THE ECOLOGY AND TAXONOMY OF MARINE DINOFLAGELLATES IN SCOTTISH SEA-LOCHS

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BY

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For my Father

ABSTRACT

The ecology and taxonomy of dinoflagellates was investigated in 1982 and 1983 in sea-lochs and coastal waters of north-western Scotland, in order to provide a better understanding of conditions leading to blooms harmful to mariculture. Because such blooms are rare the ecology of all common thecate dinoflagellates was studied, particular attention being paid to the cyst stage and its role in bloom initiation. Creran, a fjordic sea-loch near Oban, was the main site of study; water column sampling was carried out regularly in 1982 and 1983 and the sediments were sampled for cysts in 1983. Distribution of motile dinoflagellates and their cysts on the west coast of Scotland was also investigated on cruises of the R.V. Calanus in the summers of 1982 and 1983. Identification of cells was carried out by light microscopy supplemented by studies using scanning electron microscopy. Links between cysts and motile stages were made by hatching experiments, and these and scanning electron microscopy have led to the discovery of some new cyst-theca relationships.

In Loch Creran the first peak of dinoflagellate numbers occurred in May or June with warming of the water column and was dominated by Scrippsiella spp., accompanied in 1983 by Gonyaulax tamarensis. During July and August there was a mixed population, including Scrippsiella spp., Heterocapsa triquetra, Protoperidinium spp. and Diplopsalis spp. Salinity stratification at the end of August preceded an autumn succession of G. polyedra, Prorocentrum micans and Ceratium species. Observations suggest that G. polyedra cysts sink rapidly and are retained within the loch, seeding blooms in subsequent years. Two other life strategies were hypothesized as the causes for different observed patterns of seasonal distribution. One involves non-cyst-forming species (for example Protoperidinium

bipes and Prorocentrum micans) present in the loch as motile cells in small numbers throughout the year, and occasionally reaching high concentrations. The other involves species (for example Protoperidinium depressum and Ceratium furca) whose motile cells are transported to the loch by tidal exchange or estuarine circulation from the sea outside.

Seventy-two species of motile thecate dinoflagellates were found in the distributional study. Dinoflagellate abundance and variety were greatest in well- or partially-stratified water columns. Of potentially toxic species only Gonyaulax tamarensis was found to be widespread in 1983. Cysts varied in their distribution, with numbers higher in sea-lochs than in Firths and Sounds. Considerable sub-surface populations of cysts were noted in the sediments and viable cysts were encountered at 5 cm depth.

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CHAPTER 1

INTRODUCTION

The Scottish west coast is creased by large and small inroads of the sea (Fig. 1.1). The small indentations, the sea-lochs, are sheltered, unpolluted bodies of sea water well suited for the siting of marine fish farms. The past decade has seen a rapid rise in the number of such farms in these apparently ideal conditions. In 1979 and 1980, however, there were losses of many tonnes of farmed Salmon. These losses were attributed to phytoplankton blooms.

The incident in 1980 (in Loch Fyne) was clearly associated with a bloom of the dinoflagellate Gyrodinium aureolum (Jones, Ayres, Bullock, Roberts, and Tett, 1982). Dinoflagellate blooms or red tides are a well known phenomenon (for examples see LoCicero, 1975; Taylor and Seliger 1978). They are frequently monospecific and certain causative species are known to be toxic. Toxins can either cause direct mortality of marine organisms (e.g. the toxic effect of G. aureolum, English Channel in 1978; Boalch, 1979) or they can be transmitted through the food chain to cause mortality of higher organisms (e.g. Gonyaulax tamarensis, east coast of Great Britain in 1967; Coulson et al., 1968). The former problem causes economic difficulties (e.g. the value of dead stock or the cost of insuring against bloom losses) and the latter is a direct health threat (as in the case of paralytic shellfish poisoning).

During 1980, because of the concern about phytoplankton blooms a general research programme was begun by the Scottish Marine Biological Association (S.M.B.A) entitled "Phytoplankton and Mariculture". As part of that study it was decided to investigate the ecology and taxonomy of dinoflagellates in sea-lochs and it is the results of this work that are contained in

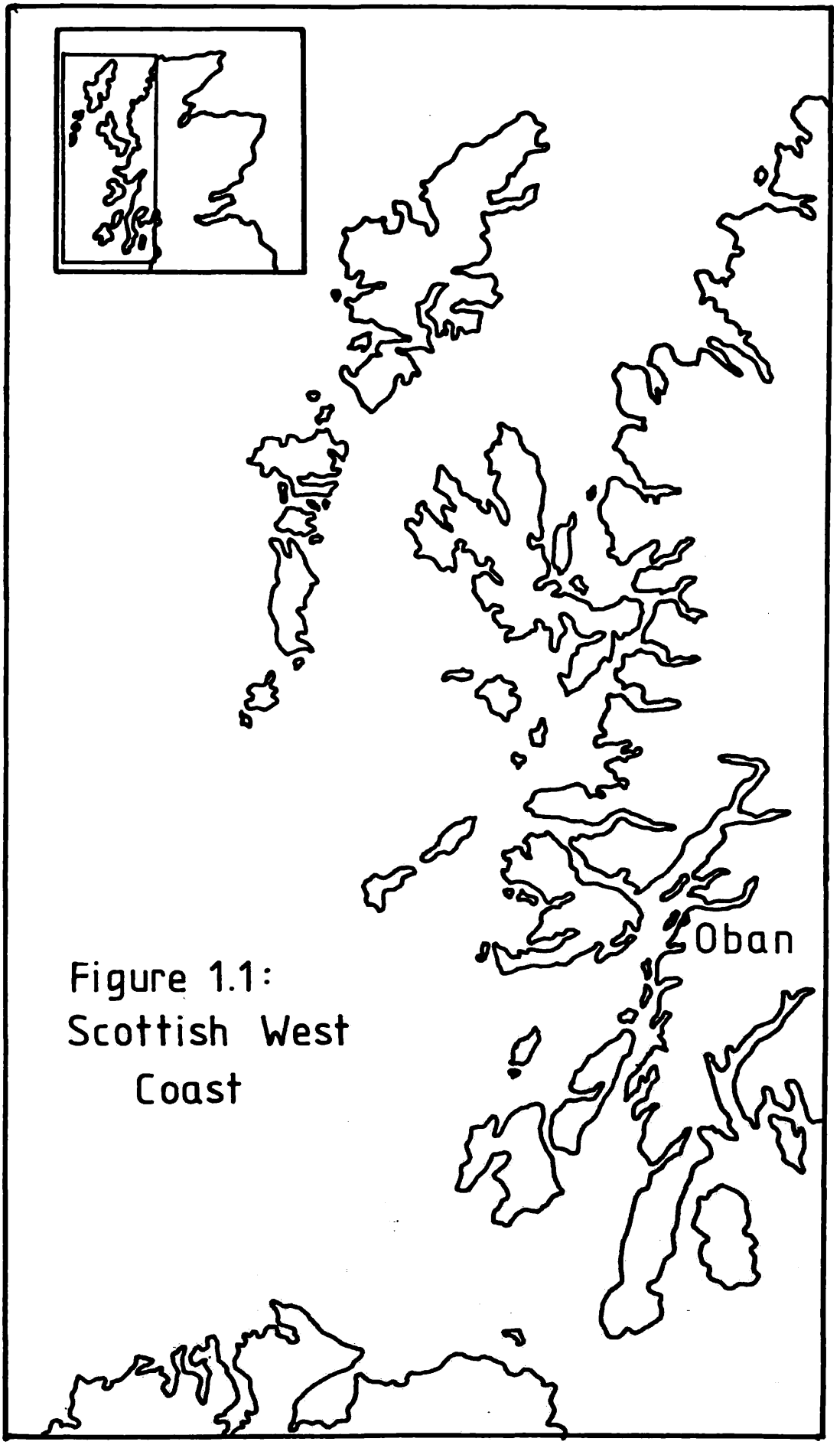


Figure 1.1:
Scottish West
Coast

the present thesis. The aim was to improve the understanding of dinoflagellate ecology within sea-lochs with a view to being able to predict blooms and decide on the suitability of sites for fish farming. A summary of other work is given by Gowen (1984).

Toxic blooms of phytoplankton have, however, been a rare and unpredictable occurrence in Scottish waters, so the project was intended to concentrate on the general ecology of dinoflagellates although allowing the possibility of studying blooms when they happened. During the sampling period (April 1982 - November 1983) only one relevant incident involving a fish farm occurred. The organism that was implicated in this case was not a dinoflagellate but a small flagellate ("X") of unknown affinity (Gowen and Lewis and Bullock, 1982).

The classical picture of the seasonal distribution of dinoflagellates descibes their first increase in numbers after the spring bloom of diatoms, maintenance of high numbers during the summer / early autumn with a gradual drop in numbers after this (for example see Lebour, 1925). This picture is somewhat enlarged by the suggestions of Margalef (1978) that dinoflagellates are associated with low turbulence and low nutrient concentrations unlike diatoms which are associated with turbulent waters and high nutrient concentrations. These hypotheses refer to 'steady-state' conditions. In the sea-lochs short-term physical processes (with time-scales of several days, comparable to the time-scale of dinoflagellate population growth) can be important and therefore conditions are unlikely to reach a steady state so far as species composition is concerned. However, Gowen (1984) suggests that the phytoplankton composition found in Scottish coastal waters is in general agreement with Margalef's hypothesis, the greatest dinoflagellate biomass being found in waters columns of intermediate and strong stratification.

In addition to the structure of the water column, factors likely to affect species composition are other physical processes, especially flushing of sea-lochs (e.g. Gowen et al., 1983); grazing (Stoecker et al., 1981) and the life cycle events of the dinoflagellates. The latter has been largely neglected in ecological studies.

The life-cycle of some dinoflagellates includes a cyst stage, which may spend part of the year in the benthos. Until recently and apart from occasional mention in the older phycological papers (e.g. Nordli, 1951) cysts have been studied almost exclusively by palynologists. Their possible role in the initiation of red tides (Steidinger, 1975) has led to a great deal of study in this context (e.g. Anderson, 1980). However, little work has been done in the context of the cysts' role in the general ecology of marine dinoflagellates. This study includes consideration of this aspect of dinoflagellate ecology.

Dinoflagellate identification requires detailed examination of thecal structure, which often can only be carried out easily with the scanning electron microscope. Cysts and cyst hatching experiments provide further information on the identification and systematic position of the motile stage. A final aim of the project was with the aid of these techniques to improve the taxonomic quality of previous studies of dinoflagellates in sea-lochs near Oban. The work thus has a strong taxonmic as well as an ecological component, and because of the diversity of literature associated with each aspect, it was felt better to deal with the literature piecemeal. Thus each chapter starts with a review of material pertinant to its subject.

CHAPTER 2

MATERIALS AND METHODS

PHYTOPLANKTON COLLECTION

Two main strategies were devised to investigate the ecology of dinoflagellates in the sea lochs. The first involved sampling on a regular basis in one loch and the second involved sampling over a wide area to obtain a nearly synoptic view on single occasions. Loch Creran was chosen as a suitable site for regular sampling, partly because of its ready accessability by road and by boat and partly because there is already extensive background information available about this loch (for example Tett and Wallis, 1978). The distributional sampling was carried out on a number of cruises over the period of study.

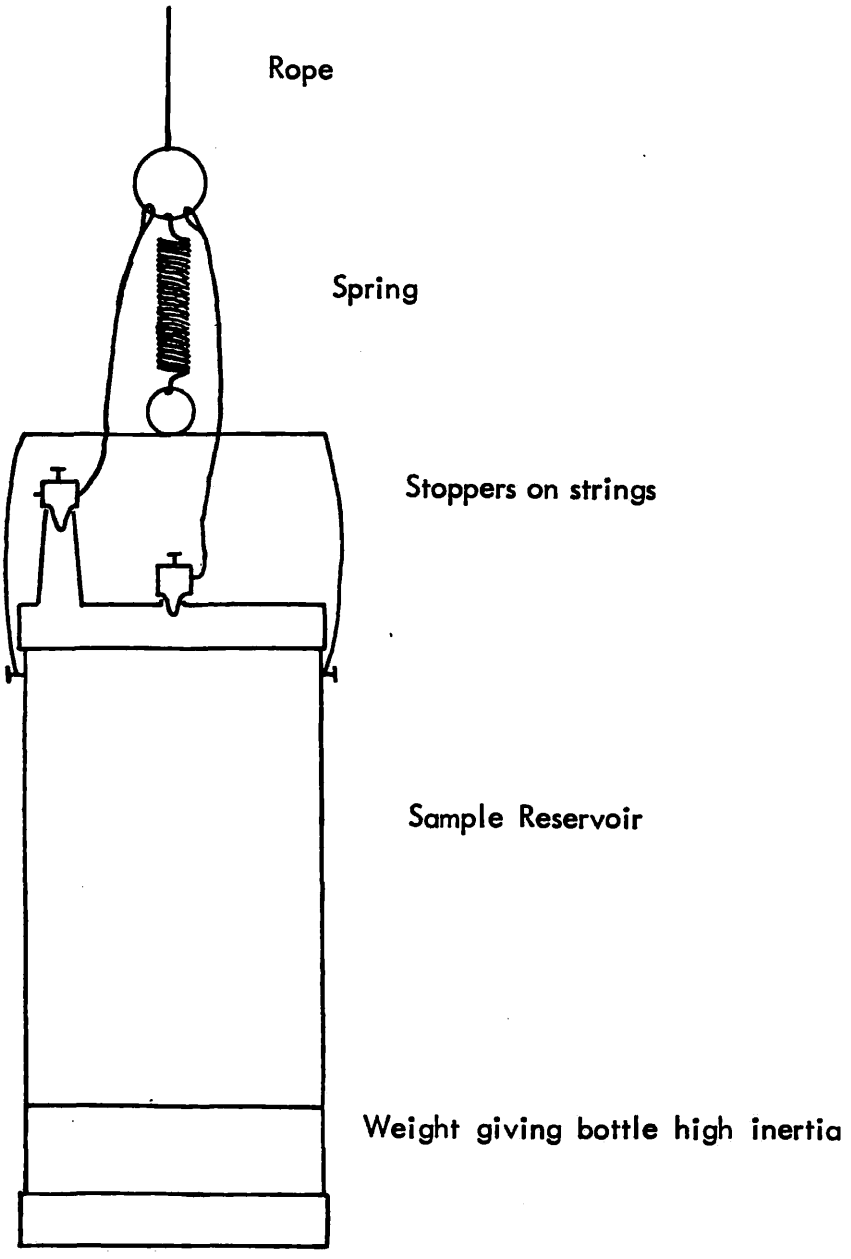
When on board ship water samples for phytoplankton enumeration were collected using an N.I.O. pattern water bottle deployed on a suitable hydrographic wire. When sampling from a pier, a small boat or at shallow depths a Collin's hand sample bottle was used (see Fig. 2.1). Both of these sampling techniques give just over one liter of water from a particular depth. The water sample taken was used to rinse and fill a one liter thermos flask which enabled the samples to be kept in good condition until they could be processed in the laboratory usually within 3-4 hours.

Net samples using a hand operated 56 μm mesh net were occasionally taken in surface waters to provide supplemental material for S.E.M.

For most of the year the concentration of dinoflagellates in the lochs is less than 1 per cm^3. Counting a reasonable number of cells in a suitable time therefore can be a problem so it was decided that samples needed to be concentrated. The method of

Figure 2.1

COLLINS HAND SAMPLER



The sampler is lowered to required depth, where a jerk on the rope removes the stoppers allowing the reservoir to be filled with water. When bubbles cease it is returned to the surface.

concentration used was suggested by and modified from Tett (1969). Using the appropriate Millipore apparatus the water sample was concentrated on to an 8 μm MF-Type Millipore membrane filter by gravity filtration. When the filter was just drained it was placed quickly into a petri dish with 10 cm^3 of the filtrate produced. Using a fine brush the filter was cleaned into the filtrate. If a live count was to be made 1 cm^3 of the sample was withdrawn from the petri dish. The remainder of the sample was transferred to a labelled glass universal bottle containing formalin (neutralised by addition of hexamethylenetetramine) to give a final concentration of 0.4% (Throndsen in Sournia, 1978). The bottle was inverted several times to ensure thorough mixing.

Formalin was chosen as a fixative because it preserves thecate dinoflagellates in an identifiable condition and no further fixation or cleaning is required for Scanning Electron Microscopy (S.E.M.). It has the disadvantage that it does not preserve naked species. An alternative is Lugol's iodine and although it preserves naked species it rarely leaves them identifiable. It also stains cells darkly leaving thecate species difficult to identify. It was decided that to enumerate naked dinoflagellates it would be preferable to count live samples. Other more powerful fixatives were considered (for example glutaraldehyde) but it was felt they were too dangerous for normal use.

Routinely 500 cm^3 of the water sample was filtered as this usually provided a reasonable number of cells per count but did not take a long time to pass through the filter. In exceptional circumstances, however, cell numbers were so great that 500 cm^3 could not be filtered by gravity filtration because of clogging, at these times a smaller sub-sample was filtered.

For counting of phytoplankton cells from the concentrated sample a 1 cm^3 Sedgewick Rafter Chamber was used on a Vickers binocular microscope under bright field illumination at x60 magnification. For most species the whole chamber was counted but where there were large numbers of a particular species a smaller area of the chamber was counted (see later discussion). It was not possible with the Sedgewick Rafter Chamber to rotate the cells to aid identification but this is a problem with most quantitative methods of cell counting. If a cell of interest or an unknown cell was found it was picked out after the count using a micropipette and examined under a higher power on a glass microscope slide or kept for later S.E.M. Finally cell counts were converted to numbers of cells per liter using the following equation:-

$$\frac{\text{number of cells counted}}{a} \times b \times \frac{1000}{c} \qquad \text{.....(1)}$$

Where a = Proportion of the chamber scanned
b = Volume of concentrated sample (cm^3)
c = Amount of water originally filtered (cm^3)

Usually this would be :-

$$\frac{\text{no. of cells counted}}{1} \times 10 \times \frac{1000}{500} = 20 \times \text{no. of cells counted}$$

The accuracy of various parts of the method was investigated to quantify the errors associated with the counts obtained. Description and discussion of these tests is given below in the section on statistical considerations.

In addition to the dinoflagellate motile cells any dinoflagellate cysts that were found in the phytoplankton samples were also counted. Some work on zooplankton grazing indicates

that there may be selectivity in their feeding. There are few large zooplankters in Loch Creran (Gowen, 1981) but the tintinnia are well represented. Stoecker et al. (1981) describes Favella ehrenbergii as selectively preying on dinoflagellates and requiring them as a food source. Therefore it was decided to count tintinnids. These were counted as a group but species of Tintinnopsis, Favella, and Heliocostomella were observed. Occurrences of tintinnid cysts (Reid and John, 1978) were also noted. These groups were counted in both preserved and fresh samples.

Identification of motile dinoflagellate cells

Motile dinoflagellate cells can be divided into groups on the basis of their cell covering or amphiesma. When the amphiesma is composed of cellulose plates the cell is described as thecate and where these plates are reduced or absent the cell is described as athecate or naked. Naked dinoflagellates could only be examined live whereas thecate dinoflagellates could be identified and counted in both fresh and preserved material.

Naked species

The taxonomy of the naked dinoflagellates is confused because observations must be made on living cells which frequently move at great speeds. As soon as cells start to die (or are fixed) considerable changes in shape take place. This often results in incomplete or inaccurate taxonomic descriptions. The problem with wild samples, is therefore purely practical - if one spends too long trying to identify a particular cell the other cells present may die or become distorted before they can be counted. With this difficulty it is clear that for a complete identification and description large numbers of cells need to be studied. Occasionally this is possible in wild samples if there is a bloom of a particular species, but more often one is struck

by the variety of naked forms to be observed in a sample. An alternative to the study of blooms is the isolation and study of cultures. Work by Kimball and Wood (1965) implies that because of the variability of a single species this may be the only way to get complete and accurate taxonomic descriptions. To date little work of this type has been carried out and it was beyond the scope of this project to attempt it.

Live samples were studied whenever possible in Loch Creran. It was originally intended to enumerate and identify the naked species but this ideal proved impossible to realise. So a system was devised whereby naked cells were enumerated under particular shape and size classifications using simplified diagrams on the counting sheet. This gave some indication of the variety of species present and their numbers. Whilst on cruises on board the R.V. Calanus enumeration was impracticable due to the difficulty of using a microscope on a vibrating moving vessel. Examination of live material was restricted to qualitative observations of small samples pipetted directly from sea water on glass slides. For taxonomic information Dodge (1982), Drebes (1974), and Kofoid and Swezy (1921) were used.

Thecate species

The identification of thecate species was hampered by having a single view of the cell. Where identification was impossible the cell was assigned to a family (for example *Gonyaulax* sp.). When plates cannot be distinguished it is difficult to separate apical views of *Protoperidinium* and *Diplopsalis* species and so these were grouped together when this occurred. Further discussion of the taxonomy of thecate species is contained in Chapter 3. For taxonomic purposes Dodge (1982), Drebes (1974), and Lebour (1925) were used.

Statistical considerations

Statistical aspects of phytoplankton sampling were divided into three parts. The first consideration was to decide how many cells should be counted to give reasonably repeatable results. The second consideration was to determine the errors that should be applied to the numbers obtained. Finally because the results were to be used in conjunction with previous data obtained at the S.M.B.A. consideration was given to the comparability of the two different counting techniques. These considerations are each treated separately below.

How many cells should be counted?

Many authors have come up with different replies to this question (for discussion see Venrik in Sournia, 1978) and it seems best that the question should be answered for each particular sampling problem. So in the first year of study a series of duplicate counts were carried out on 15 samples of different characteristics. Three species were chosen - again each with a different pattern of occurrence and a graph plotted of mean against variance of raw counts. The variance increased proportionately to the mean as would be expected for a Poisson distribution so the following theoretical table is applicable.

mean count	variance	s.d.	coefficient of variation
1	1	1	100%
2	2	1.41	71%
5	5	2.24	45%
10	10	3.16	32%
20	20	4.47	22%
50	50	7.07	14%
100	100	10.00	10%
200	200	14.14	7%

With due regard to samples where few cells were present even after concentration it was decided that for a single species a raw count of 20 cells (coefficient of variation 22%) was suitably precise. Where counts were very low at least 20 cells of the dominant species were counted even if this meant examining more than one chamber. However, some samples contained so few cells that this would have taken too much time, in these cases the samples were designated "very thin" and are accordingly marked in the tables of results. Where cell counts were very high an area smaller than the whole chamber was counted. Different counting regimes included half a chamber, several rows of a chamber, a single row of a chamber and (very rarely) a number of squares of a chamber.

With a routine 500 cm^3 sample a count of 20 cells in a whole chamber would convert to 400 cells per liter (see equation (1)). To represent concentrations lower than this + signs have been used.

+ representing 0-199 cells l^{-1} and ++ representing 200-399 cells l^{-1}

Analysis of errors

There are three sets of errors to be considered in this sampling programme.

a) Differences between samples taken.

i.e. "patchiness" of dinoflagellates in the loch

b) Differences between sub-samples taken.

i.e. differences between samples taken from a single thermos flask

c) Differences between counts.

i.e. differences between counts made on the same concentrated sample

These errors were assessed by taking appropriate duplicate samples:-

a) at a particular sampling point.

b) from a particular thermos flask.

c) from a particular preserved sample.

In addition fixed errors were assessed by microscopic examination of washings from apparatus used in the concentration technique.

All the data were log transformed for calculation of means and other statistics. This copes with the difficulties inherent in the fact that phytoplankton grow exponentially (for explanation see Barnes, 1952). Variances between samples were calculated only on those species that had means of greater than or equal to 400 cells per liter (see previous section).

Results

TABLE 2.1 : ERRORS IN COUNTS OF CELLS BELONGING TO A SINGLE SPECIES

(All data log transformed)

	df	var.	%	s.d.	c.v.
A Due to variation between samples (including B + c)	50	0.0844	100	0.30	-
(a small-scale patchiness above)	-	(0.0408)	(46%)	-	-
B Due to variation within flasks (including c)	56	0.0476	-	0.22	-
(b sub-sampling alone)	-	(0.0414)	(47%)	-	-
c Due to counting error	34	0.0062	7%	0.08	20%

TABLE 2.2 : ERRORS IN ESTIMATES OF TOTAL NUMBERS OF CELLS

	df	var.	%	s.d.	c.v.
A Due to variation between samples (including (B + c)	10	0.1012	100	0.32	-
(a small scale patchiness above)	-	(0.0287)	(28%)	-	-
B Due to variation within flasks (including c)	12	0.0725	-	0.27	-
(b sub-sampling alone)	-	(0.0563)	(56%)	-	-
c Due to counting error	14	0.0162	(16%)	0.13	-

TABLE 2.3 : CELLS LOST IN CONCENTRATION TECHNIQUE

Sample	Brush	Filter	Dish	TOTAL	Loss l^{-1}	Cell count	% loss
M329	677	59	536	1272	2544	28900	8.8
M333	252	22	1783	2057	4114	47780	8.6
M339	96	11	342	449	898	11760	7.6

Discussion

The logarithmic standard deviation for a single sample including the effects of small-scale patchiness is 0.30 (Table 2.1, (A)) (as this is log transformed data this is equivalent to $x/\div 2$) this compares well with a logarithmic standard deviation of 0.34 reported by Tett (1969). The sources of this variation are revealed in Table 2.1. The variation (c) caused by counting a single species in a sub-sample from the concentrated sample is very low but this is because of the method of calculation of the statistics (i.e. on species with cell numbers greater than 400 and for which the expected coefficient of variation is 22% or less). Variation between two samples taken from the same flask (b = B - c) is higher than might be expected and clearly care must be taken to mix the contents of flasks thoroughly before subsampling. The final important component of variation is that caused by small scale patchiness within the loch (A - B). The statistics calculated for the cell totals show similar trends although most of the values are higher. This is perhaps because of the accumulation of errors throughout the sample.

