THE ECOLOGY OF EPIPELIC DIATOMS IN LOCH GOIL

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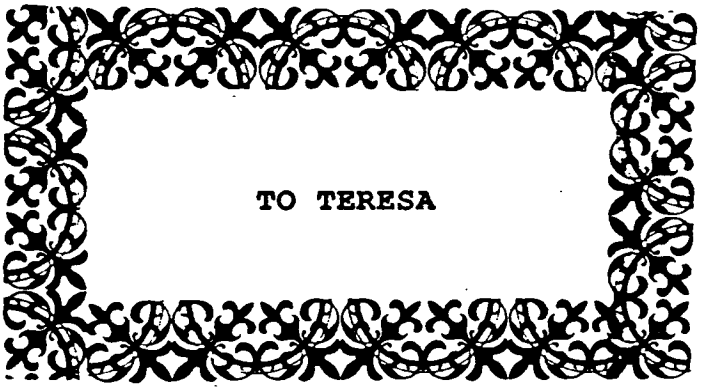

O Lord, how manifold are Your works!
In wisdom You have made them all.
The earth is full of Your
possessions - This great and wide sea,
In which are innumerable teeming things,
Living things both small and great.

Psalm 104, verses 24-25.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS i

DECLARATION i

ABSTRACT OF THESIS ii

CHAPTER 1 GENERAL INTRODUCTION 1

1.1 **MARINE EPIPELON - A GENERAL REVIEW** 2

1.1.1 Vertical migratory rhythms 3

1.1.2 Patterns of distribution 4

1.1.3 Effects of pullution 7

1.1.4 Effects of grazing 7

1.1.5 Subtidal marine epipelon 8

1.2 **SCOTTISH SEALOCHS - A REVIEW OF PREVIOUS MARINE BIOLOGICAL STUDIES** 9

1.3 **AIMS OF MY RESEARCH** 13

1.4 **LOCH GOIL** 15

1.4.1 Site description 16

1.4.2 Physical data and bathymetry 17

1.4.3 Pollution inputs to Loch Goil 19

CHAPTER 2 METHOD DEVELOPMENT 21

2.1 **INTRODUCTION** 22

2.2 **SAMPLING THE SEDIMENT - method development** 22

2.2.1 Experimental comparison of two sampling strategies 23

2.2.1.1 Large cores 24
2.2.1.2 Small cores 24

2.3 **EXTRACTING THE ALGAE - method development** 25

2.3.2 The experimental comparison of harvesting substrates as a means of extracting epipelic algae 25

2.3.2.1 Introduction 25
2.3.2.2 Materials and methods 28

2.3.2.2.1 Preparation of poly-l-lysine treatments 30
2.3.2.2.2 Preparation of agar gel treatment 30
2.3.2.2.2 Test of the pattern of dispersion of algae on the surface of polythene and glass 31
2.3.2.3 Results 31
2.3.2.4 Discussion 34
2.3.2.4.1 The number of algae 34
2.3.2.4.2 Community composition 35
2.3.2.4.3 The standard extraction method - a summary 37

2.4 **DETERMINATION OF OPTIMUM HARVESTING TIME - method development** 37

2.4.1 Introduction 37

2.4.2 Methods 38

2.4.3 Results 39

2.4.4 Discussion 39

CHAPTER 3 STANDARD METHODS 41

3.1 **SAMPLING THE SEDIMENT - standard methods** 42

3.2 **EXTRACTING THE ALGAE - standard methods** 43

3.2.1 The settling/extraction chamber 43

3.2.2 Extraction methods 44

3.2.2.1 Analysis of epipelic community structure 45
3.2.2.2 Analysis of epipelic abundance 46
3.2.2.3 Analysis of epipelic biomass (pigment analysis) 46
3.2.2.4 Acid-cleaned algae, for taxonomic identification 47

3.3 **ENUMERATION OF THE SAMPLE OF EPIPELIC ALGAE - standard methods** 48

3.3.1 Estimation of epipelic abundance 49

3.3.2 Estimation of epipelic community structure 50

3.3.2.1 Proportion of dominant algal species 50
3.3.2.2 Total number of species 51

3.3.3 Estimation of epipelic biomass; the measurement of pigment concentration 51

3.4 **PHYSICAL PARAMETERS - standard methods** 52

3.4.1 Vertical light extinction coefficient 52

3.4.1.1 Secchi disc method 53
3.4.1.2 Photocell method 53

3.4.2 Depth (pressure) 54

3.4.3 Temperature 54

3.4.4 Dissolved oxygen 55

3.4.5 Salinity 55

3.4.6 Sediment particle size analysis 55

3.5 **STATISTICAL ANALYSES** 56

3.5.1 Multivariate analyses 56

3.5.2 Tests of significance and correlation 57

3.5.3 Spatial pattern analysis 58

3.6 **LIMITATIONS AND DISCUSSION OF METHODS** 59

3.6.1 Field sampling 59

3.6.1.1 Number and size of sample 60
3.6.1.2 Sediment depth of the sample 61
3.6.1.3 Frequency of sampling 61

3.6.2 Extraction 62

3.6.2.1 Screening the algal preparation 62
3.6.2.2 Illumination of the sediment during extraction 62
3.6.2.3 Loss of algae within supernatant and interstitial water 63

3.6.3 Enumeration 64

3.6.3.1 Pigment analysis 64
3.6.3.2 Analysis of species proportions 65
3.6.3.3 Estimation of algal abundance 67

3.6.4 Sampling variance 67

CHAPTER 4 THE EPIPELON 69

4.1 **SPATIAL HETEROGENEITY (PATCHINESS) OF THE EPIPELON ON THE BOTTOM OF LOCH GOIL** 70

4.1.1 Introduction 70

4.1.2 Methods 70

4.1.2.1 Sampling method 70
4.1.2.2 Laboratory methods 71
4.1.2.3 Statistical analyses 72

4.1.3 Results 73

4.1.3.1 Large scale features 73
4.1.3.2 Small scale features 74

4.1.4 Discussion 76

4.2 **DISTRIBUTION OF EPIPELIC ALGAE ALONG THE GRADIENT OF A STRAWBERRY WORM (Eupolymnia nebulosa) MOUND** 80

4.2.1 Introduction 80

4.2.1.1 *Eupolymnia nebulosa* 80

4.2.2 Methods 82

4.2.2.1 Sampling method 82
4.2.2.1.1 Core sampler 83
4.2.2.1.2 Settling/extraction chamber 83
4.2.2.2 Laboratory methods 83
4.2.2.3 Analysis of gut contents 84

4.2.3 Results 84

4.2.3.1 Sediment 85
4.2.3.2 Gut contents 86
4.2.3.3 Epipelic community 86

4.2.4 Discussion 88

4.2.4.1 Grazing loss 89
4.2.4.2 Burial loss 90
4.2.4.3 Other loss processes 91
4.2.4.4 Sediment characteristics

4.3 **BATHYMETRIC DISTRIBUTION OF EPIPELON** 93

4.3.1 Introduction 93

4.3.2 Methods 96

4.3.2.1 Sampling methods 96

4.3.2.2 Laboratory methods 97
4.3.2.3 Data analyses 97
4.3.2.4 Sampling and analysis of the phytoplankton 98

4.3.3 Results 98

4.3.3.1 Epipelic abundance and biomass 98
4.3.3.2 Epipelic commnunity analysis 99
4.3.3.2.1 June 1989 99
4.3.3.2.2 July 1990 101
4.3.3.3 Physicochemical gradients 102
4.3.3.4 Phytoplankton 103

4.3.4 Discussion 104

4.4 **SEASONALITY OF THE EPIPELON** 113

4.4.1 Introduction 113

4.4.2 Methods 114

4.4.3 Results 115

4.4.3.1 Seasonal changes in epipelic standing crop 115
4.4.3.2 Seasonal changes in epipelic community structure 116

4.4.4 Discussion 118

4.4.4.1 The epipelon 119
4.4.4.2 Effect of depth 121
4.4.4.3 Effect of grazing 122
4.4.4.4 Effect of temperature and light attenuation 124
4.4.4.5 Nutrient effects 125
4.4.4.6 Other effects 127
4.4.4.7 Future studies 129

4.5 **EXPERIMENTAL INVESTIGATION OF THE SUCCESSIONAL COLONISATION OF SEDIMENT BY EPIPELIC DIATOMS** 131

4.5.1 Introduction 131

4.5.2 Methods 134

4.5.2.1 Experimental design 134
4.5.2.2 Data analyses 136

4.5.3 Results 136

4.5.4 Discussion

CHAPTER 5 THE RELATIONSHIP BETWEEN BENTHIC INVERTEBRATES AND EPIPELON IN LOCH GOIL 143

5.1 **BATHYMETRIC DISTRIBUTION OF BENTHIC INVERTEBRATES** 144

5.1.1 Introduction 144

5.1.2 Sampling methods 145

5.1.2.1 Core sampling method 146
5.1.2.2 Photographic method 147

5.1.3 Limitations of the method 148

5.1.4 Results 149

5.1.4.1 Community structure 149

5.1.5 Discussion 151

5.1.5.1 The faunal community 151
5.1.5.2 Epipelic algae and the macrofauna - trophic relationships 153
5.1.5.3 Influence of epipelon on invertebrate distribution 154
5.1.5.4 Biogenic disturbance 155
5.1.5.5 Hypotheses and future work 156
5.1.5.6 Conclusion 157

5.2 **EXPERIMENTAL INVESTIGATION INTO THE RELATIONSHIP BETWEEN** Ophiura albida **AND THE EPIPELON** 158

5.2.1 Introduction 158

5.2.1.1 Aims of the investigation 159
5.2.1.2 The ophiuroid *Ophiura albida* 160

5.2.2 Methods 161

5.2.2.1 Experimental design 161
5.2.2.2 Experiment 1 - response of epipelon to a gradient of grazing pressure by the ophiuroid *Ophiura albida* 162
5.2.2.3 Experiment 2 - to determine the efficacy of the barriers at maintaining normal levels of epipelic algae 163
5.2.2.4 Statistical analysis 164

5.2.3 Results 164

5.2.3.1 Experiment 1 164
5.2.3.2 Experiment 2 165

5.2.4 Discussion 166

CHAPTER 6 GENERAL DISCUSSION 171

6.1 **THE EPIPELON OF LOCH GOIL** 172

6.2 **BIOLOGICAL INTERACTIONS WITH THE EPIPELON** 177

6.2.1 The trophic relationships between the epipelon and invertebrates 177

6.2.2 Other biological interactions with the epipelon 182

6.3 **EPIPELON AND THE PHYSICOCHEMICAL ENVIRONMENT OF LOCH GOIL** 184

6.4 **ANTHROPOGENIC INFLUENCES AND FUTURE TRENDS** 187

6.5 **SCOPE OF THESIS** 187

REFERENCES 189

APPENDIX 1 Atlas and catalogue of the epipelic diatom types found within the sediments of Loch Goil 211

APPENDIX 2 Taxonomic references 257

APPENDIX 3 The seasonal variation of the salinity of sea water at the sediment/water interface - erroneous data 261

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DECLARATION

This thesis has been composed by myself and all work detailed in it is my own.

ABSTRACT OF THESIS

This study investigated the ecology of subtidal epipelic diatoms in a sea-water loch. A methodology for the sampling and measurement of subtidal epipelic algae was established. The spatial heterogeneity and seasonal distribution of epipelon was investigated and related to physicochemical (salinity, temperature, light) and biological parameters (grazing and disturbance). The relationships between the epipelon and invertebrates were examined by survey and field experiments.

The epipelic flora of Loch Goil consisted almost entirely of diatoms (163 spp, 39 genera) and was characterised by a few numerically dominant species (*Navicula* cf. *tripunctata*, *Navicula sp. H*, *Navicula forcipata* var. *densistriata*; *Amphora proteus*). The proportion of these species remained relatively constant with depth and season.

The abundance of epipelic diatoms was found to be related to micro-topography with relatively high densities concentrated on the sides and bases of sedimentary mounds formed by the polychaetes *Arenicola marina* and *Eupolymnia nebulosa*. Analysis of the pattern using a "Paired-Quadrat Variance" method showed clumping at intervals of 40cm, 2m and 3m.

The bathymetric (6-40m) distribution of epipelic diatoms was investigated and found to be divided into shallow (6m, 12m, 15m) and deep (20m and 30m) water zones, with differences in the density of algae and composition of the rarer species along the depth gradient.

The seasonal variability of the epipelon was determined from 1988 to 1990 at 9m and 11m depth. Maximum epipelic growth was recorded from May to September followed by an over-winter period (October to April) of minimum growth. The seasonal distribution of epipelic abundance and chlorophyll-a was found to be correlated with annual cycles of water temperature, irradiance and water clarity.

The invertebrates were surveyed along a bathymetric gradient (6-40m) and the species assigned to isotrophic feeding groups: carnivorous predators (28 spp, 35.4%); deposit feeders (10 spp, 12.7%); surface detrital feeders (11 spp, 13.9%); water column detrital (suspension) feeders (29 spp, 36.7%) and scrapers (1 spp, 1.3%). The invertebrate community was found to be characterised by the polychaete *Eupolymnia nebulosa* and the ophiuroid *Ophiura albida*. The trophic relationships between the invertebrates and epipelon are discussed. Detailed examination of the small-scale spatial distribution of the epipelon provided evidence of non-selective grazing of epipelon by *E. nebulosa* and the burial of algae by defaecated sediment. The effect of grazing and disturbance by the ophiuroid *Ophiura albida*, on a natural assemblage of epipelic algae, was investigated by manipulating the density of ophiuroids within barriers situated on the bottom of the loch.

CHAPTER 1

GENERAL INTRODUCTION

This study is concerned with the ecology of epipelic algae that inhabit the subtidal sediments of Loch Goil, a sealoch in Argyll, Scotland. Epipelic algae are associations that move on and in the surface sediments and grow on sand and silt both in the intertidal and subtidal (Round and Hickman, 1971). The epipelon typically consist of motile, pennate diatoms and to a lesser extent filamentous or coccoid blue-green algae, dinoflagellates and euglenoid flagellates. The subtidal zone refers to the region below low (spring) tide and is synonymous with the sublittoral region often referred to in studies of marine habitats.

1.1 MARINE EPIPELON - A GENERAL REVIEW

Much of the research involving marine epipelon has focused on intertidal habitats. This section reviews a number of these studies which examine key areas of research, including: rhythmic motility, patterns of distribution and the relationships between epipelon and physical, chemical and biological parameters. A study by Smyth (1955) on the subtidal epipelon of a Scottish sealoch is reviewed in this section while the other literature, related to subtidal epipelon, are examined in the relevant sections of this thesis. A more comprehensive review of the literature, particularly in relation to the subtidal region, are provided by Round (1971), McIntyre and Moore (1977), and Round (1981):

Round (1971) took a broad view of the benthos and discussed all habitats involving diatoms that are permanently or tidally covered by the sea. This review examined all the major literature concerning benthic marine diatoms in relation to: methodology, taxonomy, morphology and cytology, physiology and ecology.

McIntyre and Moore (1977) provided a selective review of the literature concerning marine and estuarine benthic diatom assemblages. In particular they were concerned with ecological aspects of epilithic, epiphytic, epipsammic and

epipelic assemblages (see section 6.1 for definitions) and the general distribution patterns of these algae along chemical and physical environmental gradients. Their floristic review included studies from various geographical locations, world wide (Africa, Arctic, Asia, Caribbean, Europe, Galapagos, North America and the British Isles). They examined primary productivity and the grazing of microalgae and discussed the use of laboratory ecosystems as a tool for investigating simplified microalgal communities. In particular, the need for a rigourous quantitative approach to the study of distribution patterns in nature was emphasised.

The comprehensive review of the epipelon by Round (1981) examines the intertidal and subtidal marine epipelon and includes aspects of their rhythmic motility and depth distribution.

1.1.1 Vertical migratory rhythms

Epipelic diatoms tend to be positively phototaxic (Round, 1981) which allows them to reorientate on the sediment surface following burial. Burial may be due to the deposition of suspended sediment in the water column or by biogenic disturbance. A number of studies have demonstrated the existence of tidally modified vertical migratory rhythms in intertidal marine epipelon (Hopkins, 1963, 1966; Palmer and Round, 1965, 1967; Round and Palmer, 1966). By maintaining a surface position, the epipelon permit maximum photosynthesis whereas their descent prior to tidal inflow effectively reduces the loss of algae (by displacement) when the incoming tide recovers the sand. Not all species of epipelon respond to the influence of tide and insolation. Perkins (1960) found that littoral diatoms in the River Eden estuary have a diurnal migratory rhythm that is dependant only on light intensity. Similarly, studies by Round and Palmer (1966) and Round (1979) report that some species of epipelon (eg. *Tropidoneis lepidoptera*) respond to insolation only.

Paterson (1986) utilised low temperature scanning electron microscopy (LTSEM) to monitor the migratory behaviour of epipelic diatoms maintained in the laboratory. He reported that species of *Navicula* and *Nitzschia* were the first to migrate to the surface of marine sediments and concluded that species may require different light densities to initiate a phototaxic response.

1.1.2 Patterns of distribution

Plante *et al* (1986) studied the spatial distribution of epipelic chlorophyll-a in shallow (30-60cm) sandy bottoms on the Mediterranean shore. They documented several scales of patchiness which was related to the size scales of sedimentary features: large scale (km) patchiness was related to the degree of exposure of the shore; medium scale (m) epipelic chlorophyll-a was found to be accumulated in the depression of sand waves; and on a small scale (cm), related to ripple marks. The seasonal change in the vertical distribution of epipelic chlorophyll-a, within sediment, was also investigated. A sampling strategy was proposed that maximised the dispersal of samples within a sampling area.

Grant *et al* (1986) used field and laboratory flume studies to examine the stabilization of intertidal sands by diatom mucus films. They found diatom films to be patchy on a scale of centimetres, corresponding to the structure of sand ripples. Diatom films were found to stabilise local areas of the sea bed which were transposed to new locations on sand ripples as the bedform moved through the film.

Cammen and Walker (1986) investigated the relationship between benthic microalgal and bacteria in mudflats in the Bay of Fundy, Canada. They reported significant relationships between microalgal and bacterial abundance which they attributed to the release of soluble extracellular metabolites by the algae.

Colijn and Dijkema (1981) used field observations to described the seasonal distribution of epipelic diatoms on an intertidal flat in the Dutch Wadden Sea. They related variations in community structure and chlorophyll-a to fluctuations in levels of abiotic factors such as wave action, rainfall and irradiance levels (see 4.4.4.1). In contrast to this study Admiraal *et al* (1984) adopted an experimental approach to the study of seasonality in intertidal epipelon. The growth and decline of *Navicula salinarum* and *Navicula pygmaea* were analysed in experiments with one- and two-species cultures and with natural samples of sediment and algae collected from the Ems-Dollard estuary. Admiraal *et al* demonstrated that parts of the natural seasonal succession patterns could be simulated using natural populations in controlled laboratory conditions. Their experiments demonstrated the importance of the following selection mechanisms in controlling seasonality: (1) temperature dependence of cell division; (2) interspecific competition; vertical zonation of species in micro-layers in the mud; (3) occurrence of stress factors (eg. desiccation) (4) grazing by herbivorous meiofauna. The seasonal succession of species on the mudflat was also found to follow broadly recurrent patterns in four successive years.

Round (1960) provided a detailed floristic account of the distribution and frequency of epipelic diatom on a salt marsh in Cheshire. The distribution of the species down the marsh was found to be a reflection of salinity, but was also complicated by the changing physical and chemical nature of the substratum. Distinct floras found at different points along the salt marsh were associated with the type of sediment and degree of higher plant cover, however, these two factors could not be separated. The general pattern of seasonal change was one of a rise in numbers during April/May, a maxima in June/July followed by a smaller autumn growth in September/October.

Asmus (1982) measured the production and species composition of phytoplankton and intertidal benthic microalgae, over a period of a year (1978-1980), in the Dutch Wadden Sea. Seasonal variation was related to temperature, salinity, insolation, nutrients and grazing by invertebrates.

Oppenheim (1988) studied the distribution of epipelic diatoms along an intertidal shore (saltmarsh, sandflat and mudflat) in Somerset and related changes in community structure to gradients in light, salinity, pH, tidal innundation, sediment water loss and organic matter. Oppenheim recorded gradients in all physical factors and related these to the distribution of different epipelic taxa along the shore.

Admiraal (1977 a) studied the influence of light and temperature on the growth rate of the epipelic species *Amphiprora* c.f. *paludosa*, *Navicula arenaria*, *Nitzschia* c.f. *dissipata*, and *Nitzschia sigma* grown in culture. The growth rates of the diatoms were determined at different combinations of temperature, day length, and quantum irradiance and found to be comparable to the response of planktonic diatoms. Admiraal (1977 b) also investigated the influence of herbivorous ciliates and nutrient concentrations (silicate, nitrate, phosphate), on the density and succession of benthic estuarine diatoms collected from the Dutch Wadden Sea. Using mixed diatom populations maintained in laboratory microecosystems he demonstrated that grazing by ciliates caused a reduction in the density and change in the species composition of the epipelon. No effect of adding extra nutrients or wastewater (from a sugar mill) to the microecosystem, was detected.

Wilderman (1987) measured the distribution patterns of planktonic and benthic diatoms in the Severn River Estuary (Maryland) and related these to environmental gradient using multivariate statistical analyses. It was concluded from this study that assemblages were

distributed in a complex but orderly fashion, with major discontinuities occurring between seasons and between planktonic and benthic algae.

1.1.3 Effects of pollution

A number of studies have concentrated on the effects of industrial and urban discharges on the epipelon that inhabit the intertidal mudflats of estuaries. A series of papers presented by Jonge (1992) represent the results of a multi-disciplinary study of the influence of discharges of waste water into the Ems estuary. The aims of the research included quantifying the various aspects of the many species that comprise the microphytobenthos: their properties, activities and importance as food for herbivores. These papers investigate: Ludox-TM method for the quantitative separation of benthic diatoms; the fluctuations in organic carbon to chlorophyll-a ratios for benthic diatom populations; the dynamics of microphytobenthos biomass (chlorophyll-a and carbon); primary productivity of microphytobenthos; the epipsammic community; wind and tide induced re-suspension, and gross transport of sediment and microphytobenthos in the Ems estuary.

In the Firth of Forth, Scotland, Mills (1985) studied the productivity and distribution of benthic microalgae. Using a combination of *in situ* measurements and laboratory experiments he found that the highest levels of primary productivity occurred around effluent outfalls and demonstrated tolerance to industrial effluent by natural populations of epipelon.

1.1.4 Effects of grazing

The trophic relationships between intertidal microalgae and invertebrates has been established by many authors and include the following groups of invertebrates: bivalves (Reise, 1983); gastropods (Connor and Teal, 1982; Morrisey, 1988; Pace *et al*, 1979; Levington and Bianchi,

1981); amphipods (Sundbäck and Persson, 1981; Hargrave, 1970; Lopez *et al*, 1977; Decho, 1988; Brenner, 1976); polychaetes (Bianchi and Rice, 1988; Bianchi *et al*, 1988); meiofauna (Montagna, 1984; Admiraal *et al*, 1983); and protozoan (Barlow *et al*, 1988). Details of the complex responses of epipelon to these grazing pressures are discussed in later sections.

1.1.5 Subtidal marine epipelon

Compared with the intertidal region there have been relatively few studies involving subtidal marine epipelon. These include a range of habitats comprising the: Black Sea (Bodeanu, 1964, 1968, 1971; Manea and Skolka, 1961) Kattegat (Sundbäck, 1986) Mediterranean (Plant-Cuny, 1969); NW coast of Madagascar (Plant-Cuny, 1973) and a Scottish sealoch (Smyth, 1955). These studies are reviewed and discussed later in the thesis (see 4.3.1 and 6.1). However, the study by Smyth (1955), of epipelon in Loch Sween (Argyll), has particular relevance to my research of Loch Goil as both lochs may have similar subtidal habitats and epipelic flora. Smyth investigated the epipelon using a combination of a glass slide method and cores samples (see 4.3.1). The epipelon were sampled from 13 sites within Loch Sween from depths ranging from 1-40m. Smyth described the composition of the diatom flora and estimated abundance in relation to substratum, depth and seasons. The sequence of diatom colonization of glass slides was investigated and it was found that slides were quickly colonized by relatively motile forms, but more sessile forms became dominant later (see 4.5.1). The epipelon was found to consist of 41 commoner species of diatom and was dominated by: *Amphora coffeaeformis*, *A. laevis*, *A. macilenta*, *A. marina*, *Cocconeis scutellum*, *Navicula bahusiensis*, *N. pygmaea* and *Nitzschia closterium*. The diatom flora of Loch Craiglin was also investigated and found to differ significantly from that of Loch Sween.

Further discussion and examination of this work can be seen later in this thesis.

1.2 SCOTTISH SEALOCHS - A REVIEW OF PREVIOUS MARINE BIOLOGICAL STUDIES

Loch Goil has been the subject of a number of scientific investigations in recent history. The bathymetry and nutrient status of the loch have been examined in detail (Edwards and Sharples, 1986; Edwards *et al*, 1986; Mackay and Halcrow, 1976; Grantham, 1991) but there have been few investigations of its biological communities (Holt and Davies, 1991; CRPB unpublished data; MacDonald, 1927).

The most detailed description of biological habitats of both the intertidal (4 sites) and subtidal (11 sites) regions of Loch Goil was recently carried out by Holt and Davies (1991) as part of a biological survey of all the sealochs on the west coast of Scotland, from the Mull of Galloway to Cape Wrath. Their semi-quantitative surveys utilised diving, dredging, hand-core sampling and photography to describe the abundance of conspicuous species and to classify habitats on the basis of: invertebrate and macroalgal species; situation; salinity; exposure; tidal streams; zone/range (depth) and substratum type. The principal aim of their research was to assess the scientific interest and conservation importance of the north Clyde sealochs. Holt and Davies documented two very rare species in Loch Goil, the holothiurian *Ocnus planci* and the ascidian *Styela gelatinosa*. They recognised the fragility of the sublittoral habitats within Loch Goil and that the deep water basin is vulnerable to the effects of eutrophication and resulting anoxia from sewage pollution. Holt and Davies concluded that Loch Goil remains largely unaffected by anthropogenic influence and should be maintained for its unusual communities and habitats, which are of high scientific interest.

More generally there is a long history of marine research within other Scottish sealochs, including the Firth of Clyde, the Firth of Lorne and various coastal locations within Argyll. The intertidal communities on the rocky shores of Argyll have been described by Kitching (1935) and Lewis and Powell (1960). Strathclyde University surveyed the rocky shore fauna in the Gareloch and Loch Long (Barnett, 1974). Similarly a biological survey of the shores in the Clyde Sea area was carried out by the Paisley College of Technology in 1978 and 1979 (Holt and Davies, 1991). Norton and Milburn (1972) provide a descriptive account of the depth distribution of macroalgae of Argyll. Using diving they examined eleven sites from Oban to the Kyles of Bute and described the zonation of macroalgae in relation to depth. They concluded that light and grazing echinoderms were the principal controlling factors in controlling algal distribution. Norton (1974) also provided a review of the literature related to seaweeds in the Clyde Estuary and Firth. McLean *et al* (1986) investigated the seasonal distribution of epilithic diatoms within various intertidal regions of the Clyde Estuary. They recorded a total of 307 species and found their succession to be highly variable within the estuary

Studies on the ecology of the macrobenthic fauna of the Lochs Linnhe and Eil in the Firth of Lorne have been carried out by Pearson (1970); Pearson (1971); Feder and Pearson (1988) and Pearson *et al* (1986). Similarly, Gage (1972, 1974) investigated the community structure of benthos in Loch Etive and Loch Creran, and Gage and Geekie (1973) described the large-scale patchiness of the benthic fauna in Loch Etive. A semi-quantitative survey of the major biological features of Loch Nevis and Loch Hourn was carried out by Breen *et al* (1986). They surveyed 36 sites, using diving, and documented each habitat in terms of topography and substrate. A similar study of the shallow sublittoral ecosystems of the Inner Hebrides was carried

out by Mitchel *et al* (1983) to provide data for reviewing the marine nature conservation importance of the area.

Much of the early data on the biology of the sealochs of the northern Firth of Clyde is found in the "Fauna, flora and geology of the Clyde Area" edited by Elliott *et al* (1901) and in data presented by King (1911) and Chumley (1918). The Sottish Marine Biological Association (SMBA) at Millport published a series of volumes on the fauna of the Firth of Clyde (Millar, 1960; Clarke, 1960; Allen, 1962; Bagenal, 1965; Allen, 1967; Machline, 1971; Moore, 1984; Morgan and Lampard, 1986; Wilkie, 1989). A symposium on the "Environment of the Estuary and Firth of Clyde" was organised by the Royal Society of Edinburgh in 1985 covering topics such as geography, geology, ornithology, benthic ecology, natural resources, pollution and conservation. The symposium is reported in a volume edited by Allen *et al* (1986).

Perhaps the most intensive multidisciplinary study of Scottish sealochs is "The Loch Eil and Loch Linnhe Projects" carried out by the Dunstaffnage Marine Laboratory (DML, 1992). These projects were concerned with identifying and measuring the processes involved in the exchange between the water column and sediment in sealochs. The parameters which were measured included nutrient concentrations in the water, phytoplankton concentrations and productivity, organic and inorganic settlement to the sediment, sediment/water fluxes of nutrient and oxygen, aerobic and anaerobic organic degradation rates within the sediments and sediment profiles of nutrients and metals in both solid phase and pore water. The lochs were chosen for intensive field sampling but data has also been obtained from detailed laboratory studies. An example is their use of laboratory cultures of *Skeletonema costatum* to investigate the effect on the sediment of degradation of phytoplankton at the sediment surface. Also at the DML, in conjunction with the University College of North Wales, nutrient levels have

been monitored in the Clyde Sea from the North Channel to the outer basin of Loch Fyne and in Loch Striven. The purpose of this study was to determine the potential for nuisance phytoplankton blooms (DML, 1991). Currently there are no studies at DML involving the floristic assessment of epipelon in sealochs although Tett (1982) has investigated sediment-pigment concentrations (phyto-plankton and epipelic algae) in Loch Eil and the Firth of Lorne. Currently the Dunstaffnage Marine Laboratory are concentrating their research of benthic systems on the Humber Estuary.

Since the late nineteenth century there has been considerable scientific interest in Loch Sween, Argyll. More recently Glasgow University and the SMBA have investigated the benthic ecology and plankton of the loch, particularly in relation to the impact of fish and shellfish farming. Because the habitats of Loch Sween remain relatively undisturbed by mans activities it has been proposed, by the Scottish Natural Heritage (SNH), as a marine nature reserve for Scotland.

The paucity of floristic, ecological or long-term distribution studies of the epipelon in Scottish sealochs contrasts with the intensive studies carried out on the phytoplankton. The Clyde River Purification Board currently monitor phytoplankton chlorophyll-a, micronutrient concentrations and basic environmental parameters in the Firth of Clyde and its sea lochs. Similarly the phytoplankton of various sealochs have been analysed by DAFS for various purposes including the monitoring of toxic species of algae. More detailed aspects of phytoplankton ecology have also been carried in the inner Firth of Clyde (Boney, 1986; Hinton, 1974) and within the sealochs: Loch Creran (Tett and Wallis, 1978); Loch Striven (Marshall and Orr, 1927, 1928, 1930) Lochs Striven and Fyne (Tett *et al*, 1986) and Loch Eil in the Firth of Lorne (Tett, 1982). Studies have also been carried out by the SMBA in Loch Striven following blooms

of toxic phytoplanktonic algae (Tett, 1980; Tett *et al*, 1986). Gowen *et al* (1992) have recently investigated the relationship between phytoplankton chlorophyll-a and nitrate levels using data from quasi-synoptic surveys of Scottish coastal waters (sea lochs, firths and sounds; including data feom Loch Goil) in an attempt to predict marine eutrophication.

Zooplankton studies include work on the feeding and vertical migration of euphausiids in Loch Striven, Loch Long and Loch Goil (MacDonald, 1927). Marshall *et al* (1934) and Marshall (1949) investigated the distribution patterns of copepods in relation to phytoplankton in Loch Striven.

1.3 Aims of my research

Few ecological data exist on subtidal marine epipelon either in Britain or more generally throughout the world. Round (1981) in his review of marine, subtidal epipelon indicated that:

"Of all the important algal habitats, I can think of none which is so understudied as that of the subtidal sediments".

The paucity of scientific studies on subtidal epipelon is undoubtedly related to the difficulties associated with sampling sediments from submerged habitats, which generally requires the use of either a research vessel or divers. Also the difficulty of maintaining marine epipelon in natural environmental conditions within the laboratory, poses problems to the scientist investigating the typical relationships between microalgae and the biological, physical and chemical environment. It is not surprising, therefore, that our knowledge of the ecology of epipelic algae is so incomplete. In reviewing the literature, it became apparent that the study of the epipelon from this fascinating and inaccessible habitat is still very much in its infancy. Similarly, little information exists on

epipelic algae (Smyth, 1955), or biological communities in general, from within the sea lochs of Scotland or comparable habitats.

Consequently, my present study was commenced with many aims, at several levels of importance. At a fundamental level the species involved in the subtidal epipelic algal association needed to be identified. Another primary aim was to quantify the variability of the epipelon, both spatially and temporally within Loch Goil. I also wanted to explain the spatial and temporal variations in the levels and composition of epipelon by studying the relationship between natural assemblages of algae and physicochemical and biological parameters. By examining the community of animals living on and within the subtidal sediments I attempted to gain an insight into some of the relationships between the invertebrates and epipelon of loch Goil. In particular I hoped to characterise the subtidal fauna in terms of their trophic behaviour. This would allow basic inferences to be made regarding the role of the epipelon in the food web of Loch Goil. The lesser aim of the study was to develop a method for the sampling and measurement of the epipelic algae from submerged sediments. The general approach to sampling was by means of diving.

The study was divided into the following main sections which also represent a synthesis of the aims of the present study:

A. To establish a methodology for the sampling and measurement of subtidal epipelic algae.

B. Document the spatial herogeneity of epipelon at a range of scales and along a depth profile.

C. Document the temporal (seasonal) heterogeneity in relation to the abundance and composition of epipelon.

D. To describe the epipelic community in Loch Goil and to seek to understand B and C in relation to the physicochemical parameters and/or biological parameters.

E. Investigate the relationship between the invertebrates and the epipelon in Loch Goil.

The aims of my research determine the order of this thesis. The remainder of Chapter 1 provides a detailed description of Loch Goil and discusses its relationship with the northern Firth of Clyde. Chapter 2 deals with the development of the standard methods of sampling the sediment and extracting the epipelic algae. Chapter 3 describes the standard methods used in my study of Loch Goil and discusses their limitations. Chapter 4 reports on my investigations of the natural distributions of epipelic algae including the determination of their: patchiness, small-scale distribution, bathymetric distribution, seasonality and colonisation (succession). Chapter 5 reports on the benthic invertebrate community of Loch Goil (along a bathymetric gradient) and investigates the trophic relationship between a key herbivorous grazer (*Ophiura albida*) and the epipelon. Each section contains a review of the relevant literature and the results are discussed independently. Chapter 6 is a general discussion of my findings in relation to the aims of my research.

1.4 Loch Goil

Loch Goil is one of a number of sea lochs which connect to the northern Firth of Clyde. The loch branches off approximately half way down the west side of Loch Long, which stretches northward from the Clyde, 27km up a narrow glacial valley (Fig. 1). Loch Goil is relatively short (8km), covering an area of $8.5km^2$ at high water. Only 4% (HW area) of the loch is intertidal, with a deep

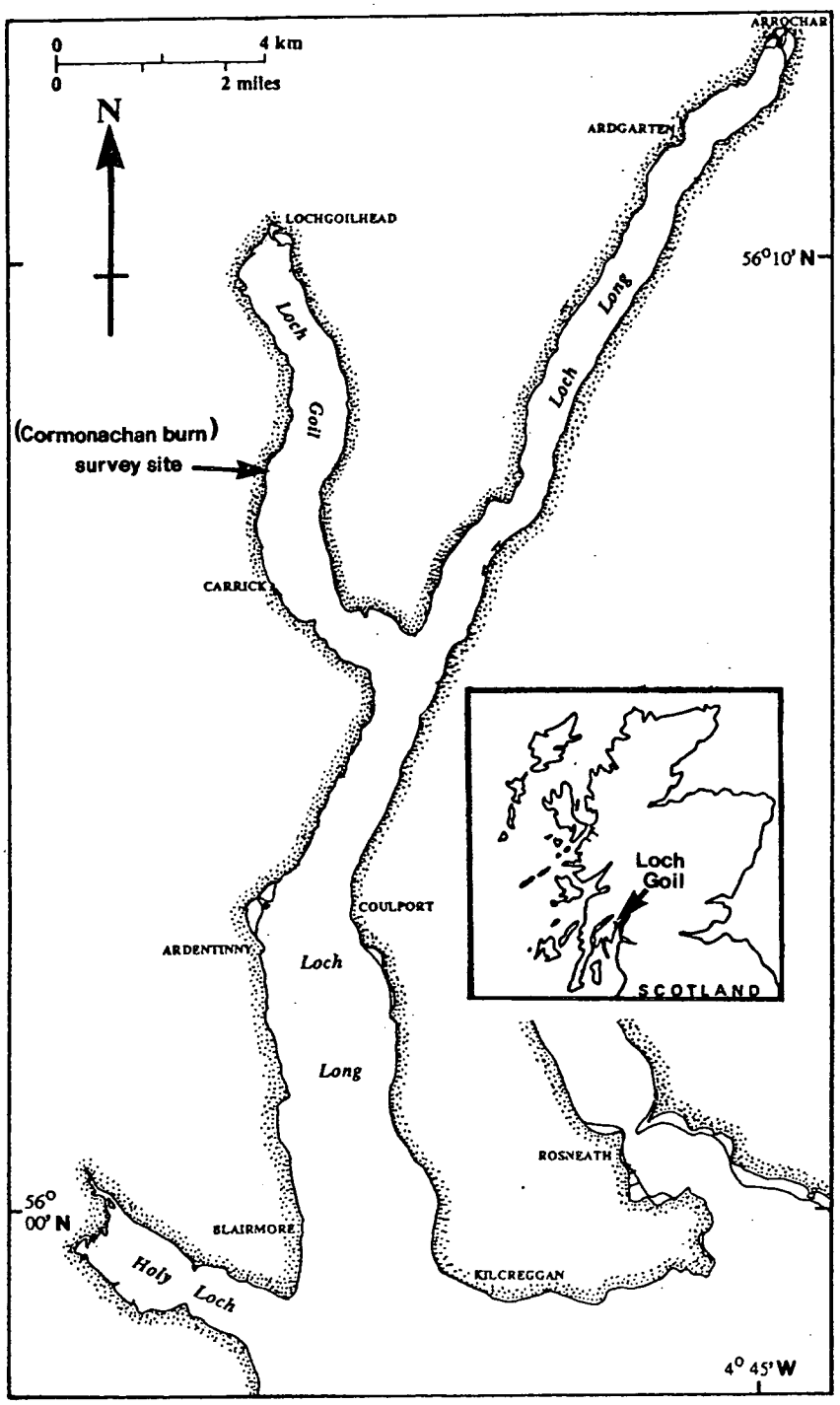


Fig. 1. Location of the survey site in Loch Goil. Inset shows the position of the loch in Western Scotland.

basin (50-93m) forming approx 60% of its area (Admiralty chart no. 3746, Edwards and Sharples, 1986). The basin is separated from Loch Long by a gently shelving region of mud that forms a shallow sill (16m) at the mouth of the loch. Approx 5km of shoreline adjoining the east side of the basin is steep, and this continues subtidally to form spectacular rocky slopes and cliff faces that descend to a depth of 30-40m. The remaining 18km of shoreline is more gently shelving and generally gives way, in the shallow subtidal, to areas of muddy sand and gravel and to silty clays in the deeper regions of the loch below approx. 25m (pers.observ.; Holt and Davies, 1991).

Loch Goil is surrounded by mountains (367-701m high) and lies on Precambrian igneous and metamorphic rocks of the Dalradian group (British Geological Survey sheet 55N). The mountains shelter most of the waters of the loch from all but southerly and northerly winds so that the sea state is therefore generally low.

1.4.1 Site description

The survey site (56^{o} 07.70'N, 04^{o} 54.20'W) is located approx. 5km from Lochgoilhead along the western shore of Loch Goil, approx. 75m from the confluence of a small stream called Cormonachan Burn (Fig.1). The site was chosen from a number of sealochs as it fulfilled the following requirements:

1. Preliminary observations of the epipelon within the subtidal sediment showed there to be a diverse and abundant community of microalgae.

2. There is a gently sloping plane of muddy sand in the subtidal region at a depth (9-12m below MLWS) that is ideal for prolonged (approx. 1h) and repeated dives. Because of the sheltered nature of the site and the relative stability of the sediment, good underwater visibility was predicted for most of the year.

3. Shelter from the prevailing westerly winds allows sampling throughout most of the year. Even with extreme

northerly or southerly winds the short wavelength of the waves would not prevent diving or disturb experimental apparatus positioned on the sea bed (9m depth below MLWS).

4. The site is isolated and unlikely to be used as a bathing beach or site for sport divers. Experimental apparatus positioned in the shallow subtidal region was therefore unlikely to be disturbed or vandalised.

5. Loch Goil is one of the closest sealochs to Edinburgh (104 miles) and is accessible by road. There is space for parking vehicles and good access to and from the water along a gently sloping, stony beach.

6. The site is isolated (approx. 5km) from any major source of urban discharge.

Because of the proximity of the site to Cormonachan Burn preliminary measurements were taken of the gradient in salinity with depth (0-11m). These showed a layer of slightly brackish water (29ppt) to exist in only the upper few centimetres of water with the remaining water column at 33 ppt. However, it was expected that changes in the flow within the burn may introduce seasonal variations in salinity, temperature and micronutrient concentration of the sea-water. Because the macroinvertebrate, macroalgal and epipelic community were of marine origin, the site was considered to be typical of the shallow subtidal regions of Loch Goil (pers. observ.) which receive freshwater from many similar burns and through ground water influx. The levels of dissolved oxygen recorded at the sediment/water interface from 1988-1990 (9m depth) were less variable than deep water levels (Mackay and Halcrow, 1976) and ranged from 5.5ppm (September) to 11ppm (January).

1.4.2 Physical data and bathymetry

The catchment area of the loch is approx. 107km^2 with an approx. annual rainfall of 2500mm per annum. The volume of the loch at low water is approx. 305.8 x 10^6 m^3 with an estimated flushing time of 9 days (Edwards and Sharples, 1986). Freshwater runoff from the surrounding

mountains reduces the salinity of Loch Goil by an estimated 0.6ppt from levels in coastal sea-water (Edwards and Sharples, 1986). However, freshwater inputs to the loch may have more localised effect, particularly after prolonged periods of rain (Holt and Davies, 1991). The salinity within Loch Goil during the period 29/1/87 to 29/11/90 ranged from 18.73-32.17 at 1m depth and 32.66-33.14 ppt at 80m depth (in the centre of the loch: [56 08.5'N 04 53.3'W] or at the mouth of the loch, over the sill; CRPB, unpubl. data).

Two distinct hydrographic regimes have been shown to occur in Loch Goil (Edwards et al, 1986; Mackay and Halcrow, 1976; CRPB unpublished data). In summer the loch stratifies causing stagnation of the deep waters in the basin. Because of this, the temperature of the deep water (approx. 50-80m) remains relatively constant through the year (7-11 ^{o}C, CRPB unpubl. data). Oxygen levels have been measured to drop below 2ppm (Edwards et al, 1986) and 5-15% saturation (CRPB, 1985) in summer due to the mineralisation of the phytoplankton and of sewage-derived organic matter. In the winter the deep water is displaced by cold, dense surface water and the oxy- and thermo-cline are disrupted by strong winds which mix the water column (Edwards et al, 1986).

Mackay and Halcrow (1976) have described the remarkable fluctations in dissolved oxygen that occur in the bottom waters of Loch Goil. They also point out that less extreme examples of this seasonal pattern can be observed in other fjordic and semi-fjordic sea lochs in Scotland.

Tidal currents within Loch Goil have not been measured. However, it is evident from the bathymetry of the loch (Admiralty chart no. 3746) that a range of bottom current velocities must exist and it is expected that velocities in the deep basin would be appreciably dimminished. Tidal ranges within Loch Goil are normal for the sea lochs of the Firth of Clyde, for example, tidal

heights at Lochgoilhead (spring and neap tides; height in metres above chart datum) are as follows: MHWS, 3.2; MHWN, 2.9; MLWN, 0.7; MLWS; 0.1 (Admiralty Tide Tables 1990).

1.4.3 Pollution inputs to Loch Goil

Lochgoilhead discharges untreated sewage into Loch Goil via an outfall, inshore of the 10m depth contour. The annual sewage loadings of Loch Goil have been estimated at 14 tonnes BOD (biological oxygen demand) and 16 tonnes suspended solids (CRPB, 1976). There is also strong evidence (CRPB, 1985; CRPB pers.comm.) that the Clyde Estuary is an important source of pollutants for several of the Clyde sea lochs, especially Loch Goil, Long, Gare Loch and Holy Loch. Elevated levels of nutrients, trace metals and organochlorine pesticides exist in the Clyde estuary, which receives effluents from industry and approx. 2.5 million people, almost half Scotland's population (Mackay and Leatherland, 1976). Using salinity and silicate as conservative tracers, Mackay and Halcrow (1976) and Mackay and Leatherland (1976) have quantified the amount of fresh water in the surface layers of Loch Long and Loch Goil that is derived from the Clyde Estuary. Following a period of prolonged heavy river flows and strong southerly winds the proportions of water derived from the Clyde Estuary ranged from 20-40% near the confluence of Loch Long and Loch Goil, 10-29% at the centre of Loch Goil and 1-14% at Lochgoilhead.

As a sea loch, Loch Goil, in common with other UK coastal waters, is subject to legislation to prevent and control water pollution. Loch Goil supports a small commercial harvest of the bivalve *Modiolus modiolus* and under the "Quality Required of Shellfish Waters" EC Directive (Section 4 of E.C. directive 79/923/EEC), is designated an area needing protection and improvement. As a consequence of this, the Clyde River Purification Board (CRPB) monitor the loch for faecal coliform bacteria both in the water and in mussels (CRPB, 1986). The eutrophic

state of Loch Goil is also monitored by the CRPB every three months or so by the measurement of major physical and chemical parameters (temperature, salinity, dissolved oxygen concentration, dissolved micronutrient concentration [NH_3-N, NO_2-N, NO_3-N, PO_4-P, SiO_2], phytoplankton chlorophyll-a and secchi depth) from the surface to the bottom (1-80m) of the loch. Some of these data, for the period 1988-1990, can be seen in Table. 11; the relationship between these data and variations in the epipelon is discussed in section 4.4.4.5.

The loch is used as a tourist amenity around Lochgoilhead where there are chalet and caravan complexes. Water sports are also popular and include activities such as yachting, canoeing, fishing and diving. The Royal Navy bases in the Clyde region use the deep area of the loch as an anchorage for nuclear submarines and surface support craft. Until recently there was also a U.S. Nuclear Submarine Base in Holy Loch, situated 12km to the south of Loch Goil (Fig. 1). Radioactivity from discharges by the Nuclear Submarine Bases and from the operation of the submarines themselves, are monitored in Lochs Long, Goil and Fyne. The results show that levels are negligible in terms of public health (CRPB, 1985).

CHAPTER 2

METHOD DEVELOPMENT

2.1 INTRODUCTION - METHOD DEVELOPMENT

The measurement of epipelic diatom abundance, chlorophyll-a and the assessment of the epipelic community structure requires: (1) a quantitative sampling method that accurately samples the natural community; (2) a quantitative method of extracting the algae from the sediment and (3) an accurate method of enumerating the harvested algae. Ultimately these methods are aimed at obtaining quantitative data on the standing crop of the motile epipelon. The standing crop at any one time is the balance resulting from the rate at which the diatoms have been growing and the rate of loss (of the initial standing crop) by, for example, grazing (Boney, 1976).

This chapter reports on the development of the standard methods (sampling, extracting and enumerating the epipelic algae) used in my investigations of the epipelon of Loch Goil.

2.2 SAMPLING THE SEDIMENT - METHOD DEVELOPMENT

In order to decide on a method that adequately samples the epipelic diatom community of Loch Goil, consideration had to be given to the following: the distribution pattern of the epipelon on the sediment surface (regular, random or contagious), the appropriate dimension of the sampling unit, and the number of sampling units in each sample.

The dispersion of the epipelon on the bottom of Loch Goil appeared, through visual inspection, to be clumped. In particular, coloured patches of copper-brown were apparent indicating dense areas of epipelic diatoms (this assumption later proved to be valid as an investigation of the dispersion pattern, at a depth of 9m, showed the epipelon to be distributed in patches at a range of scales; see 4.1.). The replication of a small sampling unit was therefore considered to be more efficient than a

few larger samples (Elliott, 1971). Elliott suggested that a small sample unit has a number of advantages over a larger unit: (1) more small samples can be taken for the same amount of labour involved in processing (extraction and enumeration of algae); (2) with increased replication the statistical error is reduced, as there are more degrees of freedom; and (3) many small samples cover a wider range of habitat than a few large units, and are therefore more representative. Plante *et al* (1986) investigated spatial patterns in marine epipelic biomass on a range of scales (cm, m, km) and found replication of samples to be essential in order to improve precision and overcome small scale (m) spatial variability of the epipelon. The sampling and extraction method must also collect a high proportion of the species present in the population as well as provide an acceptable estimate of population numbers (Holme and McIntyre, 1971).

2.2.1 Experimental comparison of two sampling strategies

Two different sampling strategies (three 45.6 cm^2 sediment cores and nine 15.2 cm^2 sediment cores) were compared for their efficacy at sampling the epipelon within an approximately 25 m^2 area of the bed of the loch (9 m depth). Two sides of the, square, 25 m^2 area were calibrated with a tape measure to allow random sampling of the sediment using randomly produced coordinates. The cores were collected, by hand, and were hermetically sealed underwater. Both cores sampled the sediment to a depth of 2 cm, and incorporated a 2 cm column of sea-water. The area of sediment sampled by a large core sample was precisely three times that of a single small core sample, so that the total area of sediment sampled after replication was identical (136.8 cm^2).

2.2.1.1 Large cores

These were constructed from perspex tube (4 cm high x 7.6 cm internal diameter), permanently sealed at one end by a perspex plate, and at the other by a removable lid. A flange, positioned 2 cm from the mouth of the core, limited the depth of the sample (Fig.5). The sample units were later homogenised and treated according to the standard method described in sections 3.2 and 3.3. An estimate was made of the epipelic diatom abundance and of the number of taxa collectively sampled by this method.

The variation between algal counts (between secondary sub-samples) was found to be unacceptable (SE=50% of $\bar{x}$) and a total of 51 species of epipelic diatom were recorded (for a definition of "secondary sub-samples" see 3.3). The implications of this variability is discussed in section 3.6.

2.2.1.2 Small cores

Polystyrene containers (4.4 cm internal diameter), sealed by a tight fitting polyethylene lid (Azlon, J. Bibby Science Products Ltd. Stone, Staffordshire, England.) were cut down to a height of 4cm. A number of small fishing weights (non-toxic shot) were attached to the side of the core with autoclave tape in order to render the unit negatively buoyant. The edge of the tape was positioned 2cm from the mouth of the core to indicate the depth to which the core sampler was to be pushed into the sediment when sampling. The nine replicate sample units (sediment) were then combined, in groups of three, into settling chambers (see Fig. 5), homogenised, and treated according to the standard method described in sections 3.2 and 3.3.

The variation was found to be a significant improvement over the use of three larger sampling units (SE=22.9 % of $\bar{x}$), with 72 species of epipelic diatom recorded.

The use of nine smaller cores improved the statistical accuracy of the sampling method and increased the number of species that was recorded. The variance was sufficiently low to allow distinctions to be drawn between natural variability in the epipelon and the residual variability introduced through limitations of the sampling method. This method was therefore adopted as standard for the monitoring of spatial and temporal patterns in the epipelic population of Loch Goil (see 3.1).

2.3 EXTRACTING THE ALGAE - METHOD DEVELOPMENT

2.3.2 THE EXPERIMENTAL COMPARISON OF HARVESTING SUBSTRATES AS A MEANS OF EXTRACTING EPIPELIC ALGAE

2.3.2.1 Introduction

The particular problem with the extraction and enumeration of epipelic algae arises from the myriads of minute sediment particles, dead diatom cells and particles of organic material with which they are closely associated. Unfortunately there are few methods which will quantitatively extract epipelic algae from sediment.

Eaton and Moss (1966) compared the accuracy of three principal methods of estimating the number and community structure of epipelic algae in sediment: by direct counting of algae within a suspension of sediment, or by allowing algae to adhere to coverglasses or fabric in response to their phototactic movement. They rapidly deduced that direct counting was inefficient and time consuming and subsequently developed a standard method of extracting epipelon from damp sediment using lens tissue (double layer of Grade 105 lens tissue). A harvesting efficiency (numbers) of 87.5% was reported for lens tissue and the similarity between direct and lens tissue estimates of species proportions was 94.02%. They found the tissue method to be more efficient than the coverglass method in efficiency of harvesting (75.5% covergalsses) and estimation of species proportions. They also

identified that the major problem with the coverglass method was the uneven distribution of epipelon on the glass, thus making enumeration by standard counts difficult. Mills (1985) utilised the lens tissue method of Eaton and Moss (1966) in his study of the epipelon of the Firth of Forth and recorded an overall efficiency of 37.1% of that found by direct counts. Colijn *et al* (1976) compared the lens tissue method, a density centrifugation technique (de Jonge, 1979) and a direct count of microalgae from the sediment. When the data was expressed in relation to the direct sediment count (assumed to be 100%) the lens tissue method was found to give an overall efficiency of 40.5% whereas the density gradient method had an efficiency of 87.8%. The method of separating epipelon from marine sediments by density centrifugation in Ludox was developed by De Jonge (1979) and subsequently modified (simplified) by Blanchard *et al* (1988). This technique allows the non-destructive extraction of cells for taxonomic identification, counting or pigment analysis. The method relies on differences in specific gravity between the epipelic algae and the sediment particles to achieve separation with a mean recovery rate of 82% (de Jonge, 1979). Paterson and Crawford (1986) developed a method utilising low-temperature scanning electron microscopy (LTSEM) to determine the composition, and orientation, of natural epiplic diatom assemblages. They compared the efficiency of the method relative to the standard lens tissue technique of Eaton and Moss (1966) and found differences in the composition of the epipelic assemblage measured by the two techniques. They indicate the usefulness of the LTSEM technique as a supplement rather than a replacement of the usual methods, particularly in the study of epipelic patchiness (in both 2 and 3 dimensions) of natural diatom assemblages. More comprehensive reviews of the literature on methods of extracting epiplic algae can be found in Round (1981), Round and Hickman (1971) and Round (1971).

Before adopting a standard method, I tried the three methods used by Eaton and Moss (1966) on the sediments of Loch Goil. I found that all three methods extracted the indigenous epipelic flora but also included a large fraction of fine inorganic particles of sediment that were prevalent in the soft subtidal sediment. The methods also extracted a large fraction of dead diatoms and, with the glass and tissue methods, even experimenting with the degree of moistness of the sediment did not alleviate the problem of contamination. The particles made counting and identification of the algae difficult and inaccurate, and for large numbers of samples this proved to be time consuming and tedious. The inclusion of dead (empty frustules) diatoms in the sample is particularly unsuitable for ecological study of the epipelon. Round (1971) points out that comment on ecological aspects of benthic marine diatoms is:

"misleading unless the living or at least the living and recently living diatoms are separated from the often abundant contaminants washed into the area".

Similarly, Round (1971) indicates that:

"contamination from dead frustules is present in all sampling techniques and must be minimised".

I recognised the importance of using a well-tried method to provide continuity of data with the literature. However, because of the large number of samples that I was to analyse during the course of my investigations I needed to use a method that was economical in time and labour, as well as efficient at removing the living epipelic algae.

The following section reports on the experimental investigation of different harvesting substrates. The aim was to optimize the extraction of epipelic algae while minimising contamination of the sample. The results of the analysis were to be used as a basis for the adoption of a standard method of extracting the epipelon from the subtidal sediments of Loch Goil.

To this aim, the effect of screening the harvested algae from detritus, sediment particles and dead diatom

cells was investigated. Also a number of solid substrates (glass, polythene, acetate and agar gel) were compared for their efficiency at removing algae from damp sediment. The effect of coating a substrate with the polymer adhesive "poly-L-lysine" (an adhesive used for the attachment of nanoplankton in electron microscopy; Marchant and Thomas, 1982), was also studied.

Unfortunately, during the earlier months of my postgraduate research a lack of transport made it impossible to use sediment from Loch Goil in these experiments. Instead I had to use sediment from a small, fresh-water, eutrophic pond located close to the laboratory in Edinburgh (GR NT 253 709). The submerged sediment of Blackford Pond harbours a diverse assembalge of epipelic diatoms and both the pond mud and Loch Goil mud were very similar in texture. I make the basic assumption that the results of these trials are applicable to the subtidal sediments of Loch Goil.

2.3.2.2 Materials and Methods

In November 1987 approximately 3 litres of surface sediment and water were collected using the glass-tube method described by Round (1953). The sediment, on arrival at the laboratory, was transfered to a large measuring cylinder and vigorously shaken to homogenise the sediment. The sample was allowed to settle in the dark (6h) in order to eliminate migration of algae due to phototaxis and hence maintain some degree of homogeneity of algae within the sample. Following the removal of excess water, which was achieved using a vacuum pump, the sample was again vigorously shaken. Equal volumes of the mixed sample were then poured into two trays (23x33cm) and the sediment in one tray couverd with a single layer of lens cleaning tissue (No. 105, Whatman International Ltd, Maidstone, England).

The following treatments were tested in triplicate on both "tissue-covered" and "uncovered" sediment:

A glass coverslip (22x22 mm)
B glass coverslip, poly-L-lysine coated
C agar gel
D polythene (20x20 mm)
E polythene, poly-L-lysine coated
F acetate sheet (20x20 mm)
G acetate sheet, poly-L-lysine coated
H double layer of lens-tissue (20x20 mm)
I lens-tissue, poly-L-lysine coated

"Glass coverslips" (22 mm x 22 mm; Chance Propper Ltd. Smethwick, Warley, England); "lens cleaning tissue" (No. 105, Whatman); "acetate" (1 mm 'acetat', over-head projection sheets, Staedtler); "polythene" utilised polythene bags (Azlon, J. Bibby Science Products Ltd. Stone, Staffordshire, England.).

In order to avoid bias the test materials were distributed randomly on the sediment surface using co-ordinates from randomly produced numbers. The two trays were placed at the base of a tall (27cm) open-topped box covered with four layers of cotton muslin to diffuse the light and produce even illumination. The sediment was continuously illuminated overnight (15 hrs) by two fluorescent strip lights positioned 50 cm above the trays. Treatments were removed between 09.00-10.00 hrs to coincide with expected period of optimal density of eipelic diatoms on the sediment surface due to vertical migration rhythms of the algae (Round and Eaton, 1966; Round and Palmer, 1966).

To compare the relative efficiancy of the treatments at harvesting a diverse assemblage of epipelic diatoms, the relative abundance of six species was determined. The "test" species were selected for the ease with which they can be identified without the need to clean the frustules, and for their size which ranged from 15-300 um as follows: *Cymatopleura solea* (30-300 um), *Nitzschia linearis* (70-180 um), *Sellaphora* (=Navicula) *menisculus* (25-30 um), *Navicula pupula* (15-60 um), *Navicula hungarica* var. *capitata* (20-25 um), and *Amphora sp* (15-60 um). Counts were made of diatom cells (preserved with 1% glutaraldehyde) under 400x magnification, along a randomly

chosen 20mm long transect of the treatment's surface, defined by a graticule of parallel glass fibres, 200 um apart. I constructed the graticule using strands of extruded glass according to the method described by Lund, et al (1958). Counts were made of the tissue treatments (H,I) along the standard transects of three subsamples of 3ml aliquots (the volume suggested by Eaton and Moss, 1966) taken from each of the homogenised treatments and mounted under a glass coverslip. To enable direct comparison of counts obtained from both solid (A-G) and tissue (H,I) treatments, the counts from H and I were first converted to numbers per cm^2 and then to a count representative of the same area of a standard transect at 400x magnification.

Chi-squared analysis [X^2] (3.5.2) was carried out using a contingency table in order to compare the proportion of the six test species sampled by the different treatments from tissue-covered and uncovered sediment. The analysis tested the null hypothesis (H_o) that the proportion of species in the two treatments are the same.

Prior to the experiment the preparation of the poly-L-lysine and agar treatments were carried out as follows:

2.3.2.2.1 Preparation of poly-L-lysine treatments

A drop of 1.0 mg ml^{-1} poly-L-lysine hydrobromide (polylysine; MW=22,000; BDH Chemicals Ltd, Poole, England) dissolved in filtered pond water, was appplied to the glass coverslips, polythene and lens tissue for two minutes at room temperature. The materials were then rinsed in a stream of filtered pond water for 30 s and air dried for later use.

2.3.2.2.2 Preparation of agar gel treatment

An agar gel was prepared (8 ml l^{-1}) from Agar No.1 dissolved in filtered pond water. The gel was applied, while hot, to the glass coverslips forming a thin, even

layer on one surface only. The gel was air-dried and cooled to room temperature before use. The glass was present in the treatment only to provide support for the gel.

2.3.2.2.3 Test of the pattern of dispersion of algae on the surface of polythene and glass

In order to decide on the number and size of the secondary sub-sample (standard cell counts) it was necessary to determine the pattern of algal dispersion (random or contagious) on the surface of the glass and polythene substrates. Epipelic algae were harvested on to glass and polythene using mixed sediment collected from Loch Goil covered with tissue. Counts were then made of algal cells (x400 mag.) within 80 randomly chosen fields of view. The data were tested for agreement with a Poisson series using Chi-square (X^2) test (Elliott, 1971). Agreement with a Poisson series was accepted at the 95% probability level ($P>0.05$) for both glass ($X^2=8.27$); polythene ($X^2=9.52$). The algae are therefore dispersed randomly over the substrates and can themselves be (secondarily) sub-sampled.

2.3.2.3 Results

The overall effect of harvesting epipelic algae through a layer of lens tissue was to reduce the number of algae collected by the treatments (Fig. 3). An exception was found only with polythene coated with poly-L-lysine (E) which harvested more algae (6.8%) through a tissue screen. Comparison of the these data by ANOVA shows the effect of screening to be significant with both the tissue treatments (H: $P<0.05$ and I: $P<0.01$) and with the glass method (A $P<0.05$). The results of ANOVA are summarised in Fig. 3. The tissue screen had the greatest effect on the lens tissue treatments (H and I) which showed a 47.1 % and 50.2 % difference compared with a 24.9 % difference with glass (A). The largest number of algae were collected using either of the polythene treatments (D and E), on tissue-covered or uncovered sediment, or using lens tissue

on uncovered sediment (H and I). The use of agar and acetate proved to wholly inefficient at harvesting algae. In particular, acetate was found to curl in contact with the moisture which caused the loss of data seen in Fig 3.

The effect of a tissue screen on the proportion of test species can be seen in Table 3. which also shows the results of the X^2 analysis. The proportion of taxa were significantly different [tissue-covered vs uncovered] ($P<0.05$) for all treatments except with the use of glass ($P>0.01$), agar gel ($P>0.05$) and acetate ($P>0.05$). However, both agar and acetate have been shown to be inefficient at extracting the algae from the sediment in appreciable numbers.

The general effect of coating a treatment with adhesive polymer, poly-L-lysine, was to reduce the number of algae harvested (except with tissue on uncovered sediment). However, none of these differences were significant at the 5% level (ANOVA, $P<0.05$). The effect of poly-L-lysine on the proportion of species harvested from the sediment was varied. With the polythene treatment on uncovered sediment, X^2 showed there to be no significant difference ($P>0.05$) in the sample community. However, the addition of poly-L-lysine on all other combination of treatments (covered and uncovered) was to modify significantly the sample community (see Table 1). With the glass and polythene methods, the effect of using a tissue screen was to compound the effect of the poly-L-lysine and indicates a deterioration in the quality of the sample. However, without knowing the structure of the epipelic community present in the sediment the effect of poly-L-lysine, on the efficiency of the different methods, is inconclusive.

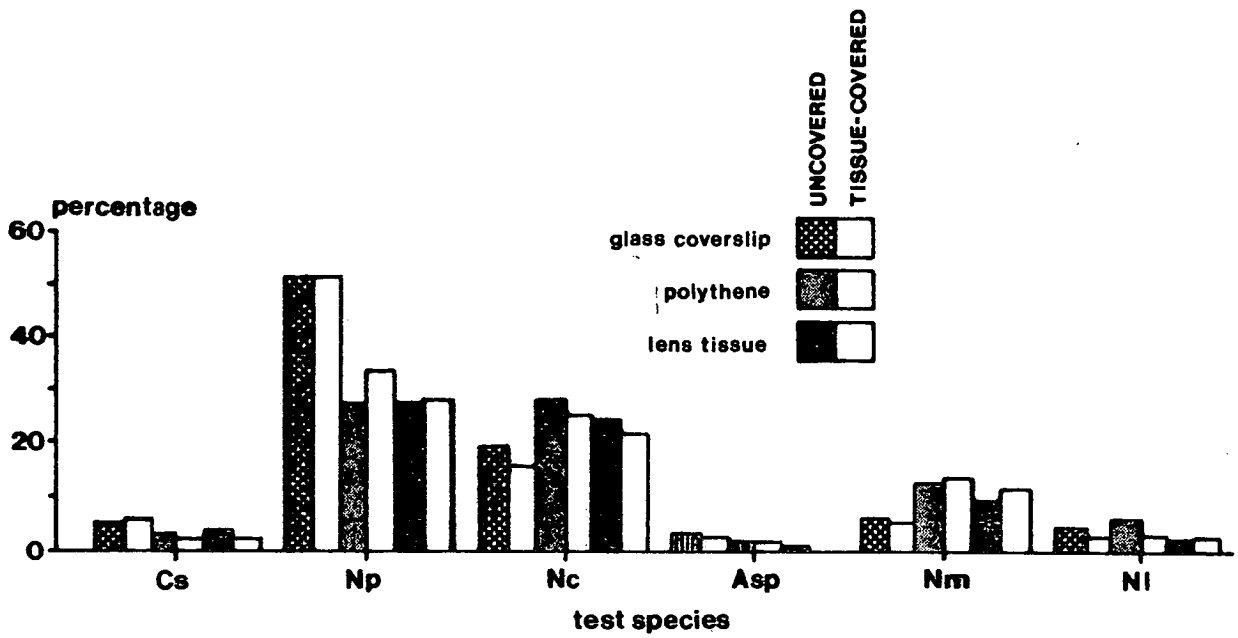


Fig. 2. The proportion of test species recovered from the sediment using the glass, polythene and lens tissue method (see text). The histogram compares the effect of harvesting the algae using tissue-covered and uncovered sediment. Key: C.s = Cymatopleura solea; N.p = *Navicula* pupula; N.c = *Navicula* capitata; A.sp = Amphora sp; N.m = *Navicula* menisculus; N.l = Nitzschia linearis;

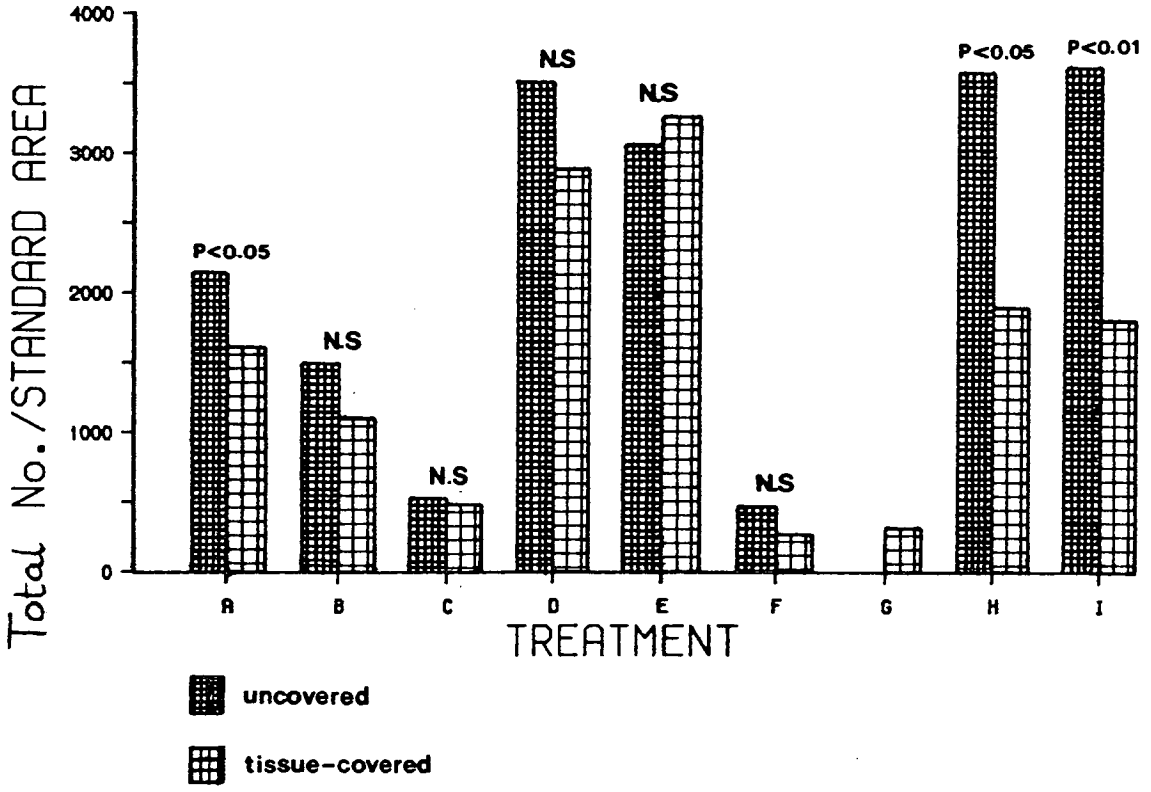


Fig. 3. The number of epipelic algae harvested from sediment using a range of treatments (glass coverslip [A]; glass coverslip with poly-l-lysine [B]; agar gel [C]; polythene [D]; polythene with poly-l-lysine [E]; acetate sheet [F]; acetate sheet with poly-l-lysine [G]; lens tissue [H]; lens tissue with poly-l-lysine [I]). The histogram compares the effect of harvesting the algae using screened and unscreend sediment. Analysis of the data by ANOVA show there to be: N.S = no significant difference ($P>0.05$) between the number of algae recovered from covered and uncovered sediment. $P<0.05$ / $P<0.01$ = a significant difference at the 5% and 1% level (respectively).

	Chi-squared analysis		
"u"	glass vs glass + p	16.17	**
"t"	glass vs glass + p	65.75	***
"u"	polythene vs polythene + p	10.92	N/S
"t"	polythene vs polythene + p	25.66	***
"u"	tissue vs tissue + p	11.43	*
"t"	tissue vs tissue + p	14.36	*

Table 1. The results of X^2 analysis comparing the effect of poly-L-lysine on the proportion of test species harvested from uncovered ("u") and tissue-covered ("t") sediment. Key: p = poly-L-lysine; "N/S" = no significant difference ($P>0.05$); * = significant differnce ($P<0.05$), ** = highly significant difference ($P<0.01$) and *** = very highly significant difference ($P<0.001$).

The effect of the tissue screen on the quality of the sample and ease of analysis was two-fold. 1) It effectively eliminated the adhesion of particulate matter and dead (empty) diatom frustules from the samples and 2) stabilized the sediment during the extraction proceedure so that excess water could be readily removed from the surface without losing sediment material or algae (data not provided).

Because the principal aim of this investigation was to "optimize the extraction of epipelic algae while minimising contamination of the sample by sediment particles", a more detailed comparison was made of those treatments that appeared to be most efficient at harvesting large numbers of algae while remaining relatively unaffected by the tissue screen. Fig 2 compares the proportion of taxa harvested using the glass (A), polythene (D) and lens tissue (H) method. The comparison of these data by X^2 revealed that the greatest similarity existed between the polythene and lens tissue method, sampled on tissue-covered sediment (Table. 1). However, compared with the community obtained with glass, both polythene and tissue significantly underestimated the

number of the small (15-60um) naviculoid diatom *Sellaphora* (=Navicula) *pupula* (Fig. 2).

		Chi-squared analysis	
		polythene	tissue
glass	"u"	316.80	223.88
	"t"	244.013	198.43
polythene	"u"		80.75
	"t"		17.71

Table 2. The results of X^2 analysis comparing the similarity of sample communities harvested by the glass, polythene and tissue methods (tissue covered vs tissue covered; uncovered vs uncovered). The results show that the greatest similarity exists between the polythene and tissue methods when used on tissue-covered sediment. However, the difference is still significant at the 1 % level ($P<0.01$), but not at the 0.1 % level ($P>0.001$). Key "t" = tissue covered sediment; "u" = uncovered sediment.

2.3.2.4 Discussion

The results of this investigation clearly suggest that, out of the nine treatments tested, the glass, polythene and lens tissue were the most efficient at isolating epipelic algae.

2.3.2.4.1 The number of algae

I found that isolating epipelon from uncovered sediment caused problems with the counting and identification of algae owing to the presence of inorganic particulate matter. These were picked up by adhesion or capiliarity on to the surface of all the substrates. The use of a single layer of lens tissue as a screen proved to be highly effective at eliminating this source of error. However, some reduction in the number of algae that were harvested did occur (glass 24.9%, polythene 17.8%, lens tissue 47.1%). Although there are clear advantages in collecting as many of the epipelic algae from the sediment as possible (eg. to reduce the chance of missing any

TREATMENT		% C.s	% N.p	% N.c	% A.sp	% N.m	% N.l	% others	No.x10⁴/m² total	S.E.	X^2
	u	4.4	50.8	18.6	2.4	5.7	3.9	14.2	2142	43.1	(P>0.01)
A glass	c	5.3	50.9	15.1	2.1	5.0	2.4	19.0	1608	33.5	13.2
	u	2.5	45.4	20.5	3.4	5.3	4.0	18.8	1492	97.2	S/D
B glass + p.	c	4.3	38.9	17.5	2.1	12.2	2.7	22.5	1094	135.4	57.9
	u	4.6	40.1	16.3	3.3	4.0	4.2	27.4	521	48.2	(P>0.05)
C agar gel	c	2.9	47.3	12.4	1.7	5.2	3.6	26.9	476	15.2	10.9
	u	2.7	26.9	27.4	1.2	12.0	5.9	23.9	3499	39.0	S/D
D polythene	c	1.8	32.8	24.9	1.0	13.1	2.8	23.7	2876	109.8	63.5
	u	3.2	28.0	24.8	1.2	11.3	7.2	24.3	3044	112.8	S/D
E polythene + p.	c	2.0	37.7	21.4	0.9	11.1	2.2	24.7	3251	143.0	143.5
	u	3.0	45.9	24.1	3.0	1.8	1.5	20.7	460	27.3	(P>0.05)
F acetate	c	0.8	49.3	21.6	1.5	2.7	1.2	23.1	264	33.3	7.2
	u	-	-	-	-	-	-	-	-	-	
G acetate + p.	c	1.0	49.4	16.5	1.6	3.6	1.3	26.6	308	17.5	
	u	3.1	27.3	24.0	0.4	8.8	2.0	34.4	3574	57.0	S/D
H tissue	c	2.0	27.9	21.5	0.0	11.3	2.5	34.8	1891	115.6	27.7
	u	2.3	29.8	25.1	0.3	7.7	2.0	32.9	3613	51.0	S/D
I tissue + p.	c	3.5	29.0	18.5	0.0	10.3	1.9	36.9	1801	79.5	65.8

Table 3. The proportion of species (percentage) and total number of epipelic algae harvested, using different treatments (A-I), from tissue-covered (c) and uncovered (u) sediment from a fresh-water pond. Analysis of the six test species (X^2) shows there to be a significant difference (S/D) between sample communities (tissue covered vs uncovered sediment) in treatments B, D, E, H and I, with rejection of the Ho at the 5% level ($P<0.05$). However, no significant difference was found for treatments A, C and F with acceptance of the Ho at the 1 %(A) and 5 % level (C, F).

Key: *C.s = Cymatopleura solea; N.p = Navicula pupula; N.c = Navicula capitata; A.sp = Amphora sp; N.m = Navicula menisculus; N.l = Nitzschia linearis;* others = all other species; total = total number of cells per standard count (see text); S.E. = standard error.

additional species) a reduction in the number could be acceptable as long as the effect of screening on the composition of the isolated algae is understood and quantified. I assume that any effect of the tissue screen in reducing levels within the sample is constant. This is an obvious requirement of the method was to allow discernment of pattern within any community data.

It appears from the results of this study that polythene used in conjunction with a tissue screen would be the most efficient method of collecting algae for the estimation of epipelic abundance. I also found that the polythene sample could be easily preserved in a semi-permanent preparation (Fig. 5) and because of the tenacity of the algae to the polythene surface the position of the cells on the slide remained fixed. This had the advantage (over eg. the tissue method) of enabling me to relocate a particular cell at a later date.

Eaton and Moss (1966) found that one of the principal disadvantages of the coverglass method was that algae distributed themselved unevenly on the surface of the glass making accurate enumeration difficult. It appears from my results that one of the advantageous effects of screening the sediment with a single layer of lens tissue is to alleviate this source of error as algae were randomly distributed on both polythene and glass substrates.

2.3.2.4.2 Community composition

There was clearly an effect on the composition of the sample community isolated from the sediment when this was screened by tissue. The reason for this is not clear although the tissue may have formed an additional barrier to the transfer of algal cells. However, there was no consistent pattern in the data of a bias favouring the smaller species *Sellaphora (=Navicula) pupula*) or limiting the larger diatoms (*Cymatopleura solea* and *Nitzschia linearis*) when sampled through a tissue screen. This indicates the effect is non-selective, resulting in an

overall reduction in levels of all species within the community.

The glass treatment was the only method that showed all three of the following attributes: (1) ability to harvested a sample community that was unaffected by the tissue-screen ($P>0.05$); (2) was efficient at collecting a relatively large number of algae (Fig 3) and (3) showed no significant ($P<0.01$) reduction in numbers when used on tissue-covered sediment (although the difference was significant at the 5% level). Consequently I decided to adopt the use of glass, through a tissue screen, to extract epipelon for the estimation of community structure. The adhesion of algal cells on to the glass would enable subsequent clearance of all organic matter by incineration, using a furnace. The empty frustules could then be identified to species and estimates made of the proportion of taxa.

Although Eaton and Moss (1966) found that lens tissue is the most efficient method of extracting epipelon from sediment all their experimental investigations were carried out on uncovered sediment. This investigation of the effects of screening (harvested) algae from contaminants represents a modification of their basic method. In particular my method could be applied to other studies of marine and fresh water epipelon when the investigator finds contamination by dead diatom cells, sediment and detritus a problem. Further analysis of the method is required to determine the efficiency of the method at extracting algae from sediment. This will involve lengthy comparisons of the number and community structure of harvested algae in relation to direct assessment of algae within the sediment. To facilitate the comparison Paterson and Crawford's (1986) method of utilising low-temperature scanning electron microscopy could suppliment direct counts of algae.

Ideally calibration of the standard method should have been carried out on the natural epipelon and sediment

from Loch Goil. However, because of a constraint on time I considered that further experimental analysis of the method was beyond the scope of my research.

2.3.2.4.3 The standard extraction method - a summary

This section gives a basic summary of the standard method of extracting epipelon for assessment of abundance, chlorophyll-a and community structure. A detailed account of the standard methods are provided in the following chapter (4).

Diatoms are isolated from damp sediment by placing pieces of polythene, glass and lens cleaning tissue on the surface of sediment, screened with a single layer of lens tissue. Algae are then allowed to adhere to these substrates overnight. The epipelon sampled by the **glass cover slip** are oven-cleaned and used for the taxonomic identification of algae and in the assessment of epipelic community structure. The **Polythene** harvested algae are used in the assessment of algal abundance whereas algae collected with **lens tissue** are used in the spectrophotometric measurement of pigment concentration to provide an estimate of biomass. Following these extractions I harvest any remaining algae using lens tissue. These are used to provide acid cleaned cells which help with the taxonomic identification of the epipelon and are examined for the presence of additional rare species.

2.4 DETERMINATION OF OPTIMUM HARVESTING TIME - METHOD DEVELOPMENT

2.4.1 Introduction

Rhythmic behaviour in epipelic algae is common and a number of authors confirm the existence of tidally modified (diurnal) vertical migratory rhythms (Perkins, 1960; Hopkins, 1963, Hopkins 1966; Palmer and Round, 1965; Palmer and Round, 1967; Round and Palmer, 1966; Round,

1979) and similar rhythms in fresh water (Round and Eaton, 1966). Round (1981) emphasises the importance of taking into account the rhythmic behaviour of epipelon in a particular habitat, so as to remove harvesting substrates at the optimum time of day. To this aim the period of optimum density in sediment from Loch Goil was determined experimentally using standard lighting condition. I made no attempt to describe the natural rhythmic behaviour of the epipelon of Loch Goil. In addition this experiment did not separate the natural rhythmic behaviour of the algae from the (phototactic) re-orientation of algae on the sediment surface following burial by the homogenisation process (described below).

2.4.2 Methods

Approximately 2 litres of surface sediment (approx. 2cm) was collected from the bottom of Loch Goil at a depth of approx. 9m. On arrival at the laboratory, appox. 250ml of sea water was added to the sediment in a large measuring cylinder which was vigorously shaken to homogenise the sediment. A portion of the homogenate was transferred to a shallow tray (23cm x 33cm x 4cm). The sediment in the tray was allowed to settle in the dark for 2h, after which time excess water was removed by means of a vacuum pump. The sediment was then covered with a single layer of lens tissue. Replicate polythene substrates (20mmx20mm) were placed at random on the surface of the sample at 17:00h and removed periodically (1h or 2h) over a 24h period. Replicate treatments were also placed on the sample periodically over 24h. These treatments were left on the sample for a period of only 2h. The reason for comparing the efficiency of the harvesting method using continuous (from the start of the experiment) or short term (2h) exposure was to determine whether or not the period of exposure had a significant effect on the number of algae harvested from sediment.

