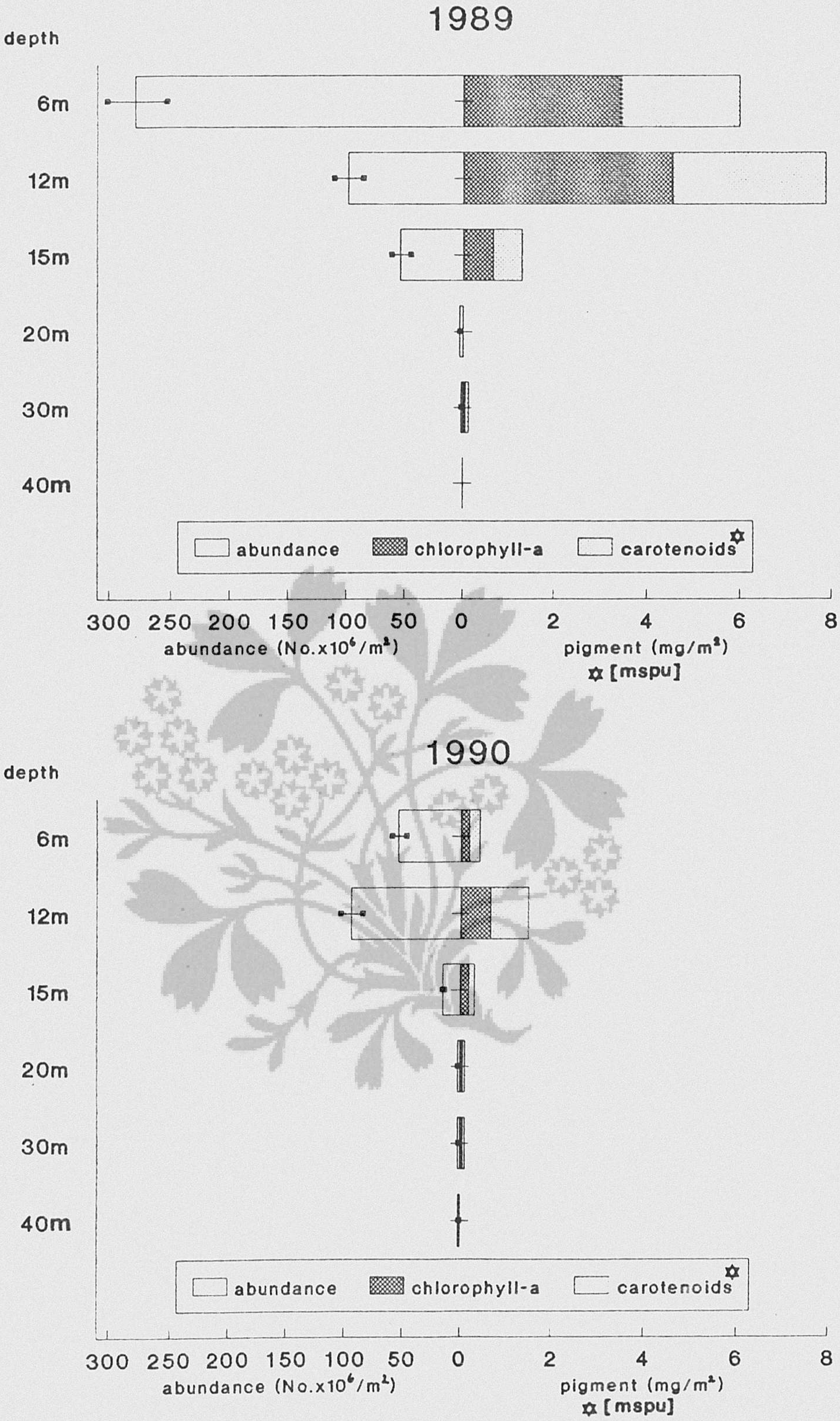


Fig. 18. Distribution of estimated diatom abundance and biomass (pigments) along a depth gradient in June 1989 and July 1990. (Bars indicate standard error).

enumeration procedure. However, 21 live algal cells were extracted from the sample using the standard lens tissue extraction method (see section 3.2.2.4) used to aid taxonomic identification.

The greatest reduction in abundance, in relation to both spatial and vertical separation of the sample stations, was from 6m to 10m. This is consistent with observed reductions in temperature (Fig. 27) and salinity (Fig. 28) and expected attenuation of light intensity. Levels of chlorophyll-a and carotenoids are positively correlated ($P=<0.050$), but their bathymetric distribution indicates a peak in the epipelic biomass at 12m depth (4.545 mg chl-a.m^{-2}; 3.296 MSPU carotenoids m^{-2}) wheras the greatest density of algae was recorded at 6m.

In July 1990 there were notably fewer epipelic algae recorded along the bathymetric profile of Loch Goil compared with the previous year (Fig. 18). Epipelic abundance was negatively correlated ($P=<0.050$) with depth, however the maximum standing crop (98.726×10^6 cells m^{-2} was recorded at a depth of 12m depth, decreasing to 1.11×10^6 cells m^{-2} at a depth of 40m. Chlorophyll-a, carotenoid and abundance data are all positively correlated ($P=<0.050$) and show a similar bathymetric distribution.

4.3.3.2 Epipelic Commnunity Analysis

There was generally a very diverse asssemblage of epipelic algae recorded over the two years, comprising 108 taxa representing 34 genera (Tables 6 and 7). The epipelic algal communities were dominated by diatoms, with one species of silicoflagellate (Chrysophyceae).

4.3.3.2.1 June 1989

Cluster anlysis of the 1989 sample community data (Fig. 19) shows the epipelic communities from the three shallowest sites (6m, 12m, 15m) to be very similar whereas the 20m and and 30m communities are clearly grouped as separate. The species composition recorded at 40m depth is

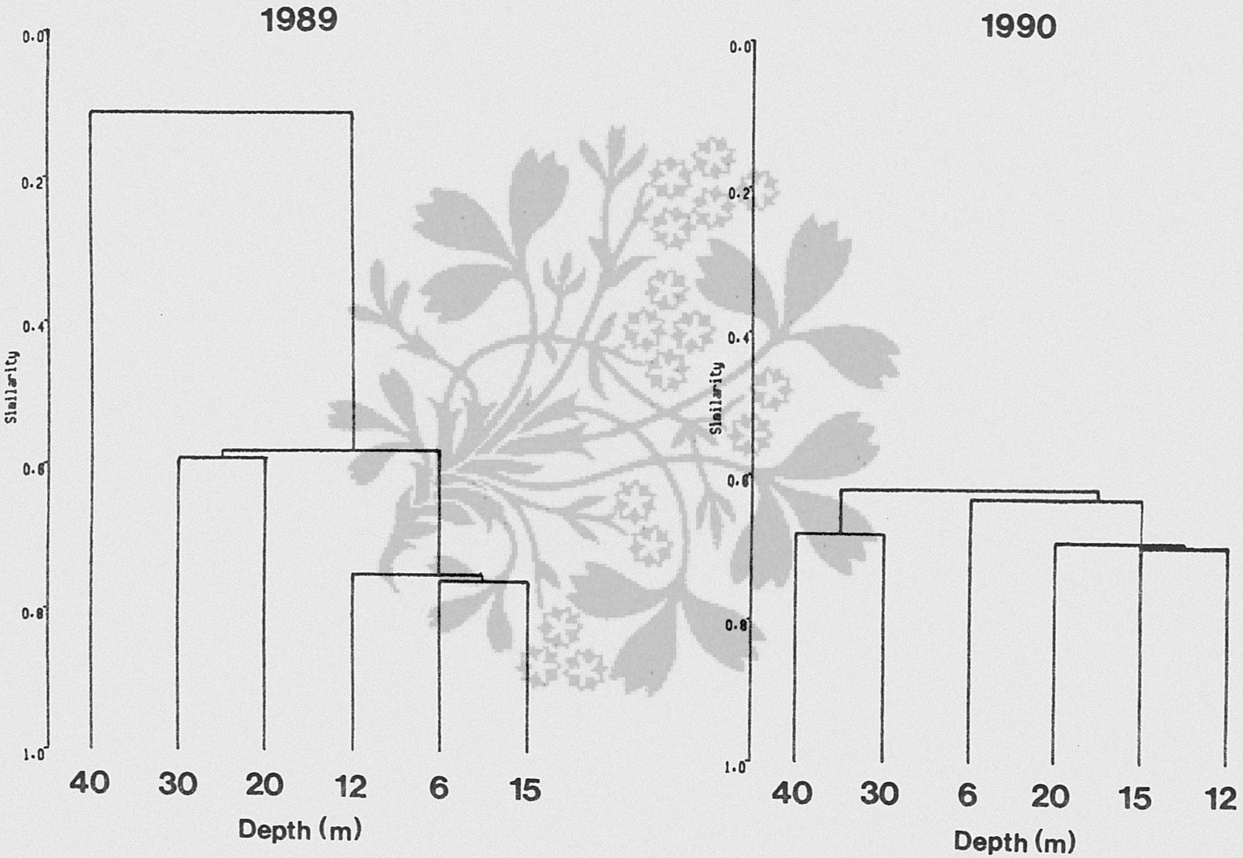


Fig. 19. Dendrograms drawn using group average sorting (Bray-Curtis coefficient) showing the similarity of the epipelic communities recorded along a bathymatric gradient in Loch Goil, 1989 and 1990.

substantially different from the two main clusters. However, this is attributed to the small number of cells (21 cells) used to estimate the community structure at this station.

The ordination plots (Fig. 20. 1989) from the DECORANA analysis, separates the sample communities into shallow (6m, 12m, 15m) and deep (20m, 30m, 40m) community types along axis 1, the stongest gradient (eigenvalue = 0.291, 82.67 % of the variability). Similarly TWINSPAN analysis shows the same separation of sample communities. Examination of the TWINSPAN matrix (Fig. 21, 1989) reveals the reason for this grouping, with several of the taxa showing highly restricted distributions along the bathymetric gradient. For example: *Navicula crucigera*, *Nitzschia distans*, *Tropidoneis vitrea* and *Amphora plicata* were only recorded within the shallow subtidal region (6-15m). However, *Nitzschia hybrida* cf. var. *pellucida*, *Tropidoneis lepidoptera*, *Pinnularia divergens* are examples of taxa recorded only at the deeper stations (20-40m).

The bathymetric distribution pattern of the sample communities are seen in Table 6. and the 24 most abundant taxa are shown graphically in Fig. 22. These data show that despite some differences in the community with depth, the most abundant taxa (*Navicula* cf.*tripunctata*, *Navicula forcipata* var. *densistriata*, *Navicula distans*, *Navicula arenaria*, *Navicula* sp.F/G/H, *Amphora* cf. *proteus* var. B) appear to form the greatest proportion of the sample communities along the entire bathymetric gradient (6-40m). This is summarised in Fig.23 (A) which divides the sample communities into the relative proportions of the major genera. This graph also highlights the increase in the proportion within the sample community of *Nitzschia* sp *B/C* at 20m and 30m depth and the planktonic diatom *Skeletonema costatum* at 30m and 40m depth.