Various regimes of sampling and analysis were adopted, and appropriate standard errors to be applied to the resulting concentrations can be calculated from

$$s.e. = \sqrt{\frac{V_a}{n_a} + \frac{V_b}{n_b} + \frac{V_c}{n_c}}$$

where V_a, V_b and V_c are the variances given in Tables 2.1 and 2.2, and n_a, n_b and n_c are the number of replicate samples taken or counts repeated at each level of analysis. Thus for an estimate of total cell concentrations based on two water samples for each of which one sub-sample was preserved, one of the sub-samples being counted once and one twice, $n_a = 2$, $n_b = 2$ and $n_c = 3$ and hence

$$s.e. = \sqrt{\frac{0.0287}{2} + \frac{0.0563}{2} + \frac{0.0162}{3}}$$

$$= 0.22$$

Values of standard error are given in Table 2.4.

TABLE 2.4 : VALUES OF STANDARD ERRORS

Regime	s.e. of counts of cells belonging to a single species	s.e. in estimates of total numbers of cells
Single sample	0.30	0.32
Double sample	0.21	0.23
One sample, 2 replicates from flask	0.25	0.26
1 sample, 1 flask, 2 replicates from tube	0.29	0.31
2 samples, 1 with 2 replicates from flask	0.21	0.22
2 samples, 2 replicates from each flask	0.21	0.22

The results given in Table 2.3 estimate a loss of about 8% of cells through using a concentration step. When considered in context of the variation discussed above this is probably acceptable. Clearly, however, the technique could be improved by introducing a step involving rinsing of the dish into the final concentrated sample.

Comparability between counting techniques

The method currently used at the S.M.B.A. for phytoplankton counting is a sedimentation chamber technique using an inverted microscope (Tett, 1973). It is quite unlike the method employed for this study and to test the comparability of the two techniques a large volume of a thick culture of *Gyrodinium aureolum* was taken. A series of six 5:1 serial dilutions were carried out. At each dilution step two sets of samples were prepared for each sampling technique. In addition a count was made on the Coulter counter to determine initial cell numbers. The results are shown in Tables 2.5 & 2.6 and Figure 2.2.

These demonstrate that the two counting methods give generally similar results. Each has about the same variation within itself. Most of the differences between the two techniques occur at the lowest cell concentrations used in this experiment (approximately 10^4 cells l^{-1}). As expected, because of the concentration step, the results of the technique used in this study are an under-estimate being up to 15% lower than those of the S.M.B.A. technique. Counts made by the S.M.B.A. technique agree with the projected cell numbers from the initial Coulter count and so can be regarded as the more accurate of the two techniques. As 10^4 cells l^{-1} is quite a large figure compared with the numbers of dinoflagellates usually counted (typical dinoflagellate concentrations recorded in this study were between 10^2 - 10^4 cells l^{-1}) any interpretation must take into account the possible underestimation at 10^4. It should however be noted that

Figure 2.2: Comparison of counting techniques

—•— This study

r = 0.99

slope = 0.82

intercept = 2.66

---▼--- S.M.B.A. technique

r = 0.99

slope = 0.69

intercept = 3.35

⊙ Coulter counter value

..... theoretical line (calculated from initial coulter counter value)

r = 1

slope = 0.699

intercept = 3.33

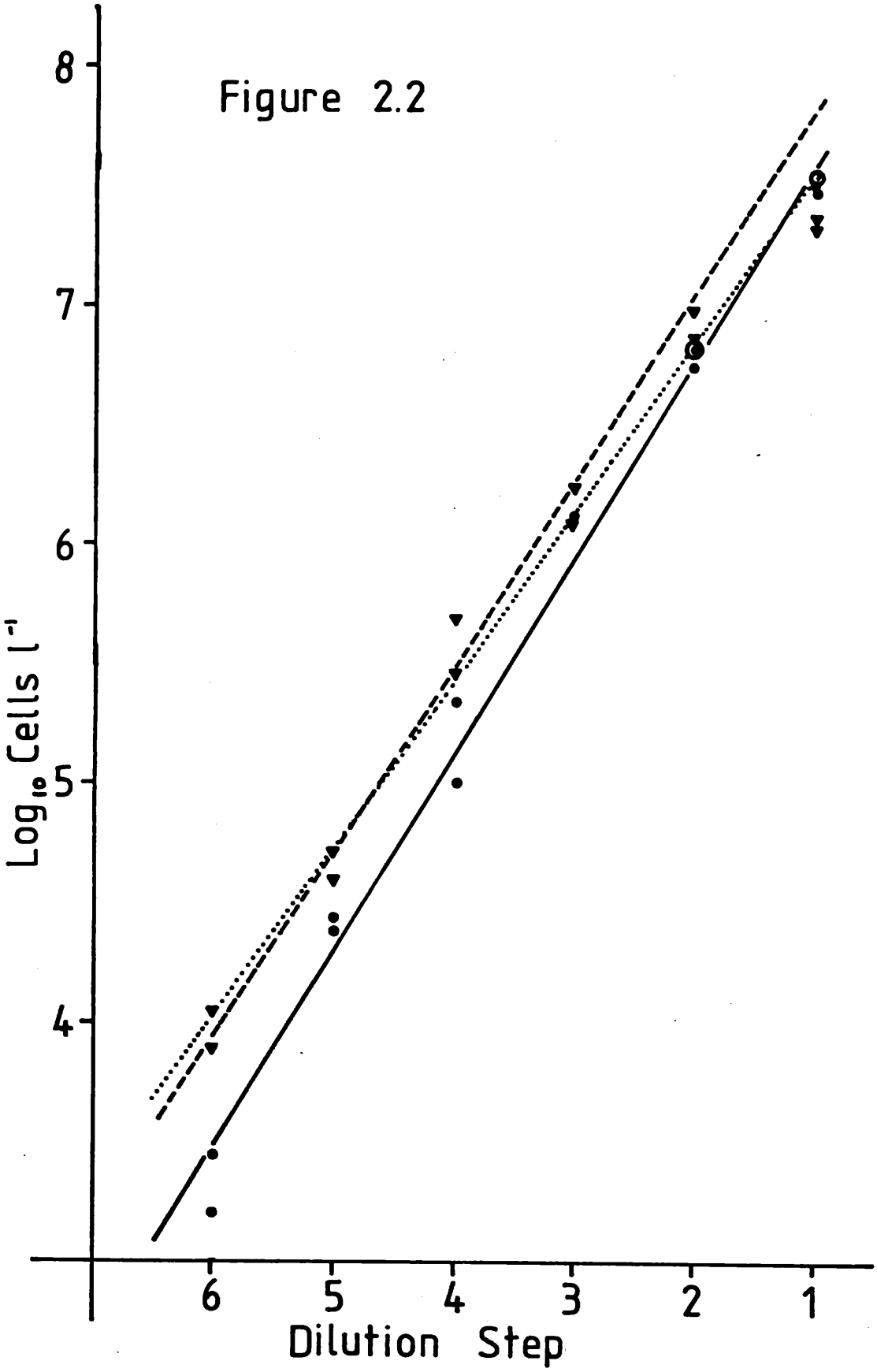


Figure 2.2
8
7
6
5
4
Log10 Cells l-1
6
5
4
3
2
1
Dilution Step

the technique used in this study is more likely to pick up species of cells that are present in low numbers as comparatively more water is examined.

TABLE 2.5 : COMPARABILITY OF COUNTING METHODS

1 denotes method of this study; 2 denotes S.M.B.A. method

Sample	log cell nos l^{-1}:1	log cell nos l^{-1}:2	mean 1	mean 2	variance
1a	7.46	7.32			
1b	7.49	7.34	7.48	7.33	0.01125
2a	6.81	6.96			
2b	6.74	6.85	6.77	6.90	0.00845
3a	6.11	6.08			
3b	6.08	6.23	6.10	6.16	0.0018
4a	5.34	5.46			
4b	5.00	5.69	5.17	5.58	0.08405
5a	4.43	4.6			
5b	4.38	4.71	4.41	4.66	0.03125
6a	3.20	3.89			
6b	3.45	4.05	3.33	3.97	0.2048
		variance	0.0155	0.01025	
		s.d.	0.1245	0.1025	

Total variance = 0.0569 s.d. = 0.239

TABLE 2.6 : COULTER COUNTER VALUES

	log cell nos l^{-1}		log cell nos l^{-1}
1a	= 7.51	2a	= 6.85
1b	= 7.52	2b	= 6.78
Average	= 7.52	Average	= 6.82

CYST COLLECTION

There were two purposes to the collection of sediment samples. The first was to assess the distribution of dinoflagellate cysts in sea lochs and the second was to provide material for incubation experiments. Two strategies were devised to assess the distribution of dinoflagellate cysts in the lochs. The first was to sample over as wide an area as possible. The second was to sample over a seasonal cycle in one place. The aim in both cases was to be able to relate what was found in the sediments to what happens in the water column and so sediment sampling was always carried out in conjunction with phytoplankton sampling. The distributional sampling was carried out during various cruises in 1982 and 1983 and the seasonal sampling was carried out in Loch Creran during the same years.

Ideally material for incubation studies should be collected at the beginning of April so that the cysts present in the sediment have undergone any overwintering or dormancy period required before hatching and also before new cysts had been produced for that year. Samples for this purpose were therefore collected in April of the second year of study from a variety of lochs close to the marine station. These had been shown in the first year to contain different cyst assemblages giving a wide variety of cysts to work on.

Sediments were sampled with a Craib corer (Craib, 1965) which gives relatively undisturbed cores of sediment and overlying water. The overlying water and the top 5 cm of sediment were taken and stored at 4°C for later study.

For counting or for incubation experiments sediment samples were treated in the same manner. A small amount of sediment (0.5 -0.75 g) was sonicated gently in sea water for one minute then passed through 63 µm mesh and retained on 38 µm mesh sieves using a standard amount of filtered sea water. The material collected on the 38 µm sieve was washed off into a small amount of culture medium or sea water and then poured into a gridded petri dish. It was examined under a Wild binocular microscope, using x80 magnification at which it was possible to count the number of cysts present. It was also possible to remove cysts for incubation experiments or for S.E.M. using a micropipette. Sieves were thoroughly cleaned after use and control samples run showed no evidence of contamination between samples.

During sampling and counting some checks were made to estimate the loss of cysts during processing. Water overlying the cores was collected, sieved and examined in the usual manner. The material that was collected on the 64 µm sieve and that which passed through the 38 µm sieve was also collected and examined. In the case of the overlying water and the material retained on the 64 µm sieve a small number of cysts were found but these were considered to be insignificant compared to the numbers of cysts counted in the main sample. The material passing through the 38 µm sieve, however, did contain a significant number of small cysts (particularly of the Scrippsiella group). This fraction of the sample contained a large amount of debris and no successful technique was developed to include these in the cyst counts.

Cyst counts were made of a known area of the petri dish. Unless there were very few cysts present in the sediment about 200 cysts in total were counted. It was thus possible to estimate cysts per unit wet weight of sediment. A sub-sample of the sediment was weighed, dried and reweighed to give a measure of water content and this was used to correct sample wet weight to dry weight. A simple calculation (equation 2) of numbers of cysts per dry gram of sediment then allows comparison of different sediment samples.

$$\text{Number of cysts counted} \times \frac{\text{Area of dish}}{\text{Area scanned} \times \text{sub-sample weight} \times D} \quad \ldots.(2)$$

where D = the ratio of $\frac{\text{Dry weight}}{\text{Wet weight}}$ of the sediment counted

Identification of cysts

As some dinoflagellate cysts are relatively delicate or calcareous no chemical procedures such as those used by palynologists to dissolve background material (for example Sarjeant, 1974) were used in preparing samples. This enabled the observation of natural material. It also meant, however, that there was a lot of background material present in the samples analysed. Indeed it was quite amazing the variety of things besides sand grains that were found in this size fraction. Inevitably therefore some cysts were missed and some misidentification was likely. Recognition and identification of cysts proved difficult early on in the period of study and so as far as possible only the most recent and therefore inter-comparable data has been presented. Because of the presence of background material and because there was also a tendency to count only those organisms that were without doubt dinoflagellate cysts some underestimation of numbers was likely. Finally some

groups of cysts were counted together. These were those of the "Spiniferites" group and the round, brown cysts. There were two reasons for this. At the magnification used these groups were difficult to separate and also it was felt that before excystment the round, brown cysts were impossible to separate (for further information see Chapter 3).

For taxonomic information Dale (1977a,b; 1978), Harland (1981; 1982), Reid (1974; 1977), Wall and Dale (1968a,b) and Wall et al. (1970) were used.

Statistical considerations

Due to the sieving steps in this procedure concentrations of cysts obtained are not absolute. Efforts were, however, made to standardise the procedure and although there was not time to rigorously test the statistical aspects of this type of sampling it is possible to speculate on the largest sources of errors. These are most likely to have been "between sample variation" and variation betweeen sub-samples taken from the original core sample. Replicate counts have been carried out on six cores. Variance and standard deviation were calculated on the log transformed data (Table 2.7). In the case of species counts and when all data were included the standard deviation was large (0.7068, equivalent to x/+ 5). When, however, the total variance was recalculated for data where on average at least 10 cysts were counted, the standard deviation was 0.0537 (x/+ 1.7). It was therefore decided to adopt a system similar to that for phytoplankton counts representing cyst numbers where less than 10 cysts were counted by +.

TABLE 2.7 : STATISTICS OF CYST COUNTS

	Variance	s.d.
Between all species counts	0.4995	0.71
Between species counts of more than 10	0.0537	0.23
Between species counts of more than 20	0.0439	0.21
Between cell totals	0.0142	0.12

COLLECTION OF OCEANOGRAPHIC DATA

Phytoplankton, as their name implies, are completely dependent on the water in which they are contained for their dispersion, nutrient supply and light requirements. No study of planktonic organisms therefore is complete without knowledge of the water column in which they exist. Temperature and salinity are the principle determinants of water column structure in the sea so these and chlorophyll were measured on most sampling occasions.

Temperature and salinity

Vertical distributions of temperature and salinity were measured using a Braystoke STM 500 submersible temperature salinity probe. This was calibrated against reversing thermometers and precision salinometer measurements on discrete samples. On board ship analogue temperature and salinity voltages were logged on to a 9825A Hewlett Packard desk top computer via a HP 6940 B multiprogrammer and the resultant graphs of temperature, salinity and density were used to assess where water samples should be taken. In more primitive conditions readings were noted directly from the probe display and sample depths were determined on the basis of these.

Chlorophyll

Chlorophyll was measured by the method of Tett and Wallis (1978). This is a standard fluorescence method with an acidification step. A known volume of sea water was filtered through a GF/C filter. If facilities were not available for immediate extraction the filter was frozen and stored in aluminium foil. Pigments were extracted by placing the filter in acetone for at least 20 hours. After extraction the sample was shaken, centrifuged for 5 minutes, reshaken and recentrifuged for a further 5 minutes to ensure complete solution of the pigments. The fluorescence of the supernatent was measured on a Turner designs model 10 fluorometer, with appropriate filters, before and after acidification. Blanks were also measured to give correction factors.

The chlorophyll concentration was calculated as follows :-

If F_O and F_A are original readings, and F_{OB} and F_{AB} are the equivalent blanks

Then $f_O = (F_O - F_{OB})/R$

and $f_A = (F_A - F_{AB})/R$

Chlorophyll $= k\ (f_O - f_A)\ E/V$ mg m^{-3}
Phaeopigment $= k\ (Hf_O - f_A)\ E/V$ mg m^{-3}

Where k = calibration factor (0.083)
E = extract volume (ml)
V = sample volume (l)
H = calibration factor (2.02)
R = range factor

The calibration factor $k = 1/(F_c(1-1/H))$

and $H = F_c/F_p$

Where F_c and F_p are the specific fluorescence coefficients of chlorophyll a and phaeophytin.

The range factor is the relationship of the fluorometer sensitivity ranges calculated using pure chlorophyll, and varies from 1 - 31.6.

SCANNING ELECTRON MICROSCOPY

Individual cysts or thecate stages were selected for S.E.M. using a micropipette. Fresh material was fixed in neutralised formalin in a 5 cm watch glass enclosed in a petri dish. If the S.E.M. was not to be carried out immediately the organisms were transferred to small capsules for later treatment. Isolated organisms were washed in distilled water before being mounted on Nuclepore filters in a suitable holder. These were dehydrated in a critical point drier using carbon dioxide. Filters were glued to suitable stubs and after sputter coating with gold-palladium, organisms were examined in a JEOL 25S S.E.M. With care this method achieved about a 70% sucess rate of viewing organisms that had been picked out. Obviously then, to examine a species from all angles it is desirable to pick out a number of cells (between 5 - 10 individuals).

CHAPTER 3

TAXONOMIC CONSIDERATIONS

INTRODUCTION

This chapter describes the taxonomic difficulties encountered with the thecate motile dinoflagellates and their cysts. Problems with naked dinoflagellates are described in Chapter 2. To begin it is necessary to look at the stucture of motile cells and cysts and to explain some items of terminology.

Motile cells

The armoured dinoflagellates are so called because of their covering of cellulose plates. These plates and their characteristics are used as the basis of taxonomic divisions within the group. Kofoid (1909) developed a system of nomenclature for these plates that is described in Figure 3.1, a-d. As will be seen from the taxonomic descriptions quite small variations in the numbers of plates or the way in which they touch other plates can divide species or even genera. The ecologist studying numerous samples by light microscopy cannot determine the complete plate structure of every armoured dinoflagellate encountered. With some experience of looking at dinoflagellates, however, it is clear that certain species can be distinguished using gross morphological charateristics. Nevertheless there remain a number of groups of species that are difficult to distinguish. The key is perhaps to have looked at a range of samples allowing comparisons of a wide variety of species to be made. It is often not until a particular species has been seen on more than one occasion or in large numbers that it is recognised for what it is.

Figure 3.1: Description of terms used in thecate taxonomy

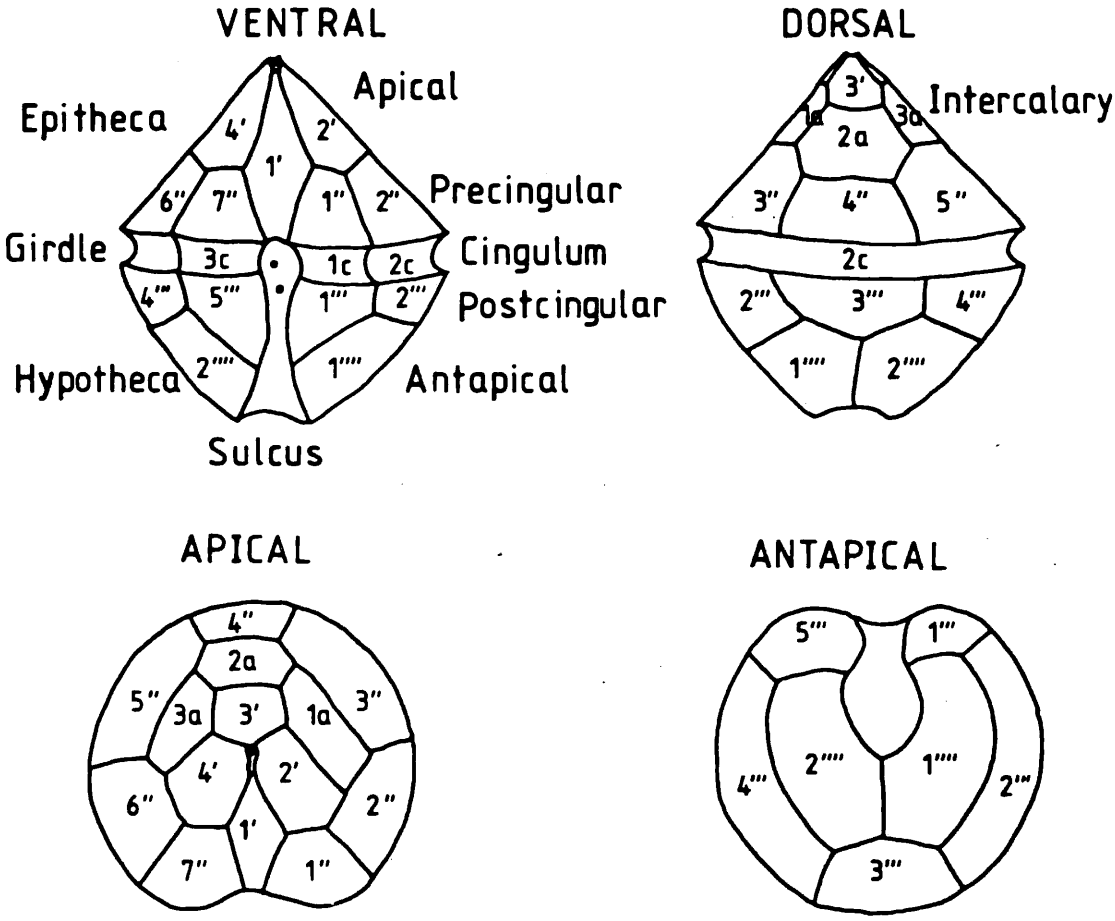
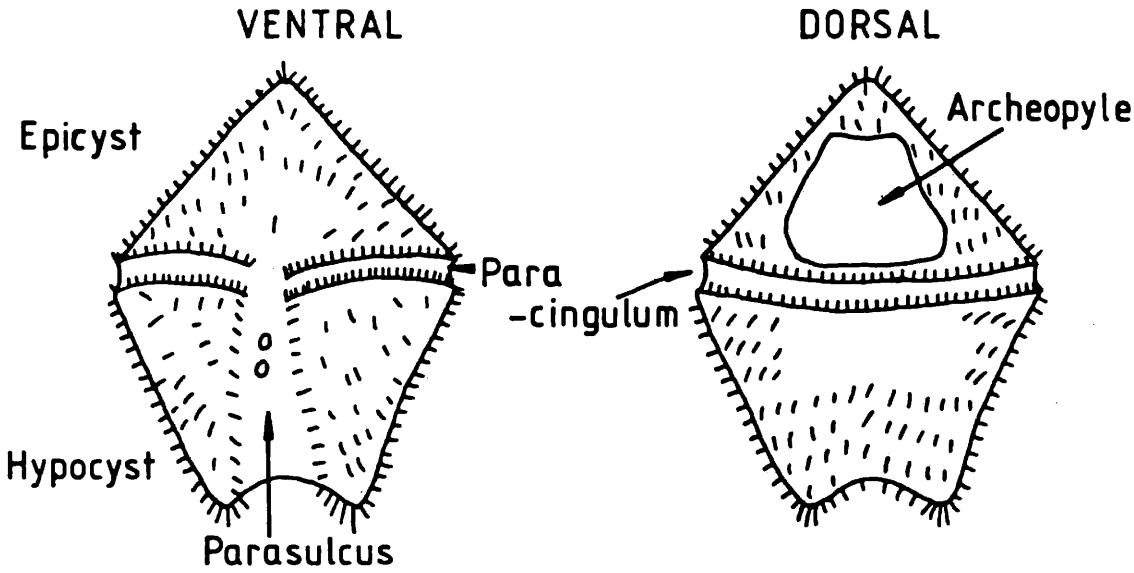


Figure 3.2: Description of terms used in cyst taxonomy



In this study motile cells were routinely identified on their gross morphological features. Where there was uncertainty and where the cells were present in sufficient numbers to justify it or where cells were potentially toxic Scanning Electron Microscopy (S.E.M.) was carried out to aid identification. In some cases by relating light microscopy to features elucidated by the S.E.M. this enabled the identification of the species on later occasions; in others it merely served to classify species in a group that cannot routinely be separated by light microscopy.

Cysts

The study of dinoflagellate cysts has largely been carried out by palynologists, whereas motile cells have largely been studied by phycologists, resulting in a dual system of nomenclature for cysts and motile cells. (The historical aspects of this are described in Chapter 8). As far as possible in this study both names are included when reference to cysts is made. This is not always possible as for example when the motile stage of a cyst has not been determined or where the cyst does not possess a palaeontological description. The term cyst as used in this study implies a dinoflagellate resting spore routinely found in the sediments. These have a very resistant wall composed of a substance akin to sporopollenin. Other non-motile stages that have been termed temporary cysts, pellicle cysts, or ecdysal cysts are not generally found in the sediments and are not included in this category.

Many cysts have some degree of reflected tabulation. That is, certain features of the motile stages are also recognisable on their cysts. This cyst tabulation is pre-fixed by the word 'para-' to distinguish it from that of the motile cell. For

example a paracingulum is frequently discernable on cyst walls (Fig. 3.2, a-b). Paratabulation can be discerned by presence or absence of spines, ridges or other small ornamentation along the plate sutures. It is sufficient in some cases to indicate the motile species to which the cyst is related. In other cases it is totally absent. An important diagnostic feature of cysts, and one used extensively in palaeontological taxonomy, is the archeopyle (the aperture that enables excystment of the motile cell). It is formed by the loss of one or more opercular piece(s). These opercular pieces are frequently related to paraplates and they are named on this basis. The genetic basis for these morphological features and their relation to motile cells is further discussed in Dale (1983).