The tray was placed at the base of a tall (27cm) open-topped box covered with four layers of cotton muslin to diffuse the light and produce even illumination. The sediment was continuously illuminated by two fluorescent strip lights positioned 50cm above the trays. Algal numbers were estimated using the standard method of enumeration (3.3.1).

2.4.3 Results

The optimum algal harvest occurred at 10:00h and was un-affected by the period of exposure of the polythene treatments (Fig. 4). After 10:00h the number of algae harvested decreased rapidly to a mid-day low, followed by a steady increase in density.

2.4.4 Discussion

The results indicate that the precise time at which the substrates are positioned on the sediment is not critical. In addition the period (minimum 2h) which the harvesting substrate is exposed to the algae appears to be relatively unimportant. Because of these results the overnight period of exposure of the harvesting substrates (under conditions of standard illumination) can be approximate. This had important practical implications as the time of arrival of samples in the laboratory varied. None the less the period of extraction adopted throughout this study (see 3.2.2) was maintained within +/- 2h of the standard 12h period.

The timing of the peak in algal abundance (Fig. 4) coincides with the expected period of optimum density of diatoms (found on the surface of fresh water sediments) that is attributable to their vertical migration rhythms (Round and Eaton 1966). Eaton and Moss (1966), however, recorded an optimum in algal numbers an hour earlier at 9:00h. The decrease in numbers from 10:00 to mid-day is comparable to the net downward migration of algae demonstrated after midday by Eaton and Moss (1966). These

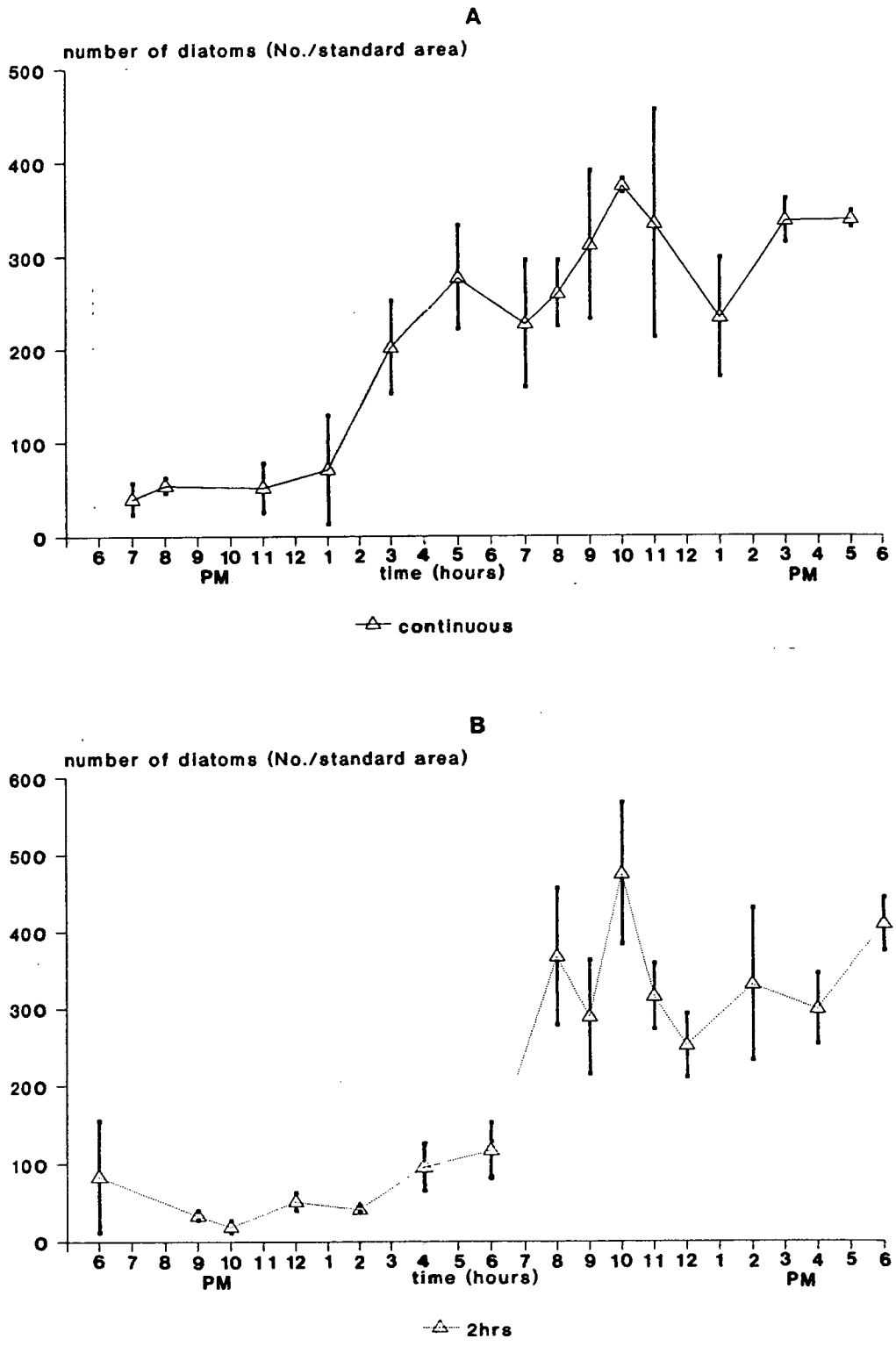


Fig. 4. Variation of epipelic diatom numbers extracted from sediment, over a 24hr period, using two methods: A: substrates positioned on sediment at 5pm so that harvesting continued over night (continuous), and B: substrates positioned on sediment 2hrs prior to removal. (bars indicate standard error).

results represent the net effect of homogenising the sediment combined with any persistent migratory behaviour. The pattern of emergence of algae on the sediment surface in the laboratory does not necessarily reflect the natural migration of epipelon in nature.

CHAPTER 3

STANDARD METHODS

3.1 SAMPLING THE SEDIMENT - STANDARD METHODS

Sampling of the subtidal sediment was carried out by hand using nine replicate sediment core samplers of 4.4cm diameter (described in 2.2.1.2). All samples were collected at random, by a pair of divers, by converting randomly produced numbers into the number of effective fin strokes (approximate distance) taken between samples.

Because of the extra complications associated with sampling underwater using diving, a detailed description of the procedures are provided. A major requirement of the core sampling method was to collect a precise area of sediment without disturbing the surface layer of epipelic diatoms (Jones, 1971) which was sometimes flocculant. This was dependent on the careful and practised technique of the sampler and required a slow movement of the hands. The direction of the sampling was dependent on the state of tide, always working into the prevailing current so that disturbed sediment drifted away from the sample area. Fin and body movements were minimized in order to reduce the disturbance of the sample area. The core was positioned carefully in the sediment, a hole was dug alongside (with the fingers), and the lid inserted and pushed across to seal the chamber. The core was removed with the lid held in position and hermetic sealing of the core sample was then secured by the removal of shell or stone fragments from the lid seal. Cores were flooded with sea-water prior to the survey dive and retained in replicate groups within sealed (flooded) polythene bags. The bags of cores were most effectively retained within closeable string bags attached to the diver by a quick-release clip. Cores were passed to the sampler, by an assistant, as they were required. The samples were retained by the sampler in a closeable string bag; replicate samples from different stations were therefore clearly and permanently marked so as to be distinguishable both underwater and in the laboratory. In addition to the nine replicate core

samples, a spare was collected in case of damage or loss of one of the sample units. To insulate from extremes of temperature samples were transported to the laboratory in an upright position within a closed polystyrene box. The samples were kept in the dark (approximately 5h) in order to eliminate migration of algae due to phototaxis and hence maintain some degree of homogeneity of algae within the sample.

The nine replicate sample units (sediment) were then combined, in groups of three, into settling chambers (see Fig. 5), homogenised, and treated according to the standard method described in the following section.

3.2 EXTRACTING THE ALGAE - STANDARD METHODS

Diatoms were isolated from the damp sediment by placing pieces of polythene, glass and lens cleaning tissue on the surface (Fig. 5); algae were then allowed to adhere to these following phototactic movement.

Care was taken during the extraction procedures to avoid cross-contamination from different algal associations, through careless splashing or transfer of sediment material. Apparatus and microscope slides were clearly and unambiguously labelled to avoid samples, sub-samples and preparations being confused.

3.2.1 The settling/extraction chamber

The settling chamber (Fig.5) was equivalent in volume to three core samples, and utilised the large perspex core samplers (see 2.2.1.1). The core was inverted and modified by the addition of a 7mm hole drilled in its base and sealed with a removable, rubber subaseal (No. 9, William Freeman & Co. Ltd, Staincross, South Yorkshire S76 8DH). At the bottom of the chamber a single layer of lens cleaning tissue (No. 105, Whatman International Ltd, Maidstone, England), was held in position by a tightly fitting circle of (500 um aperture) mesh (Lockertex.

P.O.Box 161, Warrington, Cheshire WA1 2SU). The chamber was seated on an open petri-dish.

3.2.2 Extraction

The sample units, on arrival at the laboratory, were transferred in groups of three (the grouped units will henceforth be referred to as a "sample") to a settling/extraction chamber. The chamber was then temporarily sealed with a petri-dish (90mm diameter) and vigorously shaken to homogenise the sediment. Samples were allowed to settle in the light for 3 hours. Supernatant was then removed using a vacuum pump, care being taken to avoid the re-suspension of the deposited material on the sediment's surface. The moist sediment was covered with a single layer of lens cleaning tissue (see 2.3.2.4.3) and the following substrate's were placed on top of the tissue-covered sediment in order to harvest the epipelic diatoms (Fig. 5):

Glass cover slips (22mm x 22mm; Chance Propper Ltd. Smethwick, Warley, England) harvest epipelic algae which were then oven-cleaned and used for the taxonomic identification of algae and in the assessment of epipelic community structure.

Polythene (22mm x 22mm) harvested algae used in the assessment of epipelic diatom abundance.

Lens cleaning tissue (double layer 30mm x 60mm) collected epipelic diatoms for the spectrophotometric measurement of pigment

concentration, providing an estimate of biomass. This is based on the lens tissue method of Eaton and Moss (1966).

The bung was then removed from the base of the chamber in order to allow excess interstitial water (approx. 10ml) to drain, overnight, from the sediment. The tissue layer at the base of the chamber filtered the interstitial water and retained algal cells within the sample (see 3.6.2.3). The settling chambers were then covered with the lids of petri-dishes and illuminated overnight (approx. 12h). Samples were illuminated by two 2ft. fluorescent strip lights (Thorn, 20W natural) positioned parallel to each other (2cm apart) and 50cm above the settling chambers. Light was diffused, to produce even illumination, by a double layer of cotton muslin and samples were distributed randomly beneath the light source. The harvesting substrates were removed with forceps, at 10.00h (see 2.4) the following day, and treated as follows:

3.2.2.1 Analysis of epipelic community structure.

The **glass cover slip** was placed, algae uppermost, onto the mouth of a small glass vial and allowed to dry at room temperature for 30 mins. 1ml of distiled water was then carefully transferred on to surface of the cover slip and the meniscus allowed to stand, undisturbed, for 10 minutes. The water was found by experimental trial to extract the sea salts (which would reduce the quality of the preparation) without a significant loss of diatoms from the glass (data not shown). The water was removed by tilting the cover slip with forceps and pouring the liquid on to the end portion of a glass microscope slide. This was then dried in an oven (100 ^{o}C) until the water had evaporated. The microscope slide and cover slip were then heated in a furnace at 540 ^{o}C for 20 mins, to clean the diatom frustules by the combustion all organic

material. The cover slip was allowed to cool and then mounted on the clean end of the microscope slide using Naphrax (a high refractive index diatom mountant in toluene). Assessment of the mounted algae, and the small number of cells displaced by the desalination procedure, enabled the taxonomic identification of the epipelic algal sample. Section 3.3.2 describes the method used for the estimation of epipelic community structure by utilising this, and the acid-cleaned preparations.

3.2.2.2 Analysis of epipelic abundance.

Polythene was mounted, algae uppermost, between a microscope slide and a glass cover slip. A drop of preservative (40% aqueous glycerol solution, with Lugol's Iodine or glutaraldehyde) was placed above and below the polythene square (Fig. 5) to improve both the optical quality of the preparation and to preserve the algae for future reference. For prolonged preservation the preparation was surrounded by petroleum jelly, extruded through a hypodermic needle. See section 3.3.1 for the method of counting the extracted algae.

3.2.2.3 Analysis of epipelic biomass (Pigment analysis)

The double layer of lens tissue was placed on a piece of filter paper (GF/A glass microfibre paper, Whatman International Ltd.) and dried in a desiccator, in the dark, for 3 h. The lens tissue and filter paper were then placed in a centrifuge tube to which was added 0.3 g of finely powdered anhydrous magnesium carbonate (light weight or "Levis" grade) to prevent degradation of the pigments during the extraction process. 15ml of 90% aqueous acetone (AnalaR) solution was then added to the tube, which was sealed with a lid and shaken vigorously to suspend the powder. The pigment was then extracted according to the method described by Strickland and Parsons (1972) with only minor procedural changes: The extinction of the supernatant liquid was measured spectrophotometrically (SP8-100 spectro-photometer, Pye

Unicam Ltd. Cambridge, England) in a 1cm path-length glass cuvette, against a cell containing 90% acetone. Measurement was to the nearest 0.001 unit, at: 665, 510 and 480nm. The extinction values were adjusted against the reading made at 750nm (turbidity blank) according to the correction factors described by Strickland and Parsons (1972). The extract was then decanted back into the centrifuge tube, to which was added 10 drops of 10% hydrochloric acid in order to convert the extracted pigments to their degradation products. The extract was left in the dark for 10 mins after which the degradation was halted by the addition of a small amount of magnesium carbonate. The extract was then centrifuged, transferred to a cuvette and the extinction values re-measured. The chlorophyll-a content was calculated according to the equations described in section 3.3.3.

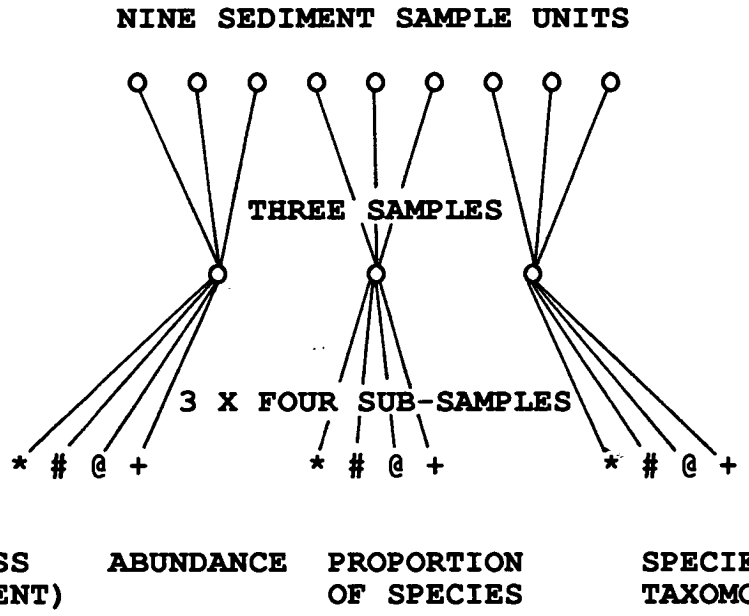
3.2.2.4 Acid-cleaned algae, for taxonomic identification

Following the removal of the harvesting substrates the bung was replaced in the settling/extraction chamber and the interstitial fluid, within the petri-dish, was poured on to the sediment surface. This returned algal cells to the sample that were lost with the interstitial fluid. The sediment rapidly absorbed this liquid; the sample was then covered by a single layer of lens cleaning tissue, and the chamber covered by the lid of the petri-dish. The remaining epipelic algae were then extracted from the sediment over a 24 h period under conditions of continuous illumination. The tissue was removed (not the tissue "screen") and the harvested algae from the three samples were then combined and acid-cleaned by boiling in nitric acid (fuming, AnalaR). The acid destroyed the tissue fibres and other organic matter, leaving only cleaned diatom valves and sand particles, picked up by the lens tissue. The valves were then washed free of acid by a succession of centrifugations and re-suspensions in distiled water until litmus paper showed the liquid to be neutral. The suspension was then transferred to a glass

cover slip and allowed to evaporate at room temperature. The preparation sometimes required dilution with water to reduce diatom cell density in the final preparation. Glass cover slips were mounted on microscope slides in Naphrax. This technique has been used in the quantitative analysis of epipelon from deep sea sediments (Round, 1971). Section 3.3.2 describes the method used for the estimation of epipelic community structure by utilising this, and the oven cleaned preparations.

3.3 ENUMERATION OF THE SAMPLE OF EPIPELIC ALGAE- STANDARD METHODS

The following flow chart summarises the sampling procedure. Nine sediment **sample units** were grouped into three **samples**. Three sets of **sub-samples** (lens tissue "*", polythene "#" and glass "@") were then harvested from the sediment.



These were used to estimate biomass, abundance and the proportion of the epipelic algal species. Lens tissue "+" was then used to provide a qualitative sub-sample of the epipelic algae to assist in the taxonomic identification of species and add to the species list.

The large number of algal cells that were harvested by the polythene and glass substrates (2.4×10^4 to 2.2×10^5 cells *per* substrate area [$484mm^2$]) precluded the counting and identification of all the cells. It was therefore necessary to take randomly selected **secondary sub-samples** (see below) from each of the glass and polythene substrates. The method of random selection was statistically accurate as the pattern of algal dispersion on the surface of the substrates was found to be random, conforming to a Poisson series (see 2.3.2.2.2).

3.3.1 Estimation of epipelic abundance

The number of cells that contained chloroplasts was counted along three randomly chosen transects (400 x mag.) of each of the three "polythene" sub-samples. Each transect was 22mm long, defined by a graticule of parallel glass fibres, 200*um* apart (Fig. 5). The graticule was constructed according to the method described by Lund *et al* (1958). This resulted in a total secondary sub-sample area of $39.6mm^2$. Only algae with 50% or more of their cell within the graticule boundary were counted. Dividing cells were recorded as one individual, and cells of fragmented or complete colonies were counted individually. The numerical bias that may result from counting individual cells of a colony was considered to be insignificant, as colonial species were rare within the epipelon of Loch Goil.

The nine sets of cell counts were converted to an estimated figure of the epipelic algal abundance ($No.m^{-2}$) and a standard error of the mean (n=9) calculated (see 3.6.4).

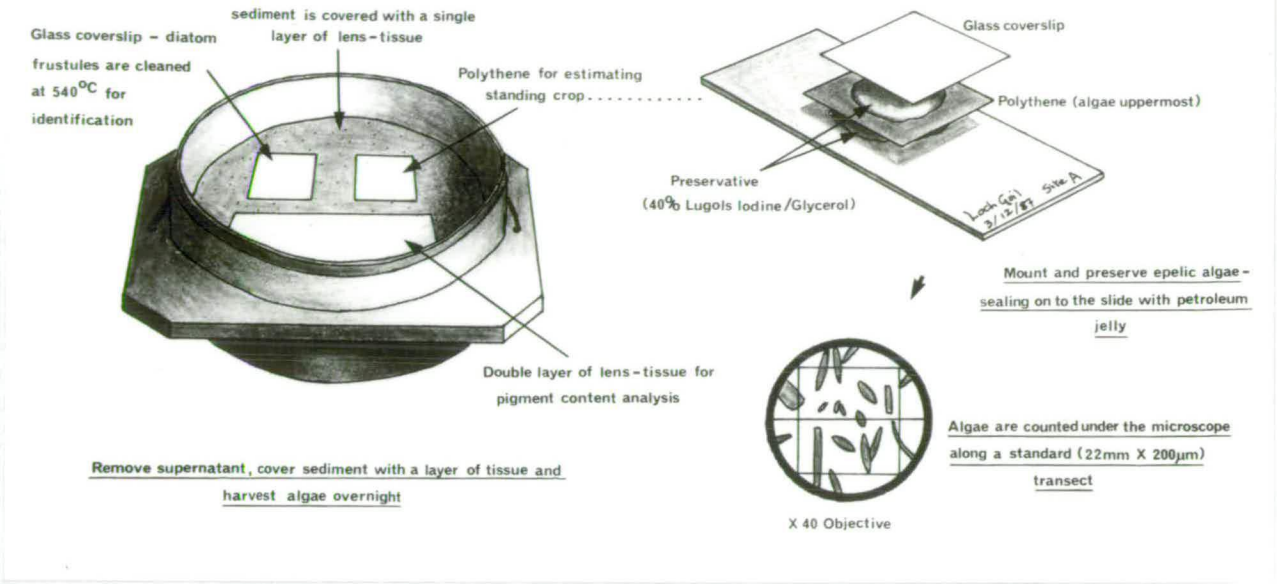


Fig. 5. A summary of the method and apparatus used to extract epipelic algae from sediment; and the procedure for mounting and enumerating the harvested cells. Three of the nine "sample units" collected at each station were combined into this chamber and the motile algae extracted, through a screen of tissue, using a number of substrates. Glass cover slips were used to harvest algae for taxonomic identification, where as the number of algae adhering to polythene was used to estimate algal abundance. Pigment analysis of the algae harvested by the double layer of lens tissue provided an estimate of epipelic biomass.

3.3.2 Estimation of epipelic community structure

3.3.2.1 Proportion of dominant algal species

The number of individuals of each species were counted within randomly chosen fields of view (x 400 mag.) along five random transects (22mm x 200um) of the three glass cover slips. Counting continued to a total cell count of approx. 500. The proportion of these predominant species was expressed as a percentage.

3.3.2.2 Total number of species

The entire surfaces of the three glass substrates were then examined (x200 and x400 mag.) for rare species that had not been encountered by the random search. A search was also made of the algal cells displaced by the desalination procedure (3.2.2.1). 100 random fields of view (x400 mag.) were then examined for rare species on each of two acid-cleaned preparations. The entire surface of the acid-cleaned preparation was then examined at low power (x30 mag.) for additional, large species of diatom.

Rare species were recorded as "present" ("*" in the tabulated community data) and contributed to the total number of species recorded from each population sample. However, these rare species were not included in the calculation of the proportions of taxa within the sample communities.

The comparison of the epipelic community structure from different sample stations is achieved both graphically and by the tabulation of the sample community data. The number of species recorded in each sample community provides a crude indication of algal diversity at each station.

3.3.3 Estimation of epipelic biomass; the measurement of pigment concentration.

The spectrophotometric equation of Lorenzen (1967) was used for calculating chlorophyll-a content, which included a correction for any phaeo-pigment present in the extracts. All values are given in mg chlorophyll-a m^{-2}, or in mg phaeopigment m^{-2}, according to the equations:

$$\text{chl-a.} = \frac{A \times K\ (E664_o - E664_a) \times v}{V_f \times l}$$

or

$$\text{phae.} = \frac{A \times K\ (R \times E664_o - E664_a) \times v}{V_f \times l}$$

where A (A=11.4) and K are constants as defined by Lorenzen (as an improvement to the original constant, the value of K was modified to K=1.76, E. J. Cox, personal communication), v is the volume of acetone (ml), E665 is the extinction at 665nm before ($_o$) and after ($_a$) acidification, V_f surface area of the sample (cm^2) and l the optical path length cuvette (cm). A correction was made for turbidity at 750nm. In some of my investigations an approximation of carotenoid concentration was made using the equation given in Parsons and Strickland, (1963), converted to calculate pigment concentration per unit area. The content is expressed as millispecific pigment units of carotenoids (MSPU m^{-2}). The limitations of both these methods are discussed in section 3.6.3.1.

3.4 PHYSICAL PARAMETERS - STANDARD METHODS

Changes in the epipelic standing crop may be governed by a complex interplay of environmental condition in a manner analogous to the phytoplankton found in aquatic and marine habitats. Measurement of the principal physical parameters of sea water (light intensity, temperature, oxygen, salinity, sediment particle size) was therefore an important aspect in the description of the abiotic marine environment of Loch Goil and in the understanding of their effects on the epipelic community.

3.4.1 Vertical light extinction coefficient

Two methods were adopted for the determination of the light attenuation with depth. Because of difficulties with the availability of the light meter equipment (equipment ordered before the beginning of my Ph.D did not become available for over a year after I had begun my studies) the secchi disc method was routinely employed in assessing

the underwater light regime. An additional consideration was that the selenium photocell method could only be used from a boat. The secchi disc method, however, required the use of diving equipment only, and was therefore utilised in the seasonal monitoring programme.

3.4.1.1 Secchi disc method

A round white disc of 10cm diameter was lowered from a hand reel by a floating diver until it disappeared from view. I adapted this method from the standard 50cm diameter secchi disc that is lowered vertically from a stationary survey vessel. According to Siedler (1972) the correlation between the depth of visibility (s) measured in this manner and the vertical extinction coefficient (b) is:

$$b.s = 0.95$$

The reduction in the size of the disk was to facilitate its use by a diver. I consider that the observation of the secchi disc, from directly beneath the water surface (using a face mask) is a considerable improvement on the standard method, although my method is restricted to diving or small boat operations. The method described by Siedler (1972) relies on the assessment of the depth of disappearance (of the disk) from above the water. In practice this is dependent on the aspect of the boat in relation to the sun and is particularly effected by the stability of the water's surface (pers. obs.).

3.4.1.2 Photocell method

A more accurate, objective measure of the rate of light attenuation in the water column involved the use of selenium photocells. A portable monitoring unit was used (Benham and George, 1981) capable of measuring water temperature, light attenuation and depth of operation. The current from the probes is conveyed to the surface via a multicore cable and the data displayed instantaneously on a liquid crystal digital panel meter. The light sensors are two selenium photocells: one lowered photocell is

directed upwards and the irradiance it measures compared automatically with a reference photocell on the surface. With the sub-surface cell just below the surface the variable gain is initially adjusted to read 100% of the surface cell reading. When the sub-surface cell is lowered further through the water column the reading displayed show the percentage of light falling on the submerged cell compared with the surface cell. The system can respond to a range of light intensities (c. 0.5-1500 $uE\ m^{-2}\ s^{-1}$) at ratios of up to 1/100 or 1%.

3.4.2 Depth (pressure)

The depth sensor, attached to the sub-surface photocell, is a sealed diaphragm pressure transducer with a full scale range of 50m (Type 4-308, Bell and Howell Ltd, Basingstoke, Hants). The transducer is temperature-compensated and provides a linear output with an accuracy of +/- 1% of the full range (Benham and George, 1981).

3.4.3 Temperature

Samples of interstitial water were collected at the sediment/water interface using a polypropylene syringe (50ml; Becton Dickinson, Cowley, Oxford OX4 3LY). The temperature (and oxygen and salinity concentration) of the water samples were measured within a few minutes of their collection. Temperature was measured, to an accuracy of +/- 0.6 ^{o}C, using two precision thermistors built into the dissolved oxygen probe (see below).

Vertical temperature profiles were measured using a thermolinear thermistor network (Type YSI 44202, Yellow Springs Inc., U.S.A. supplied by Sasco, Crawley, Sussex). The thermistor is mounted on the sub-surface photocell of the portable probe system (Benham and George, 1981) and gives a direct temperature reading (0.00 - 19.99 ^{o}C) to an accuracy of +/- 0.1 ^{o}C.

3.4.4 Dissolved oxygen

The concentration of dissolved oxygen (DO) in sea water was measured using a portable, YSI Model 57 Dissolved Oxygen Meter (Yellow Springs Instrument Co. Yellow Springs, Ohio 45387). The probe uses a Clark-type membrane covered polarographic sensing element and indicates DO in parts per million over a range of 0-20 ppm to an accuracy of +/- 1% or 0.1ppm. The probe is automatically temperature compensated and manually salinity compensated.

3.4.5 Salinity

The salinity of sea water was determined by conductivity measurement using a platinum-in-glass electrode (Phillips Type PW 9510) and portable conductivity meter (Phillips PW 9504/00). Since the specific electrical conductivity of sea-water is dependent on temperature and pressure (a rise of Δ L = 0.01 mS/cm for an increase in temperature of Δ T = 0.01 ^{o}C and pressure of Δ p = 20 decibars) it was necessary to take an accurate temperature measurement simultaneously with the conductivity measurement. The probe was initially calibrated for a range of sea-water temperatures (0-20 ^{o}C) to facilitate the transformation of conductivity measurement (Holmes) into salinity readings (ppt). Because the maximum depth at which sea water sample were collected did not exceed 40m, the pressure difference with the surface did not exceed 4 bars. The error in the determination of salinity would therefore be minute and well within the accuracy of the conductivity probe (+/- 1%).

3.4.6 Sediment particle size analysis

Textural analysis was carried out on the combined sediment samples (see 3.4.6), following the extraction of epipelic algae and the removal of the tissue screens from the sediment surface.

Two approx. 30g portions of the sediment were oven dried at 110 ^{o}C and weighed to 0.01g before being immersed separately in dispersant (aqueous sodium hexametaphosphate). The sediment was periodically agitated for 1h before being washed through a 2mm and 63um mesh. The <63um and >63um fraction of one of the portions was dried at 55 ^{o}C and the proportion of silt (<63um) and sand (>63um) was determined by weighing. Particle size analysis was carried out on the second portion of sediment. The silt fraction (<63um) was ultrasonicated for 2 mins. and the particle size distribution was determined using a Coulter counter (LS-100). The sand fraction (>63um) was dried at 55 ^{o}C and sieved while being agitated by a shaker for 20 mins. The fraction of sediment retained on each sieve was weighed to 0.01g.

The size frequency and cumulative frequency distribution of the grain size distribution data was plotted. Values derived from these plots were used to characterize the data by calculating the mode, median, mean and sorting statistic (McManus, 1988). The proportion of silt (mud) to sand was also used as an indication of the sedimentary environment.

3.5. STATISTICAL ANALYSIS

The following section briefly describes the methods of statistical analyses applied to the different data collected during my research. References are provided for more detailed explanation of both the methods and their limitations.

3.5.1 Multivariate analyses

The following multivariate statistical analyses are used to determine the level of similarity between epipelic commmunity data. These analysis were performed using the Forth River Purification Board's VAX computer incorporating an "Interactive Biological Statistical Package" (FRPB's IBSP) :

(1) DENDROGRAM - Classification or cluster analyses computes a similarity matrix using group average sorting according to Bray-Curtis (continuous data) coefficients. This method was used to group the sample communities and provide quantitative estimates of dissimilarity between communities (FRPB's IBSP).

(2) TWINSPAN (Two-way Indicator Species Analysis) is a development of an ordination technique that forms an ordered two-way table of species and samples. This arrangement throws salient features of the data into sharp relief by grouping ecologically like species with like, and ecologically like samples with like (Hill, 1979 [a]).

(3) DECORANA - is a computer program that makes ordinations of species in a set of samples by the method of detrended correspondence analyses (DCA). DCA is development of the simpler methods of ordination known as reciprocal averaging or correspondence analysis (Hill, 1979 [b]).

3.5.2 Tests of significance and correlation

(1) Product-moment correlation coefficient (r) is used to measure the degree of correlation between two variables (eg. epipelic abundance and chlorophyll-a).

Use of this coefficient requires a bivariate normal distribution and as this condition is never fulfilled by counts of a species, transformation (log) of the data is necessary (Elliott, 1971). The method of calculation is as follows:

$$r = \frac{\sum_{i=1}^{n} (x_i - \bar{x})(y_i - \bar{y})}{\left\{ \sum_{i=1}^{n} (x_i - \bar{x})^2 \sum_{i=1}^{n} (y_i - \bar{y})^2 \right\}^{\frac{1}{2}}}$$

where x is one variable with mean $\bar{x}$, and y is the other variable with mean $\bar{y}$. There is a value of y for each x, and the total number of pairs =n. The correlation is either positive or negative and ranges from -1 to +1 indicating the degree of association (Neave, 1979; Elliott, 1971).

(2) One-way analysis of variance (ANOVA) was used for the analysis of experimental data (see 5.2.2.4). ANOVA tests for significant difference between the levels of epipelic algae in diferent experimental treatments compared with the residual variation recorded between sample replicates. A null hypothesis (H_o) is tested which is the hypothesis of "no difference between levels of algae in different experimental treatments". Log-transformation of the data is necessary to comply with the assumptions of this technique (Elliott, 1971).

(3) Chi-squared analysis was used to measure significant differences between levels of epipelic algae recorded at different sample sites. The analysis tests a null hypothesis (H_o) which is the hypothesis of no association between the classification schemes by rows and by columns in a contingency table. The expected frequency in any cell is (its rows subtotal) x (its columns subtotal) - (total number of observations), and the number of degrees of freedom v is (number of rows -1) x (number of columns -1). Large X^2 values are significant and critical regions are of the form X^2 > tabulated value (Neave, 1979).

(2) SPEARMAN RANK - correlation analysis is a significance test used to analyse relationships between scores on "DECORANA" axis (derived from species abundance data) with epipelic biomass data and environmental variable values. Non-linearity cannot be too extreme for this method as it assumes that the relationships are monotonic, ascending or descending with no maxima or minima (Green, 1979; FRPB's IBSP).

3.5.3 Spatial pattern analysis

Analysis of the spatial pattern of the epipelon was achieved from data (numbers of epipelic algae) collected from fixed intervals along a straight transect. Data were analysed using a method of **Paired-Quadrat Variance** ([PQV] Ludwig and Reynolds, 1988) whereby variances are

calculated for all possible paired sample units at a given spacing (1, 2, 3...). Data analysis was carried out on an EPSON PC AX computer using the BASIC program "PQV.BAS" supplied with Ludwig and Reynolds, 1988. The variances obtained from the analysis were plotted against spacing. Interpretation of the plots was based on the following criteria:

If the epipelon is **dispersed randomly** over the study area the variance will randomly fluctuate with the different spacing. **Uniform distribution** results in low variance that does not fluctuate with different spacing, whereas **clumped dispersion** causes peaks in variance at a spacing equivalent to the radius of the clump mean area. The average distance from centre to centre of the clumps will be twice this spacing. The size and definition of the peaks indicate the form of the clumps: high and sharp peaks suggests distinct clumps with areas of low algal density between patches; whereas, low peaks that span more than one spacing suggests a pattern of poorly defined clumps.

The PQV method of calculating variance at a spacing of 1 (space between sample units) is as follows:

$$VAR(X)1 = [1/(N-1)]\{[\tfrac{1}{2}(x_1-x_2)^2]+[\tfrac{1}{2}(x_2-x_3)^2]+\ldots. +[\tfrac{1}{2}(x_{N-1}-x_N)^2]\}$$

3.6. LIMITATIONS AND DISCUSSION OF METHODS

There were inherent errors in the measurement of the epipelic algal population. These occurred through inefficiency at the (1) sampling, (2) harvesting and (3) secondary sub-sampling stages of the procedure, and included error resulting from counting bias.

3.6.1 Field sampling

The collection of epipelic algae using core samplers has been commonly utilised for intertidal studies (Aleem,

1950; Hopkins, 1963; Round and Palmer, 1966). Round (1971) and Round and Hickman (1971) reviewed the sampling apparatus that can be used for collecting epipelic algae from shallow and deep water assemblages which include the use of mechanical grabs and coring devices. Little information was available in the literature on methods of sampling sublittoral sediments by hand, using diving (Jones, 1971). The possibility of extracting the epipelon directly from the sediment is discussed by Eaton and Moss (1966). Although they emphasise the difficulty of using artificial substrates for sampling motile epipelic algae underwater owing to substrates floating off and algae being lost as the fabric of substrate is removed.

In reference to my standard core sampling method, the efficiency of the core at collecting sediment without losing the living epipelon has not been quantified. However, care was taken to avoid disturbing the flocculant, surface layer of sediment and I consider that the loss of diatoms from the population sample, at this stage in the procedure, was minimal.

3.6.1.1 Number and size of sample

The methods for defining the optimum number and size of sample units, have been developed primarily for benthic invertebrate studies (Elliott, 1971; Longhurst, 1959) and are both time- and labour-intensive. The sampling characteristics were therefore investigated for only a limited area of Loch Goil (9m depth) and not the entire survey area (6-40m depth). An assumption was therefore made that the dispersion pattern of the epipelic algae was similarly contagious at all stations within the study area.

In addition to the time constraint, the size and number of cores that could be effectively and safely be carried by a pair of divers, was a limiting factor. An increase in replication, over the nine sample units, would reduce the variance (of the estimated mean algal abundance) and improve the recruitment of algal species

(Elliott, 1971). A compromise had to be made, however, between statistical accuracy and logistical considerations.

3.6.1.2 Sediment depth of the sample

A basic assumption during sampling of the epipelon of Loch Goil was that algal cells existed only within the upper 2cm of sediment. The epipelic population is unlikely to be underestimated, however, as algal cells are normally restricted to the upper 5mm or less of sediment (Estrada *et al*, 1974; Williams, 1962; Perkins, 1963). Plante *et al* (1986), however, found that the depth of epipelic penetration within the sediment of a shallow (30-60cm) sandy shore was dependent on the degree of sediment mixing. Noticeable amounts of chlorophyll-a were recorded in sediment depths of 18cm following windy conditions, but in calm conditions the greatest concentration of living cells occurred in the surface layers (0-2cm). Within Loch Goil, concentration of algal cells in the surface sediment is likely as the degree of water turbulence (sediment mixing) was minimal at the depths (6-40m) sampled. The fine, silty nature of the sediments of Loch Goil (eg. 9m depth: mode = 4 phi [62um]) would also limit the penetration of algae within the sediment, compared with the situation in course unimodal sandy sediments.

3.6.1.3 Frequency of sampling

The frequency of the sampling within the distribution studies of this project were limited in number, due to time and logistical constraints. It is important to realise, therefore, that all data represent an instantaneous measurement of the community only at that particular place in time and space. Although data may be presented as a continuum (eg. Fig. 30), important changes in the epipelic population may have occurred between sample points.

3.6.2 Extraction

3.6.2.1 Screening the algal preparation

The use of a tissue screen during the extraction procedure meant that only the motile, epipelic community was sampled. Population estimates, therefore, excluded epipsammic, planktonic (sedimented) or dead algal cells as these were not actively motile, and were normally retained within the sediment by the tissue. The occurrence of the occasional planktonic species (see Appendix. 1) within the qualitative tissue sub-samples is attributed to a process of extraction by capillarity. The method of screening the algal preparation from particulate matter, was found to reduce the number of algae harvested (by 24%) with no significant effect on the composition of algal species, that were harvested (see Fig. 2).

3.6.2.2 Illumination of the sediment during extraction

The illumination of the samples during the extraction phase was designed to guarantee standard lighting conditions and to evoke a phototaxic response. The use of constant lighting conditions was used in preference to a natural illumination cycle because of the unavailability of a growth room to control lighting periodicity. I found it impractical to control lighting conditions (for a large number of samples) on a laboratory bench. This is contrary to the recommendations of Round and Eaton (1966) who state that:

"constant illumination can stimulate an increase in diatom division rates and result in elevated counts. The sediment should not, therefore, be artificially illuminated at night, during their extraction, but experience a natural day/night cycle".

However, modification of algal numbers within the samples was minimised by harvesting the epipelic algae within approx. 20 h. of the sample's collection.

The standard method of illumination contributed to the maintenance of a relatively constant air temperature (18-25 ^{o}C) surrounding the sediment during the extraction

phase. It is not known whether the 7°C temperature variation had an affect on the efficiency of algal extraction or the growth rate of cells within the sediment during the 20h period. The effect of temperature variation on the efficacy of diatom extraction does not appear to be documented in the literature. It was considered impractical to create a standard temperature environment for the sediment because of the vibration that is associated with a water-bath apparatus or a growth cabinet. Vibration affects the fluidity of the mud and would probably have interfered with the adhesion of diatoms to the extraction substrates.

3.6.2.3 Loss of algae within supernatant and interstitial water

Draining of interstitial sea water from the sediment overnight was found to be necessary in order to ensure a standard degree of sediment moisture. Without this drainage, the settling of the sediment caused pooling on the sample surface, reducing the area of algal contact with the glass and polythene substrates. It's important to note that the degree of moisture was found to be dependent on the sediment particle size and could introduce an element of bias when comparing samples of different sediment type.

The period (3h) allowed for algae to settle within the extraction chamber (following the addition of the sample units) was determined by the logistics of travelling, sampling and extracting within the period of a day.

Analysis of the method showed there to be a loss of algae (relative to the number of algae harvested) within the supernatant (6.97%) and interstitial fluid (0.4%). The analysis did not, however, account for algal cells trapped within the sediment. Estimation of this fraction was not possible due to the problems associated with counting algae obscured by particulate matter. The loss of algal cells within the supernatant and interstitial water may

result in the **algal abundance being underestimated.** However, this loss was assumed to be standard for all samples. The loss of algal species within the interstitial water was minimised by returning the fluid to the sample prior to extracting algae for taxonomic identification. Algae within the supernatant water could not be returned to the sample, as suspended mineral particles would reduce the quality of the acid-cleaned preparation.

3.6.3 Enumeration

3.6.3.1 Pigment analysis

There is a large amount of literature concerned with the methods of extraction of algal pigments for the determination of an estimate of biomass. Richards and Thompson (1952) offered the first trichometric equations based on extinction coefficients formulated by MacKinney (1941). Subsequently, Parsons and Strickland (1963) and Smith and Benitez (1955) improved methods of determination of chlorophylls in plant extracts. Lorenzen (1967), Yentsch (1965) and Yentsch and Menzel (1963) provided the first methods for measuring phaeophytin levels. Subsequently methods of pigment analysis have been refined (Parsons and Strickland (1972) and established methods, which mainly utilise acetone as an extraction medium, have been adapted to use aqueous methanol (Marker, 1972) and ethanol (Marker and Jinks, 1982).

During my investigation of the epipeon of Loch Goil I utilised the method of Parsons and Strickland and the equations of Lorenzen (1967); an established methodology recommended to me by Dr. E. J. Cox (pers. comm.).

The equation of Lorenzen (1967) corrects for the concentration of phaeopigments (phaeophorbide and phaeophytin). However, chlorophyllide is indistinguishable by this method. Consequently the data reported in this project represents epipelic chlorophyll-a plus chlorophyllide. Moreover, Barrett and Jeffrey (1964) and Jeffrey (1974) have found chlorophyllide as a major

degradative product of chlorophyll-a in marine muds and sea water. The concentration of chlorophyllide would, however, be proportional to chlorophyll-a content so would not interfere with the use of chlorophyll-a as a measure of epipelic biomass. Lorenzen and Jeffrey (1980) estimated the errors involved in measurement of chlorophyll-a (<1% error) and carotenoids. The measure of carotenoid concentration can only be approximated since they are a mixture of several compounds with different extinction coefficients and are therefore expressed as millispecific pigment units of carotenoids (MSPU) (Parsons and Strickland, 1963).

In using chlorophyll-a as an estimate of epipelic biomass I am assuming that it forms a constant relationship to the total organic (dry) weight of the epipelon. De Heur (1974) found that the chlorophyll-a of epipelic algae to be an average of 3% of the organic carbon whereas de Jonge (1980) showed that the ratio of chlorophyll-a to organic carbon varied. He found that chlorophyll-a determination may lead to an underestimation of biomass in summer and an overetimation during the remaining seasons (mean 2.5%, range 1-4%). Similarly, Foy (1987) points out that:

> "The disadvantage of using chlorophyll-a is that it is a constant proportion of neither biomass nor cell volume. In addition to intraspecific differences, chlorophyll-a content can be altered, for example, by irradiance, day length, temperature or nutrient status"

Care should therefore be used in the interpretation of seasonal differences in epipelic chlorophyll-a in Loch Goil. This is the principal reason why my standard method for assessing epipelic standing crop incorporates both an estimate of biomass (chlorophyll-a) and an estimate of cell numbers based on a standard count.

3.6.3.2 Analysis of species proportions

The method of enumerating the proportion (%) of the predominant species is statistically valid, as the distribution pattern of algae on the harvesting substrate

was shown to be random, corresponding to a Poisson series (see 2.3.2.2.2).

Analysis of all the community data derived during this project revealed that an average of 59% (range: 49-68%) of the total number of species recorded from each population sample were identified from the proportional count of 500 cells. "Predominant species" in this project are species that constitute 2% or more of the epipelic population.

The criticism remains that it is not known precisely what proportion of the species present within the population are sampled by the methods adopted in this project. In order to define this, the addition of new species with increased number of sampling units must be examined experimentally. It is assumed, in this project, that the abundant species are adequately sampled before the asymptote of the recruitment curve is reached. That these are sampled adequately is indicated by the low value of standard error (SE=22.9% of $\bar{x}$) associated with the estimated abundance of epipelon using the standard sampling methods (see 2.2.1.2).

The principal disadvantage of my standard method of estimating species proportions is that the method is selective, collecting only those species which are both motile and positively phototactic. However, preliminary observations of the flora made by direct observation within the sediment showed the epipelon to be almost entirely of motile, pennate diatoms. Although any method of harvesting algae can never be completely thorough, I am confident that the flora identified during my investigations of Loch Goil are representative of the natural community present within the sediment at the time of sampling.

The main problem associated with comparing floras from different samples, is that large changes in the abundance of a few dominant species may mask small scale fluctuations in the population abundance of rarer species.

This should be considered when interpreting the results displayed in the tables or illustrated graphically.

3.6.3.3 Estimation of algal abundance

In order to express abundance per unit area (m^{-2}) from a secondary sub-sample ($39.6mm^2$), the mean (n = 9) algal counts were multiplied up to the standard (No. m^{-2}). This appears to be valid in relation to the aims of this project, which are concerned with the comparison of epipelic communities and not with the definition of absolute abundance. The efficiency of the standard methods of extraction and enumeration are unknown. In order to evaluate efficiency comparison would have to be made with levels within the sediment by means of direct counts (Eaton and Moss, 1966).

The abundance of individual species was derived from the product of the estimated abundance of epipelic algae and the proportion of that species within the population sample. These figures serve as an estimate of abundance in nature and should be interpreted with caution as the precise **number of species per m^2 is not known**. The precision of this estimate would be Improved by an increase in the replication of sample units.

3.6.4 Sampling variance

The standard error (SE) of the estimated population mean was calculated for all sample estimates. SE is related to sample variance (s^2) by the formula (Elliott, 1971):

$$SE = \bar{x} +/- \frac{s}{\sqrt{n}}$$

The SE, calculated from **secondary sub-samples** (n=9, see 3.3), incorporates two sources of variation:

(1) variation between the three sets of pooled sample units. This reflected the variation that resulted from spatial heterogeneity of the algae on the surface of the

sea bed. The pooling of sample units meant that it was not possible to calculate the variance associated with the entire (9 units) sample set.

(2) variation within the homogenised sediment of each "sample" pool, including error resulting from counting bias. The variation resulting from the heterogeneity within the "sample" pool would have been minimal as analysis showed the algal distribution pattern to be in agreement with a Poisson series.

The concentrations of algal pigments (chlorophyll-a and carotenoids) were not derived from an arithmetic mean of replicate measurements and therefore did not include a measure of variance. Analysis of the method showed that the concentration of algal pigments within each sub-sample was often insufficient to produce an accurate measurement of extinction when measured independently. The magnitude of the extinction values were, therefore, increased by combining the replicate tissue substrates before extracting the algae. The sensitivity of the method could not be controlled, by increasing the area of the tissue extract or decreasing the volume of the acetone (90%), due to procedural constraints.

CHAPTER 4

THE EPIPELON

4.1 SPATIAL HETEROGENEITY (PATCHINESS) OF THE EPIPELON ON THE BOTTOM OF LOCH GOIL

4.1.1 Introduction

Patches of brown, discoloured sand observed in the shallows (5-11m depth) of Loch Goil indicated that the distribution of the epipelon may be heterogeneous. Mounds and tracks were also a notable feature of the sea bed and appeared to be a consequence of bioturbation from the activities of invertebrates (Polychaetes, Gastropods, Echinoderms and decapod Crustacea).

The aims of the investigation reported below were to describe the dispersion pattern of the epipelon (random or contagious) and investigate the effect of small scale topographic features on the pattern of algal distribution in nature. An understanding of the dispersion pattern was critical in the development of the standard sampling strategy to be used in the seasonal and depth distribution studies of this project. Interpretation of the relationship between topographic and algal distribution generated hypotheses regarding the precise causal factors that determine epipelic distribution.

4.1.2 Methods

4.1.2.1 Sampling method

Sediment topography and epipelic distribution were investigated at different distribution scales using systematic samples at intervals of 25cm and 10cm. Sampling was carried out, in June 1990, along a 16.75m long transect, laid parallel to the shore, at a depth of 9m. The end of the transect was selected at random and its length defined by a weighted tape measure. A tightly sprung line, was positioned around 20cm above the sediment, parallel to, but 30cm away from the transect line. The line was made horizontal, using a spirit level, and supported by weighted retort stands positioned half

way along, and at either end of the transect. Care was taken to avoid disturbance of the sediment within the defined experimental area and a period of 24 h was allowed to pass before sampling. The delay in sampling minimised the effect of any disturbance by allowing affected areas to be re-colonised by epipelon and come into equilibrium with the surrounding sediment. The experimental area was marked with a buoy to facilitate its relocation the following day.

68 sediment cores (standard 15.2 cm^2) were positioned at an intervals of 25cm along the entire (16.75m) length of the transect. Starting at a randomly selected distance (5m) along the transect, 21 samples were positioned at intervals of 10cm over a distance of 2m. In order to simplify the interpretation of data and detect smaller-scale heterogeneity, a number of extra sediment cores were positioned up to 5cm either side of the sampling interval to coincide with the summit of a mound or a depression within the sediment. The total number of cores used was limited by the amount of sampling equipment that could be safely carried by two divers.

After all the cores were systematically positioned in the sediment, the variations of topography were recorded by measuring the vertical distance from the centre of each core to the levelled line. Sediment samples were then retained in the usual way. The identity of each core sample and the corresponding topographic data was recorded in situ, on a water proof slate.

Ideally analysis of spatial pattern would be carried out on data from a series of contiguous samples. However, this was not possible (using the hand-coring method) due to small scale (approx. 5cm) lateral disturbance of the sediment's surface caused during the insertion of the core.

4.1.2.2 Laboratory methods

Epipelic algae were harvested from each sample unit using a modification of the standard extraction method

(3.1) to allow for the smaller volume of sediment. The sediment within each unit was homogenised and allowed to settle in the light for 3h. Supernatant was then removed using a vacuum pump; care was taken to avoid the re-suspension of the deposited material on the sediment's surface. The moist sediment was covered with a single layer of lens cleaning tissue and the epipelic algae harvested overnight, using polythene (22mm x 11mm) and a double layer of lens tissue (30mm x 15mm) placed on top of the tissue layer. Excess water was removed from the surface of the sample, periodically (3h) during the extraction period, to maintain a standard degree of sediment moisture.

Epipelic algal pigment was extracted using a modification of the standard method (see 3.2.2.3) to allow for the smaller volume of sediment involved (5ml 90% acetone, 0.1mg chl-a. Mg_2Co_3, 3 drops H_2NO_3). The concentration of chlorophyll-a was calculated to provide an indication of epipelic biomass. Algal cells adhering to the polythene substrate were counted (see 3.2.2.2) to provide an estimate of epipelic algal abundance.

4.1.2.3 Statistical analyses

The product-moment correlation coefficient (r) was used to measure the degree of correlation between epipelic algal abundance and biomass (chlorophyll-a), and the estimated (detrended) topography of the sea bed. The height and depth of the sedimentary features were estimated by relating the measured topography to a detrended profile of the sea-bed. This was calculated from a moving average (length 1.5m) along the length of the transect (Fig. 8.). The data were analysed after transformation of the series (log: abundance and chlorophyll-a; log+1: carotenoids).

Analysis of the spatial pattern of the epipelon was achieved using a method of **Paired-Quadrat Variance** ([PQV] see section 3.5.3). PQV analysis was carried out on the small and large scale sample data (intervals of 10cm and

25cm). The variances obtained from the analyses were plotted against spacing, and assessed for scale and pattern of dispersion (random, uniform or clumped).

The pattern of epipelic distribution was also compared with the sediment topography by graphical means.

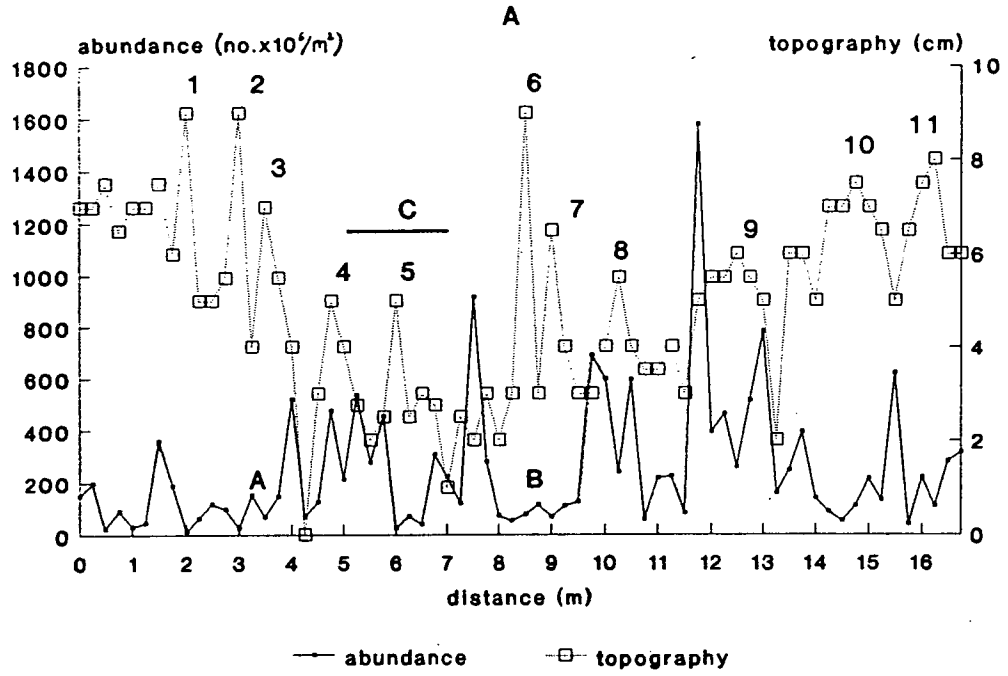
4.1.3 Results

4.1.3.1 Large scale features

Fig. 6. shows the pattern of epipelic abundance and biomass (chlorophyll-a) along the transect (16.75m) using large scale (25cm) sampling intervals. The spatial change in chlorophyll-a concentration was approximately proportional to the change in estimated algal abundance.

Inspection of Fig. 6. show there to be eleven notable topographic features along the length of the transect. Numbers 1-11 represent the summits of sediment mounds; these occurred at irregular intervals of 0.5m to 2.5m apart and ranged in height from 3cm-7cm. The mounds were found (by collection and identification) to be associated with the burrows of either the strawberry worm *Eupolymnia nebulosa* (Fig. 12) or the lugworm *Arenicola marina* (Fig. 13). There is a clear association between micro-topography and epipelic abundance and biomass at most of the sampling points. With the exception of mound "4", relatively low densities of algae occurred on the summits of the mounds. The greatest epipelic abundance and biomass occurred either within the hollows between successive peaks (between mounds: 1/2, 2/3, 5/6, 10/11) or on the sides of the mounds (between mounds: 3/4, 8/9, 9/10). The greatest difference in epipelic Abundance and biomass, between the furrow and summit of a mound, occurred on mound "9" (summit: 1575.46×10^6 cells m^{-2}, [5.13 mg chl-a.m^{-2}]; furrow: 258.86×10^6 cells m^{-2} [2.45 mg chl-a.m^{-2}]).

PQV analysis of the large scale pattern of distribution (Fig. 7) shows the epipelon to be clumped. Variance peaks at spacing of 4 and 6 intervals (25cm)



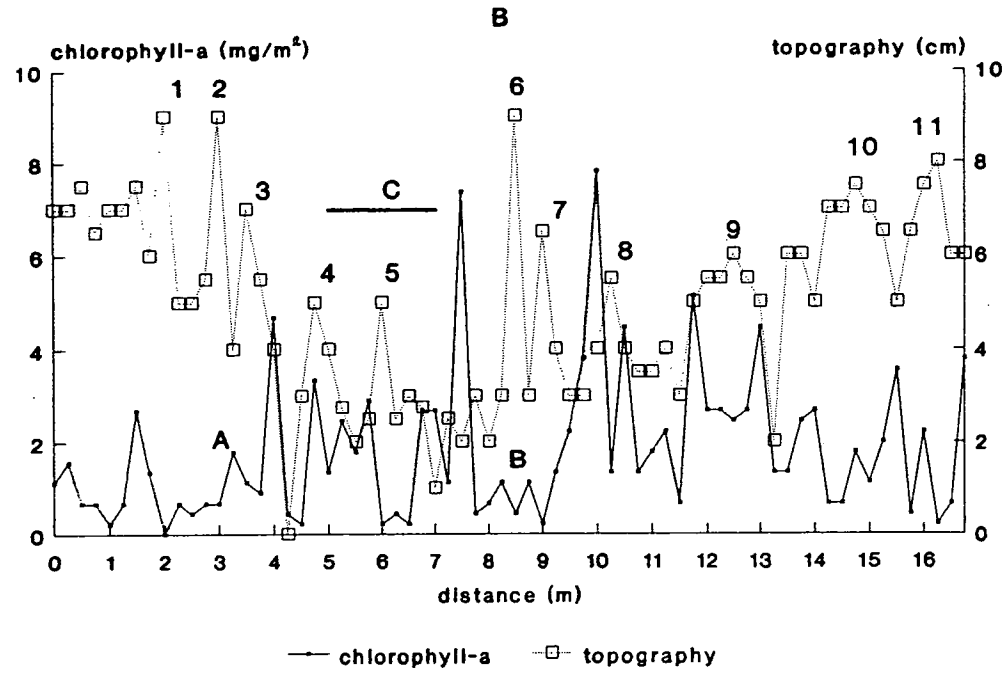


Fig. 6. Spatial distribution pattern of estimated abundance (A) and biomass (B) [chlorophyll-a] in relation to sedimentary features. Sample points were taken at intervals of 25cm along a 16.75m transect of the sea bed (9m depth). 1- 11 indicate the main sediment mounds; A, B indicate the apparent suppression of algal density between mounds situated in close (50cm) proximity. C represents the area of transect investigated in more detail, using a 10cm sampling interval.

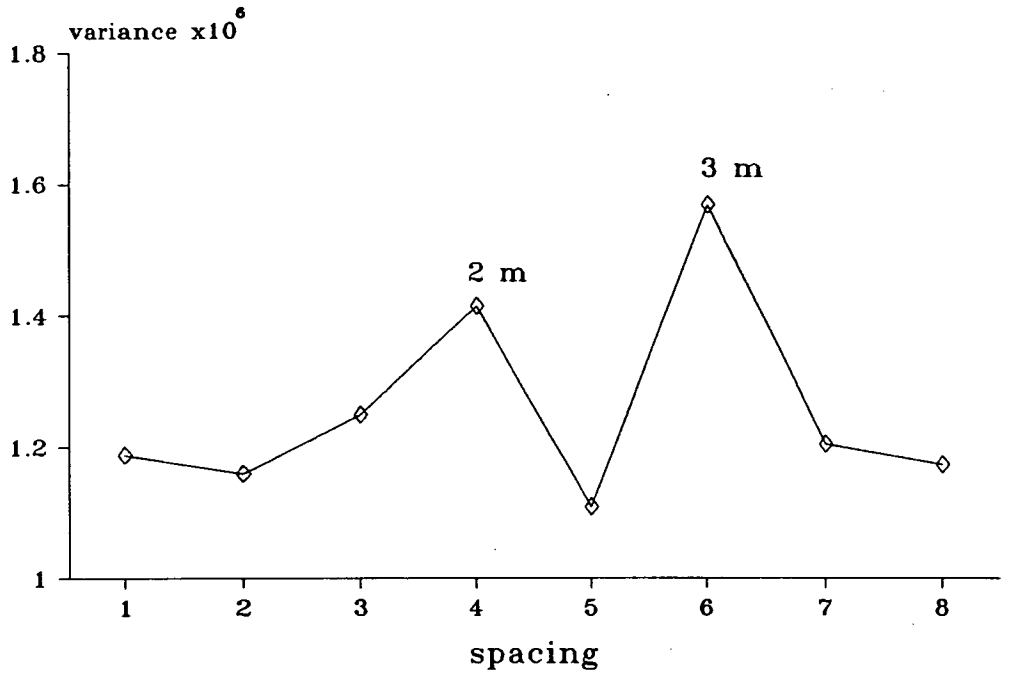


Fig. 7. Spatial pattern analysis of the dispersion of epipelon in Loch Goil using a paired-quadrat variance method (PQV). Spacing of the core-samples is at (large-scale) intervals of 25 cm over a distance of 16.75 m. The variance peaks at a spacing equivalent to the radius of the clump; indicating an average distance of 2 m and 3 m between areas of high epipelic abundance.

indicates well defined patches, separated (on the average) by a gap of 2 and 3m.

Correlation analysis showed there to be only a slight negative correlation between estimated height above the detrended topography and epipelic abundance (r=-0.075), chlorophyll-a (r=-0.135) and carotenoids (r=-0.140). The reasons for this are seen in the plot of epipelic biomass (chlorophyll-a) and height/depth of the sedimentary features (Fig. 9). There is a greater incidence of high epipelic abundance and biomass along the sides of mounds. Also the occurrence of high epipelic abundance and biomass on the summit of mound "4" (474.09 x 10^6 cellsm^{-2} [3.34 mg chl-a.m^{-2}]) and relatively low (66.59 x 10^6 cellsm^{-2} [0.45 mg chl-a.m^{-2}]) levels within the furrow between mounds "3" / "4" and "9" / "10".

4.1.3.2 Small scale features

The smaller sampling intervals (10cm) revealed a similar relationship between small scale topographic features and the abundance and biomass of epipelon. In particular the peaks in epipelic density that were recorded 20cm apart, between mounds "x/y" (235 x 10^6 cellsm^{-2} [1.56 mg chl-a.m^{-2}]) and "y / z" (239.55 x 10^6 cellsm^{-2} [1.78 mg chl-a.m^{-2}]) correspond to small (2cm deep) hollows within the sediment. These small scale features were inadequately recorded by the coarser sampling interval (C in Fig.6.).

PQV analysis of the small scale pattern of distribution (Fig. 11) shows the epipelon to be "clumped" but does not reveal a clearly defined pattern of separation between patches of high epipelic density. The shallow peak in variance at a spacing of 2 intervals (10cm) indicates that, on the average, patches are separated by gaps of 40cm.

Mound "x" provides a detailed study of the gradient of epipelic density along a feature that was also sampled by the large scale survey (mound 5 Fig. 6.). Compared with the summit (24.32 x 10^6 cellsm-2 [0.22 mg chl-a.m^{-2}]),

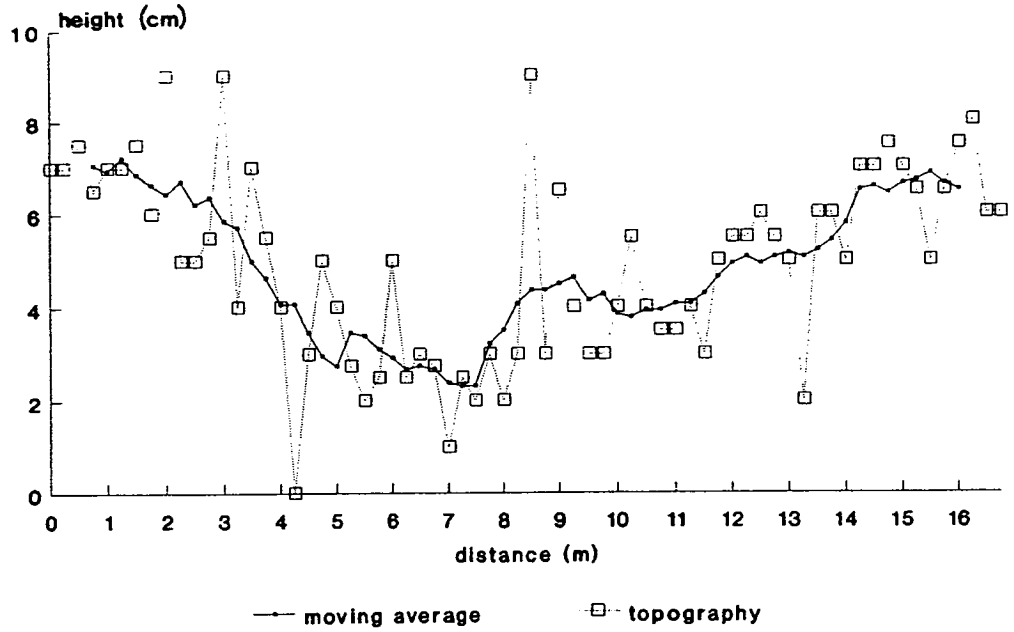


Fig. 8. The topography of the sea bed along the length of the transect. The moving average, with a length of 1.5 m, shows the detrended profile of the sediment and was used to estimate the height and depth of the sedimentary features.

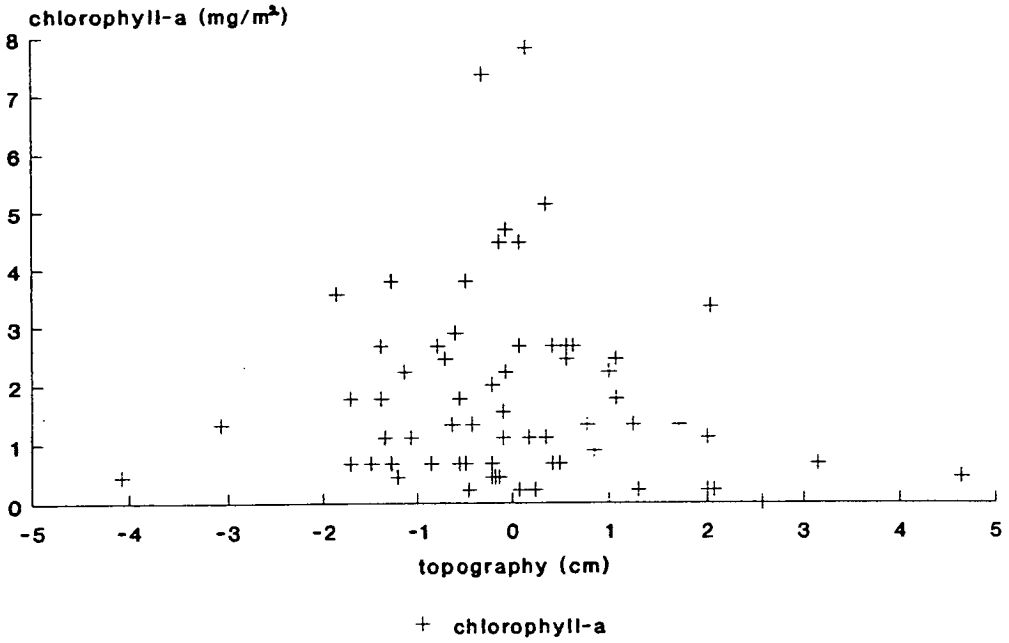


Fig. 9. Plot of epipelic biomass (chlorophyll-a) against the estimated height and depth of the sediment in relation to the sedimentary features recorded along the 16.75 m transect of the sea bed. Topography is calculated relative to the detrended profile of the sediment.

greater epipelic density occurred on both sides of the mound (550.23 x 10^6 cellsm-2 [4.24 mg chl-a.m^{-2}] and 140.23 x 10^6 cellsm-2 [1.12 mg chl-a.m^{-2}]) with another peak in algal density (235 x 10^6 cellsm-2 [1.56 mg chl-a.m^{-2}]) corresponding to the base that is shared with mound "y".

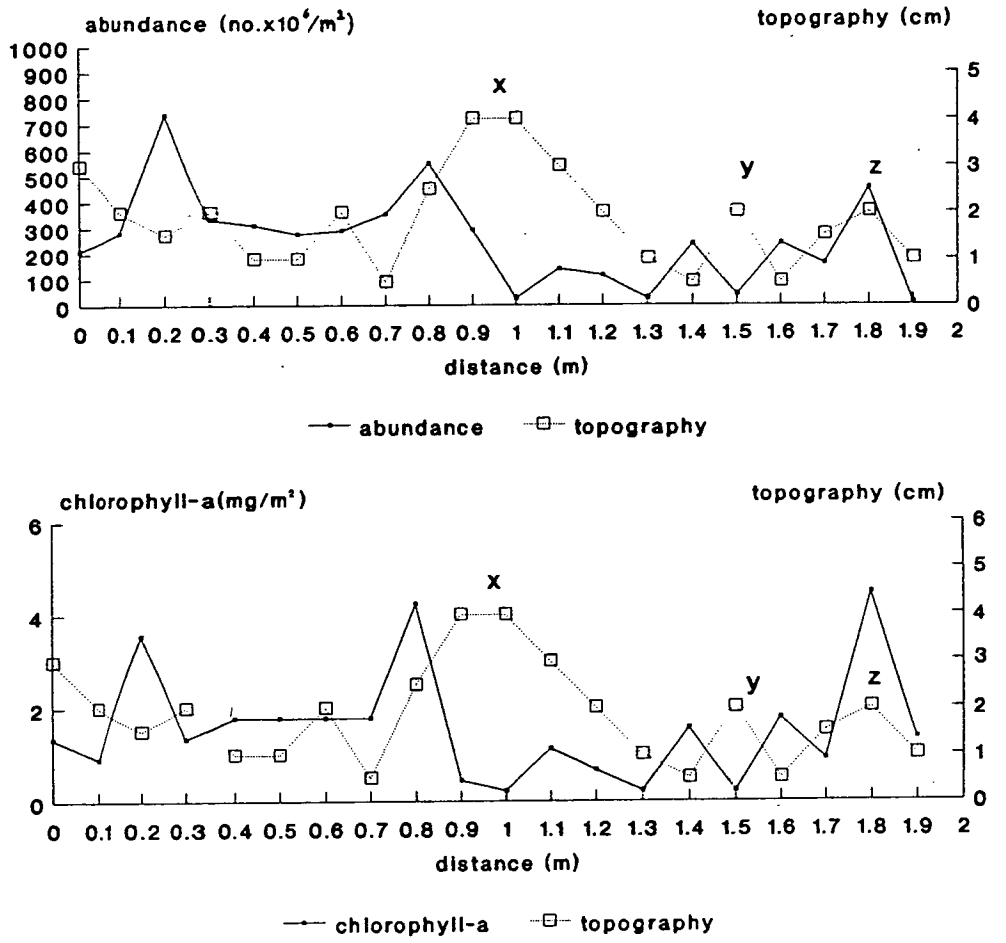


Fig. 10. Small scale (10cm sampling interval) distribution pattern of epipelic abundance (A) and biomass (B) [chlorophyll-a] in relation to sedimentary features along a 2m transect of the sea bed. "x,y,z" indicate three sedimentary features, discussed in the text.

The occurrence of a peak in algal density (451.36 x 10^6 cellsm-2 [4.46 mg chl-a.m^{-2}]) at the summit of mound "z" illustrates that the relationship between topography and algal distribution is not a simple one.

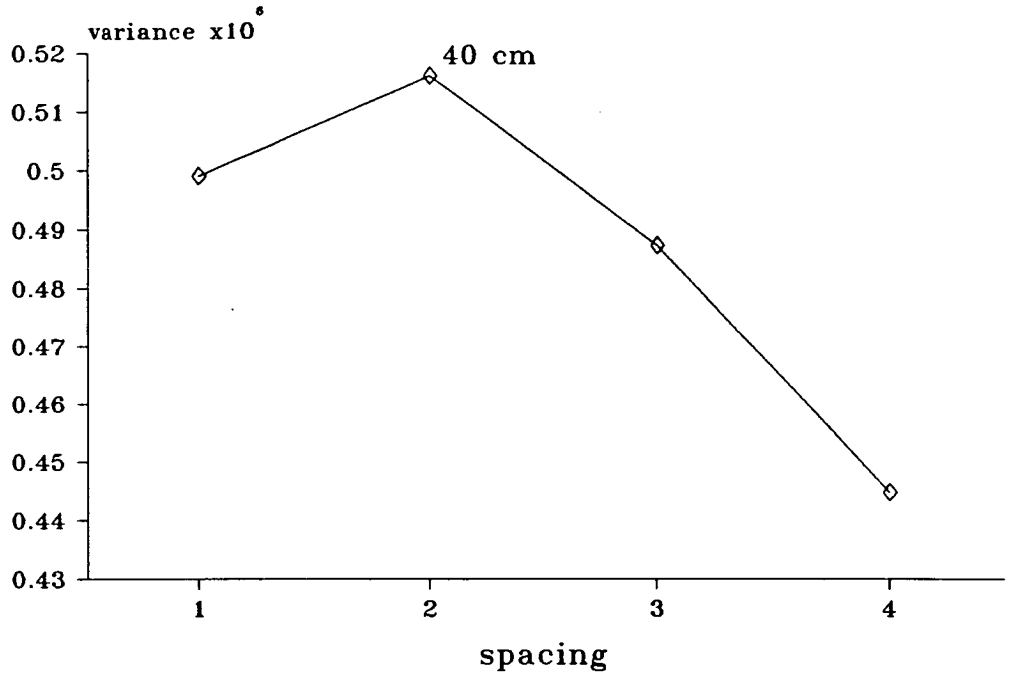


Fig. 11. Spatial pattern analysis of the dispersion of epipelon in Loch Goil using a paired-quadrat variance method (PQV). Spacing of the core-samples is at (small-scale) intervals of 10 cm over a distance of 2 m. The variance peaks at a spacing equivalent to the radius of the clump; indicating an average distance of 40 cm between areas of high epipelic abundance.

4.1.4 Discussion

A study of the data and the results of the PQV analysis show the epipelon to be clumped on the bed of Loch Goil. Analysis of the epipelon at periods of 10cm and 25cm show the pattern of clumping to be (on average) at intervals of 40cm, 2m and 3m. The large scale pattern of dispersion (2m and 3m) appears to be in response to the pattern of distribution of sedimentary mounds caused by the polychaetes *A. marina* and *E. nebulosa*, whereas the small scale pattern (40cm) reflects the dimension of the sedimentary features (mounds). The high densities of algae that occurred on the sides and bases of most of the mounds produced the concentric circles of discoloured sand that were seen to surround many of the larger mounds at this depth (9m). The PQV analysis showed there to be only a poorly defined pattern of dispersion at a small scale and can be attributed to small (<10cm) patches of high epipelic density associated with undulations in the bottom of the loch.

This study appears to be the first documentation of a relationship between the distribution of marine sub-tidal epipelon and sedimentary features. Previous investigations, however, have recorded a similar relationship in shallow intertidal marine sediments (Plante *et al*, 1986; Grant *et al*, 1986). The effect of erosion on tropical sub-tidal algal mats has been investigated (Neumann *et al*, 1970) and biogenic structures such as burrows have been attributed to the disruption of mucus binding of the sediment surface. Plante *et al* (1986) described the accumulation of algal biomass (chlorophyll-a) in the depressions of sand ripples in a shallow (30cm-60cm), sheltered, Mediterranean shore. Minimal microalgal biomass on the ridges of ripples was attributed to increased grain mobility, settlement of algal cells in the depressions and exposure during low tide. Grant *et al* (1986) found, from field and laboratory flume studies, that diatom films were patchy on a scale of centimetres, corresponding the structure of sand ripples. They found

that storms homogenised the distribution of chlorophyll-a compared to calm conditions when algal films had a patchy distribution on the sediment surface. High chlorophyll-a concentration was recorded on all surfaces of sand ripples, and was attributed to sediment transport involving processes of erosion, burial and exposure. Skjoldal (1982) suggested that thorough mixing of sand was the cause of the homogeneous distribution of chlorophyll-a recorded in the crests and troughs of intertidal ripples on a subtropical beach.

The factors (eg. erosion) supposed to cause algal patchiness on intertidal sediments are not necessarily analogous to the sub-tidal environment. The sedimentary features observed in Loch Goil (9m depth) appear to be formed by biogenic (bioturbation) rather than by tidal streams, wave movement or the other sedimentary processes that are associated with the intertidal region.

A number of possible explanation can be suggested for the pattern found in the shallow sub-tidal region of Loch Goil. The mounds that were associated with *A. marina* were caused by the deposition of ejested sediment, at one end of its U-shaped burrow, by the lugworms continual defecation cycle (Wells, 1950). The periodic deposition of sand particles would result in the burial of algal cells. This may inhibit colonisation of the upper region of the mound by epipelon and limit algal growth. The epipelon at the top of the mound may also be limited to species that can rapidly re-orientate themselves, following burial.

The physical characteristics of the sediment may have been modified either by its passage through the gut of *A. marina* (Rhoads, 1974) or through particle size selection by *E. nebulosa* (Gremare, 1988). Cadee (1976) found that sediment and detrital particles smaller than 300-400 um are preferentially ingested by *A. marina* causing courser particles (and organic matter) to be concentrated at the worms feeding depth. The distribution pattern of epipelic algae may be a response to small scale changes in the

sediment particle size along the profile of mounds caused by the defecation of fine sediment. De Wilde (1975) suggests that the funnel, which operates as a sediment trap at the feeding-end of the worm's burrow, provides a larger surface area for benthic microalgae which might result in a higher primary production. This would cause patchiness of the epipelon, with small (probably <10cm) dense patches of algae associated with each *A. marina* mound.

Mounds that were associated with *E. nebulosa* were readily identified by the presence of tentacles protruding from a small hole at the mound summit (see Fig. 12, A). The area of low algal density on the summit and upper slope of these mounds may be a result of tentacle activity, which according to Gremare (1988) harvest particulate matter from the sediment surface for either feeding, predominantly on benthic diatoms, or tube-building. The area of algal denudation surrounding the polychaete worm would be limited by the tentacle length (approx. 20cm). The touching of two adjacent feeding areas would account for the apparent suppression of algal abundance that occurred between mounds situated in close proximity (A, B in Fig. 6.).

The relationship between sediment elevation and algal density shows some variation since chance events (eg. disturbance by a fish or crabs) may disrupt the sediment and its associated epipelic community. The removal of surface sediment by other infaunal deposit feeders (including *A. marina*) or displacement by the trails and burrows of benthic invertebrates may further promote spatial patchiness of the epipelon.

This investigation has identified a contagious distribution of epipelic diatoms on the sediment of Loch Goil with zones of relatively high epipelic biomass on the sides of mounds and within the furrows of sub-tidal sedimentary features. The implication of this patchiness on the development of the standard sampling strategy was

to use small replicate sample units (cores). The close agreement between chlorophyll-a and epipelic numbers seen in Fig. 6 indicate that the methods of extracting and enumerating the epipelon from small volumes of sub-tidal sediment are effective at estimating natural levels of epipelic algae.

Further investigations were then carried out to identify the precise causal factors that determine the patchy distribution of epipelon on *E. nebulosa* mounds in nature (see 4.2).

4.2 DISTRIBUTION OF EPIPELIC ALGAE ALONG THE GRADIENT OF A STRAWBERRY WORM (Eupolymnia nebulosa) MOUND.

4.2.1 Introduction

The results of the investigation of spatial patchiness (see 4.1) suggest that a relationship exists between the sub-tidal sedimentary features and epipelic algal distributions in nature. Qualitative observations made in the shallow (6-11m) sub-tidal region of Loch Goil showed that most of the sedimentary features were formed by the polychaetes *Eupolymnia nebulosa* and *Arenicola marina*. The aim of this investigation was to determine the causal factors responsible for this relationship by more detailed examination of one of these types of sedimentary mound.

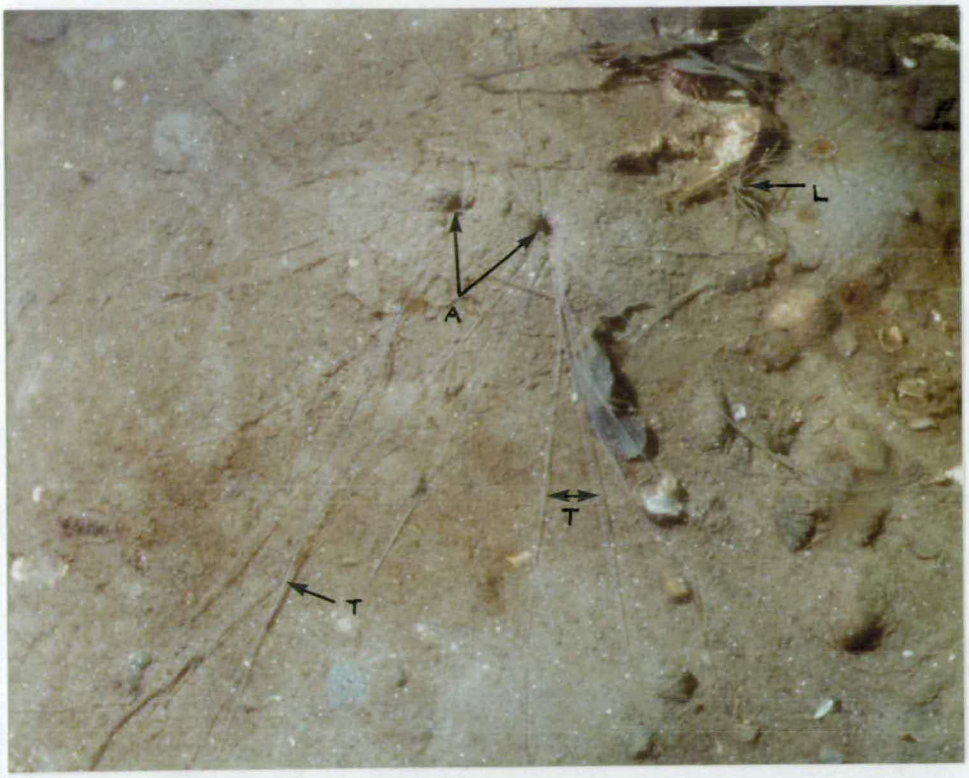
The hypothesis that "epipelic algal biomass is lost from sediment mounds, associated with *E. nebulosa*, by a process of grazing" was tested by examining the small-scale spatial variability of epipelic density and biomass along the profile of an *E. nebulosa* mound. The pattern of distribution was related to the feeding behaviour of the worm, and the contents of *E. nebulosa* guts were analysed. Selective grazing of particular epipelic algal species was investigated by examining the composition of species along the mound. The sediment of the mound was analysed to see if biogenic activity, by *E. nebulosa*, results in a gradient in particle size that can be related to the small-scale distribution pattern of the epipelon.