The approximately linear decrease in epipelic numbers and chlorophyll-a with increasing depth (Fig. 18, 1989) can be attributed to diminishing abundance of all the

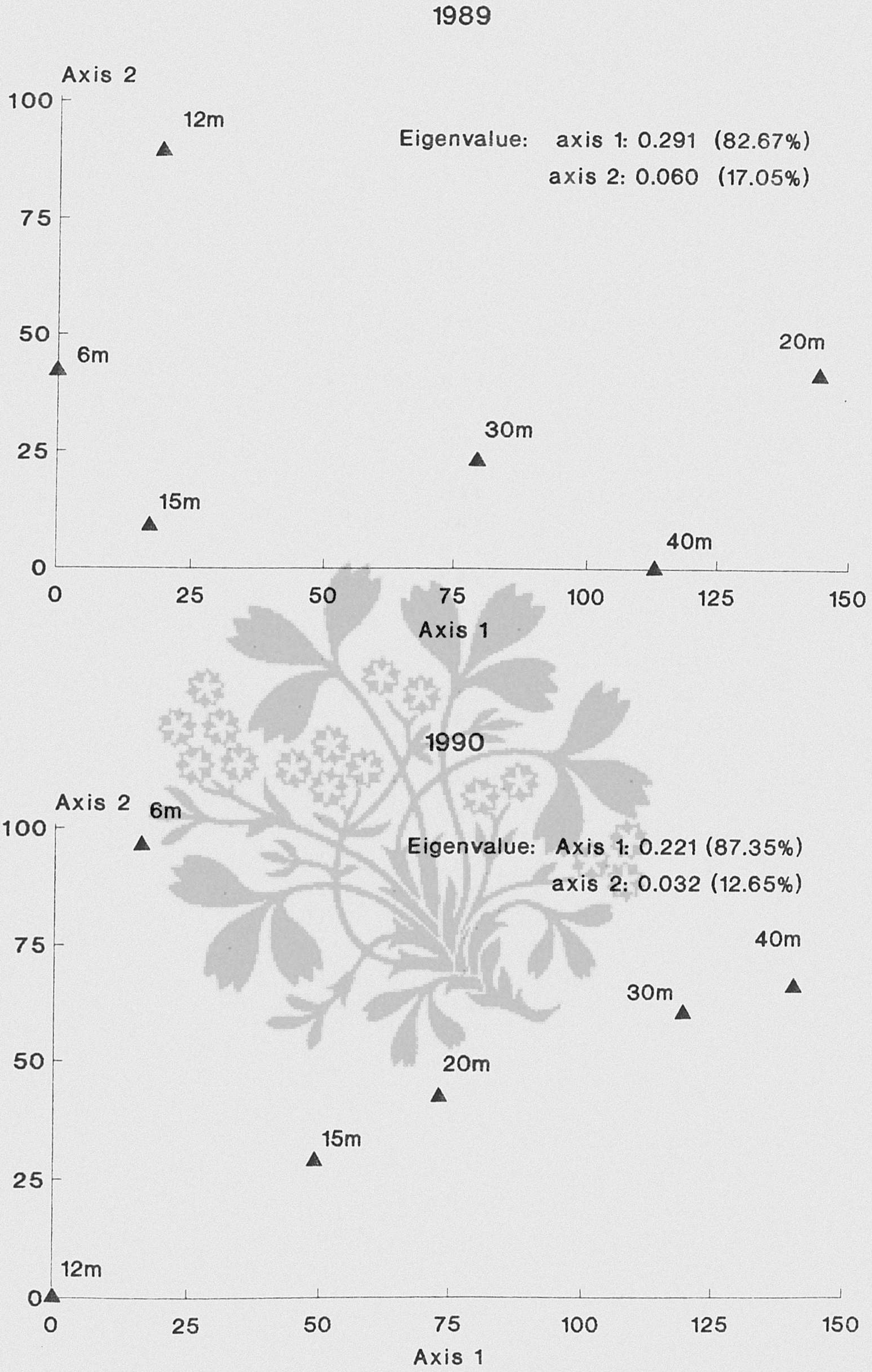
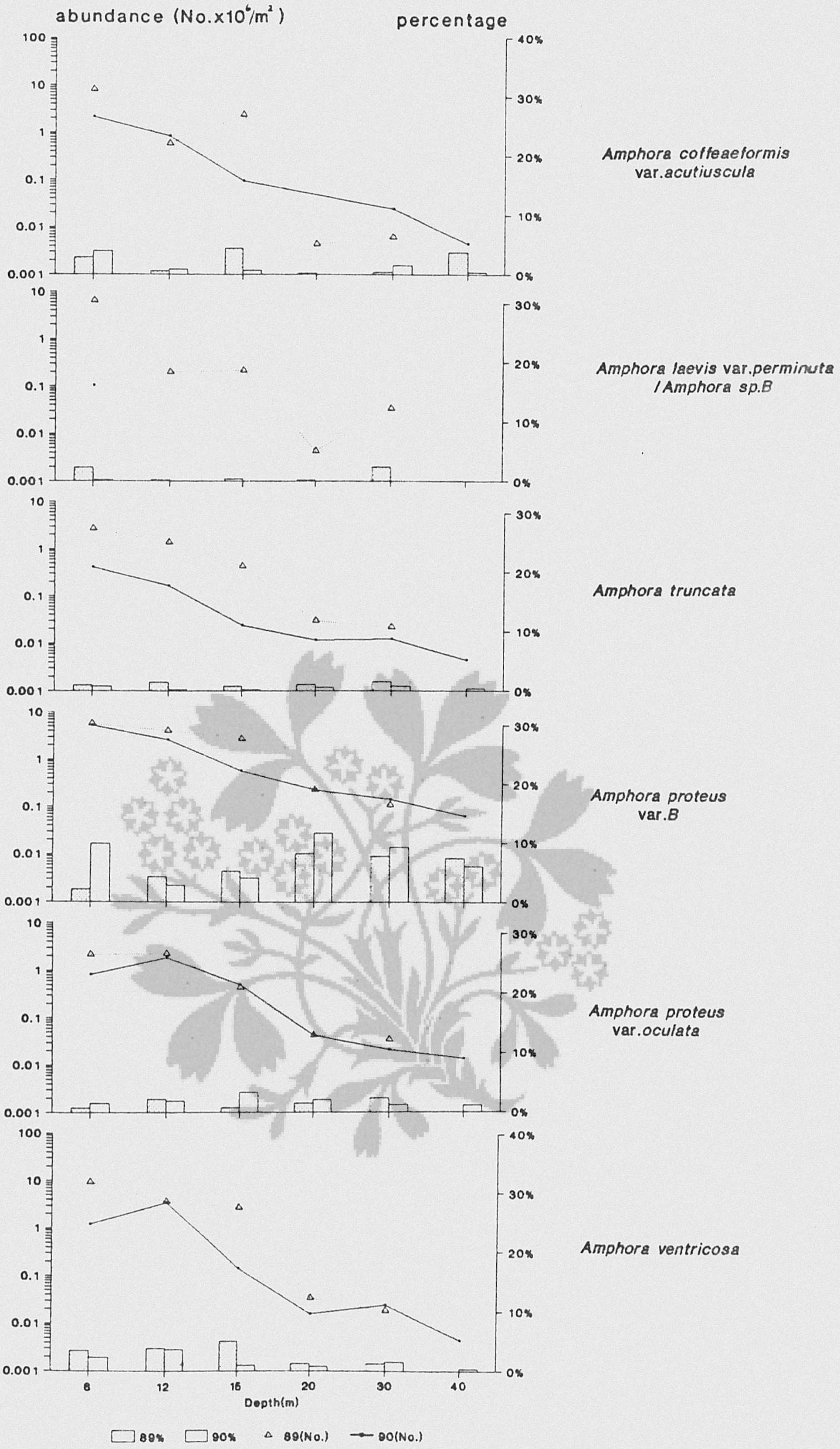


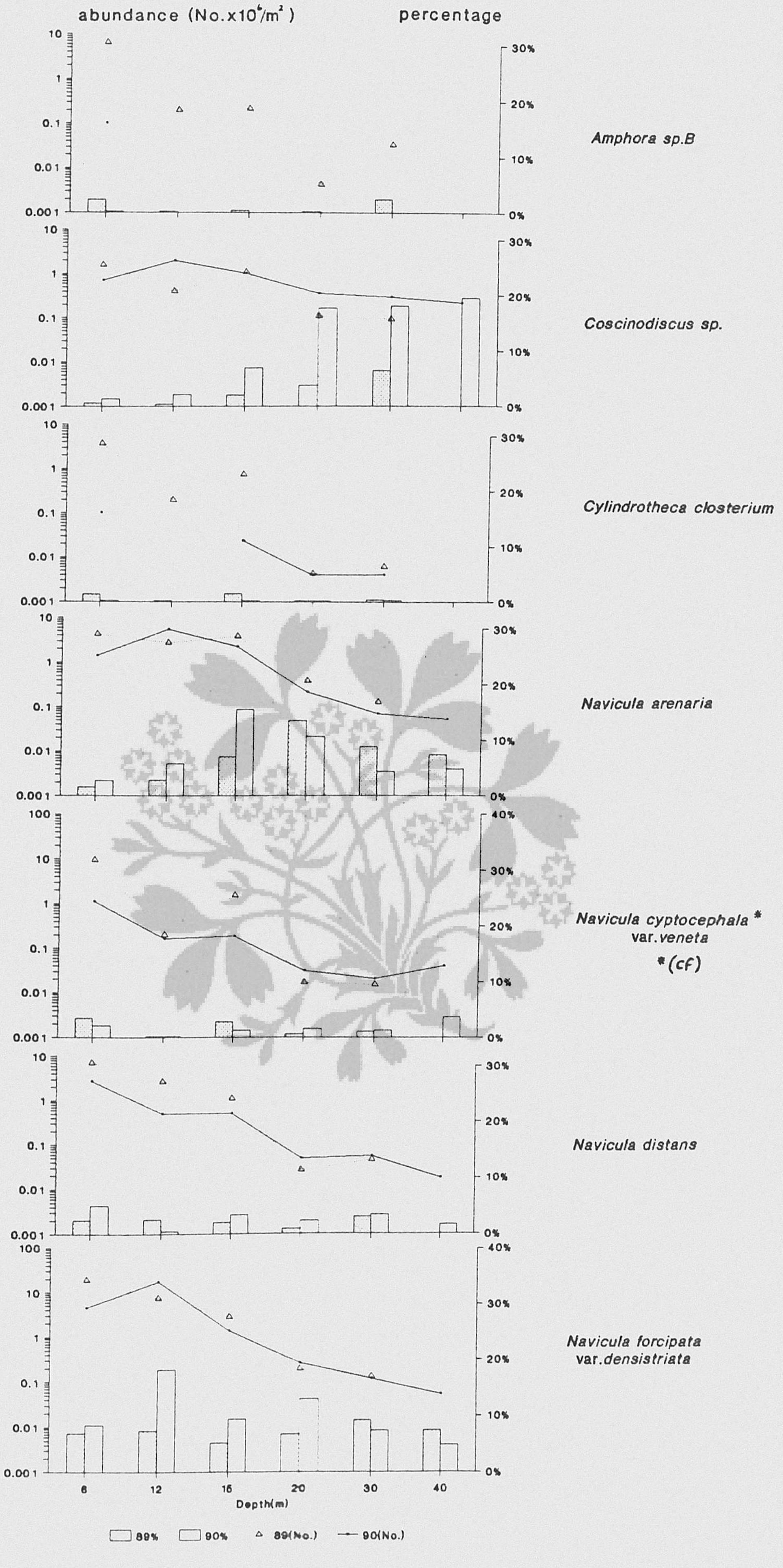
Fig. 20. Ordination plots for the epipelic community recorded from a series of depths (m) in Loch Goil during 1989 and 1990. Axis 1 and axis 2 data are derived from detrended correspondence analysis (DECORANA). The Eigenvalue and percentage variabily are shown for each axis.