The concern of many palynologists has been biostratigraphy where as much 'splitting' of species as possible is often desirable. To this end a vast compendium of terms has been built up to define cyst features. Glossaries of these terms (e.g. Williams and Sarjeant, 1973) are therefore very useful. The taxonomy of cysts is complex and often based on specimens that have undergone rigorous chemical treatments. Some difficulties were experienced initially in the present study when fresh material from the sediments was examined. These were, however, mostly resolved using S.E.M. and incubation studies (Chapter 8). Descriptions of cysts given here are intended to cover those species not mentioned in Chapter 8 and also as far as possible to define what species were included in the collective groups used for counting purposes.

TAXONOMIC DESCRIPTIONS

Phylum: Pyrrophyta Pascher
Class: Dinophyceae Fritsch
Order: Prorocentrales Lemmermann
Family: Prorocentraceae Stein
Genus: Prorocentrum Ehrenberg

Prorocentrum micans Ehrenberg, Prorocentrum gracile Schütt, Prorocentrum scutellum Schröder

Fig. 3.3, a-c; Pl. 3.1, figs.1-4

Size (after Dodge, 1982):- P. micans 35-70 µm long
20-50 µm wide
P. scutellum 35-57 µm long
30-45 µm wide
P. gracile 40-60 µm long

All these species are typical members of the Prorocentrales, the major part of the body consisting of two plates joined at the edges. The flagellar pore area is anterior and is made up of a number of small plates bearing an anterior spine. The surface of the theca is covered with small depressions containing trichocyst pores. Dodge (1982) notes the possibility that P. gracile and P. scutellum are intermediate forms related to P. micans. The main criterion for separation of these species is size and shape. Certainly P. micans appeared in this study to be the most common member of this group. It was only when a mixed population of P. micans and P. scutellum was encountered in Loch Sween in 1982 that P. scutellum was recognised as being clearly a distinct species. Light microscope observations showed the shapes of the two species to be quite different (Fig. 3.3, a-b) and those identified as P. scutellum also had a shorter spine at their anterior end. Examination by S.E.M. showed that the thecal

PLATE 3.1

All figures S.E.M.s unless otherwise stated

Fig. 1 : Detail of surface patterning of *Prorocentrum micans*; x 15,632; Loch Sween.

Fig. 2 : Detail of surface patterning of *Prorocentrum scutellum*; x 10,439; Loch Sween.

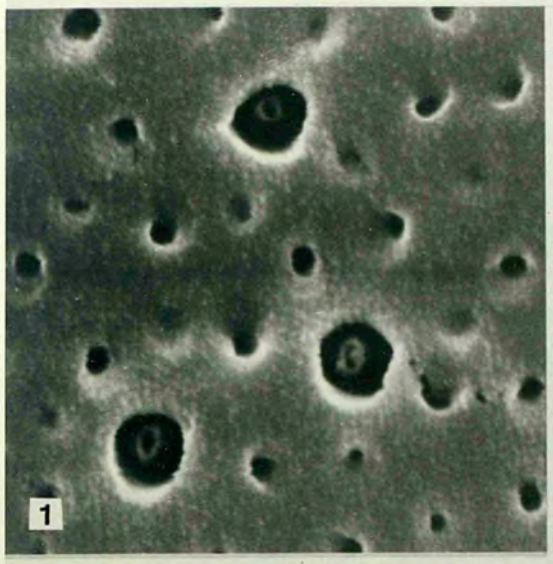
Fig. 3 : *P. micans*, 46 µm long (excluding spine); Loch Sween.

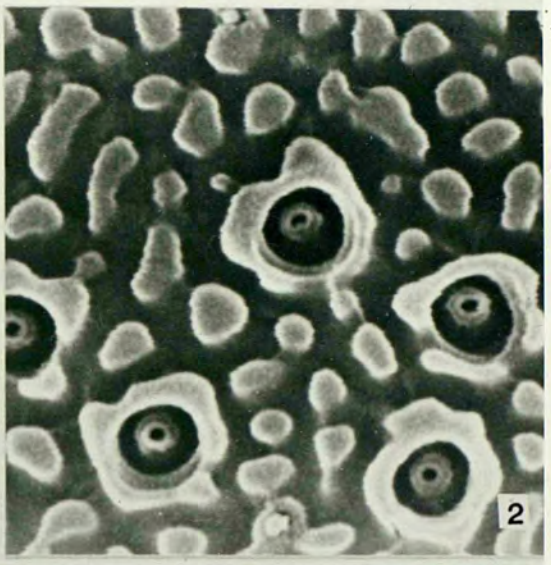
Fig. 4 : *P. scutellum*, 46 µm long (excluding spine); Loch Sween.

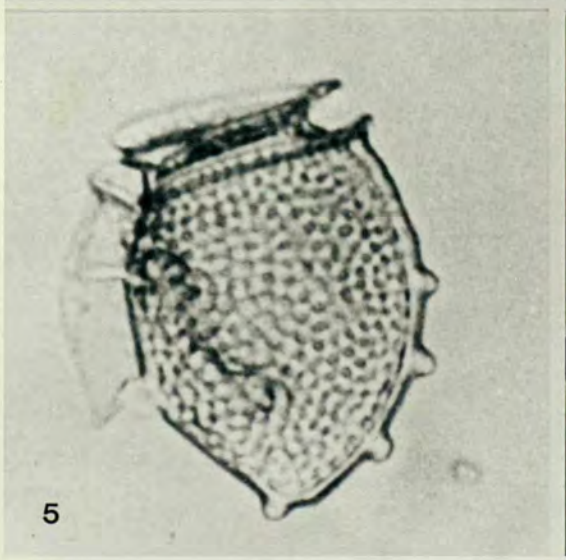
Fig. 5 : Light micrograph of *Dinophysis norvegica*, 60 µm long; North Minch.

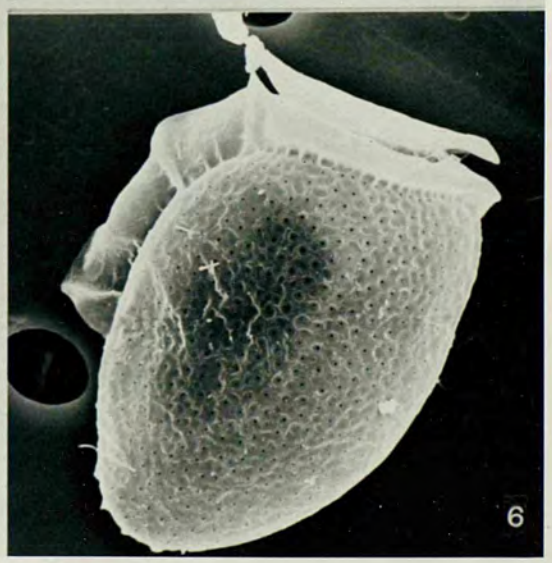
Fig. 6 : *Dinophysis acuminata*, 37 µm long; Loch Creran.

Plate 3.1









patterning of these species was also distinct. Although the trichocyst pores on both species had identical structures (Pl. 3.1, figs.1-2) the thecal ornamentation differed. The theca of P. micans was smooth whereas that of P. scutellum was covered with small protrusions and each trichocyst pore was partly or wholly surrounded by a ridge (Pl. 3.1, fig.3-4). This is in accordance with Lebour (1925) and Schiller (1937) who note the presence of small spines over its surface. S.E.M.'s of P. gracile (Dodge and Saunders unpubl.) showed it to have similar thecal ornamentation to P. micans but it was much narrower in shape with a larger anterior spine (Fig. 3.3, c).

Order: Dinophysiales Lindemann
Family: Dinophysiaceae Stein
Genus: Dinophysis Ehrenberg

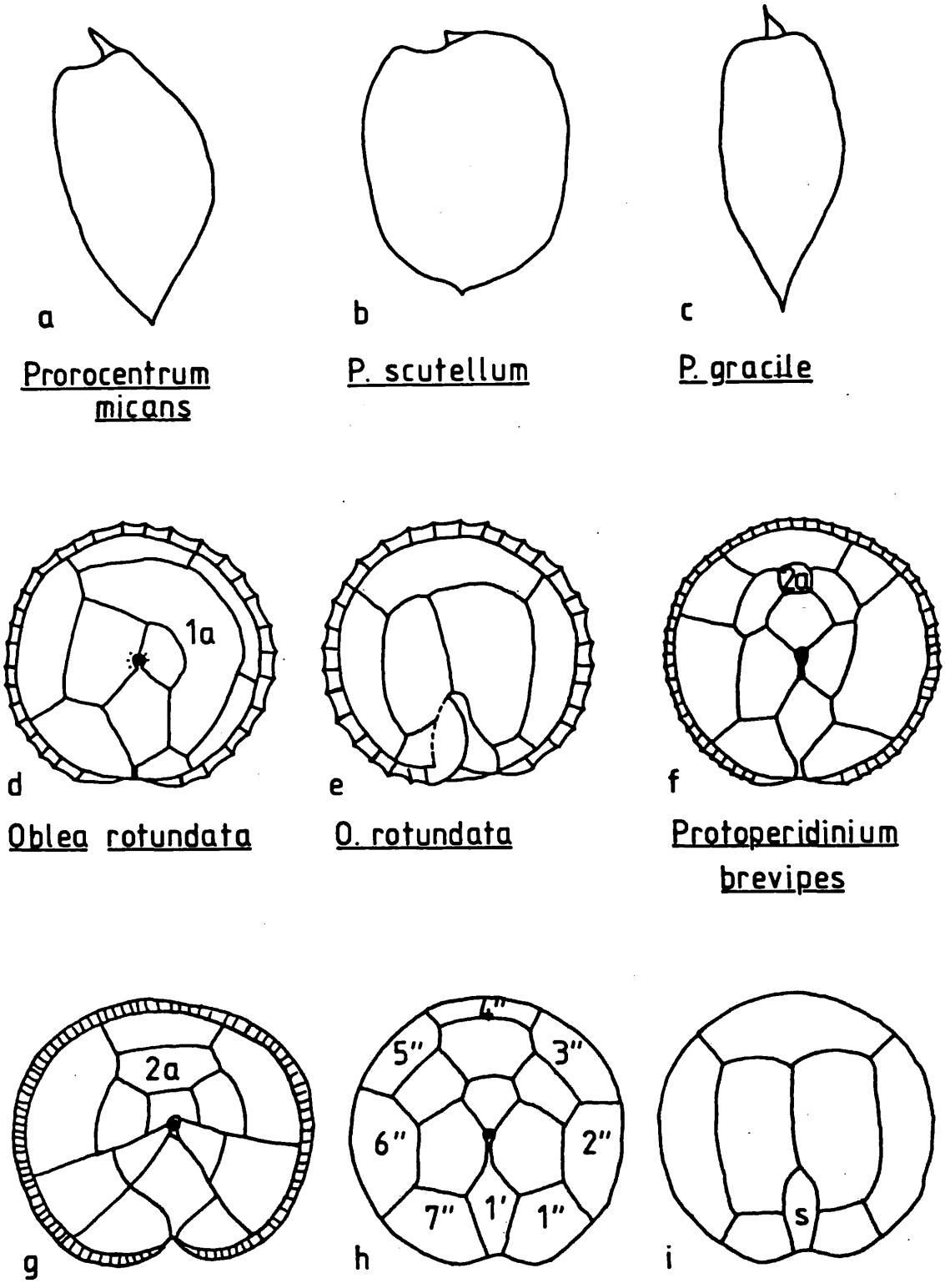
Dinophysis acuminata (Claparède & Lachman)

Pl. 3.1, figs.5-6

Size (after Dodge, 1982): 38-58 μm long

This species has been associated with diarrhetic mussel poisoning (Kat 1982, 1983a,b) and so it was felt important that definite identification was made. It is a typical member of the Dinophysiales, having a large hypotheca (composing the majority of the cell) an indented cingulum, and a small flattened epitheca. The cingulum is surrounded by lists and there is also a list on the hypotheca supported by ribs. The original description by Claparède and Lachman (1859) has been much modified. The species is very variable (Solum, 1962) and has a close resemblance to Dinophysis lachmanii Paulsen and a broad resemblance to Dinophysis norvegica Claparède and Lachman. Dodge (1982) considers D. lachmanii to be synonymous with D. acuminata. D. acuminata has a more weakly rounded body shape than

Figure 3.3



Prorocentrum micans — P. scutellum — P. gracile

Oblea rotundata — O. rotundata — Protoperidinium brevipes

Protoperidinium diabolum — Scrippsiella trochoidea (after Wall and Dale 1968b)

D. norvegica which has a distinctly pointed hypotheca. Scanning micrographs of cells in this study showed fairly smooth thecal plates in D. acuminata (Pl. 3.1, fig.6); D. norvegica usually has a heavily ornamented theca (see Dodge, 1982; Pl.II, a). Both species can possess knobs along the cell edge but these were relatively uncommon in D. norvegica. In the present study they tended to be at the bottom of the cell in D. acuminata but were sometimes right round the cell edge in D. norvegica (Pl. 3.1, figs.5-6). It was felt that the S.E.M.'s confirmed the identification of this species as D. acuminata. Those found in this study closely resembled that figured by Kat (1983a; Fig. 2.).

Order: Peridiniales Haeckel
Family: Peridiniaceae Ehrenberg
Genera: Diplopsalis Bergh;
Dissodium Abé;
Zygabikodinium Loeblich and Loeblich

The taxonomy of the Diplopsalis group was extremely confused until it was in some measure sorted out by Dodge and Hermes (1981). The group consists of species with small globular or lenticulate cells with an equatorial girdle bordered by lists. All species have a distinctive list to the left of the sulcus. They all lack chloroplasts, the protoplasm being pink in colour. When seen from above using light microscopy these cells are difficult to distinguish from Protoperidinium and so were grouped with them in counts when this happened. Without detailed plate analysis most cells of similar size within the group are difficult to distinguish. Hence in counts cells of this group were frequently assigned to Diplopsalis spp. In some counts Diplopsalis lenticula Bergh was distinguished but this almost certainly contained some cells of Zygabikodinium lenticulatum (Mangin) Loeblich and Loeblich. D. lenticula and Z. lenticulatum

differ only in epithecal plate detail . Cysts of both these species have been found and hatched from sea-loch sediments (Chapter 8). Scanning microscopy confirmed the presence of both species. Cells of Dissodium asymmetricum (Mangin) Loeblich were also distinguished by their relatively larger size compared to the previous two. On the whole the aforementioned species were never present in very large numbers. Futher detailed research was therefore not carried out for this group except on one very small species which was found to be occasionally common in Loch Creran and whose description now follows.

Genus: Oblea Balech

Oblea rotundata (Lebour) Balech ex Sournia

Fig. 3.3, d-e; Pl. 3.2, figs.1-3

Size:- 17-25 µm wide
17-25 µm long

The cell was globular with an equatorial girdle (Pl. 3.2, fig.1). The girdle lists were supported by prominent spines and there was a sulcal list. The complete epithecal and hypothecal tabulation was determined by S.E.M. (Fig. 3.3, d-e) and was sufficient to assign it to Oblea rotundata. The distinguishing features of its plate patterning were the 'meta' first apical plate, the large first intercalary plate and the two antapical plates (Pl. 3.2, fig.3). Although it was smaller in size and had a different plate pattern there was a striking similarity between this species and other members of the Diplopsalis group (see Chapter 8).

PLATE 3.2.

All figures are S.E.M.s

Fig. 1 : Ventral view of Oblea rotundata, 26 µm across; Loch Creran.

Fig. 2 : Apical view of O. rotundata, approximately 20 µm across; Loch Creran.

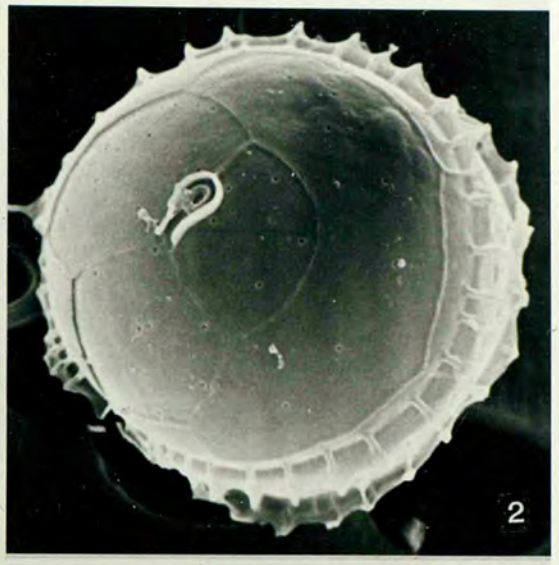
Fig. 3 : Antapical view of O. rotundata, approximately 21 µm across; Loch Creran.

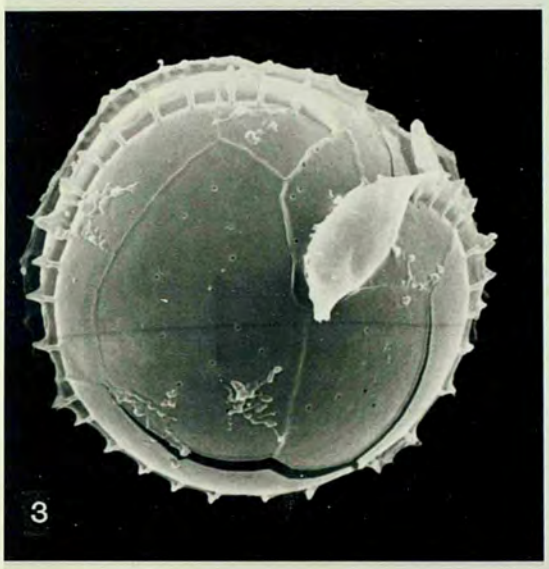
Fig. 4 : Side view Glenodinium sp., 19 µm across; Loch Creran.

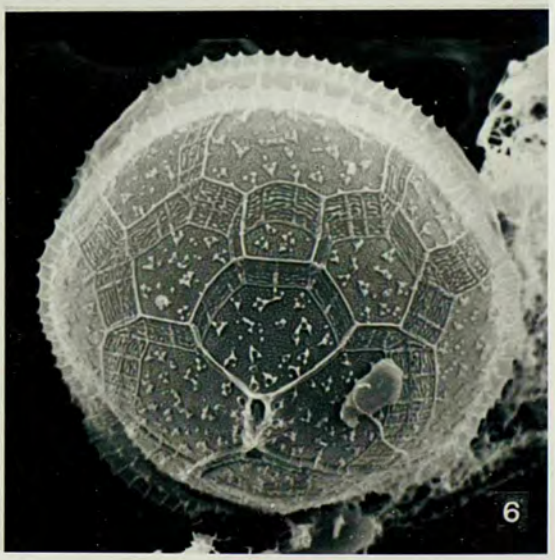
Fig. 5 : Ventral view Protoperidinium brevipes, 32 µm across; West Loch Tarbert.

Fig. 6 : Dorsal / apical view of P. brevipes showing 2a plate, approximately 25 µm across; Loch Creran.

Plate 3.2







Genus: Glenodinium Ehrenberg

This genus was formally taken to include those species which have thickened thecal plates but no obvious plate tabulation. In general the hypotheca and epitheca are more or less equal (Dodge, 1982). Species described from this genus only have these tenuous relationships and the genus is thus something of a taxonomic 'dustbin'.

Glenodinium spp.

Size:- <20 µm across

The cells ascribed to this heading were small with a median girdle dividing the epitheca and hypotheca evenly. With routine light microscopy these cells were impossible to separate. Occasional S.E.M. observations suggested that a variety of species were included in this category. Most (that survive the S.E.M. processing) had some indications of plate tabulation (Pl. 3.2, fig.4) and some had unusual plate patterning (Dodge and Saunders, unpubl.). S.E.M. observations have also shown that at least some of those cells counted as Glenodinium spp. in this study were very small Gonyaulax tamarensis cells.

Genus: Protoperidinium Bergh

Many species of Protoperidinium were hatched from cysts. The taxonomy of the hatched motile cells and that of their cysts is described in Chapter 8. As most Protoperidinium species were either rare or easily distinguished, futher investigations were only carried out on two species. The first of these species was frequent in Loch Creran in 1982 and 1983 and the second was found to be common in some areas in the summer of 1982.

Protoperidinium brevipes (Paulsen) Balech

Fig. 3.3, f; Pl. 3.2, figs.5-6

Size (after Dodge, 1982):- 18-38 µm long
28-34 µm wide

This small but distinct species was not easily identified by the routine light microscopy used for counting. The lobed hypotheca was clear but the small spines at the base of these lobes were not obvious. With S.E.M. it was immediately apparent that the cell was P. brevipes. The cell was rhombic in ventral view. It had a lobed hypotheca with two antapical small spines. The first apical plate was meta (Pl. 3.2, fig.5) and the second intercalary (2a) was characteristically small and almost square (Fig. 3.3, f; Pl. 3.2, fig.6). The theca was covered by small spines and even smaller reticulations (Pl. 3.2, fig.6).

Protoperidinium diabolum (Cleve) Balech

Fig. 3.3, g; Pl. 3.3, fig.1

Size (after Dodge, 1982):- 50-75 µm long
42-60 µm wide

The motile thecate cell was pyriforme with a long apical horn and two solid, divergent antapical spines (Pl. 3.3, fig.1). The first apical plate was 'para' and the second intercalary was 'hexa' (Fig. 3.3, g). The antapical spines were winged and the left one had a small accessory spine at its base.

Some initial difficulty was experienced in separating this species from Protoperidinium pellucidum and Protoperidinium pallidum. After S.E.M. it was clear this species could be distinguished by light microscopy on the basis of cell body shape and the struture of the antapical horns.

Round, brown cysts

In the cyst counts the heterogeneous group of 'round, brown cysts' was counted as a single entity. This was because the cysts themselves were indistinguishable, and after excystment certain species were still difficult to distinguish (see Chapter 8). This group probably included many Protoperidinium species and also some Glenodiniacean species. Incubation work (Chapter 8) showed that the group included Protoperidinium avellana, P. conicoides, P. denticulatum, P. excentricum, ?P. hangoei, P. subinerme, P. thorianum, and ?P. thulesense; and also Diplopsalis lenticula and Zygabikodinium lenticulatum. It is possible it also contains the species Protoperidinium punctulatum, Diplopsalis orbicularis (Wall and Dale, 1968) and others as yet unidentified (Dale, 1983).

Genera: Scrippsiella Balech ex Loeblich III
Peridinium Ehrenberg

The taxonomy of the small orthoperidinioid dinoflagellates is extremely confused. This is partly because of their small size and the consequent difficulties in distinguishing plate tabulation and partly because of the close similarities between the motile thecate stages. In addition to these problems there are many cultures of species from this group and new descriptions have been made when possibly there has not been sufficient inter-comparison of material.

The taxonomic difficulties with this group can be eased if the cyst stage is taken into account (Dale, 1978). Three genera of this group are separated by minor thecal plate differences amonst the motile stages: Scrippsiella has six cingular plates, Peridinium has five cingular plates, and Ensiculifera has five cingular plates the first of which has an elongate projection into the epitheca. These differences are hard to see even using the S.E.M. The morphology of their cysts is, however, very different.

In this study examination of thecate motile stages (from water column samples) suggested that Scrippsiella trochoidea and Peridinium faeroense were present in the sea-lochs. Studies of cysts (from sediments and the water column) suggested a further species Scrippsiella ?sweeneyae. Thus Scrippsiella spp. as used in this study in reference to thecate motile stages therefore includes at least three species. The two cyst types found were separated in counts as they were quite distinct.

Scrippsiella trochoidea (Stein) Loeblich III

Fig. 3.3, h-i; Pl. 3.3, figs.2-3

Size (after Dodge, 1982):- thecae 16-36 µm long
20-23 µm wide
cysts (inc. spines) 26-37 µm across

Thecae

These were typical of the small orthoperidinioid dinoflagellates. They had smooth thecal plates with randomly scattered, simple trichocyst pores. The plate tabulation is shown in Figure 3.3, h-i. In the past this species has been confused with Peridinium faeroense (see for example the discussion in Steidinger and Balech, 1977). Lebour (1925)

PLATE 3.3

All figures are S.E.M.s

Fig. 1 : Ventral view of Protoperidinium diabolum, approximately 44 µm across; Loch Melfort.

Fig. 2 : Apical view of recently encysted Scrippsiella trochoidea cell, approximately 30 µm across; Loch Creran, water sample.

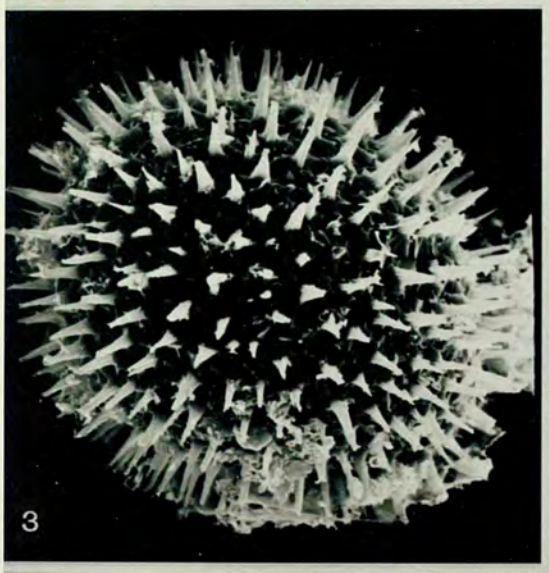
Fig. 3 : S. trochoidea cyst, 39 µm across (including spines); Firth of Clyde sediment sample.

Fig. 4 : Detail of surface patterning of sulcal area of Peridinium faeroense motile cell, x 7,000; Firth of Lorne.

Fig. 5 : Ventral view of Gonyaulax spinifera, 37 µm long; Loch Creran.

Fig. 6 : Ventral view Spiniferites bentori (Gonyaulax digitale), 55 µm long (including spines); Sound of Jura sediment.