4.2.1.1 Eupolymnia nebulosa

E.nebulosa is a terebellid polychaete that lives within soft substrates (silt, sand, between boulders and sediment) from the shallow sublittoral to a depth of 500m (Holthe, 1977). Its distribution within the United Kingdom was, until recently, poorly documented with observations of its occurrence limited to Shetland and the Scottish east coast (Holthe, 1977). It has now been recorded around

Fig. 12. A: Protruding from the muddy sediment are the thread-like tentacles (T) of the strawberry worm *Eupolymnia nebulosa*. Radiating from a burrow (A), usually situated at the apex of a mound, the pink tentacles writhe over the sediment surface collecting particles of food, denuding epipelon from a circular area of sediment. The worm tube of the sand mason polychaete *Lanice conchilega*(L)protrudes about 5cm. The frayed end of the tube, together with the tentacles of the worm, trap particles of water-borne food which probably includes suspended epipelic algae.

B: A concentric band of discoloured sediment (C) surrounds the mound usually at a constant distance from the central burrow (A). The band corresponds to an area of high epipelic abundance. Tracks (B) of unknown origin often encircle the mounds.



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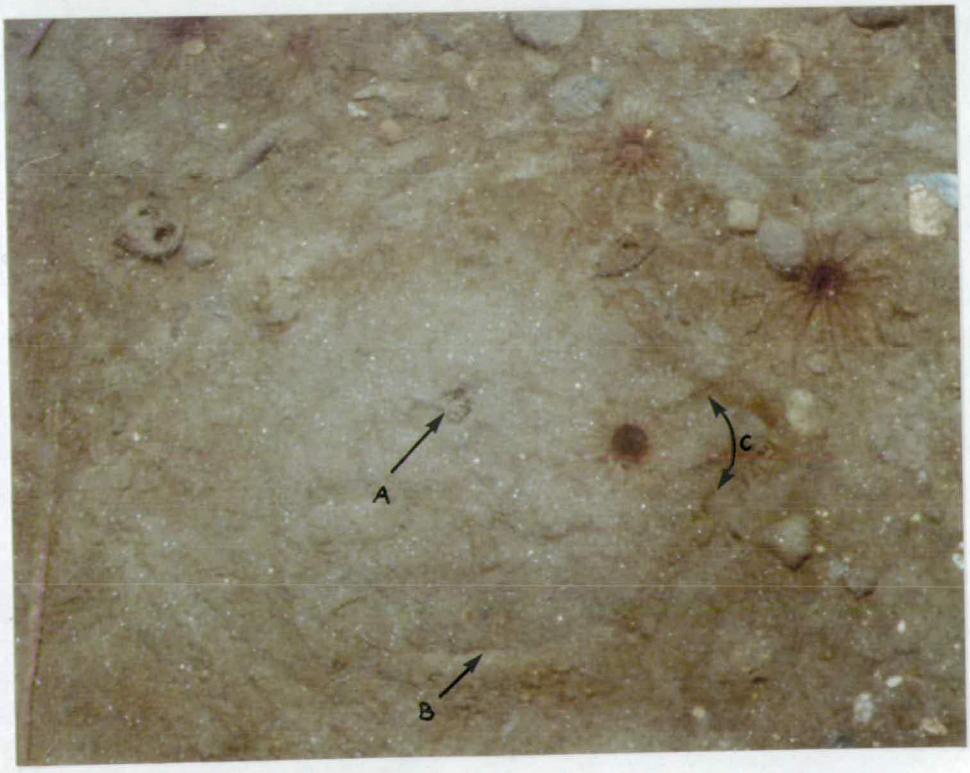
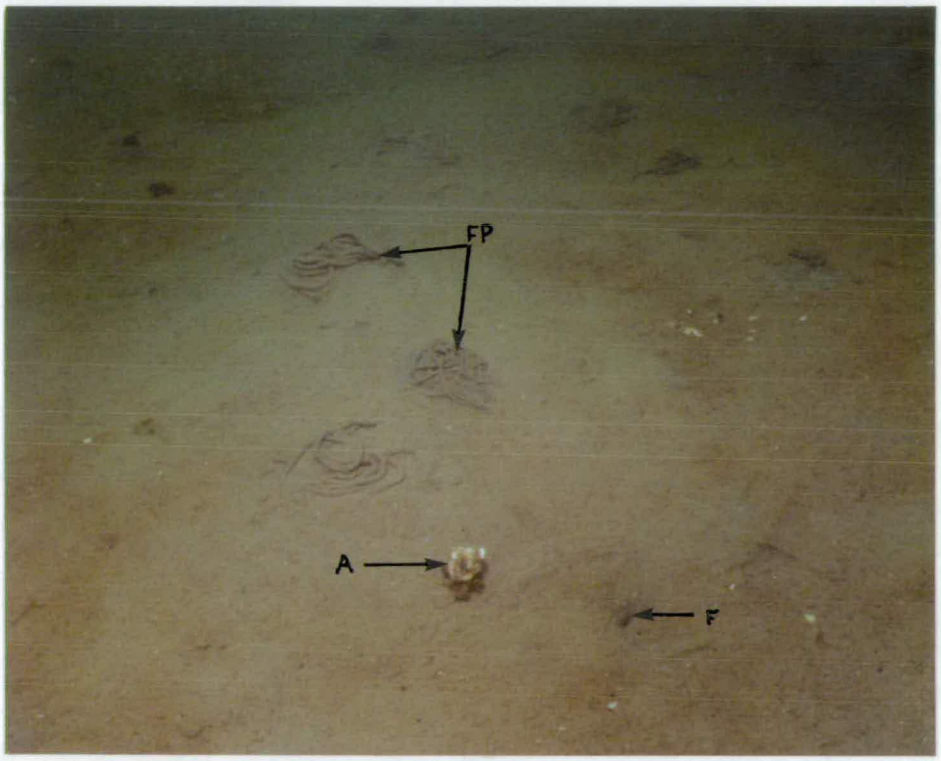


B

Fig. 13. The casts and depressions associated with the lugworm *Arenicola marina* are especially abundant in the shallow water (6m). The surface of the sea-bed appears "well-worked" by the feeding activity of the lugworm. Excavations of the sediment surface occur due to feeding depression (F), and the formation of mounds and faecal piles (FP) at the end of the U-shaped burrow in which it lives. Foraging by the common hermit crab *Pagurus bernhardus* (A) causes a network of tracks amongst the mounds and hollows.


FP
A
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most of Britain, north-west Europe, the Mediterranean, Red Sea, Arabian Gulf, Indian Ocean and Pacific (Hayward and Ryland, 1990). During a survey of sealochs in the northern Firth of Clyde (Holt and Davies, 1991) *E. nebulosa* was recorded within Loch Riddon, Gareloch and Loch Goil. Within Loch Goil my observations show that the strawberry worm population is a notable feature of the benthic invertebrate community over a wide range of depth (1-40m).

E. nebulosa is a tentaculate surface deposit-feeder (Fig. 12, A) which is mainly sessile, but capable of intermittent motility (Gremare, 1988; Fauchald and Jumars, 1979). According to Gremare (1988) the species is nocturnal in habit although I have observed tentacular activity throughout the day within the sediments of Loch Goil. The method of feeding by *E. nebulosa* has been described in detail by Gremare (1988). During periods of activity the extensile tentacles of *E. nebulosa*, as in other terebellids, collect particles from the sediment surface for either feeding or tube-building. Smaller particles are preferentially selected when it feeds (<60*um*) whereas particles greater than 2 mm in size (mainly of detrital origin) are selected for tube building (Gremare, 1988). The nutrition of *E. nebulosa* consists of detritus, small adult and larval invertebrates, and unicellular algae including diatoms (Fauchald and Jumars, 1979). According to Gremare (1988) food is predominantly of diatoms, with preferential ingestion of smaller (<15*um*) species; other micro-organisms such as foraminiferans and coccolithophores constitute the remainder of the diet. The bacterial fraction of the sediment may also serve as food for *E. nebulosa* (Taghon *et al*, 1978). Analysis of the gut contents of *E. nebulosa* from Loch Goil showed their diet to be of sediment particles containing predominantly epipelic diatoms (see 4.2.3.2.).

The mainly vertical burrow is 2 or 3 times the length of the worm, which can be up to 175 mm long (Holthe, 1977)

and is roughly U-shaped (Dales, 1955). Feeding and defaecation behavioural studies show that both processes occur at either ends of the burrow, as worms frequently reverse their direction within the burrow (Dales, 1955). According to Fauchald and Jumars (1979) there is conflicting evidence as to whether the tubes of most terebellids are blind-ended or open at both ends.

The effects of *E. nebulosa* on the substrate may be considerable. The tentacles of the population observed in Loch Goil appear to cover a substantial area of the sediment surface; densities of 15 worms m^{-2} were observed at 40m depth (see 5.1) where the sea bed appeared to be covered in a matrix of pink tentacles (Figs. 12 and 43, C). Terebellids are known to significantly modify sediment processes (Price and Thayer, 1983) and form mounds of sand (Fauchald and Jumars, 1979) but the relationship between *E.nebulosa* and epipelon has been ignored in such studies.

4.2.2 Methods

4.2.2.1 Sampling method

In June 1990 two mounds (A and B) were selected at random from the sea bed (9m depth) by divers. The maximum tentacle length of the worms were measured over a 5 min. period and the height of the mounds recorded. Care was taken to avoid any disturbance of the mounds or the surrounding sediment. The mounds were then photographed and surveyed using a method of stratified random sampling (Elliott, 1979). Replicate sediment cores (3x6.16cm^2) were randomly positioned at corresponding distances from the mound summit.

Mound A: 1, 4, 7, 11 and 15cm.
Mound B: 1, 5, 11, and 18cm.

Sediment samples (2cm deep) were then retained in the usual way and hermetically sealed by means of a screw cap. The identity of each core sample, in relation to its

sampling zone, was recorded *in situ* on a water proof slate.

4.2.2.1.1 Core sampler

The core samplers were made from polypropylene centrifuge tubes (28 mm internal diameter; Bibby, Stone, Staffordshire). The tubes were cut and then shortened (4.5cm long) by bonding the closed and threaded ends of the tube together, with heat. A number of small fishing weights (non-toxic shot) were attached to the side of the corer with autoclave tape to render the unit negatively buoyant in sea water. This prevented the units from floating off, if accidently dropped while sampling.

4.2.2.1.2 Settling / extraction chamber

The settling chamber was equivalent in volume to the core sampler, and utilised a 4cm section of a polypropylene centrifuge tube, sealed at one end by a screw cap. The lid, which formed the base of the chamber, had a 4mm drainage hole drilled in its centre, sealed with a removable plug of putty. At the bottom of the chamber a single layer of lens cleaning tissue was held in position by a tightly fitting circle of (500*um* aperture) mesh. The chamber was supported, on match sticks, above an open petri-dish.

4.2.2.2 Laboratory methods

The sample units, on arrival at the laboratory, were transferred to settling/extraction chambers, and treated according to the method described in section 3.2. Epipelic algae were harvested from the moist (tissue covered) sediment using: lens tissue (2 cm^2); a piece of glass cover slip (1 cm^2) and polythene (1 cm^2).

Epipelic algal pigment was extracted using a modification of the method described in section 3.2.2.3 (5 ml 90% acetone, 0.1 mg Mg_2CO_3, 3 drops H_2NO_3) and the concentration of chlorophyll-a and carotenoids calculated to provide an indication of epipelic biomass (see 3.3.3). Algal cells adhering to the polythene substrate were

counted to provide an estimate of epipelic algal abundance (see 3.3.1). An estimate was made of epipelic community structure using the method described in section 3.3.2. Because the counting and identification of epipelic algae is particularly time consuming, the analysis of algal community structure was carried out on only one (mound A) of the two mounds surveyed. Similarly, sediment particle size analysis was carried out only on the sediment from mound "A", using the combined samples of each zone (see 3.4.6 for method).

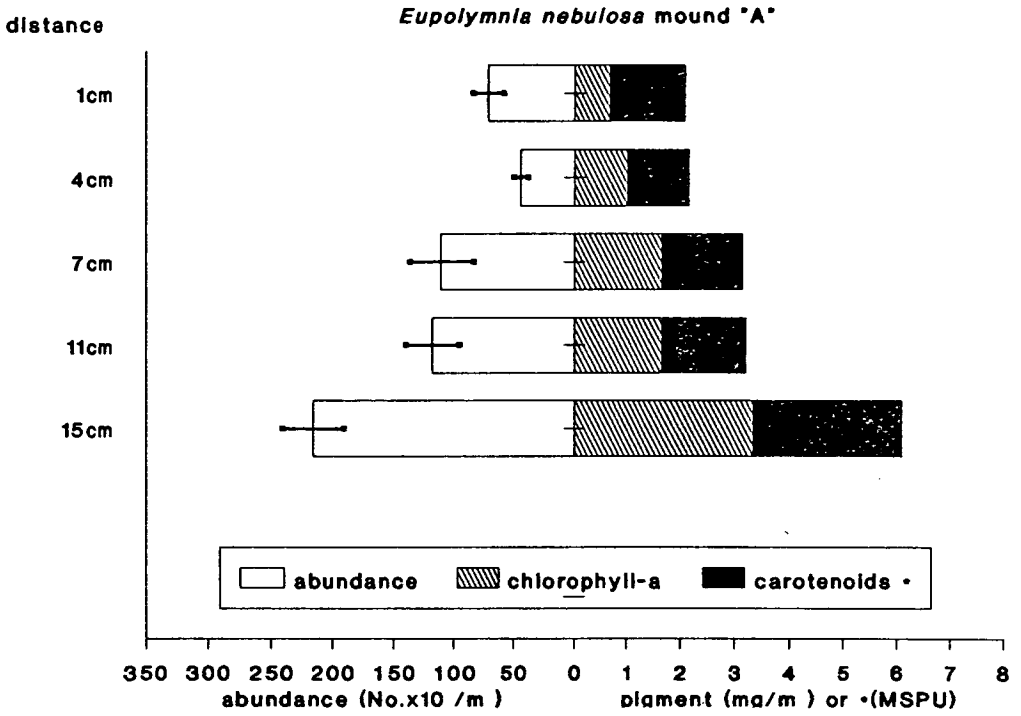
4.2.2.3 Analysis of gut contents

Three worms were collected from similar, undisturbed mounds, using a trowel, and preserved in 4% formalsaline. Their guts were later dissected-out and examined microscopically. Because of the large sediment fraction, it was found that identification or measurement of ingested algae was not possible. Analysis was therefore limited to establishing the main contents of the gut.

4.2.3 Results

The *E. nebulosa* mound "A" was 4cm high; the maximum length of the extended tentacles of the resident worm was 12cm. The sediment surrounding the mound was discoloured (copper-brown) and formed a concentric band around its base. Another sedimentary feature, with a similar concentric pattern of discolouration (shown in Fig. 12: B) was situated 35cm away (distance between summits). This mound showed no tentacular activity. No other mounds were evident within a radius of approx. 1m.

Examination of Fig. 14 (A) shows the pattern of epipelic algal abundance and biomass (Chlorophyll-a, carotenoids) along the gradient of mound "A". The biomass distribution broadly reflects the abundance distribution, although the biomass at the 1cm zone may be influenced by an increase in the abundance of a few smaller species eg. *Nitzschia panduriformis* cf. var. *minor* or *Navicula forcipata* var. *densistriata* (see Fig. 15).



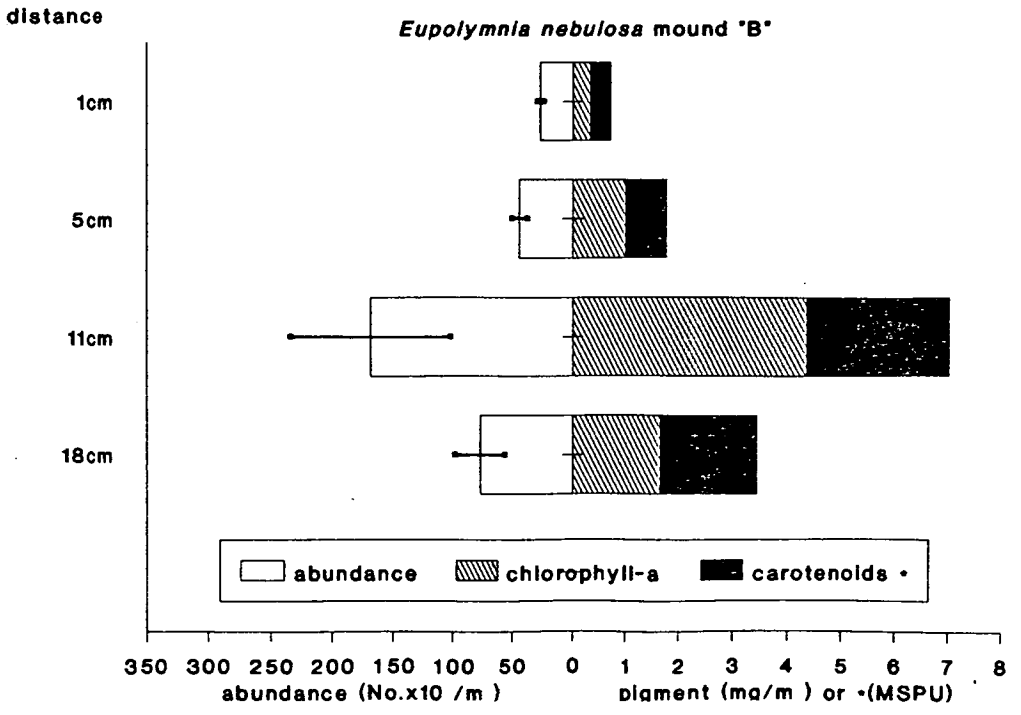


Fig. 14. The micro-distribution of epipelic diatom abundance and biomass (pigment) along the gradient of sediment mounds ("A" and *"B") created by Eupolymnia nebulosa*. Distance is measured from the mound summit. (bars indicate standard error).

The greatest abundance and biomass of epipelic algae was recorded at the base of the mound (216.01 X 10^6M^{-2}; chl-a: 3.34 mg m^{-2}; carotenoids: 2.74 MSPU m^{-2}), whereas the lowest was recorded 1cm (71.72 X 10^6M^{-2}; chl-a: 0.69 mg m^{-2}; carotenoids: 1.41 MSPUm^{-2}), and 4cm (44.14 X 10^6M^{-2}; chl-a: 1.0 mg m^{-2}; carotenoids: 1.15 MSPUm^{-2}) from the mound summit. The density of epipelon at both the 7cm (110.76 X 10^6M^{-2} chl-a: 1.67 mg m^{-2}, carotenoids: 1.47 MSPUm^{-2}) and 11cm (117.98 X 10^6M^{-2}; chl-a: 1.67 mg m^{-2}; carotenoids: 1.53 MSPUm^{-2}) zone were of a similar order of magnitude. The density of epipelon at the 11cm zone was approx. 50% (no: 54.6%; chl-a: 50%; carotenoids: 55.9%) of that recorded only 4cm away at the base of the mound.

Fig. 14 (B) shows the pattern of epipelic numbers and biomass recorded along the side of mound "B". The mound was 3cm high and there were was no tentacular activity visible on the sediment surface. A concentric band of discoloured sand encircled the pile at its base which was surrounded by three other *E. nebulosa* mounds between 35cm and 50cm away (dist. between summits). The visible band of discoloured sediment corresponds to the relatively high epipelic numbers and biomass recorded at the 11cm zone. An area of sediment containing relatively low epipelic biomass was recorded on the top and side of the mound. Sediment at the outer (18cm) zone contained relatively less epipelic algae (no: 45.86%; chl-a: 38.5%; carotenoids: 66.9%) than that recorded 7cm away at the base of the pile.

Both mound "A" and "B" showed similar patterns of algal distribution. In particular, both mounds showed evidence of algal denudation on the top and sides of the pile with relatively greater algal growth around the base.

4.2.3.1 Sediment

The sediment of mound "A" was a unimodal deposit and can be described as mainly (82.5%-87.6%) "very fine sand" with the remaining fraction being of the "very corse silt" type (McManus, 1988). Examination of the particle

size data (Table 4) shows the sediment to be similar in all zones along the mound gradient (mode: 4 *phi* [62*um*] at all zone, median: 3.35-3.5 *phi* [84*um*-93.5*um*]). The less sorted and most corse sediment was recorded at 1cm (M:S = 0.17, sorting = 0.75), 11cm (M:S = 0.14, sorting = 0.68) and 15cm (M:S = 0.16, sorting = 0.73) from the summit. The finest sediment was at the 4cm (M:S = 0.21) and 7cm (M:S = 0.18, sorting = 0.63) zone. The sorting statistic shows the sediment to be of a "moderately sorted/moderately well sorted sediment" type (McManus, 1988). Unfortunately there are no statistical data on the sediment from the 4cm zone.

zone	% mud (<63 um)	%sand (>63um)	mud:san ratio	mean (phi)	media (phi)	mode (phi)	sorting
1 cm	14.84	85.16	0.17	3.35	3.4	4.0	0.75
4 cm	17.55	82.45	0.21	*	*	*	*
7 cm	15.16	84.84	0.18	4.93	3.5	4.0	0.63
11 cm	12.38	87.62	0.14	4.61	3.4	4.0	0.68
15 cm	13.90	86.10	0.16	3.29	3.4	4.0	0.73

Table 4. Distribution of sediment particle size (% mud (silt),% sand, mud:sand ratio, mean, median, mode and sorting statistic) along the slope of a sedimentary mound formed by *Eupolymnia nebulosa*. (* no data)

4.2.3.2 Gut contents

Gut contents analysis showed the diet of the three specimens of *E. nebulosa* to consist entirely of epipelic diatoms and inorganic sediment material. Presumably the diet also included bacteria which could not be seen with a light microscope. Subjective assessment of the algal community within the guts showed there to be no selective ingestion of particular diatom species or of cells (<15*um*) or particles (<60*um*) of small dimension (Gremare, 1988).

4.2.3.3 Epipelic community

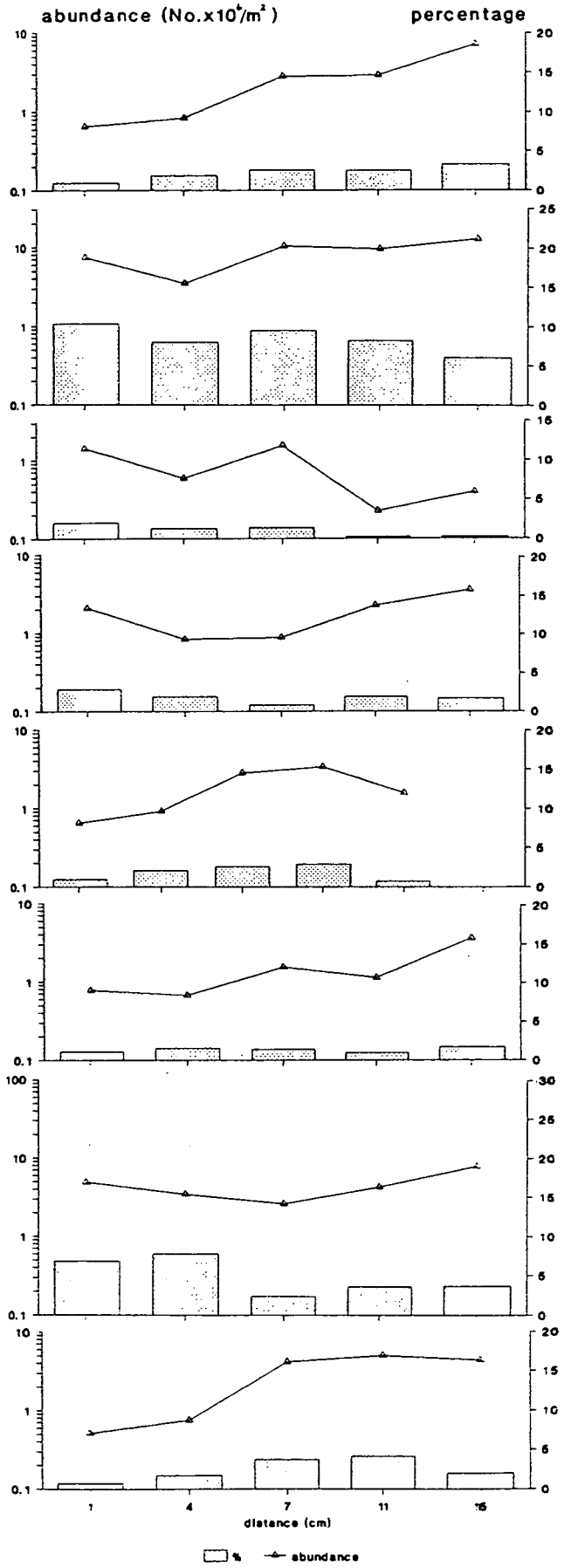
Table 5. shows the epipelic diatoms that were recorded along the gradient of the mound and the estimated

Table 5. List of epipelic species and their percentage abundance in sample communities recorded along the slope of a sediment mound by the strawberry worm Eupolymnia nebulosa. Distance is from the centre of the mound (cm). Key: * = rare species [see section 3.3.2]

Taxa distance (cm):	1	4	7 (%)	11	15
Achnanthes fimbriata	*	*			
Achnanthes sp.		0.8		0.8	0.4
Amphiprora plicata			*		
Amphora cf.arcus	*	0.4	0.4	*	*
Amphora coffeaeformis var.acutiuscula	1.3	1.9	2.7	2.6	3.6
Amphora laevis var.perminuta		0.4	0.4	0.6	0.4
Amphora ostrearia var.ostrearia		*			*
Amphora cf.proteus var.B	10.6	8.2	9.8	8.5	6.3
Amphora proteus var.oculata	2.2	1.4	1.4	0.4	0.4
Amphora proteus var.proteus	0.6	*	*	*	
Amphora truncata	*	0.6		0.4	
Amphora ventricosa	3.0	1.9	0.8	2.0	1.7
Amphora sp.B	*		0.4	*	
Amphora sp.C		0.4		*	*
Caloneis liber var.excentrica					*
Chaetoceros sp.		*	0.6		0.6
Cocconeis scutellum	*	1.0	*		
Coscinodiscus sp.	0.9	2.1	2.7	3.0	0.8
Cylindrotheca closterium		*	0.4	*	1.3
Diploneis ovalis	1.1	*	*	*	*
Diploneis smithii var.smithii	*	*	0.4	*	*
Diploneis splendida	*			*	
Donkinia reticulata	*		*		*
Gyrosigma rectum				*	0.8
Navicula arenaria	1.1	1.6	1.4	1.0	1.7
Navicula crucigera		*	*	0.6	0.4
Navicula cryptocephala*(cf) var.veneta	7.0	8.0	2.4	3.7	3.8
Navicula cf.delognei		*	0.8		
Navicual distans	0.7	1.8	3.9	4.3	2.1
Navicula forcipata var.densistriata	22.4	19.1	21.8	13.4	26.0
Navicula palpebralis var.angulosa			*		
Navicula phyllepta		0.6			
Navicula plicata var.constricta	*	0.8	*	*	*
Navicula retusa var.gregorii	0.4	1.0	*	0.4	*
Navicula tripunctata* *(cf.)	22.2	18.9	19.6	31.3	20.9
Navicula sp.A	0.4	*	*		0.4
Navicula sp.B.	2.0	1.0	2.0	4.3	5.3
Navicula sp.C/D	*	0.6	1.2	3.1	1.3
Navicula sp.F/G/H	15.9	16.6	13.7	9.6	13.5

continued..

Taxa	distance (cm):	1	4	7 (%)	11	15
Nitzschia angularis		*	*	1.2	1.2	0.6
Nitzschia angularis cf.var.affinis		0.6	1.8		*	2.7
Nitzschia aff.distans		*			*	*
Nitzschia hybrida cf.var.pellucida				*		
Nitzschia insignis var.smithii		0.4		*	*	*
Nitzschia marginulata var.marginulata		*				
Nitzschia panduriformis/punctata		4.6	1.2	1.6	0.8	1.5
Nitzschia sigma var.?						*
Nitzschia sigma var.intercedens				*	*	*
Nitzschia socialis var.socialis		*	1.6	0.6	0.8	0.4
Nitzschia sp.B/C		0.4		0.6	0.8	0.8
Pleurosigma aestaurii var.candida		1.7	0.4	4.5	4.3	2.7
Pleurosigma strigosum						*
Rhoicosphenia abbreviata				*	0.4	
Skeletonema costatum		0.6	6.2	4.5	1.4	*
Stenoneis sp.						*
Surirella fastuosa var.fastuosa					*	
Synedra pulchella				*		*
Tabellaria floculosa			*	*	0.4	
Trachyneis aspera var.aspera						*
Tropidoneis vitrea var.scaligera		*	*		*	*
Number of species:		37	40	42	42	45
Number of cells identified:		540	513	490	508	527



Amphora coffeaeformis var.*acutiuscula*

Amphora proteus var.*B*

Amphora proteus var.*oculata*

Amphora ventricosa

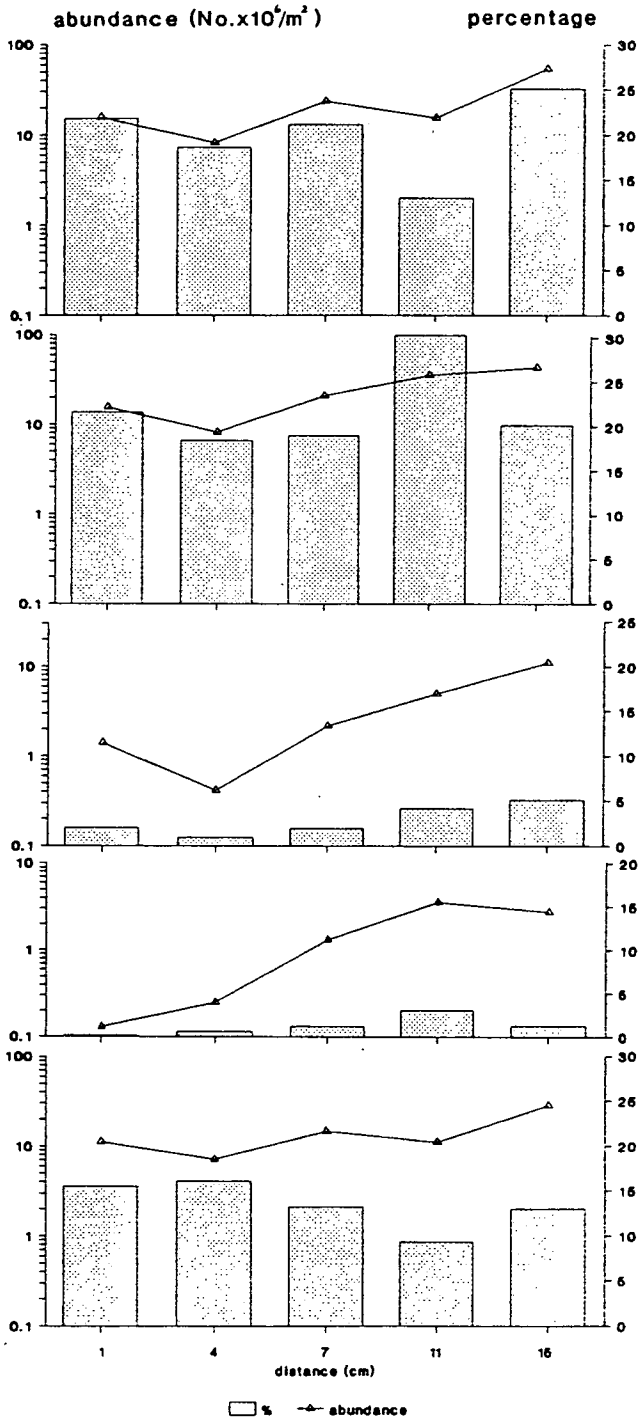
Coscinodiscus sp.

Navicula arenaria

Navicula cryptocephala[#] var.*veneta*

[#](cf.)

Navicula distans



Navicula forcipata var.*densistriata*

*Navicula tripunctata**

*(cf)

Navicula sp.B

Navicula sp.D

Navicula sp.H

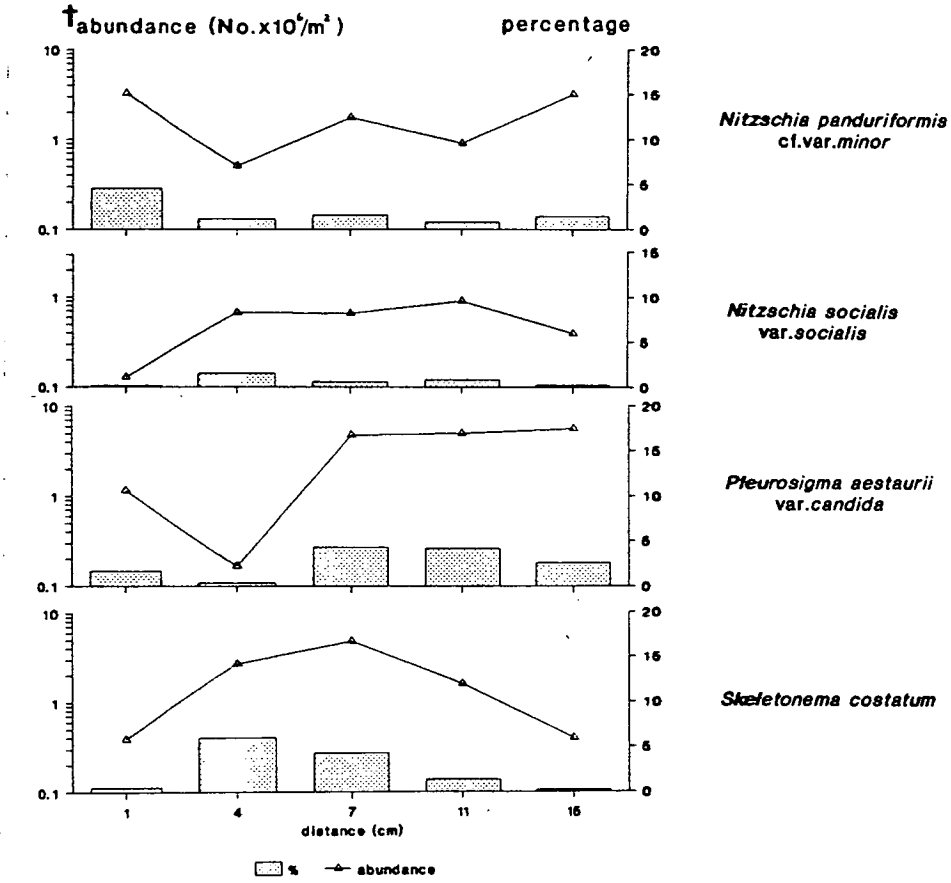


Fig. 15. The small scale distribution pattern of the predominant species of epipelic diatom along the gradient of a sediment mound (3cm high) formed by a strawberry worm *Eupolymnia nebulosa*. Distance is measured from the mound summit.

NB. Note log scale †

proportion of the separate species. The distribution pattern of the most abundant species are summarised graphically in Fig. 15. The estimated abundance is shown on a logarithmic scale and the proportion of the species recorded at the separate zone are compared in a histogram.

Fig. 16 (A) provides a summary of the whole community data by comparing the proportion and abundance of the main generic groups of the epipelon and the change in species diversity (numbers) along the mound profile. Examination of this basic community structure reveals that the proportions of the major epipelic genera remained fundamentally unchanged, despite significant change in the abundance (Fig. 16, B) and diversity of algae along the mound profile. *Navicula* species constitute 64.8-72.7% of the epipelic community whereas *Amphora* species make up 11.9-17.1% and *Nitzschia* species 3.4-5.7%.

The centric diatoms, *Coscinodiscus sp.* and *Skeletonema costatum*, are of planktonic origin and are non motile. Both species showed some variation with the smallest proportions recorded at the top and base of the mound. Because of their inability to re-orientate on the sediment surface, their levels are particularly useful indicators of a burial process.

The consistency of the epipelic community-structure along the mound is illustrated by the small variation in the proportions of most of the epipelic species (see Fig. 15). The only notable exception to this is a shift in the relative proportions (by approx. 10 %) of the two most abundant species, *Navicula forcipata* var. *densistriata* and *Navicula* cf.*tripunctata*, that occurred at the 11cm zone. The small variations in the proportions suggested by the data must be interpreted with caution due to limitations in the enumeration procedure (see 3.6.3).

The increase in the number of epipelic species, from 20 recorded at the summit to 45 recorded at the base of the mound, approximately reflects the pattern of algal

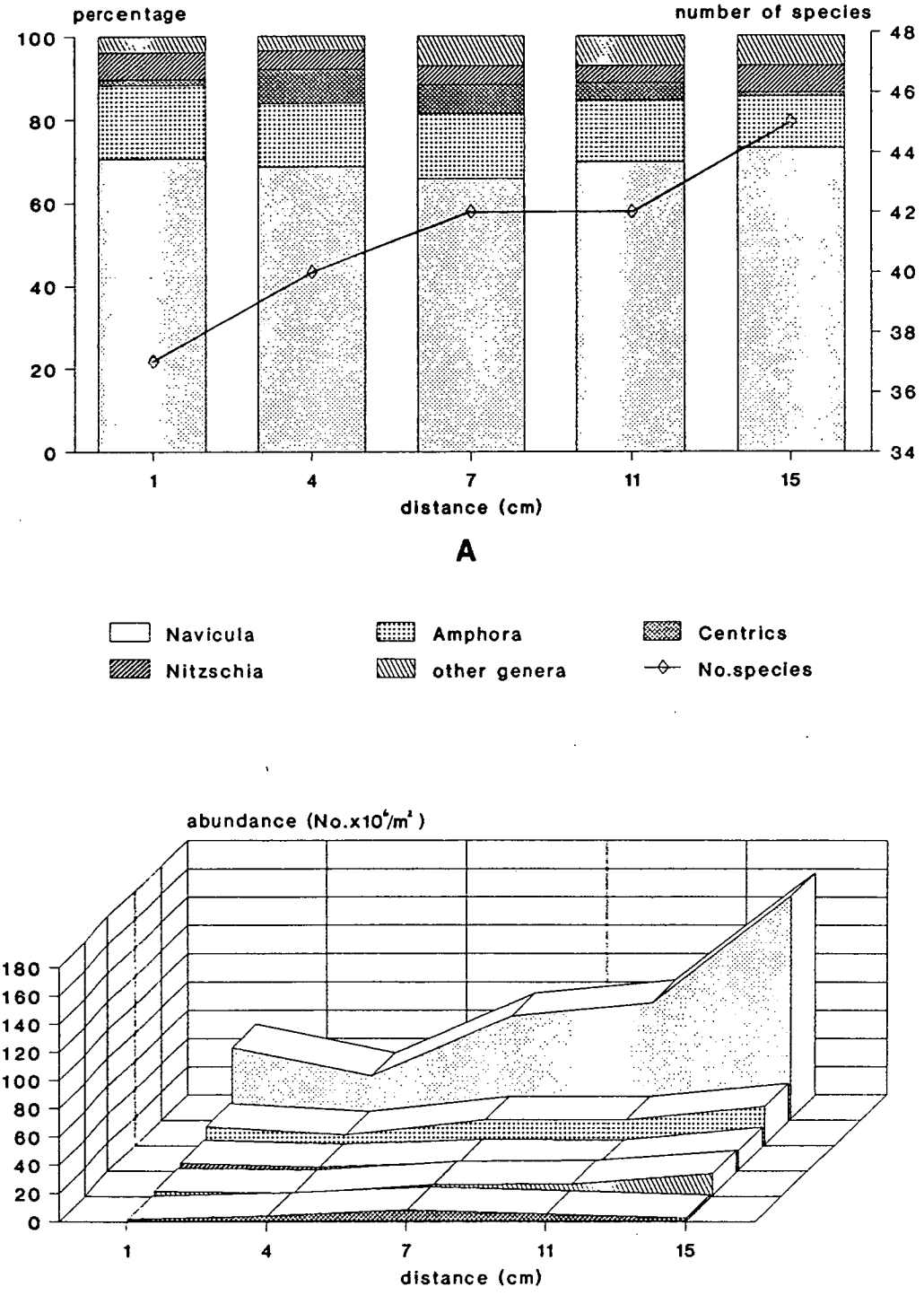


Fig. 16. The spatial change in the community structure of epipelic diatoms along the profile of a strawberry worm mound (3cm high). Indicated by A: percentage occurrence of major genera and number of species B: estimated abundance of major genera.

abundance and biomass found along the mound profile (see Fig. 14 (A).

Examination of Fig. 16 (B) shows a decline in the abundance of *Navicula* species from the mound summit to the 4cm zone. This is followed by a notable increase in the abundance of *Navicula* species, and to a lesser extent *Amphora*, *Nitzschia* and other species, from the 4cm zone to the base (15cm) of the mound. This is attributed to the pattern of distribution of a few predominant species of diatom (see Fig. 15). In particular: *Navicula forcipata* var.*densistriata* (8.21- 54.2 x 10^6 M^2); *Navicula* cf.*tripunctata* (8.12- 43.52 x 10^6 M^2); *Navicula* sp. H (7.12- 28.09 x 10^6 M^2); *Amphora proteus* var. B (3.52- 13.06 x 10^6 M^2) and *Navicula* cf.*cryptocephala* var. *veneta* Other, less abundant, species also showed a similar pattern of distribution, including *Navicula* sp. B; *Nitzschia panduriformis* cf. var. *minor*; *Navicula arenaria*; *Amphora ventricosa* and *Pleurosigma aestaurii* var. *candida*.

Species that showed a continuous increase in abundance from the summit (1cm zone) to the base of the mound included: *Navicula distans*; *Navicula sp.* D and *Amphora coffeaeformis* var. *acutiuscula*. *Nitzschia socialis* var. *socialis* and the planktonic species *Skeletonema costatum* and *Coscinodiscus sp.* were most abundant along the side of the mound (4- 11cm zone) and showed similar patterns of distribution. *Amphora proteus* var. *oculata* was the only species to be found in lower numbers at the base of the mound, than recorded at the summit.

4.2.4 Discussion

The data show that sediment mounds formed by *E. nebulosa* affect the small-scale distribution of epipelic algal abundance and biomass, without greatly modifying the epipelic community structure. The gradient in epipelic biomass from the summit to the base of the mound indicates that a loss of algal biomass is occurring within the tentacle radius (12cm) of the strawberry worm. The

hypothesis that: "epipelic algal biomass is denuded from sediment mounds, associated with *E. nebulosa*, by a (loss) process of grazing" has not been conclusively accepted or rejected. The results indicate that loss processes of both **grazing** and **burial** are responsible for the denudation of algae from the mounds; seen in both this study and the preliminary patchiness study (see 4.1):

4.2.4.1 Grazing loss

The presence of epipelic diatoms within the guts of *E. nebulosa* clearly shows that epipelon is being consumed; this agrees with the trophic status of *E. nebulosa* described in the literature (Gremare, 1988; Fauchald and Jumars, 1979; Taghon *et al*, 1978). The reduced epipelic biomass (< 50% of the 15cm zone) of the four zones within the observed radius of the tentacles in mound "A" also suggests that a grazing process is responsible for algal denudation. The area of algal denudation surrounding the polychaete worm does appear to be limited by the tentacle length. Unfortunately, because of the extensible nature of the tentacles (Gremare, 1988) the maximum measured length (12cm in mound "A") may not represent the maximum reach of the worm. This uncertainty makes interpretation of the results inconclusive, although the length is comparable to that of other worms inhabiting similar sized mounds. It is not clear how tentacle length could be measured with accuracy as collecting and preserving causes a worm to retract. Survey design could, however, be improved by the collection of a replicate sample further out from the mound centre.

There is also evidence that grazing of epipelic algae is a non selective process involving the ingestion of all species irrespective of their size. No clear difference was seen between the epipelic community within the feeding radius of the worm (12cm) and the community recorded outside the range of the tentacles (15cm zone). Qualitative assessment of gut contents also showed there to be no obvious selection of diatom species. The

proportion of the smaller species (eg. *Navicula* cf.*cryptocephala* cf. var. *veneta*, *Navicula sp.H*, *Navicula forcipata* var. *densistriata*) remaining in the sediment appeared to be unaffected. This suggests that the particle size selection, described by Gremare (1988), was not occurring in *E. nebulosa*.

4.2.4.2 Burial loss

Qualitative observations of the *E. nebulosa* community within Loch Goil show that their mounds often occurred in pairs situated in close (approx. 30cm) proximity, with no evidence of faecal pellets or casts. This indicates that both feeding and defaecation occur at either opening of a burrow (Dales, 1955; Fauchald and Jumars, 1979) and implies that both grazing and burial loss process are operating on the same area of sea bed. This can be contrasted with the depressions and faecal casts associated with *A. marina* (Fig. 13), where feeding and defaecation occur at opposite ends of a U- or J-shaped burrow (Wells, 1949).

The existence of an elevated mound is, in itself, evidence that a sediment deposition process is occurring. The low levels of non motile (planktonic) algae recorded at the top of the mound can be attributed to the spilling of defaecated sediment from the mounds summit, as these algae would be unable to re-orientate themselves on the sediment surface. However, relatively low levels of planktonic algae were also recorded at the base of the mound where deposition of sediment by *E. nebulosa* is unlikely to occur. The reason for this is not clear, although the base of mounds are relatively sheltered from tidal streams and may accumulate detrital material deposited from the water column.

It is unlikely that *E. nebulosa* would have developed a feeding strategy that involved limiting the productivity of its own food supply by its defaecation behaviour. The worm could avoid depleting its epipelic food supply by alternating its feeding between two or more burrow

openings, thus allowing the re-colonisation of the denuded mound by either the buried epipelic algae or by motile cells migrating in from the surrounding area. The relocation of *E. nebulosa* to form a new burrow is also likely to occur in nature, as *E. nebulosa* in aquaria have shown intermittent motility by means of peristaltic crawling or by pulling themselves across the substratum with the help of the tentacles (Gremare, 1988). It is not known how often *E. nebulosa* moves around in nature, however, Gremare (1988) found that motility is not required for efficient feeding by worms kept in aquarium.

4.2.4.3 Other loss processes

I consider it unlikely that sediment transport or erosion processes (from tidal stream water-movement) are the cause of the algal denudation. Both these processes have, however, been attributed to the patchiness of diatom films observed on migrating sand ripples (Grant et al, 1986). Qualitative observation of the dynamical processes occurring at this site in Loch Goil (during various tidal and weather conditions) has shown the tidal current to be negligible. The elevated algal biomass recorded at the 15cm zone (mound "A") and 11cm zone (mound "B") cannot, therefore, be attributed to diatom proliferation in sheltered microsites (ie. troughs, lee slopes), suggested by Grant et al (1986) for diatom films on intertidal sands. Gravity may however, have had an effect by causing the downward movement of surface sediment and its associated epipelic algae. This would tend to concentrate algae and organic debris (of low specific gravity) at the base of the pile and may be the cause of the visible, concentric band of relatively high algal biomass.

4.2.4.4 Sediment characteristics

There is no evidence that the pattern of epipelic algae distribution is in response to the small scale changes in sediment characteristics (eg. particle size). Because both feeding and defaecation appear to occur at

either ends of the burrow, the redepositing of faecal and pseudofaecal (sediment handled by the worm but not ingested) material on the sediment surface makes it difficult to identify any preferential ingestion of small (<60um) sediment particles (Gremare, 1988).

E. nebulosa may exert a strong influence on porosity, water content, cohesion, and compaction of the sediment as a consequence of its deposit feeding activity (Watling, 1988). This modification of the sediment, by the binding of grains into faecal pellets, may be a less desirable habitat for the motile diatom cells, limiting their abundance on the top of the mound. The method of particle size analysis (which involves the drying and sieving of the sediment; see 3.4.6) can only describe the sediment's content and not the true nature of the sediment in the field. Modification of the sediment by burrowing animals can increase the area of the interface between sediment and water a thousand times (Young, 1990). The effect on the provision of living space within the photic zone of the sediment may be profound, causing algae to proliferate. This may be the cause of the high standing assemblage of diatoms that surrounds sediment mounds, outside the tentacles' feeding range.

This investigation has identified a relationship between an ecologically important infaunal species and the epipelic community in Loch Goil. Experimental work remains to be done, however, to confirm the processes of algal loss that have been proposed for *E. nebulosa*. In particular, observation of the feeding and defaecation behaviour of *E. nebulosa* would be best achieved using specimens maintained in aquaria. The monitoring of epipelic algal loss from an algal culture maintained in a laboratory micro-ecosystem could be used to quantify algal loss rates. The relationship between small-scale variations the epipelic assemblage and the distribution of organic matter also needs to be explored.

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.

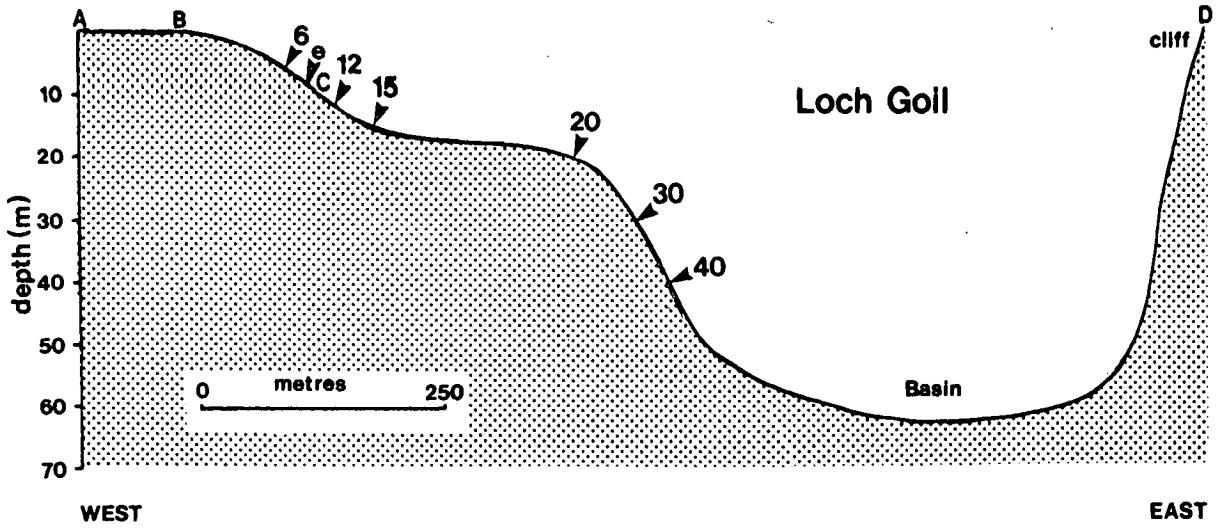


Fig. 17. Cross section of Loch Goil showing the location of the sample stations (6m, 12m, 15m, 20m, 30m, and 40m) along a bathymetric gradient (drawn from Admiralty chart no. 3746) . AB is the intertidal zone, A is at the position 56 07.73'N 04 54.45' W; B is the position of Chart Datum; C is the sample 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 disturbance, grading of 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_0): "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

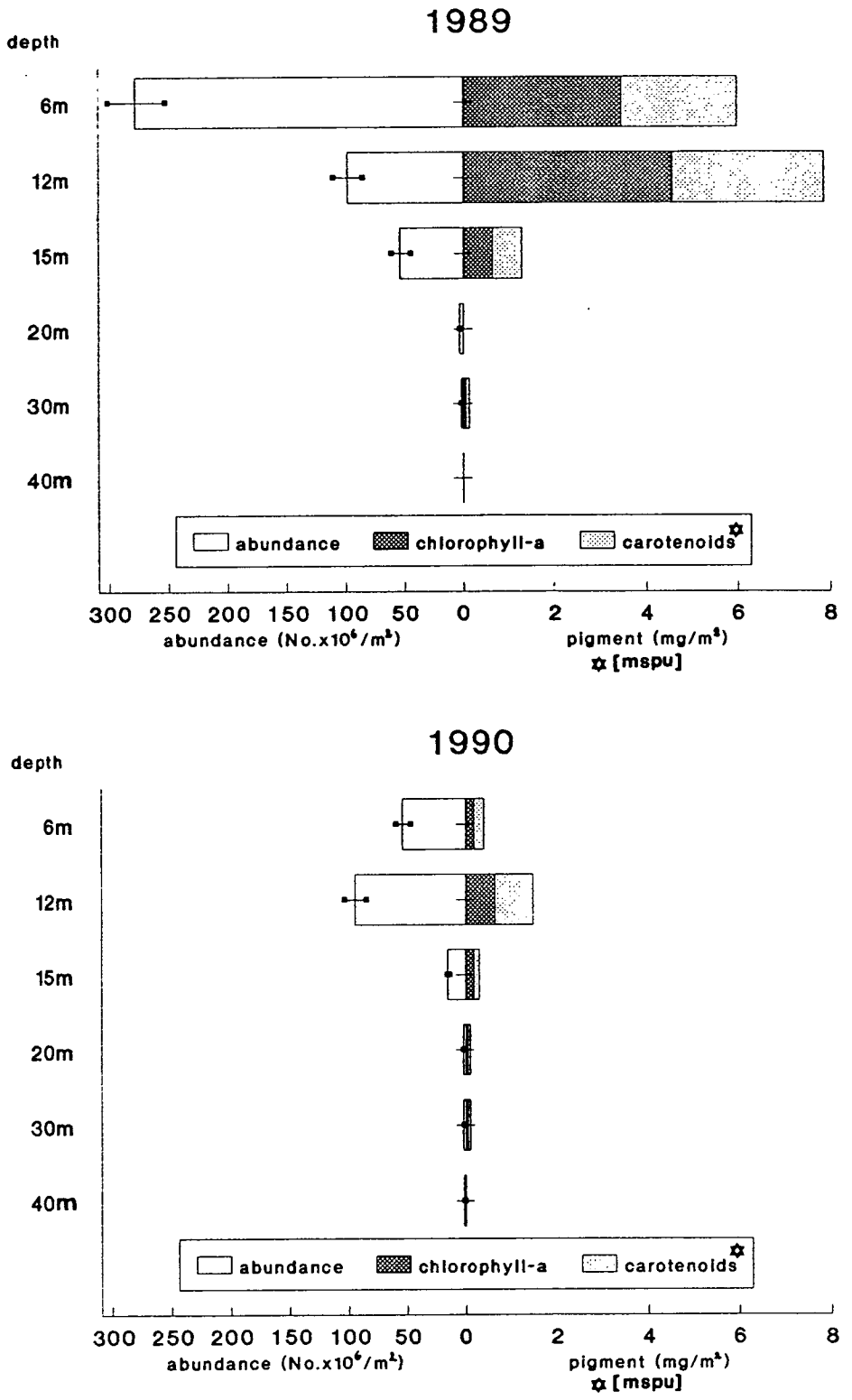


Fig. 18. Distribution of estimated diatom abundance and biomass (pigments) along a depth gradient in June 1989 and July 1990. (Bars indicate standard error).

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 x 10^6 cells m^{-2} was recorded at a depth of 12m depth, decreasing to 1.11 x 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

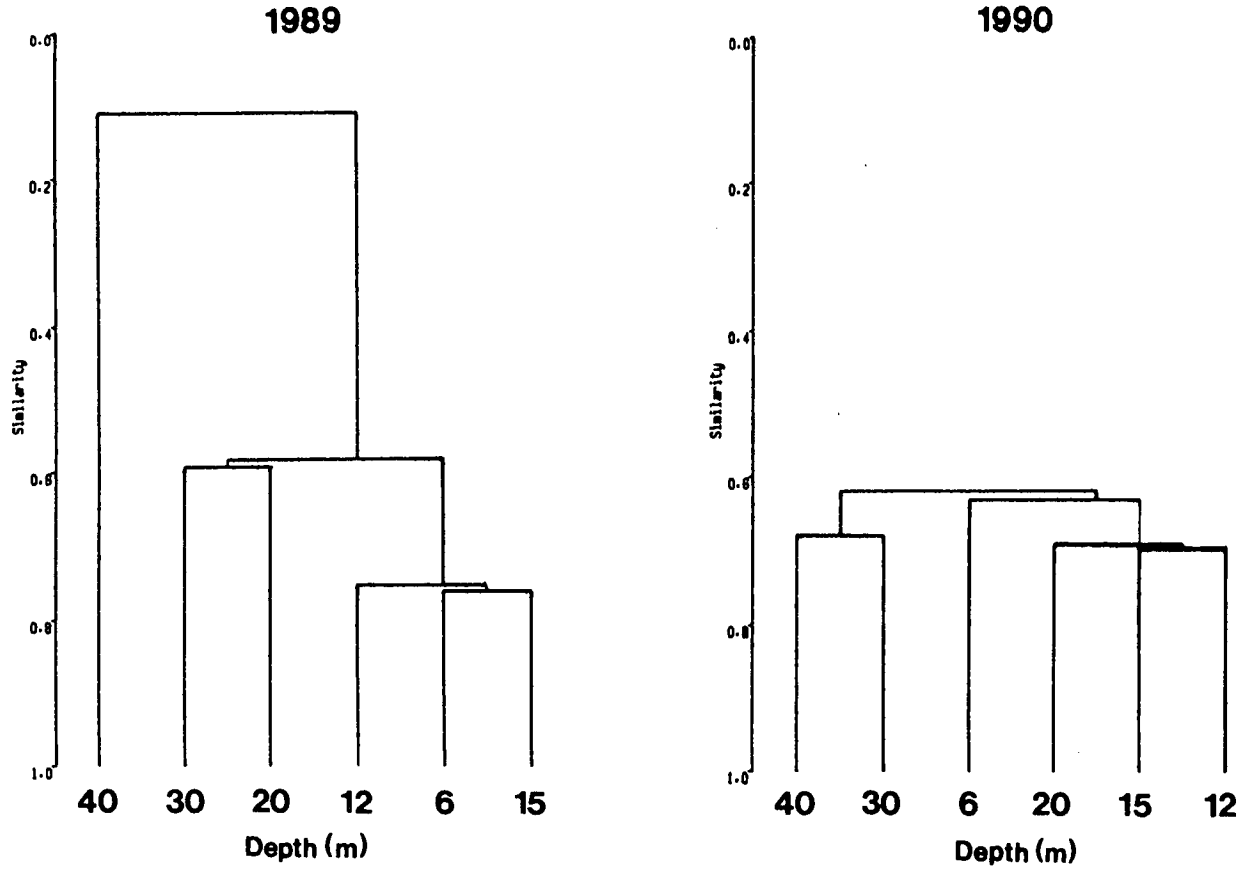


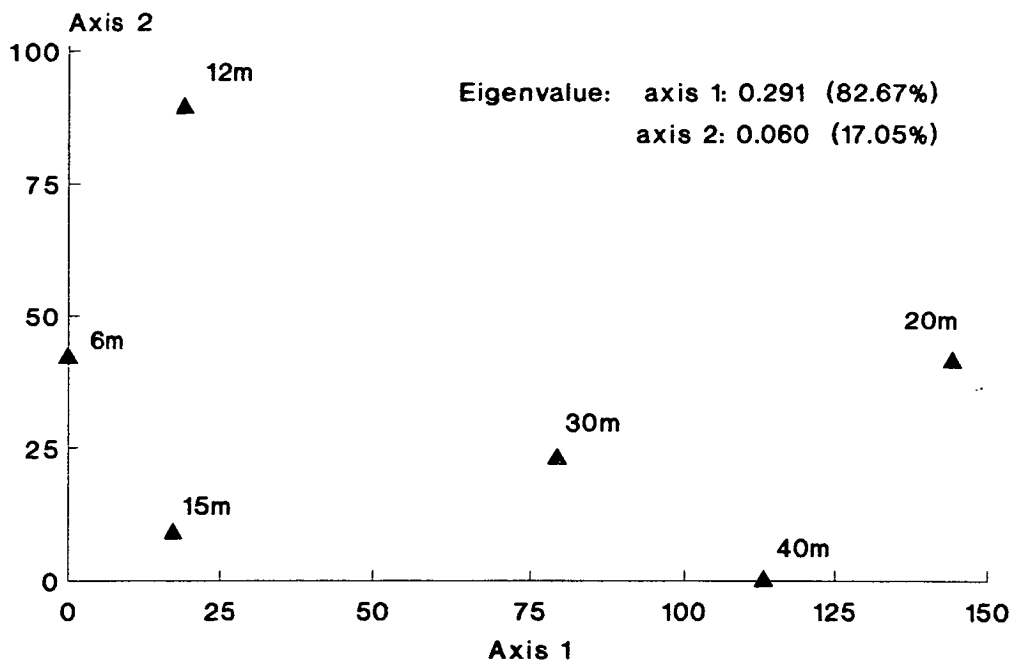
Fig. 19. Dendrograms drawn using group average sorting (Bray-Curtis coefficient) showing the similarity of the epipelic communities recorded along a bathymatric gradient in Loch Goil, 1989 and 1990.

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



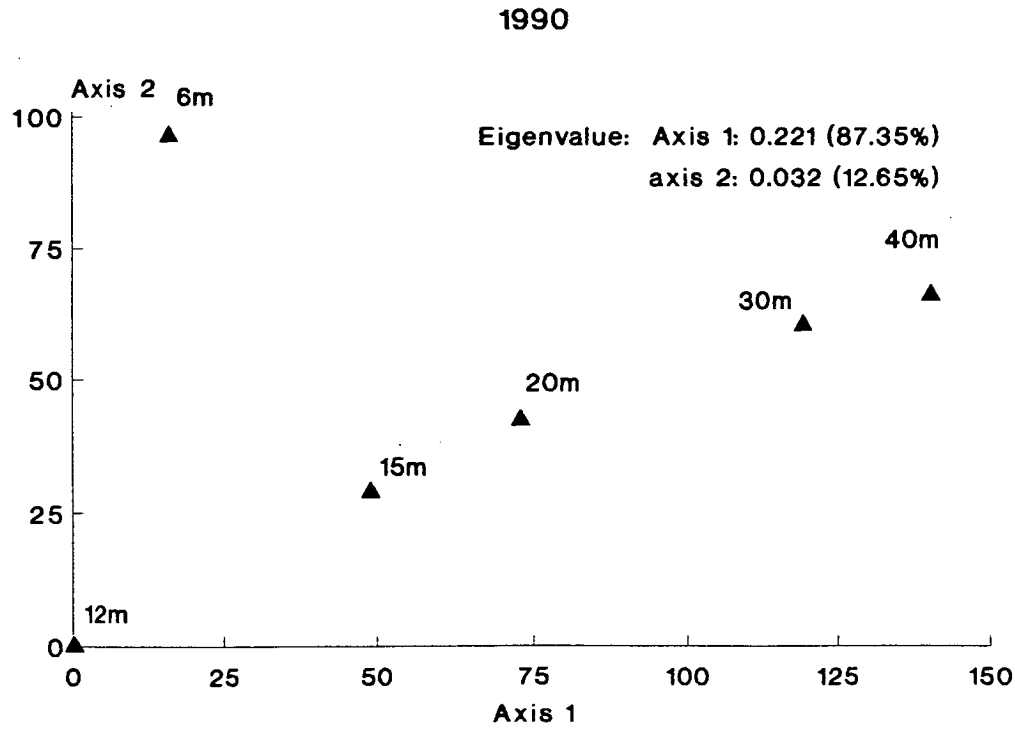


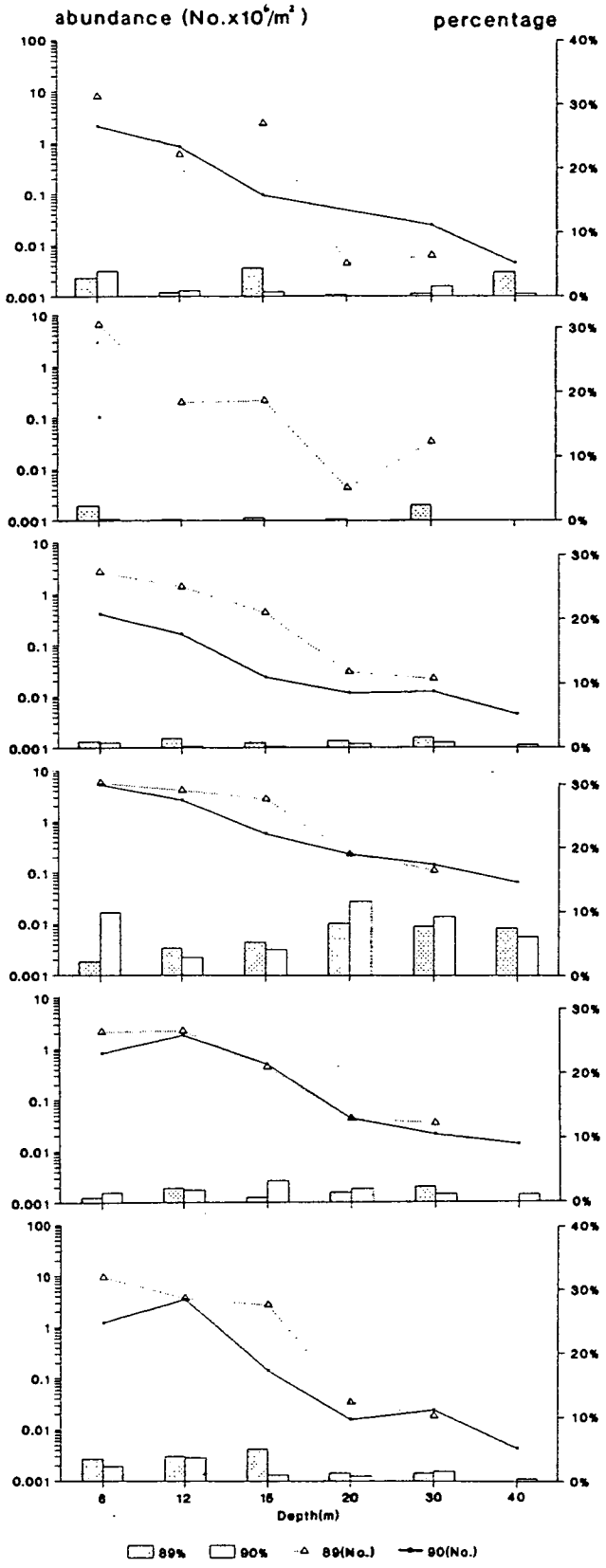
Fig. 20. Ordination plots for the epipelic community recorded from a series of depths (m) in Loch Goil during 1989 and 1990. Axis 1 and axis 2 data are derived from detrended correspondence analysis (DECORANA). The Eigenvalue and percentage variabily are shown for each axis.

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
CYCI 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 PROO	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 '-'.



Amphora coffeaeformis var.*acutiuscula*

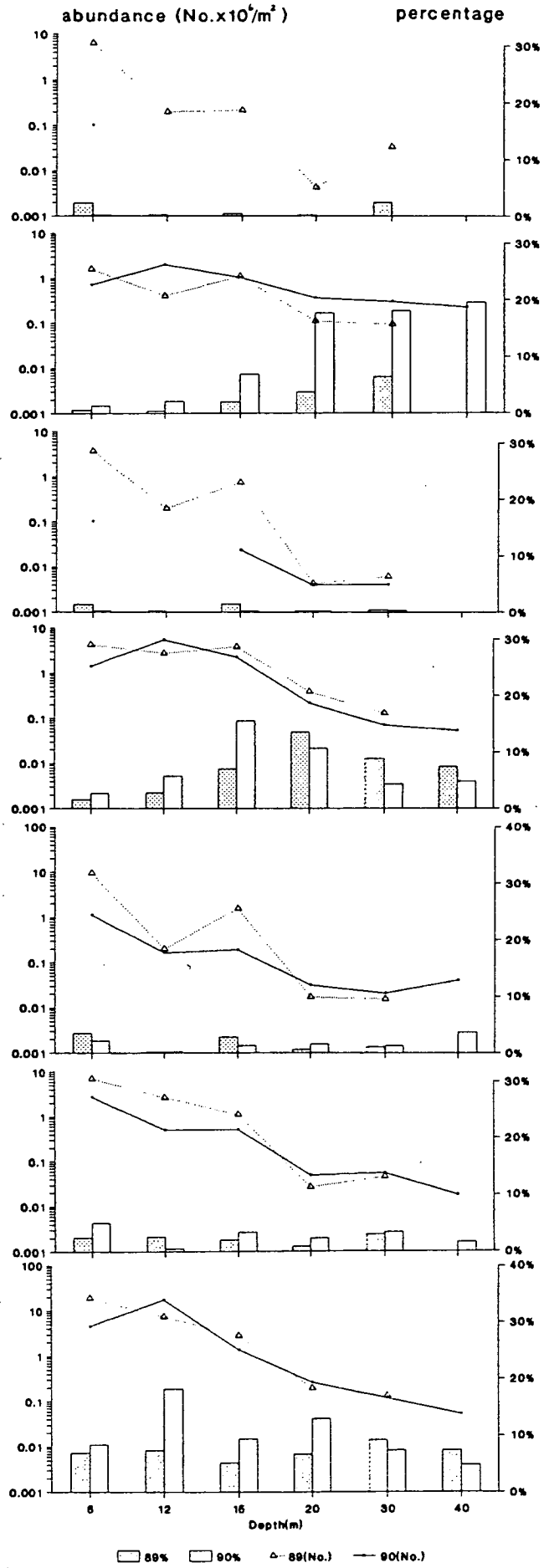
Amphora laevis var.*perminuta* / *Amphora sp.B*

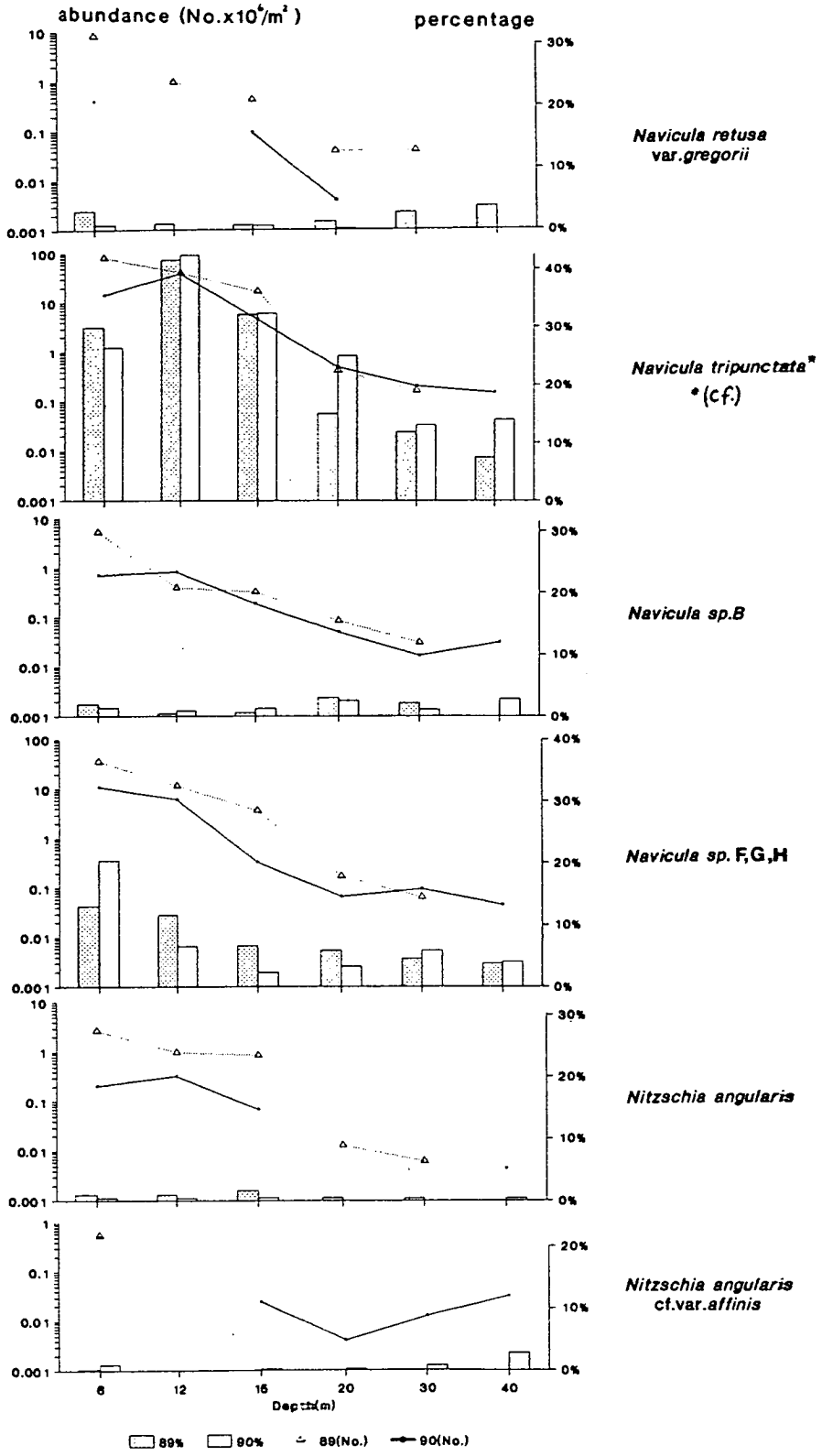
Amphora truncata

Amphora proteus var.*B*

Amphora proteus var.*oculata*

Amphora ventricosa


abundance (No.x10⁴/m²)
percentage
Amphora sp.B
Coscinodiscus sp.
Cylindrotheca closterium
Navicula arenaria
Navicula cyptocephala * var.veneta
*(cf)
Navicula distans
Navicula forcipata var.densistriata
Depth(m)
6
12
16
20
30
40
89%
90%
89(No.)
90(No.)


abundance (No.x10⁴/m²)
percentage
Navicula retusa var.gregorii
Navicula tripunctata*
*(cf.)
Navicula sp.B
Navicula sp. F,G,H
Nitzschia angularis
Nitzschia angularis cf.var.affinis
Depth(m)
89%
90%
89(No.)
90(No.)

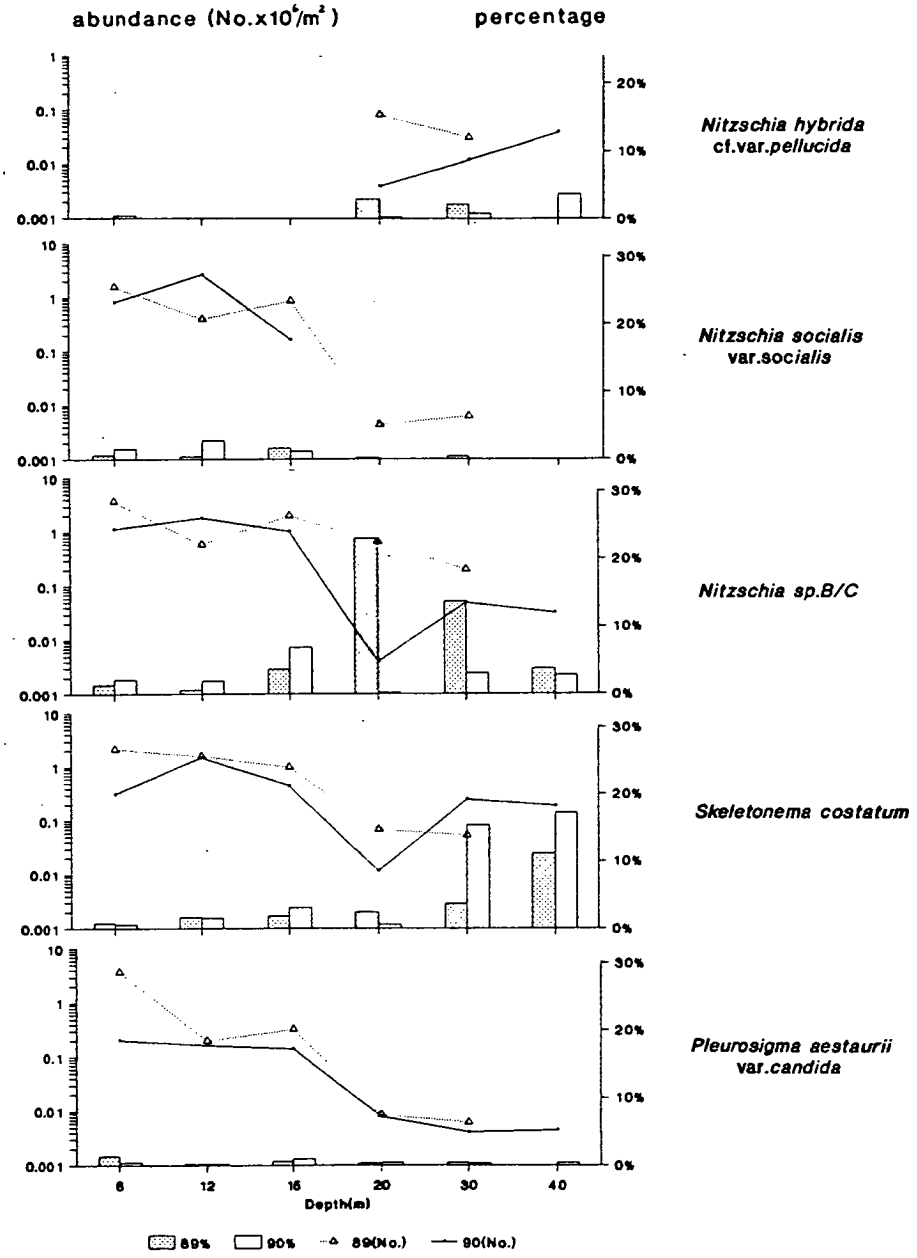
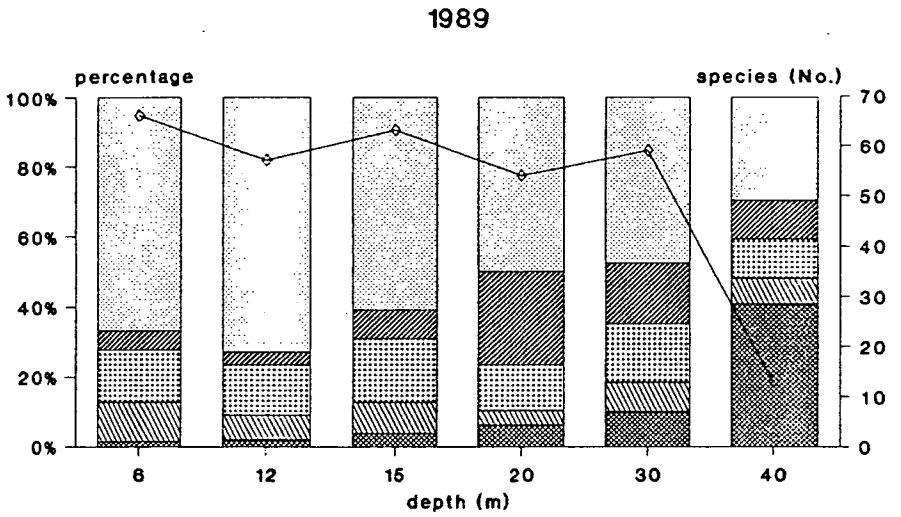


Fig.22.The depth distribution pattern of the predominant species of epipelic diatom recorded from 6-40m depth in 1989 and 1990 indicated by estimated abundance.



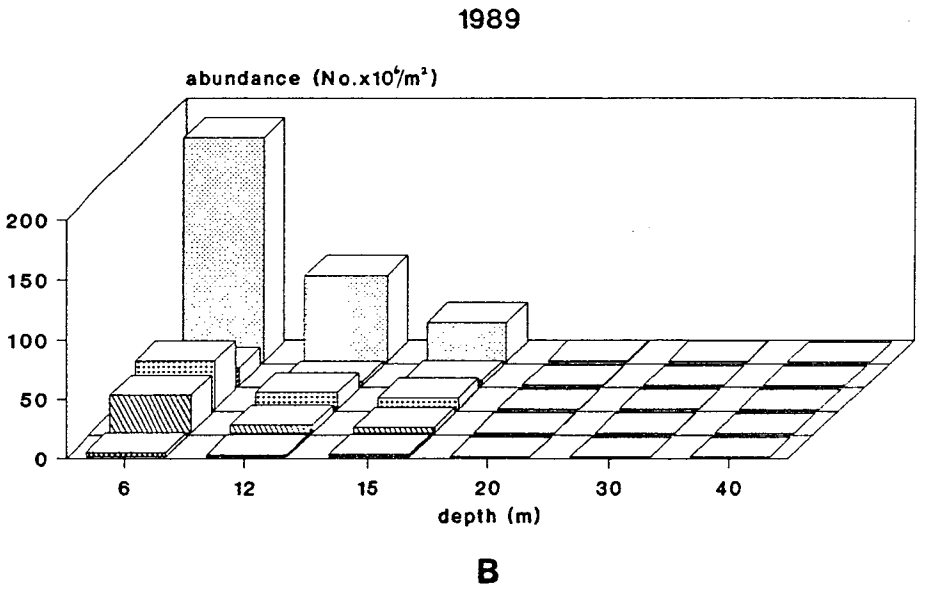


Fig.23. The spatial change in the epipelic community structure along a depth gradient (6-40m) in 1989.
A: Estimated pertage occurrence of the major epipelic diatom genera and number of species.
B: Estimated abundance of major genera.

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				*	*	
Tropidoneis 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	40
Navicula forcipata var.densistriata	8.6	19.2	9.5	13.4	7.7	5.
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.
Navicula sp.A	*	*	*	*	*	
Navicula sp.B.	1.4	0.9	1.3	2.6	1.1	3.
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.
Navicula sp.I						*
Nitzschia angularis	0.4	0.4	0.5			*
Nitzschia angularis cf.var.affinis	1.0		*	*	0.8	3.
Nitzschia bilobata var.bilobata						
Nitzschia aff.distans	*	*				
Nitzschia hybrida cf.var.pellucida	0.4			*	0.8	3.
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.
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.
Rhabdonema minutum	*					*
Rhoicosphenia abbreviata				*		*
Skeletonema costatum	0.6	1.7	3.1	0.6	16.0	18.
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;

Depth (m)		30 20	12 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 20	12 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 "-".