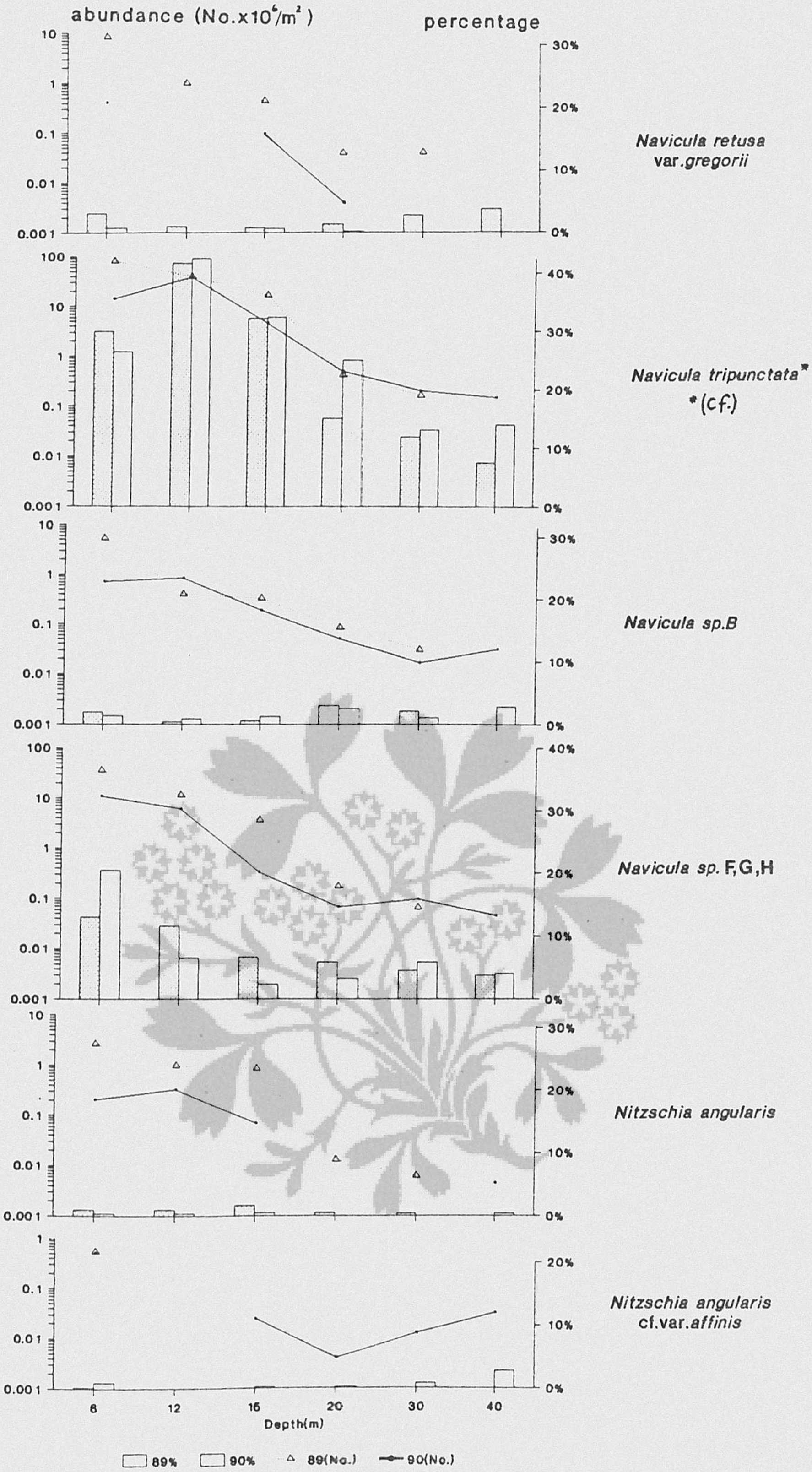
```
Depth (m)         12 15 6 20 30 40
                   \ \ | / / /
STEN ONSP   -13---   000
NAVI DICY   -1----   000
RHOI ABBR   1-----   000
NAVI CRUC   211---   000
STEN INCO   --1---   000
ACNA CONS   --1---   000
EUNO TISP   --1---   000
CAMP FAST   11----   000
AMPH OSPC   --1---   000
NITZ SIGI   -22---   000
NITZ DIST   111---   000
NITZ MARG   --2---   000
NITZ BILO   -1----   000
NITZ SIGM   2-----   000
NITZ ANGA   --1---   000
PLEU NAVI   11----   000
GYRO DIST   -11---   000
AMPH PLIC   2-1---   000
TROP VITR   -22---   000
GYRO TENU   -11---   000
CALO LIBE   1111--   001
DIPL AESD   111-1-   001
SURI FAST   1111--   001
OPEP MART   1111--   001
AMPH OSPA   1-2-1-   001
AMPH ARCU   2-11--   001
NITZ INSM   212-1-   001
PLEU FORM   1111--   001
PLEU AUST   21--1-   001
NAVI CRYP   14423-   010
NAVI CSPC   42332-   010
NAVI BRYO   -2--1-   010
DIPL SMIT   122-2-   010
TABE FLOC   11--1-   010
DIPL SPLE   11--1-   010
AMPH VENT   45433-   010
AMPH COFF   254121   010
NITZ SOCI   23212-   010
PLEU AEST   23322-   010
PLEU STRI   22212-   010
PLEU SALI   22-11-   010
PLAG TAYR   -111--   010
CYLI CLOS   13312-   010
NAVI CSPA   32323-   011
NAVI TRIP   555552   011
NAVI FORC   555552   011
NAVI PHYL   12313-   011

            12 15 6 20 30 40
             \ \ | / / /
NAVI GREG   -212--   011
NAVI DIST   44434-   011
NAVI CSPF   555551   011
DIPL AESF   11111-   011
DIPL OVAL   21112-   011
COCC SCUT   221111   011
AMPH OSPB   -2414-   011
AMPH LAEV   11221-   011
AMPH OSTR   -2212-   011
AMPH PROD   43344-   011
AMPH TRUN   32333-   011
AMPH PROT   554552   011
NITZ SSPB   243551   011
NITZ ANGU   333222   011
NITZ PAND   21222-   011
DONK RETI   1-211-   011
STAU SALI   11112-   10
NAVI PALP   -1222-   10
NAVI CSPB   22454-   10
NAVI RETG   324341   10
NAVI ATLA   -2--2-   10
NAVI HENN   2--11-   10
ACNA NTHE   --2-2-   10
NAVI AREN   453552   10
ACNA FIMB   --2-2-   10
TRAC ASPE   11121-   10
SYNE TABU   --11--   10
AMPH PROP   -1-1--   10
EUNO SEPT   -1-1--   10
GYRO ALGO   2-222-   10
DICT SPEC   111111   10
SKEL COST   332442   10
ACNA ANGU   --111-   110
COSC INSP   242553   110
NAVI PLIC   ----1-   111
PINN USPA   ----1-   111
PINN DIVE   ---1--   111
PINN RUPE   ----1-   111
SURI HYBR   ----1-   111
DIPL CRAB   ----1-   111
PLAG STAU   ---1--   111
FRUS RHOM   ----1-   111
NITZ HYBR   ---44-   111
TROP LEPI   ---11-   111

            000111
```

Fig. 21.

1989: TWINSPAN classification of epiplic communities recorded in Loch Goil at a range of depths in 1989. Abbreviations of species names are shown at the left; sample numbers along the top. The classification of species and samples are indicated along the right and bottom margins (Hill, 1979 [a]). The main dichotomy for the samples is indicated by a vertical separation. Values indicate a scale of abundance, with absence of a species represented by the symbol "-".


abundance (No.x10⁶/m²)
percentage
100
10
1
0.1
0.01
0.001
40%
30%
20%
10%
0%
Amphora coffeaeformis var.acutiuscula
Amphora laevis var.perminuta /Amphora sp.B
Amphora truncata
Amphora proteus var.B
Amphora proteus var.oculata
Amphora ventricosa
6
12
15
20
30
40
Depth(m)
89%
90%
89(No.)
90(No.)


abundance (No.x10⁶/m²)
percentage
10
1
0.1
0.01
0.001
100
30%
20%
10%
0%
40%
Amphora sp.B
Coscinodiscus sp.
Cylindrotheca closterium
Navicula arenaria
Navicula cyptocephala *
var.veneta
*(cf)
Navicula distans
Navicula forcipata
var.densistriata
6
12
16
20
30
40
Depth(m)
89%
90%
89(No.)
90(No.)


abundance (No.x10⁶/m²)
percentage
10
1
0.1
0.01
0.001
100
30%
20%
10%
40%
0%
Navicula retusa var.gregorii
Navicula tripunctata*
*(cf.)
Navicula sp.B
Navicula sp. F,G,H
Nitzschia angularis
Nitzschia angularis cf.var.affinis
6
12
16
20
30
40
Depth(m)
89%
90%
89(No.)
90(No.)

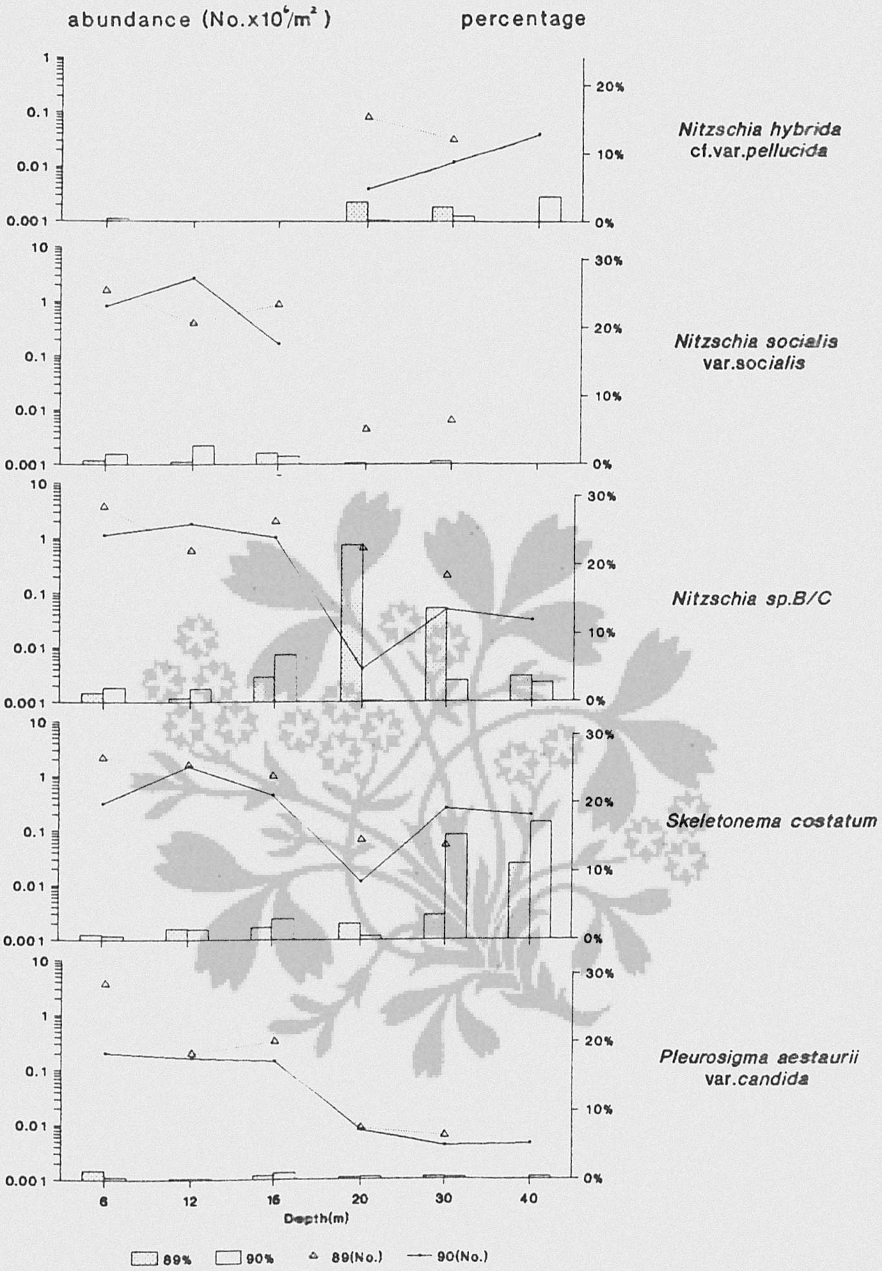


Fig.22.The depth distribution pattern of the predominant species of epipelic diatom recorded from 6-40m depth in 1989 and 1990 indicated by estimated abundance.