Plate 3.3



distinguished these species by the wider first apical plate and more prominent apical horn of S. trochoidea. Dale (1977b) distinguished P. faeroense because of its distinctive trichocyst pore structure; its five cingular plates and the difference in cyst types. The morphology of the thecae of S. trochoidea (as described by Wall and Dale, 1968b) and Scrippsiella sweeneyae (as described by Balech, 1959) appear to be identical and the species thus seem only separable by their cyst types.

Cysts

The cysts were round or slightly ovoid and covered in spines of various lengths (Pl. 3.3, figs.2-3). That this ornamentation is calcitic (Wall et al., 1970) was confirmed by dissolving it away by gentle acid treatment leaving an organic inner wall. The cysts also contained a red body. It was on the basis of this distinctive cyst type that S. trochoidea was identified as being present in the sea-lochs.

Scrippsiella ?sweeneyae Balech ex Loeblich III

This species is fully described in Chapter 8. It was distinguished from S. trochoidea on the basis of its distinctive cyst type. It has been assigned to S. ?sweeneyae because of the similarity between the motile thecate stage and Balechs' original description of S. sweeneyae (Balech, 1959). It was probably not the same species as the S. sweeneyae described by Wall and Dale (1968b), as the cyst types and the thecal morphology differed. In view of the current confusion in the taxonomy of this group, however, it was not felt to be justified in naming a new species until comparison between this material, the S. sweeneyae type material and cysts and cells of the Wall and Dale S. sweeneyae has been carried out. Nevertheless, on the basis of the cyst types at least two species are involved.

Peridinium faeroense Paulsen

Size (after Dodge, 1982):- 28-35 µm long
15-29 µm wide

Thecae

Only motile cells of this species were clearly identified in this study. They had a less prominent apical horn than other members of this group. They also had only five cingular plates and slightly different sulcal plates to the Scrippsiella species, the Sp plate being proportionately smaller (Pl. 3.3, fig.4). The thecal ornamentation was also distinctive, the trichocyst pores being surrounded by concentric ridges (Pl. 3.3, fig.4). The cyst of this species (Impletosphaeridium bifurcatum) is organic and so quite different from the calcitic cysts of the Scrippsiella species. It was not found in this study but this may simply be due to the size of sieves used. It is possible that these cysts were lost in the smallest size fraction. Reid (1972b) found the species to be a significant part of the cyst assemblage in this region of the Scottish west coast.

Family: Gonyaulacaceae Lindemann
Genus: Gonyaulax Diesing

Only two members of this genus caused taxonomic difficulties and these are described below.

Gonyaulax spinifera (Claparède and Lachmann) Diesing
[Spiniferites spp. (Mantell) Sarjeant]

Pl. 3.3, figs.1-2; Pl. 3.4, figs.1-2

Size (after Dodge, 1982):- thecae 24-50 µm long
30-40 µm wide

Thecae

Thecae had a clearly offset, deeply excavated girdle. The epitheca had 'shoulders' and an apical horn. The hypotheca had straight sides and two or more antapical spines. The surface of the theca was often heavily sculptured (Pl. 3.3, fig.5). It seems likely that close examination of plate tabulations will reveal that more than one species is included in this group (Dodge and Saunders unpubl.). In addition this species is easily confused with others of this genus, for example Gonyaulax digitale, G. diegensis and G. alaskensis (Dodge, 1982). In this study all motile thecate cells of this type were included in G. spinifera. More than one cyst type has been found in this study so it would seem likely that more than one species is included under this heading.

Cysts

Dale (1983, Table 2.) has incubated ten cyst types which he relates to the 'G. spinifera group'. These cysts include a wide range of morphological types and belong to several cyst genera (Tectatodinium, Bitectatodinium, Planosphaeridium, Nematosphaeropsis and Spiniferites). This implies that several different species (on the basis of cysts) may have closely related thecal morphotypes (as in the case of Scrippsiella spp.) and some splitting of the thecate species should be carried out. Conversely many species of the cyst genus Spiniferites (S. elongatus, S. membranaceous, S. mirabilis, and S. scabratus) have similar morphological features and produce motile thecate stages of the 'spinifera' type, so perhaps some lumping of these cyst species should take place.

In this study all species of the Spiniferites type were counted together as Spiniferites spp. as they could not easily be distinguished by the light microscopy routinely used. S.E.M.

observations indicated a variety of species to be present including S. elongatus, S. bentori, S. bulloideus and S. membranaceous / mirabilis (Pl.3.3, fig.6; Pl.3.4, figs.1-2). It is possible more species than this were present but some difficulty was experienced in separating the palaeontological taxa. Reid (1974) found S. membranaceous, S. bulloideus and S. lazus to be present in this region of the Scottish west coast. Not all of these cyst types relate to the G. spinifera group. S. bentori is the cyst of Gonyaulax digitale and S. bulloideus the cyst of Gonyaulax scrippsae (Wall and Dale, 1968a). Motile thecate cells of G. digitale were found in water samples but motile cells of G. scrippsae were not; if they were present it is possible that they have been included in the counts of G. spinifera. Further taxonomic work including both cysts and motile stages is needed to elucidate this group.

Gonyaulax tamarensis Lebour

Fig. 3.4, a-b; Pl. 3.4, figs.3-4

Size (after Dodge, 1982) :- 24-44 µm long
20-36 µm wide

The confusion surrounding the taxonomy of the G. tamarensis-like dinoflagellates was clearly evident in 1978 when G. tamarensis was transferred to two different genera in two separate papers from the same meeting (Taylor, 1979; Loeblich and Loeblich, 1979). The problem is chronic as some species of this complex are toxic and others are not. After Lebour's original description in 1925 Braarud (1945) recognised several varieties of this species, notably G. tamarensis var excavata. Later two distinct species were recognised, G. excavata (toxic, bioluminescent, lacking a ventral pore) and G. tamarensis (non-toxic, non-bioluminescent, with a ventral pore present) (Loeblich and Loeblich 1975). Balech (1971) had previously described

PLATE 3.4

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Ventral view of Spiniferites bulloideus (Gonyaulax scrippsae), 48 µm long (including spines); Firth of Clyde sediment sample.

Fig. 2 : Dorsal view of Spiniferites mirabalis / membranaceaous (Gonyaulax spinifera group), 56 µm long (including spines); Firth of Clyde sediment sample.

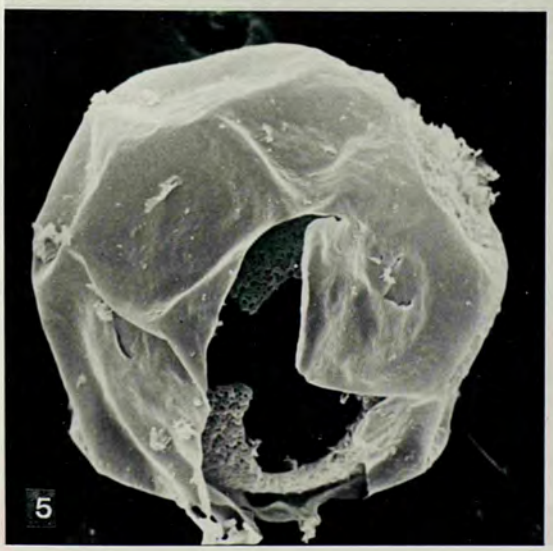
Fig. 3 : Ventral view of Gonyaulax tamarensis, 35 µm across; West Loch Tarbert, (see also Fig. 4).

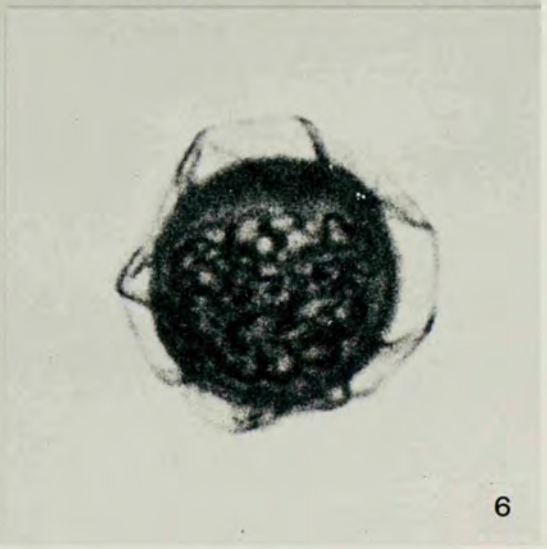
Fig. 4 : Apical view of G. tamarensis, 35 µm across; West Loch Tarbert, (see also Fig. 3).

Fig. 5 : ?Epidinium shagrinum, showing archeopyle, 37 µm across.

Fig. 6 : Light micrograph of ?E. shagrinum, showing contents; Loch Creran sediment sample.

Plate 3.4

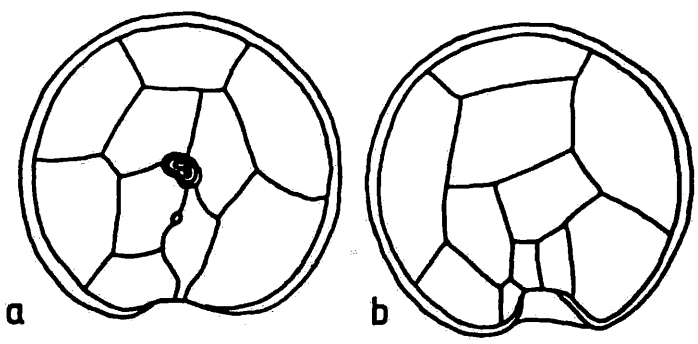




G. excavata but his description includes a ventral pore and was not considered to be the same species in this revision . Schmidt and Loeblich (1979a) relegated these two species back to varieties having found that some strains of both varieties were toxic (Schmidt and Loeblich 1979b). Thus it appears that there is no clear morphological feature to indicate toxicity. In the spirit of the suggestion that names of species of economic importance should be conserved (Steidinger, 1983) this species is referred to as G. tamarensis (the alternatives of Protogonyaulax tamarensis Taylor, and Gessnerium tamarensis Loeblich and Loeblich being ignored).

The implications of the presence of this species were such that whenever it was found, S.E.M. was carried out to confirm the identification. The cells were rounded with a slightly offset girdle and both girdle and sulcal lists (Pl. 3.4, fig.3). The thecal plates were smooth, with a ventral pore on the edge of the first apical plate (Pl. 3.4, fig.4). The plate tabulation (Fig. 3.4, a-b) and the U-shaped nucleus also helped to characterise this species.

Figure 3.4



Gonyaulax tamarensis

In commom with many of the gonyaulacoids this species also forms cysts (see for example Dale, 1977a) but none have been found in this study. It is possible that this is another of the variable features of this complex.

Family: Ceratiaceae Lindemann

Genus: Ceratium Schrank

Ceratium lineatum (Ehrenberg) Cleve; Ceratium minutum Jørgensen

These two species would seem to be end members of a complex of species. Insufficient material was collected in this study to compare these species and because of the difficulty of distinguishing them they have been lumped together as C. lineatum. Occasionally some cells were seen that might have been C. minutum.

Incertae sedis

?Epidinium shagrinum Reid

Pl.3.4, figs. 5-6

Size:- 35-39 µm across

This cyst type was found occasionally in sediment samples. Attempts at hatching were unsuccessful - the naked protoplast never properly formed its thecal plates. The cyst was cavate and the outer wall was brown (similar to cysts of Protoperidinium species). The inner wall was spherical and granular (Pl. 3.4, fig.5). The outer wall did not appear to be attached to this inner wall but was folded about it. Under the light microscope this gave the cyst the appearence of being 'frilly'. The cyst

contained many small bodies (Pl. 3.4, fig.6). The archeopyle was difficult to discern and appeared somewhat variable. Only one clear picture was obtained (Pl. 3.4, fig.5) and here the outer wall seems to have split and the archeopyle formed on the inner wall.

This cyst bore a close resemblance to Epidinium shagrinum Reid but the archeopyle was not properly determined to allow a complete comparison. Reid (1972b) did, however, find this species at its most abundant on the west coast of Scotland. Its thecal relationship is not clear but it seems most similar to Protoperidinium cysts.

CHAPTER 4

SEASONAL CYCLE OF DINOFLAGELLATES IN LOCH CRERAN

INTRODUCTION

To observe the seasonal variation in dinoflagellate populations regular sampling was carried out in Loch Creran. Loch Creran was chosen for two reasons, firstly its ready accessibility by road and boat and secondly because it is in many respects a 'typical' Scottish sea-loch (Landless and Edwards, 1976). The loch has been the site for extensive study by the Scottish Marine Biological Association (S.M.B.A.) over the last 15 years so much background information on the physical environment and the phytoplankton cycle is available.

Physical environment

As with so many of the Scottish west coast sea-lochs, Loch Creran is a submerged, glacially overdeepened river valley. It consists of two basins (Fig. 4.1). The main basin (about 11 km long and 1.5 km wide) is separated from the Firth of Lorne by a narrow entrance channel (0.2 km wide and 5m deep). The greatest depth in the main basin is 49m. The upper loch has a maximum depth of 40m, and is divided from the main basin by a narrow, shallow sill (4m deep). It is 3km long and 0.8 km wide. For further details see Milne (1972); Tett and Wallis (1978) and Tyler (1983).

Salinity distributions suggest that during much of the year the loch has a two-layer estuarine circulation driven by freshwater inflow. The brackish layer is between 4m and 8m deep (Tyler, 1983). More than half of the freshwater enters the upper basin through the River Creran and a smaller stream, in addition to this there are three other streams entering the main basin. Tyler (1983) calculates the flushing time for the loch in several different ways and considers the best estimate to be 12 days.

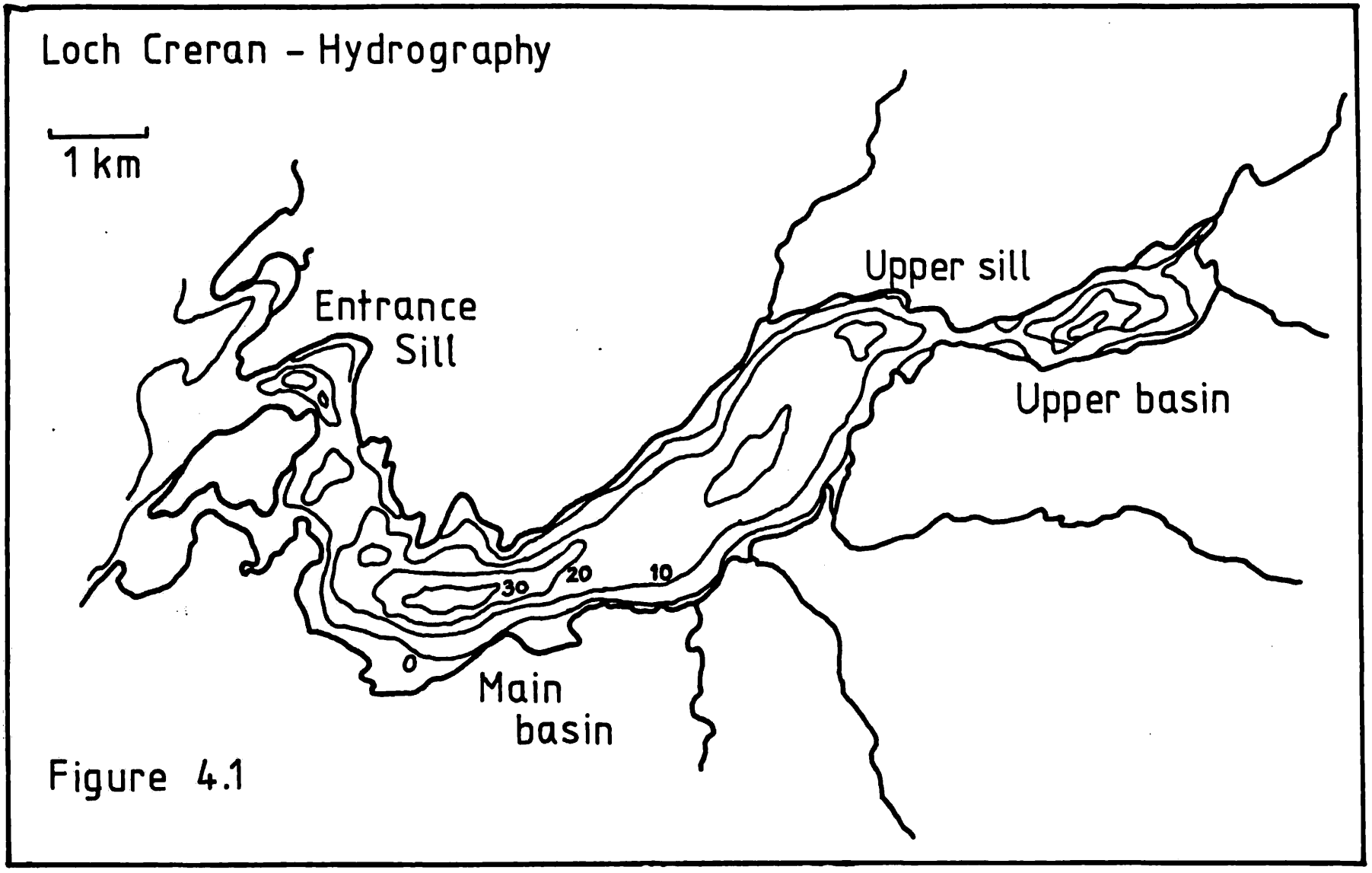

Loch Creran - Hydrography
1 km
Entrance
Sill
Upper sill
Upper basin
30
20
10
0
Main
basin

Figure 4.1

Maximal nutrient levels in surface waters in Loch Creran occur before the spring increase during February and early March. As measured by Jones (1979) in 1974-75 these were 0.55 - 0.75 µg-at dissolved inorganic phosphorous (DIP) $litre^{-1}$ and 5.5 - 7.5 µg-at dissolved inorganic nitrogen (DIN) $litre^{-1}$. During the spring increase these nutrients are depleted and summer concentrations for 1974-75 were 0.08 - 0.12 µg-at DIP $litre^{-1}$ and 0.1 - 0.25 µg-at DIN $litre^{-1}$.

Tett and Wallis (1978) report work that indicates that at least two thirds of net primary production occurred above 8m, and they take 8m to be the lower limit of the euphotic zone. The depth to which 5% of incident light penetrates can be calculated using the following equation:-

$$\frac{I}{I_o} = e^{-\lambda z}$$

where I_o is incident light at the surface, λ is the attenuation coefficient and z is depth. For Loch Creran Tyler (1983) calculates the attenuation coefficient to be between 0.20 - 0.35, it follows that for the upper end of the range

$$0.05 = e^{-0.2z}$$

$$\ln 0.05 = -0.2 \times z$$

$$z = 14.98m$$

the range of the 5% light level is thus between about 9 and 15m and this is the best estimate of euphotic zone depth. During periods of heavy rainfall, freshwater entering the loch containing humic substances causes rapid attenuation of light so that it is dark within 2 - 3m (pers. obs.).

Phytoplankton in Loch Creran

Regular sampling for amount and species composition of phytoplankton in Loch Creran has been carried out by the S.M.B.A. since 1972. Tett and Wallis (1978) describe the chlorophyll data taken over part of this time. Their combined plot (1970-1976) (Fig. 4.2) shows the general features of the phytoplankton cycle. The cycle can be divided into four periods (Tett, Drysdale, and Shaw, 1981) :-

1. Winter (December -February) <1 mg chlorophyll m^3. Dominated by small flagellates.

2. Spring-bloom (March -April) chlorophyll concentration increases to at least 10 mgm^3 then falls. Dominated by Skeletonema costatum; Thalassiosira sp. common.

3. Summer (May -September). A series of small blooms of various diatom species :- Chaetoceros spp., Leptocylindrus spp., Rhizosolenia spp. and some dinoflagellates Scrippsiella trochoidea (probably Scrippsiella spp.), Heterocapsa triquetra, Gonyaulax spp. and Ceratium spp.

4. Autumn (October -November) chlorophyll concentrations decline and there may be resurgence of some diatoms e.g. Thalassiosira and Skeletonema costatum

Although this describes the species succession in 1979 it seems applicable to most years. Skeletonema costatum dominates the phytoplankton population (particularly in the Spring). Small flagellates (some of which are probably heterotrophs) form a background at all times with Chaetoceros, Leptocylindrus, and Rhizosolenia important in the summer. Of the dinoflagellates

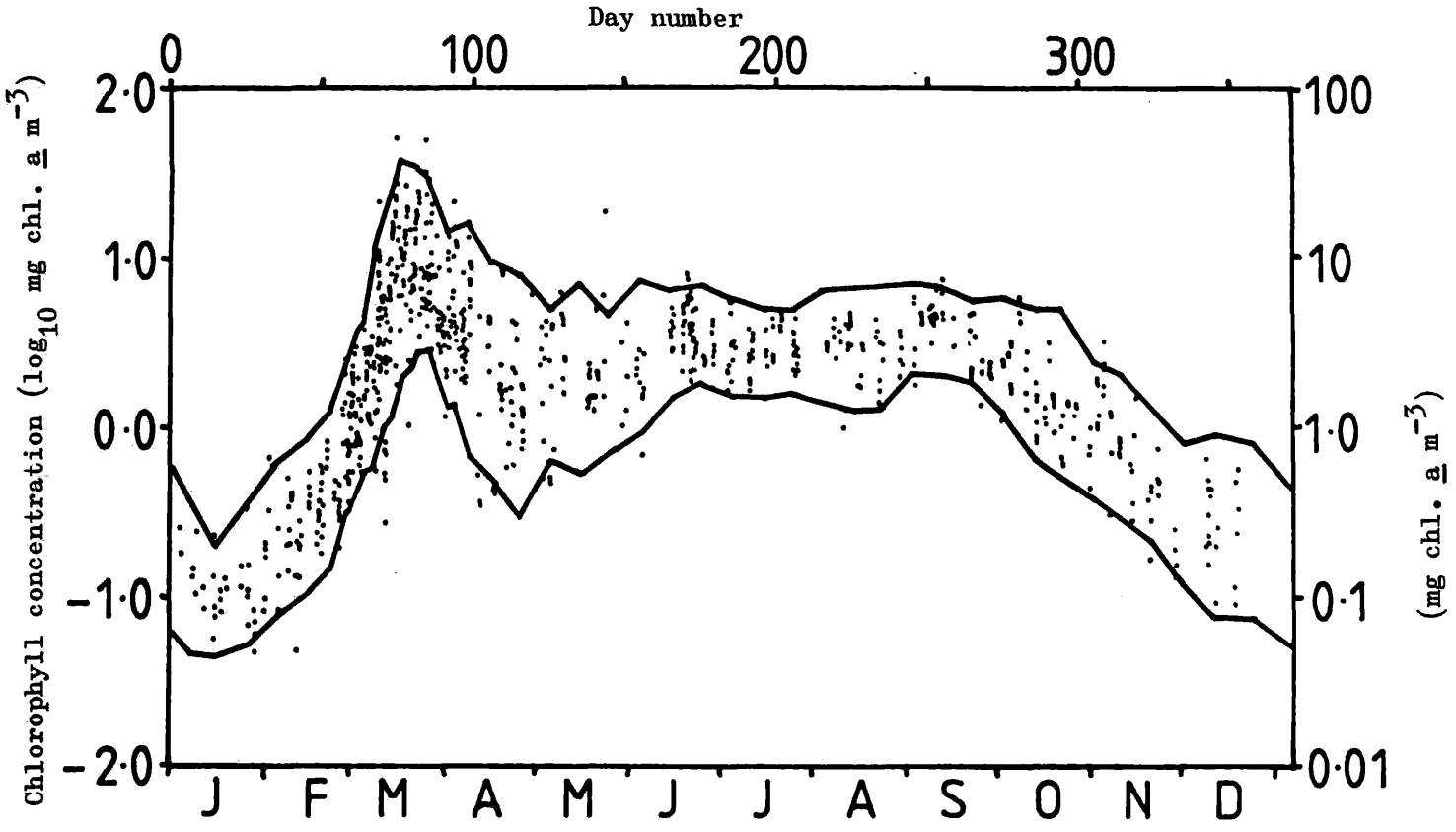


Figure 4.2 : Combined logarithmic plot of all chlorophyll data from the main basin of Loch Creran, 1-8 m depth zone, from 1970 until 1976. (after Tett and Wallis, 1978).

Scrippsiella trochoidea is the most common. These conclusions are, however, based upon the sedimentation of relatively small values (effectively 2 cm^3) of Lugol's preserved water from 1-2m depth.

The Spring increase in Loch Creran in late February / early March seems in most years to have been the result of persistant salinity stabilisation of the water column. In other coastal situations at similar latitudes stabilisation of the water column is controlled by temperature and the spring increase occurs later in the year. There is no definite occurrence of an Autumn bloom in most years, unlike waters where there is a breakdown of the summer thermocline. Tett and Wallis (1978) note that there is considerable variation in week to week run-off with consequent effects on the water column, making it remarkable that such a marked seasonality exists.

Previous phytoplankton surveys

While there have been very many phytoplankton surveys during the history of phycology few have concentrated their attention on dinoflagellate populations. This is probably because of the paucity of dinoflagellates compared to other species during most of the year. Data from different surveys can only be compared in a general way because of differences in sampling techniques and sampling areas and also changes in taxonomic nomenclature. Many phytoplankton surveys have been made with the use of nets. While this is adequate for a qualitative study of larger species it bears little relation to actual numbers or proportions of cells present, even of the larger species (personal observation). Other surveys have employed sedimentation techniques and these are considered comparable to the techniques used in this study. Surveys have been carried out in many places and for the purposes of introduction they will be divided into geographic areas.