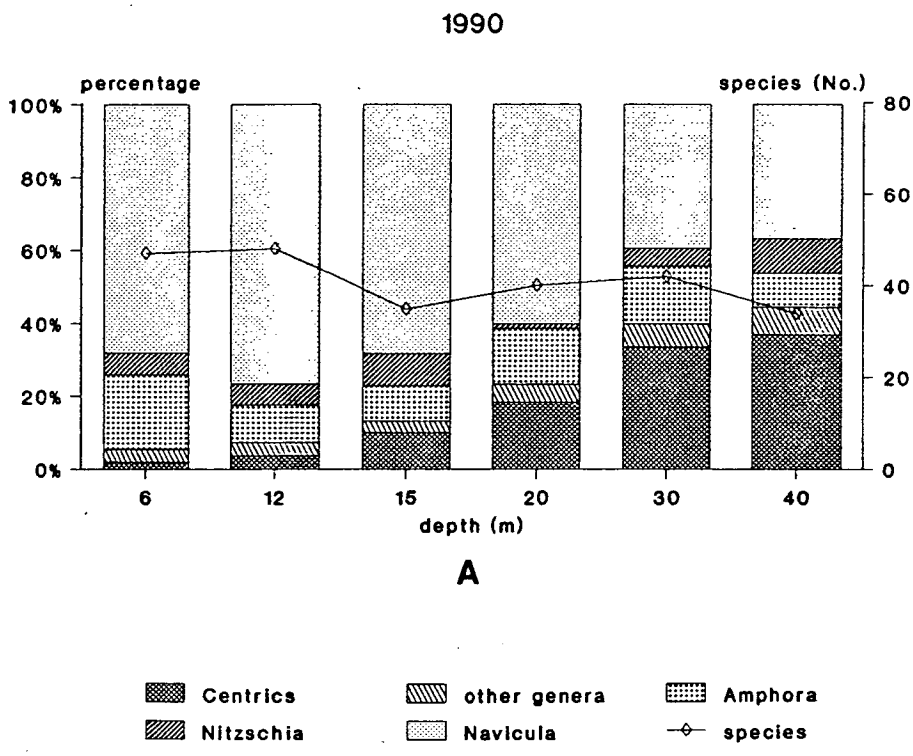


Fig. 25. The spatial change in the epipelic community structure along a depth gradient (6-40m) in 1990.
A: Estimated pertage occurrence of the major epipelic diatom genera and number of species.
B: Estimated abundance of major genera.

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

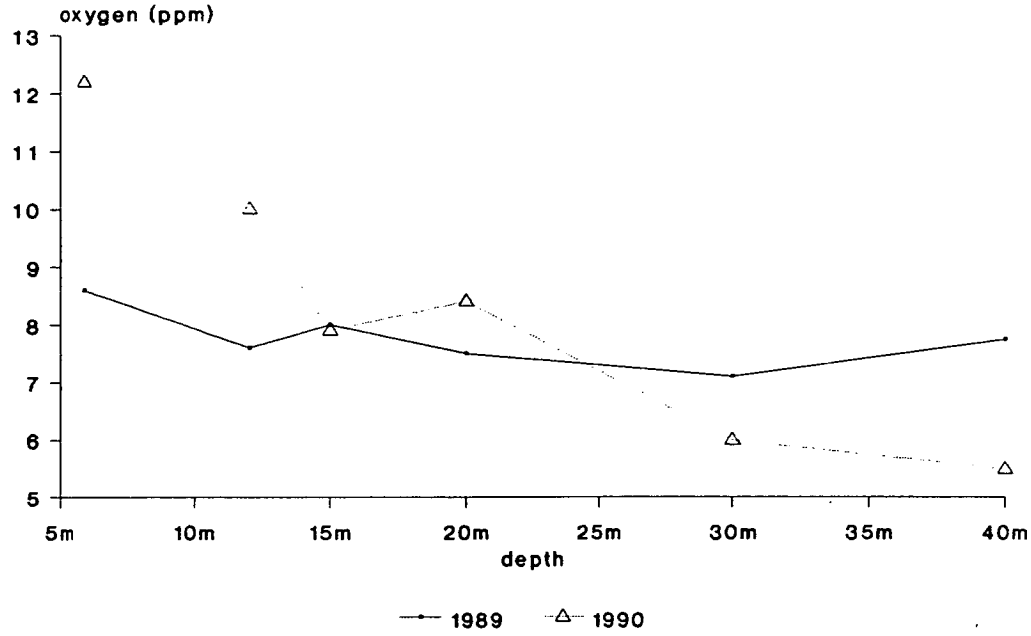


Fig. 26. Spatial distribution of oxygen (at sediment/sea water interface) along a depth gradient.

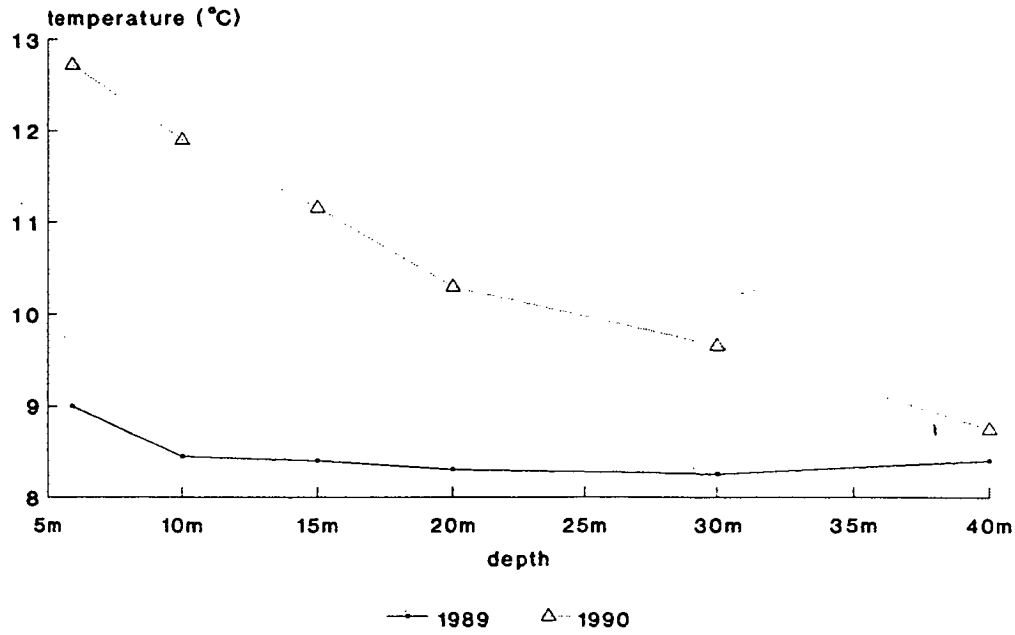


Fig. 27. Spatial distribution of temperature at the sediment surface along a depth gradient.

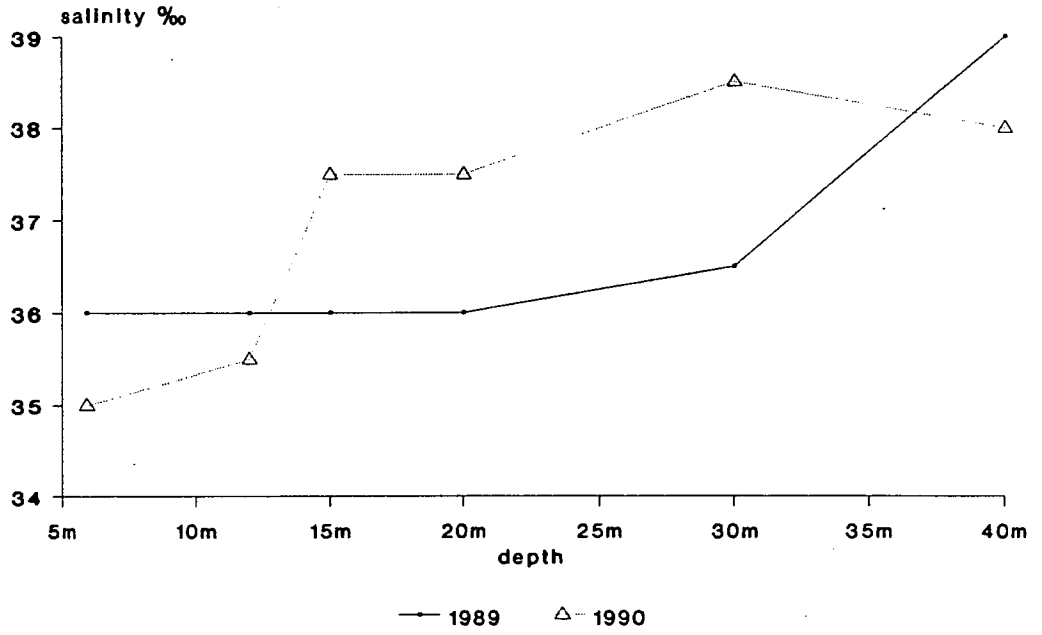


Fig.28. The salinity of seawater (recorded at the sediment surface) along a depth gradient.

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 envirnomental 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 (24-67um; 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 adaption 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

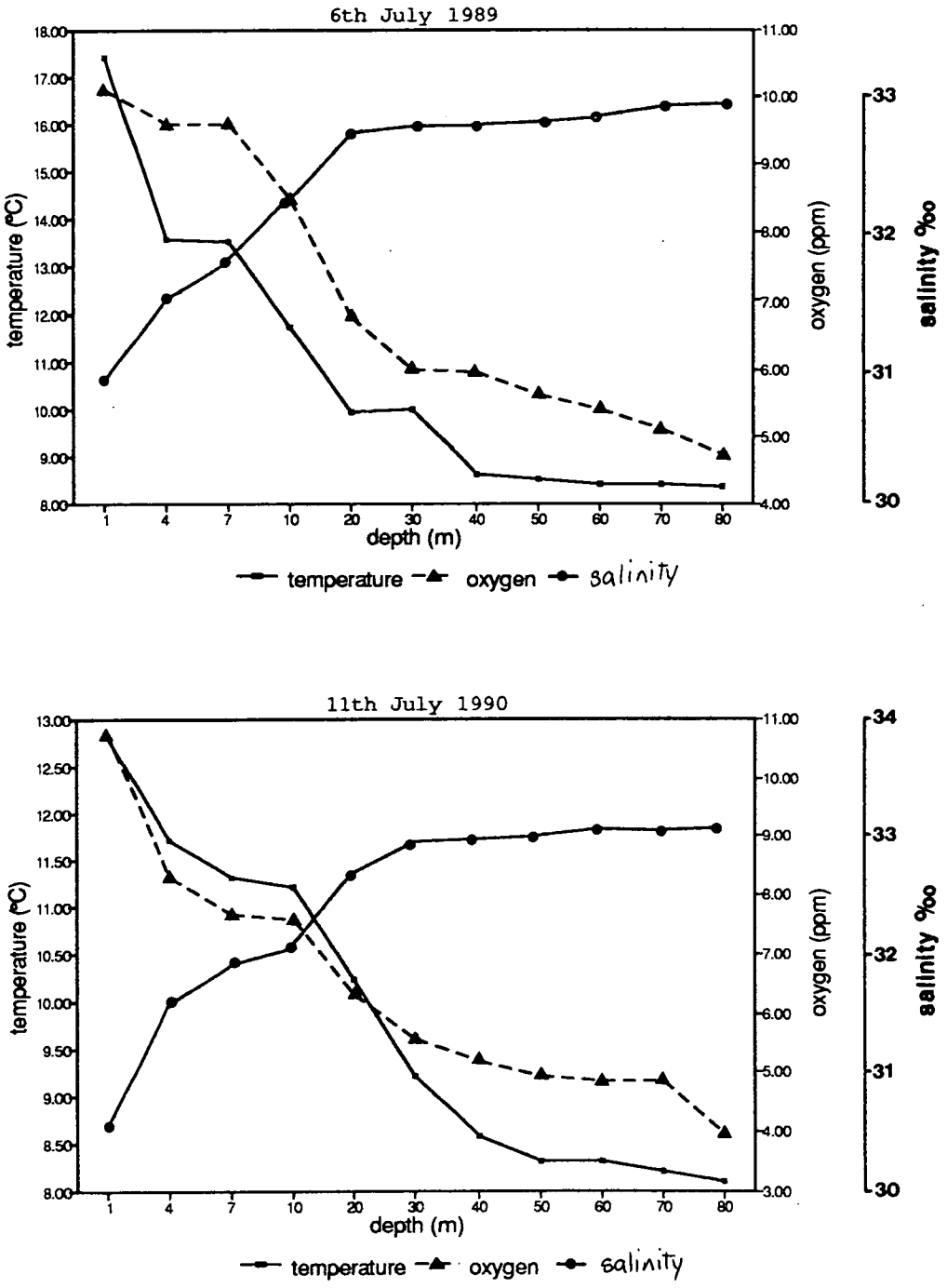


Fig. 29. Temperature, salinity and oxygen profiles along a bathymetric gradient (0-80m) in Loch Goil during July 1989 and July 1990 (CRPB unpublished data).

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_o): "there are no differences in the epipelon along a bathymetric gradient, in Loch Goil".

4.4 SEASONALITY OF THE EPIPELON

4.4.1 Introduction

There have been many studies reporting the seasonal succession of epipelic algae in fresh water habitats (Hickman, 1976; Round, 1972; Gruendling, 1971) and littoral marine habitats (Asmus, 1982; Colijn and Dijkema, 1981; Colijn et al, 1976; Round, 1960; Hopkins, 1964; Castenholz, 1967; Admiraal et al, 1984). A number of authors also describe seasonal changes in epipelic standing crop in marine (eg. Jonge, 1980; Jonge and Colijn, 1992; Smyth, 1955) and freshwater (Moss, 1969; Hickman and Round, 1970) habitats. Perhaps it is because of sampling difficulties that data on the seasonality of marine subtidal marine epipelon are scarce in the literature. Although studies may well exist, hidden in the literature, it appears that the seasonal succession of subtidal marine epipelon has yet to be fully documented.

Section 4.1 described the spatial distribution of epipelon at a range of scales within the sediments of Loch Goil. However, these studies are limited in that they describe the algae only during the summer period. The study of the temporal pattern of epipelic algal succession provides an extra dimension to the understanding of the ecology of epipelon in Loch Goil and is fundamental to the principal aims of my research (aims: C, D and E; section 1.3).

The aim of this monitoring programme was to describe the seasonal variability of the epipelon within Loch Goil. The determination of the relationships and causal factors governing this seasonality is of secondary importance since only a very limited number of physical parameters (light attenuation, salinity and temperature) were monitored.

4.4.2 Methods

Samples of sediment were collected between June 1988 and June 1990 (22 months) from depths of 9m and 11m at approx. three- or four-weekly intervals. The frequency of sampling was partly governed by the availability of financial resources (220 mile round trip) and by the logistics of finding two voluntary helpers to assist with the diving operations. Fig. 17 shows the location of the sampling sites (C and e) along the bathymetric transect. Sampling was by means of standard replicate sediment samples (9 x 15.2 cm^2; see 3.1) collected from random positions at each station. Epipelic algae were harvested from the sediment samples (see 3.2 for method) and estimates made of epipelic algal abundance and chlorophyll-a using the standards methods described in section 3.3. Analysis of the epipelic community structure was only carried out on the 9m samples in view of a constraint on analytical time. Samples of interstitial water were collected at the sediment/water interface using a polypropylene syringe (50ml), from which the temperature was measured immediately following the dive. An estimate of the vertical extinction coefficient was made on each occasion utilising a small hand-held secchi disc (see 3.4.1.1). The product-moment correlation coefficient (r) was used to measure the degree of correlation between estimated values of algal abundance and chlorophyll-a.

The salinity of sea water at the sediment/water interface was determined on each sampling occasion (see 3.4.5 for method) but the data measured by the conductivity probe appear to be erroneous. There is a major inconsistency between the magnitude of my data (max. 39 ppt) and normal levels of salinity within Loch Goil recorded by the Clyde River Purification Board (max. 33 ppt., CRPB, unpubl. data). This contradiction in the data also casts doubt on the accuracy of the seasonal pattern of salinity levels so I have not included it in the analysis (see Appendix 3). The apparent correlation between the salinity data and temperature of sea water

(Fig.31) may be attributed to the sensitivity of the conductivity electrode to temperature.

4.4.3 Results

The vertical lines in the figures related to this section approx. correspond to the time of the longest and shortest day length and provide a crude estimate of the time of greatest and least irradiance.

4.4.3.1 Seasonal changes in epipelic standing crop

The epipelon show a distinct growing season with a series of discrete maxima from the middle of May to the end of September at 9m depth, and from beginning of July to mid-September at 11m depth (Fig.30). The general trend in the data is a period of minimum growth from approx. September 1988 to April (9m) or May (11m) 1989 followed by a phase of rapid growth. The decrease in the summer level was less rapid and was interrupted, particularly at the shallow site, by a series of short periods of variable algal growth, indicated by peaks 7 and 8 in Fig. 30. Maximum levels of epipelic standing crop were recorded at 9m depth on the 27th May and 5th August 1989 (441.49 x 10^6 m^{-2} and 448.58 x 10^6 m^{-2} respectively) whereas at 11m depth the maximum level was less (371.56 x 10^6 m^{-2}), peaking at the beginning of July 1989. Levels of algae were also consistently lower at the deeper station throughout the winter and spring period. This was particularly noticeable from September 1988 to April 1989 when levels at 11m ranged from approx. 50-100 x 10^6 m^{-2} compared with 75-200 x 10^6 m^{-2} at 9m depth. Although the data do not span two complete years, the pattern of growth does appear to be cyclical.

The data showed a good correlation between estimated abundance and chlorophyll-a; indicated by the results of the correlation analysis (9m r=0.78; 11m=0.903) and Fig. 30. The difference between the levels of correlation of the data from 9m and 11m depth indicates a difference in the epipelic community structure between these two

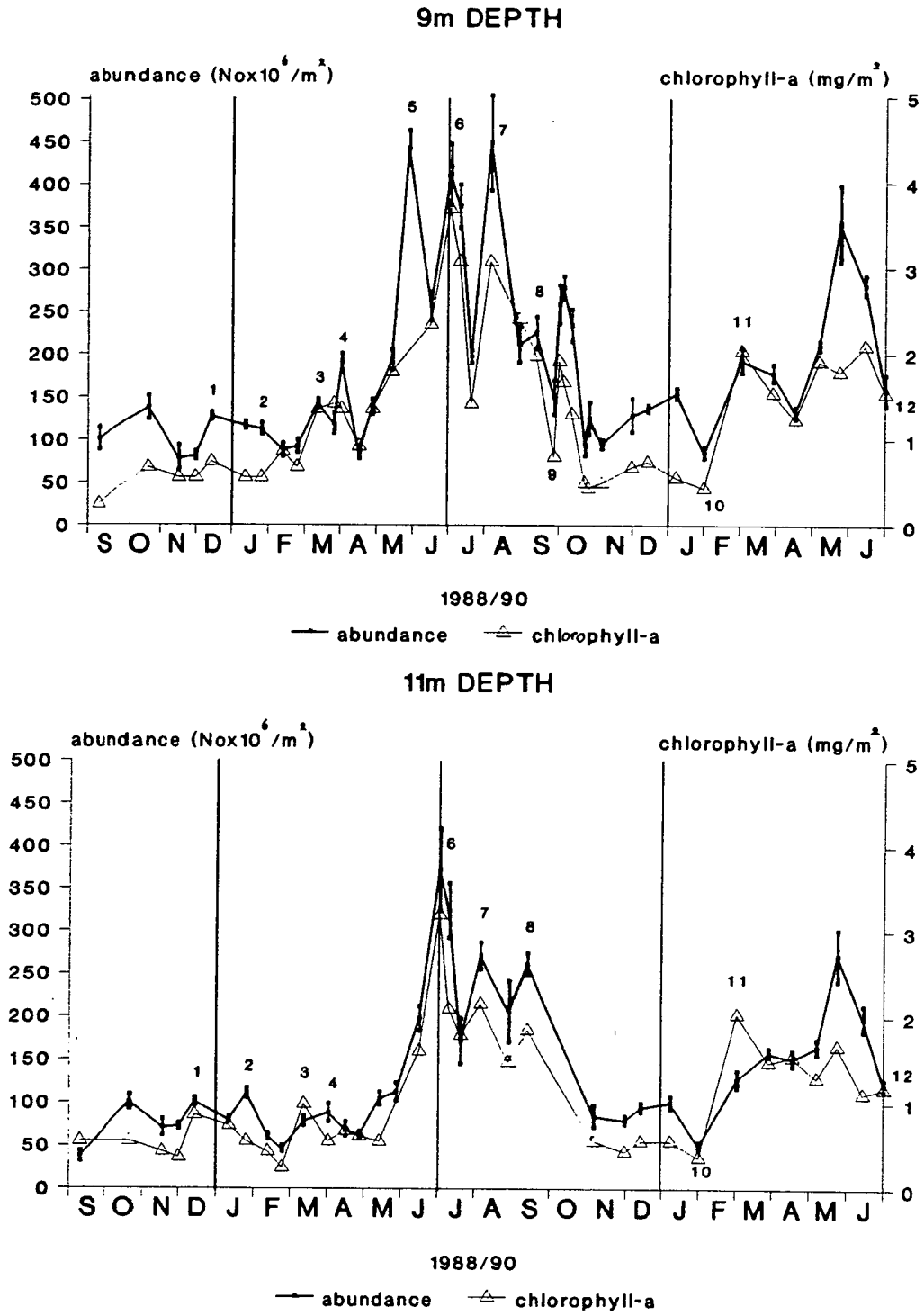


Fig. 30. Seasonal variation in epipelic abundance and chlorophyll-a from September 1988 to June 1990 at 9 m and 11 m depth. The numbers on the graphs provide a reference (see text) to levels of epipelon on particular dates and assist in the comparison of data. (standard error indicated by bars)

stations. The relatively high level of correlation (r=0.903), recorded at the deeper station, suggests a greater seasonal continuity of the size structure (and cell volumes) of the epipelic community.

Comparison of Figs. 30 and 31 show that the cyclic pattern of summer growth of epipelon closely follows the seasonal change in water temperature. The maximum temperature (19.5 ^{o}C) peaked in mid-June and approx. corresponded to the longest day. The lowest sea water temperatures (6-9 ^{o}C) occurred throughout the winter and spring from December to April. There was little difference between the water temperatures recorded from the different depths, indicating that the water column was well mixed to at least 11m depth over all the seasons.

The seasonality of the water clarity data (Fig. 32) roughly follows the change in water temperature (Fig. 31) with the lowest visibility over the winter period. This was attributed to a higher incidence of southerly and northerly winds during the winter resulting in wave-induced turbidity. Also water clarity was reduced by seasonal rainfall which would have carried higher levels of suspended solids into Loch Goil via ground and river water.

The effect of water clarity (visibility) on the pattern of epipelic growth appears to have been significant, particularly at the deeper station (see Figs. 30 and 32; the numbers on these graphs [1-12] provide a reference for the data on a selection of dates). At the shallow station (9m) small peaks in growth during the winter periods appear to correspond to incidents of increased water clarity (2,11), or increased clarity and temperature (1,3), whereas periods of reduced temperature and visibility correspond to drops in epipelic standing crop at 4, 10, and 12. The effect of water clarity on the epipelon is more noticeable at 11m depth. Clear water correspond to peaks in growth during the winter months (2,11) and during the summer (6,8). whereas poor water

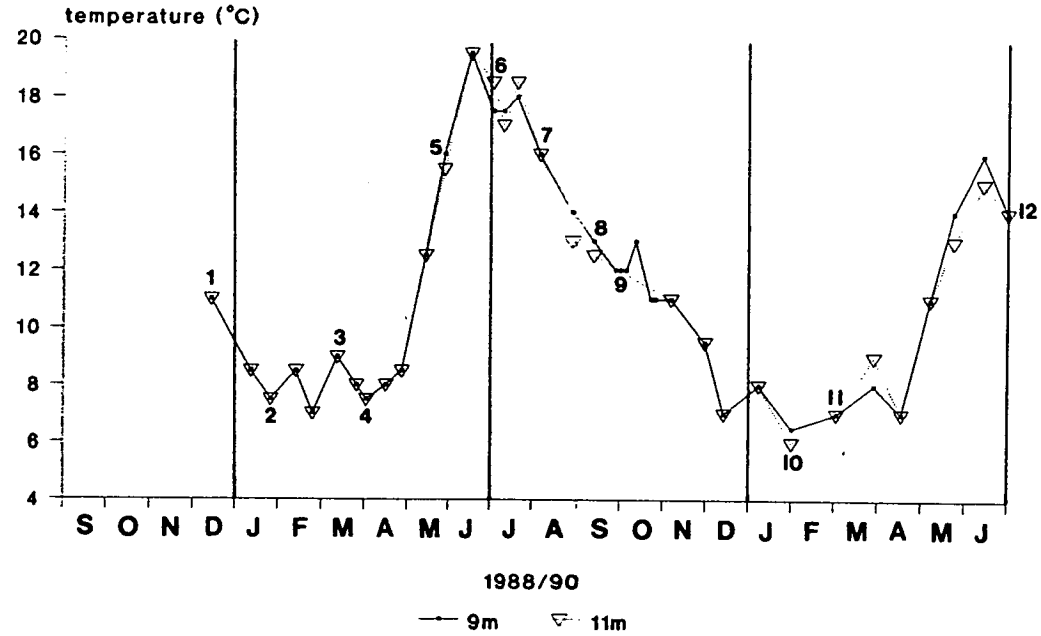


Fig. 31. Seasonal variation of sea water temperature sampled at the sediment surface. Numbers relate to particular sampling dates discussed in the text, and correspond to the numbers in Fig. 30.

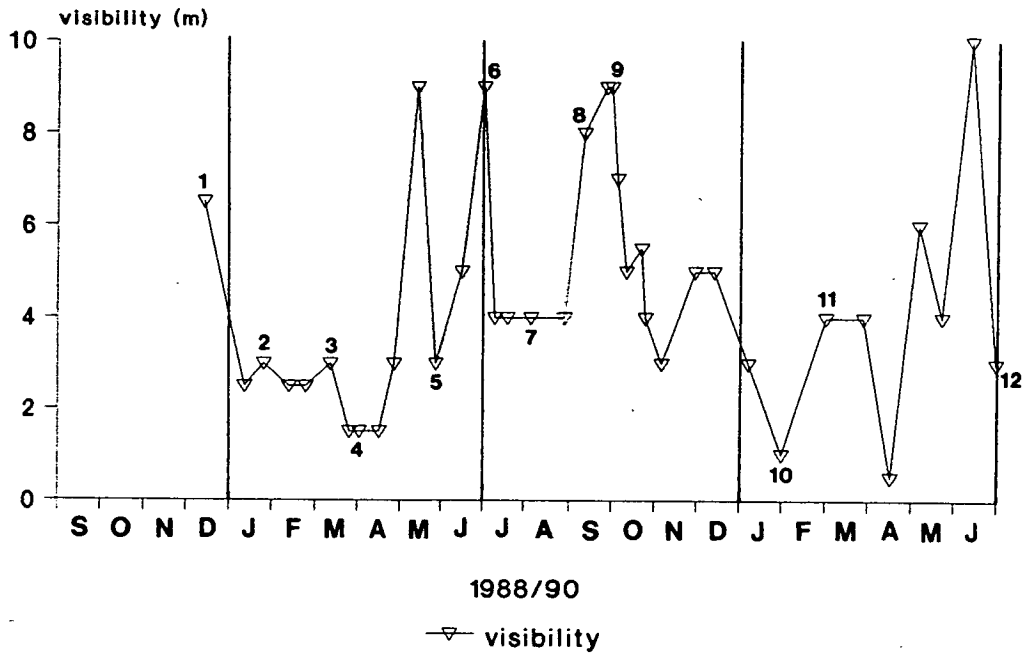


Fig. 32. Seasonal variation of estimated light attenuation based on the (vertical) clarity of the water column. Numbers correspond to those shown in Figs. 30, 31 .

clarity may have suppressed the growth of algae during July and August 1989 (7) and (combined with a drop in temperature) in February and June 1990 (10,12).

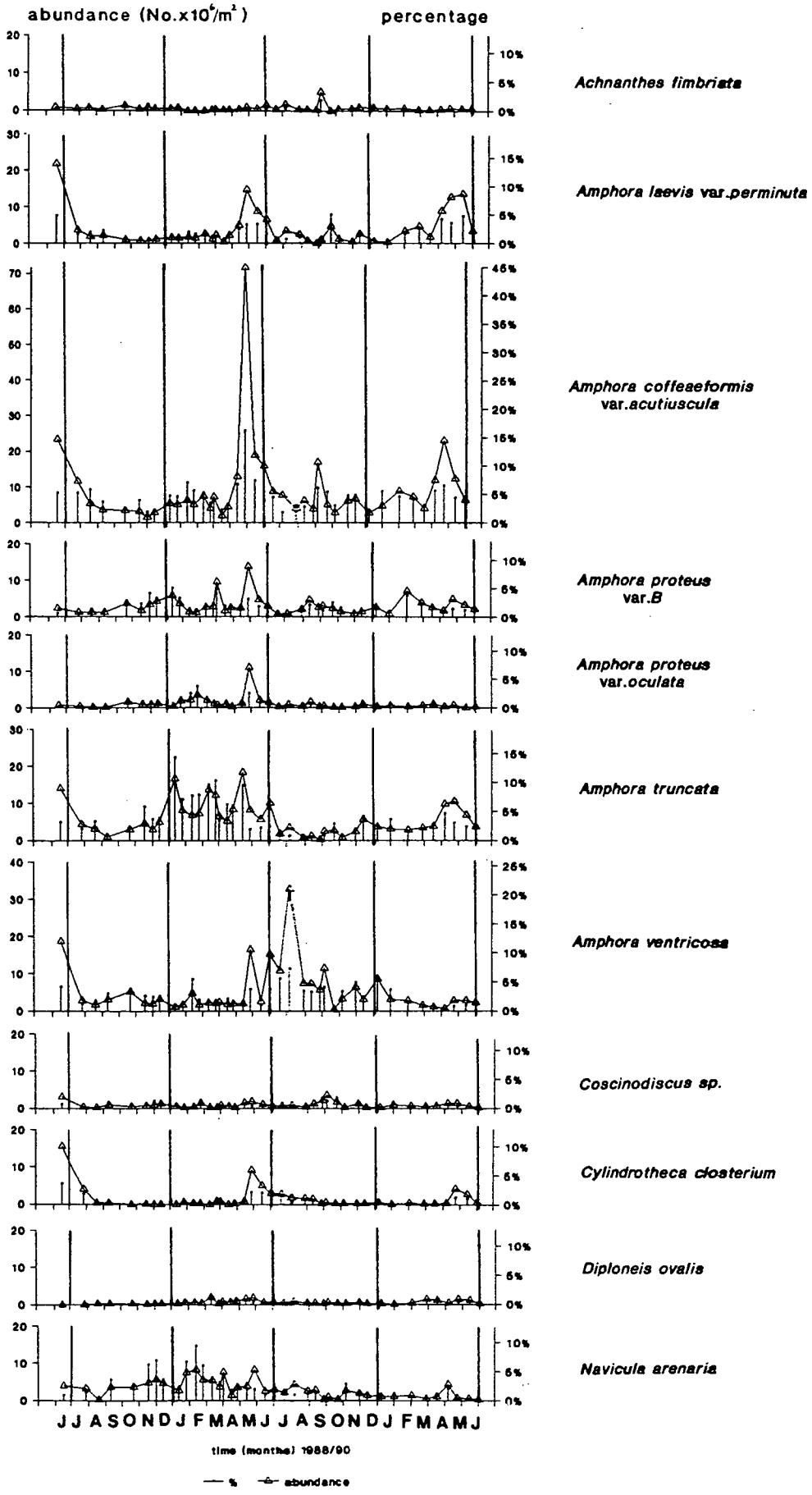
4.4.3.2 Seasonal changes in epipelic community structure

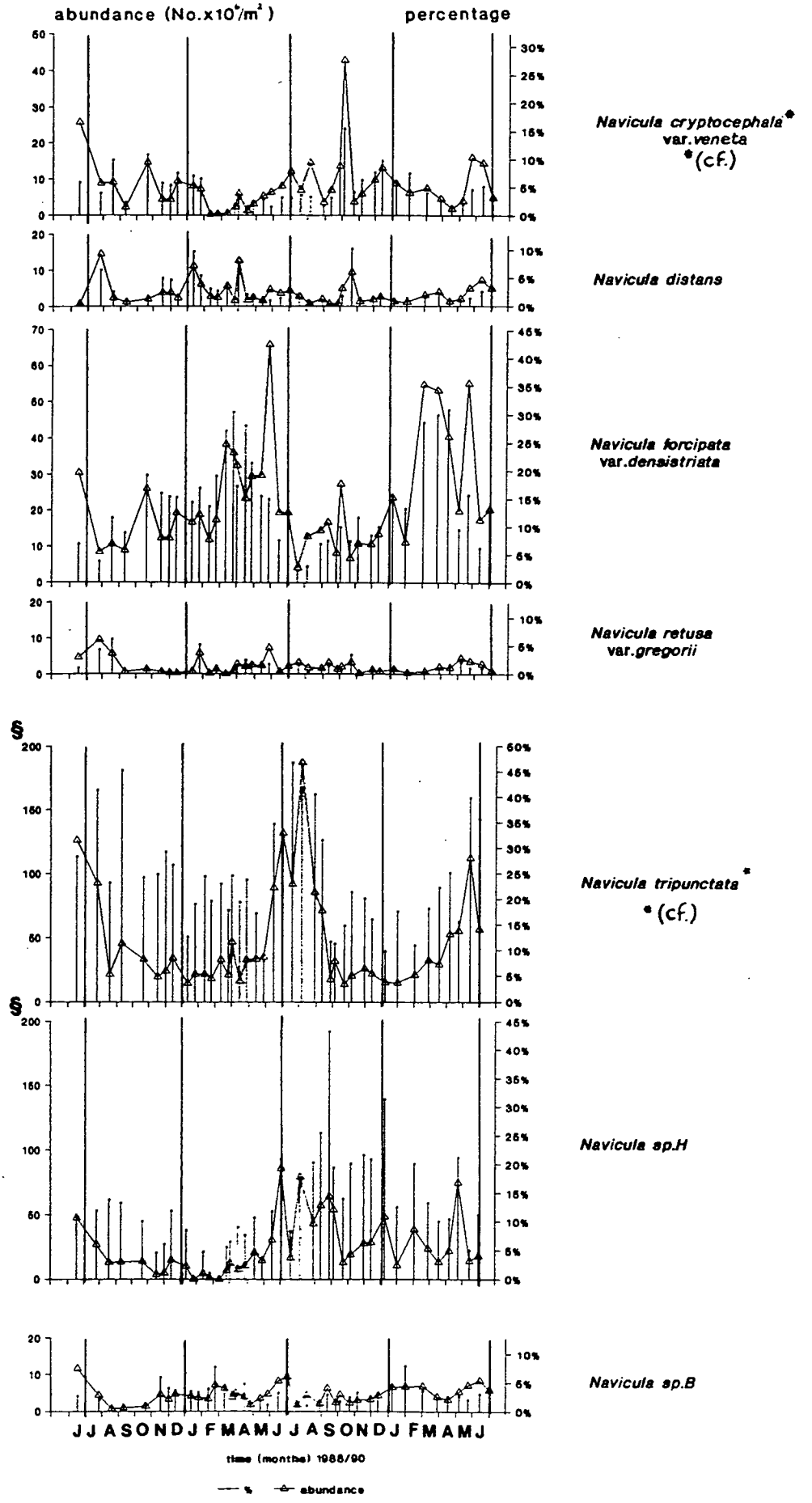
The sequence of the predominant epipelic algal species from June 1988 to June 1990 can be seen in Fig. 33. The temporal change in the community as a whole is shown in Table 10.

The most notable feature of the epipelon over the 22 month period is the dominance of *Navicula* cf.*tripunctata*, *Navicula sp.H* and *Navicula forcipata* var.*densistriata*. These species appear to grow throughout the year and seasonal fluctuations in their numbers mask the more subtle fluctuations in the density of the rarer species within the community. The continuity of the major components of the epipelon is illustrated in Fig. 34, which summarises the general pattern of the community (by genera) over time. Underlying this overall pattern there appears to be a complex succession of species over the seasons and many of these events appear to be cyclical from 1988 to 1990.

Examination of Fig. 30 show that the spring peak in algal growth in both 1989 (peak No.4) and 1990 (peak No.11) corresponds to the increased growth of *Navicula forcipata* var.*densistriata*, *Navicula sp.H*, *Navicula* cf.*cryptocephala* var.*veneta*, *Amphora proteus* var.*B*. and *Navicula distans*.

Numbers of algae increased sharply in May 1989 (peak No. 5) and 1990, attributed mainly to the growth of *Amphora coffeaeformis* var.*acutiuscula*, *Pleurosigma aestaurii* var.*candida* (especially in 1989) *Navicula* cf.*tripunctata* and *Navicula forcipata* var.*densistriata*. Peaks in growth were also seen in: *Amphora truncata*, *Amphora laevis* var.*perminuta*, *Amphora proteus* var.*B*, *Cylindrotheca closterium*, *Navicula sp.D*, *Navicula* cf. *cryptocephala* var. *veneta*, *Nitzschia angu laris*, and *Nitzschia sp.B*. Some other species showed increased growth


abundance (No.x10⁶/m²)
percentage
Achnanthes fimbriata
Amphora laevis var.perminuta
Amphora coffeaeformis var.acutiuscula
Amphora proteus var.B
Amphora proteus var.oculata
Amphora truncata
Amphora ventricosa
Coscinodiscus sp.
Cylindrotheca closterium
Diploneis ovalis
Navicula arenaria
J J A S O N D J F M A M J J A S O N D J F M A M J
time (months) 1988/90
% abundance


abundance (No.x10⁴/m²)
percentage
Navicula cryptocephala* var.veneta *(cf.)
Navicula distans
Navicula forcipata var.densistriata
Navicula retusa var.gregorii
§
§
Navicula tripunctata*
*(cf.)
Navicula sp.H
Navicula sp.B
J J A S O N D J F M A M J J A S O N D J F M A M J
time (months) 1988/90
% abundance

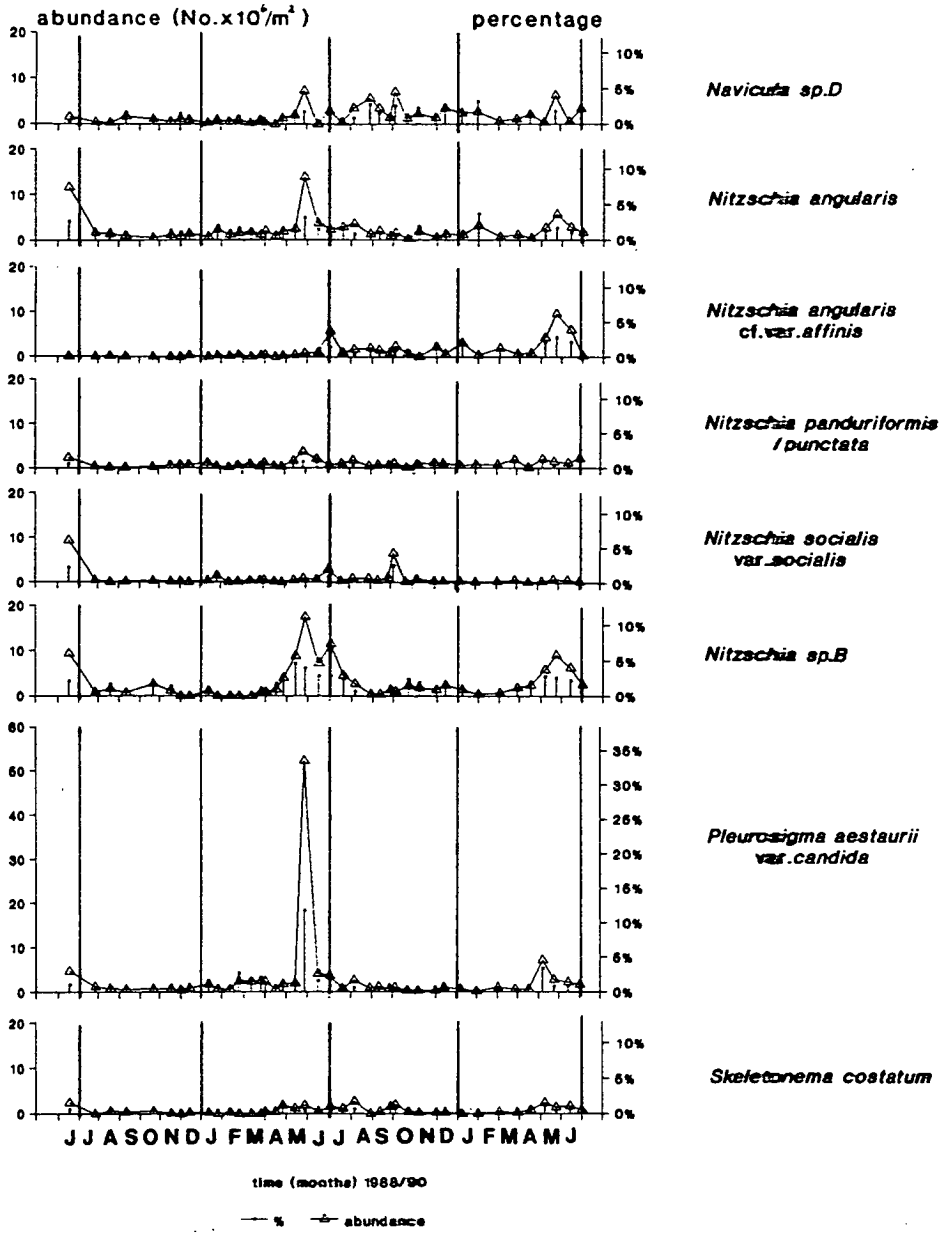


Fig. 33. Seasonal change in the estimated proportion and abundance of the major species of epipelon in Loch Goil, at 9 m depth, between June 1988 to June 1990.

§ Note the different scale

Table 10. Seasonal cycle of epipelic algae (estimated proportion of taxa [% abundance]) within Loch Goil at a depth of 9m. Based on observations made between June 15th 1988 and June 30th 1990. The table also shows the estimated abundance of epipelon (No.x10^6), the number of cells identified during the analysis of community composition and the total number of species within each sample community. Key: * = rare species (see section: 3.3.2.).

June 1988 to June 1989.

TAXON	Jn15	Jy26	A18	Sp9	Oc27	Nv16	Nv30	Dc13	Ja11	Ja25	Fb11	Fb22	Mc11	Mc25	Ap1	Ap15	Ap26	My13	My27	Jn15
Achnanthes conspicua var.conspicua																				
Achnanthes delicatula																				
Achnanthes limbriata	•	•	0.8	•	1.2	0.4	1.3	0.4	0.6	0.7				•	0.4	•	•	0.4	0.4	•
Achnanthes longipes f.lata																				
Achnanthes angustata																				
Achnanthes sp.	0.4	•	0.6	•	1.0									•		•	0.4	0.6	•	1.3
Amphiprora plicata	•		•	•		•					0.4			•	•		•	0.4	•	•
Amphora cf.arcus	0.4	•		•	•	•					•				•		•	•	•	•
Amphora coffeaeformis var.acutiuscula	5.4	5.5	6.3	3.8	2.9	4.2	2.0	2.4	4.9	5.3	7.5	5.9	5.9	3.9	4.4	2.6	4.0	7.7	17.6	7.8
Amphora coffeaeformis var.borealis		•																		
Amphora graeffii var.minor											•				0.4					
Amphora laevis var.perminuta	2.9	1.1	1.3	1.7	0.8	0.8	0.5	0.6	0.8	0.7	•	0.9	0.6	0.8	1.5	0.8	1.1	1.9	1.7	2.3
Amphora cf.lineolata	•																			
Amphora ostrearia var.ostrearia	•	•	•	•		•														•
Amphora cf.proteus var.A								•												
Amphora cf.proteus var.B	0.5	0.6	1.3	1.3	2.9	2.4	4.3	3.6	5.4	3.4	1.5	1.3	1.9	2.4	5.5	2.0	1.9	1.3	3.3	1.9
Amphora proteus var.oculata	0.5	0.4	0.8	0.6	1.4	1.6	1.4	1.4	1.2	2.1	3.1	4.4	1.9	1.0	1.1	1.6	0.4	0.8	3.1	1.0
Amphora proteus var.proteus	0.4	•	•	•	0.4	1.4	0.5	1.2	0.8	0.7	1.1	0.9	0.6	0.6	1.3	1.2	•	0.8	•	
Amphora truncata	3.2	2.1	3.5	1.1	2.5	6.2	3.8	4.3	15.5	8.0	8.2	8.5	10.4	11.2	3.7	6.6	6.5	10.0	2.0	2.3
Amphora ventricosa	4.3	1.3	1.9	3.2	4.1	2.8	2.5	2.8	1.0	1.6	5.7	2.0	1.7	1.8	1.3	2.2	1.5	1.0	3.9	1.0
Amphora sp.A	0.4	•	0.6	•	•	•	0.4	•	•	•	0.4	•		•	•	•	•	•	•	•
Amphora sp.B	2.2	0.9	0.8	0.8	0.4	•	0.5	0.8	1.0	1.1	2.1	1.3	1.5	0.6	•	0.4	1.0	1.3	1.7	1.5
Amphora sp.C	0.7	0.6	0.6	•	1.0	0.4	0.7	•			0.4	0.7	0.6	1.0	•	•	1.1	1.7	1.3	0.6
Amphora sp.D																				
Amphora sp.E								•												
Biddulphia aurita																	•			
Caloneis crassa																				
Caloneis crassa var.distoma																				
Caloneis liber var.elongata					•		•	•	•		•	•	•		•		•		•	
Caloneis liber var.excentrica									•								•	•		
Campylodiscus fastuosa		•	•		•		•	•	•	•	•	•	•		•	•		•	•	
Cocconeis scutellum cf.var.scutellum	•		•		•		0.4	0.4	0.4	•	•	•	•	•		•	0.4		•	•
Coscinodiscus sp.	0.7	•	•	1.1	0.4	0.8	1.3	1.0	0.4	•	0.4	1.5	•	•	0.4	0.6	•	0.8	0.4	0.4
Cymbella cistula var.genuina																				
Cylindrotheca gracilis	0.4														•		•			
Cylindrotheca closterium	3.6	1.9	0.4	0.4		•				0.5	•	•		0.8	0.4		•	0.4	2.2	2.1
Cymbella sp.																				
Dictyocha speculum var.speculum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Dimeregramma minor var.minor													•							
Diploneis aestiva var.delicata		0.4			•		•		•			•		•	•		•			•
Diploneis aestiva var.fusca								•		•		•		•	•	•	•	•		
Diploneis crabro					•		•	•		•	•	•			•	•				•
Diploneis ovalis			•	•	•	•	0.4	•	•	0.5	0.6	0.4	1.5	•	0.4	0.8	0.8	0.8	0.4	•
Diploneis smithii var.smithii	0.4	0.4	0.6	0.4	•	•	0.4	•	•	•	•	0.4	•	0.4	0.4	0.4	0.4	0.4	•	0.4
Diploneis splendida			•	•			•			•	•		•		•		•			
Donkinia reticulata	0.5	•	0.4	•	•	•	•			•	0.6	•	0.6	•	•	0.4	0.4	0.6	•	•
Eunotia cf.pseudopectinalis															•					
Eunotia cf.septentrionalis					•	•							•					•	•	
Eunotia sp.																				
Frustulia rhomboides var.rhomboides					•	•	•	•	•			•	•				•			
Frustulia rhomboides var.saxonica f.undulata								•								•				
Gyrosigma algoris	•		•	•		•			•					•	•	•			•	•
Gyrosigma distortum var.parkeri																				
Gyrosigma rectum	0.4	•	•	•		•	•		•					•	•	0.4	•	•	•	
Gyrosigma tenuirostrum	•	•			•	•						•	0.4		•	•	•	0.4		•
Navicula abrupta																				
Navicula arenaria	0.9	1.5	•	3.8	2.9	6.6	7.2	3.9	2.5	7.1	10.0	6.3	4.0	3.2	4.4	1.8	2.7	2.1	2.0	1.0
Navicula atlantica		0.4	0.4											•			•			
Navicula cf.bryophila																		•		
Navicula crucigera	0.4				•				•									•	•	
Navicula cf.cryptocephala var.veneta	5.9	4.2	10.4	2.3	11.5	6.0	5.6	8.1	7.4	6.9	0.4	0.4	0.4	2.0	3.5	1.6	2.5	2.9	1.5	3.4
Navicula cf.delognei		1.1	0.4													•				
Navicula cf.digito-radiata var.B													•							
Navicula cf.digito-radiata var.C								•												
Navicula digito-radiata var.cyprinus																				
Navicula distans	•	6.8	2.7	1.3	1.8	5.2	4.8	2.0	10.3	5.7	3.3	2.8	4.2	1.4	7.2	2.2	1.9	0.8	1.1	1.5
Navicula forcipata var.densistriata	7.0	4.0	12.1	9.3	20.2	16.7	15.8	16.4	15.3	17.8	14.4	20.0	28.6	32.3	18.6	29.4	23.0	16.3	15.7	8.0
Navicula gregaria	1.1	•		•		0.6	0.5	0.6	0.4	1.1	1.1	1.1	0.4	•	•			0.8	0.4	0.8
Navicula hennedyi var.hennedyi	•			•					•	•							•			
Navicula latissima						•		•			•									

June 1988 to June 1989 continued...

TAXON	Jn15	Jy26	A18	Sp9	Oc21	Nv16	Nv30	Dc13	Ja11	Ja25	Fb11	Fb22	Mc11	Mc25	Ap1	Ap15	Ap26	My13	My27	Jn15
Navicula lyroides		•																		
Navicula meniscus																				
Navicula palpebralis var.angulosa			•	•	•	0.4	•	•	•	•	•	1.3	•	•	•	•	•	•	•	•
Navicula palpebralis var.minor																				
Navicula phyllepta		1.7	1.7		•	0.4	•	0.6	•	1.4	0.4		0.4	•	0.7	•	•	•	•	
Navicula plicata var.constricta	•	•																		
Navicula retusa var.cancellata																				
Navicula retusa var.gregorii	1.1	4.5	6.5	0.6	1.0	0.8	0.4	•	0.6	5.5	•	1.5		0.8	1.5	2.6	1.9	1.3	1.7	•
Navicula cf.rhombica																				
Navicula subinflatoides																				
Navicula cf.tripunctata	29.1	43.4	24.4	47.7	25.8	26.0	30.3	28.8	13.4	20.1	25.9	20.7	24.4	18.9	26.8	20.5	25.7	18.2	8.3	36.5
Navicula sp.A	0.5	0.4	1.2	0.4	•	•	•		•			0.7	0.4	1.4	1.3	0.8	1.9	1.3	1.3	•
Navicula sp.B.	2.7	2.1	0.8	1.1	1.0	6.2	4.1	3.9	3.7	3.4	4.0	8.1	4.7	3.4	2.9	5.0	1.3	1.9	1.1	3.4
Navicula sp.C/D	0.4	•	•	1.7	0.8	0.6	1.4	0.8	•	0.9	0.6	1.1	•	0.8	•		1.0	1.0	1.7	
Navicula sp.F/G/H	11.0	12.5	14.6	14.0	10.6	4.8	6.3	12.8	9.1		5.0	1.1		5.9	7.0	9.5	8.2	11.3	3.5	12.4
Navicula sp.I																				
Nitzschia acuminata																				
Nitzschia angularis	2.9	0.8	1.5	1.1	0.6	1.4	1.3	1.4	0.6	2.3	1.5	2.0	1.5	1.0	1.3	1.0	1.5	1.3	3.5	1.7
Nitzschia angularis cf.var.affinis			•					•		•	•	0.4		•	•		0.4	•	•	0.4
Nitzschia bilobata var.bilobata														•						
Nitzschia aff.distans					•		•	•	•	•	•	•	•	•	•	•	•	•	•	•
Nitzschia hybrida cf.var.pellucida					•	•		•			•						•	0.4	0.7	0.6
Nitzschia insignis cf.var.spathulifera		•																		
Nitzschia insignis var.smithii	0.5			•	0.6	•	•	•	0.4	0.7	•		0.4	0.8	0.4	0.6	0.8	0.4	0.7	0.6
Nitzschia marginulata var.marginulata	•		•	•			•	•	•	•					•	0.4		•		
Nitzschia panduriformis/punctata	0.5	•	•	•	•	0.8	0.9	0.6	1.0	0.5	•	0.7	0.6	•	0.7	0.6	•	0.8	0.9	0.8
Nitzschia sigma var.?			•						•				•							
Nitzschia sigma var.intercedens	0.5	0.4	0.6	0.6	0.4	0.4	•	0.4	•	•		•	•	•	•	•	0.4	0.6	0.4	0.8
Nitzschia sigma var.rigida								•			•									
Nitzschia socialis var.socialis	2.2	•		•	0.4	•	0.4	•	•	1.4		•	•	•	•	•		•	•	0.4
Nitzschia sp.B/C	2.2	0.4	1.7	0.6	2.0	1.4			1.0					0.8	0.4	1.8	3.1	4.8	4.1	2.9
Opephora martyi								•							•		•	•		
Pinnularia ambigua		•	•	•	•										•					
Pinnularia ergadensis var.ergadensis																				
Pinnularia lata var.?																				
Pinnularia quadratarea var. subproducta								•					•							
Pinnularia subcapitata var.hilseana								•												
Pinnularia viridis var.mayeri																	•			
Plagiogramma stauophorum								•	•											
Plagiotropis tayrecta	0.4	•	•		•	•		0.4	0.4		0.4	0.4		•	0.4	0.6	0.8	•	•	
Pleurosigma aestuarii var.candida	1.1	0.6	0.8	0.6	0.6	1.0	0.5	0.6	1.6	0.7	0.8	2.8	1.7	2.2	1.3	0.8	1.3	1.0	12.4	1.7
Pleurosigma australe					•	•	•			•	•	•	•	•	•	0.6	•	•	•	
Pleurosigma formosum																•		•		•
Pleurosigma naviculaceum	•										•	•	•				•			
Pleurosigma nubecula																				
Pleurosigma salinarum	•	•	•	•	•	•		•	•		0.4	•		0.4	•	•	•	•	•	•
Pleurosigma strigosum	0.4	•	•	•	0.4		•	•		•	•	•	0.4	•	•	•	0.4	0.4	0.4	•
Rhabdonema minutum			•																	
Rhoicosphenia abbreviata																				
Scoliotropis latestriata																	•			
Skeletonema costatum	0.5		0.6	0.4	0.4	•		•	•		•				•	0.4	1.3	0.6	0.4	•
Stauroneis phoenicenteron var.phoenicentero											•		•							
Stauroneis salina var.lagerstedtii					•				•						•					
Stauroneis sp.								•												
Stenoneis inconspicua		•	•						•	•					•			•		
Stenoneis sp.	0.5			•	•								•				•	•		
Surirella fastuosa var.fastuosa	•			•	•		0.4	•	•	•	•	•	•	•	•	•	•	•		•
Synedra cf.fasciculata								•												
Synedra pulchella	1.1		•		•				•	•		0.4	•		•		•		•	
Tabellaria flocculosa	•		•			•	•	•				•	•	•	•	•	•	•		
Trachyneis aspera var.aspera		•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•		•
Tropidoneis lepidoptera														•			•			•
Tropinoneis vitrea var.scaligera		•			•			•	•	•	•	•	•	•	•			•		0.4
No. identified	557	530	521	472	489	503	558	507	485	437	522	459	472	493	456	503	522	478	459	477
Est. abundance (No.x10^6)	446	224	93	100	137	78	81	127	116	112	88	92	142	119	190	84	138	194	443	256
No. species	57	54	57	51	60	52	51	63	57	49	55	53	53	57	68	56	71	65	56	54

July 1989 to June 1990.

TAXON	Jy1	Jy19	A5	A28	Sp11	Sp26	Oc4	Oc22	Nv5	Nv29	Dc13	Ja7	Ja31	Mc4	Mc28	Ap16	My6	My23	Jn13	Jn3
Achnanthes conspicua var.conspicua										•										
Achnanthes delicatula							•													
Achnanthes fimbriata	0.4	•	0.4	•	0.4	0.4	2.3		0.7	0.4	0.9	0.7	0.6	0.4	•	•	•	•	•	0.4
Achnanthes longipes f.lata										•	•									
Acnanthes cf.angustata								•												
Achnanthes sp.	0.6	1.9	3.1	3.0	0.4	1.7	1.5	3.6	0.9	1.4	1.5	1.1	1.3	0.9	1.1	0.9	0.7	1.9	1.5	1.4
Amphiprora plicata	•	•	•	•	•	•	0.4	•	0.6	0.4		•	•	•	•	0.3	•	•	0.4	0.4
Amphora cf.arcus	•	1.1	•	0.4	•	•	•	•		•	•	•	•				•	•	•	•
Amphora coffeaeformis var.acutiuscula	4.8	5.1	2.1	2.2	3.1	3.5	7.5	5.7	3.6	5.5	5.6	2.0	6.1	4.9	5.3	3.4	6.1	7.1	5.1	4.3
Amphora coffeaeformis var.borealis																				
Amphora graeffii var.minor								0.4			•		•		•	•	•			
Amphora laevis var.perminuta	1.5	•	0.8	1.4	0.4	•	0.6	2.3	0.9	0.6	2.1	0.4	0.6	2.1	2.6	1.0	3.6	2.3	1.9	1.1
Amphora cf.lineolata									•	•										
Amphora ostrearia var.ostrearia	0.4	1.3	0.8	•	0.4	•	0.6	1.0	0.4	•	•				•			•	0.4	•
Amphora cf.proteus var.A					•															
Amphora cf.proteus var.B	0.7	0.4	•	1.0	2.2	1.9	1.2	2.7	1.7	0.8	1.1	1.8	1.1	4.0	2.3	2.1	0.9	1.5	1.3	1.4
Amphora proteus var.oculata	0.6	•	0.4	0.4	1.1	•	0.4	0.6	0.4	0.4	0.9	0.4	0.9	0.4	0.5	1.0	0.3	0.4	•	0.4
Amphora proteus var.proteus	0.6	•	•		0.4						•	•	•	•	0.9	•	•	•	0.4	0.4
Amphora truncata	2.6	0.9	0.8	0.4	0.5	•	1.0	3.1	0.9	2.0	4.5	2.5	3.9	1.5	2.0	3.1	5.0	3.2	2.5	2.4
Amphora ventricosa	3.9	5.9	7.8	3.7	3.5	4.1	4.4	0.4	3.6	5.3	2.4	5.9	3.9	1.5	0.9	0.9	0.3	0.8	1.1	1.4
Amphora sp.A	•	•	•	•	•	•	•	0.4	•	•	•	•	•	•	•	•	•	•	•	•
Amphora sp.B	0.4	•	0.6	0.4	•		•	3.6	0.6	•	•	•	•	•	0.5	0.5	1.0	1.7	3.4	1.1
Amphora sp.C	0.6	•	1.0	•	0.7	•	•	•	2.1	1.2	0.4	1.1		0.8	0.5	0.5	0.3	1.5	1.3	1.3
Amphora sp.D																•				
Amphora sp.E																				
Biddulphia aurita																				
Caloneis crassa								0.4												
Caloneis crassa var.distorna							•													
Caloneis liber var.elongata	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•			•	
Caloneis liber var.excentrica		•	•	•	•		•	•									•		•	
Campylodiscus fastuosa	•	•	•	•		•	•		•	•	•	•	•	•	•	•	•			
Cocconeis scutellum cf.var.scutellum	•	0.4	0.4	0.4	•		0.4	1.3	0.4	0.4	•	0.4	0.4		0.3	0.3	•	•	•	
Coscinodiscus sp.	•	0.4	•	•	0.5	1.5	1.3	1.9	•	1.0	•	•	1.1	0.4	0.3	0.5	0.7	0.4	•	•
Cybella cistula var.ginuina										•	•								•	
Cylindrotheca gracilis	•	•	•	•	•	•			•				•	•		•	•	•	•	•
Cylindrotheca closterium	0.7	1.5	0.4	0.8	0.7	•	•	•	•	•	•	0.4	•	•	•	•	•	1.3	1.1	0.4
Cymbella sp.							•			0.6							•			
Dictyocha speculum var.speculum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
Dimeregramma minor var.minor											•									
Diploneis aestiva var.delicata	•	•						•		•	•		•	•		•	•	•	•	•
Diploneis aestiva var.fusca			•		•	•	•	•		•	•		•	•	•	•				
Diploneis crabro						•	•		•			•	•		•	•				
Diploneis ovalis	•	•	•	•	•	•	•	•	•	0.4	•	•	•	•	0.8	0.9	•	0.4	0.4	•
Diploneis smithii var.smithii	0.4	0.6	0.4	•	0.4	0.4	0.6	0.6	0.4	0.4	0.6	0.4	0.6	0.4	0.3	0.5	0.3	0.4	0.4	0.4
Diploneis splendida	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	
Donkinia reticulata	•	•			•	•	•	0.4	•	•	•	•	0.4	•	•	•	•	•	•	•
Eunotia cf.pseudopectinalis						•	•					•								
Eunotia cf.septentrionalis								•	•							•				
Eunotia sp.								•			•						•			
Frustulia rhomboides var.rhomboides		•												•			•			
Frustulia rhomboides var.saxonica f.undulata																				
Gyrosigma algoris			•	•				•	•	•	•	•	•		•	•	•	•		•
Gyrosigma distortum var.parkeri								•						•	•		•	•		
Gyrosigma rectum				•			•	•	•	•							•			
Gyrosigma tenuirostrum	•	•	•	0.4	•				•			•	•	•	•	•	•	•		
Navicula abrupta											•									
Navicula arenaria	0.7	1.1	1.0	1.2	1.3	•	0.4	•	3.0	1.6	1.1	0.7	1.3	0.8	0.3	0.9	2.3	•	•	•
Navicula atlantica	•	•				0.4	0.4	0.6			•			0.4					•	
Navicula cf.bryophila																				•
Navicula crucigera	•		•			•	•			•			•		•		•	•	•	
Navicula cf.cryptocephala var.veneta	3.1	3.8	3.5	1.8	3.3	9.8	16.6	4.4	6.7	8.2	10.5	6.1	8.0	4.2	2.8	1.5	2.1	4.8	5.5	3.3
Navicula cf.delognei		0.4			•	•		•		•	•				•		0.3	•	0.4	
Navicula cf.digito-radiata var.B																	•			
Navicula cf.digito-radiata var.C																				
Navicula digito-radiata var.cyprinus		•				•										•				
Navicula distans	1.1	1.5	•	1.2	0.5	0.6	1.9	10.9	1.5	1.8	2.3	1.1	1.7	1.7	2.3	1.2	1.0	1.5	2.8	3.3
Navicula forcipata var.densistriata	5.0	2.3	3.1	7.3	7.8	5.9	10.6	7.8	12.3	9.0	10.7	16.3	14.1	30.6	31.8	32.6	10.2	16.6	6.6	13.4
Navicula gregaria	1.8	•	0.4				•			•		0.4								
Navicula hennedyi var.hennedyi						•							•							
Navicula latissima											•									

TAXON	Jy1	Jy19	A5	A28	Sp11	Sp26	Oc4	Oc22	Nv5	Nv29	Dc13	Ja7	Ja31	Mc4	Mc28	Ap16	My6	My23	Jn13	Jn
Navicula lyroides								0.4									1.7	•		
Navicula meniscus							•													
Navicula palpebralis var.angulosa	•	•					•		•	•	•	•	•	•	•	•	•	•	•	•
Navicula palpebralis var.minor											•		•	•	•					
Navicula phyllepta		0.4			•	0.6	0.4	1.5					0.4	•	0.3		0.7	•	0.6	•
Navicula plicata var.constricta			•	•	•		•	•	•		•		•	•	•	•	0.3	•	•	
Navicula retusa var.cancellata							•	•						•	•				•	
Navicula retusa var.gregorii	0.6	1.7	0.4	0.8	1.5	0.9	0.8	3.6	•	1.0	0.6	0.9	0.4	0.4	1.1	1.4	2.3	1.1	1.1	0.
Navicula cf.rhombica		•						•	•			•		•	•				•	
Navicula subinflatoides								•												
Navicula cf.tripunctata	33.8	49.8	44.7	42.8	33.2	12.4	12.1	15.9	22.8	21.5	17.3	10.4	18.8	11.8	19.3	23.6	27.0	16.6	42.4	37.
Navicula sp.A	0.9	1.3	1.4	0.6	1.3	0.6	0.6	1.3	0.6	0.8	0.6	0.7	0.7	1.3	0.6	0.9	2.4	0.4	0.4	1.
Navicula sp.B.	2.4	0.9	1.0	1.0	2.9	1.7	1.7	2.5	3.4	2.7	3.4	4.5	8.4	3.8	2.3	2.6	2.8	2.1	3.2	3.
Navicula sp.C/D	0.7	•	0.8	2.8	1.6	0.9	2.7	1.3	2.4	1.2	2.8	1.6	3.3	0.4	0.6	1.7	•	1.9	•	2.
Navicula sp.F/G/H	22.0	8.9	18.9	21.5	26.8	45.9	20.8	14.9	21.5	23.0	22.6	33.1	13.4	21.4	14.0	10.6	11.3	22.5	5.3	11.
Navicula sp.I																	•		•	
Nitzschia acuminata		•								•	•			•			•			
Nitzschia angularis	0.7	1.7	1.0	0.8	1.1	0.7	1.0	0.4	2.2	0.6	1.1	0.9	4.1	0.6	0.8	0.5	1.6	1.9	1.3	1.
Nitzschia angularis cf.var.affinis	1.5	0.6	0.4	1.0	0.7	0.7	1.0	1.0	•	2.0	0.6	2.1	0.6	1.1	0.5	0.7	2.3	2.9	2.3	•
Nitzschia bilobata var.bilobata		•	•						•											
Nitzschia aff.distans	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	0.4	•
Nitzschia hybrida cf.var.pellucida	0.6	•	•	•	•	•			0.4	•	•	0.4	•		•	0.3	0.9	•		
Nitzschia insignis cf.var.spathulifera								•												
Nitzschia insignis var.smithii	0.9	0.8	0.8	0.4	0.7	0.6	1.0	0.8	0.6	1.4	1.1	1.1	0.9	1.3	0.8	0.7	0.7	•	0.8	0.5
Nitzschia marginulata var.marginulata						•			•						•				•	•
Nitzschia pandurliformis/punctata	•	0.6	0.4	•	0.4	0.4	0.4	•	0.9	1.0	0.8	0.4	0.9	0.4	1.1	•	1.0	0.4	0.4	1.4
Nitzschia sigma var.?																				
Nitzschia sigma var.intercedens	0.6	0.6	0.6	0.8	0.7	0.7	0.6	0.4	0.7	0.8	0.8	0.5	0.6	0.4	0.3	0.3	0.3	•	0.6	•
Nitzschia sigma var.rigida											•									
Nitzschia sociala var.socialis	0.7	•	•	0.4	•	0.9	2.7	•	0.7	0.6	0.4	•	0.6	0.6	0.6	0.9	0.3	0.4	0.4	0.7
Nitzschia sp.B/C	3.0	2.5	0.6	•	•	0.9	0.4	2.5	2.1	1.2	1.9	0.9	0.4	0.4	1.1	1.9	2.9	2.7	2.3	1.6
Opephora martyi						•			•			•				•	•			
Pinnularia ambigua	•		•		•							•			•	•	•			
Pinnularia ergadensis var.ergadensis															•	•	•			
Pinnularia lata var.?																	•			
Pinnularia quadratarea var. subproducta			•	•			•							•	•	•				
Pinnularia subcapitata var.hilseana																				
Pinnularia viridis var.mayeri																				
Plagiogramma staurophorum							•	•				•	•							
Plagiotropis lepyrecta	0.4	•				•	•	•		•	•	•		•	•	•	•	•	•	
Pleurosigma aestuarii var.candida	0.9	0.4	0.6	0.4	0.5	0.6	0.4	0.4	0.4	•	0.8	0.4	•	0.6	0.3	0.5	3.6	0.8	0.8	1.1
Pleurosigma australe									•		•		•			•	•			
Pleurosigma formosum	•		•	•			•		•	•	•	•	•	•			•			
Pleurosigma naviculaceum								•		•	•									
Pleurosigma nubecula	•						•		•				•							
Pleurosigma salinarum			•	•	•				•		•	•	•	•	•	•	•		•	
Pleurosigma strigosum	•	0.4	•	•	0.4	•	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3	0.5	•	0.4	•
Rhabdonema minutum							•		•		•		•	•		•	•			
Rhoicosphenia abbreviata																				
Scoliotropis latestriata												•							•	
Skeletonema costatum	0.4	0.6	0.6		•	1.1	0.8	0.4	•	•	•			•	•	0.7	1.2	0.4	0.6	0.5
Stauroneis phoenicenteron var.phoenicentero																				
Stauroneis salina var.lagerstedtii		•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	
Stauroneis sp.																				
Stenoneis inconspicua	•					•	•	•	•	•			•	•	•	•	•	•		
Stenoneis sp.	•		•		0.3		•			0.5			•	•	•		0.7			•
Surirella fastuosa var.fastuosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
Synedra cf.fasciculata																				
Synedra pulchella								•												
Tabellaria flocculosa	•		•			•	•	•	•	•		•	•	•	•	•	•		•	•
Trachyneis aspera var.aspera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Tropidoneis lepidoptera					•						•				•		•	•		
Tropinoneis vitrea var.scaligera	0.4	0.4	0.4	0.4	0.4	•	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3	•		•	
No. identified	542	528	486	493	549	540	519	523	535	512	532	559	538	527	642	585	577	476	472	552
Est. abundance (No.x10^6)	411	197	449	211	226	149	279	93	95	128	136	154	85	193	178	132	211	355	282	158
No. species	64	66	66	57	61	63	74	72	69	69	73	65	70	69	74	70	81	60	66	51

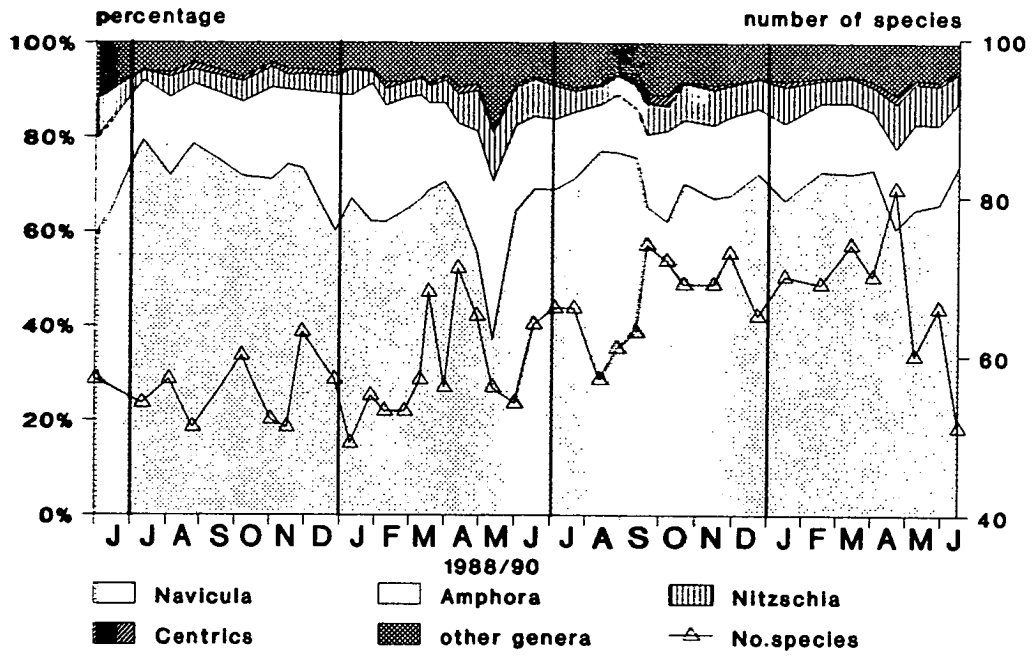


Fig. 34. Seasonal variation in the number of species of epipelic algae and in the change of community structure, indicated by the proportions of the main genera. June 1988 to June 1990.

at this time of the year but this occurred somewhat later in June 1988 (*Navicula retusa* var. *gregori*) or in June 1989 (Navicula cf.cryptocephala var.veneta and *Navicula sp.H* and *Nitzschia angularis* cf.var.*affinis*).

In the early summer of 1989 growth of *Navicula* cf.*tripunctata* and *Navicula sp.H*, *Nitzschia sp.B*, *Amphora ventricosa* and *Amphora truncata* resulted in a peak (No. 6) in epipelic density which diminished with the onset of a planktonic bloom of algae (Fig. 30). This community gave way to an assemblage dominated by *Amphora ventricosa* and *Navicula* cf.*tripunctata* (peak No.7). This was succeeded at the end of September and beginning of October (1989) by an autumn bloom of epipelic growth characterised by the dominance of *Navicula sp.H*, *Navicula* cf.*cryptocephala* var.*veneta*, *Navicula distans* and *Navicula forcipata* var.*densistriata*. The following species also showed increases in their growth during the autumn: *Navicula sp.D*, *Nitzschia socialis* var.*socialis*, *Amphora laevis* var.*perminuta*, *Amphora coffeaeformis* var. *acutiuscula* and *Achnanthes fimbriata*. The pattern of succession in the summer and autumn of 1989 is similar to the sequence in 1988 but there is some variation in the timing and occurrence of growth of some of the rarer species (eg. *Navicula distans*). Examination of Table 10 shows that many of the rarer diatom species showed no clear seasonal pattern of growth or had irregular seasonal cycles with apparently random fluctuations in population numbers (eg. *Navicula phylepta*)

4.4.4 Discussion

The seasonality of epipelic growth within the shallow (9 and 11m) subtidal region of Loch Goil appears to be responding to annual cycles of water temperature and irradiance. Underlying the pattern of a summer growth period (approx. May to September) and an over-winter period of minimum growth (approx. October to April), the epipelon experienced short-term fluctuations in standing

crop. These appear to follow changes in water temperature and visibility (light attenuation). Peaks in epipelic standing crop during the growth period are associated with sequential growth of different diatom species and are dominated by the growth of a number of key species (Fig. 33). Unfortunately much of the detail of the development and senescence of these bloom events are lost by the frequency of the sampling (approx. biweekly). This has undoubtedly resulted in the missing of the more subtle variations and successions of the epipelon, especially those species with short growing periods.

The period of epipelic growth in Loch Goil starts later in the year than the spring increase in phytoplankton (>1 mg chl-a m^{-3}), which typically occurs during March in Scottish west coast sea lochs and Norwegian fjords (Tett and Wallis, 1978). In Loch Creran, in the northern Firth of Clyde, a spring increase in phytoplankton reaches a peak (12 to 37 mg chl-a m^{-3}) at the end of March (1970-76) with fluctuating levels up to mid-September and minimal growth from October to January. Unlike the epipelon of Loch Goil (which showed a distinct period of growth in September and October 1989 at 9m depth) there is no regular recurring autumnal bloom of phytoplankton in Loch Creran. In lochs Striven and Fyne spring increase takes place in March or early April with growth continuing through summer with typically an early autumn bloom of dinoflagellates in September. Similarly, Tett (1982) recorded seasonal spring and summer increases in phytoplankton growth (May, June and July 1976) in Loch Eil and the Firth of Lorne. It appears that the growing period of epipelon starts later and finishes later than that of the phytoplankton.

4.4.4.1 The epipelon

A striking feature of the epipelon of Loch Goil, over the observation period of 2 years (1988-1990), is that the flora was composed almost entirely of diatoms with only one species of silicoflagellate (*Dictyocha speculum* is

generally considered to be phytoplanktonic). The prevalence of diatoms in the subtidal epipelon is not uncommon and has also been documented by Bodeanu, 1964 and Plante-Cuny, 1969.

The seasonal fluctuation of epipelic standing crop in Loch Goil is very similar to the pattern of fluctuation of epipelic chlorophyll-a recorded in an intertidal mudflat in the Dutch Wadden Sea (Colijn and Dijkema, 1981). They recorded a characteristic period of low over-winter growth followed by a spring bloom that started in March (comparable to peaks 3 and 4 in Fig. 30). Similarly their spring bloom was followed later by a period of maximum growth in May and June. They also recorded a distinct summer depression in July which was succeeded by an early autumnal bloom which extended from August to October. Colijn and Dijkema related fluctuations in levels to abiotic factors such as the washing away of diatoms by severe wave action or by heavy rainfall. The annual cycle of epipelic growth was related to irradiance levels with the summer low attributed to photosynthetic inhibition by high light intensities. However, because of the absorption and scattering of light by sea water, photosynthetic inhibition is unlikely to be a factor that limits the growth of epipelon in the subtidal sediments of Loch Goil. Another parallel between the intertidal flora reported by Colijn and Dijkema and the flora of Loch Goil is the dominance within the epipelic community by a few species which appear to be indifferent in their spatial distribution. In Loch Goil *Navicula cf.tripunctata*, *Navicula sp.H* and *Navicula forcipata* var.*densistriata* were the most abundant species and examination of Fig. 22 in section 4.3.3.2 shows these species to be dominant (and *Amphora proteus* var.*B*, *Navicula arenaria*) at all the observed depths (6-40m) within the loch. However, although there are some similarities in the floras of these different habitats, only *Navicula arenaria*, *Navicula cryptocephala* and *Amphora coffeaeformis* were found in

abundance in both their study and mine. Conversely, *Navicula forcipata*, which formed over 30% of the diatoms during early spring in Loch Goil, formed less than 5% of the intertidal flora in the Wadden Sea. Unfortunately the most abundant species their "*Navicula spec. 10*" which contributed almost exclusively to the peaks of high biomass in their data was not identified to species level by Colijn and Dijkema. Comparison of levels of epipelic chlorophyll-a from my study with those of Colijn and Dijkema (1981) shows my data (max. 4.5 mg m^{-2}) to be approx. an order of magnitude lower than levels in the Wadden Sea (average value of 65 mg m^{-2}). However the disparity in the data can be attributed to methodological differences as Colijn and Dijkema extracted pigment directly from the upper 2cm of sediment whereas my method extracted pigment only from motile cells harvested into lens tissue (see 3.2.2.3).

The seasonal fluctuation in epipelic standing crop in Loch Goil also corresponds with the pattern of growth recorded in Loch Sween between 1944-46 (Smyth, 1955). Smyth recorded peaks in growth in February and April followed by a steady high summer population, a rise again in August, and a slow decrease to the winter level.

There is some similarity between the seasonal pattern of epipelic growth in Loch Goil and that recorded by Plante-Cuny (1969) in the Mediterranean off Marseilles. In this detailed seasonal survey the period of maximum growth was found to occur during the spring months April to May. Plante-Cuny also observed fluctuating levels during the summer months with a low period in June and July (1964) which is comparable both to my data and to that recorded by Colijn and Dijkema (1981).

4.4.4.2 Effect of depth

There is clearly an effect of depth below the water column on the general level of epipelon and on the timing of some of the peaks in algal growth (Fig. 30. peak no.5). This is similar to the pattern of epipelic growth (and

production) in the freshwater lakes Windermere and Blelham Tarn (Round, 1961), where it was found that deeper stations tend to peak in production later in the year than the shallow stations. The relationship between algal density and depth is also consistent with the results of my investigation of the bathymetric distribution of epipelon in Loch Goil during the summer of 1989 and 1990 (section 4.3). This study showed there to be little difference in the community structure of the epipelon over the 6-15 m depth range in 1989 and 6-20 m depth range in 1990. Therefore the remarkably similar pattern of seasonal variation recorded at 9m and 11m depth (Fig. 30) probably represents a similar sequence of growth of diatom populations.

4.4.4.3 Effect of grazing

The diminished levels of epipelon at 11m are likely to be related to lower irradiance levels. However, there is evidence that the level of grazing by macro-invertebrates is different at these two stations (see Table 15, section 5.1). In particular, peaks in abundance of *Abra alba* (bivalve) and *Eupolymnia nebulosa* (polychaete) at station '12m' (located approx. 20m away from the 11m station of this study) may limit the abundance of epipelon at this depth. Grazing by animals may contribute to the demise or limitation of overall levels of epipelon. However it would require selective grazing of different diatom species to influence the successional change of the epipelic community structure by the proliferation of inedible (larger) species of diatom. This would cause species-specific differences in the equilibrium of growth and mortality and would result in changes in the community structure of epipelon.An example of this in the literature is a study by Admiraal et al (1983) who found that rapid development of meiofauna on an intertidal mudflat caused a change in the dominance of epipelic species.

Evidence from my study of the benthic macrofaunal community of Loch Goil (section 5.1) showed there to be a

diverse and abundant community of surface feeding detritivores. The inference is that this community of invertebrates graze extensively on the subtidal epipelon. Nevertheless, the effect of grazing at the micro- (<0.062mm; eg. protozoan), meio- (0.062-0.5mm; eg. nematodes) and macro-faunal (>0.5mm; eg. polychaetes) levels on the seasonality of epipelon is unknown. Certainly in the plankton, the zooplankters increase their populations later than the algae as their growth is more sensitive to temperature so that for a time grazing may be unimportant (Moss, 1988).

In Loch Goil there will undoubtedly be seasonal changes in the abundance and composition of invertebrates. For example a study by Buchanan *et al* (1978) of an invertebrate community off the Northumberland coast (50-80m depth) reported a clear annual cycle in the invertebrate community. They recorded an increase in numbers and biomass in the summer followed by a large winter mortality. The main reason for the annual fluctuation in the invertebrate community is the larval recruitment that occurs in the summer. In addition the composition of large, motile invertebrates (eg. *Ophiura albida*), may change in Loch Goil as a result of their migratory behaviour. The effect on the epipelon of annual changes in the benthic fauna may be profound. The summer recruitment of post-larval invertebrates occurs during a period of optimal epipelic growth and may be synchronised with this event (as well as temperature). The post-larval invertebrates are small enough to be meiofauna (0.062-0.5mm) and it is likely that the maximum size of diatoms consumed by eg. polychaete larvae would change with the growth of the animals. The effect of grazing by herbivorous larvae on the seasonality of the epipelon (levels and community composition) is likely to be complex and is an area worthy of further study.