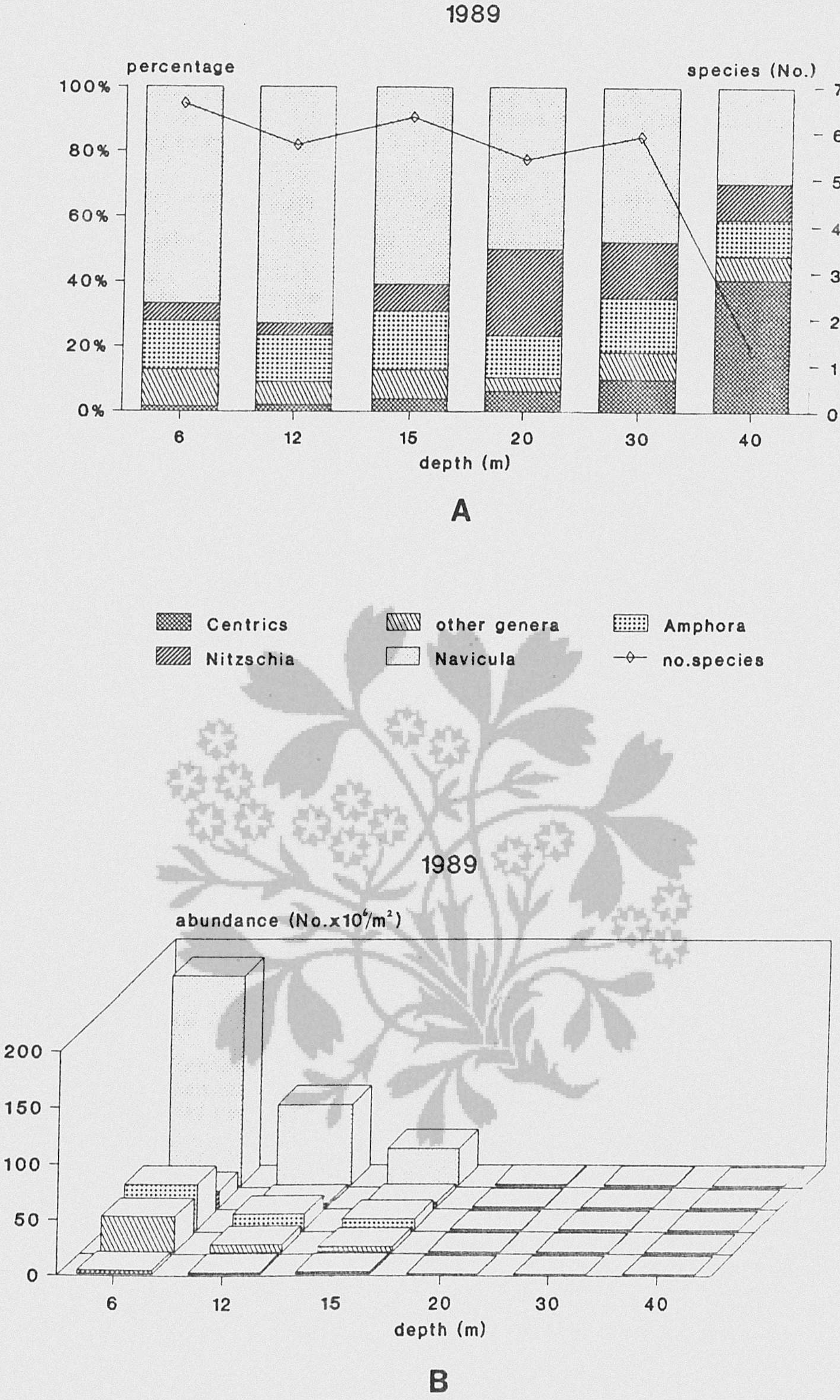


Fig.23. The spatial change in the epipelic community structure along a depth gradient (6-40m) in 1989.
A: Estimated pertage occurrence of the major epipelic diatom genera and number of species.
B: Estimated abundance of major genera.

Table 6. List of epipelic species and their percentage abundance in sample communites recorded along a bathymetric gradient (6 - 40m), within Loch Goil, in June 1989. Depth is in metres below chart datum. Key: * = rare species (see section 4.3.2.2).

Taxa 1989:	6m	12m	15m	20m	30m	40m
Acnanthes cf.angustata	*			*	*	
Achnanthes conspicua var.conspicua	*					
Achnanthes fimbriata	0.4				0.5	
Achnanthes sp.	0.4				0.5	
Amphiprora plicata	*	0.4				
Amphora cf.arcus	*	0.4		*		
Amphora coffeaeformis var.acutiuscula	3.0	0.6	4.9	*	0.5	*
Amphora laevis var.perminuta	0.8	*	*	0.3	*	
Amphora ostrearia var.ostrearia	0.4		0.4	*	0.7	
Amphora cf.proteus var.B	2.2	4.4	5.5	8.5	8.1	9.5
Amphora proteus var.oculata	1.2	2.9	1.3	1.7	2.5	
Amphora proteus var.proteus		0.4	*	*		
Amphora truncata	1.0	1.5	0.9	1.1	1.6	
Amphora ventricosa	3.6	4.0	5.3	1.3	1.4	
Amphora sp.A	0.4	*			*	
Amphora sp.B	2.4	*	0.4	*	2.5	
Amphora sp.C	*	*				
Caloneis liber var.elongata		*	*	*		
Caloneis liber var.excentrica	*					
Campylodiscus fastuosa		*	*			
Chaetocerous sp.						
Cocconeis scutellum cf.var.scutellum	*	0.4	0.4	*	*	*
Coscinodiscus sp.	0.6	0.4	2.1	3.9	6.8	38.1
Cylidrotheca gracilis						
Cylindrotheca closterium	1.4	*	1.5	*	0.5	
Dictyocha speculum var.speculum	*	*	*	*	*	*
Diploneis aesteva var.delicata	*	*	*		*	
Diploneis aesteva var.fusca	*	*	*	*	*	
Diploneis crabro					*	
Diploneis ovalis	*	0.6	*	*	0.9	
Diploneis smithii var.smithii	0.4	*	0.4		0.5	
Diploneis splendida		*	*		*	
Donkinia reticulata	0.6	*		*	*	
Eunotia cf.septentrionalis			*	*		
Eunotia sp.	*					
Frustulia rhomboides var.rhomboides						
Frustulia rhomboides var.saxonica f.u					*	
Gomphonema parvulum var.exilis						
Gyrosigma algoris	0.4	0.4		0.6	0.5	
Gyrosigma distortum var.parkeri	*		*			
Gyrosigma rectum						
Gyrosigma tenuirostrum	*		*			
Navicula abrupta						
Navicula arenaria	1.6	2.9	7.5	14.1	9.3	9.5
Navicula atlantica			0.4		0.5	
Navicula cf.bryophila			0.4		*	
Navicula cf.decussis var.decussis						
Navicula cf.delognei						
Navicula crucigera	*	0.4	*			
Navicula cryptocephala* var.veneta (cf)*	3.6	*	3.0	0.6	1.1	
Navicula cf.digito-radiata var.B						
Navicula cf.digito-radiata						
Navicula digito-radiata var.cyprinus			*			
Navicual distans	2.6	2.7	2.1	0.9	3.2	

Continued....

Taxa 1989:	6m	12m	15m	20m	30m	40m
Navicula forcipata var.densistriata	7.3	7.8	5.5	7.1	9.7	9.5
Navicula gregaria	*		0.6	0.5		
Navicula hennedyi var.hennedyi		0.4		*	*	
Navicula palpebralis var.angulosa	0.4		*	0.3	0.5	
Navicula phyllepta	1.0	*	0.4	*	1.1	
Navicula plicata var.constricta					*	
Navicula retusa var.cancellata						
Navicula retusa var.gregorii	3.2	1.1	0.9	1.4	2.9	*
Navicula tripunctata* (cf.)*	31.3	43.5	34.1	15.7	12.4	9.5
Navicula sp.A	1.4	1.1	0.6	0.6	1.1	
Navicula sp.B.	2.0	0.4	0.6	3.1	2.3	
Navicula sp.C/D	1.8	3.6	0.6	1.1	0.5	
Navicula sp.F/G/H	13.7	12.2	7.0	6.1	4.7	*
Navicula sp.I						
Nitzschia angularis	1.0	1.1	1.7	0.5	0.5	9.5
Nitzschia angularis cf.var.affinis	*					
Nitzschia bilobata var.bilobata			*			
Nitzschia aff.distans	*	*	*			
Nitzschia hybrida cf.var.pellucida				3.0	2.3	
Nitzschia insignis var.smithii	0.4	0.4	*		*	
Nitzschia marginulata var.marginulata	0.6					
Nitzschia panduriformis/punctata	0.6	0.6	*	0.3	0.5	
Nitzschia sigma var.intercedens	0.8	0.4	0.6			
Nitzschia socialis var.socialis	0.6	0.4	1.7	*	0.5	
Nitzschia sp.B/C	1.4	0.6	3.8	24.0	14.4	*
Opephora martyi	*	*	*	*		
Pinnularia ambigua						
Pinnularia appendiculata						
Pinnularia divergens				*		
Pinnularia rupestris					*	
Pinnularia sp.A					*	
Plagiogramma staurophorum				*		
Plagiotropis tayrecta	*		*	*		
Pleurosigma aestaurii var.candida	1.8	0.4	1.5	0.3	0.5	
Pleurosigma australe		0.6	*		*	
Pleurosigma formosum	*	*	*	*		
Pleurosigma naviculaceum		*	*			
Pleurosigma nubecula						
Pleurosigma salinarum		0.4	0.4	*	*	
Pleurosigma strigosum	0.6	0.6	0.6	*	0.5	
Rhabdonema minutum						
Rhoicosphenia abbreviata		*				
Skeletonema costatum	0.8	1.7	1.9	2.5	3.8	14.3
Stauroneis salina var.lagerstedtii	*	*	*	*	0.9	
Stauroneis sp.						
Stenoneis inconspicua	*					
Stenoneis sp.	1.6		*			
Surirella fastuosa var.fastuosa	*	*	*	*		
Surirella hybrida					*	
Synedra cf.tabulata	*			*		
Tabellaria floculosa		*	*		*	
Trachyneis aspera var.aspera	*	*	*	0.3	*	
Tropidoneis lepidoptera				*	*	
Tropinoneis vitrea var.scaligera	0.4		0.4			
Number of species:	66	58	63	54	59	13
Number of cells identified:	496	476	469	637	443	27

Table 7. . List of epipelic species and their percentage abundance in sample communites recorded along a bathymetric gradient (6 - 40m), within Loch Goil, in July 1990. Depth is in metres below chart datum. Key: * = rare species (see section 4.3.2.2).