Western Scotland

Marshall and Orr (1927) recorded seasonal changes in the phytoplankton for the Firth of Clyde and Loch Striven for 1924-1928. They examined water samples which were centrifuged before counting. The only other published seasonal surveys of phytoplankton composition on the Scottish West coast are those of Wood, Tett and Edwards (1973) in Loch Etive during 1970 and 1971 and Gowen, Tett and Jones (1983) in Loch Ardbhair in 1981 and 1982. These surveys employed a sedimentation technique for counting.

A more detailed unpublished survey of Loch Etive was made in 1969 by Tett using techniques similar to those used in this study. Other relevant unpublished records include the survey already mentioned in Loch Creran (Tett, Drysdale and Shaw, 1981) and Tett's (1969) PhD thesis relating to the Firth of Clyde. For the latter samples were treated by a method similar to that described here except that microscopic analysis was made in a Bogorov tray.

Rest of the British Isles

No other area of Britain provides an environment equivalent to that of the Scottish sea-lochs. However, with regard to the species present (if not the timing of their occurrence) they provide an interesting comparison. Many of the surveys carried out around the British Isles have been dependent on net collections. Of these perhaps the most notable in scale are those of the continuous plankton recorder survey. Of their large volume of publications only two will be referred to here, those of Robinson (1965 and 1983) which describe only *Ceratium* spp. Dodge and Hart-Jones (1974 & 1977) were concerned with dinoflagellate succession in the North sea. Finally, of those surveys employing net sampling there is the recent investigation of Horwood *et al*. (1982), again in the North sea.

Lebour (1917) collected samples for a year off Plymouth and used a centrifugation technique for concentration of cells. Sykes (1969 PhD thesis, Aberystwyth University) sampled for two years in Cardigan Bay. More recently work in the Western English Channel from 1964-1976 has been described in papers by Holligan and Harbour (1977) and Maddock et al. (1981). Both sets of data collected by the Plymouth laboratory utilized a sedimentation technique. Holligan, Maddock and Dodge (1980) described the distribution of dinoflagellates around the British Isles and considered that the patterns observed in different areas (with different water column structures) could be analogous to a seasonal succession.

Other areas

Seasonal observations of phytoplankton succession have probably been carried out in most areas of the world. However, for the purposes of this study the Norwegian fjords were considered the most appropriate for comparison. Much work has been carried out on phytoplankton in the fjords notably by Braarud, Foyn and Hasle (1958) in Dramsfjord; Braarud and others (1974 and 1976) in Hardangerfjord and Sakshaug (1972) and Sakshaug and Myklestad (1973) in Trondheimsfjord.

METHODS

Sampling

During 1982, from the end of April to the end of September, water samples were collected from Barcaldine Pier (Fig. 4.3). Over the winter 1982/83 samples were collected monthly at the same place. From the beginning of April 1983 until the beginning of November 1983 samples were again collected weekly. During this time samples were collected alternately at Barcaldine Pier

and Station C5 (Fig. 4.3). At Station C5 where the depth at low water is 20m a full water column profile was worked determining temperature, salinity, and chlorophyll concentrations at a number of depths dependent on water column structure, as described in Chapter 2. These parameters were also determined on the 1982 samples from Barcaldine pier as part of the S.M.B.A.'s routine monitoring programme. Although the depth of water was 5m at low tide, the samples for counts were usually taken from 2m. This will not always reflect the maximum abundance of cells but a compromise was needed because of the necessity of sampling from the pier. It was felt that in Loch Creran, 2m was a suitable depth because it would be below any strongly brackish layer but within the euphotic zone described by Tett and Wallis (1978) where maximum production takes place.

During 1983 extra samples were taken at two particularly interesting times of the year. The first was when Gonyaulax tamarensis was present in Loch Creran, and because of the possible toxic effects of this alga a full survey of the loch was carried out on the 19th of May (Fig. 4.3) and an extra station was worked at Creagan bridge the following week (24th May). During the autumn bloom of Gonyaulax polyedra, samples were collected and counted from more than one depth to get some indication of the distribution of motile cells and cysts throughout the water column.

Comparison of counts of live and preserved samples

As mentioned in Chapter 2 counts were made of living samples as frequently as possible to estimate the number and variety of naked species. The counts of living and preserved samples for armoured dinoflagellates were apparently similar. Statistical tests were carried out to assess the comparisons objectively. For each sample for which live and preserved counts had been made, the difference between these counts was calculated for 'total armoured dinoflagellates'. A mean difference was

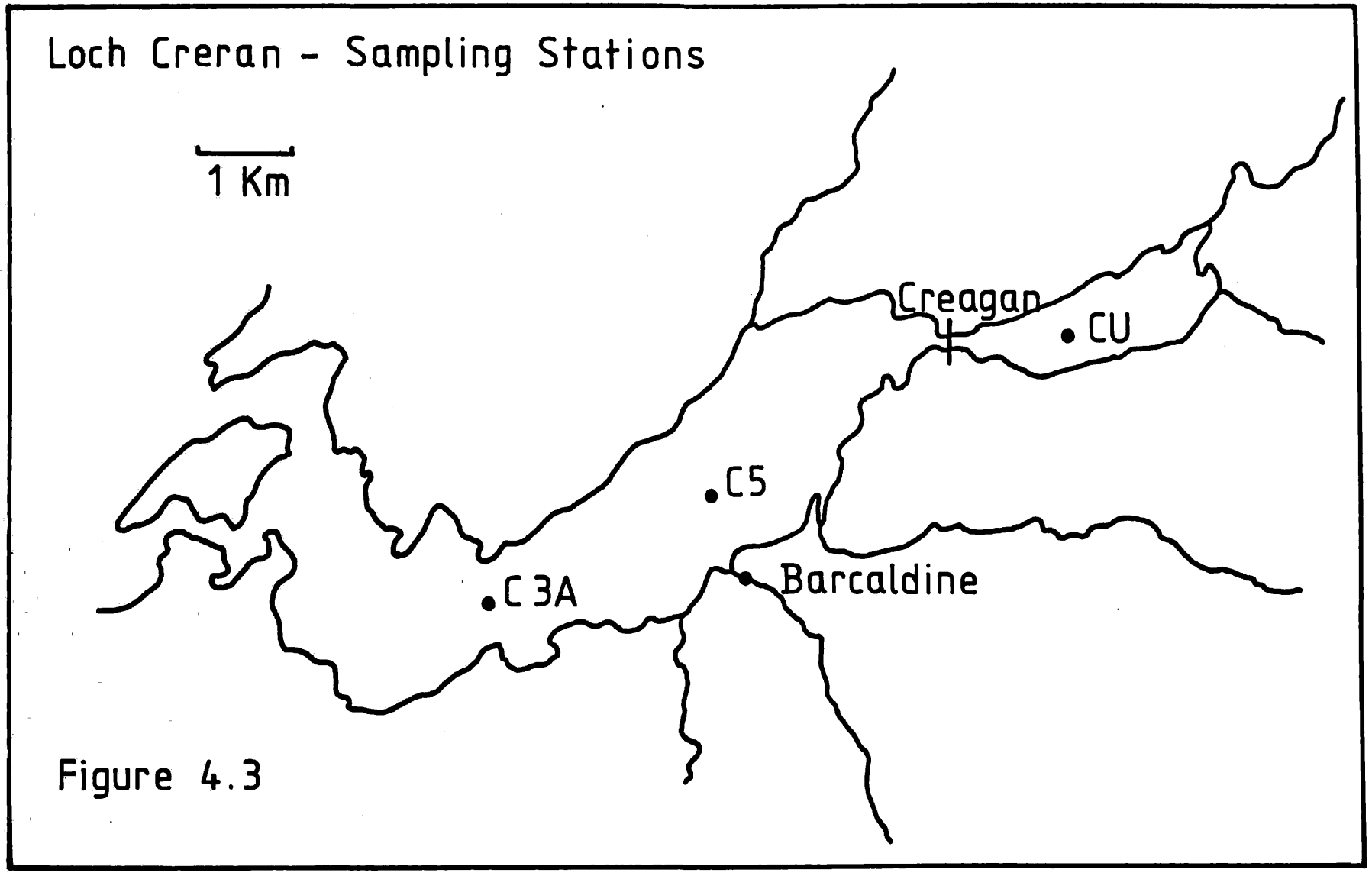

Loch Creran - Sampling Stations
1 Km
Creagan
CU
C5
C 3A
Barcaldine

Figure 4.3

calculated for 1982 and also for 1983. The standard error of the mean difference was calculated for 1982 and 1983 samples separately. From this the t-value of the mean difference was calculated. For 1982 this value implied that the difference between live and preserved counts was not significant. However, the t-value for 1983 shows the difference between the counts was significant ($0.05 < p > 0.02$). In both years the counts from the live samples were lower than those of the preserved sample, this difference was probably highlighted in 1983 because of the greater abundance of dinoflagellates in that year. As the live samples swim around, the preserved sample counts were considered more accurate and it was decided that for the purposes of seasonal description of the armoured dinoflagellates the counts from the preserved material were sufficient. So the living counts were used only to provide numbers of naked species.

RESULTS

Tables 4.1 - 4.6 are given at the end of the chapter

1982

A list of motile thecate dinoflagellate species and their occurrence as counted in preserved samples is given in Table 4.1. Table 4.2 shows numbers and occurrences of some other organisms. The reasoning behind the use of + and ++ symbols is given in Chapter 2. Graphs are given of total numbers of armoured and naked dinoflagellates (Fig. 4.4), of dominant species (Figs. 4.5 - 4.7), and of total numbers of *Protoperidinium* spp., *Ceratium* spp. and *Dinophysis* spp. since no species were individually numerically important in these groups (Figs. 4.8 - 4.10). Chlorophyll values are graphed in Figure 4.11. Full temperature, salinity and chlorophyll data are contained within S.M.B.A. internal report no. 114 (Lewis, 1983). Temperature and salinity as measured at 2m is given in Figure 4.12.

During 1982 the first maximum of dinoflagellate numbers was in early June but by the beginning of July numbers had diminished although they gradually increased to a second maximum in early September. Numbers had fallen to their low winter values by early October (Fig. 4.4). The changes in numbers of naked dinoflagellates appeared to follow those of the armoured species (taking into account gaps when no counts were made). The following account is concerned only with the armoured forms.

The first maximum of dinoflagellate numbers (13,600 cells per l) was largely composed of Scrippsiella spp. (12,400 cells per l). The bloom of Scrippsiella spp. occurred just after an increase in temperature of the surface water (maximum 14°C) and increasing salinities (from 31.2‰ on June 1st to 33.4‰ on June 29th) as measured at Barcaldine Pier. These were due to fine weather. After their initial high numbers in June, Scrippsiella spp. persisted throughout the summer until the end of August (Fig. 4.5). They were the most commonly occuring dinoflagellates during 1982. At the end of July and during August Protoperidinium spp. and Heterocapsa triquetra were seen more commonly.

At the beginning of September (max. nos. 13,800 cells per l), and during the second peak of numbers a succession of species was seen. This started with Scrippsiella spp. which disappeared towards the end of August and was immediately followed by a peak in numbers of Gonyaulax polyedra (Fig. 4.6) (max. 7,800 cells per l) at the end of August / beginning of September. This maximum also comprised Prorocentrum micans (3,100 cells per l) (Fig. 4.7); Protoperidinium spp. (900 cells per l) (Fig. 4.9) and Ceratium spp. (400 cells per l) (Fig. 4.8). Of these P. micans persisted until the end of September. As regards the hydrographic situation, the high temperatures (max. 16.4°C, min. 13.3°C) and salinities close to those of Firth of Lorne seawater

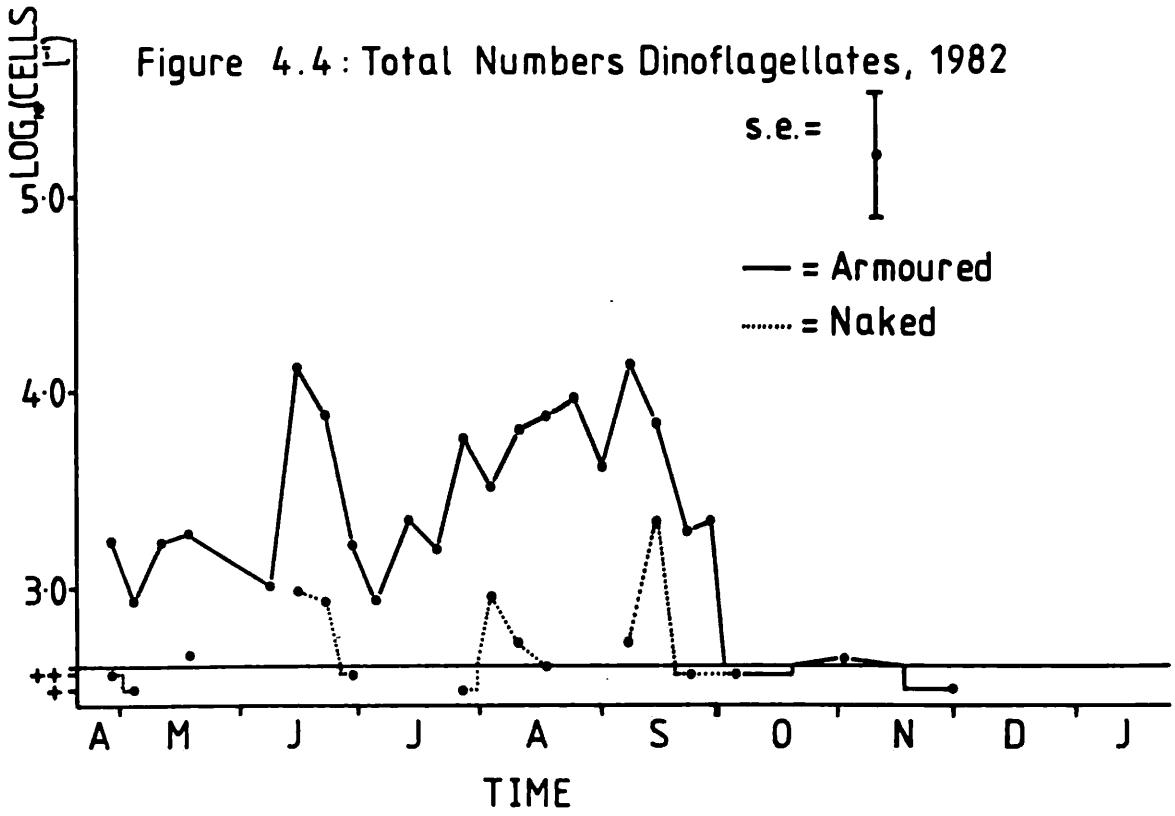


Figure 4.4: Total Numbers Dinoflagellates, 1982
s.e.=
— = Armoured
..... = Naked
LOG10(CELLS l-1)
5·0
4·0
3·0
A
M
J
J
A
S
O
N
D
J
TIME

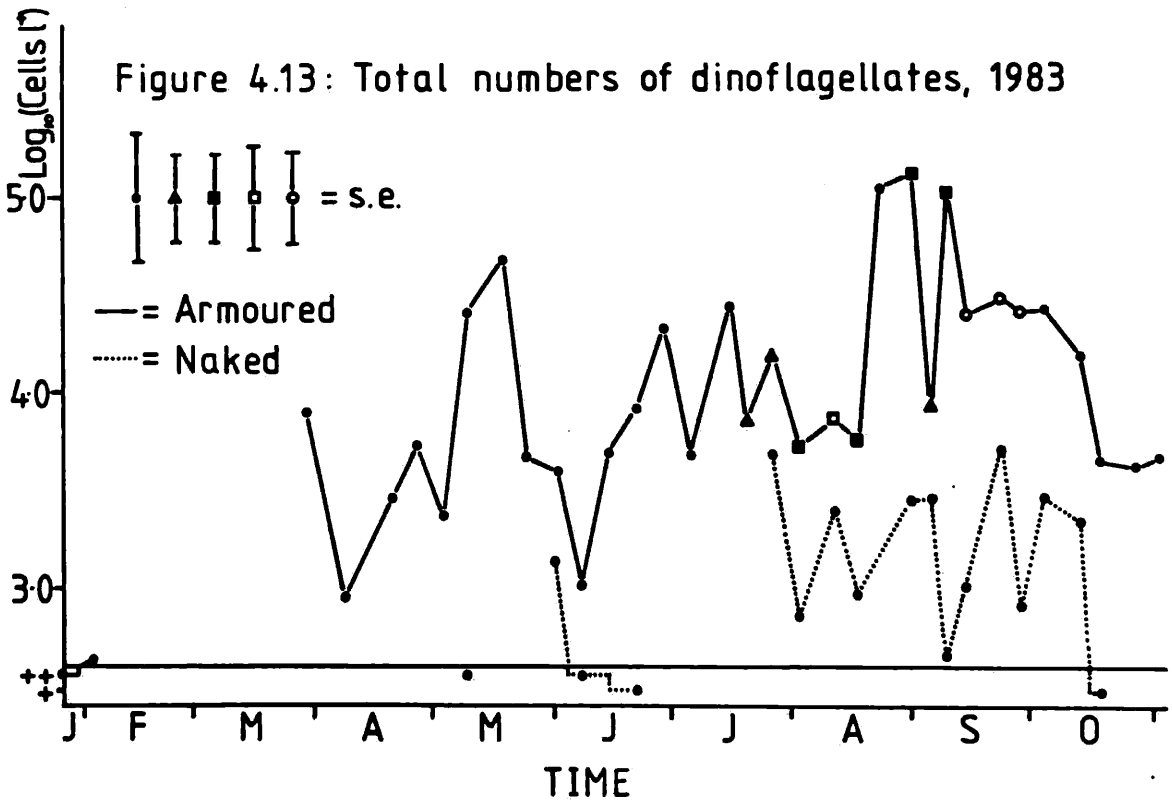


Figure 4.13: Total numbers of dinoflagellates, 1983
= s.e.
—= Armoured
.....= Naked
Log10(Cells l-1)
5·0
4·0
3·0
J
F
M
A
M
J
J
A
S
O
TIME