4.4.4.4 Effect of Temperature and light attenuation

The general seasonal pattern of changes in temperature and light attenuation can be accounted for by the normal annual cycle of air temperature, day length, and light intensity. Although I do not have irradiance data, examination of Boney's (1986) data in Firth of Clyde (1976-77) shows there to be a very similar pattern of irradiance and sea temperature change over an annual cycle. Therefore it is not possible, from this study, to separate the effects of these two determinants on the seasonality of the epipelon. The results clearly show a relationship between either or both of water temperature and irradiance on the levels of epipelic algal growth in Loch Goil. Of course, this is of no surprise as total production of algae in any habitat tends to follow the general pattern of variation of irradiance or temperature (Round, 1981). Similarly, Gruendling (1971) reported that temperature was the major determinant of seasonality (a peak in epipelic growth from May to September) at all depths in Marion Lake, British Columbia.

Examination of the light attenuation (visibility) data (Fig. 32) shows there to be some notable fluctuations in the clarity of the water, particularly in the spring and summer of 1989 and in June 1990. These can be attributed to phytoplankton blooms which occur annually at this time of the year in all the sea lochs of the northern Firth of Clyde (CRPB pers. comm.). This compares with periods of low visibility in the winter months (eg. January 1990) which coincide with storm conditions and hence very turbid conditions. Although I do not have data for all the planktonic bloom events, the reduced visibility observed in June 1990 corresponds to a spectacular bloom of *Emiliania (Coccolithus) huxleyi* which persisted throughout July. (More recently, in July 1992, the waters of Loch Goil and Loch Long have experienced prolific growth of the dinoflagellate *Scrippsiella trochoides* [Pers. obs.]). The correlation of the light attenuation data to periods of suppressed epipelic growth

clearly indicates the complexity of the relationship between cyclical events of phytoplankton and those of the epipelon. Periods of excessive phytoplanktonic growth may have had a cloaking effect, limiting the incident light reaching the sediment and reducing the growth of the epipelic algae. Conversely the effect of phytoplankton on water turbidity may be of secondary importance, with the epipelon responding to changes in water chemistry associated with the plankton blooms. Certainly in the case of *E. huxleyi*, its proliferation in the summer of 1990 can be linked to low levels of total oxidised nitrogen (0.69 *u*g atom.l^{-1}) in the surface waters of Loch Goil (see table 11). According to work by Eppley, Rogers and McCarthy (1969) conditions of low nitrate levels provide *E. huxleyi* with a competitive advantage over diatoms until upwelling of deeper waters increase nitrate levels, allowing diatom growth. This prediction appears to be confirmed by the situation in Loch Goil (Loch Goil: TON=3.2 *u*g atom.l^{-1} at 80 m depth; see Table 11). It is possible that reduced levels of nitrate within the water column may also have limited epipelic diatom growth in this instance.

4.4.4.5 Nutrient effects

The effect of nutrient levels on the seasonality of epipelon in Loch Goil would require further investigation involving measurement of micronutrient concentrations at the sediment surface or within the interstitial water. However, some discussion is possible based on the data on levels within the water column obtained by the CRPB (Table 11). Grantham (1991) also measured nutrient levels within Loch Goil during 1989, but these data are not refered to in this thesis.

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

Date/ depth	Sal ‰	Temp °C	D.O. ppm	NH_4-N	TON	PO_4-P	SiO_2	Chl-a
29/6/88								
1m	31.76	14.72	11.42	0.70	0.46	0.43	1.47	2.01
80m	32.90	9.65	5.62	11.30	15.17	2.14	16.00	0.09
28/10/88								
1m	29.01	11.31	7.77	0.00	8.01	1.51	-	0.39
80m	32.90	8.10	0.81	0.20	23.37	5.07	-	0.11
19/01/89								
1m	21.98	7.60	9.87	8.20	19.38	1.81	28.00	0.13
80m	32.72	9.33	1.46	0.30	18.30	3.93	45.00	0.02
04/04/89								
1m	25.27	7.21	14.45	0.00	13.67	0.12	-	1.47
80m	32.66	9.22	2.35	0.00	27.21	4.35	29.00	0.32
06/07/89								
1m	30.91	17.40	10.10	0.00	0.52	0.52	2.50	0.68
80m	32.86	8.35	4.75	9.30	12.03	1.95	10.20	0.10
17/10/89								
1m	26.20	12.60	7.12	0.30	11.39	1.68	11.80	0.66
80m	32.79	10.00	1.60	0.00	24.22	4.43	24.00	0.03
7/12/89								
1m	31.99	8.46	6.79	0.00	13.19	1.98	14.80	0.52
80m	32.82	9.82	0.70	0.10	21.23	4.73	31.00	0.28
08/03/90								
1m	18.73	6.90	9.90	10.00	24.60	1.22	20.00	0.15
80m	32.97	9.74	4.44	0.60	16.78	5.29	24.00	-
09/04/90								
1m	24.06	8.10	17.24	0.40	15.55	2.85	19.80	14.10
70m	*	*	4.81	0.40	22.12	3.20	25.00	0.61
80m	32.94	9.68	4.40	0.20	23.25	3.82	28.00	8.59
11/07/90								
1m	30.48	12.82	10.80	0.40	0.16	0.69	0.20	5.12
80m	33.03	8.10	3.96	0.40	17.56	3.20	8.65	0.06

Table II. Environmental parameters recorded from the surface (1m) and bottom of Loch Goil during the period **June 1988** to **July 1990.** The data include micronutrient concentrations and phytoplankton chlorophyll-a. Data was collected by the Clyde River Purification Board (unpublished) from a site (80m) at 56 08.5'N 04 53.3'W or at the mouth of the loch, over the sill (40m).

KEY: Chlorophyll-a (Chl-a, ug/l), ammoniacal nitrogen (NH_4-N, ug.at./l), TON (total oxidised nitrogen [Nitrate and nitrate] ug.at./l), Temperature (°C), Ortho-phosphate (PO_4-P, ug.at/l), salinity (sal, ppt), dissolved oxygen (D.O., ppm) Silicate (SiO_2, ug.at./l). Data flags: - = data not collected, * = data not shown.

Bowers, 1984). Conversely, in the study of a freshwater lake, Hickman (1976) observed no significant relationship between the seasonality of epipelon and levels of micronutrients in the overlying water (he also reported that temperature was not a principal controlling factor of algal growth!). I suspect that a similar relationship with water chemistry exists in Loch Goil as the intimate association between the epipelic algae and the sediment is likely to ensure adequate levels of dissolved silica and other micronutrients. This is consistent with Round *et al* (1990) who indicate that silicate is unlikely to be reduced to limiting concentrations except for epipelic communities living on highly calcareous or highly organic sediments. They therefore predict that:

"...on the whole benthic diatom populations will behave quite differently from planktonic populations."

For phytoplankton communities silicate levels of less than 0.5 *ug* atom.l^{-1} are considered limiting to algal growth (Brockmann et al, 1990). Brockmann also found inorganic nitrogen below levels 1 *ug* atom.l^{-1} (TON) were limiting to phytoplankton growth in the North Sea. As a consequence spring blooms of phytoplankton are normally characterised by a shift from predominantly diatoms to flagellate species as levels of SiO_2 become limiting but phosphate, nitrate or ammonia are still available (Reid et al, 1990; Brockmann et al, 1990).

It appears from my data that the main analogy between seasonality of marine phytoplankton and that of the subtidal marine epipelon lies in their similar response to the increase in temperature and light associated with spring and summer growth (Boney, 1986). However, the epipelon of Loch Goil does not show the same degree of succession of species (or of groups of algae) that is associated with phytoplankton (Park, 1991; Park, 1992). Based on the nutrient data available for Loch Goil during this period it appears that nutrient limitation may not be a significant controlling factor in the seasonality of the

epipelon. Certainly, the levels of total oxidised nitrogen, phosphate and silicate rarely reach limiting levels, and appear to be higher near the bottom of the loch. This is probably associated with the mineralisation of organic matter by sediment bacteria, producing higher levels of eg. nitrates at the sediment-water interface. It is likely that levels of micronutrients within my study area (particularly silicate) are likely to differ from the data recorded by the CRPB because of the proximity of Cormonachan Burn which injects fresh water into the loch close to my site (75m away). These levels are likely to be highly seasonal as, according to Schaub and Gieskes (1991), dissolved silicate input (into coastal waters) is strongly influenced by fluctuations in river discharge.

4.4.4.6 Other effects

In Hickman's (1976) study of shallow sublittoral (50cm deep) epipelon in a freshwater lake he reported a series of maxima throughout the growing season (April to late November) with the largest population at the beginning of October. These fluctuations were related to storm events causing physical disturbance and removal by wave action, whereas the growth and decline of different epipelic diatom populations was related to specific combinations of light and temperature favourable or detrimental to their growth. In Loch Goil the depth (9m and 11m) of the epipelon monitored in this study, and the sheltered aspect of the loch, means that wave-related disturbance is unlikely to be a cause of the observed fluctuations in standing crop. There is evidence (Fig. 33) that some species that showed growth in spring also produced autumnal growth (eg. *Navicula distans*, *Navicula* cf.*cryptocephala* var.*veneta*, *Amphora ventricosa*). This phenomenon has been widely reported (Hickman, 1976) and is related to similar conditions of temperature and light during these periods.

The seasonal succession of species in Loch Goil is comparable to the sudden rise and fall of freshwater

epipelic populations described by Round (1972). He related the collapse of epipelic populations to rapid change ("shock") in the aquatic habitat such as thermal stratification and destratification of the water body. Examination of the temperature data in Fig. 31 shows no evidence of an association between short-term fluctuations in water temperature and the distinct maxima in epipelic standing crop. Statification of Loch Goil does occur during the summer months but only within the deep basin at depths greater than approx. 50m (Edwards et al, 1986; CRPB unpublished data). In the winter the deep water is displaced by cold, dense surface water and the oxy- and thermo-cline are disrupted by strong winds which mix the water column (Edwards et al, 1986). This annual cycle of events may indirectly influence the seasonal pattern of epipelic growth through the release of nutrients from the basin water. The thermocline in Loch Goil occurs within the euphotic zone at a depth where levels of epipelic algae are likely to be minimal (see section 4.3.3.3) and therefore the effect of stratification and de-stratification on the seasonal (and bathymetric) distribution of epipelon may be slight.

I have made some preliminary measurements (see 1.4.2) of the gradient in salinity with depth (0-11m) but have no reliable salinity data over this study period (see Appendix 3). I found there to be a layer of brackish water (29 ppt) in the upper few centimetres of water with the remaining water column at 33 ppt. The degree (depth and salinity) of halo-stratification will undoubtedly vary with the seasons and with levels of rainfall and river flow. Reduced salinity may influence the composition of the epipelon by allowing the proliferation of euryhaline species such as *Amphora coffeaeformis* which grows well over a range (11-50 ppt) of salinities (Cooksey and Chansang, 1976). Salinity variation may have been the cause of the peak in abundance of *A. coffeaeformis* var.*acutiuscula* on May 27th 1989 (Fig. 33).

Admiraal et al (1984) describes a broadly recurrent pattern of succession of epipelic species on an intertidal mudflat. They also measured the impact of various environmental conditions on the succession of natural and cultured populations of epipelon and the importance of the following selection mechanisms were demonstrated: 1) temperature, 2) interspecific competition in dense populations, 3) vertical zonation of species in micro-layers of the mud, 4) occurrence of stress factors eg. desiccation or salinity change, and 5) grazing by herbivorous meiofauna (eg.nematodes and oligochaetes). Other suggested determinants of seasonality in epipelon include parasitism and species interaction (Round, 1972).

4.4.4.7 Future studies

Future research should include a more thorough assessment of the seasonal variation of epipelon in Loch Goil. Sampling of epipelic species and standing crop (chlorophyll-a and numbers) should be accompanied by the measurement of greater range of environmental parameters (salinity, temperature, micronutrient in the interstitial water [NH_4-N, TON, PO_4P, SiO_2], sediment redox potential, sediment organic content). Clearly, the sequence of epipelic succession in 1988 to 1990 would have been more accurately recorded if a more intensive sampling programme had been employed. Therefore future study of epipelic seasonality in Loch Goil should concentrate on more regular monitoring (eg.twice weekly) carried out during the periods of optimum growth identified in this study. In the study of phytoplankton of the Firth of Clyde, Hinton (1974) concluded that even a daily sampling programme would give an incomplete picture of successional events. The geographical isolation of Loch Goil would limit the intensity of any future sampling programme, but long-term observations of the epipelon over many years is necessary before the cyclical patterns of seasonal change can be worked out. Intensive observations should be made in both time and space (different depths and sites within Loch

Goil) to provide an overall picture of events in Loch Goil.

This study does not answer all the questions pertaining to the dynamics of epipelic seasonality. The investigation is also limited by its reliance on standing crop data which only shows the balance resulting from the rate at which the diatoms have been growing and the rate of loss (Boney, 1976). However it has described a previously undocumented flora and provides a baseline against which long-term changes in the epipelon of Loch Goil can be measured in future studies.

4.5 EXPERIMENTAL INVESTIGATION OF THE SUCCESSIONAL COLONISATION OF SEDIMENT BY EPIPELIC DIATOMS'

4.5.1 Introduction

The appearance of the bottom of Loch Goil is far from the monotonous and featureless habitat that one might associate with deep, fjordic sea lochs. Instead, the fine-sandy bed of the loch is marked by the trails of benthic invertebrates adding to the seascape of bumps, tracks, mounds and depressions. Examples of these biogenic disturbances of the sediment can be seen in the underwater photographs (Figs. 35 and 36). Measurements of the level of algae in freshly made tracks of the gastropod *Buccinum undatum* showed the level of algae to be significantly less than that in the surrounding sediment (data not provided).

My previous investigation of the patchiness of epipelon (section 4.1) identified a contagious distribution of algae on the bottom of Loch Goil. Zones of relatively high algal density were found to occur on the sides of mounds and within furrows and the scale of this clumping was correlated to the pattern of distribution of sedimentary features. I recognize that the displacement effect of trails and burrows may be superimposed on this pattern and have a significant impact on both the quantity and the composition of the epipelic community. The significance of this secondary effect of grazing on the levels of microalgae has also been recognised in a number of other studies (Bianchi *et al*, 1988; Levington *et al*, 1977; Connor *et al*, 1982; Hill and Knight, 1987; Flint and Goldman, 1975). However, there appears to be little known about the effect of sediment displacement on the community structure of the epipelon.

The colonisation of marine sediment by microbial communities has been reported by Tufail (1987) who utilised sediment collected from the interdidal region of the Clyde estuary. The purpose of his study was to measure the effect of enrichment by soil run-off and sewage

Fig.35. A: The common starfish (B) Asterias rubens (20cm long) prepares to feed on a buried bivalve. This species was seen to feed mostly on epibenthic bivalves such as *Mytilus edulis* and *Modiolus modiolus* and excavations from it's foraging activity is considered unusual behaviour (pers. observation). The anemone Cerianthus lloydii (A) escapes burial.

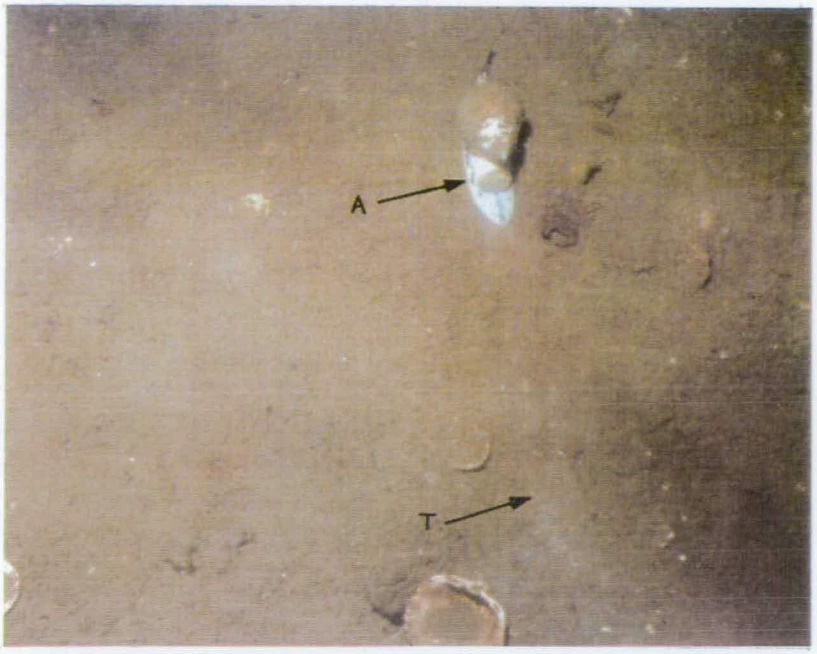
B: Sub-surface, mole-like excavations (B) by the polychaete worm *Aphrodite aculeata* (length 10-20cm) or the more ubiquitous gastropod *Buccinum undatum* leave a trace on the sediment surface. Burrowing behaviour by *B. undatum*, to a depth limited by the length of it's short siphonal canal, must result in the mixing of the upper sediment layer.

A

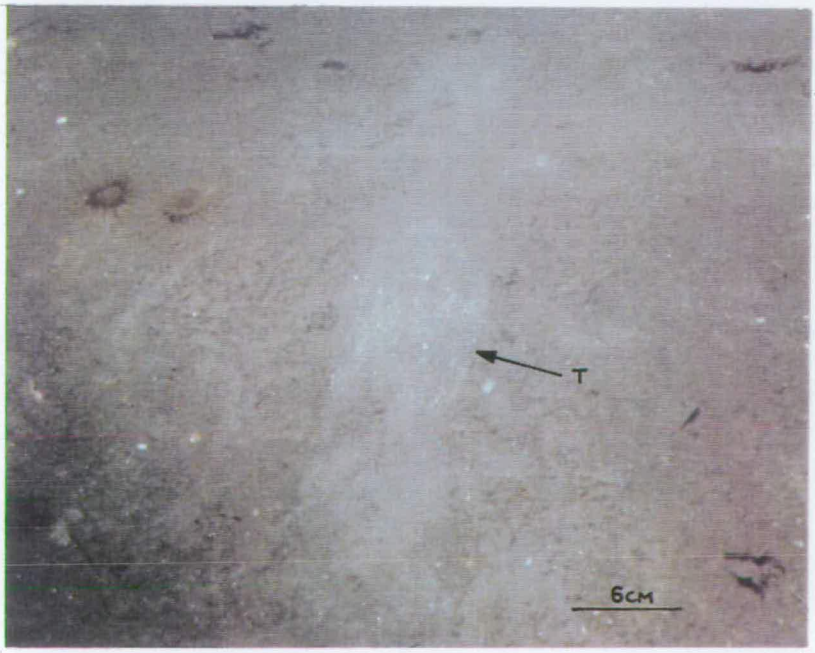
B

Fig.36. A: The largest mollusc (shell up to 8cm high) in Loch Goil *Buccinum undataum* (A) has a mainly saprophytic diet (N.Runham, pers. comm.). The tracks (T) and hollows created by its foraging behaviour displace and bury the surface layer of of epipelic algae.

B: A recent track (T) has significantly fewer diatoms than the surrounding sediment and creates a visible matrix of diatom-denuded areas on the bottom of the loch.



A



B

(simulated using growth media) on the colonising microbial comunity under light and dark conditions. Tufail measured the numbers of viable heterotrophic bacteria and microalgal cells (per mm^2) and levels of chlorophyll-a following colonisation of the sediment after a 25d incubation period. This study showed colonisation and growth of bacteria, blue-green algae, pennate diatoms and fungi. Diatom growth was reported to have been limited to the sediment enriched with "photosynthetic" medium and exposed to light conditions whereas blue-green algae were found to have grown in sediment enriched with either "photosynthetic" or "bacterial" medium under light conditions. Only three species of epipelic diatom (*Amphora spp.* and *Raphoneis sp*) and two species of blue-green algae (*Schizothrix sp.* and *Agmenellum sp.*) were found to have grown over the 25d. Tufail's investigation appears to be limited in that it was carried out *in vitro* and consequently the sediment was isolated from both natural environmental conditions and from all other microalgae, other than those already contained within the sediment. As a result Tufail's study addresses the effect of different environmental regimes on microbial communities rather than the succesional events that occur during colonisation under natural conditions.

Wilson (1925) made qualitative observations of the sequence of marine algal succession and recorded *Navicula* and *Nitzschia* spp among pioneer species colonizing cleared surfaces. Smyth observed the course of colonization of glass slides placed on the bottom of Loch Sween (2-20m). He reported a three staged series of colonization:

(1) Colonization within 3 or 4 d by *Amphora laevis, A. macilenta, A. marina, Navicula pygmaea, N. retusa, Nitzschia closterium* and other species of *Navicula* and *Nitzschia*. These species occurred in low abundance and were common throughout the year in Loch Sween.

(2) Subsequent colonisation by less actively motile species of microalgae that Smyth described as consisting

mostly of epiphytic and epilithic forms. These included: *Amphora coffeaeformis*, *Navicula bahusiensis* var. *bahusiensis* and *Cocconeis scutellum* (*C. scutellum* often became dominant. Less important secondary colonisers included *Navicula bahusiensis* var. *arctica*, *N. ramoisissima*, *Amphora acutiuscula* and very small species of *Navicula* and *Fragillaria*. Smyth indicated that there were too many variable factors (eg. proximity and activity of neighbouring colonies) to assess any time when colonization of this stage was complete.

(3) The last stage of colonization was only observed on slides heavily encrusted by mud, detritus, faecal pellets, worm tubes and other foreign matter. Under these circumstances larger species of diatom were recorded on the surface of the slide and included: *Melosira sulcata*, *Amphora proteus*, *A. truncata*, *Diploneis spp.*, *Gyrosigma rectum*, *Navicula cyprinus*, *N. palpebralis*, *N. scorpularum* var. *belgica*, *Nitzschia sigma*, *N. spathulata*, *Pleurosigma spp.* and *Tropidoneis spp.*

Although the data provided by Smyth details the floristic changes in microalgae colonizing a gass surface, this may not relate to the natural series of events that occur on the bottom of a loch following biogenic disturbance. In addition, Smyth did not demonstrate the change in abundance of algae over time and only indicated that the abundance of microalgae after 3 or 4 d:

"...remained fairly steady, not noticeably affected by longer periods of exposure".

Similarly there is no indication of the periods of time associated with stages 2 and 3 of the algal succession.

This section reports an experiment that I carried out to investigate the colonization and successional events that occur on sediment, previously cleared of all living microalgae. My approach to this investigation was one of "look and see"; I do not considered it to be comprehensive and it will require further investigation. Similarly, it

is not the purpose of this study to provide a detailed review of the literature on either succession events in epipelon or the classical theories of succession and climax communities (Clements, 1949). However, although it is not difficult to find literature on seasonal succession in the marine epipelon, I can find no reference to previous studies that have cleared areas of sediment in the subtidal zone, for the purpose of studying re-colonization.

The principal aim of this study is to identify those species of epipelic algae that are the primary colonists and to describe the succession of species over time. To this aim I measured the change in the community structure of epipelon, within artificially cleared sediment, situated on the bottom of the loch.

4.5.2 Methods

4.5.2.1 Experimental design

The experimental apparatus consisted of normal (PVC), household kitchen sieves (1mm mesh; sieve diameter 15cm; depth 7cm) with their handles removed. The purpose of using the sieves (termed "screens") was to isolate areas of sediment (177cm^2) on the bottom of the loch while allowing the transfer of interstitial water and epipelic algae through the mesh. It was assumed that this exposed treatments to normal environmental conditions.

Approx. 5l of surface sediment was collected from the bottom of Loch Goil (9m depth) and dried at 220^{o}C for 48 h. This killed the algae and removed cellular contents from within the cells. The sediment (termed "clean") was cooled and homogenised. The "screens" were lined with a single layer of lens cleaning tissue (No.105, Whatman International Ltd, Maidstone, England), to prevent loss through the mesh, and filled with the prepared sediment. The apparatus were placed in separate polythene (Tupperware) containers of similar size and shape

(diameter 17cm), which were then carefully filled with filtered sea-water.

The screens were positioned at random positions along a straight line within the "experimental area" on the bottom of the loch at a depth of 9m (see "e" in Fig. 17). They were positioned in sequence and the distance between the screens was as follows: 1-3 (105cm); 3-8 (100cm); 8-14 (52cm).

Because the epipelon are normally restricted to the upper 5mm or less of sediment (Estrada *et al*, 1974; Williams, 1962; Perkins, 1963) the mesh screens were positioned flush with the sediment surface so as to allow lateral movement of algae into the treatments. This was achieved by forming depressions in the bottom, using a hand trawl. The position of the apparatus on the bed of the loch was marked with a buoy to facilitate its relocation over the course of the experiment. Care was taken to avoid any disturbance of the apparatus or surrounding sediment when sampling and inspecting the screens.

The experiment was run over a 14d period (5th to 19th August 1990) during which time sediment was removed (3 x 6.16cm^2) from a different screen on the following days: 1, 3, 8 and 14d. On d 14, sediment (9 x 6.16cm^2) was also taken from within a "control" area of the bottom (approx. 16 m^2) located 5m to the north of the experimental area (knowing the direction aided my relocation of the area in conditions of poor light or reduced visibility). This region was defined by a weighted rope to ensure that the sediment remained undisturbed by diver activity during the experiment. These samples provided an indication of the natural ("ambient") community and levels of epipelic algae within Loch Goil at 9m depth.

Sampling was by means of replicate sediment cores (6.16cm^2) taken from random positions within the treatments and control area. The design of the core samplers and the methods of extraction and analysis of

epipelon are the same as used in a previous study, described in section 4.2.2.1.

Estimates were made of the number of epipelic algae and concentration of chlorophyll-a and phaeopigments. An assessment was made of the epipelic community structure using the standard method described in section 3.3.2.

4.5.2.2 Data analyses

Dendrogram analysis (see 3.5.1) was used to compare the species abundance data recorded from the different treatments. This was used as a descriptive tool to discern basic patterns of colonisation. The similarity matrix also provided quantitative estimates of dissimilarity between communities within the different treatment and within the natural ("ambient") community.

Chi-squared analysis (X^2; see 3.5.2) was used to measure significant differences between sample communities of pairs of treatments. The analysis was carried out on the fourteen most numerically dominant taxa and tested the null hypothesis (H_o) that "proportions of the major species of epipelic algae are the same".

4.5.3 Results

The epipelon showed a 120 fold increase in the number of algae colonising "clean" sediment over the 13 days between 1 and 14d. However, a significant difference was recorded between the number of algae within 14d old sediment, and the natural sediment situated outside of the apparatus ($P<0.05$). Fig. 37 and Table 12 show the temporal pattern of change in the levels of epipelon.

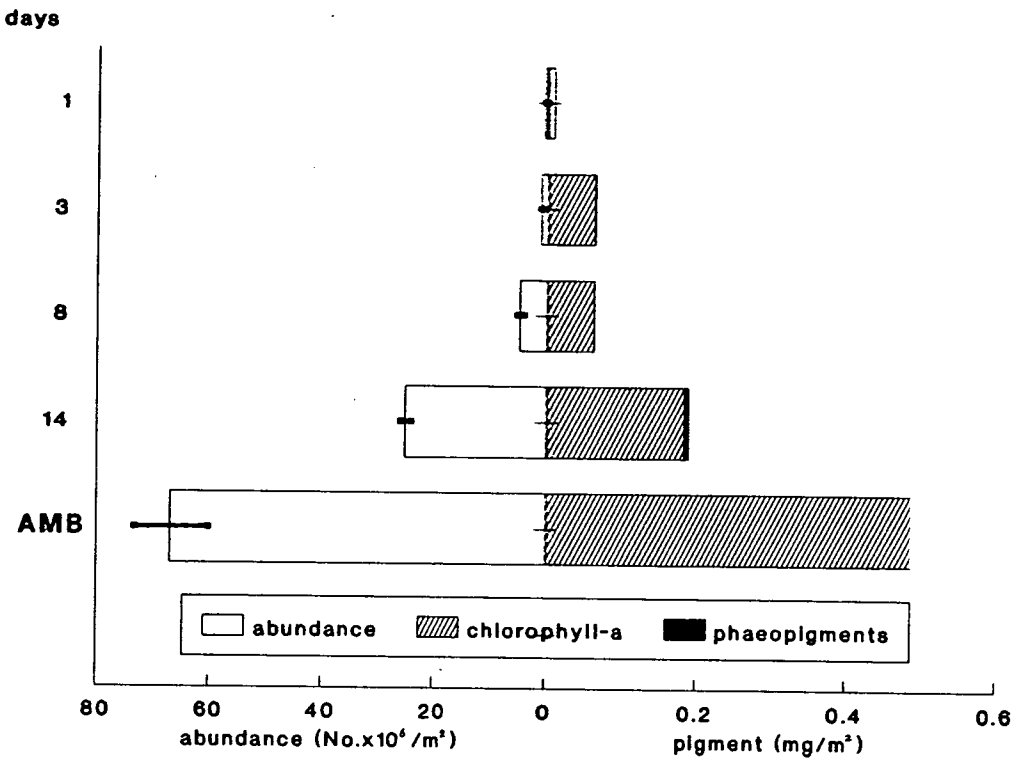


Fig. 37. The colonization of "clean" sediment by epipelic algae indicated by the change in estimated abundance and chlorophyll-a over a 14 d period. Data are compared with ambient (AMB) levels of algae recorded outside the apparatus. The histogram shows levels of phaeopigments and standard errors (indicated by bars).

colonization:	1d	3d	8d	14d	AMB
abundance	0.556	1.111	4.621	25.253	66.919
S.E.	0.166	0.158	0.601	0.971	6.675
chlorophyll-a	0.000	0.061	0.061	0.184	0.491
phaeopigments	0.007	0.001	0.000	0.004	0.491

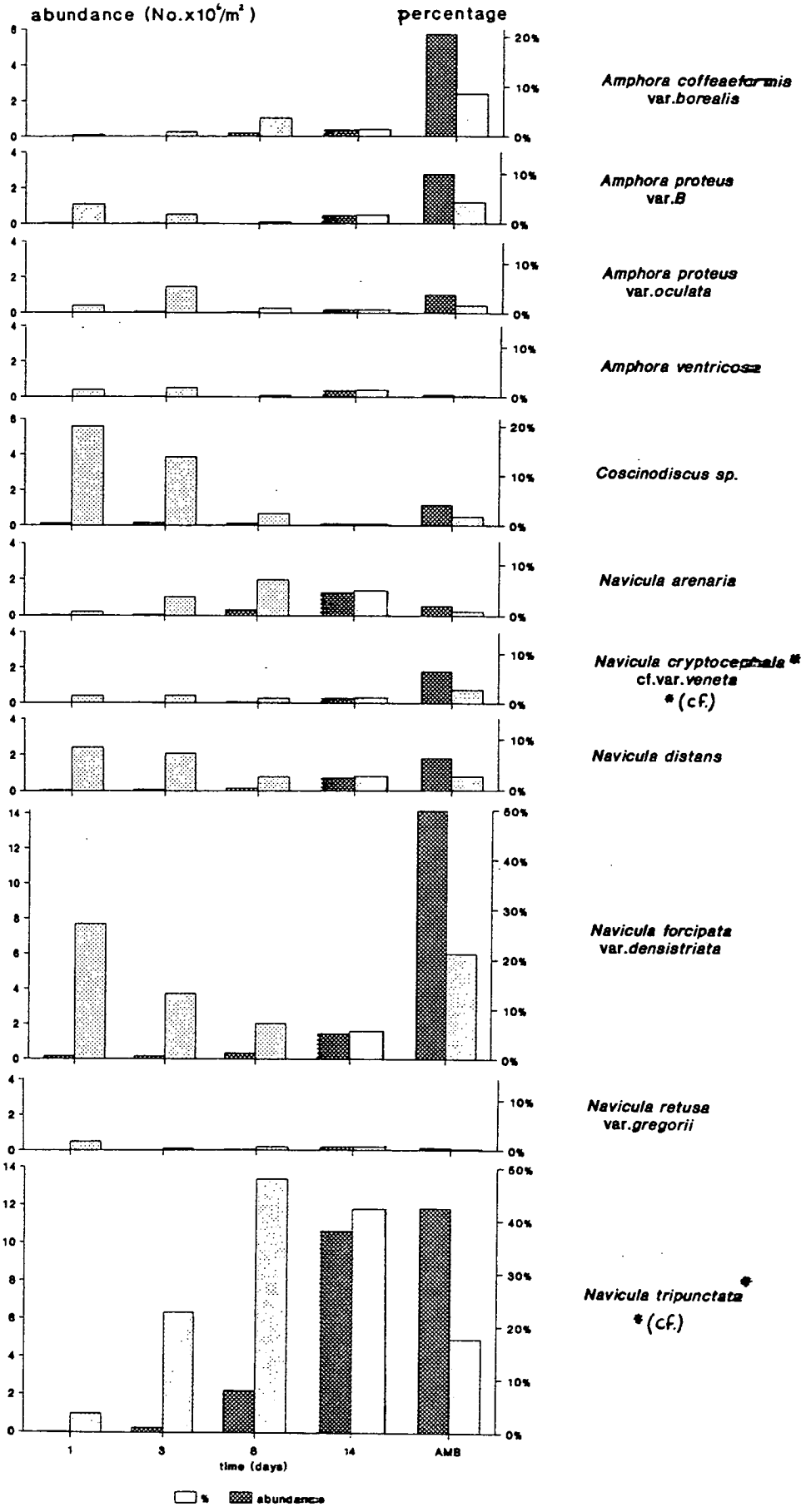
Table 12. Change in levels of epipelon (abundance [No.x$10^6/m^2$], chlorophyll-a and phaeopigments [mg/m^2]) during the colonization of "clean" sediment over 14d. Data is compared with ambient (AMB) levels (see text). S.E. = standard error (No.x$10^6/m^2$).

Although levels of algae were low (equivalent to $0.556x10^6$ m^{-2}) after one day of exposure, analysis of the community structure reveals that a diverse assemblage of epipelon had colonised the sediment; comprising 31 taxa representing 18 genera (Table 13). The diversity of algae changed little over the 14d (48 species, 16 genera by day 14), however, examination of the data reveals significant modification of community structure.

Fig 38 shows the change in abundance and proportion of the major taxa over 14d and compares them with the ambient (AMB) community. The data shows that *Navicula forcipata* var.*densistriata*, *Navicula distans*, *Coscinodiscus sp* and *Navicula sp.B* were the major species in the 1d old community. However, from d 3 a general increase in cell numbers occurred leading to a shift in the dominant taxa to a community dominated by *Navicula* cf.*tripunctata*. By d 8 and d 14, *N.* cf.*tripunctata* formed 53 and 46.5 percent of the sample community (respectively). Other species of epipelon also became progressively more prevalent including *Navicula arenaria* and *Nitzschia* sp.*B/C* (these species are grouped, as no

distinction was made between their taxonomic identification in the community analysis). A number of species demonstrated a phased occurrence, including *Nitzschia socialis var. socialis* (d3) and *Amphora proteus* var.*oculata* (d8).

Cluster analysis shows that the epipelic communities from 8d and 14d old sediment were most similar (Fig. 39). This is also confirmed by Chi-squared analysis, with the acceptance of the H_o at the 5% level ($P<0.05$) that: "proportions of the major species of epipelic algae after 8 and 14d of colonization, are the same". The cluster matrix also shows some similarity between the ambient and the 1 d and 3d community. However, this can be attributed to levels of the dominant algae *N.* cf.*tripunctata* and *N. forcipata* var. *densistriata*. Comparison of these community data by chi-squared analysis showed them to be significantly different ($P>0.05$). The ambient community was notably more diverse (71 species, 25 genera) than any of the treatment communities and was dominated by *N.* cf.*tripunctata*, *N. forcipata* var. *densistriata; N. sp.B*, *A. proteus* var.*B* and *A. coffeaeformis* var.*borealis* (Fig. 38).


abundance (No.x10⁶/m²)
percentage
Amphora coffeaeformis var.borealis
Amphora proteus var.B
Amphora proteus var.oculata
Amphora ventricosa
Coscinodiscus sp.
Navicula arenaria
Navicula cryptocephala * cf.var.veneta
* (cf.)
Navicula distans
Navicula forcipata var.densistriata
Navicula retusa var.gregorii
Navicula tripunctata *
* (cf.)
1
3
8
14
AMB
time (days)
% abundance

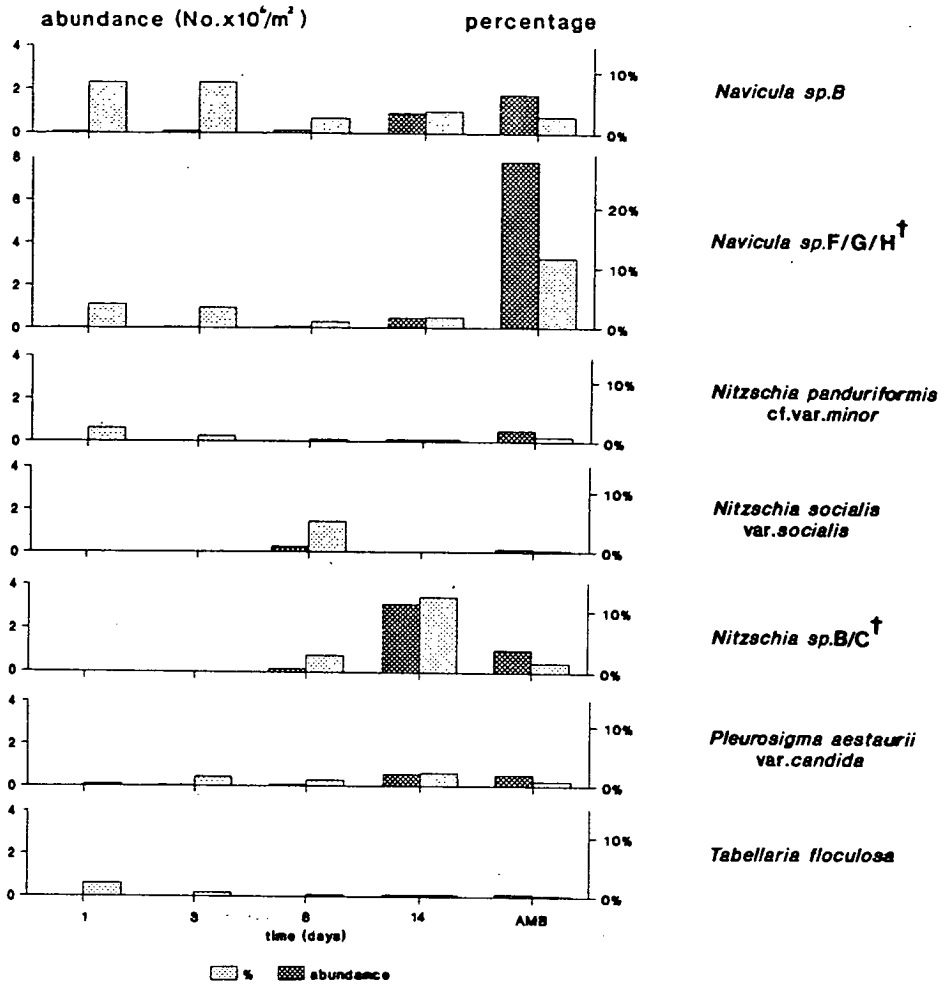


Fig.38.The temporal change in the proportion and estimated abundance of predominant epipelic diatom species over a 14 day colonization period. Data is compared with the ambient (AMB) epipelic community recorded from the sediment at the same depth on day 14.

† see text for explanation of "/"

Taxa	colonization period (days):	percentage 1	3	8	14	AMB
Achnanthes fimbriata		1.1	•		•	•
Amphiprora plicata				•		•
Amphora cf.arcus						•
Amphora coffeaeformis var.acutiuscula		•	1.0	4.1	1.6	9.3
Amphora laevis var.perminuta			1.0	1.5	1.2	•
Amphora ostrearia var.ostrearia						0.4
Amphora cf.proteus var.B		4.2	1.9	•	2.0	4.6
Amphora proteus var.oculata		1.9	5.5	1.1	1.2	2.5
Amphora proteus var.proteus			•	•		•
Amphora truncata		1.1	1.6	1.1	0.8	1.7
Amphora ventricosa		1.5	1.9	•	1.6	•
Amphora sp.A						•
Amphora sp.B			0.6	0.8		0.8
Amphora sp.C				•	•	0.6
Caloneis liber var.elongata		•	•	•	•	•
Caloneis liber var.excentrica			•		•	
Campylodiscus fastuosa		•			•	•
Chaetocerous sp.						•
Cocconeis scutellum cf.var.scutellum		1.1	1.3		•	0.6
Coscinodiscus sp.		21.3	14.5	2.6	•	1.9
Cylindrotheca closterium			•			
Dictyocha speculum var.speculum		•		•	•	•
Diploneis aestiva var.delicata					•	•
Diploneis aestiva var.fusca			•		•	•
Diploneis crabro			•	•		
Diploneis ovalis		1.9	1.0	•		•
Diploneis smithii var.smithii		0.8	1.0	•	•	0.4
Diploneis splendida		•	0.6	•	•	•
Donkinia reticulata					0.8	•
Eunotia cf.pseudopectinalis			0.6			•
Eunotia cf.septentrionalis		•				•
Frustulia rhomboides var.rhomboides		•				•
Gomphonema parvulum var.exilis				•		
Gyrosigma algoris						•
Gyrosigma tenuirostrum						•
Navicula arenaria		0.8	3.9	7.9	5.5	0.8
Navicula atlantica		•			0.8	0.4
Navicula crucigera						•
Navicula cf. cryptocephala var.veneta		1.5	1.6	1.1	1.2	2.9

Table 13. The change in community structure of the epipelon, during colonization of "clean" sediment, over a 14 d period. Values indicate the estimated proportion (percentage) of taxa within the sample community based on counts of algae extracted from sediment after 1, 3, 8 and 14 d. The composition of the epipelon are compared with the naturally occurring community (AMB), recorded outide of the experimental apparatus.
Key: • = taxa present within sample community (see methods section).

continued...

Taxa	colonization period (days):	1	3	percentage 8	14	AMB
Navicula cf.delognei						•
Navicula digito-radiata var.cyprinus					•	•
Navicula distans		9.1	8.1	3.4	3.1	2.9
Navicula forcipata var.densistriata		28.9	13.9	7.9	6.3	23.0
Navicula hennedyi var.hennedyi		•		•		•
Navicula palpebralis var.angulosa				•		•
Navicula phyllepta			0.6	•	•	0.4
Navicula plicata var.constricta			•	•	•	•
Navicula retusa var.gregorii		1.9	•	0.8	0.8	•
Navicula cf. tripunctata		3.8	23.9	53.0	46.5	19.3
Navicula sp.A		•		•	2.0	•
Navicula sp.B.		8.7	8.7	2.6	3.9	2.9
Navicula sp.C/D			•		1.6	3.3
Navicula sp.F/G/H		4.2	3.5	1.1	2.0	12.6
Nitzschia angularis				1.1	0.8	0.6
Nitzschia angularis cf.var.affinis						1.0
Nitzschia aff.distans				•	•	•
Nitzschia hybrida cf.var.pellucida						•
Nitzschia insignis var.smithii		0.8		•	0.8	0.8
Nitzschia marginulata var.marginulata			•	•		
Nitzschia panduriformis/punctata		2.3	1.0	•	•	0.8
Nitzschia sigma var.?						•
Nitzschia sigma var.intercedens		•	•	•	•	•
Nitzschia socialis var.socialis				5.6	•	0.4
Nitzschia sp.B/C				3.0	13.7	1.7
Pinnularia appendiculata					•	
Pinnularia quadratarea var. subproducta		•				
Plagiotropis tayrecta					•	
Pleurosigma aestaurii var.candida		•	1.6	1.1	2.3	0.8
Pleurosigma nubecula				•		
Pleurosigma salinarum						•
Pleurosigma strigosum				•	•	•
Rhabdonema minutum		0.8	•	•	•	•
Rhoicosphenia abbreviata			•			
Skeletonema costatum		•				2.1
Stauroneis salina var.lagerstedtii						•
Stenoneis inconspicua				•		
Surirella fastuosa var.fastuosa		•	•	•	•	•
Synedra pulchella		•				
Tabellaria floculosa		2.3	0.6	•	•	•
Trachyneis aspera var.aspera		•	•	•	•	•
Tropidoneis lepidoptera						•
Tropidoneis vitrea var.scaligera			•			0.4
No.COUNTED:		280	327	295	282	525
No.SPECIES:		38	41	47	48	71

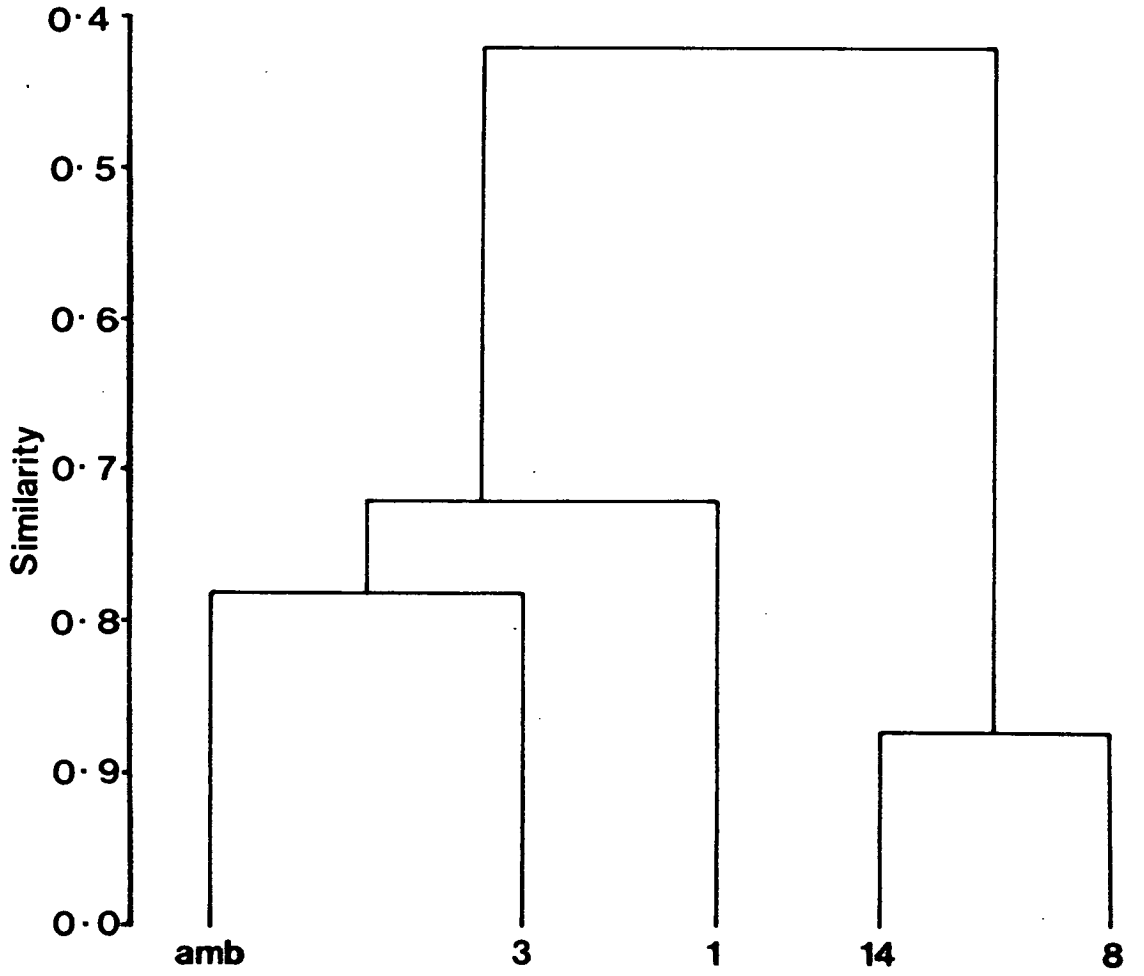


Fig. 39. Dendrograms drawn using group average sorting (Bray-Curtis coefficient) showing the similarity of the epipelic communities following colonization of clean sediment over a period of 1, 3, 8 and 14 d. Treatments are compared with the ambient (AMB) community recorded from the sediment surrounding the apparatus.

Chi-squared analysis				
	3	8	14	ambient
1	71.35	197.12	163.37	98.56
3		77.14	52.19	100.56
8			11.73	155.65
14				138.68

Table 14. Matrix showing the results of Chi-squared analysis (values of X^2) between the different treatments (1, 3, 8, 14d and ambient). The X^2 value of 11.73 (shown in bold), calculated from the comparison of treatments 8 and 14, show there to be no significant difference (v= 12, Q=0.050) between these two communities and H_o is accepted at the 5% level ($P<0.05$). All other calculated values of X^2 are well above the tabulated value of 21.03 (v= 12, Q=0.050) in Neave (1979) and H_o is rejected in these cases.

4.5.4 Discussion

The similarity of the communities after 8 and 14d suggest that the flora has reached a stage of equilibrium, although this community is significantly different from that which occurred naturally. The data shows evidence of a succession of species from a *N. forcipata* var.*densistriata* dominated community, at the start of the experiment, to a community dominated by *N.* cf.*tripunctata*.

Navicula cf.*tripunctata* may have a higher specific growth rate and shorter doubling time than other species within the community. The relatively small size of this species in Loch Goil (25-63um) may also be an indication of greater growth rate as Banse (1976) has shown that smaller species generally have higher specific growth rates and shorter doubling times. However, *N.* cf.*tripunctata* was not the smallest of the species present

within the re-colonised community (eg.*N. forcipata* var. *densistriata* [29-36um] and *Amphora coffaeformis* [21-25um]). Both these species formed only a small percentage of the sample community after 14d, dispite being a major component of the natural epiplic community in the surounding sediment.

Doubling times of marine diatoms are usually in the range of 5-60 h (Round, 1981) which could account for the recorded increase in abundance over 14d as summarised in the table below. However, it is more likely that these changes represent a combination of rates of growth and rates of immigration from the surrounding sediment.

period	days (No.)	increase.(fold)
1-3	2	2.0
3-8	5	4.2
8-14	6	5.5

The proportions of the dominant taxa in the natural sediment are significantly different from levels recorded on d 14. This suggests that *N.* cf.*tripunctata* may have a competitive advantage over other species; particularly *N. forcipata* var.*desistriata*, *Amphora coffeaeformis* var.*borealis* and *Navicula spp. F/G/H* which were also prevalent in the natural sediment community. It is unclear from these results whether competition by *N.* cf.*tripunctata* led to the mortality of other algae. However, the levels of phaeopigments recorded within the treatments were generally low (Fig. 37) and suggest that little senescence of algae occurred. The use of phaeopigments as an indicator of successional events has been demonstrated by Margalef (1967) who interpreted high levels as an indication of a later successional stage or more senescent cells in plankton communities.

It is difficult to categorize the major species into the classical framework of pioneer species (Clements,

1949) on the bases of one experiment. However, the dominance of *N.* cf.*tripunctata* from d 3 and the rapid increase in numbers of *N.* cf.*tripunctata* over the 14d period suggests that this taxa (rather than *N. forcipata* var.*densistriata*) is a pioneer species. In particular it appears to have the attributes of rapid growth and high dispersal powers that characterise an opportunist; quick to colonise an area of denuded sediment.

The main similary between my data and the series of events recorded by Smyth in Loch Sween (Smyth, 1955) is the corresponding 3 d period at which the sample populations approximated the surrounding mud population in terms of community structure. However, there is no parallel between the succession of species recorded by Smyth (see 4.5.1) and the change in community structure recorded in my study (see Fig. 37 and Table 12) although some of the species were similar (*Navicula retusa, Amphora coffeaeformis, A. proteus, Cocconeis scutellum, Tropidoneis spp., Pleurosigma spp., Diploneis spp.*).

Although the results indicate an addition of species to the treatment, this experiment may be demonstrating only a small portion of the successional events that would occur naturally in Loch Goil. Further study should relate the results of experimental studies with observations of natural communities following the exposure of denuded sediment by an animal's tracks or excavations. This work should also focus on longer-term experiments in order to measure the replacement of species over time. Round (1981) points out that the concept of climax communities is difficult to apply to algal communities owing to their rapid, seasonal variability. Accordingly, all long-term studies on succession must integrate the seasonal variation of the natural flora.

It is assumed in this study that the mesh screen and lens tissue do not present a barrier to the lateral dispersion of epipelic algae. Certainly, when dismantling the apparatus after the experiment, most of the lens

tissue had disintegrated and is unlikely to have restricted the motility of algal cells. Of course the treatments could also be colonised through water borne algae suspended by biogenic activity (A flip of a fish tail!) or lifted by tidal currents. However, the latter is unlikely in the sheltered waters of Loch Goil. The relatively constant background levels of *Coscinodiscus sp* and *Tabellaria flocculosa* (commonly found within the plankton of Loch Goil) in all the treatments indicate that seeding from the water column does occur.

The accuracy of the data could be improved in future studies by increase of replication of the treatments and by collecting more sediment samples. The experiment would also benefit from the additional of a control that measures the effect of the barriers. This could be achieved by measuring the effect of the screens on freshly collected sediment.

CHAPTER 5

THE RELATIONSHIPS BETWEEN BENTHIC INVERTEBRATES AND EPIPELON IN LOCH GOIL

5.1 BATHYMETRIC DISTRIBUTION OF BENTHIC INVERTEBRATES

5.1.1 Introduction

This investigation describes the faunal communities that inhabit Loch Goil, over a range of depth (6-40 m), in the vicinity of Cormonachon (Fig. 1). The principal aim of the study was to identify animals capable of exploiting the epipelon as a food resource. It is hoped that the results of this study will lead to the creation of hypotheses regarding processes by which epipelic biomass is lost from sediments of Loch Goil, and indicate areas for future study.

The approach used in this investigation was to assign each species of macrofauna to an isotrophic group (groups with similar feeding habits: detrital, deposit or suspension feeder), based on trophic habits recognised in the literature (Pearson, 1971; Water Research Council (WRc), 1992; Gage, 1972; Fauchald and Jumars, 1979). Some of the taxa are categorized in more detail into feeding groups that describe feeding behaviour and size of food particles normally ingested by the organism. The more detailed isotrophic groups are based on the classification by WRc, 1992. Taxa that were not categorised from the literature were assigned a trophic status postulated from: the morphology of their feeding apparatus, analysis of gut contents, and personal observations of the animal in nature.

There is little quantitative information on the benthic fauna of Loch Goil. Holt and Davies (1991) appear to have carried out the only (qualitative) biological survey of the subtidal benthos of Loch Goil, as part of a extensive survey of sea lochs on the west of Scotland. They surveyed eleven subtidal stations (0-65 m depth) along the length of the loch by a combination of diving observations, photography, hand-core sampling, and dredging. Two of their sample stations are close to the

bathymetric transect surveyed in my study: a benthic community dominated by *Amphiura spp.* and *Ophiura albida* was recorded approx. 200 m to the north (56° 07.78'N, 04° 54.10'W) at a depth of 20 m; and a community dominated by ascidians was recorded within the muddy basin at 65 m depth (56° 07.60'N, 04° 53.49'W) approx. 350 m to the east of the transect. Five of the nine stations recorded a benthos of soft mud with a diverse and varied benthic fauna. A review of comparative studies in other sealochs in Scotland is provided in Chapter 1 of this thesis, by Holt and Davies (1991) and Pearson *et al* (1986).

The purpose of this study was to: (1) identify the principal fauna that might affect the epipelon by virtue of their trophic behaviour or other biogenic activities (eg. bioturbation) (2) allow comparison to be made between the patterns of distribution of the benthic fauna, over a bathymetric gradient, and the epipelic algae (reported in section 4.3). It is not the purpose of this survey to provide a comprehensive evaluation of the benthic fauna of Loch Goil, as the aim of my research is to investigate the ecology of epipelic algae.

In this report, reference to benthic macro-fauna includes invertebrate animals and fish of greater than 0.5mm size (McIntyre and Warwick. 1971). The term "infauna" is defined by Thorson (1957) as:

"...animals inhabiting the sandy or muddy surface layers of the sea bottom - i.e., living buried or digging in a substratum (all animals associated with the level bottom)."

In this report "infauna" also includes bottom dwelling fishes and those motile invertebrates that Thorson describes as:

"intimately related to the animals of the benthos".

5.1.2 Sampling methods

In June 1989 an attempt was made to survey the benthic macro-fauna of Loch Goil, over a range of depths (6-40m), using a small (100cm^2) grab sampler operated from

an inflatable boat. However, deployment and retrieval of the grab without a winch was found to be impractical. The efficiency of the grab was also limited by the presence of shell fragments and small stones at some of the stations. In July 1990 therefore, a quantitative survey of the benthic fauna was achieved using a combination of underwater photography and core sampling. The lower limit of the survey was determined by the safe limit to which diving could be employed for sample collection and photography. Fortunately the depth range of the survey appeared to cover the entire euphotic depth of the water column.

The abundance and composition of the benthic fauna was recorded at seven stations along a bathymetric gradient (6-40 m) by a team of four divers operating from inflatable boat. Sampling was carried out concurrently with the investigation of the bathymetric distribution of epipelon (section 4.3). Fig. 17 shows a cross section of Loch Goil and the location of the sampling stations. The position of the stations were achieved using an echo-sounder and sextant.

5.1.2.1 Core sampling method

Three subtidal sediment samples were collected by hand using small (150 ml) polystyrene containers (Azlon, J. Bibby Science Products Ltd. Stone, Staffordshire, England.) as core samplers. The cores ($25cm^2$ of sediment to a depth of 6cm) were collected at random and the containers sealed underwater. Samples were later sieved through a 0.5mm mesh and the retained sediment and benthos transferred to a shallow tray, of contrasting colour, for sorting. Fine forceps were used to extract the fauna which was then preserved in borax-buffered 4 percent formosaline (Lincoln and Sheals, 1979). In the laboratory identification was made to the highest practical taxonomic level using a stereo binocular microscope to 80x magnification and compound microscope to 1000x. Decapitated specimens were rejected unless species

specificity was obvious. Unfortunately the level of identification of the polychaetes was limited both by my experience at identification and by the availability of taxonomic literature.

5.1.2.2 Photographic method

At each station the surface-living benthic macrofauna were photographed in fifteen randomly selected areas of the sea bed (see Fig. 40, A). A 50cm square (2500cm^2) quadrat (lightweight and foldable for ease of operation) was held a few centimetres above the sediment, by an assistant, and a photograph taken from a distance of approximately 50cm. Photographs were taken on 400 ASA Kodacolor Gold film (f16/60th second exposure) using a Nikonos III camera, f=35mm lens with wide angle lens attachment (subawider II, Subatec Ltd.) and Novatek III flash (Aqua-Craft Inc. San Diego California). When possible, identification of benthic invertebrates was made *in situ*. The abundance of the different taxa was later quantified from the photographic prints. Benthic invertebrates that could not be identified *in situ* were collected, preserved in formosaline for identification in the laboratory. Photographs were also taken of organisms and habitats at all of the sample stations. Animals occurring outside the quadrats were recorded separately and an assessment made of their abundance using the following criteria:

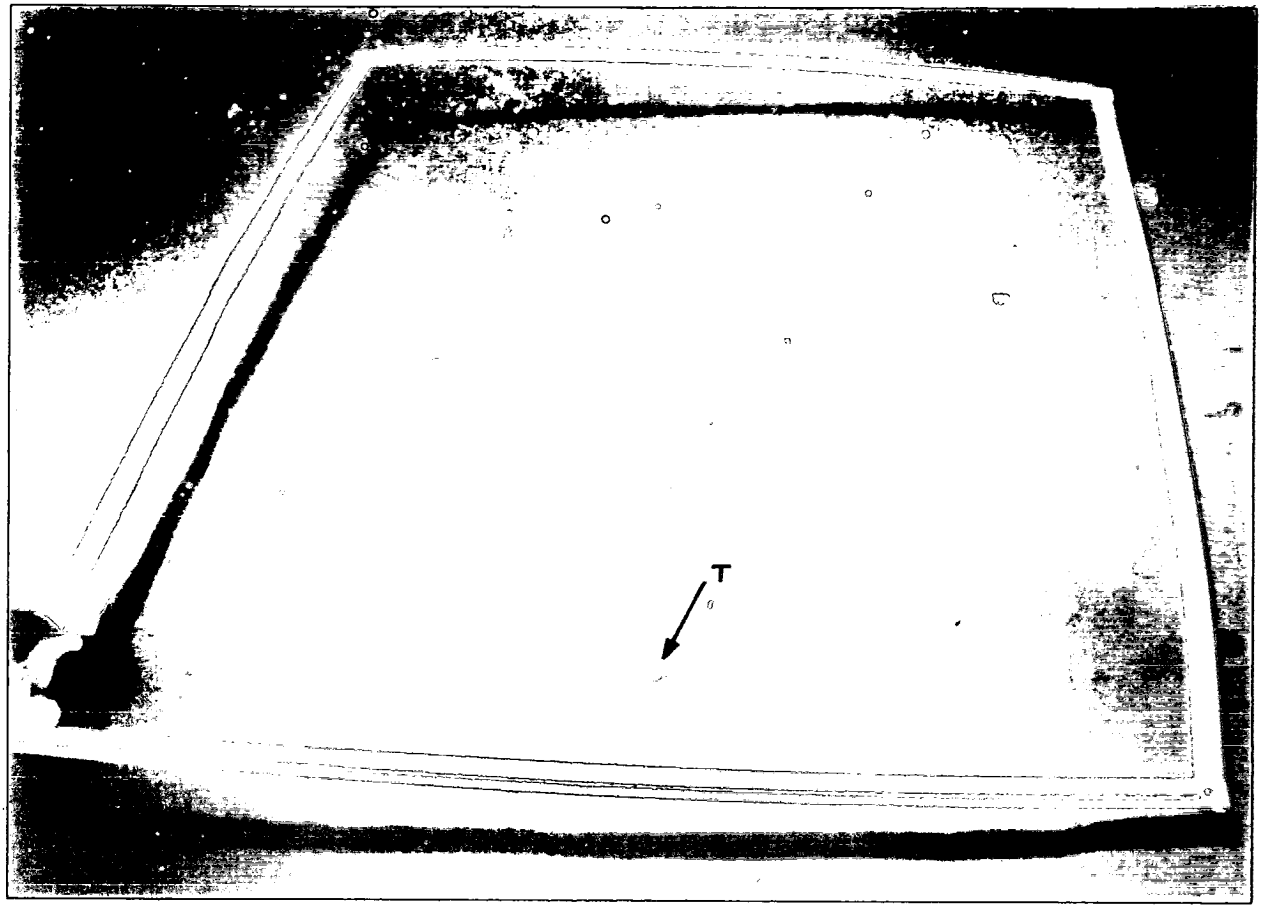
Present - 1 to 10 individuals.
Moderate abundance - 10 to 100 individuals.
Abundant - more than 100 individuals.

These qualitative observations were added to the numerical data to optimize the amount of information recorded at each station.

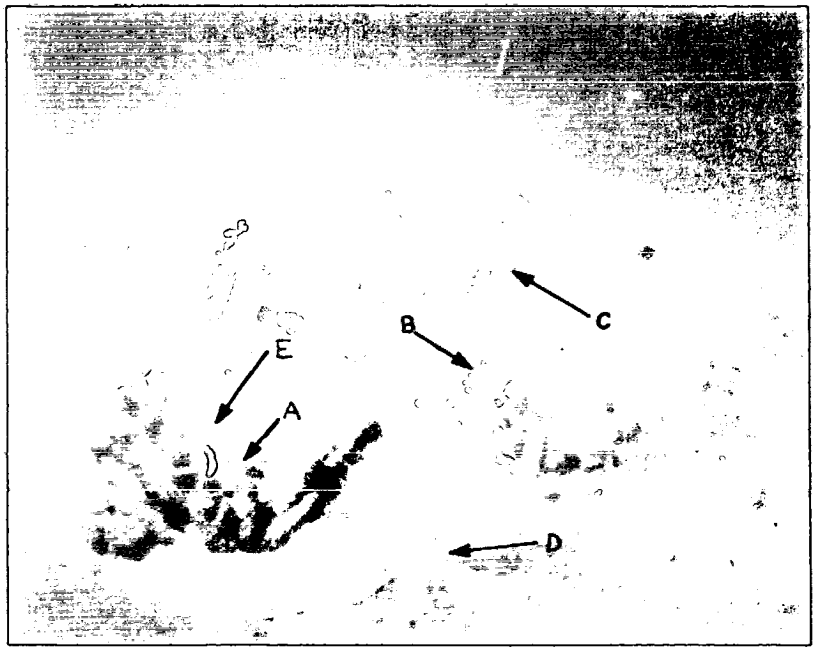
A subjective assessment was also made of biogenic disturbance of the sediment at each station based on the degree of disruption of the surface by burrows, mounds,

Fig. 40. A. A photograph is taken of the sea bed within a 50 cm square (2500 cm^2) quadrat, held a few centimetres above the sediment by an assistant. Because of the sediment consisted of fine mud the photographer had only a few seconds in which to frame and take a photograph before a cloud of silt overwhelmed the sample area. An old track or burrow bisects this area of sediment, and the mucus tube (T) of the anemone *Cerianthus lloydii* protrudes about 2 cm.

B. At 30 m depth a silt covered rock (approx. 50 cm wide) forms an apparent oasis of life in an expanse of sediment. *Galathea* sp. (A), *Cirripedia* indet. (B), *Ophiothrix fragilis* (C) *Thyone sp.* (D) and *Protula tubularia* (E),



A



B

faecal casts and tracks. This was quantified on a scale of 1 to 3 (1=slight, 2=moderate, 3=great).

5.1.3 Limitations of the method

The use of underwater photography to record habitats of subtidal communities is an established qualitative method in marine biology (Mc.Intyre and Warwick, 1971; Mitchell *et al*, 1983; Holt and Davies, 1991). However, my use of a hand-held foldable quadrat to enable semi-quantitative assessment of the benthic fauna from photographs is a useful innovation that does not appear to have been adopted in previous studies of sublittoral ecosystems.

The main limitation of the overall sampling method is the possibility that the core-sampling size ($25cm^2$), depth (6cm) and degree of replication (3 cores) may be insufficient to accurately sample the faunal community. The core sample may miss sub-surface deposit-feeding invertebrates that retract from the surface layers when disturbed by the diver. This sample-bias would affect the proportion of burrowing polychaetes that were sampled in this investigation; for example the large polychaete *Chaetopterus variopedatus* found at Cormonachan by Holt and Davies (1991) was not recorded in my study. Ideally, further investigation is required to determine optimum sample size and degree replication required to overcome the natural herogeneity that may exist within benthic macrofaunal communities of Loch Goil (Elliott, 1971).

The level of taxonomic identification of the polychaete worms can also be improved with both experience and availability of taxonomic literature.

Quantitative investigations of macrobenthic communities normally involve the measurement of biomass of the individual taxa (Mc.Intyre and Warwick. 1971). This method was not adopted in this study due to the combination of data derived from both photographs and core samples. However, the use of abundance data in determining

the pattern of distribution of sublittoral benthic fauna is valid, as other studies of the subtidal benthos (e.g. Elliott and Kingston, 1987) have found "biomass distribution to broadly reflect abundance distribution".

5.1.4 Results

5.1.4.1 Community structure

A diverse community (82 species) of macro-benthic animals was recorded over the 6 to 40 m depth range of Loch Goil, including the following groups: polychaetes (21 sp); sipunculids (1 sp); gastropods (3 spp); bivalves (8 spp); polyplacophora (1 sp); opisthobranchs (3 spp); echinoderms (10 spp); nemertines (1 sp); ascidians (2 spp); crustaceans (8 spp); porifera (1 sp); cnidaria (10 spp) and pisces (13 spp). Table 15 lists the species, their abundance along the bathymetric gradient and their isotrophic group. The number and proportion of species from the different feeding groups are as follows: carnivorous predators (28 sp, 35.4%); deposit feeders (10 sp, 12.7%); surface detrital feeders (11 spp, 13.9%); water column detrital (suspension) feeders (29 spp, 36.7%); carnivorous predators (28 spp, 35.4%) and scrapers (1 sp, 1.3%).

The following groups of species occurred regularly at all, or most, of the sites along the depth gradient and can be thought of as characteristic of this habitat within Loch Goil:

Carnivorous scavengers: *Pagurus bernhardus; Pagurus prideaux; Carcinus maenas, Liocarcinus depurator; Asterias rubens; Psammechinus miliaris; Buccinum undatum, Callionymus lyra; Limanda limanda* and *Gobius sp.*

Motile deposit and detrital feeders: *Ophiura albida; Syllidae sp.; Nephtys hombergii* and *Polychaeta spp* (5 species).

Sedentary detrital feeders: *Ascidiacea* indet.; *Eupolymnia nebulosa; Abra alba;*

axa	Depth (m):	6	9	12	15	20	30	40	Trophic	Source
RUSTACEA										
mphipoda indet.		1	-	2	2	1	-	-	WCDtF	WR *
irripedia indet.		-	-	-	-	-	+	-	SF	G
lunida rugosa		-	-	-	-	-	1	+	C	Pk
alathea sp.		-	-	-	-	-	+	2	C	Pk
agurus prideaux		-	-	-	-	+	+	-	C	Pk
agurus bernhardus		5	1	+	1	-	+	++	C	Pk
arcinus maenas		+	1	+	1	+	+	-	C	Pk
ocarcinus depurator		-	+	-	+	+	1	+	C	Pk
NIDARIA										
ennatulacea indet.		-	-	-	-	94	-	++	WCDtFpf	WR *
irgularia mirabilis		-	-	-	-	+	++	1	WCDtFpf	WR *
otanthea simplex		+	+	+	-	-	1	9	WCDtF/	Pk
erianthus lloydii		3	15	32	80	31	6	14	WCDtF/	Pk
cyonium digitatum		-	-	-	2	-	-	-	WCDtF	Pk
etridium senile		-	+	-	-	-	-	-	WCDtF	Pk
achycerianthus multiplicatus		-	+	+	-	++	++	1	WCDtF/	Pk
rticina eques		-	-	-	-	-	-	+	WCDtF/	Pk
damsia carciniopados		-	-	-	-	+	+	-	WCDtF	Pk
ubularia indivisa		-	-	-	-	-	+	-	WCDtF	Pk
CHINODERMATA										
ophiothrix fragilis		-	-	-	-	+	++	24	WCDtFp	WR *
ophiura ophiura		-	-	-	-	-	1	3	IDtF	WR *
ophiura albida		+	+	-	1	+	141	137	IDtF	WR *
ophiocomina nigra		+	-	-	-	-	-	-	WCDtF	WR *
sterias rubens		+	+	4	1	2	-	-	C	Pk
chinus esculentus		+	+	+	-	-	-	-	DF	WR #
sammechinus miliaris		+	+	+	-	+	1	1	MP	G
chinocardium cordatum		+	-	-	-	-	-	-	IDtFa	WR *
eptosynapta inhaerens		-	+	-	-	-	-	-	IDtF	WR *
pyone sp.		-	-	-	-	-	+	42	SF	G
SCES										
manda limanda		+	+	+	+	-	+	-	C	Pk
eugopterus punctatus		-	+	-	-	-	1	-	C	Pk
ngnanthus phlegon		+	-	-	-	-	-	-	C	Pk
yliorhinus canicula		+	-	-	-	-	-	-	C	Pk
onger conger		+	-	-	-	-	-	-	C	Pk
entrolabrus rupestris		+	-	-	-	+	-	-	C	Pk
allionymus lyra		+	+	+	2	2	+	+	C	Pk
olis gunnellus		+	-	-	-	-	-	-	C	Pk
rnatoschistus minutus		+	+	+	-	-	-	-	C	Pk
obiusculus flavescens		+	+	-	-	-	-	-	C	Pk
obius sp.		23	15	+	+	-	+	-	C	Pk
inachia spinachia		+	-	-	-	-	-	-	C	Pk
voxocephalus scorpius		-	+	-	-	-	-	-	C	Pk
ogenic disturbance		3	2	1	1	1	2	1		

Taxa	Depth (m):	6	9	12	15	20	30	40	Trophic	Source
ANNELIDA										
Capitella capitata		-	-	1	2	5	4	6	ISpFf	WRc
Cirratulidae indet		-	-	-	2	4	5	9	IDtFf	WR *
Nephtys hombergii		-	1	-	2	-	2	2	DF	WR #
Lagis koreni		-	-	3	-	-	-	1	IDF	WR #
Syllidae indet.		15	-	2	4	-	-	1	DtF/C	FJ
Polychaeta indet. (5 spp)		8	3	1	2	-	4	-	DS	P
Phyllodoce sp.		-	-	4	-	1	2	-	MP	P
Owenia fusiformis		-	1	1	-	-	-	-	WCDtFa	WR *
Aphrodite aculeata		-	+	-	-	-	-	1	MP	P
Arenicola marina		6	+	-	-	-	-	-	IDtFf	WR *
Lanice conchilega		4	1	-	-	+	-	-	IDtFa	WR *
Myxicola infundibulum		-	-	-	-	+	-	-	WCDtFp	WR *
Sabella pavonina		-	+	-	-	-	-	+	WCDtFp	WR *
Pomatoceros triqueter		4	5	-	-	+	-	-	WCDtF	WR *
Eupolymnia nebulosa		2	4	8	-	1	16	57	IDtFa	WR *
Sabellidae indet.		-	+	1	8	-	-	-	WCDtFp	WR *
Protula tubularia		-	-	-	-	1	1	-	WCDtFp	WR *
SIPUNCULA										
Sipuncula indet.		-	-	-	-	-	1	-	DF	G
MOLLUSCA										
Abra alba		4	9	16	9	4	3	2	IDtF	WR *
Mya arenaria		-	-	-	-	1	1	-	WCDtF	WR *
Mya truncata		+	-	-	-	-	-	-	WCDtF	Pk
Pecten maximus		-	-	+	-	-	-	-	WCDtF	Pk
Chlamys opercularis		-	-	-	+	-	-	-	SF	P
Acanthocardia aculeata		+	-	-	-	-	-	-	IDtF	Pk
Modiolus modiolus		+	+	-	+	-	-	-	SF	P
Cerastoderma edule		+	-	-	-	-	-	-	IDtF	Pk
Opisthobranchia indet.		-	-	-	1	-	-	-	C	Pk
Lacelina auriculata		-	-	-	-	-	2	-	C	Pk
Limacia clavigera		-	+	-	-	-	-	-	C	Pk
Turritella communis		-	-	-	-	-	1	-	SDF/SF	P
Aporrhais pespelecana		+	-	-	-	-	-	-	DF	Pk
Buccinum undatum		+	+	+	2	1	2	+	C	Pk
Polyplacophora indet.		+	-	-	-	-	-	-	S	Pk
NEMERTINA										
Lubulanus annulatus		-	-	-	-	-	+	-	C	Pk
PORIFERA										
Porifera indet.		-	-	-	-	-	1	-	WCDtF	Pk
ASCIDIACEA										
Ascidiacea indet.		-	2	-	4	-	+	16	WCDtF	Pk
Botrylloides leachi		+	-	-	-	-	-	-	WCDtF	Pk

Table 15. Benthic macrofauna recorded in Loch Goil along a bathymetric gradient (6 - 40m). The abundance (no. per 3.75 m) and trophic group of the taxa are shown along with qualitative observations ("+" see key) of taxa observed at each sample station. An estimate is given of the degree of biogenic disturbance of the sediment (1 - 3 see key) at each station. See Fig. for location of sampling stations in Loch Goil.

Key: TS = trophic status Source = literature on feeding mode of taxa
Qualitative observations: + = present ++ = moderate numbers +++ abundant
Biogenic disturbance 1 = slight 2 = moderate 3 = great

WRc: WRc (1992)
= organism feeds on food particles of generally <50 um but always <100 um.
= organism feeds on food particles of consistently >100um in size.

WCDtF	water column detrital feeder
WCDtFa	water column detrital feeder-active appendage capture
WCDtFp	water column detrital feeder-passive appendage capture
WCDtFpf	water column detrital feeder-pump and filter capture
IDtF	interface detrital feeder
IDtFa	interface detrital feeder-active appendage capture
IDtFf	interface detrital feeder-forage capture
ISpFf	interface specialised feeder-forage capture
DF	deposit feeder
IDF	interface deposit feeder

: Pearson (1971)

P	motile predators
	scrapers
DF	surface deposit feeders
F	suspension feeders
S	deposit swallowers

Gage (1972)

DF	deposit feeder
SF	suspension feeder

k: personal obervations and postulated feeding habits

F	deposit feeder
DF	interface deposit feeder
tF	interface detrital feeder
CDtF	water column detrital feeder
	carnivore
	scraper

Fauchald and Jumars (1979)

DtF	detrital feeder
C	carnivore
SF	suspension feeder

Cerianthus lloydii and *Pachycerianthus multiplicatus*.

The data also clearly distinguish a deep water fauna, which corresponds approximately to the 20-40 m depth range. This is characterised by a number of numerically dominant species which are all detrital feeders:

Ophiura albida and *Ophiothrix fragilis* (ophiuroids); *Thyone sp.* (sea cucumber); *Eupolymnia nebulosa* (terebellid polychaete); *Ascidiacea* indet. (tunicate); *Pennatulacea* indet. and *Virgularia mirabilis* (sea pens); and *Pachycerianthus multiplicatus* (anthozoan).

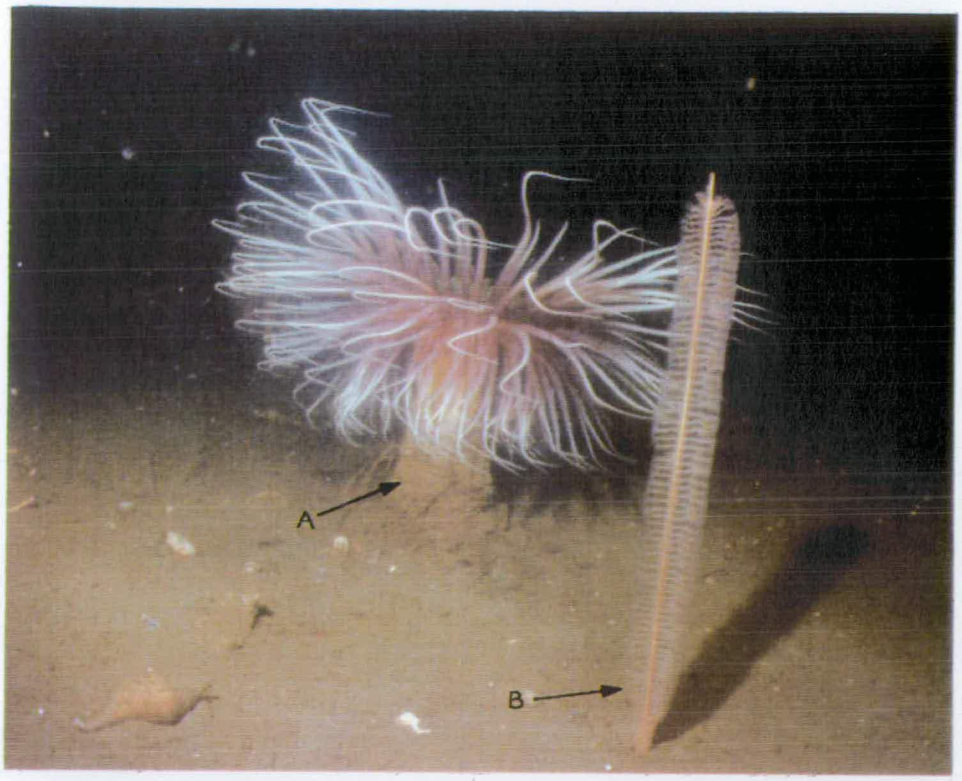
Figures 40, (B); 41 (A, B); 42 (A, B); 43 (A, B, C) show underwater photographs of this deep water community including more detailed macro-photographs of some of the characteristic species.

The data clearly show other variations in the community of fauna with depth, and distinguish a less clearly defined shallow water community, characterised by the increased abundance of *Syllidae* indet. and *Arenicola marina* (polychaetes).

Assessment of biogenic disturbance of the sediment at each of the sample stations identified the greatest bioturbation to be at the 6 m, 9 m and 30 m stations. At the two shallowest stations this is mainly attributed to: the fecal casts and mounds of the lugworm *Arenicola marina;* the dragging of gastropod shells across the sediment by *Pagurus bernhardus* and to the foraging and swimming activity of *Gobius sp.* Disturbance at 30 m depth was mainly due to the continual writhing of the ophiuroid *Ophiura albida* and scouring of the sediment surface by the tentacles of *Eupolymnia nebulosa*. Other sources of disturbance observed during this survey include: tracks and burrows made by the scavenging carnivores *Buccinum undatum, Asterias rubens* and *Carcinus maenas* (see Figs 35 and 36) and displacement of surface sediment by foraging

Fig. 41, A. The largest invertebrate recorded in Loch Goil is the burrowing cerianthid *Pachycerianthus multiplicatus* (A) seen here, at a depth of 30 m, next to a sea-pen *Virgularia mirabilis* (B). Protruding vertically to a height of about 25 cm the sea-pen is common only in the quietist waters with minimal water currents (personal observation).

B. *Urticina equis* (C) is seen here in a retracted state. The common brittle-star *Ophiothrix fragilis* (D) and the tube of a peacock worm *Sabella pavonina* (E). The strawberry worm *Eupolymnia nebulosa* (F) with tentacles radiating out over the sediment-covered surface of a rock at a depth of 40 m.