Taxa 1990:	6m	12m	15m	20m	30m	40m
Acnanthes cf.angustata						
Achnanthes conspicua var.conspicua						
Achnanthes fimbriata		*	*			
Achnanthes sp.			*	0.4	*	
Amphiprora plicata	*	*				
Amphora cf.arcus						
Amphora coffeaeformis var.acutiuscula	4.3	1.1	0.8		1.6	*
Amphora laevis var.perminuta	*			*	*	*
Amphora ostrearia var.ostrearia	0.6	*				
Amphora cf.proteus var.B	10.2	3.0	4.1	12.0	9.6	6.4
Amphora proteus var.oculata	2.0	2.2	3.6	2.4	1.6	1.3
Amphora proteus var.proteus	0.6	*	*		*	*
Amphora truncata	0.8	*	*	0.6	0.8	*
Amphora ventricosa	2.3	3.9	1.0	0.8	1.6	*
Amphora sp.A						
Amphora sp.B	*					
Amphora sp.C					0.8	
Caloneis liber var.elongata						
Caloneis liber var.excentrica						
Campylodiscus fastuosa		*				
Chaetocerous sp.		*	0.5	0.8	2.4	2.1
Cocconeis scutellum cf.var.scutellum	0.6		*	0.4	0.5	1.7
Coscinodiscus sp.	1.4	2.2	7.1	18.4	18.9	21.0
Cylidrotheca gracilis	*				*	
Cylindrotheca closterium	*		*	*	*	
Dictyocha speculum var.speculum				*	0.5	
Diploneis aesteva var.delicata	*	*				
Diploneis aesteva var.fusca		*		*		
Diploneis crabro						
Diploneis ovalis	*	*			*	*
Diploneis smithii var.smithii	*	0.4		*	*	
Diploneis splendida		*				
Donkinia reticulata				*	*	*
Eunotia cf.septentrionalis	0.4	*		0.4		
Eunotia sp.						*
Frustulia rhomboides var.rhomboides					*	
Frustulia rhomboides var.saxonica f.u						
Gomphonema parvulum var.exilis						*
Gyrosigma algoris	*	*	0.3			
Gyrosigma distortum var.parkeri						
Gyrosigma rectum				*		
Gyrosigma tenuirostrum						
Navicula abrupta			*			
Navicula arenaria	2.7	6.1	15.8	11.0	4.5	5.2
Navicula atlantica						
Navicula cf.bryophila				0.4	*	
Navicula cf.decussis var.decussis					0.5	
Navicula cf.delognei	*					
Navicula crucigera						
Navicula cryptocephala* var.veneta (cf)*	2.2	*	1.3	1.6	1.3	3.9
Navicula cf.digito-radiata var.B					0.5	
Navicula cf.digito-radiata		*				
Navicula digito-radiata var.cyprinus						
Navicual distans	5.3	0.6	3.5	2.4	3.5	1.7

Continued....

Taxa 1990:	6m	12m	15m	20m	30m	40m
Navicula forcipata var.densistriata	8.6	19.2	9.5	13.4	7.7	5.2
Navicula gregaria					*	
Navicula hennedyi var.hennedyi		*				
Navicula palpebralis var.angulosa	*	*	*	0.4		
Navicula phyllepta	0.4	*				*
Navicula plicata var.constricta		*			*	
Navicula retusa var.cancellata						*
Navicula retusa var.gregorii	0.8		0.7	*		
Navicula tripunctata* (cf)*	27.2	44.5	32.9	25.7	13.6	15.0
Navicula sp.A	*	*	*	*	*	
Navicula sp.B.	1.4	0.9	1.3	2.6	1.1	3.0
Navicula sp.C/D	0.4	1.3	1.8	1.0	1.3	
Navicula sp.F/G/H	21.1	6.8	2.3	3.4	6.1	4.3
Navicula sp.I						*
Nitzschia angularis	0.4	0.4	0.5			*
Nitzschia angularis cf.var.affinis	1.0		*	*	0.8	3.0
Nitzschia bilobata var.bilobata						
Nitzschia aff.distans	*	*				
Nitzschia hybrida cf.var.pellucida	0.4			*	0.8	3.9
Nitzschia insignis var.smithii						
Nitzschia marginulata var.marginulata						
Nitzschia panduriformis/punctata	0.4	*	*	0.6	*	
Nitzschia sigma var.intercedens	*	0.4				
Nitzschia socialis var.socialis	1.6	3.0	1.2			
Nitzschia sp.B/C	2.2	2.0	7.1	*	3.2	3.0
Opephora martyi		*				*
Pinnularia ambigua	*					
Pinnularia appendiculata			*	*	*	
Pinnularia divergens						
Pinnularia rupestris						
Pinnularia sp.A						
Plagiogramma staurophorum						
Plagiotropis tayrecta	*					
Pleurosigma aestaurii var.candida	0.4	*	1.0	0.4	*	*
Pleurosigma australe		*				
Pleurosigma formosum						
Pleurosigma naviculaceum						
Pleurosigma nubecula	*			*		
Pleurosigma salinarum		*			0.5	
Pleurosigma strigosum		0.4	0.3	0.4		0.9
Rhabdonema minutum	*					*
Rhoicosphenia abbreviata				*		*
Skeletonema costatum	0.6	1.7	3.1	0.6	16.0	18.5
Stauroneis salina var.lagerstedtii						
Stauroneis sp.				*		
Stenoneis inconspicua						
Stenoneis sp.						
Surirella fastuosa var.fastuosa						
Surirella hybrida						
Synedra cf.tabulata		*				
Tabellaria floculosa		*	0.3		*	
Trachyneis aspera var.aspera	*					
Tropidoneis lepidoptera		*		*		
Tropidoneis vitrea var.scaligera						
Number of species:	47	48	35	40	42	34
Number of cells identified:	511	541	608	501	375	233

1989	abundance	chlorophyll-a	carotenoids	salinity	temperature	oxygen	depth	axis 1	axis 2	silt (%)	median
abundance		-	-	-	-	-	N	-	-	-	-
chlorophyll-a			P	-	-	-	-	-	-	-	-
carotenoids				-	-	-	-	-	-	-	-
salinity					-	-	-	-	-	-	-
temperature						-	-	-	-	-	-
oxygen							-	-	-	-	-
depth								-	-	-	-
axis 1									-	-	-
axis 2										-	-
silt (%)											-
median											

1990	abundance	chlorophyll-a	carotenoids	salinity	temperature	oxygen	depth	axis 1	axis 2	silt (%)	median
abundance		P	P	-	P	-	N	N	-	-	-
chlorophyll-a			P	-	-	-	-	N	-	-	-
carotenoids				-	P	-	N	N	-	-	-
salinity					N	N	P	-	-	-	-
temperature						P	N	N	-	-	-
oxygen							N	-	-	-	-
depth								P	-	-	-
axis 1									-	-	-
axis 2										-	-
silt (%)											P
median											

Table 8. The relationships between scores on DECORANA axis with epipelic abundance, chlorophyll-a and environmental variables. Data was recorded along a bathymetric gradient in 1989 and 1990. Significant levels (P=<0.050) derived from Spearman rank correlation analysis. Median = median sediment particle size; '-' = no correlation; P = positive correlation; N = negative correlation.

major taxa (Fig. 23) and most of the rarer species (Fig. 22).

4.3.3.2.2 July 1990

TWINSPAN analysis of the 1990 community data separates the shallow water stations (6m, 12m, 15m) from the deeper stations (20m, 30m, 40m) in a manner similar to that seen in June 1989 (Fig. 24, 1990). However, examination of both the dendrogram (Fig. 19, 1990) and ordination plot (Fig. 20; 1990) shows that the shallow community is less distinct than that recorded in the previous year with a lower level of similarity (cluster analysis) and a greater spread along the principal ordination axis (eigenvalue = 0.221, 87.35 % of the variability). DECORANA and cluster analyses also indicate a difference between the community of the two deeper stations (30m and 40m) and the epipelon recorded at the shallower stations. This can be attributed to a marked increase in abundance of *Skeletonema costatum* at these two stations (Fig. 20).

Examination of the TWINSPAN matrix (Fig. 24, 1990) and Table 7 once again reveals the reason for this grouping, with several of the less abundant taxa showing highly restricted distribution along the bathymetric gradient. In particular, four of the taxa that characterised the shallow community in 1990 (*Amphora plicata*, *Nitzschia distans*, *Nitzschia sigma* var.*intercedens* and *Campylodiscus fastuosus*) were also limited to the same range of depth in 1989. However, of those species that characterised the two deepest stations (20m and 40m), only *Frustulia rhomboides* was common to both 1989 and 1990 communities. *F. rhomboides* is strictly a fresh water species which would have had to have been been washed in from Cormonachan Burn. None the less the cell was alive within the sediment which suggests that I may have identified this species incorectly (see appendix 1). The taxa that separate the deep and shallow water communities in 1989 and 1990 bear little resemblance;

```
              30  12
Depth (m)  20 | 40| 15 6
            \ \ | | / /

CYLI GRAC  -1----  111
DICT SPEC  12----  111
GYRO RECT  1-----  111
STAU ROSP  1-----  111
DONK RETI  111---  111
GOMP PARV  --1---  111
FRUS RHOM  -1----  111
AMPH OSPC  -2----  111
EUNO TISP  --1---  111
NAVI CSPI  --1---  111
NAVI DISC  -2----  111
NAVI RETC  --1---  111
NAVI DIGB  -2----  111
NAVI GREG  -1----  111
NAVI BRYO  21----  111
ACNA NTHE  -1----  111
RHOI ABBR  1-1---  111
CHAE TOCE  23312-  110
PLEU SALI  -2-1--  110
NITZ HYBR  123--2  110
AMPH LAEV  111--1  110
COCC SCUT  222-12  110
ACHN ANSP  2---1-  110
PINN APPE  11--1-  110
SKEL COST  255342  10
COSC INSP  555453  10
AMPH TRUN  221112  10
NAVI CRYP  333134  10
CYLI CLOS  11--11  011
TROP LEPI  1--1--  011
PLEU NUBE  1----1  011
PLEU STRI  2-222-  011
NITZ ANGA  --3-13  011
NITZ PAND  21-112  011
AMPH PROT  554455  011
OPEP MART  --11--  011
DIPL OVAL  -111-1  011
RHAB MINU  --1--1  011
DIPL AESF  1--1--  011
NAVI CSPF  454545  011
NAVI DIST  442255  011
NAVI AREN  544554  011
```

```
           30  12
        20 | 40| 15 6
         \ \ | | / /

NAVI FORC  554555  011
NAVI CSPB  423333  011
NAVI TRIP  555555  011
NAVI PLIC  -1-1--  011
PLEU AEST  211132  010
NITZ ANGU  121222  010
NITZ SSPB  143454  010
EUNO SEPT  2--1-2  010
AMPH PROO  432454  010
AMPH VENT  231534  010
AMPH PROP  -11112  010
DIPL SMIT  11-2-1  010
NAVI CSPC  33-342  010
NAVI PALP  2--111  010
NAVI CSPA  11-111  010
AMPH COFF  -31335  001
TABE FLOC  -1-12-  001
NAVI PHYL  --11-2  001
NAVI RETG  1---22  001
AMPH PLIC  ---1-1  000
PLAG TAYR  -----1  000
GYRO ALGO  ---121  000
PLEU AUST  ---1--  000
NITZ SOCI  ---433  000
NITZ SIGM  ---2--  000
NITZ DIST  ---1-1  000
NITZ SIGI  -----1  000
NAVI DELO  -----1  000
AMPH OSTR  ---1-2  000
AMPH OSPB  -----1  000
PINN AMBI  -----1  000
CAMP FAST  ---1--  000
DIPL SPLE  ---1--  000
SYNE TABU  ---1--  000
DIPL AESD  ---1-1  000
ACHN FIMB  ---11-  000
NAVI DIGC  ---1--  000
NAVI HENN  ---1--  000
NAVI ABRU  ----1-  000

           000111
```

Fig. 24.