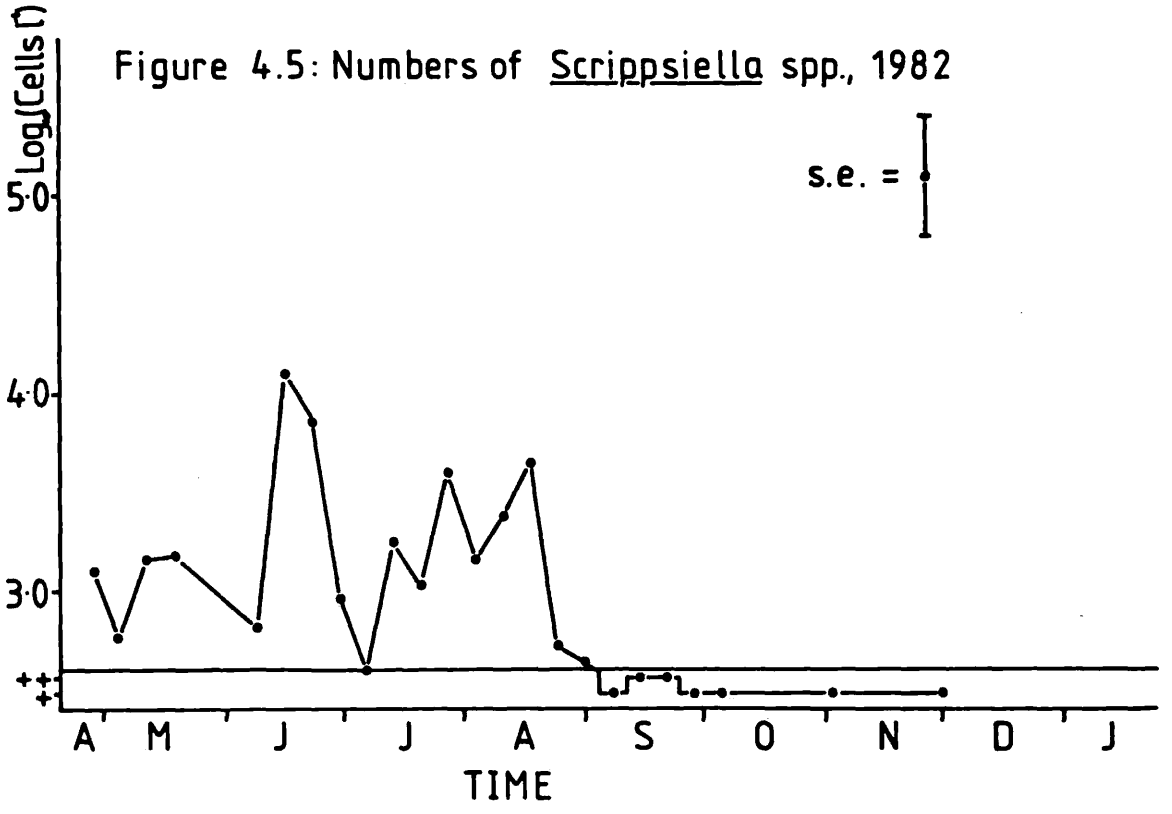


Figure 4.5: Numbers of Scrippsiella spp., 1982

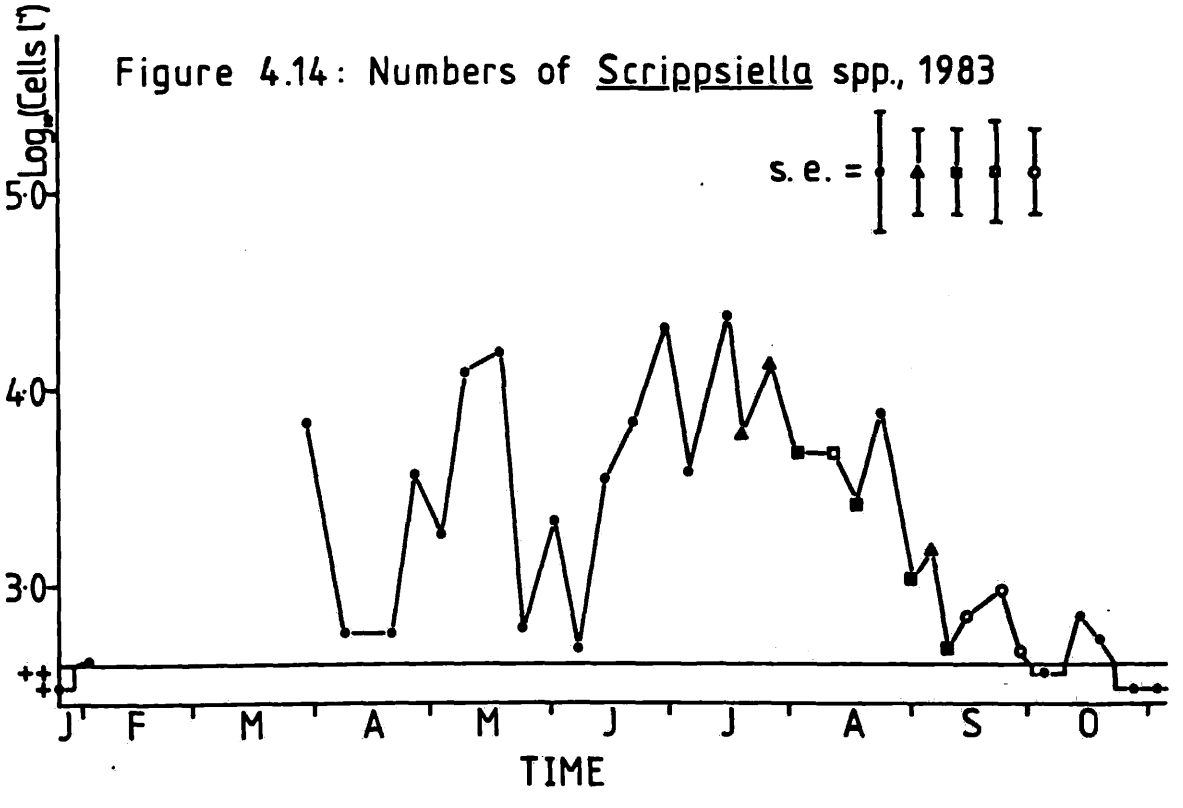


Figure 4.14: Numbers of Scrippsiella spp., 1983

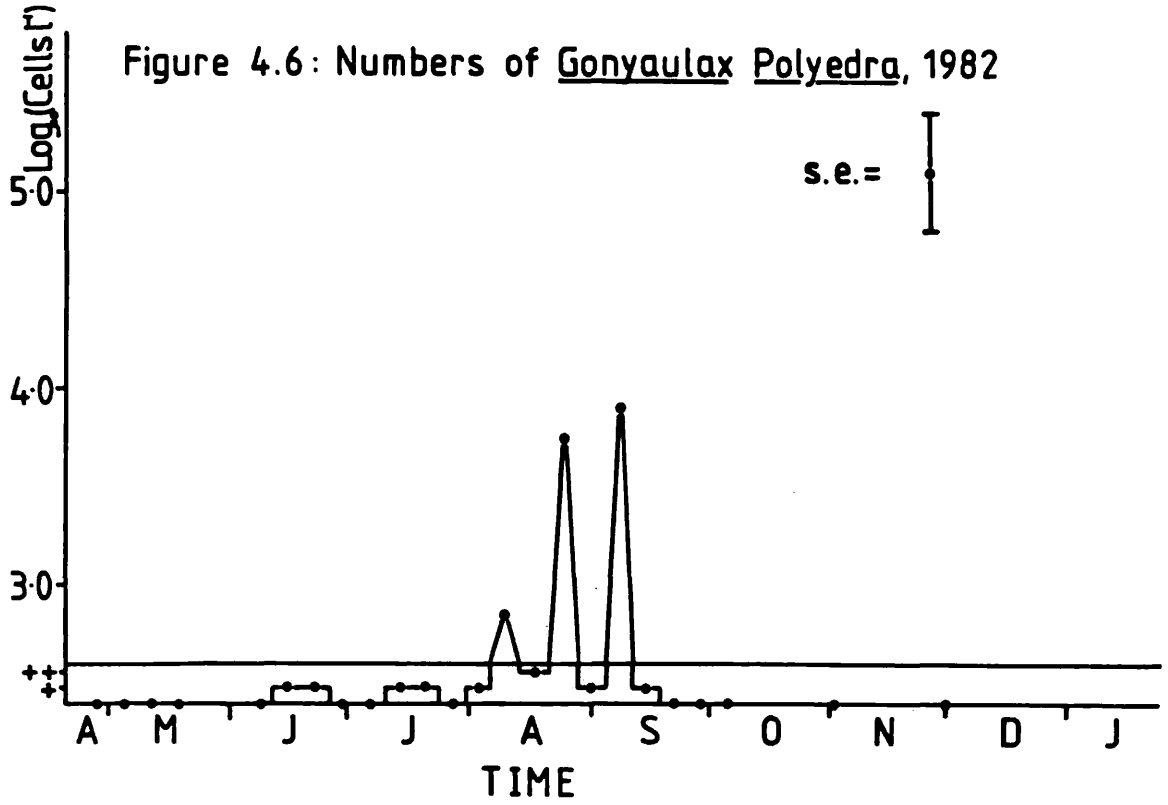


Figure 4.6: Numbers of Gonyaulax Polyedra, 1982

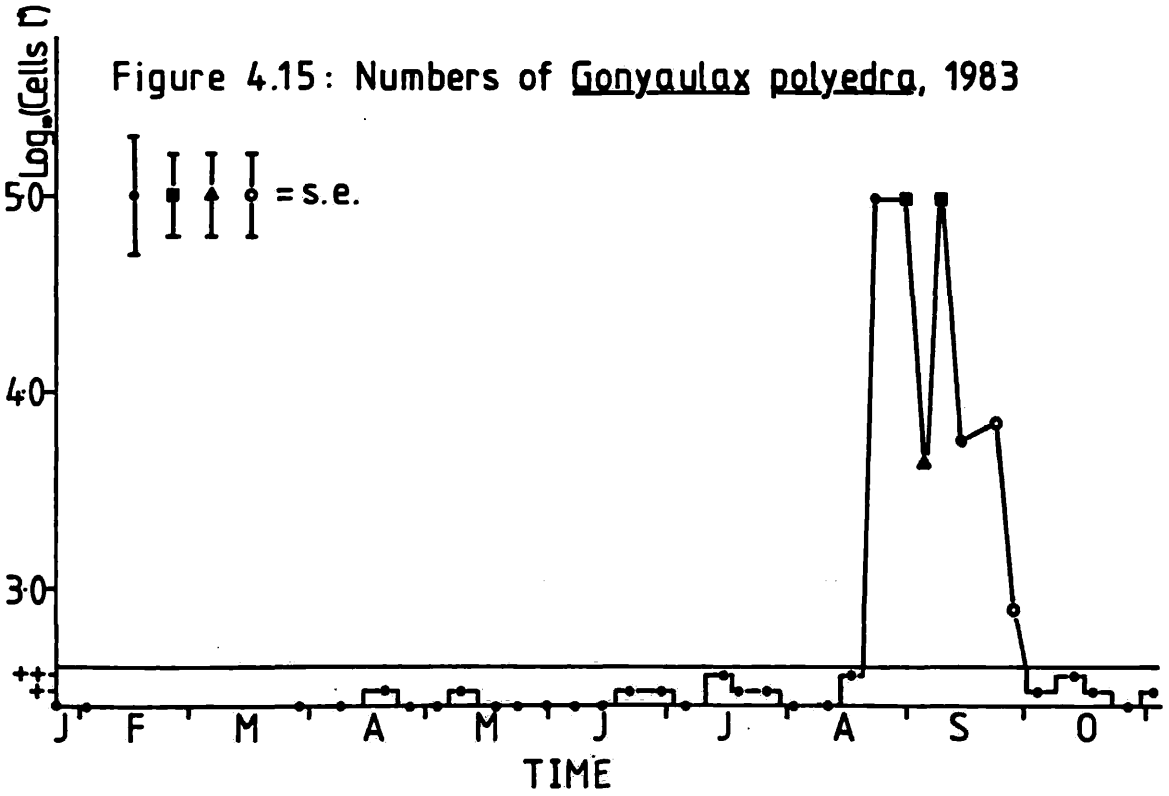


Figure 4.15: Numbers of Gonyaulax polyedra, 1983

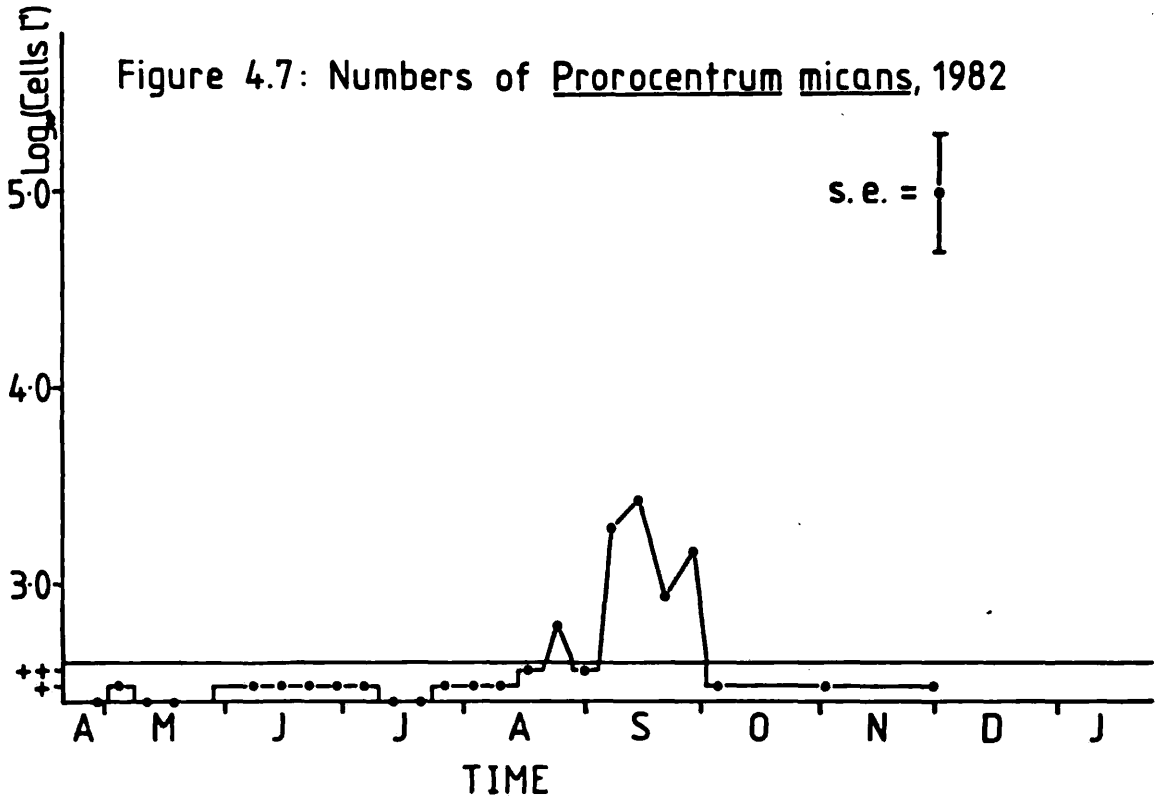


Figure 4.7: Numbers of Prorocentrum micans, 1982

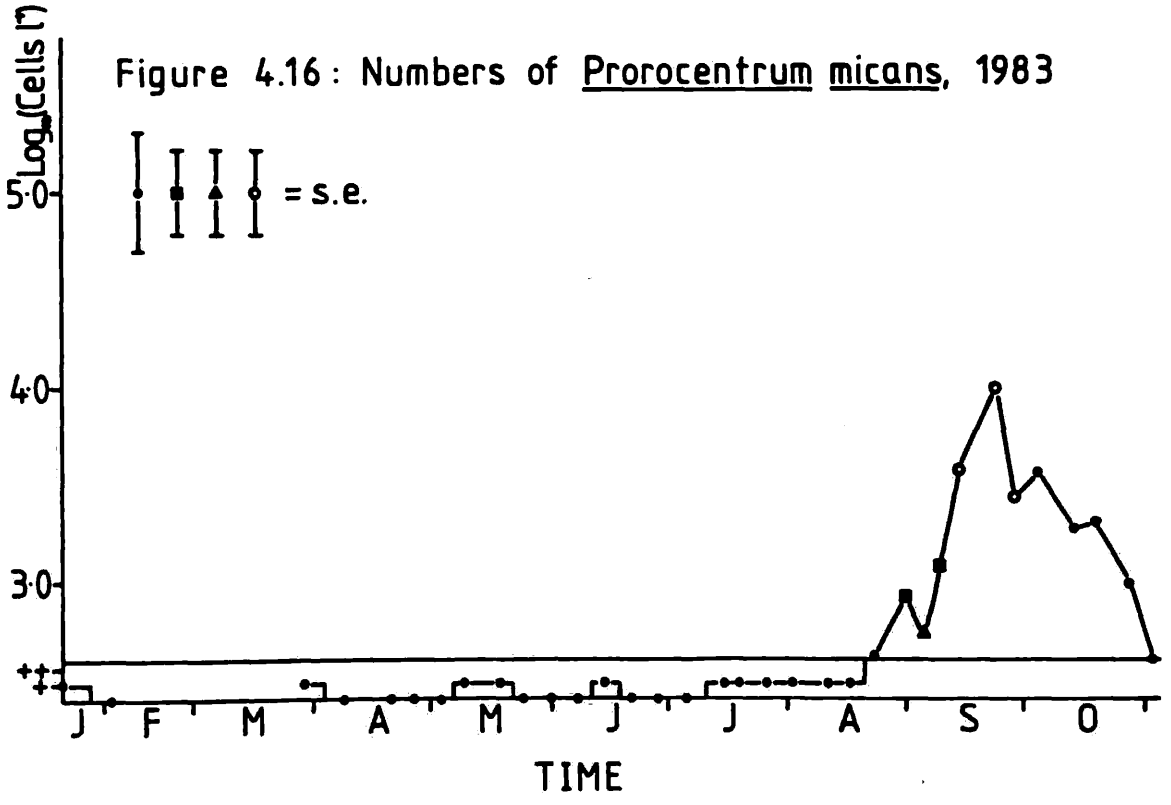


Figure 4.16: Numbers of Prorocentrum micans, 1983

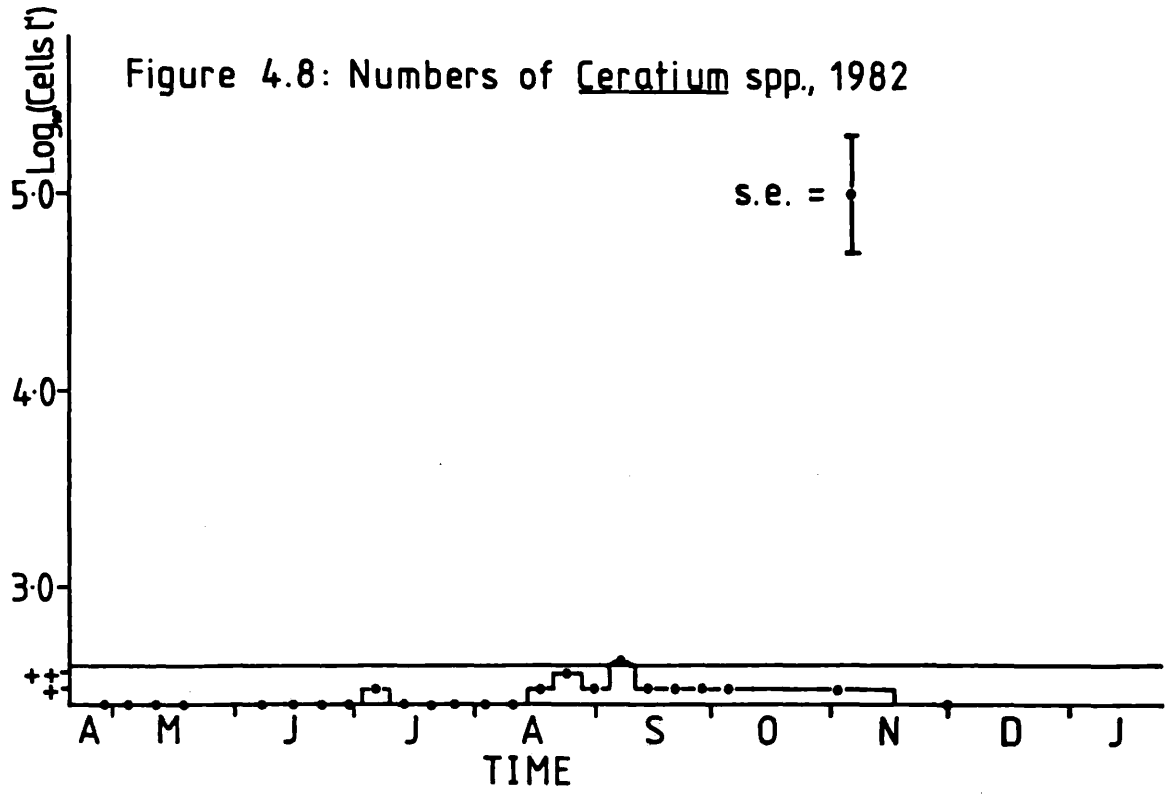


Figure 4.8: Numbers of Ceratium spp., 1982

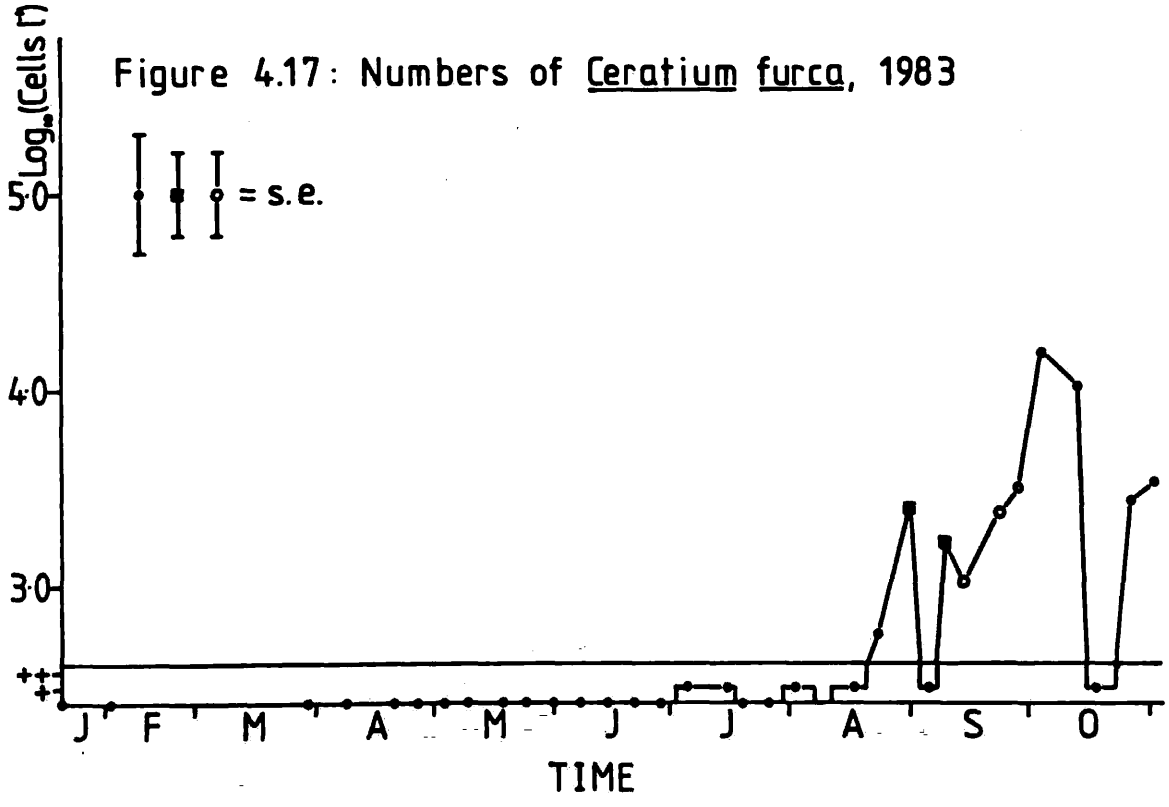


Figure 4.17: Numbers of Ceratium furca, 1983

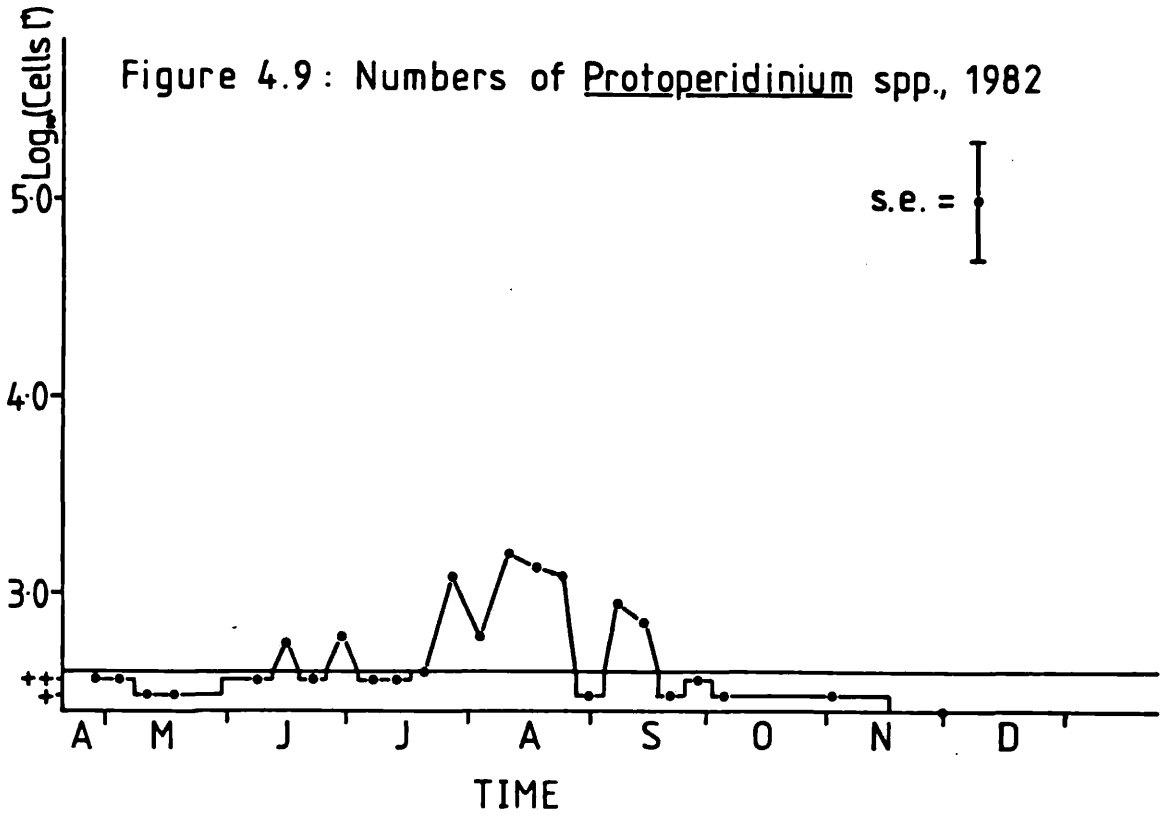


Figure 4.9: Numbers of Protoperidinium spp., 1982

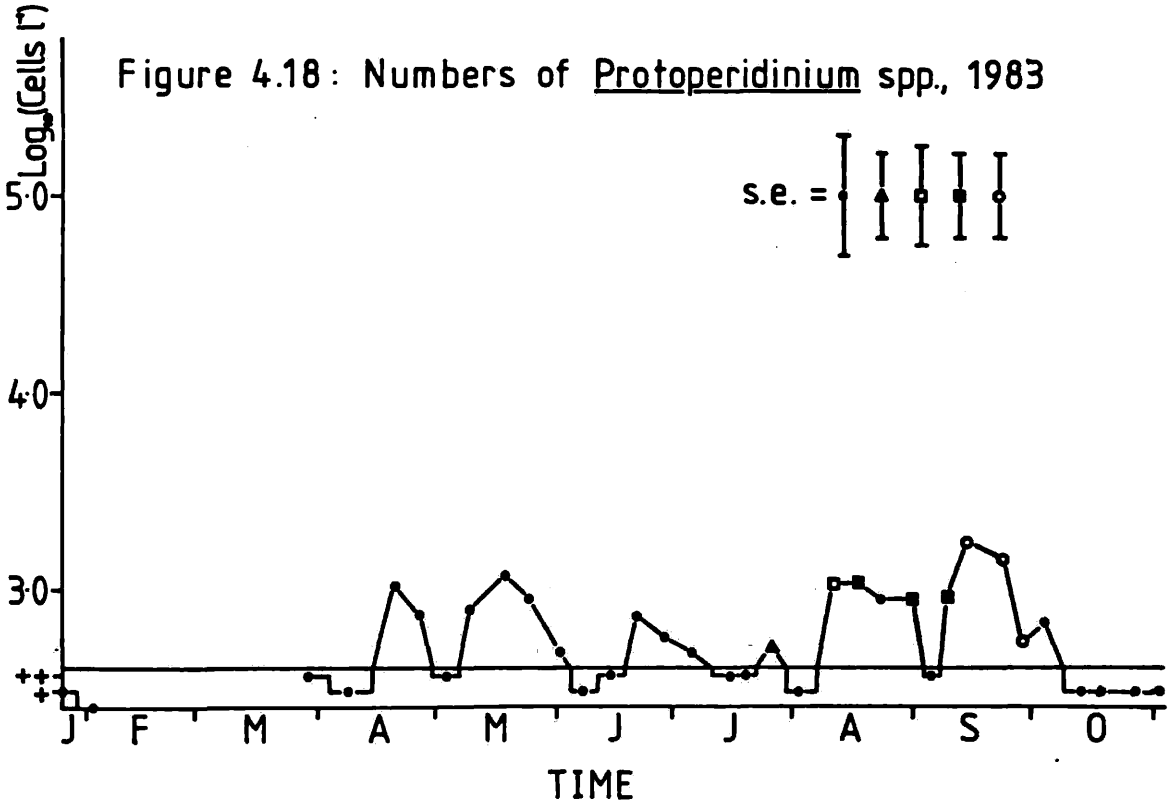


Figure 4.18: Numbers of Protoperidinium spp., 1983

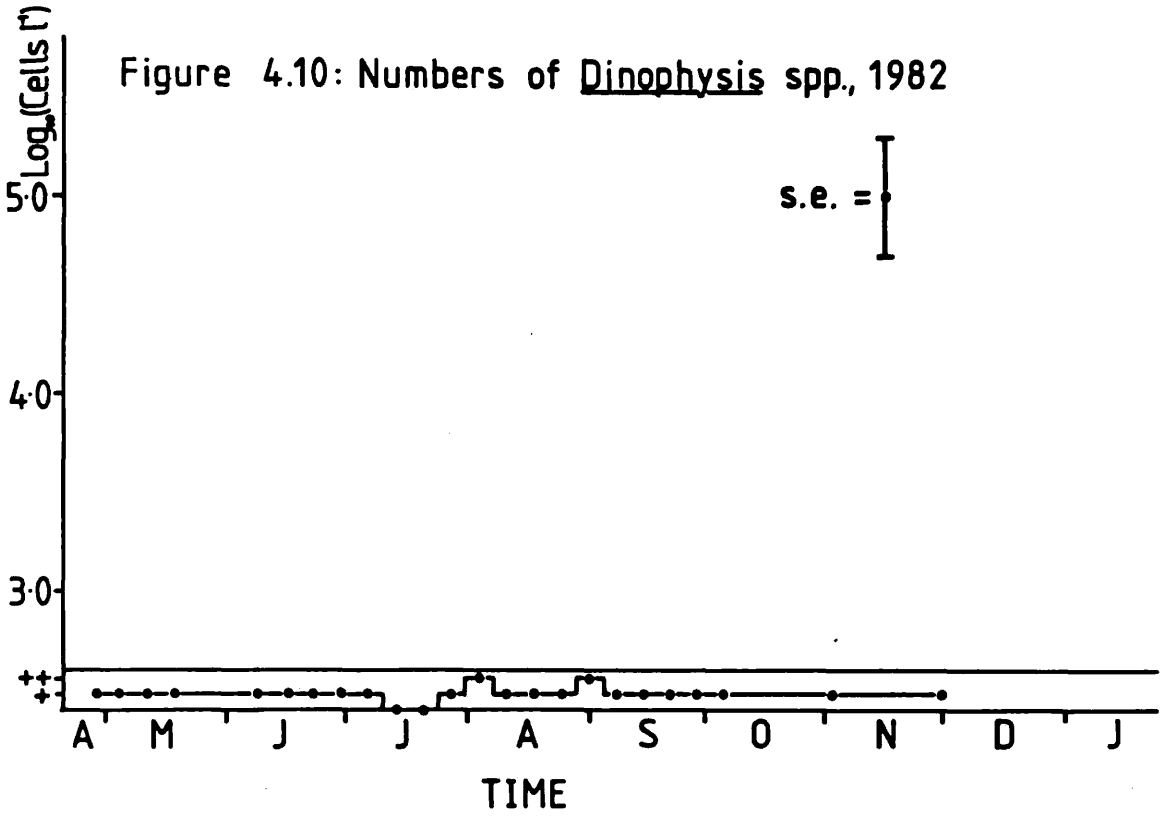


Figure 4.10: Numbers of Dinophysis spp., 1982

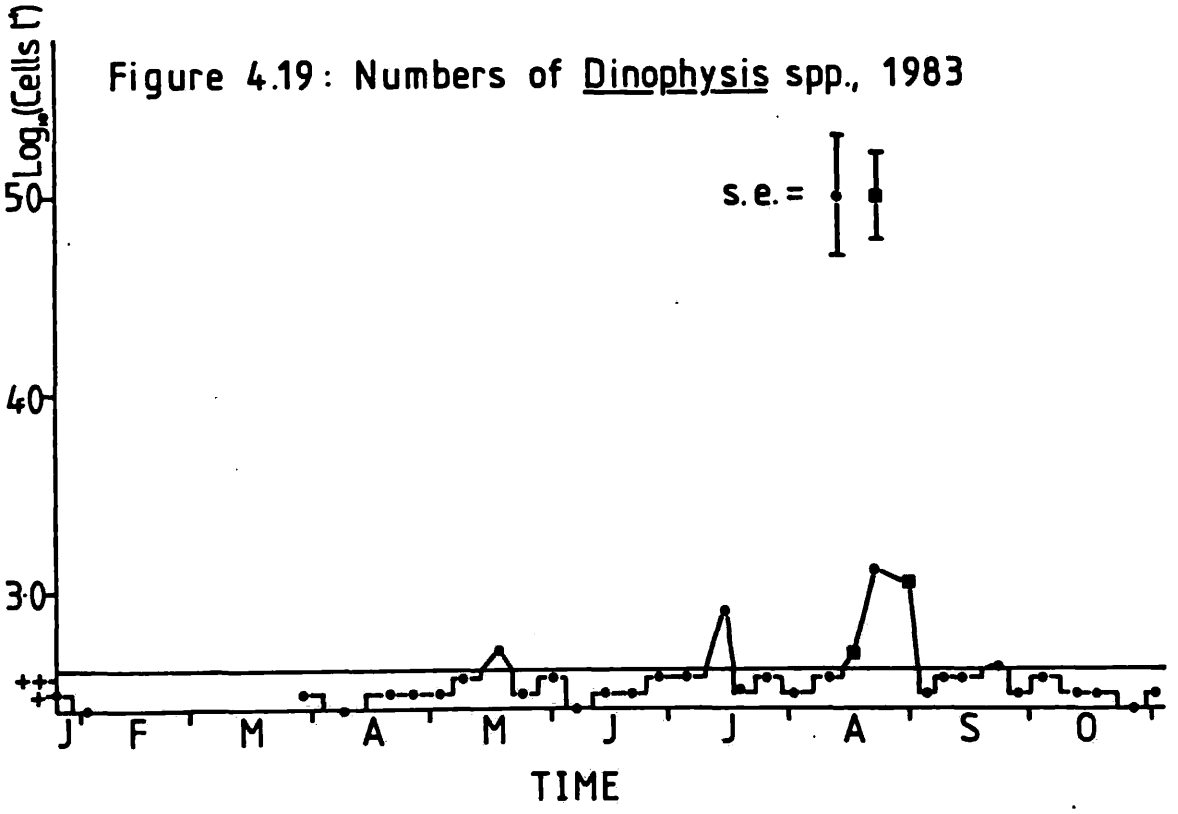


Figure 4.19: Numbers of Dinophysis spp., 1983

Figure 4.11: Chlorophyll values, 1982, Barcaldine pier

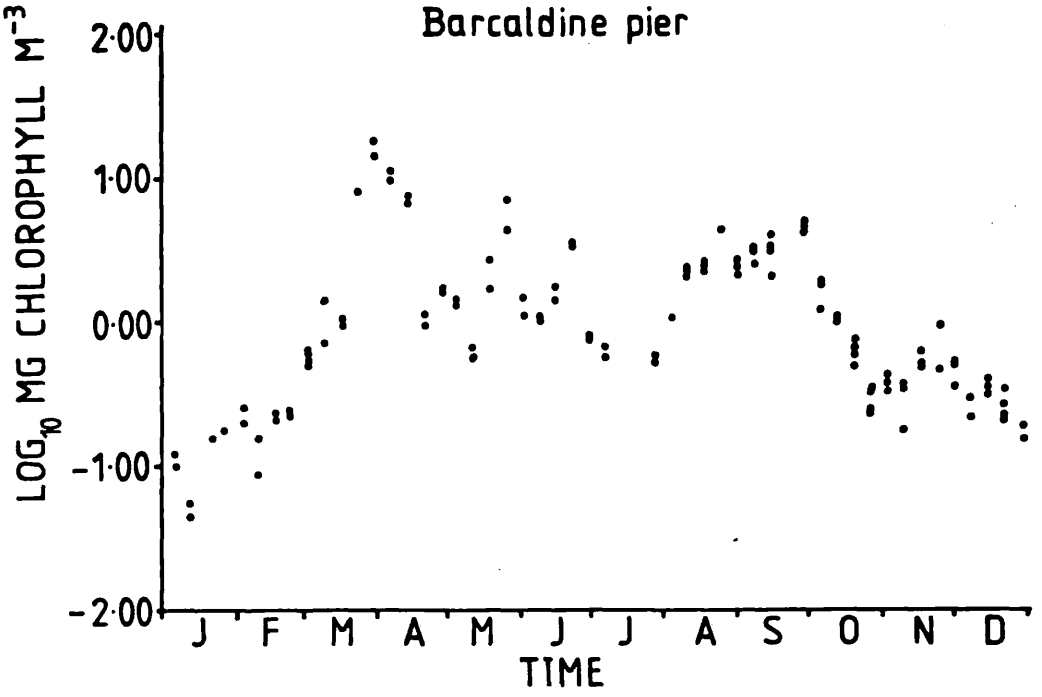
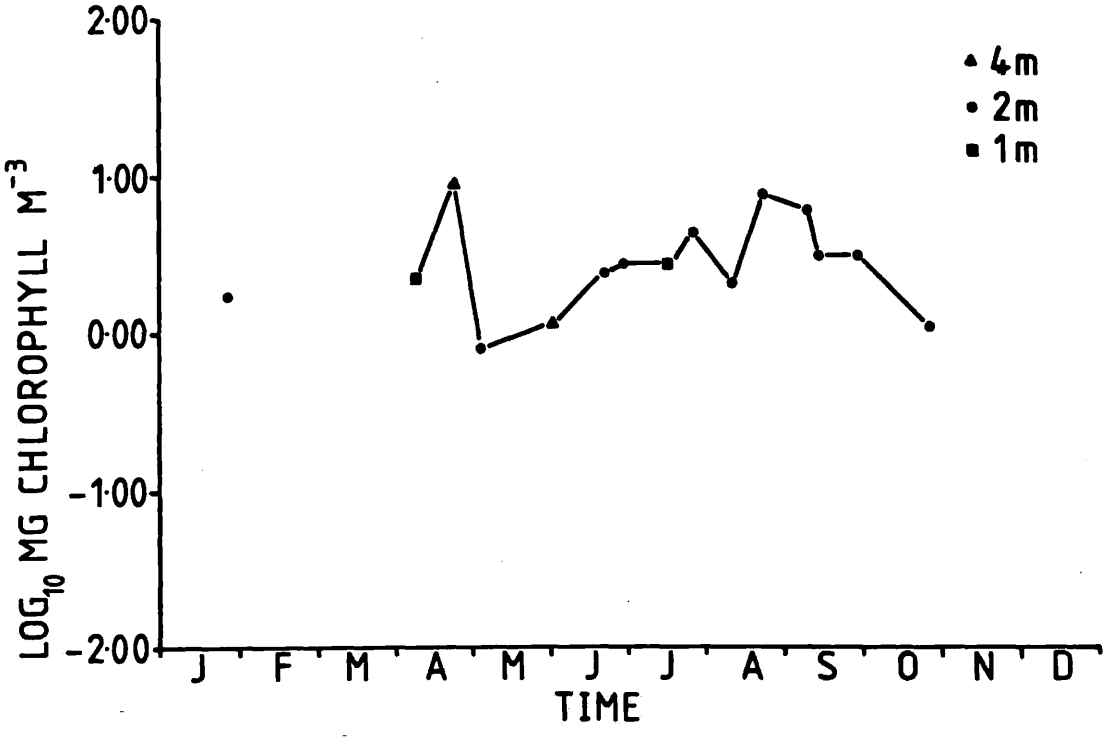


Figure 4.20: Chlorophyll values, 1983, C5



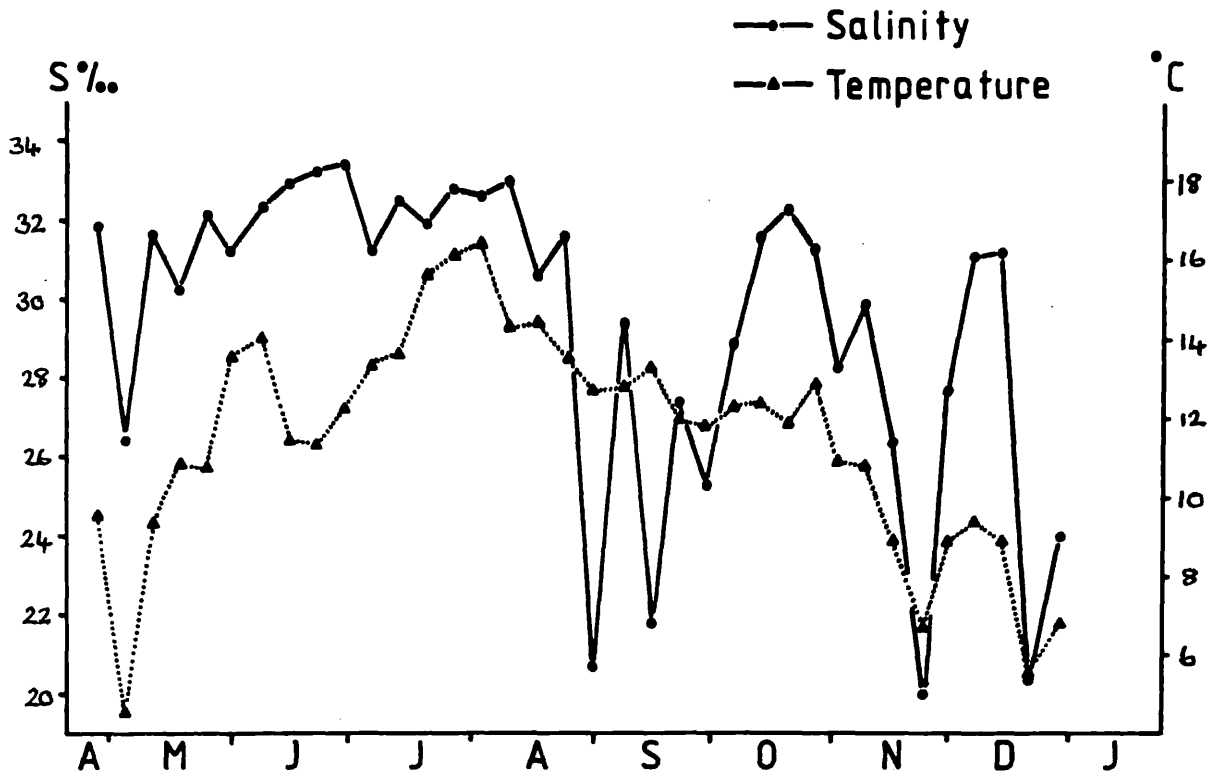


Figure 4.12 : Temperature and salinity at 2m, at Barcaldine Pier, 1982

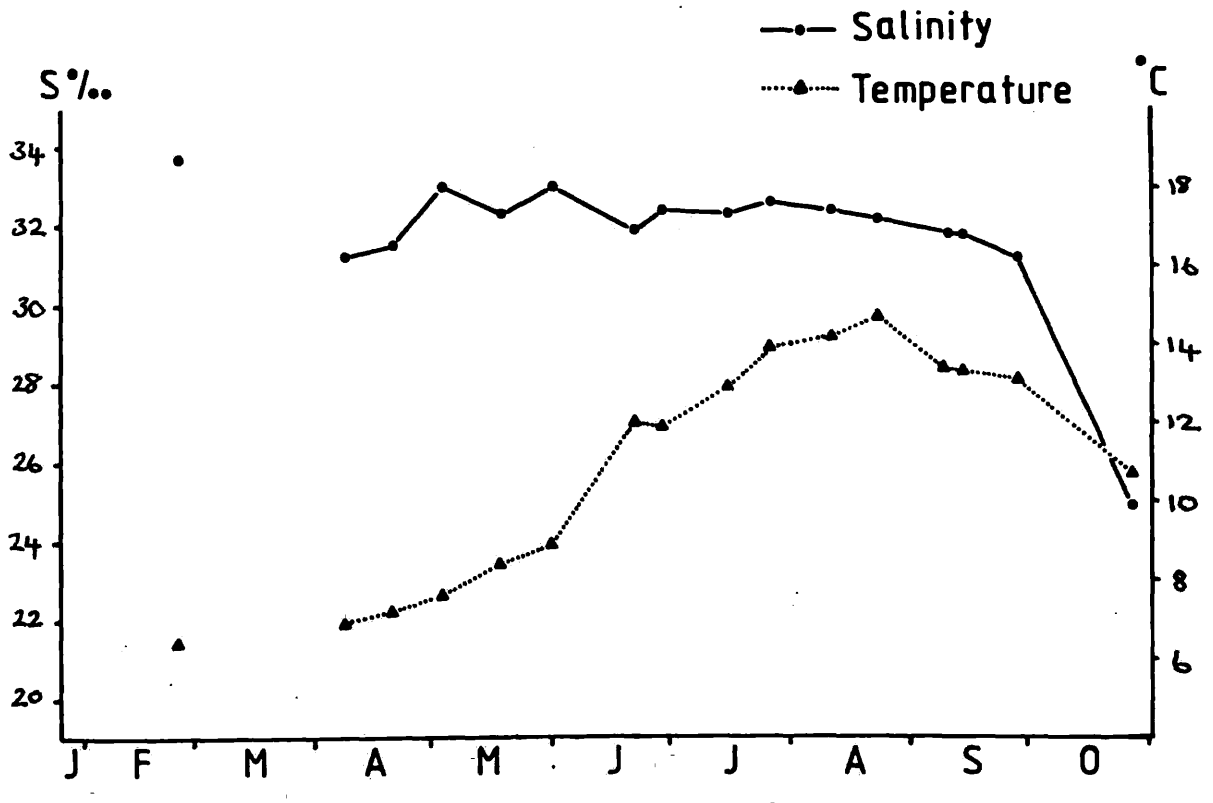


Figure 4.21 : Temperature and Salinity at 2m, at C5, 1983

(max. 33‰;min. 31.2‰) persisted throughout July until the middle of August after which the salinity began to drop due to increased rainfall. This decrease was most marked between the 24th and 31st of August when there was a drop in surface salinity of almost 11‰. This coincides with a drop in numbers of all species except G. polyedra which was abundant for the first time. By the time of the autumn maximum in dinoflagellate numbers the salinity was 29.4‰ and the temperature was 12.8°C.

Of other dinoflagellates encountered Dinophysis spp. were present for most of the year although never more than 400 cells per litre. The most abundant species of this group was Dinophysis acuminata. The most frequently occuring and the most abundant of the Protoperidinium species was P. bipes reaching a maximum of 1,300 cells per litre in mid-August. P. brevipes also occurred regularly. Other common species were P. ovatum during July and August and P. cerasus during September and October. Of the Ceratium species C. fusus and C. lineatum were the most important in 1982.

Tintinnids were present throughout most of the year, having maximum numbers around the middle of May, the beginning / middle of July and at the beginning of September. From observation of samples these peaks would seem to be related to the presence of organic debris.

1983

A list of motile thecate dinoflagellate species and their occurrence is given in Table 4.3. Table 4.4 covers other organisms. Table 4.5 gives abundances during the Gonyaulax tamarensis bloom and Table 4.6 shows the distribution of cells, with depth, during the Gonyaulax polyedra bloom. Total numbers of thecate and naked motile dinoflagellates are graphed in Figure 4.13. Abundant species (Scrippsiella spp., G. polyedra,

Prorocentrum micans and Ceratium furca) are graphed separately (Figs. 4.14 - 4.17). Figures 4.18 and 4.19 are graphs of Protoperidinium spp. and Dinophysis spp., groups where no species was numerically important. Figure 4.20 gives the chlorophyll data for C5 at 2m (or the nearest sample depth to this when 2m was not sampled). Full details of temperature, salinity and chlorophyll data collected are given in S.M.B.A. internal report number 114 (Lewis, 1983). Temperatures and salinities as measured at 2m at C5 are given in Figure 4.21.

On the whole 1983 had a greater dinoflagellate population than 1982. Chlorophyll concentrations were similar to those in 1982 if a little higher during June and July (which was unusually low in 1982). When the graph of total dinoflagellate numbers (Fig. 4.13) is compared to that for chlorophyll (Fig. 4.20) it is clear that the biomass of the April phytoplankton bloom must be mainly composed of other algal species. There was a drop in chlorophyll concentrations during May when the first peak of dinoflagellate numbers occurred. As most of these early dinoflagellates were pigmented this could imply that amounts of other phytoplankters might have dropped at this time.

The initial post-spring maximum in dinoflagellate numbers occurred in May. Numbers dropped at the beginning of June then increased a little to remain fairly stable over the rest of June and July until the second peak of numbers in the middle of August. This persisted through September and gradually tailed off in October although numbers had not dropped to their previous 1982/83 winter levels until the beginning of November.