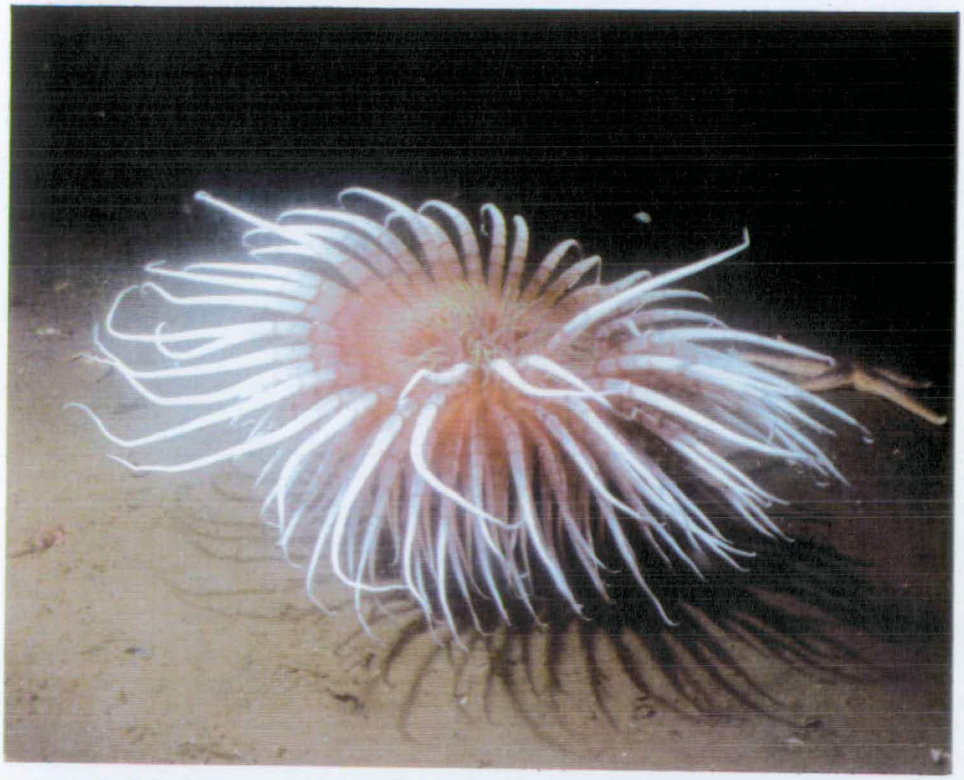


A

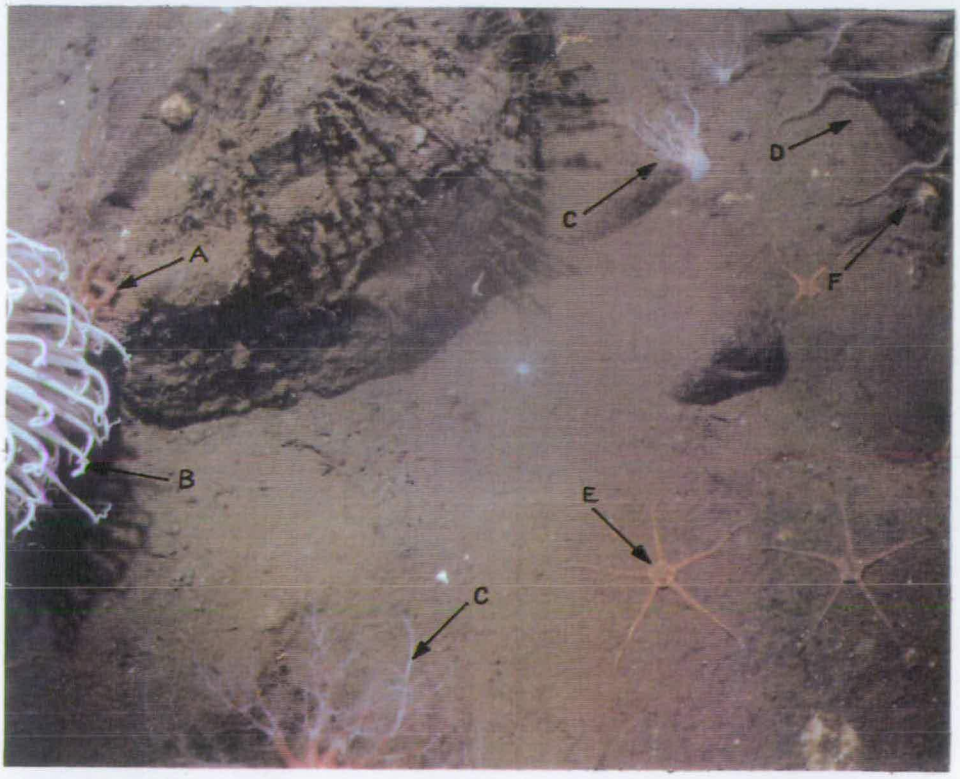
B

Fig. 42. A. The large and beautiful burrowing cerianthid sea anemone *Pachycerianthus multiplicatus* is particularly common in the deeper water (deeper than 20 m) of Loch Goil.

B. At a depth of 40 m a small area of sea bed (approx. 2500 cm^2) supports a diverse and abundant population of invertebrates: *Galathea sp.* (A), *Pachycerianthus multiplicatus* (B), *Thyone sp.* (C), the tentacles of *Eupolymnia nebulosa* (D), *Ophiura albida* (E) and *Psammechinus miliaris* (F)



A



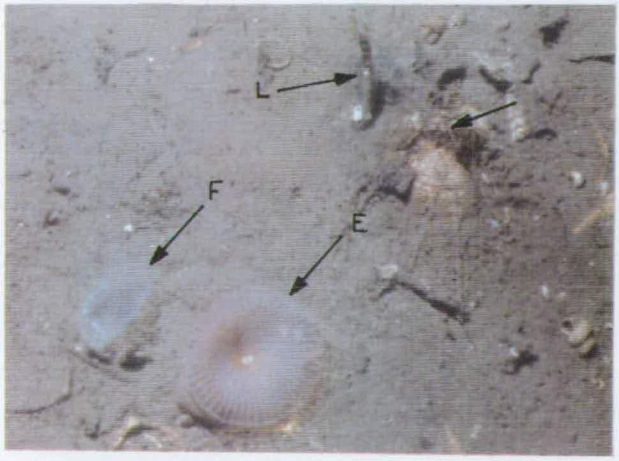
B

Fig. 43 A. The iridescent green, blue and gold hairs of the sea mouse *Aphrodite aculeata* (A) show the outline of a 10 cm specimen. This burrowing polychaete was rarely observed on the surface of the sediments of Loch Goil. The opiuroid *Ophiura albida* (B) is particularly abundant at depths of 30 and 40 m. The brittle stars writhe constantly over the surface of the fine muddy sand and occasionally bury themselves below the sediment surface. The branched tentacles of the burrowing sea-cucumber *Thyone sp.* (C) are extended for feeding but retract rapidly when the animal is disturbed.

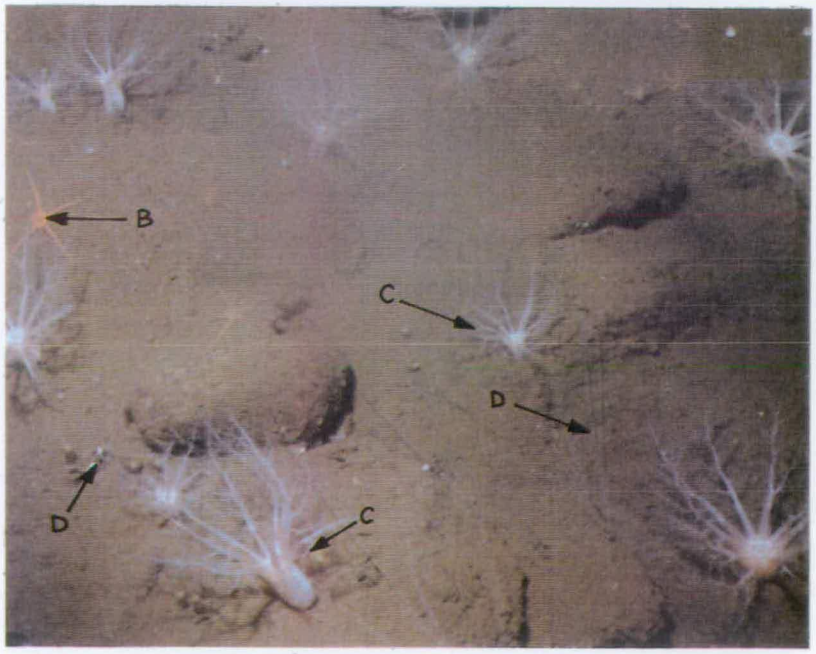
B. At a depth of 20 m the mucus and sand-grain tube of the sand mason worm *Lanice concheliga* (L) lies within the feeding radius of a strawberry worm *Eupolymnia nebulosa* (D). The fan-worm *Myxicola infundibulum* (E) and an ascidian (F) both feed on water-born particles of food.

C. At a depth of 30 m and 40 m, areas of sea bed were densely colonised by burrowing sea-cucumbers *Thyone sp.* (C) Because the animal retracted quickly when disturbed the collection of a specimen by hand, for identification to species level, was impossible in this instance. *Ophiura albida* (B) and tentacle of *Eupolymnia nebulosa* (D) feed on the surface of the fine sediment.

A



B



C

and swimming activity of other fish species and the swimming crab *Liocarcinus depurator*.

5.1.5 Discussion

5.1.5.1 The faunal community

Because of the semi-quantitative nature of the sample-data it is not strictly permissible to compare the benthic animal community of Loch Goil with the classical concept of marine benthic communities derived from Peterson (1918, 1924) and later re-defined by Thorson (1957). Nonetheless, there is some similarity between the fauna of Loch Goil and the Syndosmya (*Abra*) communities described by Thorson as characterising:

"...sheltered or estuarine areas, often with somewhat reduced salinity and a mixed to muddy bottom rich in organic material".

This community is characterised by: *Abra* (*Syndosmya*) *alba; Lagis* (*Pectinaria*) *koreni; Echinocardium chordatum; Nephtys sp.; Ophiura albida; Ophiura ophiura* (*texturata*); *Cultellus pellucidus; Nucula sp.; Corbula gibba*. Of these species, the first six were recorded in Loch Goil, although the extent of their distribution varied along the bathymetric gradient (Table 15). The geographical distribution of the *Abra* community, reviewed from the literature by Thorson (1957), includes inner parts of fjords and coastal areas of Scotland, and the Black Sea off the coast of Romania. This is particularly interesting as I have also found there to be significant similarity between the epipelon of Loch Goil and that recorded in the Romanian Black Sea by Bodeanu, (1964) (see section 4.3.4).

The deep water fauna (20-40 m) of Loch Goil appears to be similar to the community found by Holt and Davies (1991) throughout the north Clyde sealochs in: East Kyle; West Kyle; Holyloch; Gareloch; Loch Riddon; Loch Striven and Loch Long. The habitat ("NC20") is described as one of mixed sediments found over a 0-58 m depth range in enclosed coastal areas subject to weak tidal streams and

normal salinity. These characteristics are consistent with the conditions and aspect of my study area within Loch Goil. Similarly, the sediment over the bathymetric gradient have been shown to be composed of a mixture of particle sizes (see section 4.3.3.3 and Table 8). Therefore, it is not surprising that the animal species described by Holt and Davies as characteristic of this habitat include the following taxa: *Cerianthus lloydii; Ophiura ophiura; Ophiura albida; Aporrhais pespelecani; Mya truncata; Modiolus modiolus; Virgularia mirabilis; Thyone fusus; Pachycerianthus multiplicatus; Protanthea simplex; Ophiothrix fragilis; Ophiocomina nigra; Pagurus bernhardus; Pagurus prideaux; Asterias rubens; Buccinum undatum; Pomatoceros triqueter; Callionymus lyra; Gobius sp; Chaetopterus variopedatus; Psolus phantapus; Thyonidium commune* and *Lithodes maia*. All but the last four of these taxa have been recorded along the bathymetric gradient (6-40m) during my investigation (see Table 15). Although this a very strong indication that my study area is characteristic of the sealochs of the northern Firth of Clyde, it is worth noting that very different communities dominated by ophiuroid *Amphiura filiformis* and the ascidian *Styela gelatinosa* were found by Holt and Davies at 20 m and 65 m depth (respectively) close to my bathymetric transect. My survey also found a more diverse benthic community (79 species), whereas Holt and Davies found only 21 species at the 20 m station and 16 species within the basin at 65 m depth.

A noticeable exception from the list of taxa found by Holt and Davies to be characteristic of the "mixed sediment community" is the terebellid polychaete *Eupolymnia nebulosa*. I found this species along most of the bathymetric gradient (except at 12 m), and at 30 and 40 m depth it covered the sea bed in a matrix of pink tentacles (Fig. 12, A; Fig. 41, B). *E. nebulosa* has been recorded in shelly gravel in Loch Goil, Loch Riddon and Gareloch (Holt and Davies), but not as a major feature of

the benthic faunal community. However, Pearson (1971) found *E. nebulosa* to be the dominant organism in all but the deeper parts of Loch Eil in the Firth of Lorne and characterised a mixed group of fauna termed the "inner loch transition fauna". Other major species of this community include: *Aphrodite aculeata; Terebellides stroemi; Amphitrite cirrata; Ameana trilobata; Praxillura longissima* (polychaetes); *Ophiothrix fragilis; Psammechinus miliaris; Ophiura albida; Amphiura sp; Ophiopholis aculeata* (echinoderms); *Modiolus modiolus; Astarte elliptica; Thyasira flexuosa; Phacoides borealis; Cultellus pellucidus* (bivalves). The macrobenthic community of Loch Eil and Loch Goil share some similarities although Loch Eil appears to have a greater diversity of organisms. However, the diversity of fauna recorded by Pearson (1971), and from other investigations of Loch Eil (Pearson, 1970; Feder and Pearson, 1988), may be a consequence of the more intensive sampling methods adopted in these studies.

5.1.5.2 Epipelic algae and the macrofauna - trophic relationships

This investigation identifies the species of benthic macrofauna that may be utilising the epipelon as a food resource based on the assumption that:

1. detrital feeders consume epipelic algae from the sediment surface (interface detrital feeders) and from the water column (suspension and water column detrital feeders) as part of the lose detrital fraction.

2. deposit feeders consume epipelic algae from surface (surface or interface deposit feeders) or sub-surface (deposit swallowers) sediment through non-selective ingestion of "mouth-fulls" of sediment.

Based on these assumptions, It is likely that all but one of the invertebrate species (*Polyplacophora* indet.) may be consuming and utilising the epipelon of Loch Goil

as a food resource. Furthermore, based on the trophic coding scheme in the WRc (1992) review, 21 of the 51 invertebrate species (and probably more as many species are not classified in this paper) in Loch Goil feed on food particles of generally less than 50um but always less than 100um ("*" in Table 15). This includes 5 of the 7 numerically dominant organisms that were found to characterise the deep water faunal community of Loch Goil. Although little is known of the diets of many of these taxa, these data indicate that the epipelon is a major autotrophic resource to the animal community of Loch Goil.

This study also identifies the proportion of predatory species, which are comprised mainly of fish and decapod crustacea. The separation of the benthic macrofauna into these isotrophic groups allows me to construct a food web diagram which incorporates the inter-relationships of the epipelon with the macrobenthos.

This diagram attempts to partition the role of the different fauna in the food web of Loch Goil and is shown (Fig.47) and discussed in the final chapter (see 6.2.1).

5.1.5.3 Influence of epipelon on invertebrate distribution

Another aspect of the relationship between the epipelon and the invertebrate community in Loch Goil is the influence the algae may have on animal distribution patterns. The data from these investigations provides no indication of the reason for the observed "deep water" and "shallow water" invertebrate community. The variation is likely to be a response to sedimentary or hydrodynamical differences with depth. However, the influence of the epipelon on faunal distribution cannot be overlooked. A number of earlier studies have shown the epipelon to influence invertebrate communities in the marine habitat: Whitlatch (1981) found a positive correlation between deposit-feeding species diversity and the variety of food

within the sediment (eg. living diatoms, fecal pellets, organic-encrusted mineral grains and meiofauna) and suggests that food abundance may also regulate the distribution of deposit-feeding assemblages. Holland *et al* (1974) found that motile, pennate diatoms stabilise marine sediments and suggest that this could facilitate the colonisation of muddy sediments by filter feeding macrofauna and influence the distribution of meiofauna species. Jumars and Fauchald (1977) related changes in the abundance of sessile invertebrates with depth (2.4 to 5600m) to variation in sediment stability and the availability of food in relation to the optimum foraging area of the animals. However, Jumars and Fauchald (1977) also admit that the characteristics which determine the distribution of invertebrate species at particular depths, remain largely unidentified. In relation to Loch Goil, the results of sediment particle size analysis (Table. 8 section 4.3.3.3.) show there to be no clear change in sediment characteristics along the bathymetric gradient. However, the distribution of the sessile invertebrates may be responding to other sedimentary characteristics (eg. particulate organic matter) or hydrodynamical changes (eg.water movement) associated with increasing depth. In addition, the distribution pattern of adult invertebrates may reflect the pattern of dispersal (and subsequent settlement) of the their planktonic larval stages.

5.1.5.4 Biogenic disturbance

The effect of biogenic disturbance of the sediment on the epipelon is not clear. There appear to be no studies of the effect of bioturbation on the epipelon although the effect of biological activity on sediment properties is well documented (Meadows and Tufail, 1986; Holland *et al*, 1974; Eckmann *et al*, 1981; Cadee, 1976) and is known to affect: sediment stability, permeability, particle sedimentation, and pore-water chemistry (pH and Eh). The relatively large numbers of epipelon recorded at 6 and 12 m in July 1992 (Fig. 18, section 4.3.3.1) correspond to

high and moderate bioturbation of the sediment. However, only low levels of epipelic algae were found at 30 m depth where moderate biogenic activity was also recorded. Although no causality is demonstrated by these data, the influence of bioturbation on the observed distribution pattern cannot be ruled out.

5.1.5.5 Hypotheses and future work

Comparison of my data with the bathymetric distribution of epipelon (Fig. 18) clearly shows that the depth range at which the impoverished epipelic community was found (in July 1990) corresponds to the prolific, deep water fauna (see Table 15). Similarly, the depth at which the greatest biogenic activity was recorded corresponds to an area of high epipelic density. Although this does not necessarily mean causality it does indicate that processes of grazing and bioturbation may be influencing the growth and abundance of epipelon in addition to the effect of light attenuation with depth. This raises a number of hypothesis that can be tested in future studies:

> The **first hypothesis** is that: "grazing of epipelic algae by numerically dominant "water column and interface detrital feeders", in the deep water region (20-40m) of Loch Goil, limits the abundance of epipelic algae, especially in the context of the low light levels prevailing".
>
> The **second hypothesis** is that: "bioturbation of the sediment in the shallow waters of Loch Goil stimulates the growth of epipelic algae".

These are site specific hypotheses that apply only to the study area within Loch Goil, as the faunal communities in other areas of the loch appear to differ (Holt and Davies, 1991). Similarly the hypotheses would not necessarily apply to other sea lochs or coastal marine habitats.

Future research should include the testing of these hypotheses, as follows:

Hypothesis 1: (1) Laboratory and/or field experiments that monitor the response of epipelic algae to feeding activity of the major taxa identified from this study. (2) A detailed review of the literature regarding the trophic behaviour of each species. (3) analysis of gut contents. (4) observation of their feeding behaviour either in nature or in the laboratory. (5) measurement of the response of a natural population or culture of epipelic algae to the feeding activity of each species in the laboratory.

Hypothesis 2: Laboratory and/or field experiments that monitors the response of epipelic algae to bioturbation. These experiments must be carefully controlled so as to allow a distinction to be made between the grazing and bioturbation effects of organisms.

Another area of research is to determine the loss of epipelon, through grazing by the meiofauna (animals of less than 1000μm) and the protozoan communities of Loch Goil, which are currently unknown.

5.1.5.6 Conclusion

The current investigation identifies the species of benthic macrofauna that may be utilising the epipelon as a food resource and has recorded variations in biogenic disturbance of the sediment along a bathymetric gradient. However, I recognise that any relationship between these two factors and the pattern of distribution of epipelic algae (section 4.3) may be masked by a complex set of other co-varying parameters (light attenuation, depth of the halocline, wave action, nutrient levels of interstitial water, organic content of the sediment, sediment redox potential). In particular, this study emphasises the importance of examining biological and sedimentary characteristics as well as physicochemical parameters when trying to explain the distribution patterns of epipelon in nature.

5.2 EXPERIMENTAL INVESTIGATIONS INTO THE RELATIONSHIP BETWEEN Ophiura albida AND THE EPIPELON

5.2.1 INTRODUCTION

Qualitative observations made in the shallow sublittoral (6-11.5m depth) region of Loch Goil over a period of approx. six months showed that the ophiuroid *Ophiura albida* was a major element in the macrobenthic community. They were seen to move on the bottom of Loch Goil in large numbers where they appeared to be feeding. Examination of the stomach contents of 25 specimens collected from this region showed their diet to be predominantly of epipelic algae and sediment.

It was on the bases of these preliminary observations that I undertook to test a hypothesis ("first hypothesis" in section 5.1.5.5) regarding the trophic relationship between the brittlestar *Ophiura albida* (an interface detrital feeder) and the epipelon of Loch Goil. In particular this investigation measured the net effect of *O. albida* grazing on natural levels of epipelic algae.

I adopted a field experimental approach to this study in order to measure the response of a natural population of epipelon while maintaining normal environmental conditions (light, salinity, temperature and natural seawater). This method was favoured over the use of laboratory microcosms since preliminary trials at keeping algae under laboratory conditions were unsuccessful: there was a proliferation of epipelon and a modification of the community favouring the domination of only a few species of algae (data not provided).

Previous studies of the effects of herbivorous grazers on microalgae have mostly used laboratory microcosms in investigations of freshwater habitats (Cooper, 1973; Peer, 1986; Steinman *et al*, 1989) and marine intertidal mudflats (Admiraal *et al*, 1983; Bianchi *et al*, 1988; Bianchi and Rice, 1988; Morrisey, 1988; Pace *et al*, 1979; Sündback and Persson, 1981;). Collectively

these studies have monitored the response of epipelic algae to grazing by a range of herbivores including bivalves, gastropds, amphipods, polychaetes and nematodes. There has been a paucity of field experiments that investigate grazing effects on sublittoral epipelic communities. A notable exception is the study by Flint and Goldman (1975), who studied the effect of crayfish grazing on microalgae and higher plants in the freshwater habitat of Lake Tahoe. They utilised cages to exclude crayfish from artifical substrates (used to support diatom growth). Investigations of the effects of grazers on macroalgae within marine subtidal habitats have been frequent (eg. Jones and Kain, 1967; Fletcher, 1987). However, there appear to have been no previous studies of this kind on the epipelon in subtidal marine habitats or sealochs. The relationship between *O. albida* and epipelon has not previously been investigated experimentally and indeed, although they form some of the largest populations of brittle stars in the seas, the Ophiuridae (especially the genus *Ophiura*) have largely been ignored; little is known about the ecology of *O. albida* or of other ophiuroid species (Tyler and Banner, 1977).

5.2.1.1 Aims of the investigation

The purpose of this study was to determine the effect of the ophiuroid *O. albida*, on the natural community of epipelic algae and to test the hypothesis: "grazing by the ophiuroid *O. albida*, limits the abundance of epipelic algae in Loch Goil".

To this aim two experiments were carried out: Experiment 1 measured the response of natural populations of epipelic algae, following exposure to a gradient of grazing pressure by *O. albida*. Experiment 2 measured any modification the apparatus may have had on the natural levels of epipelic algae. Both studies tested the feasibility of this new experimental method, as a means of manipulating natural populations of epipelon maintained *in situ*, in a submerged habitat.

5.2.1.2 The ophiuroid Ophiura albida

O. albida grows to a maximum size of 12mm (disk diameter), living on the surface of marine sediments. It is an interface detrital feeder (WRc, 1992) eating mainly microalgae but also crustacean remains (Taylor, 1958) and occasionally macroalgal debris (Eichelbaum, 1910). *O. albida* is one of the most abundant bottom animals in the central North Sea but is generally scarce at depths exceeding 60m (Ursin, 1960). It is found in association with various communities but has the greatest affinity for the *Syndosmya* (*Abra*) community (Thorson, 1957; Tyler and Banner, 1977). Perhaps as a consequence of this affinity, *O. albida* is common throughout the north Clyde sealochs and is a major element in the subtidal benthic communities of: East Kyle; West Kyle; Holyloch; Gareloch; Loch Riddon; Loch Striven and Loch Long (Holt and Davies, 1991) and Loch Eil in the Firth of Lorne (Pearson, 1971; Pearson, 1970; Feder and Pearson, 1988). The geographical extent of *O. albida* extends from East Finmark to the Azores, and also in the Mediterranean, with a depth distribution of intertidal to 850m (Tyler, 1977).

In a study of echinoderms in the Bristol Channel, Tyler and Banner (1977) found that the distribution of *O. albida* was clumped. They also reported that the population was loosely segregated into a shallow (<10m) water population of small adults (3.3-6mm disc diameter) and a deep water community (>20m) of larger (3.9-6.9mm) and older ophiuroids. Tyler and Banner found high concentration of adult *O. albida* (max. 50 m^{-2}) in the fine-grained sediments and related both their distribution and the segregation of the population to the hydrodynamic environment, which would affect both the settlement of the meroplanktonic larvae and the sediments. The abundance and distribution of early adults (within the settlement areas) are modified by the subsequent motility and the migratory behaviour of the ophiuroids.

In terms of the utilisation of epipelon by *O. albida*, Taylor (1958) found that the availability of food is an

important factor governing gonad production in this species of ophiuroid. He also related a massive increase in gonad production, during spring, to the period of maximum food consumption. Tyler (1977) concluded that micro-algal production is a limiting factor in gonad production in *O. albida* and compared *O. albida* with *O. ophiura (texturata)*, which is not so dependant on seasonal micro-algae for gonad growth. Tyler attributed this to the more varied and omnivorous diet of *O. ophiura* and to the ability of *O. ophiura* to engage in suspension-feeding compared with *O. albida*, which is only an interface/detrital feeder (WRc, 1992).

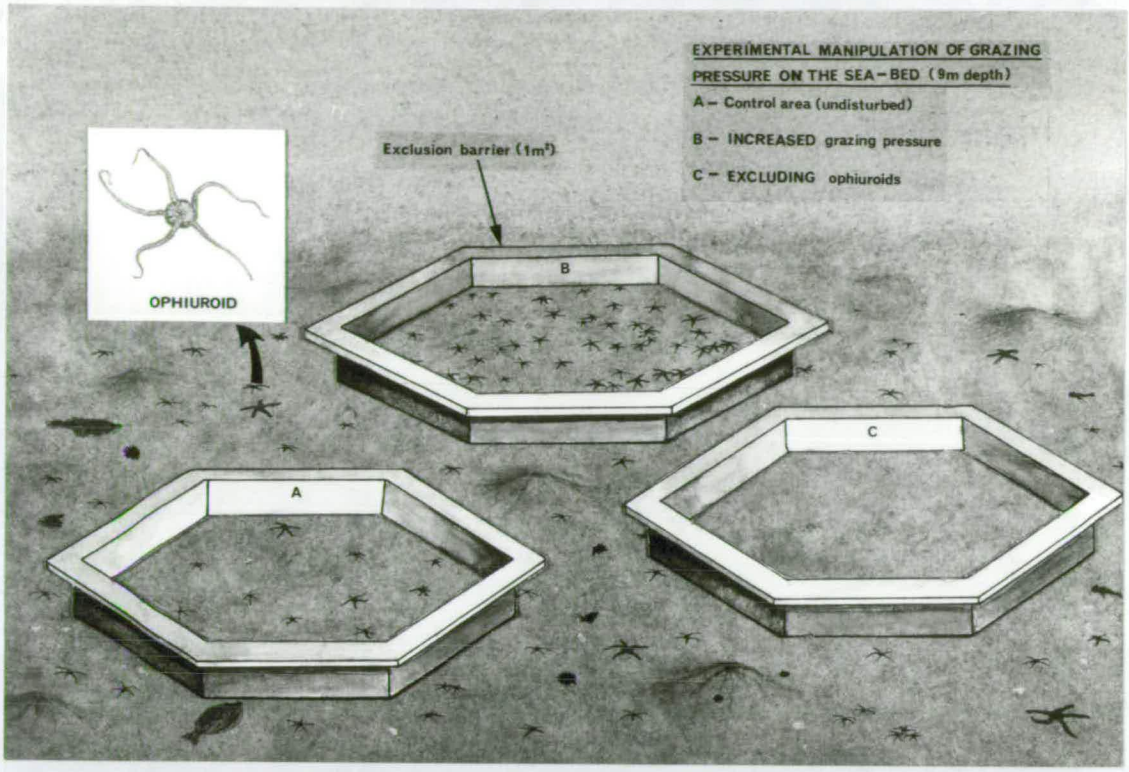
5.2.2 Methods

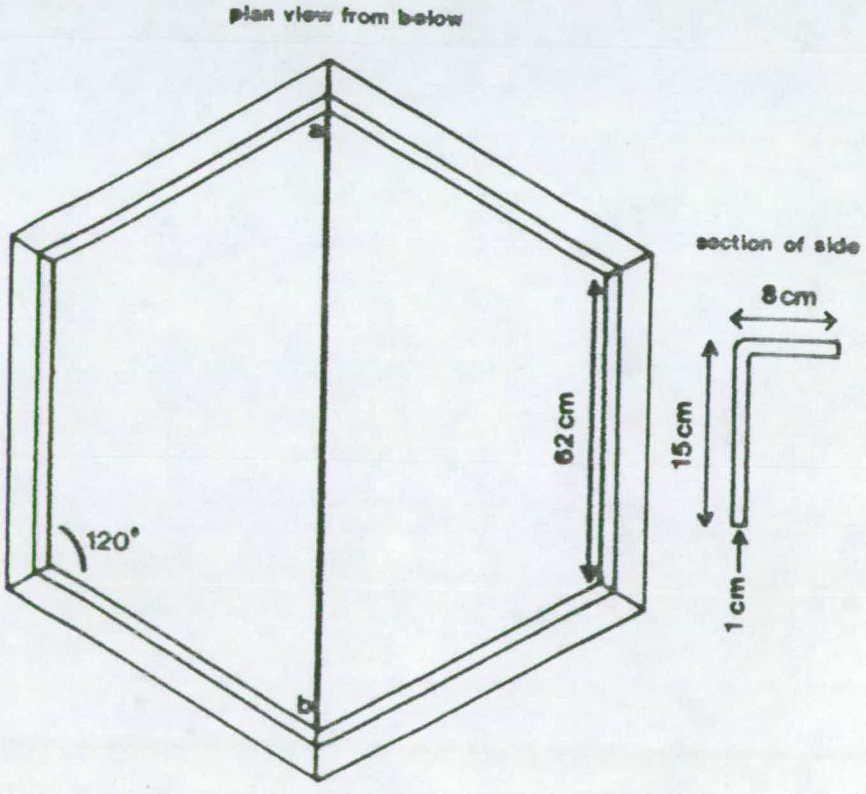
5.2.2.1 Experimental design

This investigation manipulated the density of *O. albida* on the bed of the loch by means of large (1 m^2) hexagonal barriers. The barriers regulated grazer density while minimising both shading of the algae and modification of natural environmental conditions. Because the epipelon are normally restricted to the upper 5mm or less of sediment (Estrada *et al*, 1974; Williams, 1962; Perkins, 1963) it is assumed the barriers prevent lateral movement of algae and thus effectively isolate the algae within a $1m^2$ area of sediment.

A plan of the barriers and a pictorial representation of part of the experimental area is shown in Fig. 44. The apparatus was constructed out of strips of PVC, welded together by heat, to form a hexagon. This shape minimised the length of the sides in relation to internal area, so as to reduce edge-effects on the enclosed epipelic algae. The 8cm flange increased the rigidity of the barrier and facilitated the exclusion of demersal fish and invertebrates from the apparatus. The barriers were labelled with small holes (1-6 holes) to enable identification by "feel", in conditions of poor light and low visibility.

Fig.44. A pictorial representation of part of the experimental area on the bottom of Loch Goil. Experimental barriers were used to manipulate grazing pressure, by the ophiuroid *O. albida*, on the natural community of epipelic algae while preventing incursion by other invertebrates. A plan and side view of the experimental barriers illustrates their structure. A central partition (a,b) divided a barrier into two equal halves, in experiment "2" (see text).


EXPERIMENTAL MANIPULATION OF GRAZING
PRESSURE ON THE SEA-BED (9m depth)
A – Control area (undisturbed)
B – INCREASED grazing pressure
C – EXCLUDING ophiuroids
Exclusion barrier (1m²)
OPHIUROID
A
B
C


plan view from below
120°
62cm
section of side
8cm
15cm
1cm

Six barriers were positioned at random on the bed of Loch Goil within an area of approx. 40 m^2, at a depth of 9m. Fig. 17 shows the location of the "experimental area" along the profile of Loch Goil. The sides of the barriers were pushed into the sediment to a depth of approx. 5cm and the location of the experimental area marked with a single buoy. Care was taken to avoid disturbance of the sediment while positioning the barriers on the bed of the loch. Because of logistical considerations a period of approx. 24 h passed between positioning the barriers and commencing the experiments.

5.2.2.2 EXPERIMENT 1 - RESPONSE OF EPIPELON TO A GRADIENT OF GRAZING PRESSURE BY THE OPHIUROID Ophiura albida.

A week before positioning the barriers, the density of *O. albida* (at 9m depth) was determined, within the "experimental area", by quadrat survey (30 x 625cm^2). A density of 51 *O. albida* per m^2 (mean +/- a standard error of 7) was recorded.

24h before the start of the experiment, approx. 450 specimens of *O. albida* were collected by hand from an area of sediment located approx. 500m to the east of the "experimental area"; from a depth of 6-11m. The ophiuroids were maintained in a mesh cage located next to the barriers until the start of the experiment on the following day (day 0). This period was necessary for logistical reasons and to facilitate the simultaneous introduction of the ophiuroids into the barriers. I assume that the ophiuroids could not feed during this time.

On "day 0" all surface living macrofauna were removed from within five of the barriers and the density of *O. albida* manipulated to approx. correspond with 0, 0.1, 1, 2.5 and 5 times the mean surveyed density ($51m^{-2}$). The experiment was left for 29d (4th October to 2nd November, 1988) during which time the apparatus was inspected periodically to remove any macroalgae, swimming-crabs *etc* that might have entered the barriers. After 29d the levels of epipelic algae within the barriers were compared with

levels from a similar area of sediment (1 m^2) outside the barriers. This area was the "control" and was chosen at random from an area of the bottom (approx. 16 m^2) located 5m to the west of the experimental area (knowing the direction facilitated the relocation of the area in poor conditions of light and visibility). This region was defined by a weighted rope to ensure that the sediment remained undisturbed by diver activity over the 29d period.

Replicate sediment samples (9 x 15.2cm^2) were collected by hand after 29d from randomly placed positions within the barriers and from the control area. Epipelic algae were harvested from the sediment samples (see 3.2) and estimates made of epipelic algal abundance and chlorophyll-a using the standards methods described in section 3.3.

After sampling, the efficacy of the experimental barriers (at confining the ophiuroids) was measured by collecting and counting the ophiuroids within each barrier.

5.2.2.3 EXPERIMENT 2 - TO DETERMINE THE EFFICACY OF THE barriers AT MAINTAINING NORMAL LEVELS OF EPIPELIC ALGAE.

The purpose of this experiment was to determine: 1. if the PVC barriers modify the levels of algae by their presence and 2. determine if the action of sediment removal (carried out to monitor 1.) significantly altered levels of algae due to disruption effects.

The sixth barrier was cleared of all surface-living invertebrates and divided into two halves ("A" and "B") by means of a strip of PVC, pushed into the sediment (Fig. 44).

The experiment was run over the same 29d period during which time the apparatus was inspected and replicate sediment samples (3 x 15.2cm^2) removed at the following times: from **side "A"** at 0, 4, 8, 15 and 29d and **side "B"** at 0 and 29d. Samples of sediment (9 x 15.2cm^2)

were also collected at 0, 4, 8, 15 and 29d from random positions within an approx. $16m^2$ area of the bottom located 2m to the east of the experimental area. This region was also marked by a weighted rope to ensure the sediment remained undisturbed by diver activity. These samples provided an indication of the natural ("ambient") levels of epipelic algae within Loch Goil at 9m depth.

Epipelic algae were extracted from the sediment and estimates made of abundance and chlorophyll-a using the standard methods (see 3.2.2.2 and 3.2.2.3).

5.2.2.4 Statistical analysis

The product-moment correlation coefficient (r) was used to measure the degree of correlation between estimated values of algal abundance and chlorophyll-a.

One-way analysis of variance (ANOVA) was applied to transformed (log) counts of algae to:

Experiment 1. Measure any significant difference between levels of epipelic algae in different experimental treatments compared with the residual variation recorded between sample replicates. This tested the null hypothesis (H_o): "there is no difference between levels of epipelic algae within sediment exposed to different grazing pressures or within the experimental control".

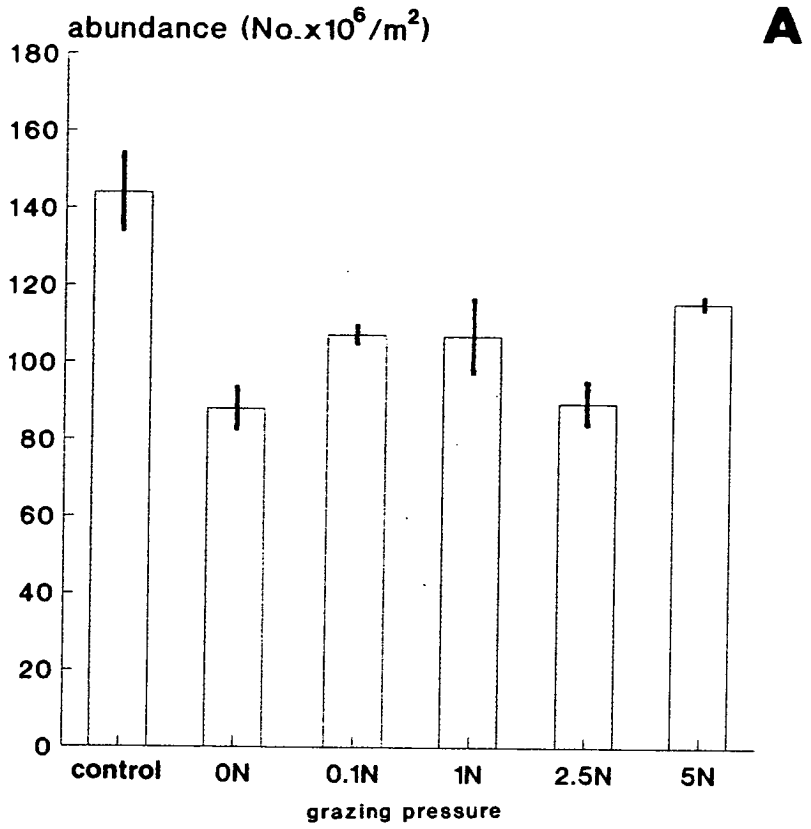
Experiment 2. Measure any significant difference between levels of algae inside and outside an experimental barrier over a 29d period. This tested the null hypothesis (H_o): "the enclosure of a natural community of epipelon by an experimental barrier has no effect on levels of algae".

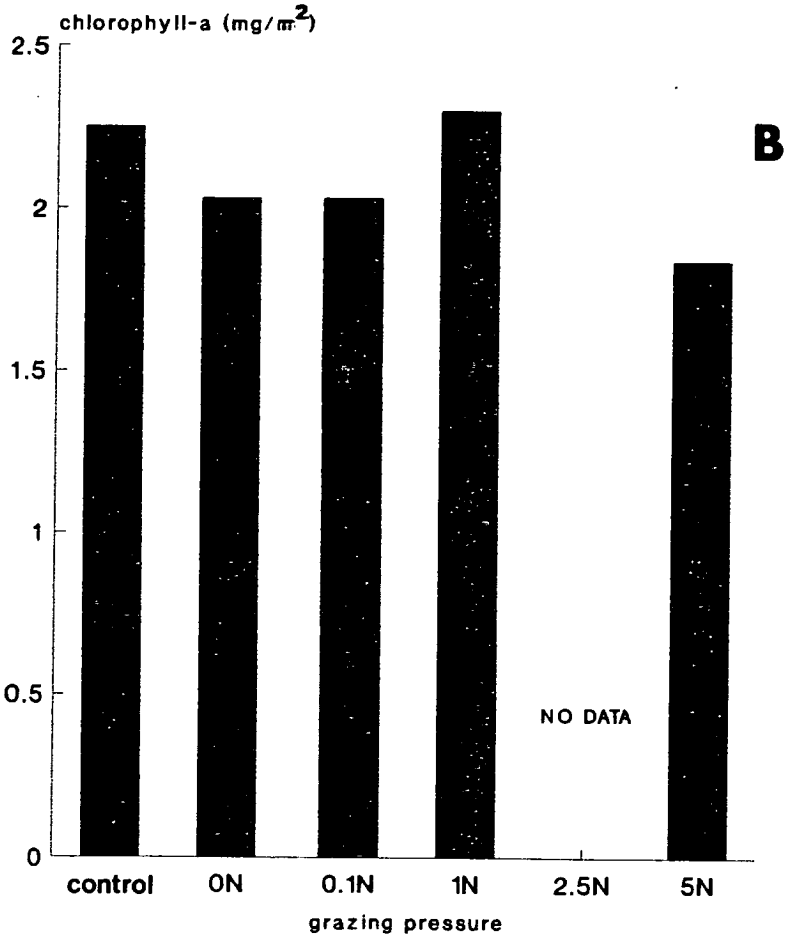
5.2.3 Results

5.2.3.1 Experiment 1

Fig 45 and Table 16 compare the levels of algae recorded in sediment, after a 29d period, exposed to a range of grazing pressure (0, 0.1, 1, 2.5 and 5 times 51 *O. albida*) with control levels. There is a poor

Fig. 45. The response of the epipelon (A: abundance No. x 10^6 m^{-2}; B: chlorophyll-a, mg m^{-2}) to a gradient of grazing pressure by the ophiuroid *O. albida* after a 29 d period. The density of epipelic algae within the experimental barriers are compared with each other and with ambient levels recorded outside of the experimental barriers. Key: 0 N, 0.1 N, 1 N, 2.5 N and 5 N times the natural density (N=51/ m^2) of *O. albida*. Bars indicate standard error.


abundance (No.x10^6/m^2)
A
180
160
140
120
100
80
60
40
20
0
control
0N
0.1N
1N
2.5N
5N
grazing pressure


chlorophyll-a (mg/m^2)
B
2.5
2
1.5
1
0.5
0
NO DATA
control
0N
0.1N
1N
2.5N
5N
grazing pressure

Ophiura albida grazing pressure N x 51 m	No. start/end of 29 d period	chlorophyll-a mg m^2	No. of algae No. x $10^6 m^2$	SE No.x$10^6 m^2$
control	-	2.25	144.0	9.9
0 N	0/0	2.03	88.0	5.3
0.1 N	5/4	2.03	107.3	2.2
1 N	51/22	2.30	106.9	9.4
2.5 N	128/114	no data	89.5	5.4
5 N	255/222	1.84	115.6	1.4

Table 16. Response of the epipelon (indicated by a change in abundance and chlorophyll-a after a 29 d period) to a gradient of grazing pressure of *Ophiura albida*. Ophiuroid numbers were manipulated to correspond to 0, 0.1, 1, 2.5 and 5 times the natural level (51 per m^2) present within Loch Goil at 9 m depth. Epipelic algae, exposed to ophiuroids over a 29 d period, are compared with algae from within a control area, situated outside of the barriers. The efficacy of the apparatus is indicated by the difference in the number of ophiuroids recorded at the start and end of the experiment. (SE = standard error).

association between estimated levels of algal abundance and chlorophyll-a (correlation analysis: r=0.318). This makes it difficult to identify any patterns in the data although there is clearly no simple response of the epipelon to increased grazing pressure.

The results of the ANOVA (Table 17) shows there to be no significant difference (P>0.05) between the mean abundances of epipelic algae within sediment exposed to different grazing pressure or within the control area. The H_o (5.2.2.4) is therefore accepted.

The ophiuroids appeared to be distributed evenly within the barriers and were assumed to be feeding normally during the 29d period.

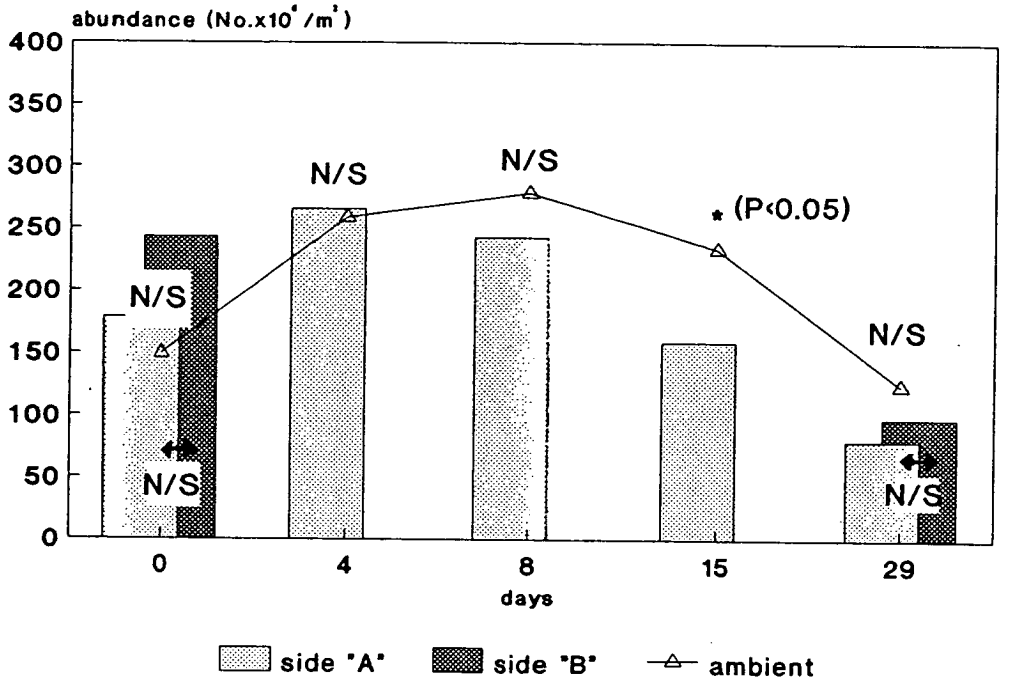
ANALYSIS OF VARIANCE				
source	DF	SS	MS	F
factor	5	0.4865	0.0973	1.65
error	12	0.7092	0.0591	
total	17	1.1957		

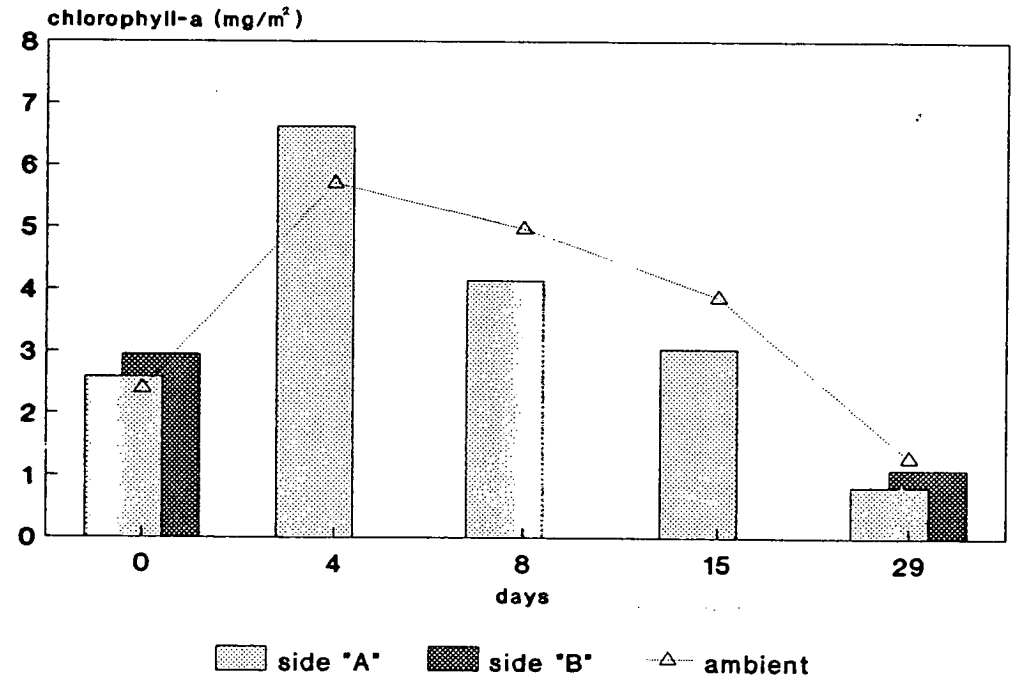
Table 17. Results of analysis of variance (ANOVA) of log-transformed abundance data. As the calculated value of F is less than the tabulated value (F=3.106 [Neave, 1979]) I accept the Ho and conclude that there is evidence that there is no significant (P>0.05) difference between the level of epipelon in sediment exposed to a range of grazing pressure or sediment outside of the experimental barriers (ambient). For further details on the form of the ANOVA results, see Ryan *et al*, 1985 and Elliott, 1971.

5.2.3.2 Experiment 2

Levels of epipelic algae within the barrier (side "A") closely followed ambient levels although a significant difference in numbers was recorded on day 15 (F=6.7; P<0.05). Fig. 46 shows the change in levels of algae over the 29d and summarises the results of the ANOVA. No significant difference was recorded between side

Fig. 46. Histograms comparing levels of epipelic algae recorded inside and outside (ambient) a barrier (A: abundance No. x 10^6 m^{-2}; B: chlorophyll-a, mg m^{-2}). The graphs also compare the effect on the epipelon of sampling continuously over a 29 d period (side "A": 0, 4, 8, 15 and 29 d) compared with sampling only at the start and end of the experiment (side "B": 0 and 29 d). Analysis of the data by ANOVA show there to be no significant difference "N/S" ($P>0.05$) between the two sides at 0 d and 29 d. Except for day 15 (* = significant $P<0.05$) there was no significant difference between levels inside (side "A") and outside (ambient) the barriers over the 29 d period. Bars indicate standard error.


abundance (No.x10⁴ /m²)
400
350
300
250
200
150
100
50
0
N/S
N/S
* (P<0.05)
N/S
N/S
N/S
0
4
8
15
29
days
side "A"
side "B"
ambient


chlorophyll-a (mg/m²)
8
7
6
5
4
3
2
1
0
0
4
8
15
29
days
side "A"
side "B"
ambient

treatment	No. of algae [No. x $10^6 m^2$] (chlorophyll-a [mg m^2]) 0	4	8	15	29	days
ambient level	149	258.7	278.7	233.6	124.5	
	(2.40)	(5.71)	(4.97)	(3.87)	(1.29)	
side "A"	178.5	265.4	242.6	159.1	80.3	
	(2.58)	(6.63)	(4.15)	(3.04)	(0.83)	
side "B"	242.9	-	-	-	98.3	
	(2.95)	-	-	-	(1.11)	

Table 18. Levels of epipelic algae inside and outside (ambient) an experimental barrier over a 29 d period. The data also show the effect, on algal levels, of sampling (sediment removal) either continuously (side "A": 0, 4, 8, 15 and 29 d) or only at the start and end of the experiment (side "B": 0 and 29 d). Ambient levels represent the natural variability of epipelon that occurred in Loch Goil within the "experimental area" (see text).

"A" and "B" at either the start or end of the experimental period. The similarity of the data on d. 29 indicates that sediment removal did not have a significant effect on the results obtained from side "A".

Correlation analysis of the data from this experiment showed there to be a clear association between the abundance and chlorophyll-a data ($r=0.955$), which is reflected in the similarity of distribution patterns seen in Fig. 46.

5.2.4 Discussion

The results appear to indicate that the ophiuroid *O. albida* has no significant effect on levels of epipelic algae within the sediments of Loch Goil. However, I must conclude that this investigation is inconclusive. In particular, the following limitations in design have become apparent:

1) In order to discern the effect of the varied grazing pressures on the epipelon, significant similarity must exist in the levels of algae within the different barriers at the start of the experiment. The basic assumption of "a homogeneous distribution of algae on the bottom of Loch Goil" is not valid as subsequent investigation showed the distribution of epipelon to be significantly patchy (see 4.1.4).

2) Experiment 1 is inadequately controlled. Although the "control" area is exposed to natural levels of grazing by *O. albida* it is also exposed to greater biological interference including disturbance by fish and grazing by motile invertebrates such as the sea mouse *Aphrodite aculeata* (polychaeta). However, the provision of an adequate biological control would be difficult to achieve *in situ* owing to the spatial patchiness of the epipelon on the bottom of the loch.

3) The type and number of other invertebrate species (eg. terebellid polychaetes) within the sediment of each barrier is unknown. It is likely that levels of grazing by

these macro-invertebrates may vary significantly between barriers which makes interpretation of these results impossible. Similarly, because *O. albida* is omnivorous (Taylor, 1958) the effect of abnormally high densities of *O. albida*, on the other heterotrophic animals within the sediment, is uncertain. Alteration of the macrofauna (>0.5mm) and meiofauna (0.5mm-0.062mm) community may have secondary effects on the levels of epipelon through alteration of other grazing pressures. This could have knock-on effects at all trophic levels as meiofauna in turn graze on protozoans, which may themselves consume algae.

Nonetheless, the results of this study are surprising considering that *O. albida* feeds predominantly on epipelic algae (Taylor, 1958; personal observations). The expected response of the epipelon to exposure of a range of abnormally high densities of *O. albida* (5-255m^{-2}) is to show a depletion of algae in proportion to the intensity of grazing. Conversely, if *O. albida* normally limits algal abundance, through grazing, then their exclusion is likely to result in a proliferation of algae within the confines of the barrier.

However, it is possible that the response of the natural community of epipelon, is more complex. Previous studies on the effects of macrofaunal deposit feeders on benthic microflora have documented mechanisms of positive feedback from consumers (nutrient excretion, increased turnover rate, disruption of the sediment by bioturbation and provision of additional surface area of sediment for algal growth) that stimulate elevated levels of algae at low levels of grazing (Bianchi *et al*, 1988; Levington *et al*, 1977; Connor *et al*, 1982; Hill and Knight, 1987; Flint and Goldman, 1975). However, conflicting results are reported by Morrisey (1988), who found that low levels of grazing by herbivores on marine sediments did not lead to an increase in microalgal standing stock. Moreover, Hargrave (1970) and Cooper (1973) reported enhancement of

microalgal density and production when exposed to natural densities of grazers. At high levels of grazing, microalgal abundance is normally reduced as removal of algal cells exceed production and growth. For instance, Sundbäck and Persson (1981) found increased chlorophyll-a and primary production with decreasing numbers of herbivorous amphipods. However, abnormally high levels of grazing may initiate a process of negative feedback whereby the release of toxic metabolites (eg. ammonia) further reduces algal growth (Hargrave, 1970).

The period of exposure (29d) utilised in this experiment may have been too long. Hence, any response the epipelon may have shown to increased grazing or the removal of grazers could have occurred earlier in the experiment. Pace *et al* (1979) measured a highly significant increase in standing stock and productivity of microalgae within three days, following removal of *Nassarius obsoletus* (Gastropoda) from a salt marsh mudflat. Further study should therefore focus on the short term temporal response of epipelon, utilising more carefully controlled experimental design either in the field or using laboratory-based microcosms.

A gradient of grazing pressure would also be accompanied by a corresponding rise in the disturbance (bioturbation) of the surface sediment attributed to the foraging behaviour and movement of animals. A reduction in algal abundance through grazing may have been masked by disturbance-related stimulation of epipelic growth. Connor *et al* (1982) found that secondary grazing processes are disproportionately important in epipelic communities. They attributed this to the short distances required to bury algal cells below the photic zone. Further work is required to determine if *O. albida* exerts its effect on the epipelon primarily via consumption or disturbance.

The reason for the poor correlation of epipelic abundance and chlorophyll-a data in experiment "1" is not clear although it may be attributed to differences in the

community structure and cell-volume of the dominant algal species within the different barriers. The accuracy of the data could be improved in future studies by increasing sample replication. This would reduce residual variation and overcome any patchiness of the epipelon within the barriers and reduce edge effects. However, because of the difficulties in handling large numbers of cores while diving, increasing sample replication may not be feasible in studies of this kind. Similarly, it would be desirable to have greater replication of treatments and controls in this investigation. However, the use of additional barriers was limited in this case by practical considerations and availability of resource.

The barriers were effective at keeping ophiuroids within the experimental areas although some loss of animals did occur. This was probably due to predation by fish and crabs. However, the loss of *O. albida* to predation is less than the 25% loss of *Ophiura* reported to occur in shallow sea lochs by Aronson (1992). He set ophiuroids as bait for predators in Loch Melford, Scotland (20-30m depth) and at a continental slope site off the coast of North Carolina (500m depth) to investigate the predation pressure experienced by brittlestar populations. The design of the experimental barriers utilised in my investigation may be improved by covering the apparatus with a mesh to exclude predators. However, the use of a mesh to exclude crayfish from periphyton in Lake Tahoe was found by Flint and Goldman (1975) to significantly reduce light penetration to the sediment.

Despite the limitations of the experimental design the results of experiment 2 indicate the possible usefulness of this method in future studies of grazer-epipelic relationships in submerged aquatic and marine habitats. However, future experiments should utilise sediment that has been voided of all other invertebrates so as to allow the incorporation of adequate biological controls. Any field experiments should be accompanied by

parallel studies using laboratory microcosms. This will facilitate the replicability,control and manipulation that are difficult in field conditions.

The reliance of *O. albida* on epipelon for at least part of its nutrition (Taylor, 1958; Tyler, 1977) may influence both the levels of epipelon within the sediments of Loch Goil and the dispersion of *O. albida* to areas of high algal density. Although no quantitative measurement of seasonal fluctuations in *O. albida* were made, qualititative observations reveal that the ophiuroid may be migrating to the shallow (6-11m depth) subtidal region of Loch Goil over the winter period. A dense population of *O. albida* (51 per m^2) was recorded at 9m depth in October 1988, whereas in July 1990 a bathymetric survey of the benthic macrofauana (recorded over a 6-40m depth range) found low density of *O. albida* at most depths except 30m and 40m, where it was recorded at a density of 38 and 37 per m^2 (respectively). I postulate that *O. albida* is migrating to the shallow water sediment to exploit epipelon for food when levels in the deeper waters may be limited by the reduced daylength, temperature and light that occurs during the winter period (pers. observ.). This would be consistent with the highly motile behaviour of adult *O. albida* observed by Tyler and Banner (1977).

In conclusion, this experiment does not separate grazing and bioturbation effects and the underlying assumptions of the experimental design are flawed. Consequently the experiments were unable to test the hypothesis: "grazing by the ophiuroid *O. albida*, limits the abundance of epipelic algae in Loch Goil". The results nevertheless suggest that the response of the epipelon to the presence of *O. albida* is complex and that a simple prey-predator model is inappropriate.

CHAPTER 6

GENERAL DISCUSSION

The aims of my research, outlined in Chapter 1, are as follows:

A. To establish a methodology for the sampling and measurement of subtidal epipelic algae.

B. Document the spatial herogeneity of epipelon at a range of scales and along a depth profile.

C. Document the temporal (seasonal) heterogeneity in relation to the abundance and composition of epipelon.

D. To describe the epipelic community in Loch Goil and to seek to understand B and C in relation to the physicochemical parameters and/or biological parameters.

E. Investigate the relationship between the invertebrates and the epipelon in Loch Goil.

In respect to these principal aims my research has been successful, although inevitably my data have evoked more questions than they have provided answers. In this chapter I will attempt to summarise the results that have been reported and discussed in the previous sections, and discuss them further in relation to the principal aims of my research (aims B-E).

6.1 THE EPIPELON OF LOCH GOIL

The epipelic flora of Loch Goil is diverse, consisting almost entirely of diatoms (163 species of diatom comprising 39 genera). The prevalence of pennate diatoms is a common feature of the submerged flora from small bodies of fresh water (eg. Hickman and Round, 1970), and of subtidal (Bodeanu, 1964, Plante-Cuny, 1969) and

intertidal marine (Colijn and Dijkema, 1981) epipelon. In contrast, the algal populations on the intertidal mudflats in the Ems-Dollard estuary were found by Admiraal *et al* (1984) to be not always composed exclusively of diatoms. They found that, during periods in spring or summer, large numbers of blue-green and euglenoid algae or mats of green alga (*Vaucheria sp.*) were prevalent.

Another characteristic feature of the epipelic flora of Loch Goil is the numerical dominance of a few species of diatom (eg.*Navicula* cf.*tripunctata*, *Navicula sp.H*; *Navicula forcipata* var.*densistriata*; *Amphora proteus*). This feature occurs throughout the year and is relatively unaffected by depth. Although the dominant species of epipelon recorded in Loch Goil and Loch Sween (Smyth, 1955) are different (see 4.3.4), it appears that a salient feature of the epipelon of both these lochs is a remarkable stability in epipelic community structure. This contrasts with the phytoplankton which generally have greater seasonal variability (Park, 1991, Park, 1992). Further investigation is required in order to confirm whether this stability in the epipelon is a general characteristic feature of sea loch and fjordic habitats.

The results of the re-colonisation experiment indicated that the algal dominants may have a competitive advantage over other algae which can perhaps be attributed to the rapid growth and high dispersal powers of these species. In particular it appears that *Navicula* cf.*tripunctata* is an opportunist species, quick to colonise an area of sediment denuded of algae (by eg. grazing).

The epipelic flora of Loch Goil appears to include some species that are commonly recognised as fresh water algae. Most of the fresh water alga were found in low abundance (*Eunotia spp; Frustulia rhomboides; Rhoicosphenia abbreviata; Tabellaria flocculosa*) and there

is little doubt that they originate from Cormonachan Burn situated close to the survey site. However, *Navicula* cf.*tripunctata* was found in abundance. *N. tripunctata* is a fresh water species (Krammer and Lange-Bertalot, 1986) and it may be that the identification of this species is incorrect, or there may be a morphologically similar species occupying similar niches in fresh and salt waters. Although the longevity of the fresh water species in Loch Goil is unknown, their existence with intact chloroplasts in marine sediments is of interest, and may be worthy of further investigation.

The average number of epipelic algae recorded from Loch Goil appears to be quite low compared with other marine and fresh water habitats reported in the literature This can partly be attributed to my method of extracting algae through a tissue screen (so as to provide a clean, easily analysed sample community; see Section 2.4.4) but may must also reflect naturally low levels.

It appears from the literature that the densities of epipelon recorded over the bathymetric profile of Loch Goil (1.1×10^6 to 2.8×10^8 cells m^{-2}) or over two continuous years (4.0×10^7 m^{-2} to 4.49×10^8 m^{-2}) are generally of an order of magnitude or more lower than levels in most other marine and fresh water sub-tidal habitats. Similarly, it is difficult to make valid comparisons between the pigment data obtained using my standard method of extraction and enumeration (see 3.2.2.3 and 3.3.3) with various methods used in other studies. With the exception of levels of abundance recorded by Manea and Skolka (1961: 5.7×10^3 to 5.15×10^4 cells m^{-2}) other studies found the following range of cell densities: Stevenson and Stoermer (1981) 9×10^9 to 3×10^{10} cells m^{-2}; Stevenson *et al* (1985) 1×10^8 to 1.2×10^{10} cells m^{-2}); Roberts and Boylen (1988) 3×10^9 cells m^{-2} maximum and Bodeanu (1964) 3.9×10^5 to 1.2×10^{10} cells m^{-2}. This difference is unlikely to be simply attributable to real differences in nature as the algal extraction methods used

in these investigations differed from mine and involved separating the algae by washing, followed by enumeration of the algae in a concentrated subsample. It is also difficult to compare the levels of epipelon in Loch Goil with the semi-quantitative measurements made by Smyth (1955) in Loch Sween. He recorded levels ranging from 1.0 x 10^6 to 7.32 x 10^9 cells m^{-2} utilising glass slides placed on to the surface of the submerged mud for periods ranging from 4-118 days. Estimates based on direct counts of algae from core samples of Loch Sween sediment showed a maximum estimated abundance of 5.8 x 10^9 cells m^{-2} at a depth of 2m (Sept. 1946).

It is unrealistic to assume that the flora of Loch Goil has been fully characterised as a result of my research, particularly as I have no evidence of the large scale (km) heterogeneous distribution of species within the loch. Also, there is likely to be a portion of the epipelic flora (eg. filamentous or coccoid blue-green algae, dinoflagellates and euglenoid flagellates) which has been unsuccessfully sampled by the standard methods adopted. Although the exclusion of these groups of algae may have been exaggerated by the use of a tissue screen (see section 2.3.2) even colonial blue-green algae can normally pass through tissue placed on a sample of sediment (D. G. Mann, pers. comm). Therefore, it is likely that these algae are either absent, or present only in very low abundance in the sediment of Loch Goil.

Similarly, this study has not considered other microalgal communities that are associated with the sediments of Loch Goil. This includes the epipsammon which consist mostly of diatoms, but also coccoid Cyanophyta and Chlorophyta attached to surface of sand grains (Round, 1981). Also the plocon which is a community of mainly centric diatoms or filamentous algae that is loosely associated with sediment but not creeping on or between the particles (Round, 1981). In addition there will be a community of epilithic and epiphytic microalgae associated

with the stones and macroalgae (respectively) which are prevalent in the shallow (0-6m) subtidal region of Loch Goil.

This study has provided a detailed floristic study of the epipelon within a small region of Loch Goil. It remains conjecture as to the extent to which this flora and its patterns of distribution is typical of sealochs in Scotland. The fact that a significant proportions of water of Loch Goil is derived from the Clyde Estuary (20-40% near the confluence of Loch Long and Loch Goil, 10-29% at the centre of Loch Goil and 1-14% at Lochgoilhead: Mackay and Halcrow [1976]; Mackay and Leatherland, [1976]) must ensure some continuity of species due to the dispersion of epipelic algae suspended in the water column. It is tempting to predict that basic similarities exist in epipelic floras of sealochs, in much the same way that the invertebrate community of Loch Goil bares a resemblance to other sealochs in the Firths of Clyde and Lorne. For example the communities of benthic invertebrates identified from this study are similar to communities recorded throughout the north Clyde sealochs by Holt and Davies (1991) and Loch Eil in the Firth of Lorne (Pearson, 1971; Pearson, 1970; Feder and Pearson, 1988). Also the geographical distribution of the *Abra* community (identified in section 5.1 as being comparable to the Loch Goil animal community) includes inner parts of fjords, coastal areas of Scotland, and the Black Sea off the coast of Romania (Thorson, 1957).

Because of the lack of comparative data on subtidal marine epipelon, much descriptive work is still required. In particular there is the enormous task of describing the diversity of epipelic algae that inhabit the many different habitats that must exist within this and other Scottish sealochs. Qualitative samples of subtidal sediments are currently being collected from sites around Scotland by the Royal Botanic Gardens, Edinburgh. These are being collected for taxonomy and there remains little

ecological research of subtidal marine habitats within Scotland. Future ecological data on epipelon (factors affecting its growth; patterns of variability; processes of loss etc) need to be integrated with existing information on the phytoplankton, water chemistry and other relevant biological information on the sealochs of the northern Firth of Clyde.

As a product of my investigations I have compiled a taxonomic atlas and catalogue (Appendix 1). This not only illustrates the flora which is discussed throughout this thesis, but may also assist any future researchers in identifying the epipelon of subtidal sediments in sealochs and elsewhere. The atlas is arranged so that taxa are grouped according to gross morphological similarity rather than taxonomic affinity and should be used to assist identification rather than as a substitute for the use of taxonomic keys.

6.2 BIOLOGICAL INTERACTIONS WITH THE EPIPELON

6.2.1 The trophic relationships between the epipelon and invertebrates

This study has successfully described the diverse (82 species) community of macro-benthic animals that inhabits a region (6-40m depth) of Loch Goil. Although the quantitative relationship between many of the these animals and the epipelon is unknown, that so many species of animal are sustained in such abundance is an astonishing testimony to the nutrient value of the epipelic diatoms and other benthic and planktonic food sources within Loch Goil. In section 5.1.4.1 the invertebrate taxa identified from my study were assigned to an isotrophic group (groups with similar feeding habits: detrital, deposit or suspension feeder) based on trophic habits recognised in the literature (Pearson, 1971; WRc, 1992; Gage, 1972; Fauchald and Jumars, 1979) or postulated from personal observations. The number and

proportion of species from the different feeding groups were found to be as follows: carnivorous predators (28 spp, 35.4%); deposit feeders (10 spp, 12.7%); surface detrital feeders (11 spp, 13.9%); water column detrital (suspension) feeders (29 spp, 36.7%) and scrapers (1 sp, 1.3%) see Table 15 in section 5.1.4.1. Based on these results it is possible to evaluate the role of different macrobenthic fauna in the food web of Loch Goil.

In its most general sense the principal food web pathway is: epipelon-invertebrate-fish-seal or bird. Fig. 47 illustrates the trophic relationship between the animals of Loch Goil and the epipelon as a whole. The food web is limited in that the association between different isotrophic groups makes no distinction between the species within each group. Thus, I assume that no preference is made for, eg. a certain species of epipelic algae or polychaete. In addition no allowance is made for those species that feed at more than one trophic level; for example, Syllidae species are both detrital feeders and carnivores (Fauchald and Jumars, 1979). This simplifies the data presentation but obviously underestimates the complexity of the food web that would naturally occur in Loch Goil.

My investigation of the invertebrates community of Loch Goil was limited to the analysis of the macrofauna (>0.5mm) and ignores all the smaller animals that passed through the 0.5mm screen. This includes the meiofauna (0.5mm-0.062mm) which usually consists of nematodes, harpacticoid copepods, turbellarians and gastrotrichs but for a time would also include most of the macroinvertebrate fauna in their the post-larval stages (Gray, 1981). It also includes the microfauna (<0.062mm) which consist almost exclusively of protozoans. The grazing of epipelic algae by these small meio- and micro-invertebrates may be significant, particularly in the light of their relatively high level of abundance compared with the macrofauna. For example, a study of an intertidal

Fig. 47. The feeding relationships within Loch Goil based on invertebrates and fish recorded between 6-40m depth in July 1990. The invertebrates are categorized into isotrophic feeding groups according to the literature (Pearson, 1971; Gage, 1972; Fauchald and Jumars, 1979) or personal observations. The food web shows the role of the epipelon and other microalgae (boxed) in the feeding ecology of Loch Goil. Arrows indicate the flow of energy. Sediment bacteria represent the main decomposers of all dead organic matter.

SCRAPER

Polyplacophora indet.

WATER COLUMN DETRITAL FEEDERS (ON SEDIMENT)

Amphipoda indet.
Thyone sp.
Pennatulacea indet.
Virgularia mirabilis
Tubularia indivisa
Modiolus modiolus
Mya arenaria
Mya truncata
Pecten maximus
Chlamys opercularis
Sabellidae indet.
Owenia fusiformis
Myxicola infundibulum
Cerianthus lloydii
Pachycerianthus multiplicatus

WATER COLUMN DETRITAL FEEDERS (EPILITHIC/EPIPHYTIC)

Ophiocomina nigra
Ophiothrix fragilis
Sabella pavonina
Protula tubularia
Pomatoceros triqueter
Cirripedia indet.
Alcyonium digitatum
Porifera indet.
Botryllioides leachi
Ascidiacea indet.
Metridium senile
Adamsia carciniopados
Protanthea simplex
Urticina eques

PREDATORY FISH

Conger conger
Scyliorhinus canicula
Zeugopterus punctatus
Myoxocephalus scorpius

SUB-SURFACE DEPOSIT FEEDERS

Polychaeta indet. (5 spp)
Sipuncula indet.
Nephtys hombergii
Syllidae indet.
Aporrhais pespelecana

CARNIVOROUS FISH

Gobius sp.
Pomatoschistus minutus
Gobiusculus flavescens
Spinachia spinachia
Callionymus lyra
Syngnanthus phlegon
Pholis gunnellus
Centrolabrus rupestris
Limanda limanda

CARNIVORES (SPECIALIST FEEDERS)

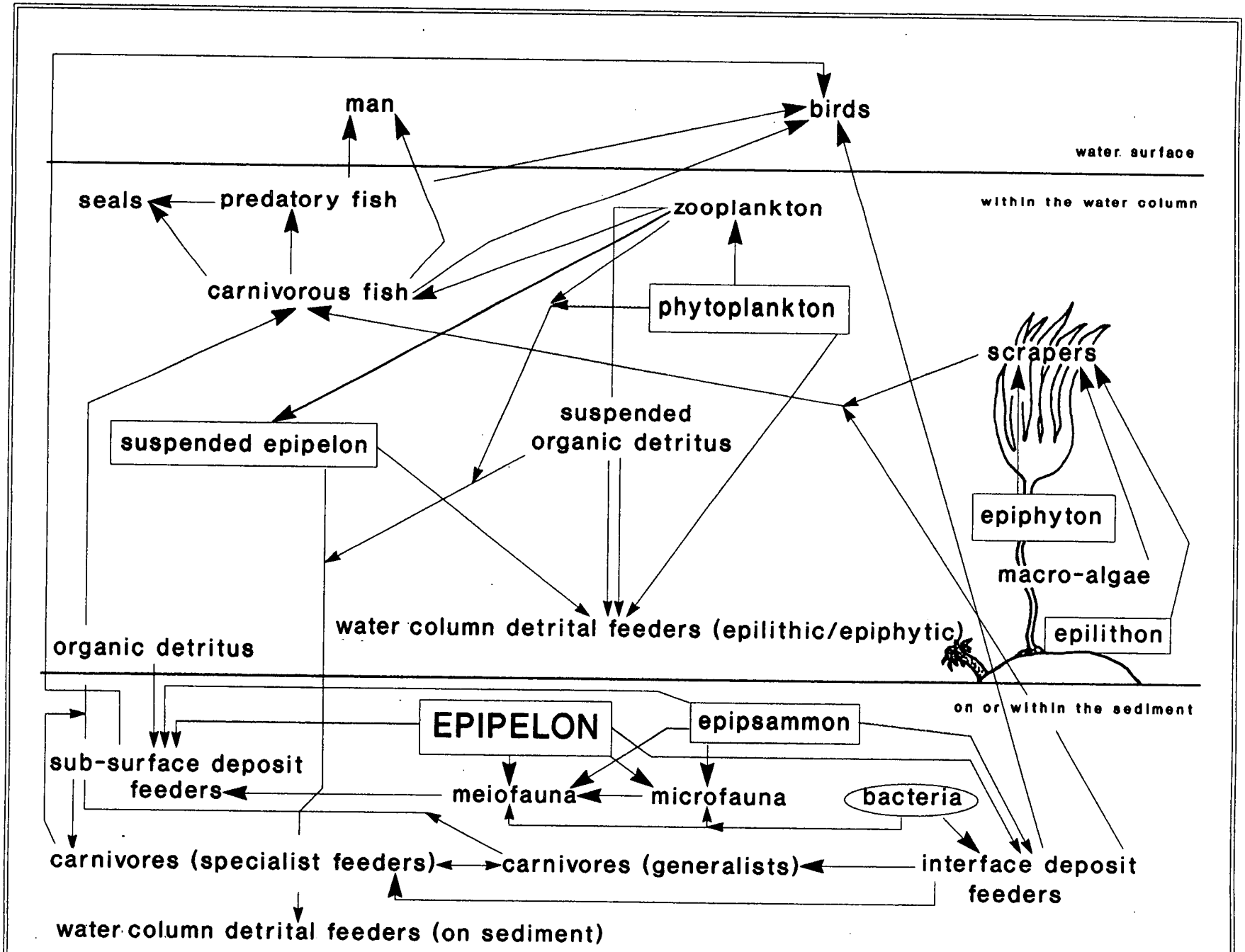
Opisthobranchia indet.
Limacia clavigera
Facelina auriculata
Tubulanus annulatus
Phyllodoce sp.
Capitella capitata
Aphrodite aculeata
Psammechinus miliaris
Asterias rubens

CARNIVORES (GENERALISTS)

Pagurus bernhardus
Pagurus prideaux
Carcinus maenas
Liocarcinus depurator
Munida rugosa
Galathea sp.
Buccinum undatum

INTERFACE DEPOSIT FEEDERS

Ophiura ophiura
Ophiura albida
Leptosynapta inhaerens
Echinus esculentus
Echinocardium cordatum
Turritella communis
Acanthocardia aculeata
Cerastoderma edule
Abra alba
Lanice conchilega
Cirratulidae indet.
Lagis koreni
Eupolymnia nebulosa
Arenicola marina


man
birds
water surface
seals
predatory fish
within the water column
zooplankton
carnivorous fish
phytoplankton
scrapers
suspended epipelon
suspended
organic detritus
epiphyton
macro-algae
water column detrital feeders (epilithic/epiphytic)
epilithon
organic detritus
on or within the sediment
EPIPELON
epipsammon
sub-surface deposit
feeders
meiofauna
microfauna
bacteria
carnivores (specialist feeders)
carnivores (generalists)
interface deposit
feeders
water column detrital feeders (on sediment)

beach by Fenchal (1978) found the microfauna (approx. 10^6-10^7 m^{-2}) and meiofauna (approx. 10^5-10^6 m^{-2}) to dominate numerically, although the macrofauna (approx. 10^3 m^{-2}) were dominant in terms of biomass. It is known that most protozoans eat whatever they find around them of a suitable size (including diatoms), like simple hunter-gathers (Finlay and Fenchel, 1989). An ecological study by Fenchel (1968) of ciliate populations inhabiting soft marine sediments in Scandinavia identified the importance of epipelic diatoms in the diets of different ciliate species. However, there appear to have been few studies that quantify the loss of epipelic algae to these myriads of tiny grazers. Research efforts should concentrate on quantifying these losses, although such studies face formidable taxonomic difficulties. In addition, difficulties in maintaining natural communities of animals in the laboratory or biological controls in the field will pose problems.

Plante-Cuny and Plante (1984) presented a clarification of consumers of marine epipelic algae in terms of the size classifications of macro- meio- and micro-fauna. They also reviewed the literature on food selection and consumption by a range of animal species within these categories. Plante-Cuny and Plante concluded that the details of whether epipelic diatoms form a major or merely accessory item of food for benthic animal remains largely unexplored. They also point out that:

> (a) the diets of many benthic animals are poorly understood; (b) that benthic diatoms may be consumed directly by non-benthic animals such as limicolous birds; (c) that phytoplanktonic food (referred to in much of literature as being ingested by benthic consumers) often consists largely of re-suspended epipelic diatoms; (d) and that the digestibility of diatoms has only recently been demonstrated for some animals.

All these remarks are relevant to my study although the classification of the feeding habits of benthic marine animals has advanced considerably since 1978 with the WRc (1992) appraisal of isotrophic groups for most marine invertebrates.

The role of sediment bacteria in the food web must not be underestimated. Cammen and Walker (1986) indicate that heterotrophic bacteria generally account for most of the organic matter that is utilised by invertebrates in marine sediments. They also found a strong correlation between micro-algal biomass (predominantly pennate diatoms) and bacterial abundance and biomass in a marine intertidal mudflat and attributed this to bacterial utilisation of algal exudates. Cammen and Walker showed that the response of sediment bacteria was linked more closely to epipelic biomass than to production. The results of my study may therefore be relevant to biologists interested in predicting bacterial levels and patterns of distributions in Scottish sealochs. This field of research has particular relevance to the Scottish Purification Boards as sediment bacteria are involved in the breakdown and mineralisation of sewage-derived organic matter. In this respect it is fortunate that the peak in levels of sewage effluent that occur during the summer months in Loch Goil corresponds to the period of optimum epipelic and thus bacterial growth.

Although this study attempts to estimate levels of epipelon it does not attempt to quantify general rates of loss through grazing or the quantity of energy transferred to primary consumers. However, the dense patches of epipelic diatoms from early spring to late autumn clearly provide a predictable source of food on which many invertebrates can depend both directly and indirectly for their nutrition. This study shows that the greatest concentration of epipelic diatoms occurs at depths of 15m or less, but also that the bathymetric distribution of live epipelon extends to the deeper reaches of the loch,

although the maximum depth was not determined. The existence of epipelic diatoms at an estimated density of 1.1 x 10^6 m2 at 40m (July 1990) appears (along with sediment bacteria, settled phytoplanktonic algae, detritus and meiofauana) to be sufficient to sustain dense populations of invertebrates, including the most abundant invertebrates *Ophiura albida* and *Eupolymnia nebulosa*. A large proportion of the nutritional value of the epipelon (biomass) can be attributed to just a few predominant species of algae such as *Navicula* cf.*tripunctata* and *Navicula forcipata* var.*densistriata*. However, the level of dominance does not necessarily reflect productivity and there may be very rapid turnover of some of the rarer species. The quantitative role of the epipelon in relation to their productivity and energy transfer within Loch Goil are areas for further study. Such studies would utilise my data on the seasonal and bathymetric distribution of epipelon in their calculation of total epipelic production within Loch Goil.

The trophic relationship between *O. albida* and the epipelon was investigated in some detail in section 5.2. Although *O. albida* was known to feed mainly on epipelic algae (Taylor, 1958; personal observations) this study has failed to demonstrate any significant grazing effects on natural levels of epipelic algae. However, these results remain inconclusive. In particular my attempt at manipulating ophiuroid grazing intensities, under arduous field conditions, was thwarted by difficulties in forming adequate biological controls. Despite these difficulties the experiment did succeed in manipulating and maintaining a natural assemblage of epipelic algae. This would have been difficult to achieve in a laboratory microcosm.

Similarly, the relationship between the terebellid polychaete *Eupolymnia nebulosa* and the epipelon was investigated by detailed observations of the small-scale distribution of algae along an *E. nebulosa* mound. This study identified a significant (non-selective) grazing

loss of epipelic biomass. In particular this grazing of epipelon by *Eupolymnia nebulosa* has profound impact on algal abundance and is a consequence on their pattern of distribution in the shallow subtidal region of the loch.