1990: TWINSPAN classification of epiplic communities recorded in Loch Goil at a range of depths in 1990. Abbreviations of species names are shown at the left; sample numbers along the top. The classification of species and samples are indicated along the right and bottom margins (Hill, 1979 [a]). The main dichotomy for the samples is indicated by a vertical separation. Values indicate a scale of abundance, with absence of a species represented by the symbol "-".

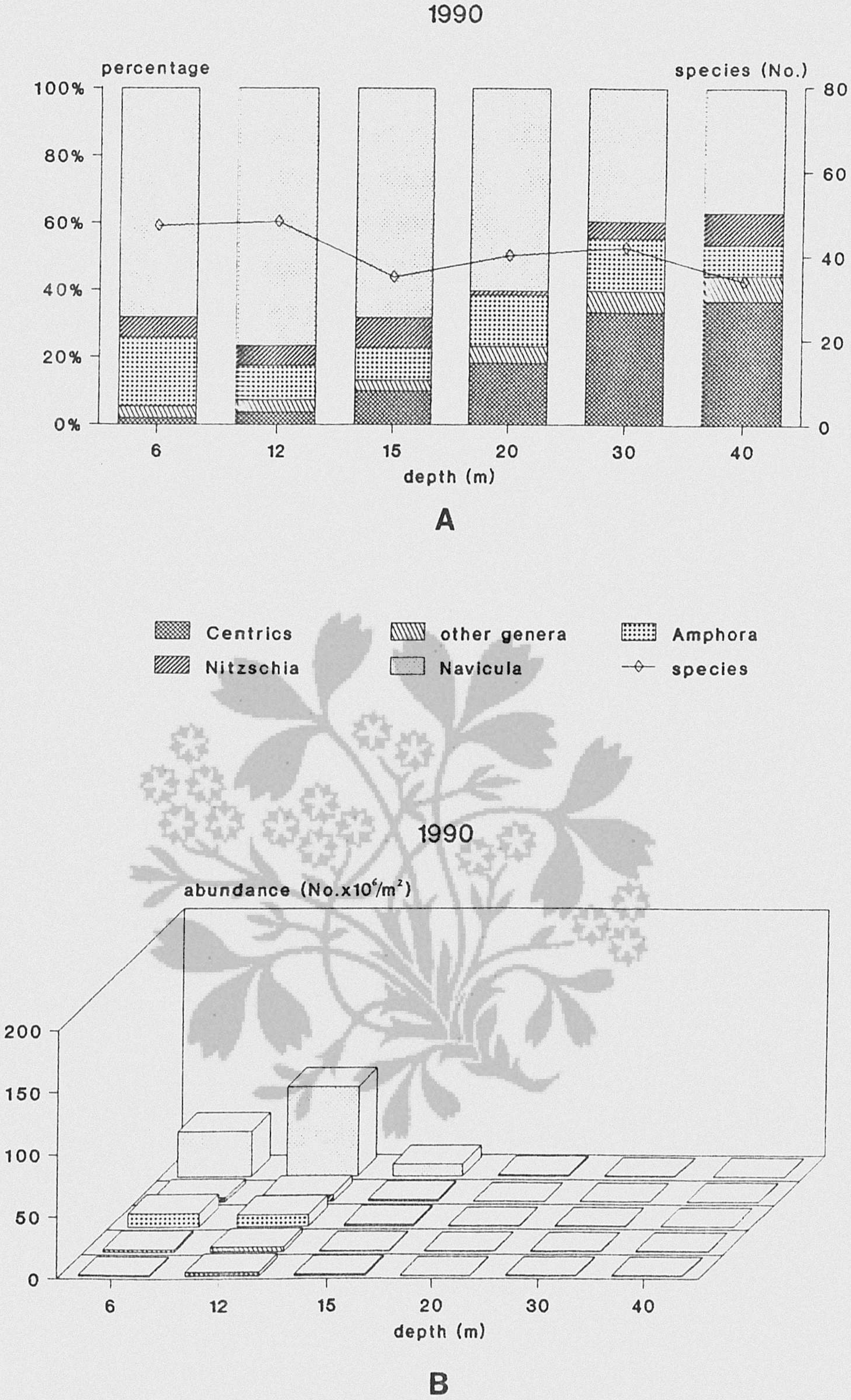


Fig. 25. The spatial change in the epipelic community structure along a depth gradient (6-40m) in 1990.
A: Estimated pertage occurrence of the major epipelic diatom genera and number of species.
B: Estimated abundance of major genera.

however, it is the re-occurrence of the most numerically dominant taxa that is most notable feature of the data. Inspection of Fig. 22. shows the similarity, between the two years, of the bathymetric distribution of the major taxa (*Navicula* cf.*tripunctata*, *Navicula forcipata* var. *densistriata*, *Navicula arenaria*, *Navicula* sp.F/G/H, and *Amphora* cf. *proteus* var. B). This similarity is summarised by comparing Fig. 23, (A) and Fig. 25, (A) which divide the sample communities of the 1989 and 1990 data (respectively) into the relative proportions of the major genera.

The most notable differences in the disitribution and abundance of the major taxa, between the two years, is the absence of a peak (recorded in 1989 at 20m and 30m depth) of *Nitzschia* sp. *B/C* and an increase in the abundance of *Coscinodiscus sp*. at 20m, 30m and 40m in 1990. Fig. 22 and Fig. 25 shows that it was an increase in the abundance of the dominant *Navicula* and *Amphora* species (*Navicula* cf.*tripunctata*, *Navicula forcipata* var. *densistriata* *Navicula arenaria*, *Amphora ventricosa* and *Amphora proteus* var.*oculata*) at a depth of 12m that was reponsible for the peek in algal density recorded at this depth (Fig. 18).

4.3.3.3 Physicochemical Gradients.

Changes in the temperature (Fig. 26) and oxygen levels (Fig. 27) with depth in both 1989 and 1990 show that the sampled habitats were within the epilimnion of Loch Goil with no evidence of stratification within the measured depth range (6-40m). In 1989 temperature (9-8.4 ^{O}C) and oxygen (8.6-7.5 ppm) showed little change as depth increased indicating a well mixed water column. In 1990 temperature (12.5-8.8 ^{O}C) and oxygen (12.2-5.5 ppm) showed greater variation with both parameters decreasing in an approximately linear fashion with increasing depth. The variation in salinity with depth can be seen in Fig.28. However, these data appear to be erroneous as levels differ considerably from those recorded from the centre of Loch Goil by the Clyde River Purification Board (CRPB) in

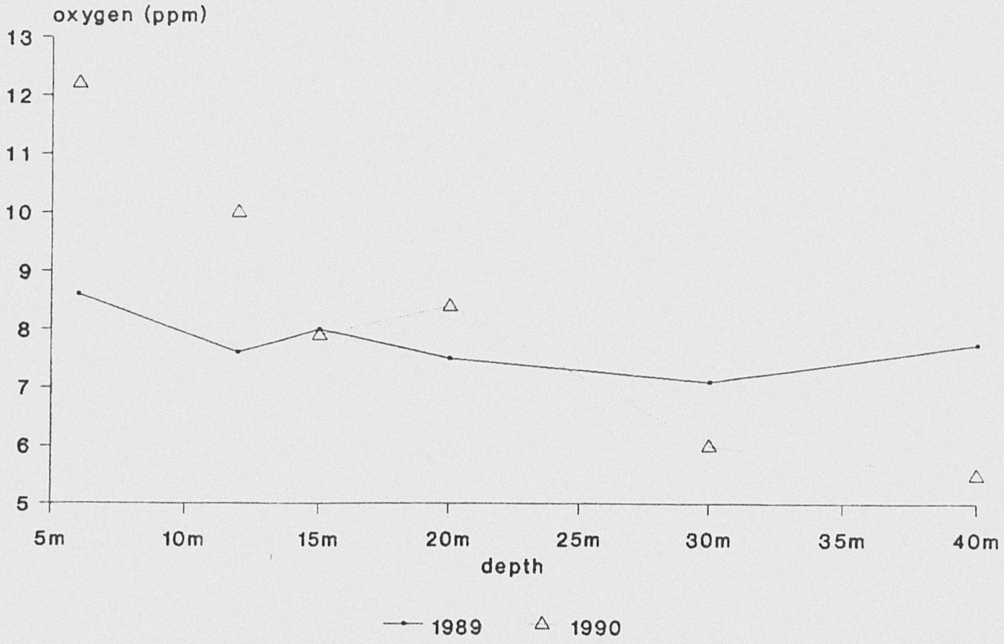


Fig. 26. Spatial distribution of oxygen (at sediment/sea water interface) along a depth gradient.

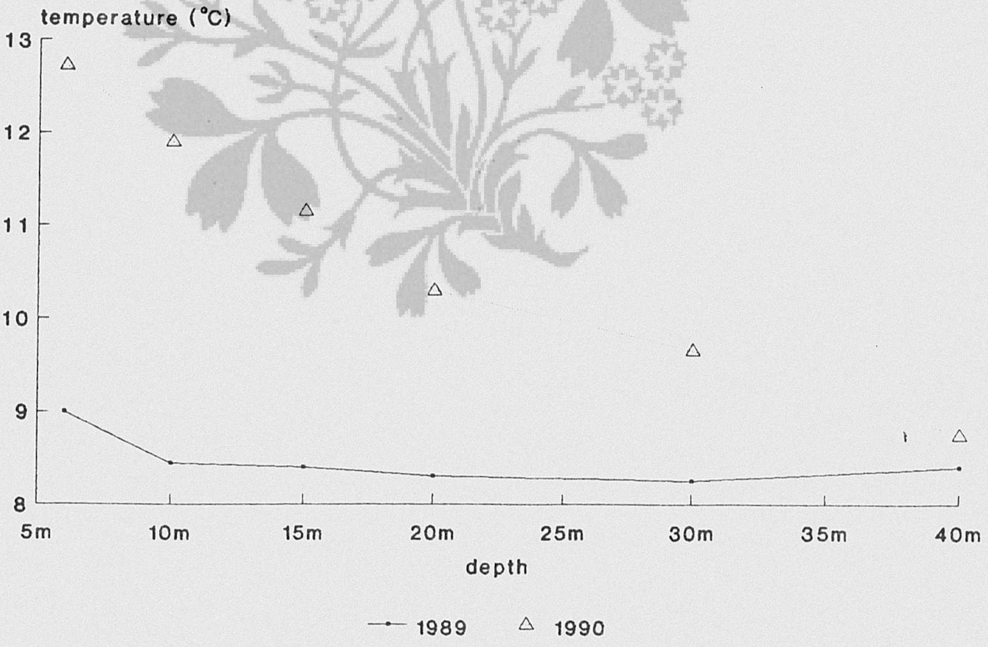


Fig. 27. Spatial distribution of temperature at the sediment surface along a depth gradient.