Numbers of naked species seemed to reflect the trends shown by the armoured dinoflagellates. There seemed to be no clear trends in the diversity of naked species but this is probably a result of the difficulties in identification.

Scrippsiella spp. (max. 15,500 cells per l) dominated in May when there was a peak in total dinoflagellate numbers (max. 47,500 cells per l), which also included Gonyaulax tamarensis (max. 14,600 cells per l); Glenodinium spp. (max. 5,700 cells per l); Gonyaulax spinifera (max. 5,200 cells per l) and Heterocapsa triquetra (max. 3,700 cells per l). At the time the surface salinities were close to those of Firth of Lorne seawater (32.3‰ at 2m) and temperatures of around 8.5°C. There had been some salinity stratification of the water column during April but this gave way to a mixed situation by the beginning of May. The water column showed some stratification at the time of maximum dinoflagellate numbers and chlorophyll values showed a peak at around 6m. After the peak of numbers in the middle of May there was a sharp drop to the beginning of June, accompanied by a better mixed water column. The increased dinoflagellate population during June and July continued to be dominated by Scrippsiella spp. The water column showed a moderate stratification during this period.

As in 1982 there was a succession of species during the autumn bloom. This started with Gonyaulax polyedra (max. nos. 98,400 cells per l at 2m) at the end of August just as the Scrippsiella spp. dropped in numbers. It was followed by Prorocentrum micans (max. nos. 9,800 cells per l) during the middle of September and finally Ceratium furca (max. nos. 15,400 cells per l) became abundant at the end of September / beginning of October. The G. polyedra bloom occurred in a water column stratified with regard to salinity. The salinity had been slightly reduced in the surface layers (down to about 5m) from the typical values throughout July and August (32.6‰ at 2m to 32.2‰ at 2m). Despite possible mixing during September / October due to high winds the heavy rainfall caused the salinity stratification to strengthen and deepen until the last sampling date at the end of October. A study by Dr R.C.T. Raine on the decrease of phytoplankton in Loch Creran in September to December

of 1983 showed that the large armoured dinoflagellates (e.g. Ceratium spp.) persisted until mid-November. After this there was an increase in small armoured and naked forms but after the beginning of December the numbers of dinoflagellates were low (Raine and Tett, 1984).

Of the other motile dinoflagellates encountered Protoperidinium spp. were present in their greatest numbers and diversity during the post-spring and autumn blooms. They were also present in lower numbers during June and July. Among the species present P. brevipes and P. bipes were the most frequent and the most abundant, P. bipes having its maximum numbers (1,000 cells per l) during August and P. brevipes in September (12,000 cells per l). P. ovatum occurred in low numbers throughout the year and P. cerasus was also present fairly frequently especially during September - October. Dinophysis spp. were present during the whole of the year but achieved their greatest numbers in late August during the autumn bloom. Of these species D. acuminata and D. norvegica were the most common.

Tintinnids were present in the loch throughout 1983 in greater numbers than in 1982 (Table 4.4). Their greatest numbers occurred (during May) at the same time as the maximum abundances of dinoflagellates. They were distributed throughout the loch, their numbers being lowest in the upper loch (Table 4.5). Some tintinnid cysts were noted in the samples shortly after this time.

The May bloom of dinoflagellates during 1983 was notable for the presence of Gonyaulax tamarensis. A survey of the loch was carried out to ascertain its distribution (Table 4.5). On the sampling day there appeared to be moderate stratification throughout the loch. The upper loch also had a strongly brackish surface layer. The abundance of thecate species throughout the main basin of the loch was fairly even in the samples from 2m.

The upper loch contained much greater numbers of Glenodinium spp. (39,800 cells per l against 15,200 cells per l at Creagan bridge) and slightly greater numbers of G. tamarensis. Like station 3a the upper loch contained few Protoperidinium spp.

The distribution of cells with depth was measured during the Gonyaulax polyedra bloom in September (Table 4.6). Salinity was reduced down to about 4m on the two occasions sampled (Figs. 4.22 - 4.23) and this stratification perhaps accounts for the chlorophyll maximum at about 4m. Most photosynthetic dinoflagellates had greatest numbers at this depth (for example G. polyedra; Figs. 4.24 - 4.25). Non-photosynthetic dinoflagellates showed a fairly scattered distribution throughout the water column (for example Protoperidinium brevipes; Figs. 4.24 - 4.25). Different again was the distribution of Scrippsiella spp. which were most abundant in the surface layers (Figs. 4.24 - 4.25).