6.2.2 Other biological interactions with the epipelon

Perhaps the most striking discovery of this study is the relationship that has been uncovered between the epipelon and the polychaetes *Arenicola marina* and *Eupolymnia nebulosa*. In section 4.1 it was found that the epipelon are distributed in patches on the bottom of the loch (9m depth) at (average) intervals of 40cm, 2m and 3m. This is related to the pattern of the sedimentary features formed by these polychaetes and produced a distinct pattern of concentric zones of dense algal growth; a phenomena that has not been previously documented. In addition to the loss of epipelic algae by the grazing action of *E. nebulosa* my results also indicate that epipelic algal biomass is being lost from the top of both *E. nebulosa* and *A. marina* mounds, through burial by defecated sediment. Whether algal burial caused by biogenic disturbance constitutes a permanent or temporary loss of biomass is uncertain. According to Colijn (1982) only 1% of incident light is transmitted through the upper 0.14 mm layer of estuarine sediment so permanent burial beneath this level would certainly limit photosynthetic production and cell growth. The ability of buried algal cells to re-orientate themselves and migrate back to the sediment surface (into the light) is not clear from the literature. Regular vertical migratory rhythms have been observed in marine (Paterson, 1986; Round, 1979; Palmer and Round, 1967) and fresh water epipelic algae (Round and Palmer, 1966) in response to light intensity and/or tidal rhythms. Plant *et al* (1986) recorded noticeable amounts of chlorophyll-a in the sub-surface sediment (up to 20cm down) and found the depth of penetration to be dependent on weather conditions and hence sediment mixing. Although

not discussed in their paper, the accumulation of degradation products below the majority of living cells (upper 2cm in calm conditions) suggests to me that buried algae are failing to return to the sediment surface. Fenchel and Staarup (1971) recorded almost constant numbers of diatoms and chlorophyll-a levels down to a sediment depth of 16cm in a beach (50cm water depth) in Denmark. However it is not known how long these cells had been buried as the beach was in an exposed locality and mixing of the sediment to this depth may have been a continual process.

Photographic evidence is provided of other sources of biogenic disturbance of the sediment surface by animals feeding and moving over the bottom of the loch. These disruptions of the sediment/water interface have been shown to affect both the level and species composition of epipelon on the bottom of the loch. The results of the re-colonisation experiment (section 4.5.3) showed that a succession of epipelic species occurs in sediment denuded of algae. This has highlighted the importance of secondary grazing and disruption processes on the epipelic community of Loch Goil. The influence of invertebrates on the epipelon is likely to be highly complex. For example modification of the sediment by burrowing animals has been found to increase the area of the interface between sediment and water greatly (Young, 1990). The effect on the provision of living space within the photic zone of the sediment may be profound, enabling algae to proliferate. Other secondary effects of invertebrates which have been documented in the literature include: nutrient excretion, increased turnover rate, disruption of the sediment, provision of additional surface area of sediment for algal growth that stimulate elevated levels of algae at low levels of grazing (Bianchi *et al*, 1988; Levington *et al*, 1977; Connor *et al*, 1982; Hill and Knight, 1987; Flint and Goldman, 1975).

Other biological interactions commonly associated with phytoplankton may also effect the epipelon of Loch Goil and include the effects of: viruses (Suttle *et al*, 1990), fungal epidemics (Canter and Lund, 1948; Canter, 1979) protozoan parasites (Canter, 1979) and chytrids (Canter, 1963). Chytrid and oomycete parasitism of epipelic diatoms is common in freshwater, though they are host-specific and tend to affects only a few species at any one time (D. G. Mann, pers. comm.). These may effect the levels and composition of the epipelon by influencing rates of mortality, growth and primary productivity.

6.3 EPIPELON AND THE PHYSICOCHEMICAL ENVIRONMENT OF LOCH GOIL

Although the phytoplankton of Loch Goil was not studied in detail, the effect of seasonal phytoplankton blooms on water clarity was recorded and has been discussed previously in section 4.4.4. In particular it appears that short-term fluctuations in the levels of epipelon appear to follow changes in water clarity. Water clarity appears to be dependent on phytoplanktonic blooms, the level of river flow (rainfall) and wind-disturbance. Future study could utilise sediment traps to investigate the effect of the sedimentation of phytoplanktonic algae on the levels, community structure and seasonality of epipelic algae.

The effect of wave action on epipelon abundance has already been discussed in section 4.4.4.6. Having experienced the influence of waves under varying wind conditions I conclude that this form of disruption and burial of epipelic algae is not significant in the subtidal habitats of Loch Goil. Even the most powerful waves did not appear to disrupt the sediment surface at 6m depth, which is the shallowest depth at which fine subtidal sediments begin in Loch Goil. This contrasts with the intertidal marine habitats where levels of epipelic algae respond to the washing away of diatoms by severe

wave action or by heavy rainfall (Colijn and Dijkema, 1981). In addition the subtidal epipelon would be subjected to sea water of relatively constant salinity. This again contrasts with the intertidal habitat where the flora must tolerate great fluctuations in salinity associated with tidal fluctuations, evaporation, rainfall and riverine input.

The textural characteristics of the subtidal sediment do not appear to control the concentration of epipelic algae in Loch Goil. However, no measurements were made in this study of other sediment characteristics, such as redox status or organic content. Tett (1982) found that sediment redox status was the most important control of sediment pigment content in Loch Eil in the Firth of Lorne. Any future studies attempting to elucidate causal realtionships involving the epipelon should include the measurement of this determinand.

Unfortunately, the accurate measurement of light and salinity were plagued by the malfunction of apparatus. The loss of salinity data in the seasonal investigation of epipelon was particularly unfortunate considering the proximity of Cormonachan Burn and the possible influence of varying salinities on the epipelon. In my study of the bathymetric distribution of epipelic algae I recorded a halocline at a depth of 12-15m in July 1990 which corresponded to a measured peak in epipelic density at that depth. This is consistent with the results of Sündback (1986) who also observed optimum levels of epipelic chlorophyll-a at 14-16m depth and related this to the depth of the halocline and the adaption of taxa to low light intensities. However, this pattern was not observed in 1989 and a disparity in the magnitude of my data with levels recorded by the CRPB means that this relationship must remain non-proven.

There is clearly a relationship between the abundance of epipelic algae and both water temperature and irradiance. Both parameters vary with depth and time and

it has not been possible to separate their effects purely on the basis of field observations. Although no successful measurements were made of absolute irradiance levels the amount of light transmitted to the substratum will clearly decrease with increasing depth, while the spectral quality of the light is modified as it passes through water (Kendrick and Kroenberg, 1986). Similarly the general levels of irradiance over an annual cycle are predictable (Boney, 1986). Based on the results of this study I postulate that light attenuation with depth is the principle determinant of variation in abundance and composition of epipelon with depth and that seasonal variations in irradiance and temperature are the principal factors influencing the temporal variablity of epipelic density. This is consistent with the view of Round (1981) who indicates that total production of algae in any habitat tends to follow the general pattern of variation of irradiance or temperature.

It is not possible to assess the relevance of my data to other subtidal marine habitats. In particular, because differences exist in the hydrodynamical conditions of sealochs and coastal waters, it is likely that some of the physicochemical factors that control the spatial and seasonal distributions of epipelon in Loch Goil may not apply to marine epipelon in coastal habitats. An example of this can be seen in phytoplankton ecology of northern temperate seas. With phytoplankton it is well known that a threshold of solar radiation, temperature and stabilisation of the water column (determined largely by wind stress and water currents) are the main triggering processes for spring and early summer diatom growth (Boney, 1986; Tett and Wallis, 1978). It is also known that the annual variation in standing crop and the succession of phytoplankton in sealochs and fjords are different from the classical marine cycles. This is attributed mainly to the importance of salinity variation in the water column of sealochs which is controlled

largely by freshwater input, sill depth and tidal mixing (Edwards and Edelsten, 1976).

6.4 ANTHROPOGENIC INFLUENCES AND FUTURE TRENDS?

Increasing urbanisation and industrialisation of the Clyde catchment (see 1.4.3) promises a future of higher levels of water borne pollutants (eg. trace metals, NH_4-N, TON, PO_4P) and greater eutrophication. These will almost certainly modify the natural levels of microalgae (epipelic and planktonic).

Recent expansion in the number of new holiday homes along the southern shore of the loch is a sign of the increasing use of Loch Goil as an amenity for water sports and as a recipient of untreated sewage and domestic effluent. This will inevitably result in a highly seasonal fluctuation in the levels of nitrogen and phosphorous which may ultimately be reflected by changes in phytoplankton and epipelon especially during the summer.

6.5 SCOPE OF THESIS

Ultimate understanding of the underlying causal processes can only be arrived at by the study of local situations and from laboratory and field experiments. The conclusions derived from my study of a single location within Loch Goil are specific to the study area though they conceivably have wider implications for other sealoch systems of similar habitat. Examples of these habitats include the sealochs of the northern Firth of Clyde and Firth of Lorne as well as fjordic sealochs further-a-field in Scandinavia or New Zealand.

There was a relative dearth of knowledge on the biology of Loch Goil at the start of my study. There was also little information on the ecology of subtidal marine epipelon anywhere in the world. In view of this, much of my work on the ecology of epipelon in Loch Goil has been of a general, descriptive nature. Description of the indigenous epipelic community and the basic patterns of

distribution (in time and space) have been achieved but the fundamental mechanisms and causal factors responsible for the observed patterns remain to be explored. Nonetheless basic descriptive information is essential before more detailed hypotheses can be formulated and provides a base-line for future studies.

Administrative Officer
Mrs D GORDON

12 January 1993

Professor F E Round
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Bristol
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Dear Professor Round

You are invited to act as external examiner of a thesis entitled "**The ecology of epipelic diatoms in loch goil**" which will shortly be presented for the degree of PhD of this University by PARK, Richard Anthony.

The internal examiner will be Dr P M Smith, Institute of Cell & Molecular Biology.

If you are willing to act, a copy of the regulations and note of guidance will be sent with the thesis. I would, however, draw your attention now to the following regulations about oral examinations:

For the PhD: "The examiners will hold an oral examination unless this, for exceptional and special reasons, waived by the committee".

For the MPhil: "The examiners will hold an oral examination unless this is, for exceptional reasons, waived by the Committee".

The fee is £68. Expenses (including first-class rail or tourist air fares) in connection with an oral examination may be reclaimed. Payments to examiners living in the United Kingdom are subject to tax deduction at the basic rate at the date of payment. If you accept this invitation to act as an external examiner and you are subject to tax being deducted at source on such payments, I should be grateful if you would include with your reply a note of your National Insurance number.

Would you please let me know whether you accept this invitation?

Yours sincerely,

Secretary
Postgraduate Studies Committee

cc: Internal Examiner (for information) ✓

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APPENDIX 1

Atlas and catalogue of the epipelic diatom types found within the sediments of Loch Goil.

The following 164 taxa, in 40 genera, were recorded from 276 samples collected from seven localities within Loch Goil (6-40 m depth), between June 1988 and September 1990.

The micrographs were taken on Kodak Technical Pan film with a POLYVAR photomicroscope, (C. Reichert AG, Hernalser Hauptstrasse 219, A-1170, Austria) equipped for brightfield and Nomarski differential interference contrast (DIC) optics. All micrographs in this work were taken with oil immersion objectives: Plan Apo 40/1.00 and 100/1.32 using either bright field or interference contrast and utilising a magnification changer module (magnification factors 0.8X, 1X, and 1.25X). The camera module was an automatic attachment (POLYMATIC camera and lamp housing control unit) with an automatic exposure meter. Diatom material was acid cleaned according to the method described in section 3.2.2.4 and mounted on slides using Naphrax, a high resolution diatom mountant. Slides are currently at the Royal Botanic Garden, Edinburgh.

Unless specified, the magnification of the micrographs is x1500. The larger species of *Nitzschia* and *Pleurosigma* are represented with a magnification of x1000, x750 or x500 owing to the constraint of page size. A small number of diatom species are represented by drawings. This method was adopted when damage to the frustule or dirt obscured structures or when a diatom was mounted in an oblique position so that a line drawing would provide substantially more information.

The atlas is arranged so that taxa are grouped according to gross morphological similarity rather than taxonomic affinity. This will increase the usefulness of the atlas and catalogue in future studies of Loch Goil. The micrographs are numbered (1-239) for reference to the taxonomic list. The treatment of a taxon in the catalogue comprises its name and authority and the taxonomic keys that I used for its identification; including reference to page numbers, plates and figures within these texts. This catalogue, and the tables of diatom assemblages that appear in the preceding sections, list the diatom genera and species in alphanumeric order.

Note: There have been some recent changes in the taxonomy of some of the species that are listed in this catalogue (Round *et al*, 1990). These include the following species: *Amphora ventricos*, *Navicula abrupta*, *Navicula atlantica*, *Navicula delognei*, *Navicula dissipata*, *Navicula forcipata*, *Navicula hennedyi*, *Navicula latissima*, *Navicula lyroides*, *Navicula pygmaea*, *Nitzschia acuminata*, *Nitzschia marginulata*, *Nitzschia panduriformis*, *Nitzschia punctata*, *Pinnularia ambigua*.

CATALOGUE

Achnanthes cf. angustata. Greville

A. brevipes Agardh. var. *angustata* (Greville) Cleve. in Foged. N. (1975) p. 7, f. 11/12, 13, 17, 18. Cleve-Euler, A. (1951-55). p. 50, f. 596h. Schmidt, A. (1874-1956). pl. 418/10-15. **Fig. 18.**

Achnanthes sp.

Raphid valve. **Fig. 58.**

Achnanthes conspicua var. conspicua. Mayer.

Hustedt, F. (1930). p. 202, f. 291. Hustedt, F. (1931-37). p. 387, f. 833a-d. Cleve-Euler, A. (1951-55). p. 38, f. 554. **Fig. 93.**

Achnanthes delicatula. Kützing

A. delicatula in: Pankow, H. (1976). p. 160, f. 328. Hustedt, F. (1930). p. 202, f. 293. Hustedt, F. (1931-37). p. 389, f. 836. Peragallo, H. and Peragallo, M. (1897-1908). p. 7. Cleve, P. T. and Grunow, A. (1880). p. 22. Cleve-Euler, A. (1951-55). p. 45, f. 583c, d. Cleve, P. T. (1895). p. 190. Van Heurck (1880-1885). pl. 27/3. **Fig. 92.**

Achnanthes fimbriata. Grunow

Ross, R. (1963). p. 72-76, f. 17-22. *A. stroemii* in Hustedt, F. (1931-37). p. 393, f. 841B. Pankow, H. (1976). p. 158, f. 334-5. Cleve-Euler, A. (1951-55). p. 19, f. 515. Schmidt, A. (1874-1956). pl. 399/45-50. **Fig. 85, 86, 90, 91.**

Achnanthes longipes Agardh. f. lata.

Convex valve with pseudoraphe. Peragallo, H. and Peragallo, M. (1897-1908). p. 5, pl. 1/10-12. and Molder, K. and Tynni, R. (1972). p. 151, f. 73, 74. *A. longipes* in Pankow, H. (1976). p. 153. Hendey, N. I. (1964). p. 174, f. 28/1-6, 42/2. Van Heurck, H (1880-5). p. 129, pl. 26/13-16. Schmidt, A. (1874-1956). pl. 419/6, 7. *A. danica* in Cleve and Grunow (1880). p. 21. **Fig. 99.**

Amphiprora plicata Gregory.

A. plicata var. *subplicata* Grunow *in* Cleve, P. T. and Grunow, A. (1880). p. 65, pl. 5/88. *A. paludosa* var. *nereis* (Lewis 1861) Cleve, P. T. (1894). p. 15. *Auricula decipiens* (Grunow in Cleve and Möller 1882; Grunow in Van Heurck 1880) in Cleve, P. T. (1894). p. 20. *Tropidoneis recta* var. *subplicata* (Grunow *in* Cleve and Grunow 1880) Cleve, P. T. (1894). p. 28. *Amphoropsis decipiens* (Grunow *in* Cleve and Moller 1882) in Van Heurck (1880-1885). pl. 22B/11. **Fig. 235, 228.**

Amphora sp. A.

Fig. 126.

Amphora sp. B.

Fig. 129, 131.

Amphora sp. C.
This species may be *A. lineolata* Ehrenberg 1838. Pankow, H. (1976). p. 274, f. 576. Hustedt, F. (1930). p. 346, f. 636. Cleve, P. T. (1894). p. 126. Schmidt, A. (1874-1956). pl. 26/51. Foged, N. (1978). p. 33, pl. 36/15. **Fig. 136.**

Amphora sp. D.
Fig. 141.
Amphora sp. E.
Fig. 152.

Amphora cf. arcus Gregory.
Peragallo, H. and Peragallo, M. (1897-1908). p. 224, pl. 50/6. Cleve-Euler, A. (1951-55). p. 101, f. 695a. Cleve, P. T. (1894). p. 127, pl. 4/4. *A. sulcata* Schmidt 1875 in Schmidt, A. (1874-1956). pl. 26/46, 47. Gregory, W. (1857). p. 50, pl. 5/88. **Fig. 127.**

Amphora coffeaeformis Agardh. var. acutiuscula.
Cleve, P. T. (1894). p. 121. Hustedt, F. (1930). p. 346. Krammer. K. and Lange-Bertalot, H. (1986a). p. 348, pl. 151/ 1-6. *A. acutiuscula* in Van Heurck, H. (1880-1885). p. 57, pl. 1/18. Pankow, H. (1976). p. 279, f. 597. Peragallo, H. and Peragallo, M. (1897-1908). p. 230, pl. 50/29. *A. lineata* in Schmidt, A. (1874-1956). pl. 26/59. **Fig. 151, 154, 155.**

Amphora coffeaeformis Agardh. var. borealis.
Pankow, H. (1976). p. 279, f. 596. Hustedt, F. (1930). p. 345, f. 634. Schmidt, A. (1874-1956). pl. 26/56, 57. Ross, R. (1963). Hendey, N. I. (1964). p. 264. Peragallo, H. and Peragallo, M. (1897-1908). p. 230, pl. 50/27. *A. borealis* in Kützing, F. T. (1844). p. 108, pl. 5/37;3/18. Cleve-Euler, A. (1951-55). p. 97, f. 685b-d. Cleve, P. T. (1894). p. 121. *A. salina* var. *minor* in Van Heurck, H. (1880-1885). p. 57, pl. 1. Krammer. K. and Lange-Bertalot, H. (1986a). p. 348, pl. 151/1-6. **Fig. 150.**

Amphora graeffii Grunow. var. minor.
Peragallo, H. and Peragallo, M. (1897-1908). p. 211, pl. 46/14-15. Hendey, N. I. (1964). p. 263, pl. 37/8.
This species can be easily confused with the larger species A. *truncata* which it resembles in both the shape of the cell and pattern of striation (19 striae *per* 10u). **Fig. 147.**

Amphora laevis Gregory. var. perminuta.
Cleve, P. T. (1894). p. 130. Peragallo, H. and Peragallo, M. (1897-1908). p. 221, pl. 49/10. **Fig. 130.**

Amphora cf. lineolata Ehrenberg.
Pankow, H. (1976). p. 274, f. 576. Hustedt, F. (1930). p. 346, f. 636. Cleve, P. T. (1894). p. 126. Schmidt, A. (1874-1956). pl. 26/51. Foged, N. (1978). p. 33, pl. 36/15. **Fig. 137.**

Amphora ostrearia Brebisson. var. ostrearia.
Pankow, H. (1976). p. 281, f. 570. Hendey, N. I. (1964). p. 266, pl. 38/5. Peragallo, H. and Peragallo, M. (1897-1908). p. 219, pl. 49, 13. Cleve-Euler, A. (1951-

55). p. 101, f. 697. Schmidt, A. (1874-1956). pl. 26/23. Van Heurck, H. (1880-1885). p. 55, pl1/25. **Fig. 132.**

Amphora cf. proteus Gregory. var. A.
Similar to *A. proteus* but striae on dorsal side (9 in 10 *um*) extend for only one third of the valve length. Striae adjacent to the raphe form finger-like projections in the middle. **Fig. 146.**

Amphora cf. proteus Gregory. var. B.
Similar to but smaller (17 *um* long, 7 *um* wide) than *A. proteus*. **Fig. 160.**

Amphora proteus Gregory. var. oculata.
The size range of this species varies prodigiously (length from 24-73 *um*). I consider that the specimens shown in Figs: 145, 156-8 and 159, 161 may represent individual varieties of *A. proteus* that have not yet been recognised formally.
A. proteus Gregory. var. *oculata* in: Peragallo, H. and Peragallo, M. (1897-1908). p. 201, pl. 44/21, 22. Cleve-Euler, A. (1951-55). p. 93, f. 673e. Schmidt, A. (1874-1956). pl. 27/42-45. Gregory, W. (1857). p. 46, pl. 5/81a-e. Foged, N. (1978). p. 34, pl. 36/12. **Fig. 145, 156-9, 161.**

Amphora proteus Gregory. var. proteus.
Pankow, H. (1976). p. 276, f. 569. Hendey, N. I. (1964). p. 262. Peragallo, H. and Peragallo, M. (1897-1908). p. 200, pl. 44/24-28. Cleve, P. T. (1895). p. 103. Cleve-Euler, A. (1951-55). p. 93, f. 673a-g. Schmidt, A. (1874-1956). pl. 27/3. Gregory, W. (1857). p. 46, pl. 5/81a-e. *A. (proteus?)* var. *kariana* in Cleve, P. T. and Grunow, A. (1880). p. 24, pl. 1/7. **Fig. 133-135, 153.**

Amphora truncata Gregory.
Peragallo, H. and Peragallo, M. (1897-1908). p. 212, pl. 47/5, 6. Cleve, P. T. (1894). p. 112, pl. 3/17, 18. Cleve-Euler, A. (1951-55). p. 95, f. 678. Schmidt, A. (1874-1956). pl. 28/5. **Fig. 148, 149.**

Amphora ventricosa Gregory.
Hendey, N. I. (1964). p. 269, pl. 38/12. *A. angusta* var. *ventricosa in* Cleve, P. T. (1894). p. 135. **Fig. 140, 143, 144.**

Amphora ventricosa Gregory. var. ?
Hendey, N. I. (1964). p. 269, pl. 38/12. *A. angusta* var. *ventricosa* Gregory. *in* Cleve, P. T. (1894). p. 135. **Fig. 142.**

Brachysira (Anomoeoneis) Pfitzer. sp. A.
Fig. 60.

Bacillaria sp. Gmelin.
Fig. 198.

Caloneis amphisbaena Cleve.
Cleve 1894. Pankow, H. (1976). p. 204. Peragallo, H. and Peragallo, M. (1897-1908). p. 77, pl. 10/10.

Cleve-Euler, A. (1951-55). p. 87, f. 1119. Schmidt, A. (1874-1956). f. 271/29, 32. **Fig. 80.**

Caloneis crassa Gregory.
Caloneis or *Navicula brevis* in: Hendey, N. I. (1964). p. 229, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 80, pl. 10/13, 14. Cleve-Euler, A. (1951-55). p.89, f. 1123b, d, e, i. **Fig. 1, 2.**

Caloneis crassa Gregory. var. distoma.
Caloneis or *Navicula brevis* var. *distoma* in: Cleve, P. T. and Grunow, A. (1880). p. 30, pl. 1/25. Cleve-Euler, A. (1951-55). p. 90, f. 1123i. Van Heurck, H. (1880-1885). p. 97, pl. 11/18. Cleve, P. T. (1894). p. 61.
This variety appears to be distinct from other forms of the species found within Loch Goil although *C. crassa* var. *distoma* is not recognised as a formal division of this species at present. **Fig. 3.**

Caloneis liber Wm. Smith. var. elongata.
Pankow, H. (1976). p. 204. Hendey, N. I. (1964). p. 229, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 71, pl. 9/5, 6. Cleve-Euler, A. (1951-55). p. 90, f. 1124e. Schmidt, A. (1874-1956). f. 50. **Fig. 84.**

Caloneis liber var. excentrica Grunow.
Pankow, H. (1976). p. 204. Hendey, N. I. (1964). p. 229, pl. 29. Cleve-Euler, A. (1951-55). p. 90, f. 1124/g, h. Peragallo, H. and Peragallo, M. (1897-1908). p. 71, pl. 9. Schmidt, A. (1874-1956). f. 50.
The taxonomic placing of *C. liber* var. *excentrica* is based fundamentally on the density of the striae, although the shape of the valve does bear a notable similarity to *C. westii* Wm. Smith 1853. [Hendey, N. I. (1964). p. 230, f. 16. Pankow, H. (1976). p. 203.] which differs in possessing a courser striate pattern of 12-14 *per* 10 *um*. **Fig. 83.**

Campylodiscus fastuosus Ehrenberg.
Hendey, N. I. (1964). p. 290, pl. 40/13. *C. thuretii* in Peragallo, H. and Peragallo, M. (1897-1908). p. 247, pl. 57:4-9. and Schmidt, A. (1874-1956). pl. 208/12. *C. parvulus* in Peragallo, H. and Peragallo, M. (1897-1908). p. 242, pl. 54/9. Schmidt, A. (1874-1956). pl. 17/12-14. **Fig. 120.**

Chaetoceros sp. Ehrenberg.
Fig. 170.

Cocconeis scutellum Ehrenberg. cf. var. scutellum.
Pankow, H. (1976). p. 148. f. 302. Hustedt, F. (1930). p. 191, f. 267. Hustedt, F. (1931-37). p. 337, f. 790. Kützing, F. T. (1844). p. 73, pl. 5/6, f. 3, 6. Hendey, N. I. (1964). p. 180, pl. 27/8. Peragallo, H. and Peragallo, M. (1897-1908). p. 19, pl. 4/5. Cleve, P. T. (1894). p. 170. Schmidt, A. (1874-1956). pl. 190/17, 18. Van Heurck, H. (1880-1885). p. 132, pl. 29/1-3.
Fig. 117, 118 (upper valve without raphe), **119** (lower valve with median line, small central area and false stauros).

Coscinodiscus concavus Ehrenberg.
Schmidt, A. (1874-1956). pl. 59/16. **Fig. 232.**

Thassiosira (Coscinodiscus) cf. eccentrica Ehrenberg.
Hendey, N. I. (1964). p. 80, pl. 24/2. Schmidt, A. (1874-1956). pl. 58/46-49. Molder. K. and Tynni, R. (1972). p. 158, f. 22. **Fig.** 234.

Thalassiosira (Coscinodiscus) Ehrenberg. sp.
Fig. 231.

Paralia sulcata Ehrenberg.
Fig. 233.

Cylindrotheca closterium Reiman et Lewis.
Nitzschia closterium Ehrenberg. in: Pankow, H. (1976). p. 295, f. 619. Hendey, N. I. (1964). p. 283, pl. 21. Peragallo, H. and Peragallo, M. (1897-1908). p. 293, pl. 74/15. Cleve-Euler, A. (1951-55). p. 92, f. 1508. **Fig. 199.**

Cylindrotheca gracilis Grunow.
Van Heurck, H. 1882. Pankow, H. (1976). p. 289, f. 609. Hendey, N. I. (1964). p. 284. Cleve-Euler, A. (1951-55). p. 95, f. 1518. Schmidt, A. (1874-1956). pl. 349/34-37. Krammer, K. and Lange-Bertalot, H. (1988) p. 134, f. 87/3. Hustedt, F. (1930). p. 393, f. 746. **Fig. 207.**

Cymbella cistula Ehrenberg.
C. cistula var. genuina *in* Cleve-Euler, A. (1951-55). p. 163, f. 1251a-c. *C. cistula* in Hustedt, F. (1930). p. 363, f. 676b. Van Heurck, H., H. (1880-5). p. 64, pl. 2:12. *Cocconema cistula* in Schmidt, A. (1874-1956). pl. 10/4. **Fig. 163.**

Cymbella Agardh sp.
Fig. 162.

Dictyocha speculum Ehrenberg. var. speculum.
Pankow, H. (1976). p. 51, f. 50. (a silicoflagellate.). **Fig. 165.**

Dimeregramma minor Gregory. var. minor.
Pankow, H. (1976). p. 140, f. 276. Hustedt, F. (1931-37). p. 118, f. 640. Hendey, N. I. (1964). p. 156, pl. 27/12. Peragallo, H. and Peragallo, M. (1897-1908). p. 334, pl. 82/13, 14. Molder, K. and Tynni, R. (1969). p. 246, f. 52. *D. minus* in Van Heurck, H. (1880-1885). p. 146, pl. 36/10. **Fig. 123.**

Diploneis aestiva (Donkin) Cleve var. fusca Gregory.
D. fusca Gregory *in* Cleve, P. T. (1894). p. 93. Hustedt, F. (1931-37). p. 654, f. 1053a. Hendey, N. I. (1964). p. 255, f. 32/4. *D. fusca* (Gregory) var. *gregorii* in Cleve, P. T. (1894). p. 94. *D. fusca* (Gregory) var. *norvegica* in Cleve, P. T. (1894). p. 93. *D. fusca* (Gregory) var. *tenuipunctata* in Cleve, P. T. (1894). p. 94. **Fig. 96.**

Diploneis aestiva (Donkin) Cleve var. delicata A. Scmidt.
D. fusca var. *delicata* (A. Scmidt) Cleve 1894 *in* Cleve-Euler, A. (1951-55). p. 81, f. 652. Schmidt, A. (1874-1956). pl. 7/1, 7, 8. Hustedt, F. (1931-37). p. 656. f. 1053b. **Fig. 95.**

Diploneis crabro Ehrenberg.
Hustedt, F. (1931-37). p. 616, f. 1028-34. Hendey, N. I. (1964). p. 225. pl. 32. Peragallo, H. and Peragallo, M. (1897-1908). p. 109-12, pl. 15/1. Cleve-Euler, A. (1951-55). p. 86, f. 660. Schmidt, A. (1874-1956). f. 11, 12, 69, 174. Simonsen, R. (1987). pl. 332. **Fig. 116.**

Diploneis ovalis Hilse.
Hustedt, F. (1931-37). p. 671, f. 1065. Peragallo, H. and Peragallo, M. (1897-1908). p. 128, pl. 21. Cleve-Euler, A. (1951-55). p. 75, f. 643. Schmidt, A. (1874-1956). f. 7/33-36. **Fig. 104, 105.**

Diploneis smithii Brebisson. var. smithii.
Pankow, H. (1976). p. 192. Hustedt, F. (1931-37). p. 647, f. 1051. Hendey, N. I. (1964). p. 225, pl. 32. Peragallo, H. and Peragallo, M. (1897-1908). p. 132, pl. 19/26, 29, 30. Cleve-Euler, A. (1951-55). p. 81, f. 654. Schmidt, A. (1874-1956). f. 7.
This species occurs in three apparent forms in Loch Goil (a-c). The elliptical form (c) also fits the taxonomic description of *D. elliptica* (Kützing) Cleve 1894. [Hustedt, F. (1931-37). p. 690, f. 1077. Peragallo, H. and Peragallo, M. (1897-1908). p. 128, pl. 21/16. Cleve-Euler, A. (1951-55). p. 77, f. 646. Schmidt, A. (1874-1956). f. 7.]. *D. elliptica* is considered to be a fresh water species (Hustedt, F. 1931-37) and is therefore unlikely to be indigenous to the sediments of Loch Goil. **Fig. 97, 98, 100, 101.**

Diploneis splendida Gregory.
Peragallo, H. and Peragallo, M. (1897-1908). p. 121, pl. 18/15-18. Cleve-Euler, A. (1951-55). p. 71, f. 633. Schmidt, A. (1874-1956). f. 13/32. **Fig. 115.**

Donkinia recta Donkin.
Cleve.P. T. (1894). p. 119. var. rectum *Donkinia recta* in Hendey, N. I. (1964). p. 251, pl. 35/7. Peragallo, H. and Peragallo, M. (1897-1908). p. 178, pl. 36/11. Van Heurck, H. (1880-1885). p. 119, pl. 17/9. **Fig. 229.**

Donkinia reticulata Norman.
Foged, N. (1975) p. 24, pl. 17:1. **Fig. 224, 225.**

Eunotia cf. pseudopectinalis Hustedt.
Hustedt, F. (1931-37). p. 314, f. 779. Cleve-Euler, A. (1951-55). p. 93, f. 410 *E. pectinalis* Hustedt 1911 *in* Schmidt, A. (1874-1956). pl. 271/8. Molder, K. and Tynni, R. (1971). p. 210, f. 58. **Fig. 167.** This is a fresh water species.

Eunotia cf. septentrionalis Østrup.
Hustedt, F. (1931-37). p. 292, f. 758. Cleve-Euler, A. (1951-55). p. 131, f. 478. **Fig. 166.** This is a fresh water species.

Eunotia sp. Ehrenberg.
A fresh water species, not indigenous to Loch Goil. **Fig. 106, 107.** This is a fresh water species.

Frustulia rhomboides De Toni var. rhomboides.
Hustedt, F. (1930). p. 220, f. 324. Hustedt, F. (1931-37). p. 728, f. 1098a. Hendey, N. I. (1964). p. 239. Cleve-Euler, A. (1951-55). p. 7, f. 1326a. Cleve, P. T. (1894). p. 122. Schmidt, A. (1874-1956). pl. 369/1, 2. Molder, K.. and Tynni, R. (1973). p. 165, pl. 43. **Fig. 168.** This is a fresh water species.

Frustulia rhomboides De Toni var. saxonica f. undulata.
Hustedt, F. (1930). p. 221. Hustedt, F. (1931-37). p. 729, f. 1099b. Cleve-Euler, A. (1951-55). p. 8, f. 1327g, h. Schmidt, A. (1874-1956). pl. 369/7. Molder, K.. and Tynni, R. (1973). p. 165, pl. 46. **Fig. 169.** This is a fresh water species.

Gomphonema parvulum Kützing. var. exilis Grunow.
Hustedt, F. (1930). p. 373, f. 713. Cleve-Euler, A. (1951-55). p. 178, f. 1269n. Cleve, P. T. (1894). p. 180. **Fig. 172.**

Gyrosigma algoris Carter and Bailey-Watts.
G. obscurum in: Krammer. K. and Lange-Bertalot, H. (1986a). p. 299, f. 116:1, 2. **Fig. 223.**

Gyrosigma distortum Wm. Smith. var. parkeri Harrison.
Pankow, H. (1976). p. 177, f. 377. Cleve-Euler, A. (1951-55). p. 12, f. 1338b. *G. parkerii* (Harrison) Elmore 1921. *in* Krammer. K. and Lange-Bertalot, H. (1986a). p. 299, f. 116:4. **Fig. 222.**

Gyrosigma tenuirostrum A. Grunow.
Cleve-Euler, A. (1951-55) p. 13, f. 1340. **Fig. 221.**

Navicula Bory. sp. A.
Fig. 13, 14.
Navicula Bory. sp. B.
Fig. 36, 40-42.
Navicula Bory. sp. C.
Fig. 59.
Navicula Bory. sp. D.
Fig. 63.
Navicula Bory. sp. E.
Fig. 69.
Navicula Bory. sp. F.
Fig. 77.
Navicula Bory. sp. G.
Fig. 78.
Navicula Bory. sp. H.
Fig. 79.
Navicula Bory. sp. I.
Fig. 94.

Navicula abrupta Gregory.
Hustedt, F. (1961-66). p. 516, f. 1588. Hendey, N. I. (1964). p. 210, pl. 33. Peragallo, H. and Peragallo, M. (1897-1908). p. 132, pl. 21/34-39. Cleve-Euler, A. (1951-55). p. 106, f. 711. **Fig. 45.**

Navicula arenaria Donkin.
Hendey, N. I. (1964). p. 196, pl. 30. Peragallo, H. and Peragallo, M. (1897-1908). p. 101, pl. 13/4, 5, 6. Cleve-Euler, A. (1951-55). p. 132, f. 763. Schmidt, A. (1874-1956). f. 47. **Fig. 66, 67.**

Navicula atlantica Schmidt.
Hustedt, F. (1961-66). p. 509, f. 1553. Hendey, N. I. (1964). p. 210, pl. 33. Peragallo, H. and Peragallo, M. (1897-1908). p. 133, pl. 21. Cleve-Euler, A. (1951-55). p. 106, f. 710/e. Schmidt, A. (1874-1956). f. 2/33. **Fig. 44, 48, 57.**

Navicula cf. bryophila Boye Patersen.
Cleve-Euler, A. (1951-55). p. 174, f. 865. Schmidt, A. (1874-1956). pl. 404/41-48. Tynni, R. (1975). p. 11, pl. 1/12. Hustedt, F. (1961-66). p. 91, f. 1237. **Fig. 62.**

Navicula crucigera Wm. Smith.
Pankow, H. (1976). p. 242, f. 4. Hustedt, F. (1961-66). p. 44, f. 1199. Hendey, N. I. (1964). p. 189, pl. 27. Cleve-Euler, A. (1951-55). p. 17, f. 1350. **Fig. 32.**

Navicula cf. cryptocephala Kützing. var. veneta.
Pankow, H. (1976). p. 235. Hendey, N. I. (1964). p. 195. Peragallo, H. and Peragallo, M. (1897-1908). p. 94, pl. 12/34-38. Cleve-Euler, A. (1951-55). p. 154, f. 813. Schmidt, A. (1874-1956) f. 272.
This species is most precisely described by the var. *veneta* in Hendey, N. I. (1964). However identification is not conclusive as no figure provided for this species. **Fig. 53**. N. cryptocephala is typically a frsh water species.

Navicula cf. decussis Østrup. var. decussis
Cleve-Euler, A. (1951-55). p. 175, f. 866A. Schmidt, A. (1874-1956). pl. 398/37, 401/12, 13. Krammer. K. and Lange-Bertalot, H. (1986a). p. 141, f. 47:10-18. **Fig. 89.**

Navicula cf. delognei Van Heurck
Van Heurck, H. (1880) p. 110. pl. 11/13. Hendey, N. I. (1964). p. 191, pl. 30/1. *Navicula grevillei* (Agardh 1830) Heiberg 1863 *in* Cleve-Euler, A. (1951-55). p. 218, f. 962a-d. Cleve, P. T. (1894). p. 152. Van Heurck, H. (1880-1885). p. 110, pl. 16/2. Peragallo, H. and Peragallo, M. (1897-1908). p. 64, pl. 8/14. *Navicula grevilleana* Hendey, 1964 in Pankow, H. (1976). p. 261, f. 556. **Fig. 138, 139.**

Navicula cf. digito-radiata Gregory. var. A.
Fig. 65.

Navicula cf. digito-radiata Gregory. var. B.

Pankow, H. (1976). p. 229. Hendey, N. I. (1964). p. 202, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 98, pl. 12/28, 29. Cleve-Euler, A. (1951-55). p. 160, f. 822. Schmidt, A. (1874-1956). f. 272/28-32. **Fig. 68.**

Navicula cf. digito-radiata Gregory. var. C.
Pankow, H. (1976). p. 229. Hendey, N. I. (1964). p. 202, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 98, pl. 12/28, 29. Cleve-Euler, A. (1951-55). p. 160, f. 822. Schmidt, A. (1874-1956). f. 272/28-32. **Fig. 71.**

Navicula digito-radiata Gregory. var. cyprinus Ehrenberg.
Pankow, H. (1976). p. 229. Hendey, N. I. (1964). p. 202, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 98, pl. 12/28, 29. Cleve-Euler, A. (1951-55). p. 160, f. 822. Schmidt, A. (1874-1956). f. 272/28-32. **Fig. 10.**

Navicula dissipata Hustedt.
Schmidt, A. (1874-1956). pl. 403/7, 8. Pankow, H. (1976). p. 216, f. 450. Hustedt, F. (1961-66). p. 549, f. 1587d. Hendey, N. I. (1964). p. 214, pl. 37/7. **Fig. 50.**

Navicula distans Wm. Smith.
Hendey, N. I. (1961-66). p. 203, pl. 27/13. Peragallo, H. and Peragallo, M. (1897-1908). p. 104, pl. 11/22, 23. Cleve-Euler, A. (1951-55). p. 133, f, 768. Cleve, P. T. (1894). p. 35. Schmidt, A. (1874-1956). f. 46/11-14. Van Heurck, H. (1880-1885). p. 87. **Fig. 70, 75, 76.**

Navicula forcipata Greville. var. densistriata Schmidt.
Hustedt, F. (1961-66). p. 531, f. 1568. Hendey, N. I. (1964). p. 211, pl. 33. Peragallo, H. and Peragallo, M. (1897-1908). p. 130, pl. 21/29, 30. Cleve-Euler, A. (1951-55). p. 105. Schmidt, A. (1874-1956). f. 70/14. **Fig. 46, 47.**

Navicula gregaria Donkin.
Pankow, H. (1976). p. 235, f. 490. Hustedt, F. (1930). p. 269, f. 437. Peragallo, H. and Peragallo, M. (1897-1908). pl. 8/7. Cleve-Euler, A. (1951-55). p. 130, f. 755a-c. Tynni, R. (1975). p. 18, pl. 1/8. **Fig. 64.**

Navicula hennedyi Wm. Smith. var. hennedyi.
Cleve-Euler (1953). p. 107, f. 713. Pankow, H. (1976). p. 221, f. 459. Hustedt, F. (1961-66). p. 453, f. 1516. Hendey, N. I. (1964). p. 213, pl. 33. Peragallo, H. and Peragallo, M. (1897-1908). p. 139, pl. 25/2, 3. Tynni, R. (1975). p. 18, pl. 4:89. **Fig. 56.**

Navicula cf. incerata Grunow.
Tynni, R. (1975) p. 20, pl8/158. Van Heurck, H. (1880-5). p. 107, pl. 14:43. Hustedt, F. (1930). p. 306, f. 542. Hendey, N. I. (1964). p. 197. Peragallo, H. and Peragallo, M. (1897-1908). p. 93, pl. 11/16. Cleve-Euler, A. (1951-55). p. 168, f. 849B. **Fig. 61.**

Navicula latissima Gregory.
Pankow, H. (1976). p. 254, 263, f. 554. Hustedt, F. (1961-66). p. 717-719, f. 1701. Peragallo, H. and Peragallo, M. (1897-1908). p. 146-7. pl. 27. Cleve-Euler,

A. (1951-55). p. 115, f. 733. Schmidt, A. (1874-1956). f. 6. **Fig. 4.**

Navicula lyroides Hendey.
N. lyra Ehrenberg. var. *elliptica* in: A. Schmidt 1874. Hustedt, F. (1961-66). p. 500, f. 1551. Hendey, N. I. (1964). p. 209, pl. 33. Peragallo, H. and Peragallo, M. (1897-1908). p. 133, pl. 22. Cleve-Euler, A. (1951-55). p. 106, f. 710/a. Schmidt, A. (1874-1956). f. 2, 129. Van Heurck, H. (1880-1885). pl. 10/2. Cleve, P. T. (1894). p. 63. **Fig. 43, 49.**

Navicula meniscus Schuman.
Krammer. K. and Lange-Bertalot, H. (1986a). p. 101, f. 30/3. **Fig. 73.**

Navicula palpebralis Brebisson. var. minor Grunow.
Hendey, N. I. (1964). p. 216, pl. 34. Peragallo, H. and Peragallo, M. (1897-1908). p. 82, pl. 10/16. Cleve-Euler, A. (1951-55). p. 4, f. 974. Schmidt, A. (1874-1956). pl. 191, 263. **Fig. 12.**

Navicula palpebralis var. angulosa Gregory.
Hendey, N. I. (1964). p. 216, pl. 34. Cleve-Euler, A. (1951-55). p. 4, f. 974. **Fig. 33-35.**

Navicula phyllepta Kützing .
Cleve-Euler, A. (1951-55). p. 139, f. 784. Hendey, N. I. (1964). p. 190, pl. 37/3. Krammer. K. and Lange-Bertalot, H. (1986a). p. 104, f. 32:5-11. **Fig. 54, 55.**

Navicula plicata Ehrenberg. var. constricta.
Hustedt 1962. Pankow, H. (1976). p. 260, f. 543. Hustedt, F. (1961-66). p. 328, f. 1443. Hendey, N. I. (1964). p. 193. Peragallo, H. and Peragallo, M. (1897-1908). p. 65, pl. 8/15. Cleve-Euler, A. (1951-55). p. 219, f. 965. Simonson, R. (1987). f. 734. **Fig. 15.**

Navicula cf. pygmaea Kützing.
This species occurs in Loch Goil in a range of frustule lengths (10-30 *um*) which at its smallest is below the range described in the taxonomic literature (20-45 *um*).
Pankow, H. (1976). p. 223, f. 464. Hustedt, F. (1930). p. 312, f. 561. Hustedt, F. (1961-66). p. 538, f. 1574. Hendey, N. I. (1964). p. 211. Peragallo, H. and Peragallo, M. (1897-1908). p. 130, pl. 21/20. Cleve-Euler, A. (1951-55). p. 105, f. 708. Cleve, P. T. (1894). p. 65. Schmidt, A. (1874-1956). pl. 70/7. Van Heurck, H. (1880-1885). p. 94, pl. 10/7. **Fig. 52.**

Navicula retusa Brebisson. var. cancellata.
N. cancellata in: Pankow, H. (1976). p. 231. Hendey, N. I. (1964). p. 203, pl. 30/18-20. Peragallo, H. and Peragallo, M. (1897-1908). p. 101, pl. 13/7, 8. Cleve, P. T. and Grunow, A. (1880). p. 36. Cleve-Euler, A. (1951-55). p. 132. **Fig. 72, 74.**

Navicula retusa Brebisson. var. gregorii.
N. cancellata var. *subapiculata* in: Peragallo, H. and Peragallo, M. (1897-1908). p. 102, pl. 13/9. *N. cancellata*

var. *gregorii* in Cleve-Euler, A. (1951-55). p. 133, f. 764. Schmidt, A. (1874-1956). pl. 46/43. Cleve, P. T. (1894). p. 30. **Fig. 38-39.**

Navicula cf. rhombica Gregory.
Hustedt, F. (1961-66). p. 325, f. 1441. Hendey, N. I. (1964). p. 192, pl. 30/3. Peragallo, H. and Peragallo, M. (1897-1908). p. 64, pl. 8/10. Cleve, P. T. and Grunow, A. (1880). p. 43. Cleve-Euler, A. (1951-55). p. 218, f. 961. Cleve, P. T. (1894). p. 152. **Fig. 6.**

Navicula cf. sparsistriata.
Hustedt, F. (1964). p. 547, f. 1586. **Fig. 51.**

Navicula subinflatoides Hustedt.
Hustedt, F. (1961-66). p. 294, f. 1416. Hustedt, F. (1977). f. 731. **Fig. 7, 8.**

Navicula cf. tripunctata Muller.
N. gracilis Eherenberg. in: Pankow, H. (1976). p. 236, f. 493. Cleve-Euler, A. (1951-55). p. 130, f. 756. **Fig. 24-31.**

Nitzschia Hass. sp. A.
Fig. 178. Probably a member of the lineares group described in Cleve, P. T. and Grunow, A. (1880). p. 93.

Nitzschia Hass. sp. B.
Fig. 179.

Nitzschia Hass. sp. C.
Probably a member of the lanceolatae group described in Cleve, P. T. and Grunow, A. (1880). p. 94. **Fig. 180.**

Nitzschia Hass. sp. D.
Member of the lanceolatae group described in Cleve, P. T. and Grunow, A. (1880). p. 94. **Fig. 206.**

Nitzschia acuminata Wm. Smith.
Pankow, H. (1976). p. 304, f. 646. Hustedt, F. (1930). p. 401, f. 764. Hendey, N. I. (1964). p. 280, pl. 39/10. Peragallo, H. and Peragallo, M. (1897-1908). p. 271, pl. 70/19-21. Cleve-Euler, A. (1951-55). p. 61, f. 1436a. Schmidt, A. (1874-1956). pl. 331/4, 5. **Fig. 188.**

Nitzschia angularis Wm. Smith.
Pankow, H. (1976). p. 312, f. 667. Peragallo, H. and Peragallo, M. (1897-1908). p. 285, pl. 73/6. Cleve-Euler, A. (1951-55). p. 70, f. 1461b. Schmidt, A. (1874-1956). f. 335/19. Cleve *and* Grunow (1880). p. 89, f. 5/99. Van Heurck, H. (1880-1885). p. 177, pl. 62/11-14. **Fig. 189, 194, 195.**

Nitzschia angularis Wm. Smith. cf. var. affinis.
Peragallo, H. and Peragallo, M. (1897-1908). p. 284, pl. 73/8. Van Heurck, H. (1880-1885). p. 177, pl. 62/11-14. **Fig. 205.**

Nitzschia bilobata Wm. Smith. var. bilobata.
Pankow, H. (1976). p. 309, f. 659. Hustedt, F. (1930). p. 405, f. 775. Hendey, N. I. (1964). p. 280, pl.

39/2, 43/15. Peragallo, H. and Peragallo, M. (1897-1908). p. 273, pl. 70/26. Cleve-Euler, A. (1951-55). p. 65, f. 1446a, b. Krammer. K. and Lange-Bertalot, H. (1986b). p. 61, pl. 46/1, 2. Van Heurck, H. (1880-1885). p. 175, pl. 60/1. **Fig. 187.**

Nitzschia aff. distans Gregory.

Clearly a member of the spathulatae group described in Cleve, P. T. and Grunow, A. (1880). p. 87. this species is most often observed with its frustule at an oblique angle.

Foged, N. (1978). p. 104, pl. 45/6. Schmidt, A. (1874-1956). pl. 334/1, 2. Peragallo, H. and Peragallo, M. (1897-1908). p. 283, pl. 73/3. **Fig. 185, 191, 192.**

Nitzschia hybrida cf. var. pellucida Grunow.

Krammer, K. and Lange-Bertalot, H. (1988) p. 61, pl. 47/4. Cleve and Grunow (1880) p. 80, f. 5/96. *N. hybrida* in Hustedt, F. (1930). p. 406, f. 778. Peragallo, H. and Peragallo, M. (1897-1908). p. 274, pl. 70/29. Cleve-Euler, A. (1951-55). p. 66, f. 1449. *N. pellucida* Cleve-Euler, A. (1951-55). p. 65, f. 1448cd. **Fig. 200, 201.**

Nitzschia insignis Gregory. var. smithii.

Cleve, P. T. and Grunow, A. (1880). p. 84. Schmidt, A. (1874-1956). pl. 333/5. Krammer. K. and Lange-Bertalot, H. (1986b). pl. 26:1. Peragallo, H. and Peragallo, M. (1897-1908). p. 295, pl. 75/3. *N. smithii* in Cleve-Euler, A. (1951-55). p. 68, f. 1454. (*Hantzschia spectabilis*) in Krammer. K.. and Lange-Bertalot, H. (1986b). p. 132, pl. 91/1-4. Van Heurck, H. (1880-1885). pl. 61/1. **Fig. 183, 184, 202, 209, 210.**

Nitzschia insignis Gregory . cf. var. spathulifera Grunow.

This species may be a separate variety of *N. insignis* (not currently recognised) as the valve is shorter, with narrow spathulate extensions to the outer margin, similar to, but smaller than (82 *um* long) *N. insignis* (*N. adriatica* var. ?) Gregory. var. *spathulifera* Grunow. Cleve, P. T. and Grunow, A. (1880). p. 85. Cleve-Euler, A. (1951-55). p. 68, f. 1454a. Peragallo, H. and Peragallo, M. (1897-1908). p. 296, pl. 75/7-9. **Fig. 181, 182.**

Nitzschia marginulata Grunow. var. marginulata.

Van Heurck, H. (1880-1885). pl. 58/13. Krammer. K. and Lange-Bertalot, H. (1986b). p. 45, pl. 33/6. Peragallo, H. and Peragallo, M. (1897-1908). p. 270, pl. 70/14, 15. *N. marginulata* var. *genuina* in Cleve, P. T. and Grunow, A. (1880). p. 72, pl. 5/93. Cleve-Euler, A. (1951-55). p. 61, f. 1434a. **Fig. 186.**

Nitzschia panduriformis Gregory. cf. var. minor Grunow.

Cleve, P. T. and Grunow, A. (1880). p. 71. Cleve-Euler, A. (1951-55). p. 55. f. 1425c. *N. panduriformis* in Pankow, H. (1976). p. 310. Hendey, N. I. (1964). p. 279. Peragallo, H. and Peragallo, M. (1897-1908). p. 269, pl. 70/6. Schmidt, A. (1874-1956). pl. 331/19, 20. Van Heurck, H. (1880-1885). p. 172, pl. 58/4. **Fig. 190.**

Nitzschia cf. punctata W. Smith. var. coarctata Grunow. f. minor.

The species found in Loch Goil is small (28-45 um long) and is most similar to the var. *minor* described by Krammer, K.. and Lange-Bertalot, H. (1988) p. 50, f. 38:14. The density of striae and the shape of the frustule is consistent with Grunow's original description of *N. punctata* var. *coarctata* although the smaller form is not reported in this, or other taxonomic texts.

Pankow, H. (1976). p. 302, f. 635. Hustedt, F. (1930). p. 401. Hendey, N. I. (1964). p. 278. Peragallo, H. and Peragallo, M. (1897-1908). p. 268, f. 26. Cleve-Euler, A. (1951-55). p. 57, f. 1429e. Schmidt, A. (1874-1956). pl. 330/16. **Fig. 193.**

Nitzschia sigma Kützing. var. ?.
Fig. 196.

Nitzschia sigma Kützing. var. intercedens Grunow.
Hendey, N. I. (1964). p. 282. Cleve-Euler, A. (1951-55). p. 75, f. 1470e. Schmidt, A. (1874-1956). pl. 336/5. Van Heurck, H. (1880-1885). p. 179. pl. 66/1. *N. intercedens* Grunow. in: Peragallo, H. and Peragallo,, M. (1897-1908). p. 290, pl. 74/7. **Fig. 173, 174, 175.**

Nitzschia sigma var. rigida Kützing.
Hustedt, F. (1930). p. 420. Hendey, N. I. (1964). p. 282. *N. rigida* in Peragallo, H. and Peragallo, M. (1897-1908). p. 291, f. 74/9. Cleve-Euler, A. (1951-55). p. 75, f. 1470c, d. Schmidt, A. (1874-1956). pl. 336/6. Tynni, R. (1980). p. 20, pl. 11:182. Van Heurck, H. (1880-5). p. 179, pl. 66:2, 5. **Fig. 204.**

Nitzschia socialis Gregory . var. socialis.
Cleve and Grunow (1880) p. 85, f. 85. Pankow, H. (1976). p. 312, f. 663. Hendey, N. I. . (1964). p. 280. Peragallo, H. and Peragallo, M. (1897-1908). p. 280, pl. 72/7, 8. Cleve-Euler, A. (1951-55). p. 69. **Fig. (197?), 203.**

Biddulphia aurita Lyngbye.
(Odontella aurita) Hendey, N. I. (1964). p. 103, pl. 24/6. Cleve-Euler, A. (1951-55). p. 119, f. 257d. Schmidt, A. (1874-1956). pl. 120/6, 7. 122/1-8. Drebes, von G, 1974. **Fig. 171.**

Opephora martyi Heriband.
Pankow, H. (1976). p. 130, f. 236. Hustedt, F. (1930). p. 132, f. 120. Hustedt, F. (1931-37). p. 135, f. 654. Molder, K.. and Tynni, R. (1969). p. 246, f. 53. *Fragilaria pinnata* var. *genuina* f. *subsolitaris* (Grunow 1862) *in* Cleve-Euler, A. (1951-55). p. 37, f. 348n-q. **Fig. 122, 124.**

Pinnularia Ehrenberg. sp. A.
Fig. 16.

Pinnularia ambigua Cleve.
Pankow, H. (1976). p. 200, f. 425. Hendey, N. I. (1964). p. 233, pl. 34/5,8. Cleve-Euler, A. (1951-55). p. 34, f. 1040. Cleve, P. T. (1894). p. 94. *A. digitus* in

Schmidt, A. (1874-1956). pl. 26/30. Schmidt, A. (1874-1956). pl. 313/20,21. **Fig. 125,128.**

Navicula lanceolata Agardh.
Hustedt, F. (1930). p. 305, f. 540. Peragallo, H. and Peragallo, M. (1897-1908). p. 100, pl. 13/2. Cleve, P. T. and Grunow, A. (1880). p. 35. Cleve-Euler, A. (1951-55). p. 134, f. 772a. Cleve, P. T. (1894). p. 21. Krammer. K.. and Lange-Bertalot, H. (1986a). p. 100, pl. 29/5-7. **Fig. 37.**

Pinnularia divergens Wm. Smith..
Foged, N. (1978) p. 114, pl. 33/1. Hustedt, F. 1930. p. 323, f. 589. Cleve-Euler, A. (1951-55). p. 51. **Fig. 17.**

Pinnularia ergadensis Gregory var. ergadensis.
Hendey, N. I. (1964). p. 216, pl. 29. Peragallo, H. and Peragallo, M. (1897-1908). p. 77, f. 14. **Fig. 108.**

Pinnularia lata Brebisson. var.?
Because the frustule was fragmented it was not possible to identify this specimen to variety level .
Hustedt,F. (1930). p. 324, f. 595. Cleve-Euler, A. (1951-55). p. 33, f. 1038. **Fig. 164.**

Pinnularia cf. microstauron Ehrenberg.
Hustedt,F. 1930. p. 320, f. 582. Foged, H. (1974) p. 98, pl. 18/14. Cleve-Euler, A. (1951-55). p. 55. **Fig. 20.**

Pinnularia quadratarea Schmidt. var. subproducta Grunow.
Cleve 1896. Pankow, H. (1976). p. 199. Peragallo, H. and Peragallo, M. (1897-1908). p. 86, pl. 11/8,9. Cleve-Euler, A. (1951-55). p. 10, f. 981. Schmidt, A. (1874-1956). f. 261/33. Fig. 22.

Pinnularia rupestris Rabenhorst.
Cleve-Euler, A. (1951-55). p. 75, f. 1105/g, h. Schmidt, A. (1874-1956). f. 45/38-44. **Fig. 21.**

Pinnularia subcapitata Gregory. var. hilseana Janisch and Rabenhorst.
Cleve-Eulr, A. (1951-55). p. 64, f. 1090. Schmidt, A. (1874-1956). f. 44,45/59,60.65 Krammer, K.. and H. Lange-Bertalot (1986a) p. 426, f. 193/1-18. **Fig. 19.**

Pinnularia viridis Ehrenberg var. mayeri Cleve-Euler.
Pankow, H. (1976). p. 199. Cleve-Euler, A. (1951-55). p. 73, f. 1103. Schmidt, A. (1874-1956). f. 42. Krammer, K. and H. Lange-Bertalot (1986a) p. 428,f. 194. **Fig.** 23.

Plagiogramma staurophorum Gregory.
Pankow, H. (1976). p. 124, f. 219. Hustedt, F. (1931-37). p. 110, f. 635. Hendey, N. I. (1964). p. 166, f. 36/1. Cleve-Euler, A. (1951-55). p. 24, f. 332. Schmidt, A. (1874-1956). pl. 209/6-8. **Fig. 121.**

Plagiotropis tayrecta.
Paddock. T. B. B. (1988). p. 25, f. 5. **Fig. 226,230.**

Pleurosigma aestaurii Brebisson. var.candida Schumann.
Peragallo, H. and Peragallo, M. (1897-1908). p. 164, pl. 33/10. *P. aesterii* in Cleve, P. T. and Grunow, A. (1880). p. 52. Cleve, P. T. (1894). p. 42. *P. angulatum* var.*aestaurii* in Van Heurck, H. (1880-1885). p. 115, pl. 18/8. **Fig. 211.**

Pleurosigma formosum W.Smith.
Hendey, N. I. (1964). p. 242. Peragallo, H. and Peragallo, M. (1897-1908). p. 156, pl. 30/1-3. Cleve, P. T. (1894). p. 45. Krammer. K. and Lange-Bertalot, H. (1986a). Krammer. K. and Lange-Bertalot, H. (1986b). Van Heurck, H. (1880-1885). p. 116, pl. 19/4. **Fig. 213.**

Pleurosigma australe Grunow.
Peragallo, H. and Peragallo, M. (1897-1908). p. 163, pl. 32/7, 8. Cleve, P. T. and Grunow, A. (1880). p. 51. **Fig. 216.**

Pleurosigma naviculaceum Brebisson.
Hendey, N. I. (1964). p. 243. Cleve, P. T. (1894). p. 36. Cleve, P. T. and Grunow, A. (1880). p. 51. Van Heurck, H. (1880-1885). p. 116, Atlas Suppl. f. 35. Peragallo, H. and Peragallo, M. (1897-1908). p. 162, pl. 32/11-13. Foged, N. (1978) p. 120, pl. 21/5,6. **Fig. 217.**

Pleurosigma nubecula Wm. Smith.
Pankow, H. (1976). p. 184, f. 388. Cleve-Euler, A. (1951-55). p. 23, f. 1375. *P. intermedium* var *nubecula* in: Peragallo,H. and Peragallo, M. (1897-1908). p. 165, pl. 32/19,20. **Fig. 218.**

Pleurosigma salinarum Grunow.
Cleve, P. T. and Grunow, A. (1880). p. 54. Pankow, H. (1976). p. 185, f. 395. Cleve, P. T. (1894). p. 39. Peragallo, H. and Peragallo, M. (1897-1908). p. 166, p. 133/16. Hustedt,F. (1930). p. 228, f. 344. **Fig. 214.**

Pleurosigma strigosum Wm. Smith..
Hendey, N. I. (1964). p. 246, pl. 36/7. *P. angulatum* var.*strgosum* Wm. Smith. in: Van Heurck, H. (1880-1885). p. 115, pl. 19/2. *P. angulatum* var. *convexum* Grunow. in: Cleve, P. T. (1894). p. 41. **Fig. 212,215,219,220.**

Rhabdonema minutum Kützing.
Hendey, N. I. (1964). p. 172. Hustedt, F. (1931-37). p. 18, f. 548a. Peragallo, H. and Peragallo, M. (1897-1908). p. 359, pl. 89/5,6. Cleve-Euler, A. (1951-55). p. 6. Schmidt, A. (1874-1956). pl. 219/14,15. Van Heurck, H., H. (1880-5). p. 166, pl. 54:17,18. Molder, K.. and Tynni, R. (1969). p. 237, f. 15. **Fig. 103.**

Rhoicosphenia abbreviata Agardh.
Krammer. K.. and Lange-Bertalot, H. (1986a). p. 381, pl. 91/20,21. **Fig. 11.** This is a fresh water species.

Scoliotropis latestriata Brebisson.
Pankow, H. (1976). p. 187, f. 400. Hendey, N. I. (1964). p. 234, pl. 29/5. Cleve-Euler, A. (1951-55). p.

87, f. 662,930. Van Heurck, H., H. (1880-5). p. 111, pl. 17/12. **Fig. 176.**

Skeletonema costatum Greville.
Pankow, H. (1976). p. 67, f. 80. Hendey, N. I. (1964). p. 91, pl. 7/3. Peragallo, H. and Peragallo, M. (1897-1908). p. 439, pl. 121/5. Cleve-Euler, A. (1951-55). p. 40, f. 47b-e. Schmidt, A. (1874-1956). pl. 321/5,6. pl. 180/45. **Fig. 208.**

Stauroneis sp. Ehrenberg.
Fig. 227.

Stauroneis phoenicenteron Nitzsch. var.phoenicenteron.
Hustedt, F. (1930). p. 225, f. 404. Hustedt, F. (1959). p. 766, f. 1118a. Cleve-Euler, A. (1951-55). p. 209, f. 944. Cleve, P. T. (1894). p. 148. **Fig. 177.**

Stauroneis salina Wm. Smith.
Hustedt, F. (1931-37). p. 258, f. 414. Hendey, N. I. (1964). p. 212. Pankow, H. (1976). p. 210. cf. var. Lagerstedtii Cleve-Euler. in Cleve-Euler, A. (1951-55). p. 212, f. 949e. **Fig. 5.**

Stenoneis inconspicua Gregory.
Pankow, H. (1976). p. 195, f. 415. Hendey, N. I. (1964). p. 222. Peragallo, H. and Peragallo, M. (1897-1908). p. 49, pl. 7/7,8. Cleve-Euler, A. (1951-55). p. 6, f. 1323. **Fig. 81, 82.**

Stenoneis sp. Cleve.
Fig. 9.

Surirella fastuosa Ehrenberg. var. fastuosa.
Pankow, H. (1976). p. 318. Hendey, N. I. (1964). p. 288, pl. 40/4. Peragallo, H. and Peragallo, M. (1897-1908). p. 248, pl. 59/2,3. Cleve-Euler, A. (1951-55). pl. 25. Schmidt, A. (1874-1956). pl. 206/7. Krammer. K.. and Lange-Bertalot, H. (1986b). pl. 123/2. **Fig. 102.**

Surirella hybrida Grunow.
Peragallo, H. and Peragallo, M. (1897-1908). p. 252, pl. 64/1,2. Schmidt, A. (1874-1956). pl. 358/1-7, 359/2,3. **Fig. 109.**

Synedra cf. fasciculata Grunow.
Cleve *and* Grunow 1880. p. 105, pl. 6/114. **Fig. 239.**

Synedra pulchella Ralfs and Kutzing. cf. var. puchella.
Pankow, H. (1976). p. 132. Hustedt, F. (1931-37). p. 160. Hustedt, F. (1931-37). p. 191, f. 688. Hendey, N. I. (1964). p. 163. Peragallo, H. and Peragallo, M. (1897-1908). p. 318. Cleve-Euler, A. (1951-55). p. 66, f. 387. Schmidt, A. (1874-1956). pl. 300/19-35. Molder,K.. and Tynni, R. (1970). p. 137, f. 51,52. Cleve, P. T. *and* Grunow, A.(1880). p. 107. Van Heurck, H., H. (1880-5). p. 149, pl. 41:1-8. **Fig. 110.**

Synedra pulchella Ralfs and Kutzing. var. **A.**
Pankow, H. (1976). p. 132. Hustedt, F. (1930). p. 160. Hustedt, F. (1931-37). p. 191, f. 688. Hendey, N. I.

(1964). P. 163. Peragallo, H. and Peragallo, M. (1897-1908). p. 318. Cleve-Euler, A. (1951-55). p. 66, f. 387. Schmidt, A. (1874-1956). pl. 300/19-35. Molder, K. and Tynni, R. (1970). p. 137, f. 51,52. Cleve, P. T. *and* Grunow, A. (1880). p. 107. Van Heurck, H., H. (1880-5). p. 149, pl. 41:1-8. **Fig. 111.**

Synedra cf. tabulata Agard.
Molder, K.. and Tynni, R. (1970). p. 137, pl. 55. Pankow, H. (1976). p. 131, f. 241. Hendey, N. I. (1964). p. 161. Cleve, P. T. *and* Grunow, A.(1880). p. 105. *S. tabulata* var. *genuina* in Cleve-Euler, A. (1951-55). p. 69. *S. affinis* var.*tabulata* in Van Heurck, H., H. (1880-5). p. 153, pl. 41:9a. Peragallo, H. and Peragallo, M. (1897-1908). p. 319, pl. 80/13. **Fig. 112.**

Tabellaria floculosa Roth.
Peragallo, H. and Peragallo, M. (1897-1908). pl. 59/16. Cleve-Euler, A. (1951-55). p. 9. Hustedt, F. (1930). p. 123, f. 101. Schmidt, A. (1874-1956). pl. 269/14-19,27,30. Van Heurck, H., H. (1880-5). p. 162, pl. 52: 10-12. Molder, K., and Tynni, R. (1969). p. 239, f. 20 a-c. **Fig. 113,114.** This is a fresh water species.

Trachyneis aspera Ehrenberg var. aspera.
Pankow, H. (1976). p. 201, f. 426. Hendey, N. I. (1964). p. 236. pl. 29/13. Peragallo, H. and Peragallo, M. (1897-1908). p. 150, pl. 29/1,2. Cleve-Euler, A. (1951-55). p. 5, f. 976. Schmidt, A. (1874-1956). pl. 48. Cleve, P. T. (1965). p. 191. **Fig. 87,88.**

Tropidoneis lepidoptera Gregory.
Pankow, H. (1976). p. 168. Hendey, N. I. (1964). p. 256, pl. 36. Peragallo, H. and Peragallo, M. (1897-1908). p. 188, pl. 39/3-7. Cleve-Euler, A. (1951-55). p. 27, f. 1386. Paddock, T.B.B. (1988). p. 39, pl. 13. **Fig. 236.**

Tropidoneis vitrea Wm. Smith. var. scaligera Grunow.
Pankow, H. (1976). p. 169, f. 355. Hendey, N. I. (1964). p. 255, pl. 36/3. Peragallo, H. and Peragallo, M. (1897-1908). p. 191, pl. 41/7,8. Cleve-Euler, A. (1951-55). p. 28, f. 1388c. **Fig. 237,238.**

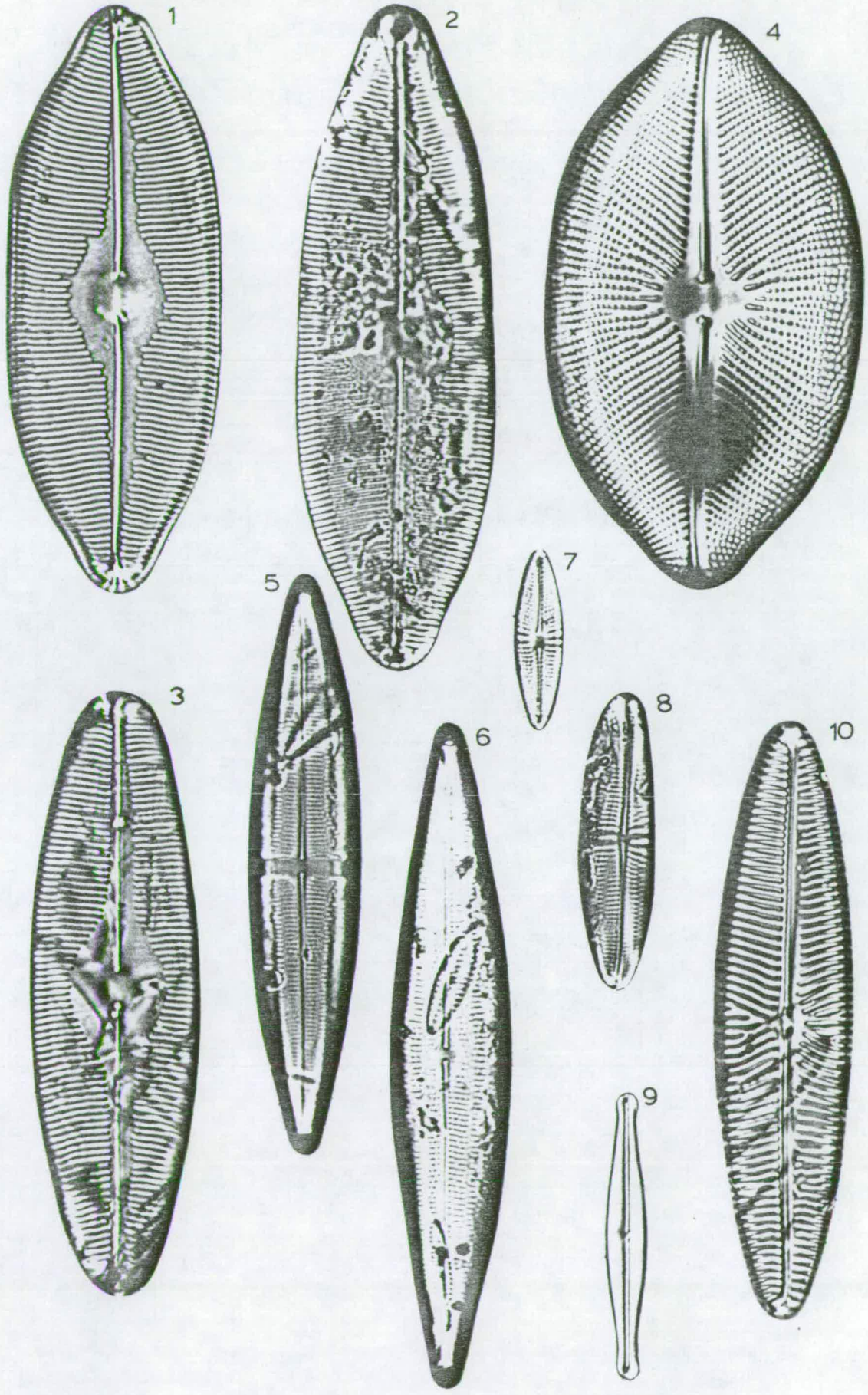
Index

1,2.....Caloneis crassa Gregory.
3.....Caloneis crassa Gregory. var. distoma
4.....Navicula latissima Gregory.
5.....Stauroneis salina Wm. Smith. cf. var. Lagerstedtii Cleve-Euler.
6.....Navicula cf. rhombica Gregory.
7,8.....Navicula subinflatoides Hustedt.
9.....Stenoneis sp Cleve.
10.....Navicula digito-radiata Gregory. var. cyprinus Ehrenberg.
11.....Rhoicosphenia abbreviata C. Agardh.
12.....Navicula palpebralis Brebisson. var. minor Grunow.
13,14.....Navicula Bory. sp A
15.....Navicula plicata Ehrenberg. var. constricta Hustedt.
16.....Pinnularia Ehrenberg. sp A
17.....Pinnularia divergens Wm. Smith.
18.....Acnanthes cf. angustata Greville.
19.....Pinnularia subcapitata Gregory. var. hilseana Janisch and Rabenhorst.
20.....Pinnularia cf. microstauron Ehrenberg.
21.....Pinnularia rupestris Rabenhorst.
22.....Pinnularia quadratarea A. Schmidt var. subproducta Grunow.
23.....Pinnularia viridis Ehrenberg. var. mayeri A. Cleve-Euler.
24-31.....Navicula cf. tripunctata Müller.
32.....Navicula crucigera Wm. Smith.
33-35.....Navicula palpebralis var. angulosa Gregory.
36,40-42.....Navicula Bory. sp B
37.....Navicula lanceolata Agardh.
38-39.....Navicula retusa Brebisson. var. gregorii
43,49.....Navicula lyroides Hendey.
44,48,57.....Navicula atlantica Schmidt.
45.....Navicula abrupta Gregory.
46,47.....Navicula forcipata Greville. var. densistriata Schmidt.
50.....Navicula dissipata Hustedt.
51.....Navicula cf. sparsistriata Hustedt.
52.....Navicula cf. pygmaea Kützing.
53.....Navicula cf. cryptocephala Kützing. var. veneta
54,55.....Navicula phyllepta Kützing.
56.....Navicula hennedyi Wm. Smith. var. hennedyi
58.....Achnanthes sp Bory.
59.....Navicula Bory. sp C
60.....Anomoeoneis sp A. Pfitzer.
61.....Navicula cf. incerata Grunow.
62.....Navicula cf. bryophila Boye Patersen.
63.....Navicula Bory. sp D

64.....Navicula gregaria Donkin.
65.....Navicula cf. digito-radiata Gregory.
var. A
66,67.....Navicula arenaria Donkin.
68.....Navicula cf. digito-radiata Gregory.
var. B
69.....Navicula Bory. sp E
70,75,76.....Navicula distans Wm. Smith.
71.....Navicula cf. digito-radiata Gregory.
var. C
72,74.....Navicula retusa Brebisson.
var. cancellata
73.....Navicula meniscus Schuman.
77.....Navicula Bory. sp F
78.....Navicula Bory. sp G
79.....Navicula Bory. sp H
80.....Caloneis amphisbaena
var. amphisbaena Cleve.
81,82.....Stenoneis inconspicua Gregory.
83.....Caloneis liber var. excentrica Grunow
84.....Caloneis liber Wm. Smith var.elongata
85,86,90,91.....Achnanthes fimbriata Grunow.
87,88.....Trachyneis aspera Ehrenberg. var. aspera
89.....Navicula cf. decussis Østrup.
var. decussis
92.....Achnanthes delicatula Kützing.
sp. *delicatula*
93.....Achnanthes conspicua Mayer.
var. *conspicua*
94.....Navicula Bory. sp. I
95.....Diploneis aestiva Donkin.
var. *delicata* A. Scmidt.
96.....Diploneis aestiva Donkin.
var. fusca Gregory.
97,98,100,101.....Diploneis smithii Brebisson.
var. smithii
99.....Achnanthes longipes Agardh. f. lata
102.....Surirella fastuosa Ehrenberg.
var. fastuosa
103.....Rhabdonema minutum Kützing.
104,105.....Diploneis ovalis Hilse.
106,107.....Eunotia sp Ehrenberg.
108.....Pinnularia ergadensis Gregory.
var. ergadensis
109.....Surirella hybrida Grunow.
110.....Synedra pulchella Ralfs and Kutzing.
cf. var. puchella
111.....Synedra pulchella Ralfs and Kutzing.
var. A
112.....Synedra cf. tabulata Agard.
113,114.....Tabellaria floculosa Roth.
115.....Diploneis splendida Gregory.
116.....Diploneis crabro Ehrenberg.
117,118,119.....Cocconeis scutellum Ehrenberg.
cf. var. scutellum
120.....Campylodiscus fastuosa Ehrenberg.

121.....Plagiogramma staurophorum Gregory.
122,124.....Opephora martyi Heriband.
123.....Dimeregramma minor Gregory. var. minor
125,128.....Pinnularia ambigua Cleve.
126.....Amphora Ehrenberg and Kützing. sp A
127.....Amphora cf. arcus Gregory.
129,131.....Amphora Ehrenberg and Kützing. sp B
130.....Amphora laevis Gregory.
var. perminuta Cleve.
132.....Amphora ostrearia Brebisson.
var. ostrearia
133-135,153.....Amphora proteus Gregory.
var. proteus
136.....Amphora Ehrenberg and Kützing. sp C
137.....Amphora cf. lineolata Ehrenberg.
138,139.....Navicula cf. delognei Van Heurck.
140,143,144.....Amphora ventricosa Gregory.
141.....Amphora Ehrenberg and Kützing. sp D.
142.....Amphora ventricosa Gregory. var.?
145,156-9,161.....Amphora proteus Gregory. var. oculata
146.....Amphora cf. proteus Gregory. var. A
147.....Amphora graeffii Grunow var. minor
148,149.....Amphora truncata Gregory.
150.....Amphora coffeaeformis Agardh.
var. borealis
151,154,155.....Amphora coffeaeformis Agardh.
var. acutiuscula
152.....Amphora Ehrenberg and Kützing. sp E
160.....Amphora cf. proteus Gregory. var. B
162.....Cymbella sp Agardh.
163.....Cymbella cistula Ehrenberg. var. ginuina
164.....Pinnularia lata Brebisson. var.?
165.....Dictyocha speculum Ehrenberg.
var. speculum
166.....Eunotia cf. septentrionalis Østrup.
167.....Eunotia cf. pseudopectinalis Hustedt.
168.....Frustulia rhomboides De Toni.
var. rhomboides
169.....Frustulia rhomboides De Toni.
var. saxonica f. undulata
170.....Chaetoceros sp Ehrenberg.
171.....Biddulphia aurita Lyngbye.
172.....Gomphonema parvulum Kützing.
var. exilis Grunow.
173,174,175.....Nitzschia sigma Kützing.
var. intercedens Grunow.
176.....Scoliotropis latestriata Brebisson.
177.....Stauroneis phoenicenteron Nitzsch.
var. phoenicenteron
178.....Nitzschia Hass. sp A
179.....Nitzschia Hass. sp B
180.....Nitzschia Hass. sp C
181,182.....Nitzschia insignis Gregory.
cf. var. spathulifera Grunow.
183/4,202,209/10..Nitzschia insignis Gregory.
var. smithii Ralfs.