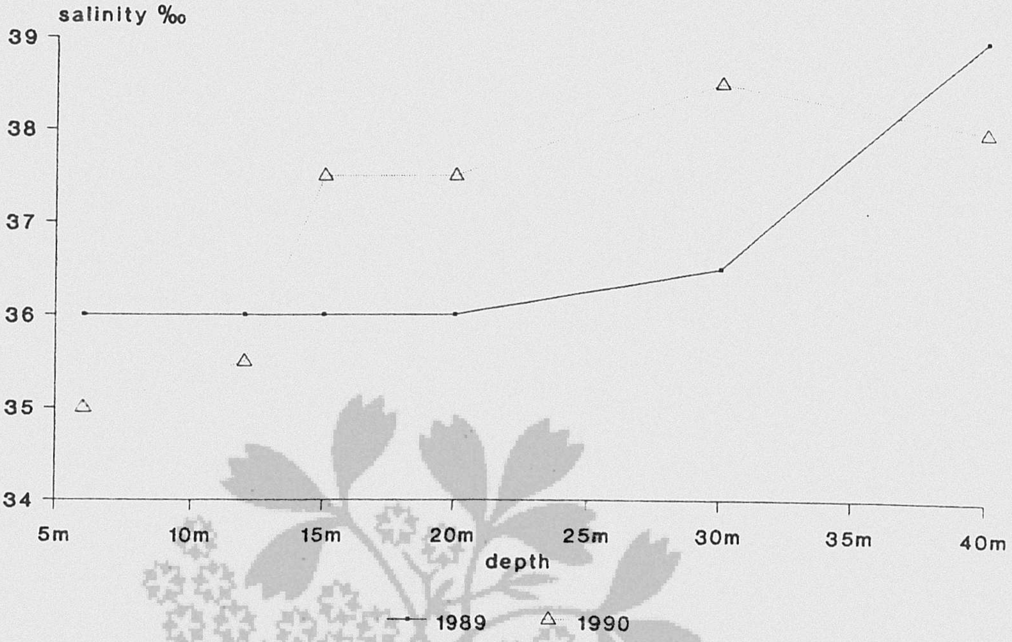


Fig.28. The salinity of seawater (recorded at the sediment surface) along a depth gradient.

depth (m)	%<63 silt	%>63u sand	silt:sand	(phi) mean	(phi) medi	(phi) mode	sorting
1989							
6m	17.1	82.9	0.21	3.40	3.45	4.00	0.80
12m	12.9	87.1	0.15	3.18	3.25	4.00	0.90
15m	5.2	94.8	0.05	1.16	1.95	-3.00	1.55
20m	35.7	64.3	0.56	5.30	3.75	4.00	1.40
30m	25.7	74.3	0.35	3.47	3.60	4.00	1.23
40m	23.0	77.0	0.30	3.56	3.50	4.00	1.12
1990							
6m	47.8	52.2	0.91	3.37	3.85	-1.75	2.83
12m	24.8	75.2	0.33	3.61	3.50	3.95	1.18
15m	22.0	78.0	0.28	3.44	3.35	3.95	1.08
20m	25.8	74.2	0.35	4.29	3.10	3.95	2.33
30m	26.0	74.0	0.35	1.98	2.90	-1.75	3.48
40m	58.6	41.4	1.41	4.68	4.45	3.95	1.95

Table 9. Sediment particle size data recorded along a depth profile (6 - 40 m) of Loch Goil in June 1989 and July 1990.

July 1989 [1m = 30.91 ppt; 40m = 32.77 ppt] and July 1990 [1m = 30.48 ppt; 40m = 32.98 ppt] (Fig. 29; CRPB, unpubl. data). Although the magnitude of the data appear to be incorrect, if the errors are consistent then a halocline existed at a depth of 12-15m in 1990.

Although no data were obtained showing light attenuation, the light available to the epipelon appeared to be limited in both 1989 and 1990 by a phytoplankton bloom. This formed a dense layer that discoloured the water green from the surface to a depth of approximately 2-5m. In July 1990 phytoplankton density in the surface water was particularly dense, causing very poor (< 0.5m) visibility in the first few meters of water; compared with approximately 2m surface visibility in 1989.

Spearman Rank analysis of the 1989 data revealed a significant (negative) correlation ($P<0.05$) between epipelic abundance and depth. However, no other associations were found between either axis 1 or abundance and any environmental variables (Table 8). In 1990 significant correlations ($P<0.05$) were found between axis 1 (DECORANA analysis) and both depth (positive) and temperature (negative). Similarly, the abundance of the epipelon was correlated ($P<0.05$) with both depth (negative) and temperature (positive).

A cursory inspection of Loch Goil suggested a transition from a coarse sand in the shallows to finer muddy sediment with increasing depth. However, Table 9 shows there to be a mixed, heterogeneous distribution of sediments with no clear pattern of variation along the bathymetric gradient in either 1989 or 1990. Spearman rank analysis showed there to be no significant relationship between the epipelon and either the proportion of silt within the sediment or median sediment particle size (Table 8).

4.3.3.4 Phytoplankton

In June 1989 the predominant species found in the water column was *Chaetoceros spp*. Other phytoplankton species present (approx. equal proportions) included: *Skeletonema costatum, Coscinodiscus sp, Diplopeltopsis minor, Noctiluca scintillans, Protoperidinium sp, Gonyaulax sp,* and *euglenoid flagellates*.

In July 1990 the turbid, green discolouration of the upper 6m of the water column was due to a bloom of the coccolithophore *Emiliania huxleyi.* Other species of phytoplankton present (approx. equal proportions) included: Dictyocha speculum, Chaetocerous spp, Thalassiosira sp, Ceratium fusus, Gonyaulax sp and euglenoid flagellates.

4.3.4 Discussion

The epipelon showed considerable variation in community composition, abundance and biomass along the depth gradient in both 1989 and 1990. The epipelon can be characterised into shallow and deep water zones, with differences in the density of algae and composition of the rarer species along the depth gradient.

The data identify a number of taxa that appear to inhabit a restricted range of depth but only four of these species were common to the shallow water community in both 1989 and 1990. Novel species occur in both years and some species (eg. *Nitzschia socialis*) that characterised the shallow zone in one year, were recorded at greater depth or at a range of depths in the other year. The selectivity of taxa for a particular depth has been observed by previous investigators in freshwater (Round, 1961; Roberts and Boylen, 1988; Kingston *et al*, 1983; Stevenson and Stoermer, 1981; Stevenson *et al*, 1985.) and marine (Bodeanu, 1964; Manea and Skolka, 1961) habitats. None of the six species of diatom recorded by Manea and Skolka (1961) in the Roumanian Black Sea were found in Loch Goil. However, 13 of the 86 taxa recorded by Bodeanu (1964) were recorded along the bathymetric gradient of Loch Goil. In particular, *Nitzschia distans*, *Nitzschia sigma* (4-10m) and *Nitzschia bilobata* (4-16m) were found by Bodeanu, and myself, to be restricted to a similar depth range within the shallow sublittoral region. Most of the other species common to both studies (*Navicula forcipata*, *Navicula* cf.*cryptocephala*, *Amphora proteus*, *Amphora truncata*, *Amphora coffeaeformis* var.*acutiuscula*, *Nitzschia hybrida*, *Surirella fastuosa*, *Cocconeis scutellum* and *Diploneis smithii*) were more cosmopolitan in distribution; recorded by Bodeanu over most of the recorded depth range (2-20m). This is consistent with my data as these species were recorded over a similar range of depth (6-20m) within Loch Goil. The only exception is *Navicula retusa* var. *cancellata*, which was only recorded in Loch Goil at a depth of 40m, but was found at 4-16m depth in the Black Sea study.

An interesting feature of the data is the dominance within the sample communities (1989 and 1990) of the following taxa: *Navicula* cf.*tripunctata*, *Navicula forcipata* var. *densistriata*, *Navicula distans*, *Navicula arenaria*, *Amphora* cf. *proteus* var. B and *Navicula* sp.F/G/H (No distinction was made between *Navicula* sp. F, G or H in the analysis). These dominant species are different from the major community (see 4.3.1) recorded in Loch Sween over a 1-20m depth range by Smyth (1955). However, comparison of the whole of both communities shows there to be a number of common species: *Amphiprora sp.*, *Amphora coffeaeformis*, *A. laevis*, *A. proteus*, *A. truncata*, *Cocconeis scutellum*, *Diploneis sp.*, *Navicula abrupta*, *N. cryptocephala*, *N. digito-radiata*, *N. forcipata*, *N. gregoria*, *N. palpebralis*, *N. retusa*, *Nitzschia sigma*, *Pleurosigma formosum*, *Rhabdonema minutum*, *Tropidoneis sp*. Although the algal dominants may differ, the proportions of the dominant algae remain relatively unchanged over this depth range in both Loch Goil (6- 30m) and Loch Sween (1-20m). However, the data collected by Smyth may not reflect the natural community present within the sediment as the methods were qualitative. In addition, because the slides were removed by lifting the exposed sample through the water column (by a cord), the sample communities are likely to have been modified through the loss of algae.

The stability of the epipelic community in Loch Goil with depth differs from the communities recorded in the Black Sea (Bodeanu, 1964). With the exception of *Amphora coffeaeformis* var.*acutiuscula*, which was found to be the most abundant taxa over the 4-12m depth range, Bodeanu generally found a shift in the major taxa with increasing depth.

Comparison of the Loch Goil epipelon with freshwater communities (Round, 1961; Roberts and Boylen, 1988; Kingston *et al*, 1983; Stevenson and Stoermer, 1981; Stevenson *et al*, 1985.) shows there to be (not surprisingly) an entirely different range of species in the marine and freshwater habitats. However, the epipelic algal community recorded by Stevenson and Stoerma (1981) was also dominated by diatoms at all recorded depths (6.5-27.4m) although the diversity of algae (255 taxa, 36 genera) and abundance of diatoms (9×10^9 cells m^{-2} to 3×10^{10} cells m^{-2}) was higher than levels recorded in Loch Goil. This is in contrast with the results of Roberts and Boylen (1988) who found epipelic diatoms to have the greatest abundance (3×10^9 cells m^{-2}) at 1m and 4m depth whereas blue-green algae were found to dominated the deepest (7m) part of the lakes.

The increase in the proportion of planktonic species (*Chaetoceros* sp, *Skeletonema costastum*, *Coscinodiscus* sp) within the deepest (30m and 40m) sample communities of Loch Goil has also been observed in fresh water lake communities (Kingston *et al*, 1983; Stevenson and Stoerma, 1981). This is attributed to the deposition of more plankton (and less epipelon) in proportion to the longer water column of deep water areas.

In relation to the density of epipelic algae along the bathymetric gradient: the shallow zone (6-15m) was characterised in both 1989 and 1990 by relatively high epipelic abundance and pigment levels (chlorophyll-a and carotenoids). The levels of algae were generally higher in 1989, particularly at the shallowest station (6m) where over five times more algae were recorded than the same depth in 1990. It was the shallowest depth in 1990 that possessed the highest algal density whereas a peak in density and biomass was recorded at a depth of 12m in 1990. The reason for the peak in epipelic pigment concentration at 12m depth in 1989, while cell numbers were proportionally lower, is not clear. However, *Navicula* cf.*tripunctata*, which formed 43.5 % of sample community at this depth, shows considerable size variation (24-67*um*; see Appendix 1) and may have been generally larger at this depth. Further analysis of the sample communities would be required to test this hypothesis.