185,191,192.....Nitzschia aff. distans Gregory.
186.....Nitzschia marginulata Grunow.
var. marginulata
187.....Nitzschia bilobata W. Smith.
var. bilobata
188.....Nitzschia acuminata Wm. Smith.
189,194, 195.....Nitzschia angularis Wm. Smith.
190.....Nitzschia panduriformis Gregory.
cf. var. minor
193.....Nitzschia cf. punctata W. Smith.
var. coarctata Grunow. f. minor.
196.....Nitzschia sigma Kützing. var.?
197(?),203.....Nitzschia socialis Gregory.
var. socialis
198.....Bacillaria sp Gmelin.
199.....Cylindrotheca closterium
Reiman et Lewis.
200,201.....Nitzschia hybrida
cf. var. pellucida Grunow.
204.....Nitzschia sigma Kützing.
var. rigida Kützing.
205.....Nitzschia angularis Wm. Smith.
cf. var. affinis
206.....Nitzschia sp D Hass.
207.....Cylindrotheca gracilis Grunow.
208.....Skeletonema costatum Greville.
211.....Pleurosigma aestaurii Brebisson.
var. candida
212,215,219,220...Pleurosigma strigosum Wm. Smith.
213.....Pleurosigma formosum W. Smith.
214.....Pleurosigma salinarum Grunow.
216.....Pleurosigma australe Grunow.
217.....Pleurosigma naviculaceum Brebisson.
218.....Pleurosigma nubecula Wm. Smith.
221.....Gyrosigma tenuirostrum Grunow.
222.....Gyrosigma distortum Wm. Smith.
var. parkeri Harrison.
223.....Gyrosigma algoris Carter and Bailey-
Watts.
224,225.....Donkinia reticulata Norman.
226,230.....Plagiotropis tayrecta Paddock.
227.....Stauroneis sp Ehrenberg.
228,235.....Amphiprora plicata Gregory.
229.....Donkinia recta Donkin.
231.....Coscinodiscus sp Ehrenberg.
232.....Coscinodiscus concavus Ehrenberg.
233.....*Paralia sulcata* Ehrenberg.
234.....Thalassiosira cf.eccentrica Ehrenberg.
236.....Tropidoneis lepidoptera Gregory.
237,238.....Tropidoneis vitrea Wm. Smith.
var. scaligera Grunow.
239.....Synedra cf. fasciculata Grunow.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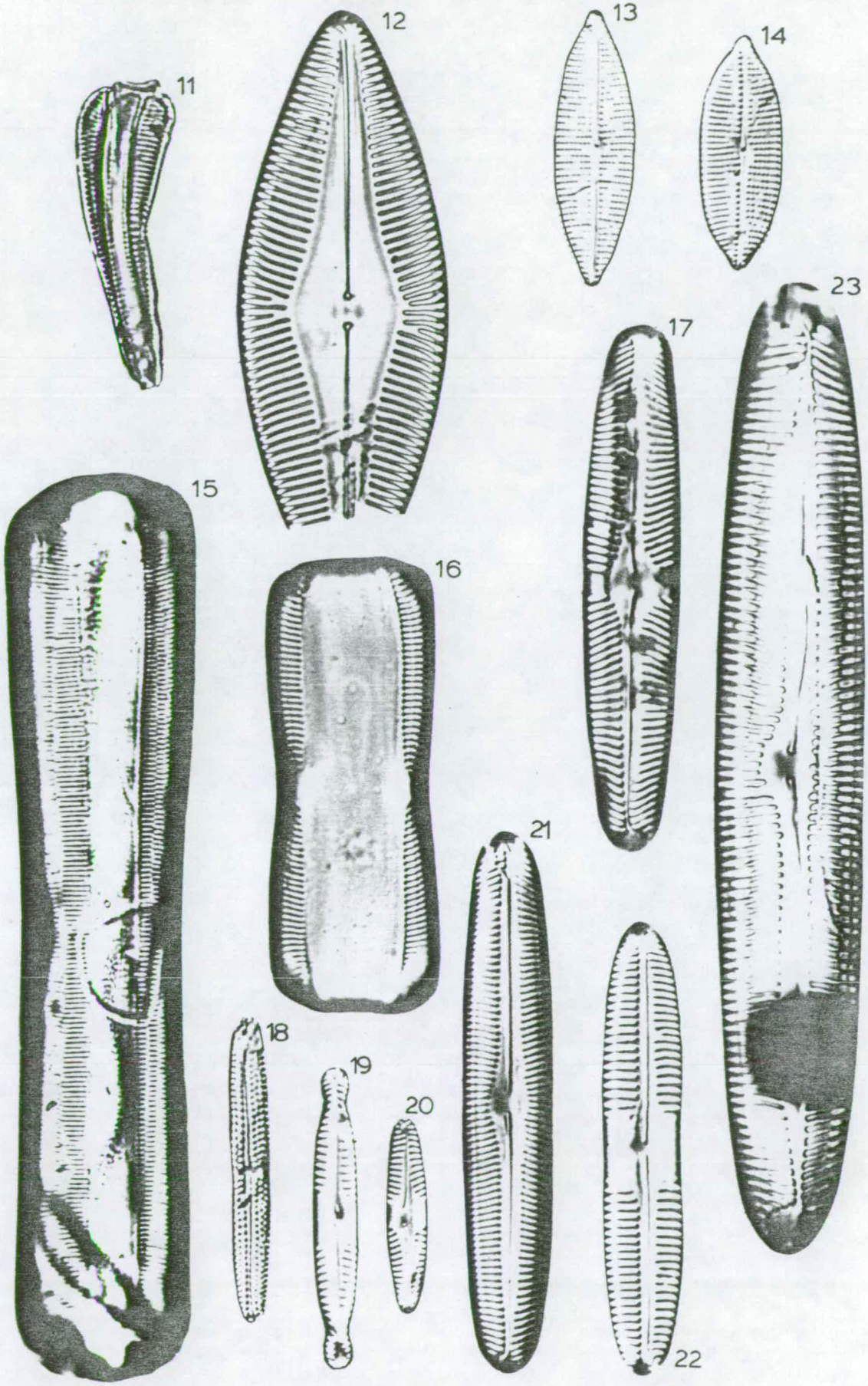
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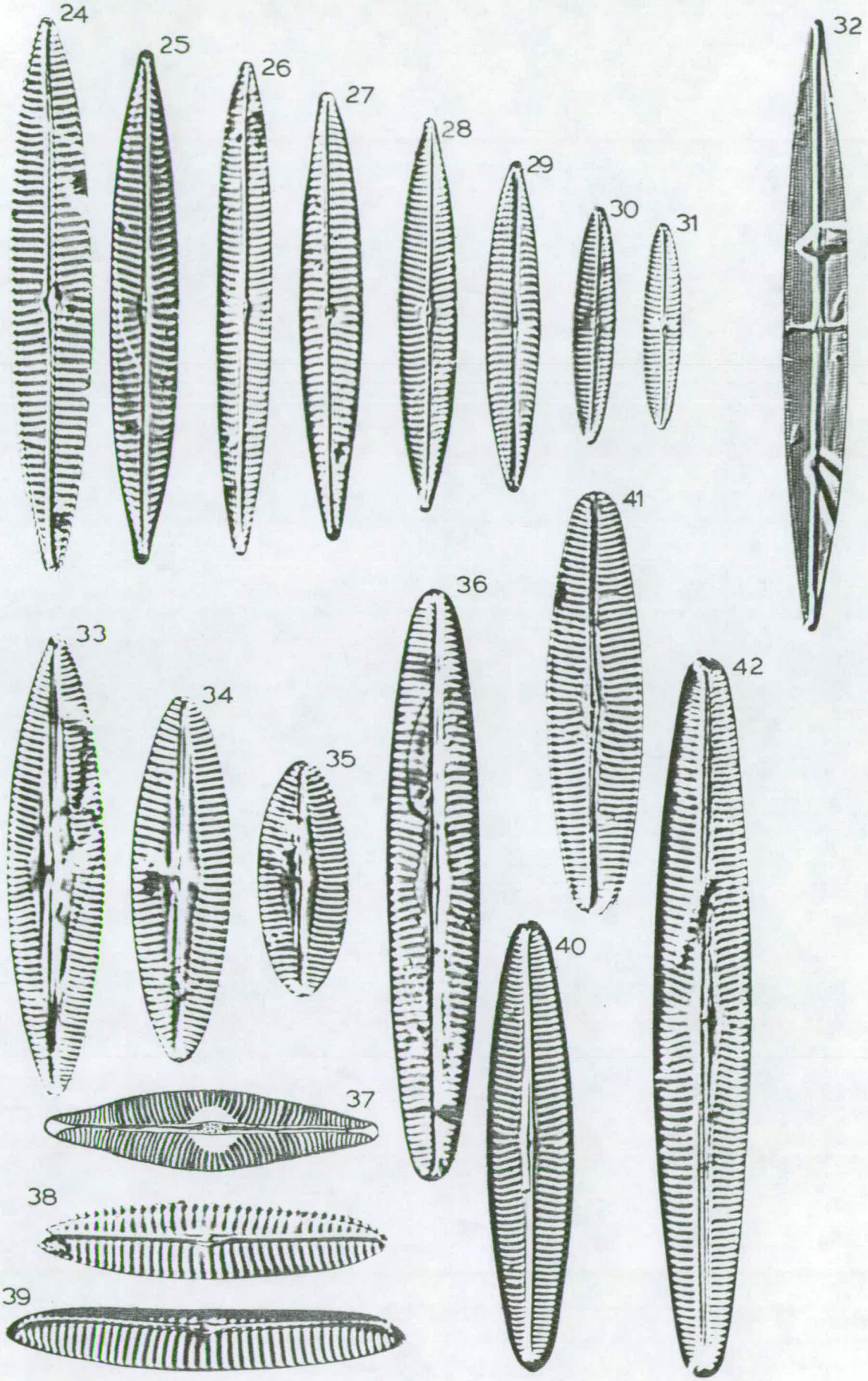
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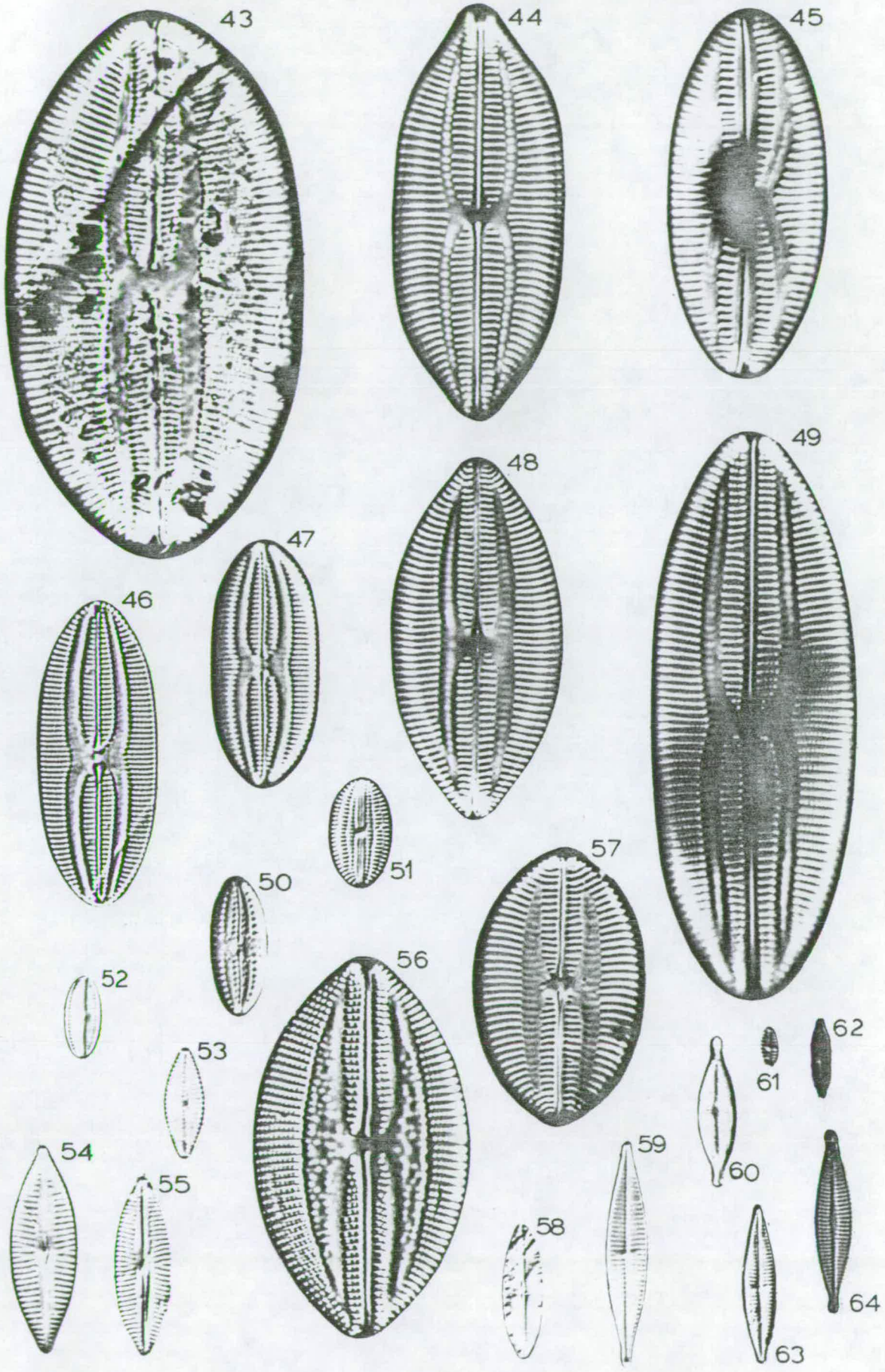
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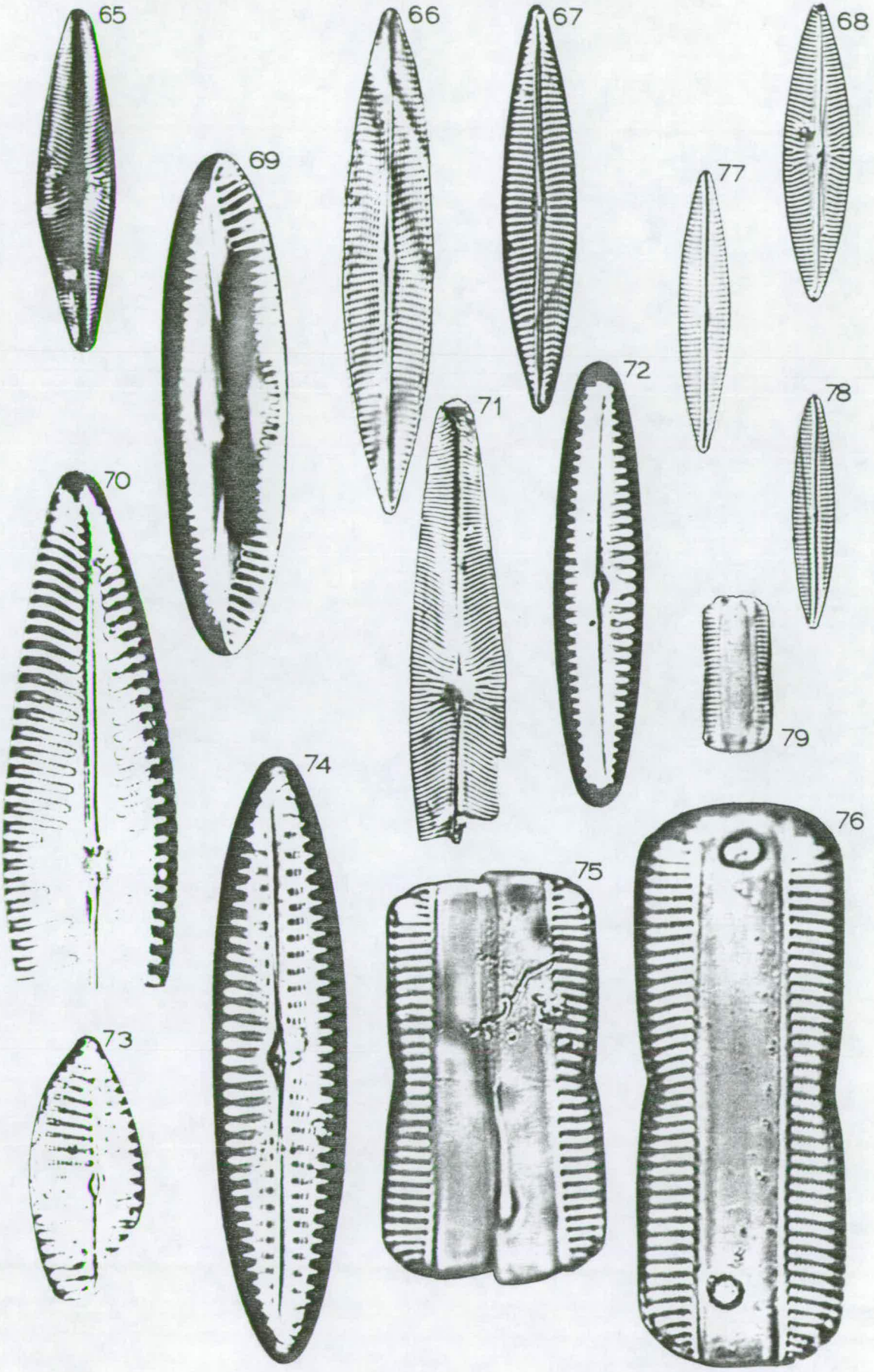
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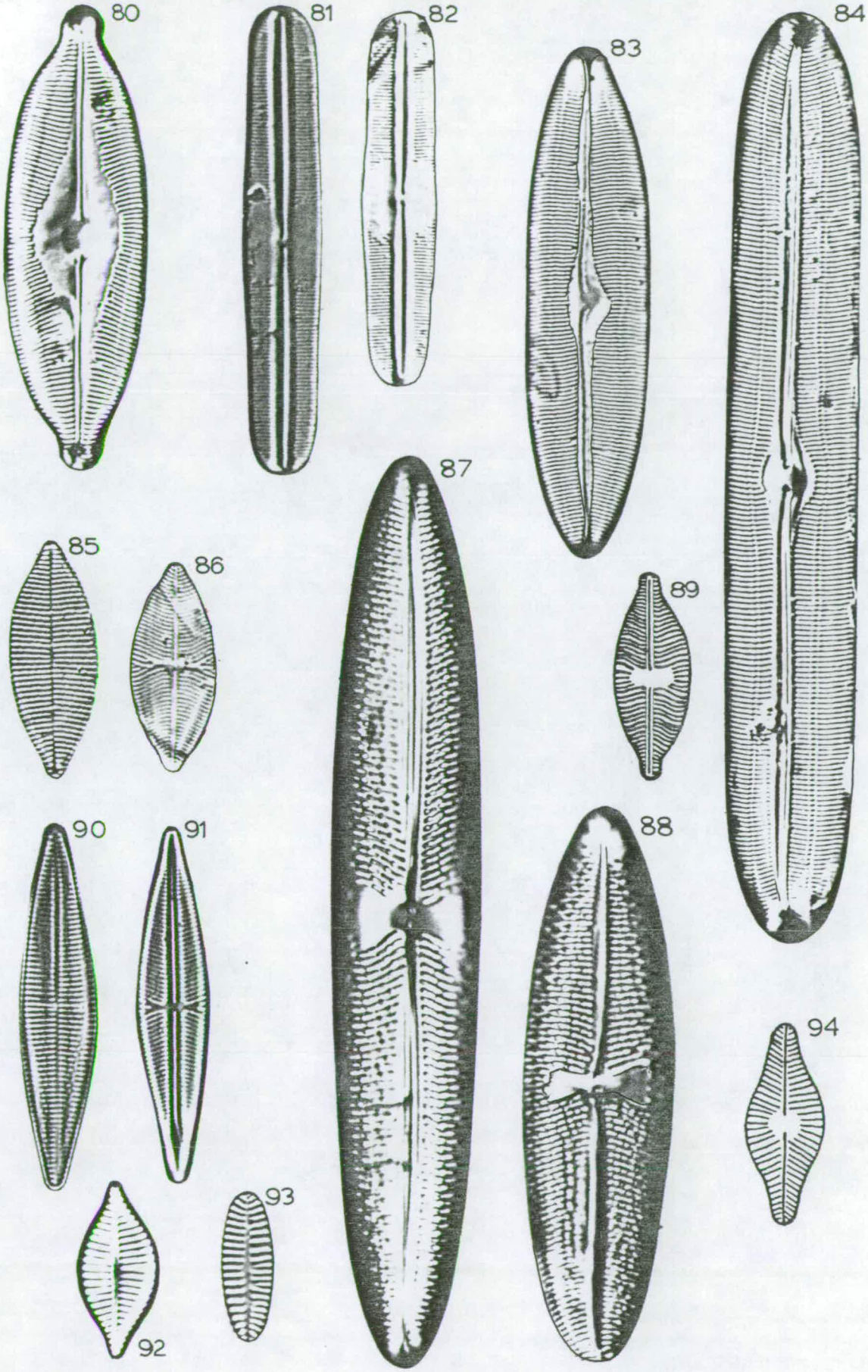
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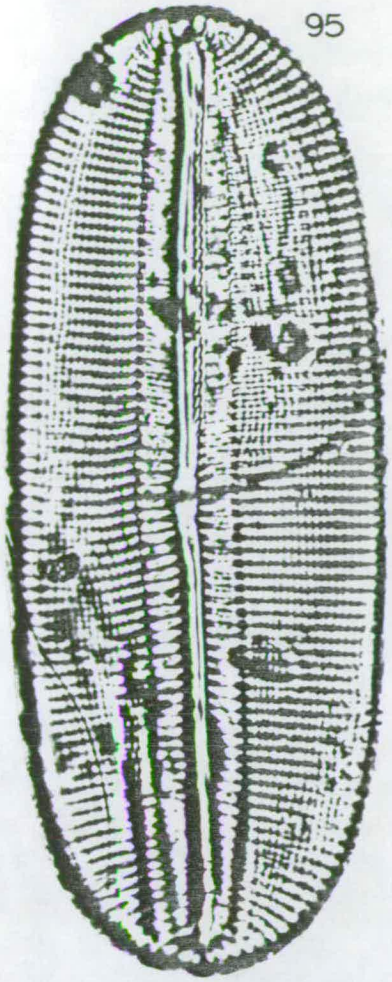
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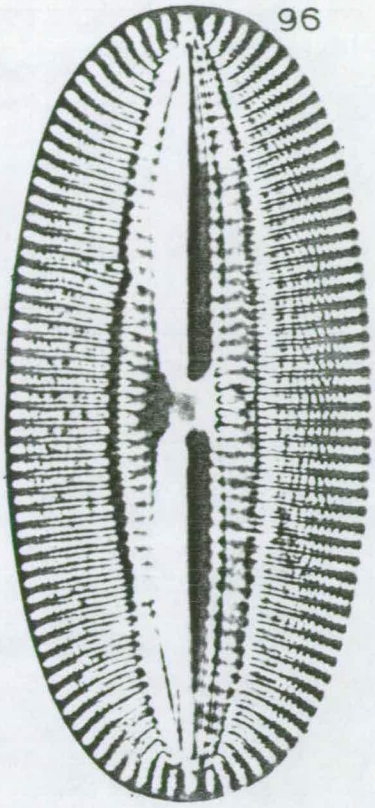
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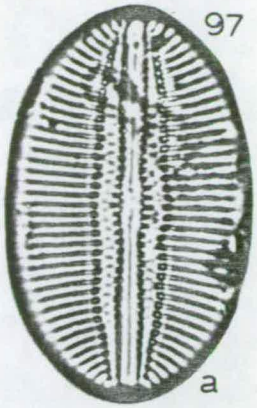
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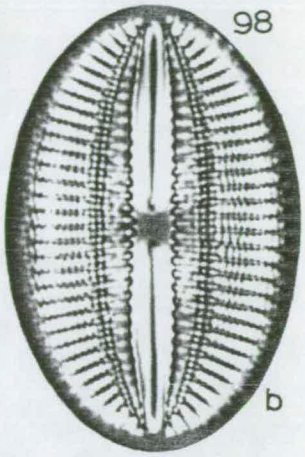
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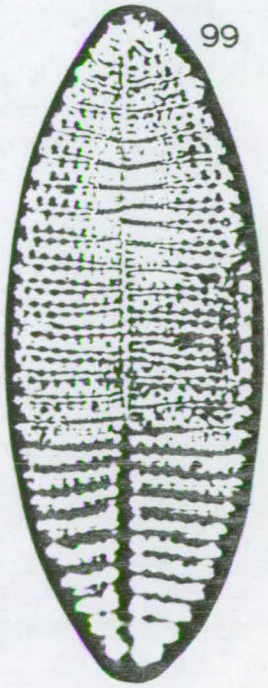
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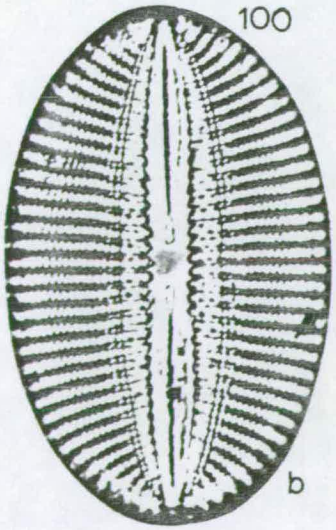
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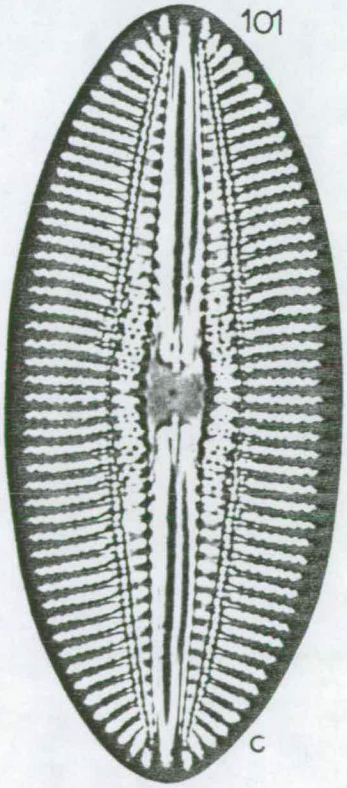
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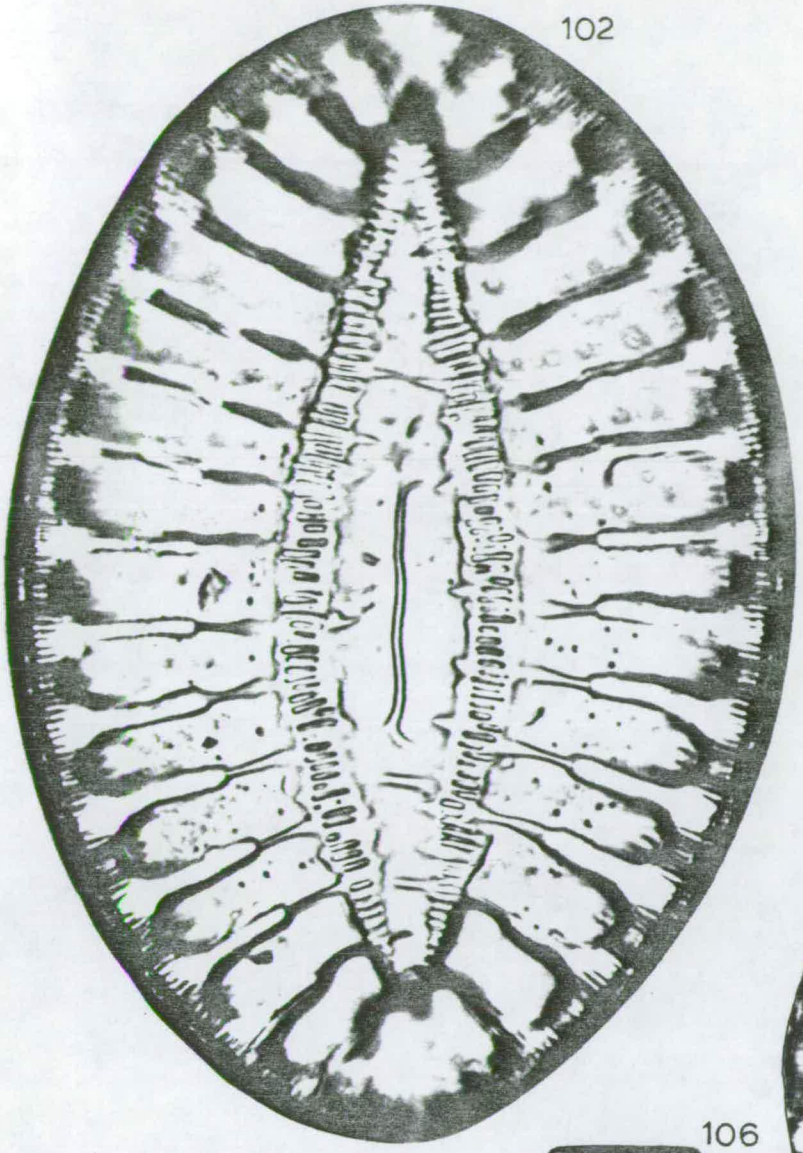
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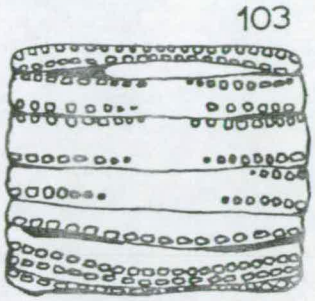
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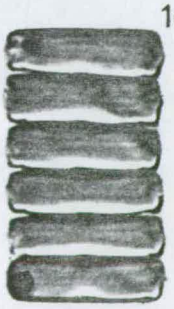
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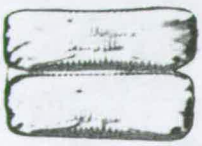
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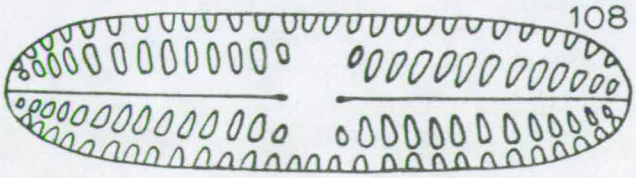
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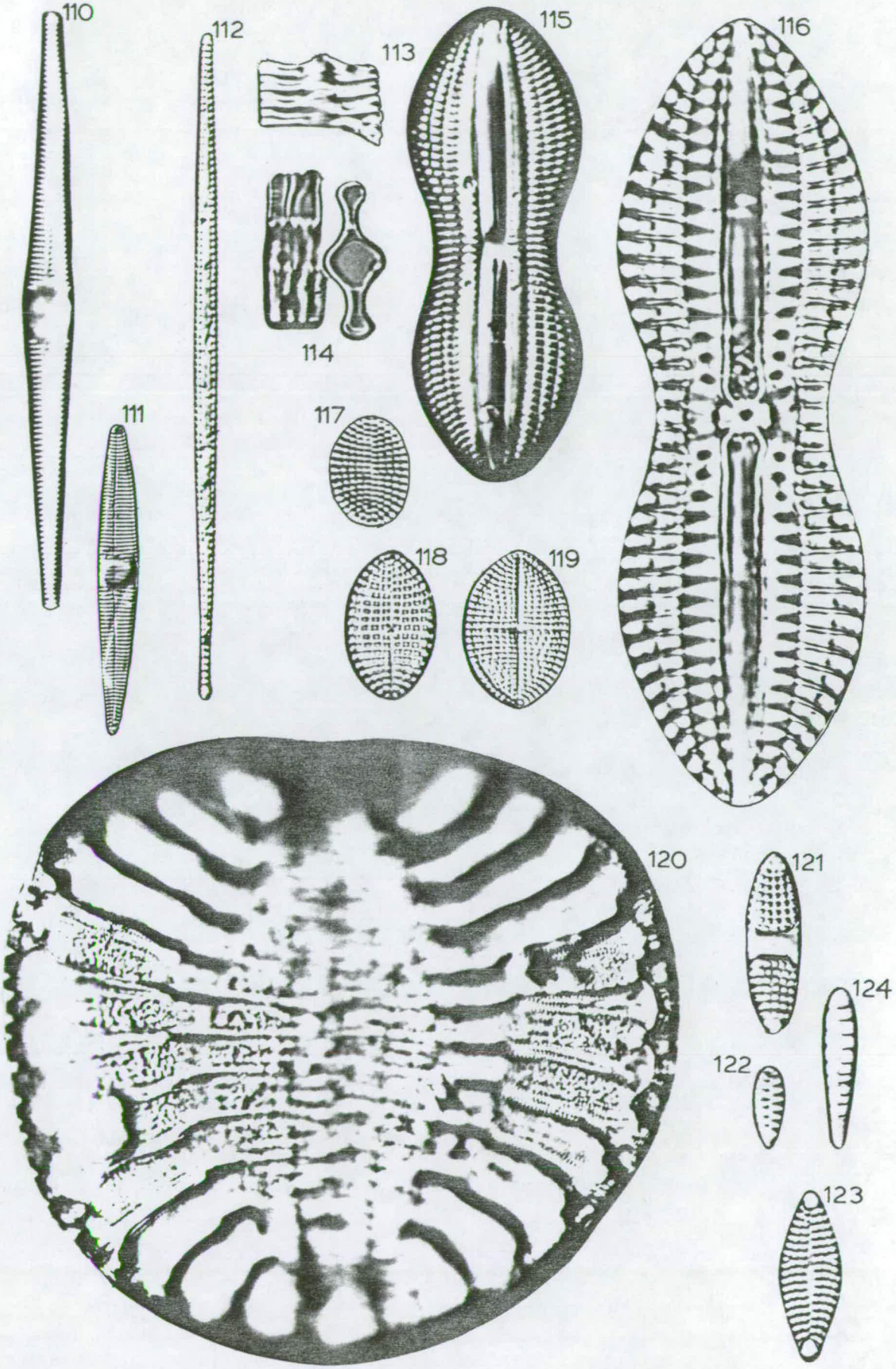
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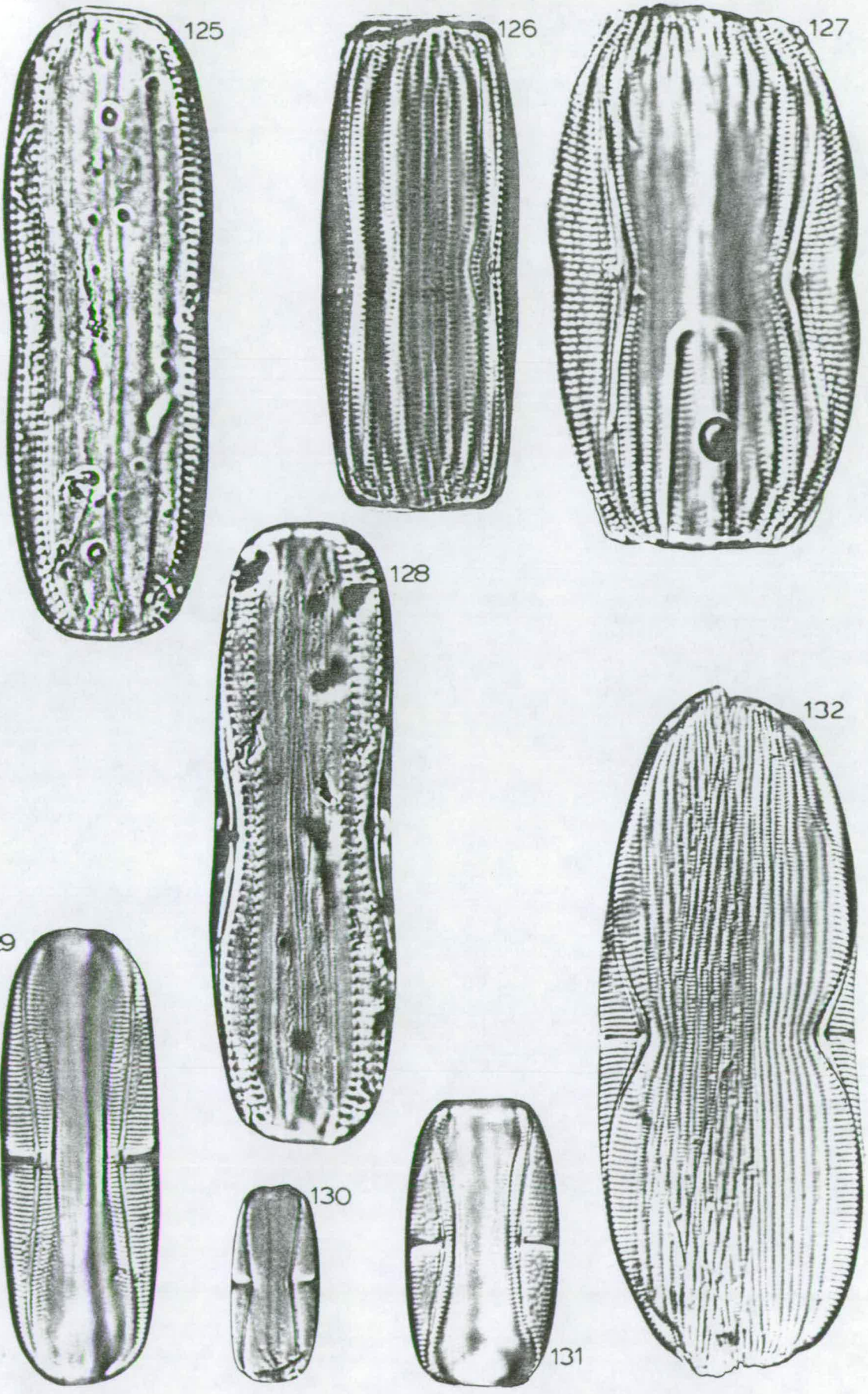
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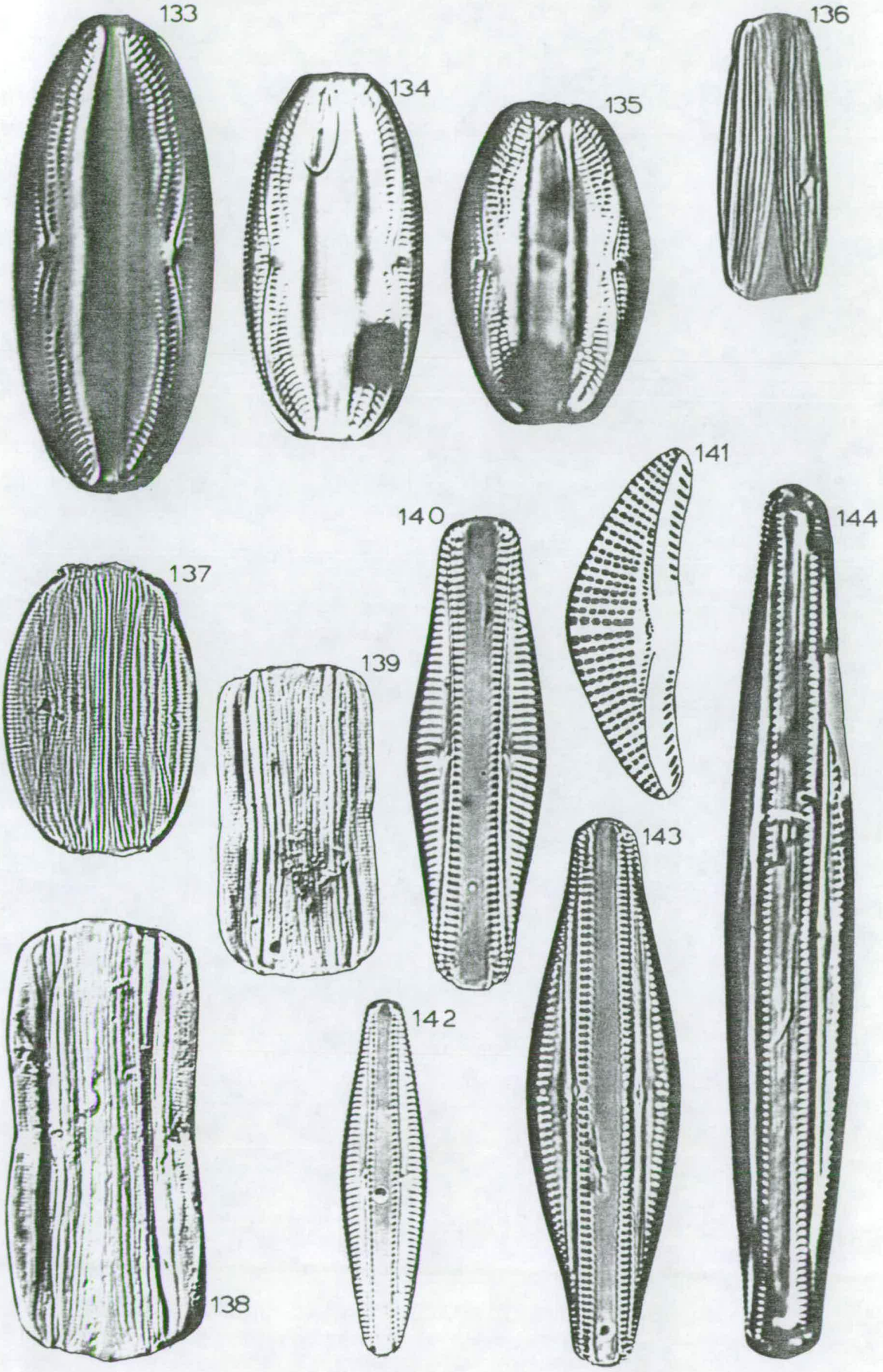
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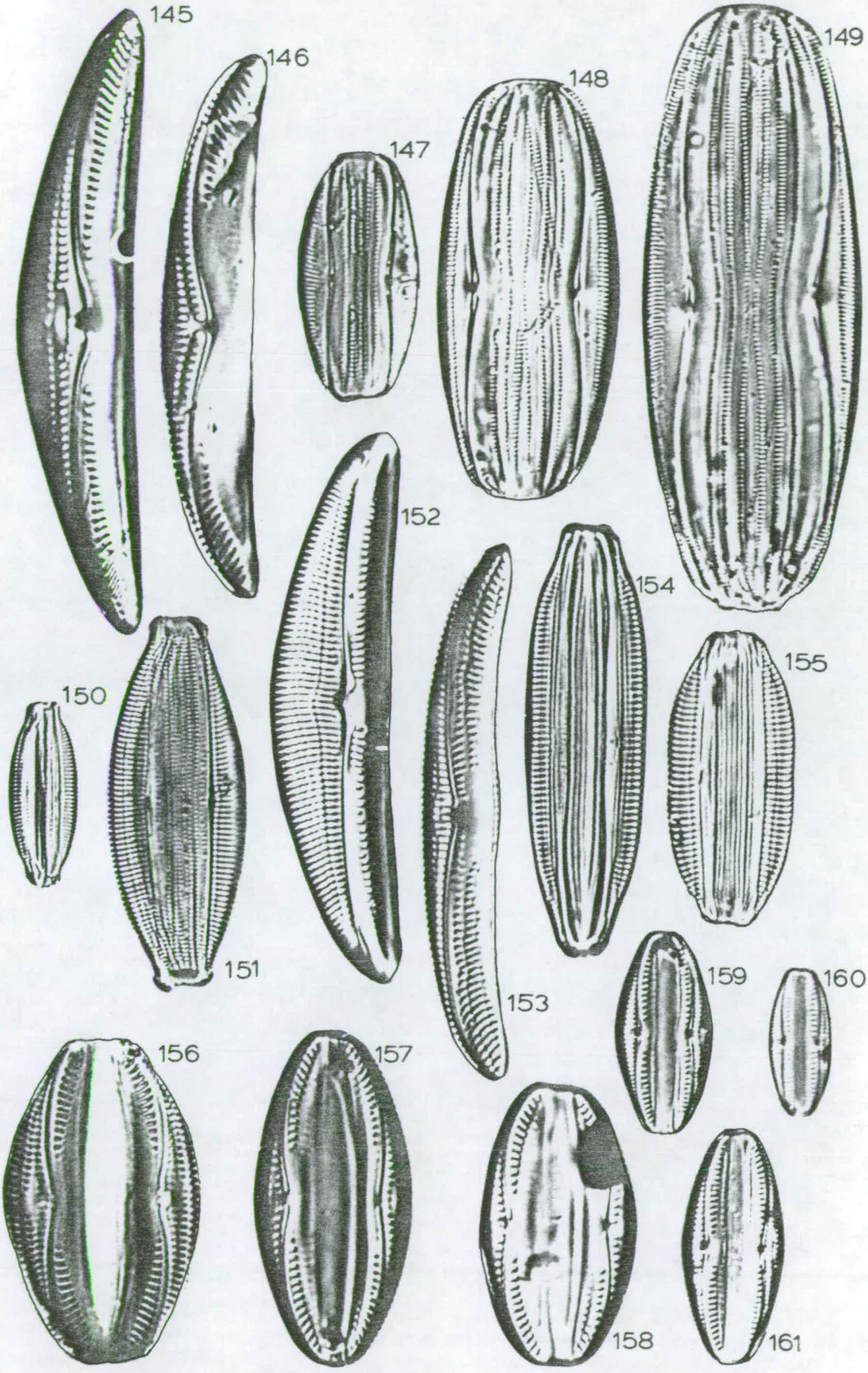
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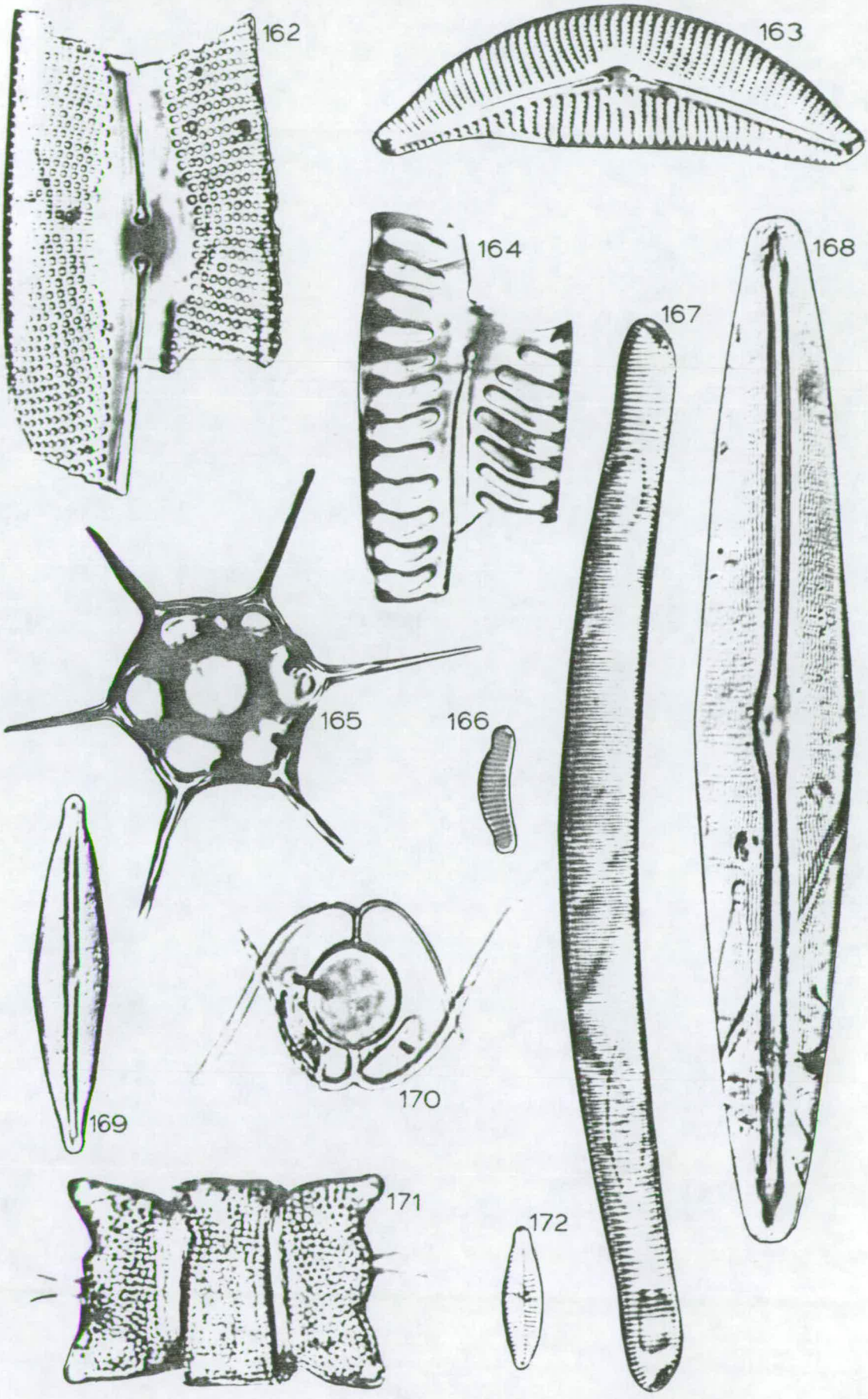
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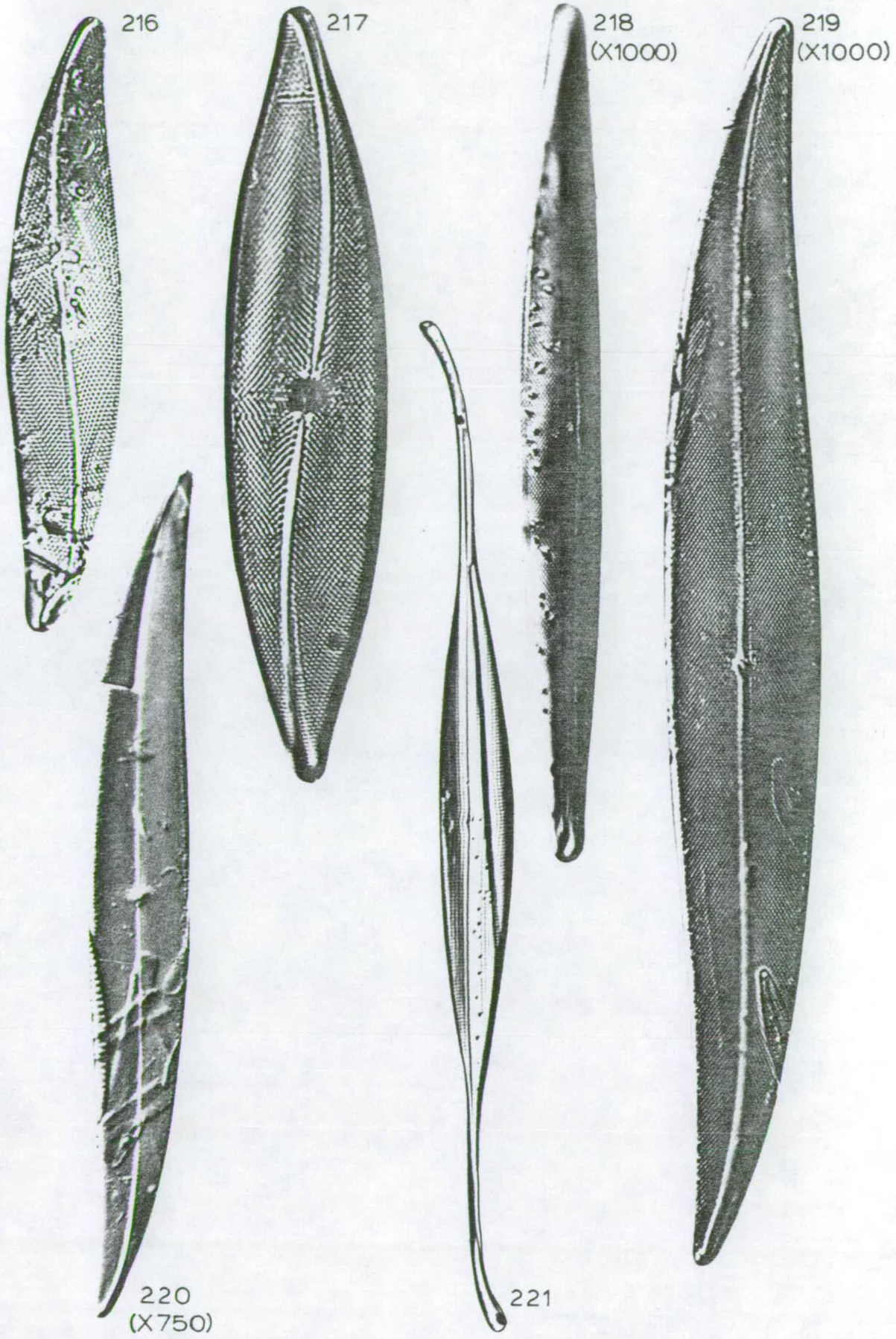
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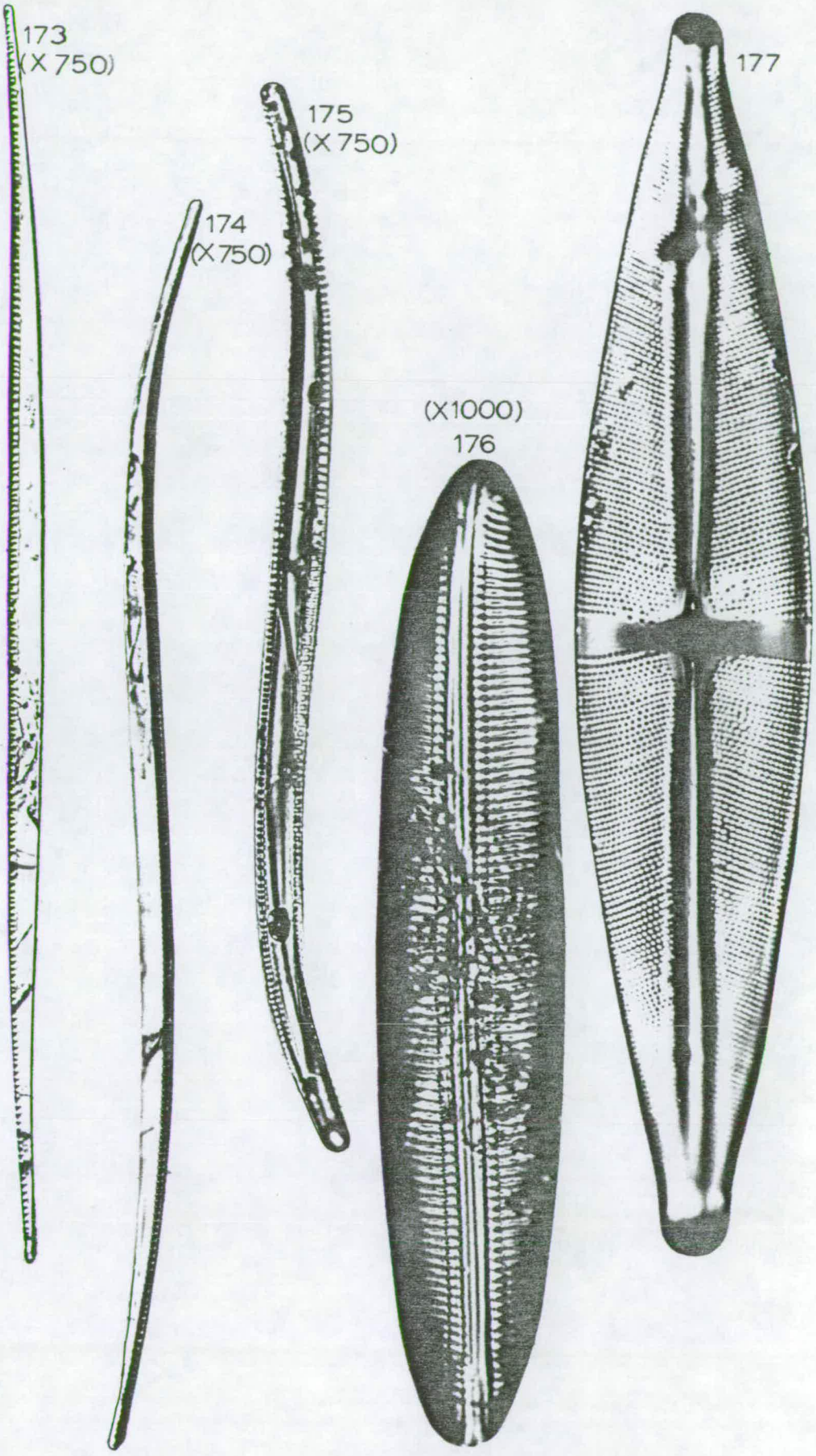
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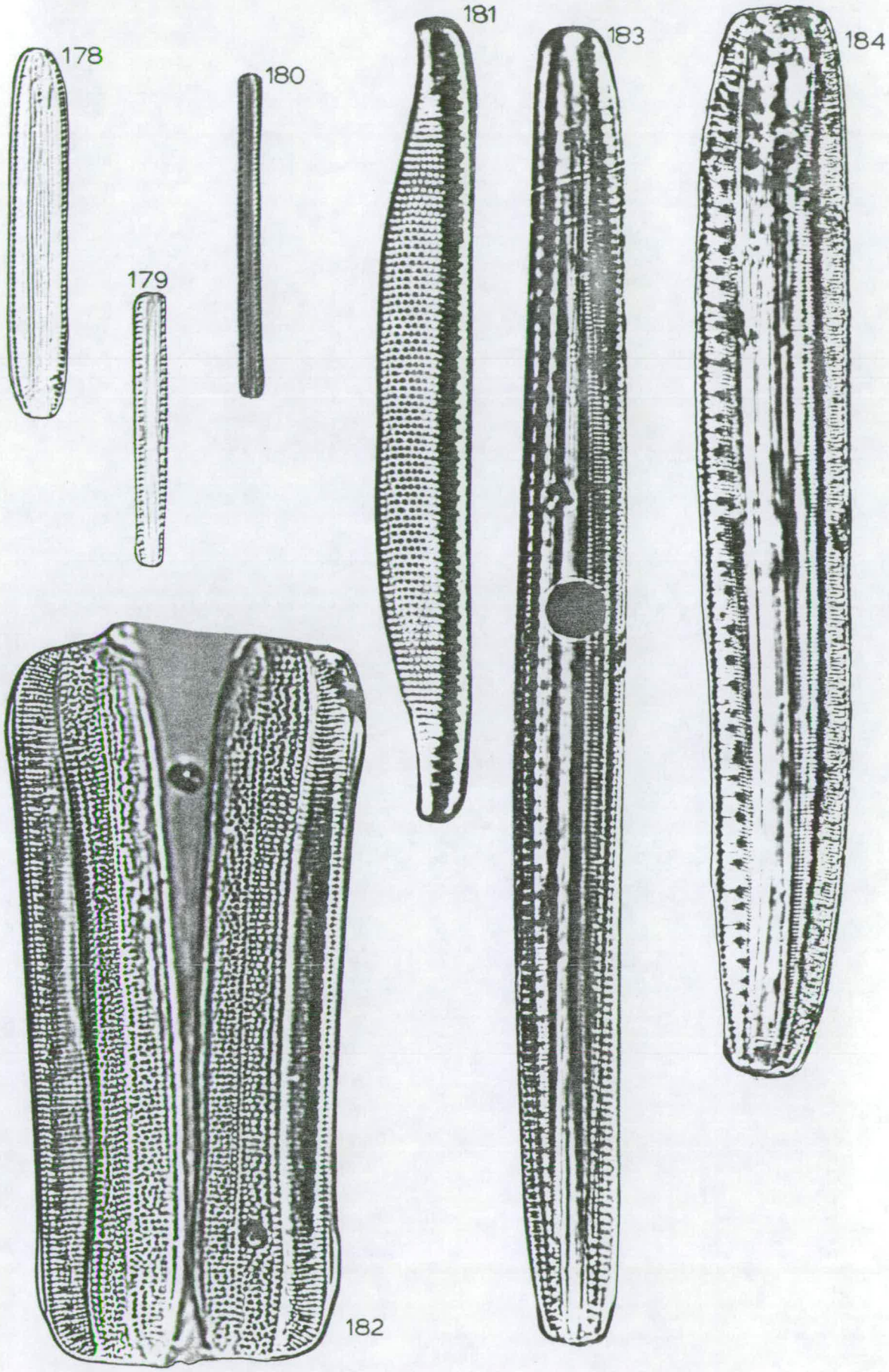
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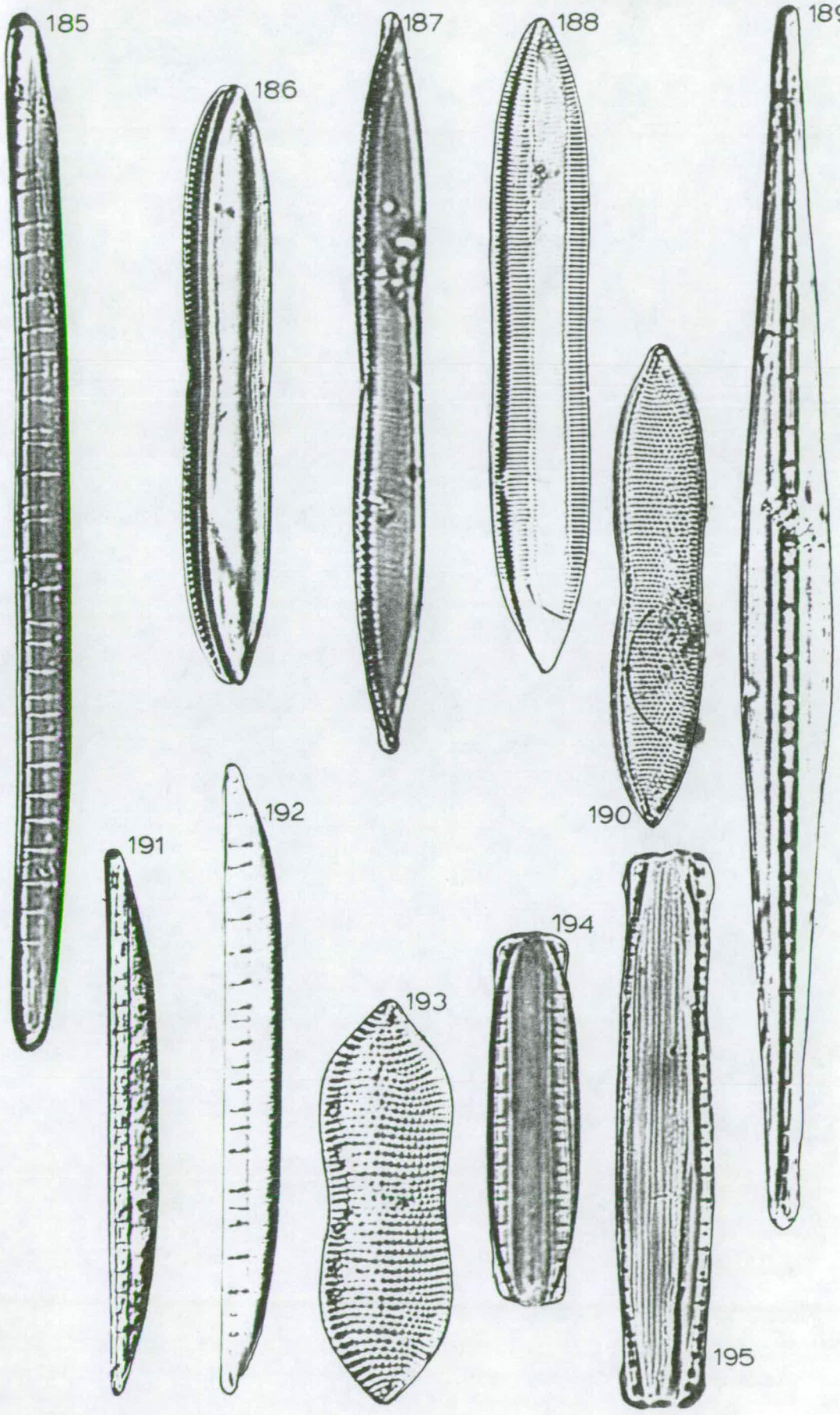
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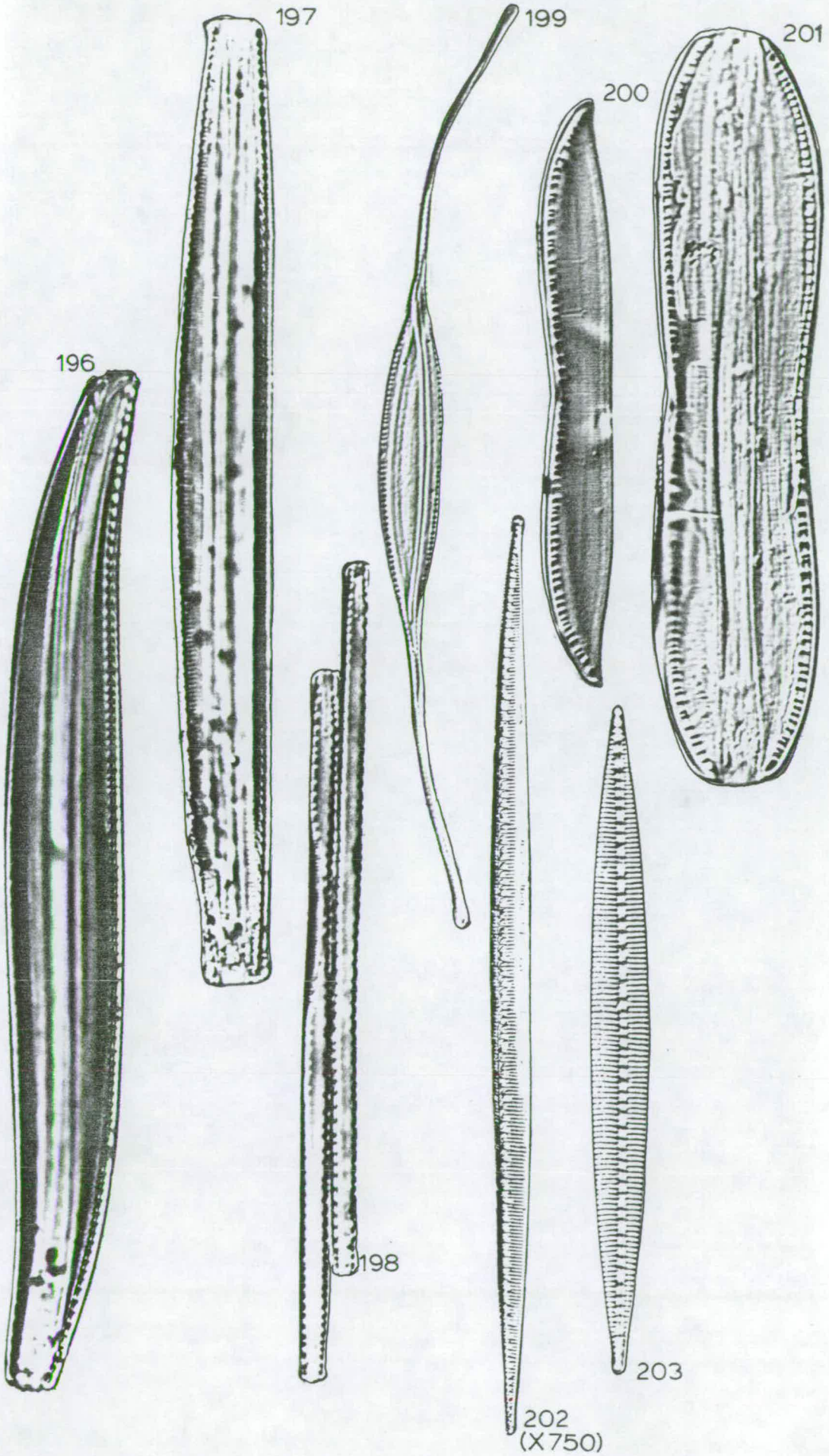
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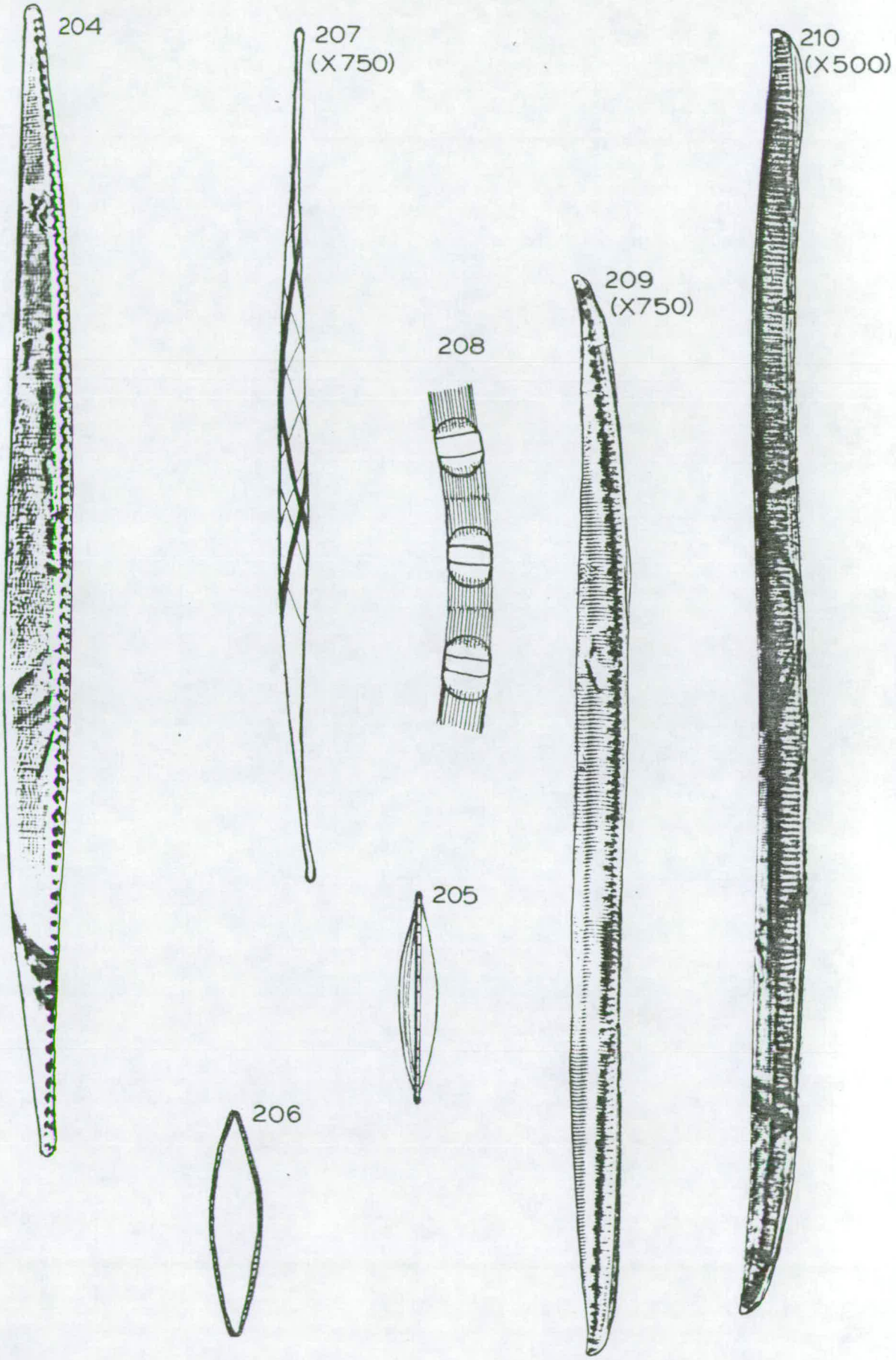
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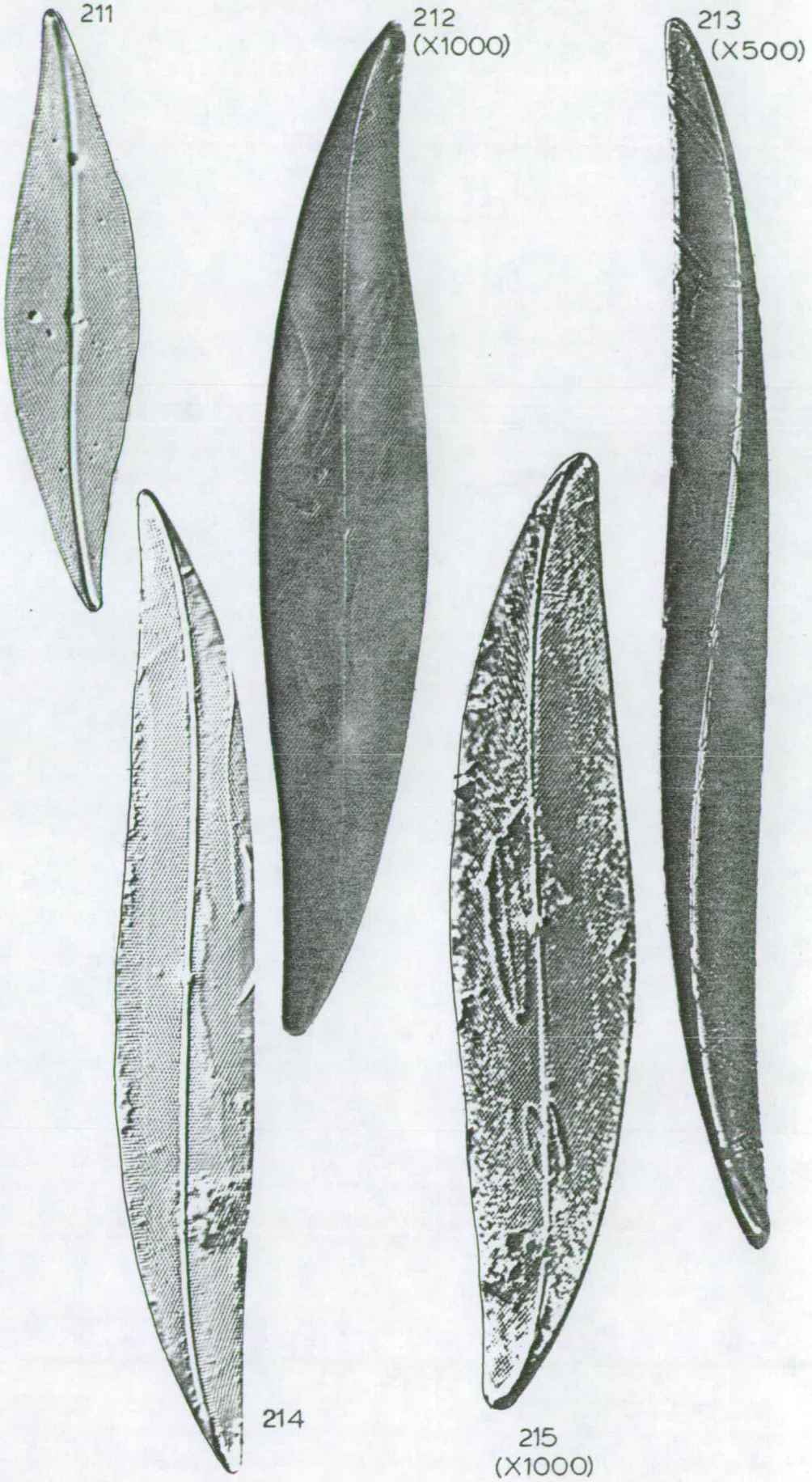
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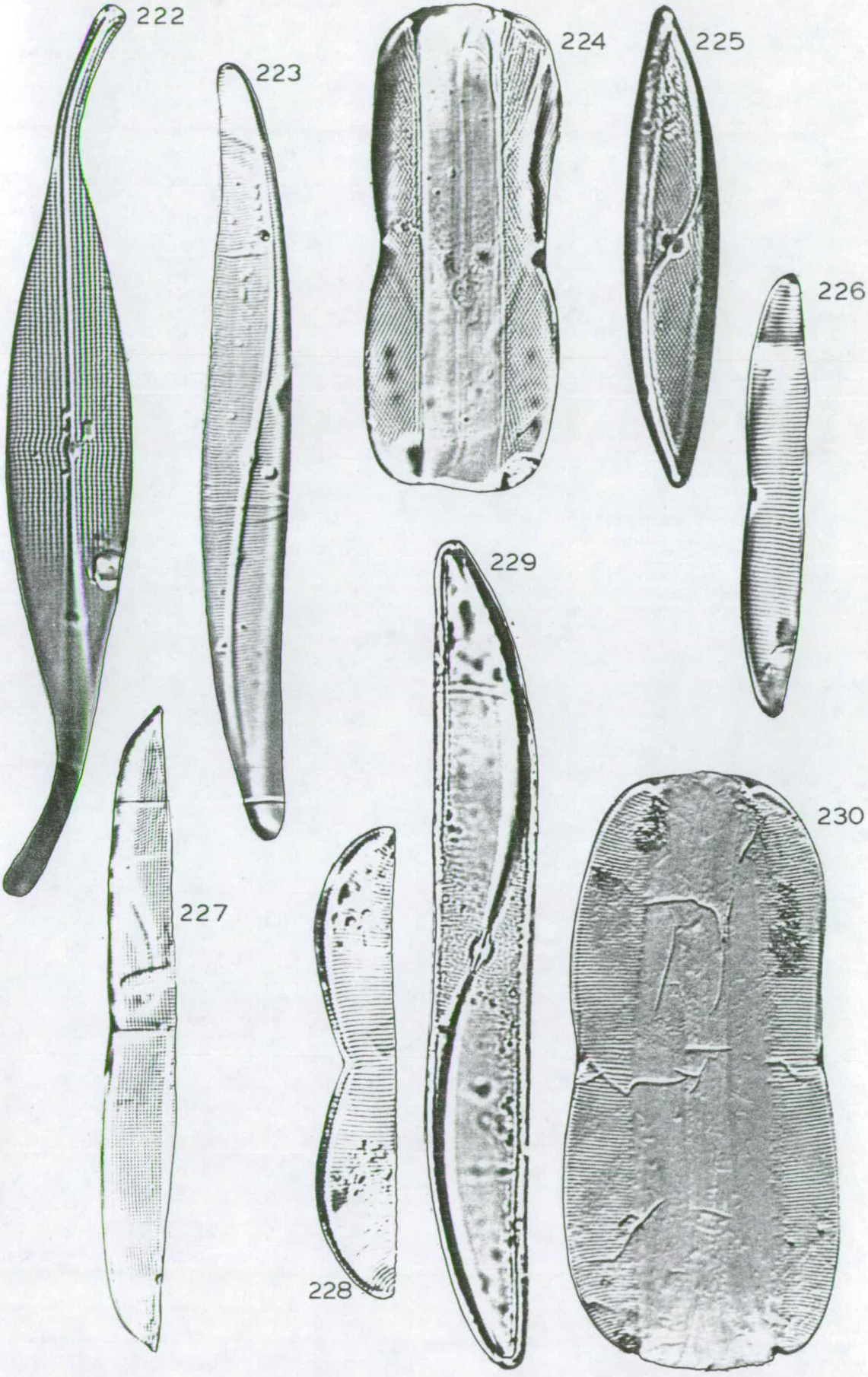
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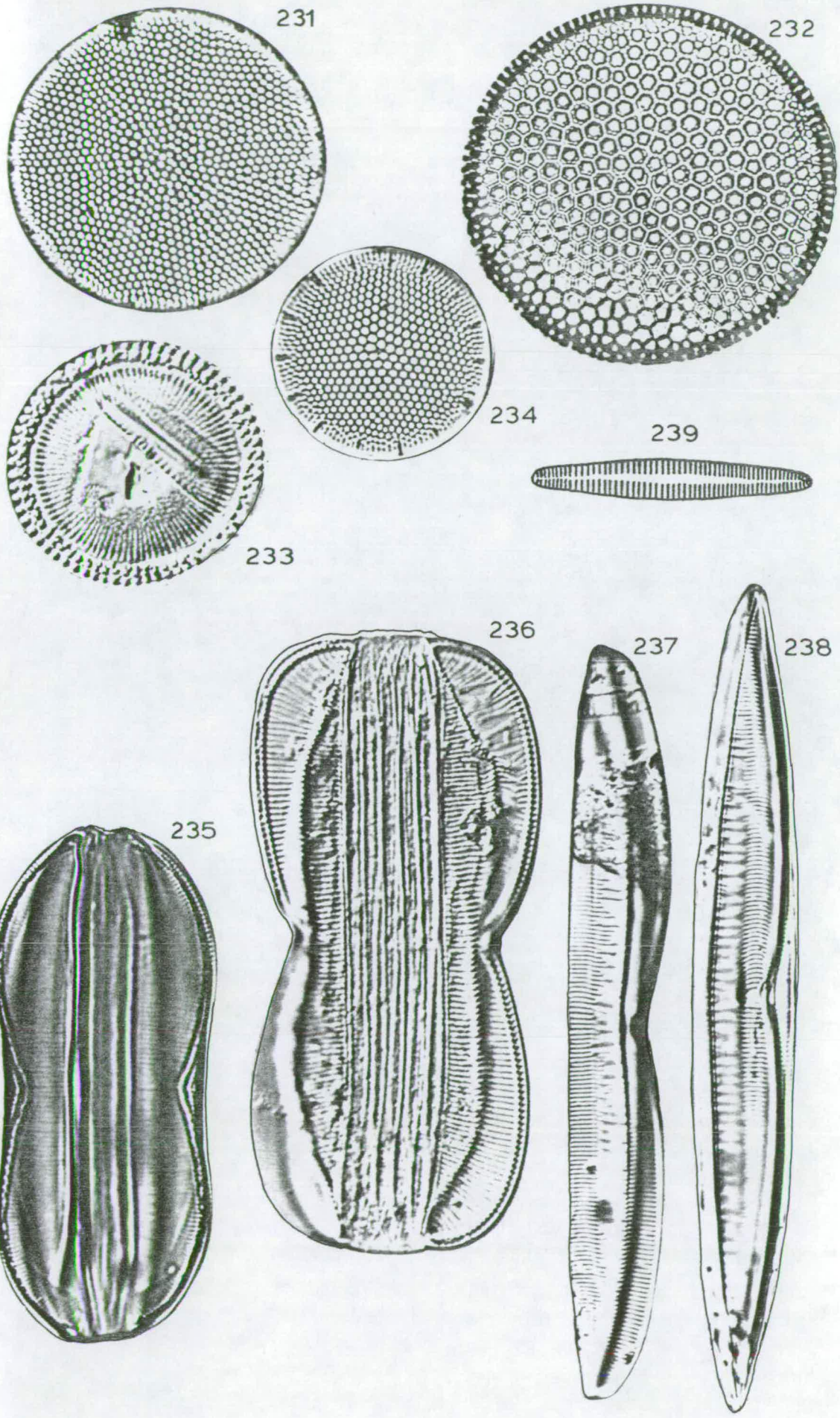
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APPENDIX 2

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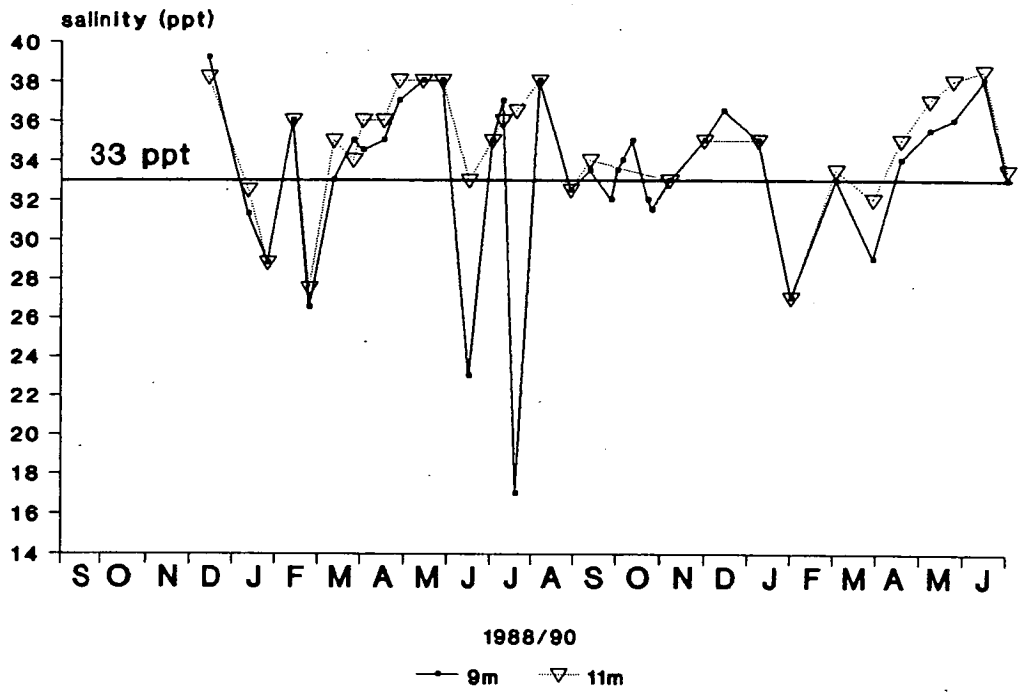
APPENDIX 3



Seasonal variation of salinity measured at the sediment/water interface at 9m and 11m depth from September 1988 to June 1990. Salinity was determined by conductivity measurement using a portable electrode and meter (Philips PW 9504/00). This data appears to be erroneous as salinity measurements collected by the Clyde River Purification Board (pers. comm.) show that levels within Loch Goil do not normally exceed 33 ppt. Consequently I doubt the accuracy of both the magnitude and the seasonal variation in salinity levels. I have not included this data in my analysis.