Round (1981) indicates that optimum standing crop of benthic algae does not always correspond to the shallowest depth, and the density of epipelon in fresh water lakes (Roberts and Boylen, 1988 and Stevenson & Stoermer, 1981) have been shown to peak at sub-surface depths of 9.1m and 4m respectively. Plante-Cuny recorded a peak of cell numbers (approx. 150 cells m^{-2} x 10^{8}) at 30-35m depth, considerably deeper and higher than the pattern recorded in Loch Goil. Plante-Cuny's detailed floristic study also recorded a greater diversity of algae at depth (eg. an average of 42 species at 40-60m depth) and revealed a few species of epipelic diatoms living at depths of 300m and one species, *Navicula pennata*, at 360m. The occurance of epipelic diatoms in these deep oceanic sediments can probably be related to the clarity of the water off the coast of Marseille compared with the relatively turbid waters of Scottish sea lochs. Another possible explaination is that the epipelic algae existing at these great depths are apochlorotic (without chlorophyll); existing heterotrophically.

The approximately linear decrease in epipelic density with depth, observed in 1989, is consistent with the pattern of distribution observed by Bodeanu (1964) although the density of algae in this study of the Black Sea is considerably greater (9×10^9 cells m^{-2} to 3×10^{10} cells m^{-2}). Similarly, Stevenson *et al* (1985) observed a negative, linear relationship between the biovolume of most epipelic algal species with depth (1-<20m) in New Hampshire lakes.

This investigation has characterised the epipelon along a gradient of depth within Loch Goil. However, it does not conclusively show the cause of these patterns of variation. Spearman rank analysis of the physicochemical data revealed significant correlations (P= <0.05) between epipelic abundance and temperature in 1990. However, in 1989 the water temperature varied only 0.5 ^{o}C over the depth gradient whereas the density and composition of the epipelon varied considerably with depth.

The negative correlation, observed in both 1989 and 1990, between epipelic abundance and depth indicates that a positive correlation would exist between the epipelic abundance and light levels. However, this assumes that water clarity is spatially constant within Loch Goil. Sündback (1986) has shown that:

> "turbidity may decrease with increasing depth, and thus light intensity at the sediment surface at 15m is not necessarily less than that at 8-10m".

Although the measurement of vertical light attenuation was not successfully made (due to faults in the electrical circuits) it is generally acknowledged that the amount of light transmitted to the substratum decreases with increasing depth and the spectral quality of the light is modified as it passes through water (Kendrick and Kroenberg, 1986). Light attenuation with depth is likely to be the principal factor influencing the bathymetric distribution of epipelic density. Benthic microalgae are known to attain light saturated photosynthesis at a range of light intensities and inhibition of photosynthesis has been recorded when light intensity is greater than 150 uE.m^{-2}.s^{-1} whereas 20 uE. m^{-2}.s^{-1} was the recorded lower limit for microphytobenthic growth (Sundbäck, 1986). Photosynthetic inhibition is unlikely to be the cause of the relatively low algal density recorded at 6m in 1990, as reduced visibility within the shallows appeared to severely limit the amount of light penetrating beneath the surface of the loch. However, the masking of light by the dense planktonic bloom of *Emiliania huxleyi* may have reduced the density of epipelon recorded along the whole bathymetric gradient in July 1990, compared with levels found in June 1989. Two weeks later (1st. August 1990), the bloom of *Emiliania huxleyi* turned the waters of Loch Goil, Holy Loch and Loch Long, a turquoise colour and reduced visibility within Loch Goil to less than 50 cm (pers. observation). This attracted the attention of both the media and the Clyde River Purification Board who attributed the colour to the scattering of light by the myriad coccolith scales released from the senescent *Emiliania huxleyi* cells (C.R.P.B pers. comm.).

The changes in the epipelic community with depth may reflect the adaptation of some taxa to low light regimes. Rosen and Lowe (1984) have observed that some diatom species (eg. *Cyclotella meneghiniana*) adapt to the low light intensities that are present at depth, by increasing chlorophyll-a concentration, chloroplast volume and thylakoid surface density. Certain species of *Navicula* and *Nitzschia* have also been shown to be facultative heterotrophs (Stevenson *et al*, 1985, Admiraal and Peletier, 1979. To determine the importance of light as a determinant, future study should include experimental manipulation of natural cultures of epipelon to varied light intensities and wavelengths. Natural epipelic communities could also be manipulated in field experiments by transplanting shallow water communities to deeper areas and by modifying the light regime, *in situ*. Future study of the bathymetric distribution of the epipelon should include accurate measurement of light intensity. It should be noted, however, that the methods used will have to be more sensitive than those routinely used in phytoplankton research, where the depth of the euphotic zone is assumed to correspond to the depth where 1% of the incident light remains.

Sundbäck (1986) also observed optimum levels of epipelic chlorophyll-a at 14-16m depth and related this to the depth of the halocline and the adaptation of taxa, recorded at that depth, to low light intensities. This is comparable to my data, as the peak in epipelic density at 12m depth (July 1990) coincides with the depth of the halocline observed both in my data (Fig. 28) and in that recorded by the CRPB (Fig. 29; CRPB, unpubl. data). The CRPB data also shows there to be thermal stratification at 30-40m in July 1989 and 40-50m in July 1990 further indicating that the sampled depth range is within the epilimnion of Loch Goil. Epipelon were found with protoplasm in them from the deepest recorded depth (40m) in both 1989 and 1990. However, future studies should sample from a greater range of depth (0-93m), in both the summer and winter months, using an automatic corer such as a "Craib" corer (Mc.Intyre and Warwick, 1971), operated from a surface vessel with winch. This would ascertain whether summer stratification, and subsequent stagnation (oxygen <2 ppm) of the deep (30-50m) waters of Loch Goil (Edwards *et al*, 1986; Mackay and Halcrow, 1976; CRPB unpublished data) is reflected in changes in the community structure of the epipelon. It would also determine the maximum depth at which the epipelon inhabits Loch Goil. Round (1972) stipulates that "epipelic populations in large (fresh) water bodies tend to occur only above the thermocline". Further investigation is required to ascertain whether or not this is true for Loch Goil and sea loch habitats in general.

Other factors that may influence the bathymetric distribution of epipelon include: wave action, nutrient levels of interstitial water, organic content of the sediment, sediment redox potential, grazing pressure and

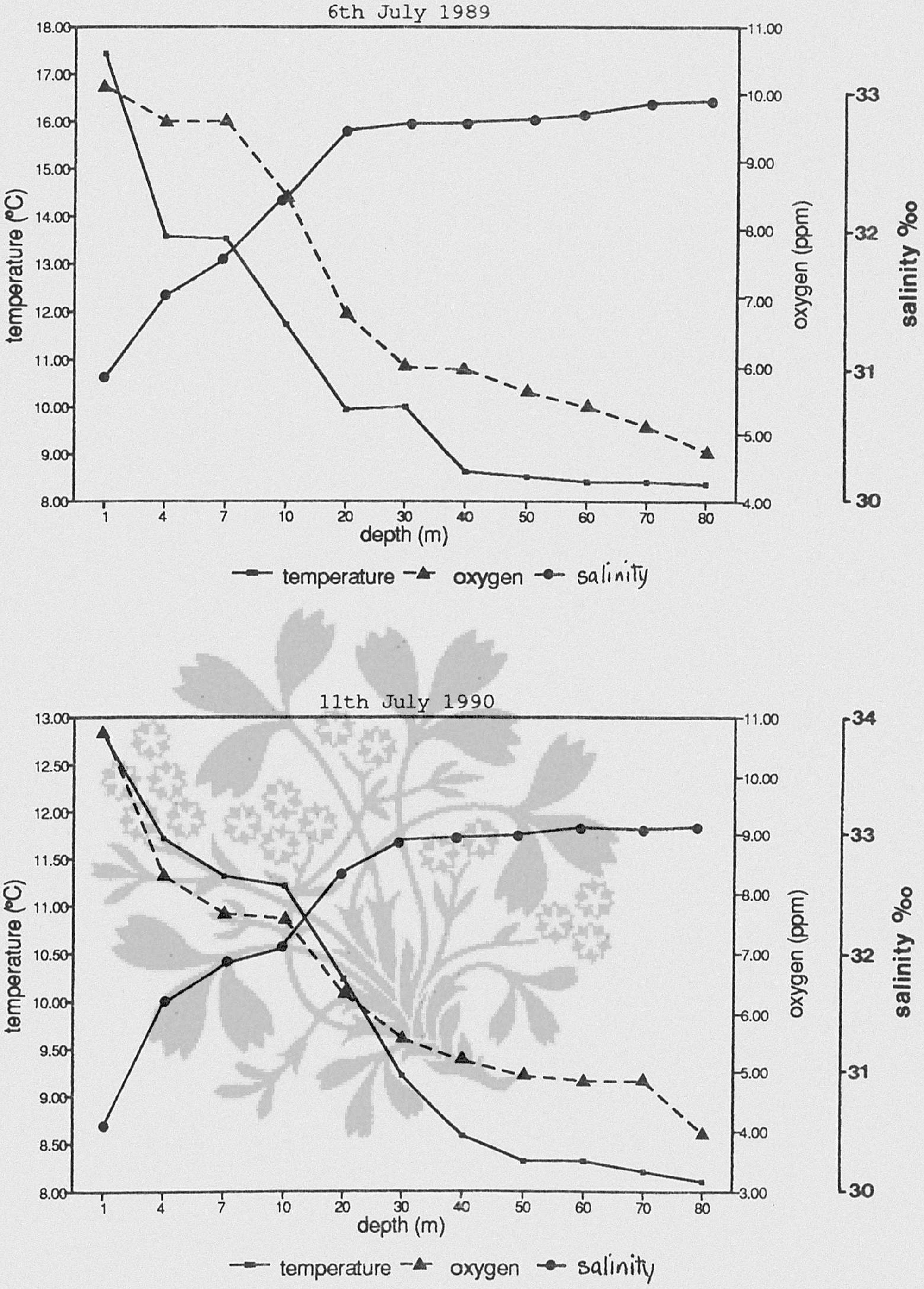


Fig. 29. Temperature, **salinity** and oxygen profiles along a bathymetric gradient (0-80m) in Loch Goil during July 1989 and July 1990 (CRPB unpublished data).

bioturbation. Wave action may disrupt surface communities in shallow water (Gruendling, 1971; Stevenson and Stoermer, 1981). However the effect on the shallow water community in Loch Goil is unlikely to be significant as the site is extremely sheltered and the intensity of winds preceding these surveys were minimal. Sediment is generally considered to be an inexhaustible source of nutrients for the epipelon, however, nutrient limitation has been demonstrated (Graneli and Sundbäck, 1985) and availability of inorganic nutrients may effect species composition (Pringle and Bowers, 1984). A future study could include measurement of micronutrient concentrations (NH_3N, TON, PO_4-P, SiO_2) within interstitial water; sediment redox potentials and the organic content of the sediment at different depths. The subtidal epipelon may also be influenced by grazing and bioturbation of benthic macro-invertebrates along the depth gradient. Qualitative observations made while sampling showed there to be an extremely diverse and spatially heterogeneous community of particularly: polychaetes, ophiuroids, anthazoans, pennatulids, holothurians, and bivalves. The effect of these animals on the abundance and community composition of the epipelon requires investigation. In particular the characterisation of the invertebrate community along the same bathymetric gradient would indicate possible trophic relationships involving the epipelon (see section 5.1). This could lead to more detailed examination of grazing and bioturbation effects through experimental investigation in the field and laboratory.

This investigation has succeeded in characterising the bathymetric distribution of epipelon in Loch Goil, providing novel data on a habitat not previously described. Graphical representation of the data and the results of the multivariate analysis provides a visual display of variations in the epipelon which, in itself, is convincing evidence of environmental and biological control of the epipelic algae over the measured depth gradient. The analyses have lead to the rejection of the null hypothesis (H_0): "there are no differences in the epipelon along a bathymetric gradient, in Loch Goil".