DISCUSSION

1982

The first peak of dinoflagellate numbers (mainly composed of Scrippsiella spp.) occurred after some warming of the water column. From work by Wall et al. (1970), Dale (1977b & 1978) and this thesis (Chapter 5) it is probably fair to say that the Scrippsiella population derived from cells excysted from resting cysts in the sediments. In the laboratory an increase in temperature is frequently used to initiate excystment although this does not appear to be a necessity (Binder and Anderson, 1983). It is possible therefore that the increasing temperatures during May allowed excystment of a suitable inoculum for the water column. Some cysts were present in the water column at this time. With the initial population available, increases in cell numbers would occur when conditions were suitable i.e. when

Figure 4.22 : Temperature, salinity, and chlorophyll profile of station C5 on 9/9/83

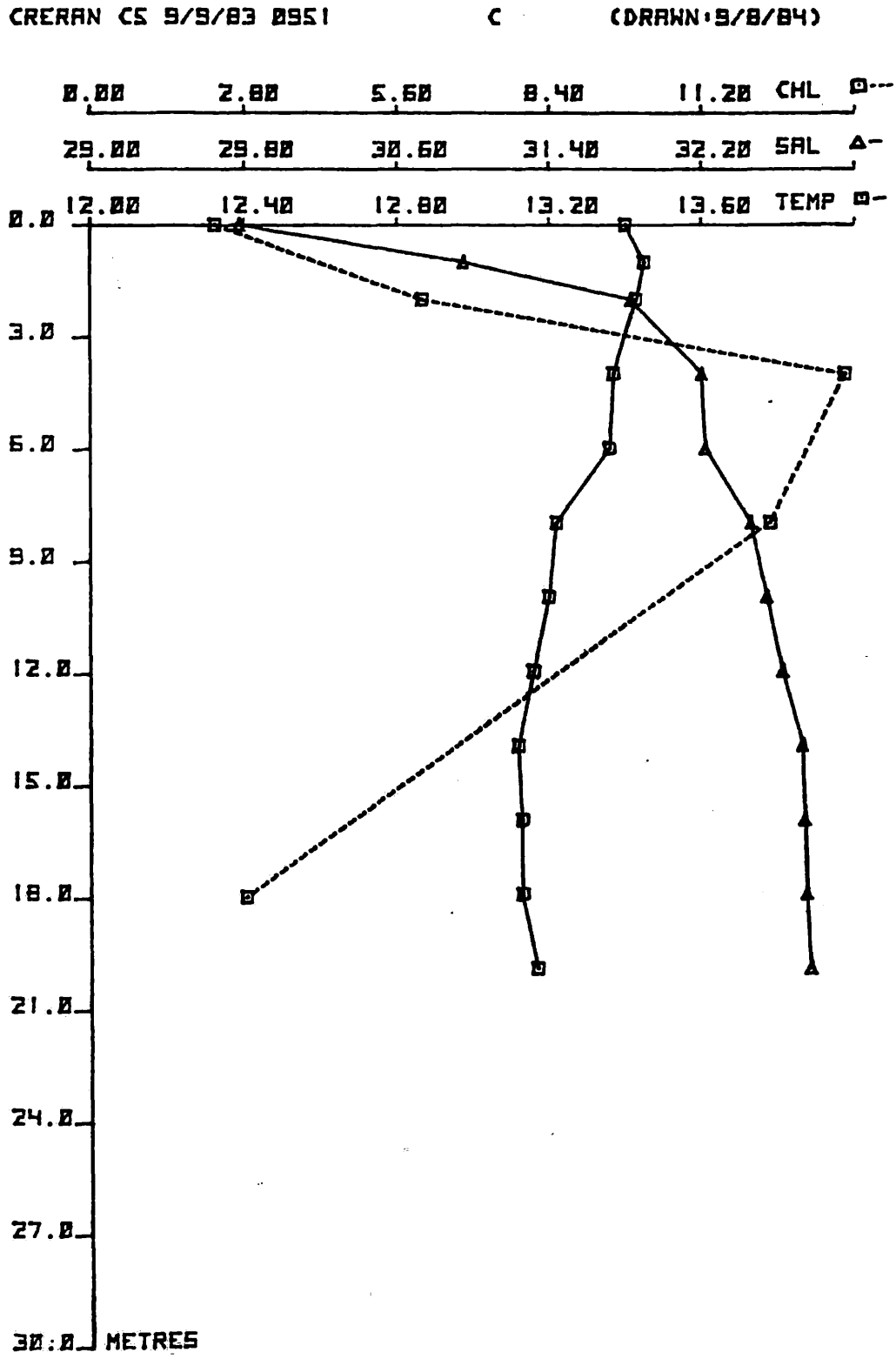


Figure 4.23 : Temperature, salinity, and chlorophyll profile of Station C5 on 14/9/83

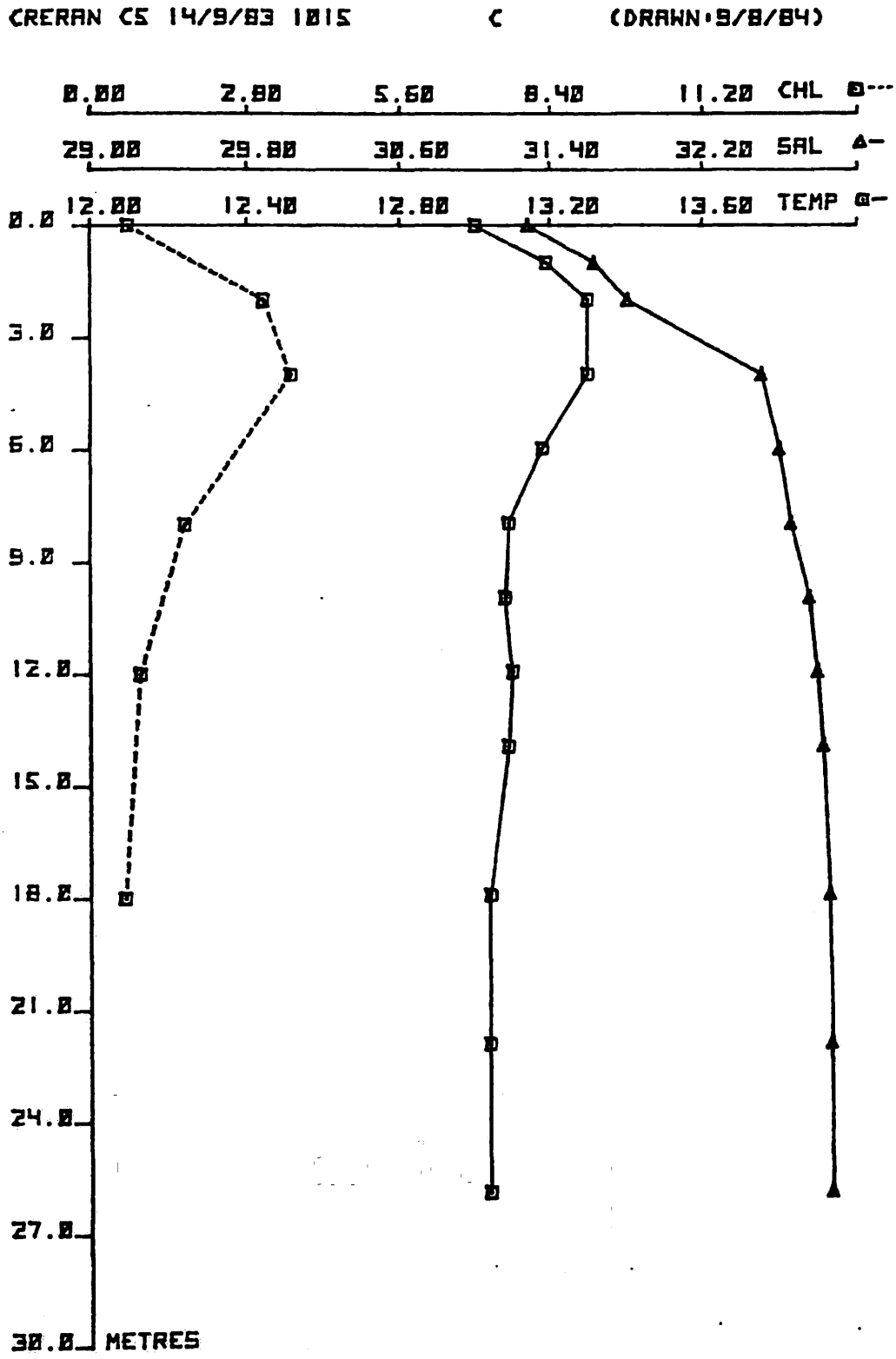


Figure 4.24: Distribution of cells with depth, 9/9/83

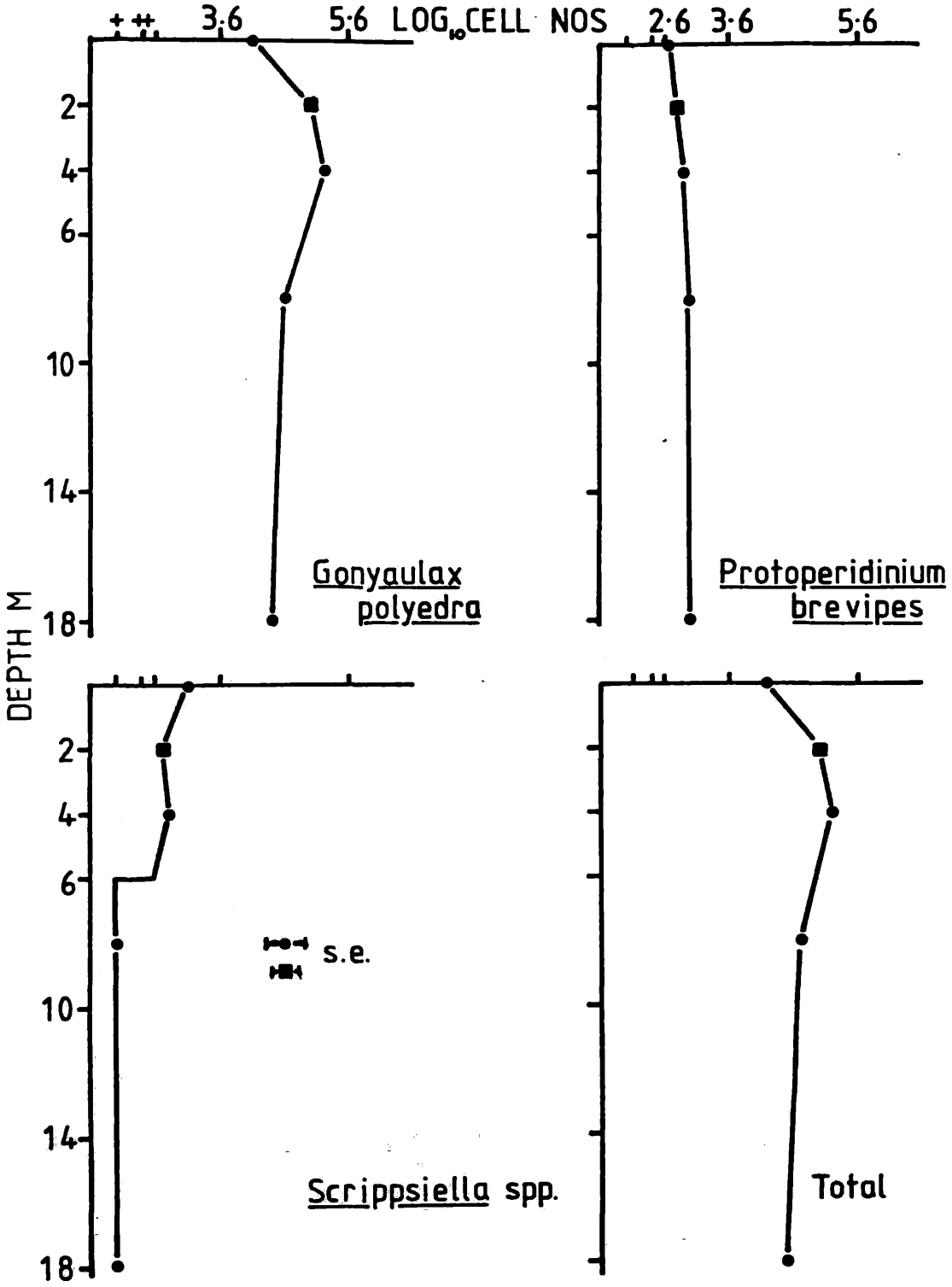
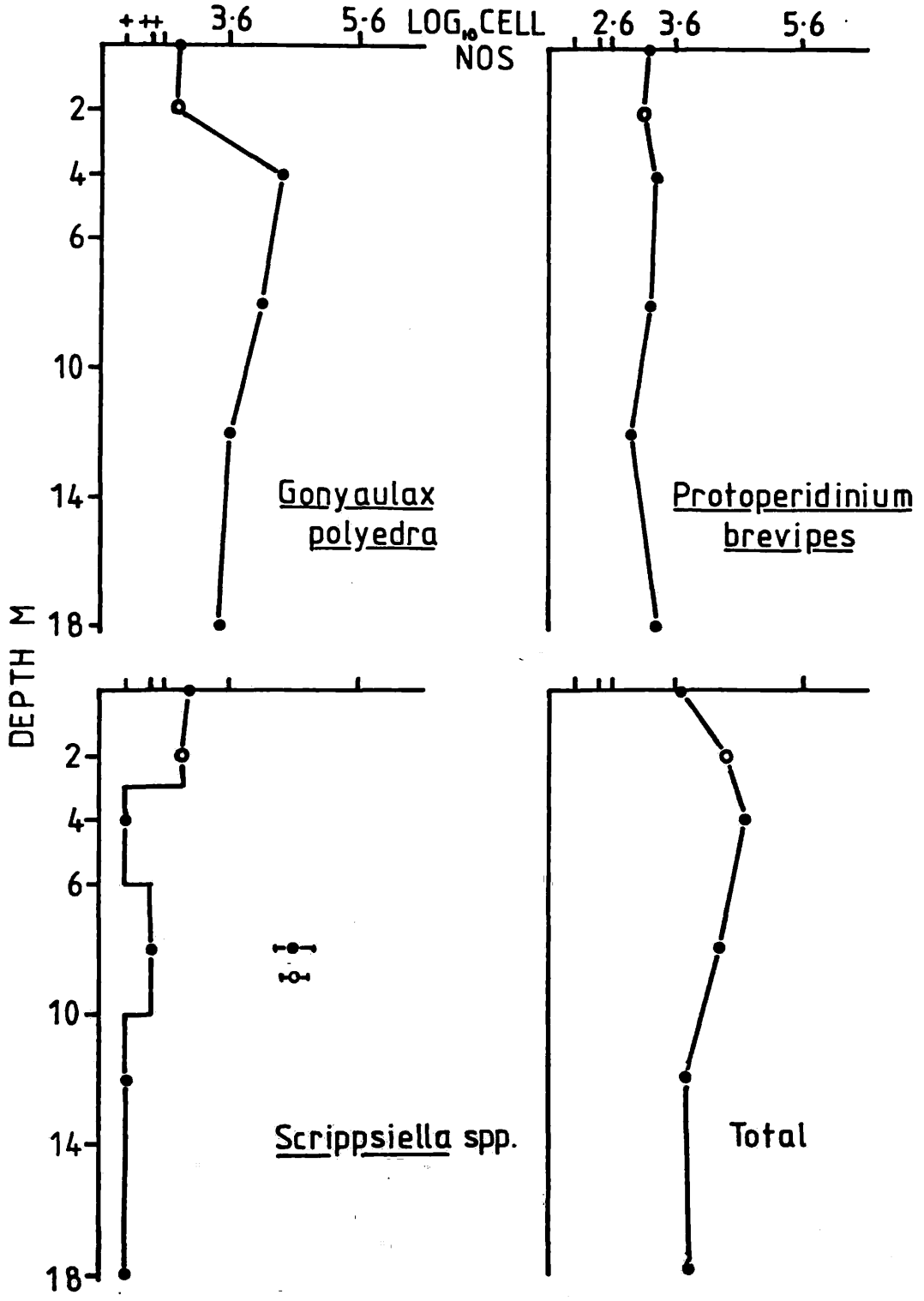


Figure 4.25: Distribution of cells with depth, 14/9/83



growth rate exceeded the sum of the rate of flushing from the loch and the rate of grazing. So why the decline in numbers at the end of August just when conditions seem most suitable for other dinoflagellates? Anderson et al. (1983) observed that populations of Gonyaulax tamarensis can be severely depleted by encystment. Observations during this study suggest that cysts once formed sink rapidly. Table 4.2 shows that cyst formation was taking place between the end of July and the middle of August, thus encystment in addition to grazing and flushing may be amongst the reasons for the decline in the Scrippsiella population.

The autumn bloom of dinoflagellates starts with Gonyaulax polyedra, a cyst-forming dinoflagellate. It appeared during June and July in small numbers implying that although cysts had hatched conditions were not suitable for its growth. It first bloomed at times of marked stratification due to decreased surface salinities. Decreased salinity or stabilisation perhaps favour its growth. This could be for a number of reasons. Decreased salinity indicates increased freshwater entering the loch, which possibly brings terrestrially derived substances with it aiding growth (for example humic materials) and might also be associated with increased exchange with the sea which leads to increased nutrient concentrations. The decreased salinity also probably indicates increased turbidity and decreased light penetration. In laboratory experiments G. polyedra has been shown to adapt to low light situations (Prézelin and Sweeney, 1979).

Prorocentrum micans followed on from Gonyaulax polyedra in the autumn succession. It appears to be present in low numbers for most of the year. Experimental work by Braarud and Rossavik (1951), Kain and Fogg (1960), and Mahoney and Mclaughlin (1979) suggest it has a wide salinity tolerance (20-40‰). The work of Braarud and Rossavik (1951), Silva (1959), and Kain and Fogg (1960) suggests an optimal growth at 20-24‰. P. micans also has

wide temperature tolerances, the maximum growth rate being found at temperatures above that normally encountered in the sea (Kain & Fogg, 1960). Barker (1935) gave the optimum temperature for its growth to be 25°C. The lowered salinity and increased temperature at this time of the year possibly favour its growth.

Ceratium spp. were also present at this time of year. They were not observed in the loch earlier in the year and as they probably do not have cysts the population probably originated from outside the loch. There is evidence for the presence of Ceratium spp. off the Scottish west coast in May, June and July (Robinson, 1965; Holligan et al., 1980) and in this study they were found in the Firth of Lorne in July (see Chapter 6).

Of other species present Protoperidinium spp. occurred in their greatest numbers during July, August and September. Protoperidinium spp. as a group possibly show several different strategies. Certainly many of them are cyst forming (see Chapter 8), some are probably brought from outside the loch (for example Protoperidinium depressum) and yet others may be constant members of the loch phytoplankton (for example Protoperidinium bipes). However, as they are never present in large numbers these differences are difficult to establish precisely. Dinophysis spp. appeared to be present throughout most of the year.

1983

The first peak of dinoflagellate numbers in 1983 occurred in May, a month earlier than in 1982. There had been a gradual warming of the water column during April although not as marked as the temperature increase that preceded the post-spring peak of numbers in June 1982 (6.9°C - 8.4°C from April to mid-May in 1983 compared to 9.3°C - 14°C in 1982. This 1983 maximum of numbers was not composed exclusively of Scrippsiella spp. Although this was the dominant group of species, considerable numbers of other

dinoflagellates were also involved, namely Gonyaulax tamarensis, Glenodinium spp., Gonyaulax spinifera, and Heterocapsa triquetra. The reasons for the differences are not clear. The salinities in 1983 were slightly higher and the temperatures slightly lower than the 1982 bloom. Scrippsiella spp., G. spinifera, and probably H. triquetra are all cyst forming species. Conditions must have been suitable for excystment earlier in the year although temperature would not appear important here. There is evidence that temperature initiation may not be a necessary corollory to excystment (see Chapter 8). Some varieties of G. tamarensis particularly recorded on the east coast of the United States form cysts (e.g. Anderson et al., 1982). However, cysts of this type have not been found in Loch Creran (see Chapter 7) or in the type locality (Tamar estuary; Dale, Pers. comm.) and it would seem that perhaps some varieties are not cyst forming. G. tamarensis has not been recorded in L. Creran previously and although this may be due to misidentification it would seem likely that it has been introduced to the loch by exchange with the Firth of Lorne. Chapter 6 shows that it was present in the Firth of Lorne later in the year. Little is known about the algae identified here as Glenodinium spp.; its increased numbers in the upper loch may indicate an ability to exploit low salinity conditions. There has been some experimental work on H. triquetra (Barker 1935, Braarud and Pappas 1951) that suggests it has a wide salinity tolerance but a lower temperature optimum than some other dinoflagellates. The lower mean temperatures may have contributed to the success of this species in 1983. There is a paucity of experimental information on conditions governing the growth of other species. Obviously conditions were more favourable in 1983 than in 1982 as not only was there a greater variety of species present earlier in the year, they were also present in greater abundance than in the previous year.

Following this first 1983 maximum, numbers decreased in much the same way as in 1982 although a little earlier than in that year. The tintinnid population was greater in 1983 at this time and may have contributed to the decline. They were frequently seen to take or contain the smaller dinoflagellates. Numbers of dinoflagellates increased during June and July. These increased numbers were mostly due to Scrippsiella spp. but as in 1982 their numbers decreased dramatically at the end of August just before the autumn bloom of other dinoflagellates. As in 1982 there was some cyst formation, although not so marked as in that year. The Scrippsiella spp. were present mostly in the surface layers of the water column (Table 4.6) and the rapid increase in freshwater entering the loch as shown by the decreased salinities (of 1982 and 1983), may have represented increased flushing of these layers, in which case they were probably washed out of the loch.

The succession of species in the autumn bloom of 1983 was more clearly defined than, although similar to, that of 1982. As in 1982 it started with Gonyaulax polyedra which reached much greater numbers in 1983 than in 1982. The slightly higher temperatures in 1983 may have contributed to this increased success, Meeson and Sweeney (1982) showed G. polyedra to have improved growth up to 20 °C. The formation of G. polyedra cysts was sufficient during 1983 for them to be found in the water column towards the end of the bloom (see Chapter 5).

Prorocentrum micans followed Gonyaulax polyedra in 1983 as in 1982; P. micans was perhaps favoured by the lower salinities and higher temperatures found at this time. Finally in the autumn succession Ceratium furca became important at the end of September. There is some evidence (see 1982) that it may originate from outside the loch. Experimental work on cultures of Ceratium furca suggests that its growth rate is similar to that of other dinoflagellates (Nordli, 1957; Meeson and Sweeney, 1982; Sakshaug et al., 1984) so its late appearence in the year

is not due to slow growth. Comparative work between Ceratium furca and Gonyaulax polyedra at different temperatures and irradiances by Meeson and Sweeney (1982) suggests that under low light conditions C. fuca can grow where G. polyedra does not survive. Nordli (1957) shows that C. furca, Ceratium fusus, Ceratium tripos and Ceratium lineatum had optimal growth at low salinities (20‰). Although there are many other complex factors at work in the natural environment this experimental evidence perhaps provides some clues to the success of Ceratium in the later part of the year with decreased light and salinity. In 1983 Ceratium reached higher numbers than 1982 presumably indicating more suitable conditions for growth in this year.

Protoperidinium spp. were more abundant during 1983 although never reaching large numbers. Certain species seem to be present most of the time (P. bipes, P. brevipes) and perhaps these are constant members of the loch phytoplankton albeit in very small numbers at certain times of the year. Others are known to be cyst forming (P. leonis. P. pentagonum) and occur sporadically throughout the summer and autumn. Finally some only appear irregularly and perhaps originate from outside the loch (P. depressum).

Dinophysis spp. were again present throughout most of the year, and cetain species (D. acuminata) could perhaps be regarded as resident members of the Loch Creran phytoplankton. They achieved their maximum numbers during the autumn bloom associated with Gonyaulax polyedra.

The vertical distribution of dinoflagellates is interesting (Figs 4.24 - 4.25). The photosynthetic dinoflagellates concentrated about the halocline. It is possible they are collected there by concentrating factors but more probably they have employed their motility to arrive at an optimal position

compromising between maximum light absorbtion and suitable position for nutrient gathering. The exception to this are the Scrippsiella spp. which concentrate in the surface layers. This may reflect a preference for the lower salinities found there, an ability to utilize very low nutrient concentrations, an ability to withstand any photoinhibition experienced in these layers or a combination of all these. The even distribution of non-pigmented dinoflagellates would seem to indicate that whatever nutrition they require is distributed throughout the water column.

Comparison between 1982, 1983 and other Creran data

To assess which species might be described as 'typical' for a year, species present in 50% or more of the samples for each year are listed in Table 4.7. As can be seen from this table, seven such species are listed for 1982 and twelve for 1983. This probably reflects the greater abundance of dinoflagellates in 1983 as the number of species recorded at least once in each year was the same (Table 4.8). Of all the species the following occur in the lists for both years and therefore are taken to represent typical species for the loch:- Dinophysis acuminata, Gonyaulax spinifera, Heterocapsa triquetra, Prorocentrum micans, Protoperidinium bipes, Protoperidinium brevipes and Scrippsiella spp.

TABLE 4.7

Species present in >50% of samples taken

1982	1983
Protoperidinium bipes	*Protoperidinium bipes*
P. brevipes	*P. brevipes*
Prorocentrum micans	*P. cerasus*
Dinophysis acuminata	*P. ovatum*
Gonyaulax spinifera	*Prorocentrum micans*
Scrippsiella spp.	*Dinophysis acuminata*
Heterocapsa triquetra	*D. norvegica*
	Ceratium lineatum
	Gonyaulax spinifera
	G. polyedra
	Scrippsiella spp.
	Heterocapsa triquetra

TABLE 4.8

Numbers of different species present

	1982	1983
Protoperidinium spp.	20	21
Prorocentrum spp.	3	2
Dinophysis spp.	6	7
Ceratium spp.	4	4
Gonyaulax spp.	6	8
Other	8	7
TOTAL	47	49

In both 1982 and 1983 the first peak in dinoflagellate numbers occurred in May / June after some warming of the water column. In both years *Scrippsiella* spp. were the dominant species although in 1983 *Gonyaulax tamarensis* also occurred at this time. In 1979 a bloom of *Scrippsiella* spp. also occured at this time at Barcaldine Pier (Tett, Drysdale and Shaw, 1981).

All of these Scrippsiella blooms were of the same order of magnitude, that is about 10-12,000 cells per litre. In all years there was after this initial maximum, a drop in numbers of Scrippsiella spp. followed by an increase in late June and steady numbers throughout July and August. Common to all these years also is the sharp decline of Scrippsiella spp. at the end of August. The main reason for this would seem to be increased flushing of the surface layers at this time and in some years it is also aided by encystment of the population. During the summer period (late June, July and August) other dinoflagellates are present including Heterocapsa triquetra, Protoperidinium spp., and Diplopsalis spp.

Late August with the decreased salinity seems to have been the start of the autumn succession of dinoflagellate species. This was started in 1982 and 1983 by Gonyaulax polyedra which may have previously excysted from the sediments. Although in neither year did the G. polyedra bloom last long, in 1983 the organism was more abundant than in 1982 (up to 100,000 cells per litre in 1983 against 10,000 cells per litre in 1982) and its 1983 bloom terminated in a period when encystment was observed. In 1979 Gonyaulacoids are figured as occuring in high numbers (30,000 cells per l) at this time and although species were not distinguished G. polyedra is illustrated below the graph (Tett, Drysdale and Shaw 1981). After this first bloom the subsequent period of relatively high temperatures and low salinities was probably found suitable by Prorocentrum micans, an alga that appeared to have been present in the loch throughout the year in small quantities. Finally in both years there was an increase of Ceratium spp. The increase was more marked in 1983 when conditions may have stayed suitable in the loch for longer. Dinophysis spp. would appear to be present in the loch for most of the year. None of these latter species are mentioned in the 1979

report, probably because of their lack of abundance. Naked species appeared to follow the abundances of armoured species and on the whole high dinoflagellate growth seems to be favoured by the onset of stratification of the water column.

Chlorophyll data for 1982 and 1983, not surprisingly do not give any helpful indication of dinoflagellate numbers and must only be regarded as an indicator of total phytoplankton biomass. However, it remains similar in amount and cycle in 1982 and 1983 and within the envelope described for Loch Creran by Tett and Wallis (1978). This implies that 1982 and 1983 can be regarded as normal years.

On the basis of this evidence three patterns of occurrence can perhaps be discerned.

1. Species present in the loch as motile cells all year round although sometimes in very low numbers. (e.g. Dinophysis acuminata, Prorocentrum micans, Protoperidinium bipes)

2. Species present in the loch all year round by virtue of encysted stages, sometimes present in the plankton as low numbers of motile cells, occasionally in abundance when conditions are suitable (e.g. Scrippsiella spp., Gonyaulax polyedra)

3. Species which are brought into the loch in sea-water from the Firth of Lorne. These occur sporadically in small numbers but occasionally remain in the loch long enough to become abundant. (e.g. Protoperidinium depressum, Ceratium fusus, Ceratium furca). These species could be described as visitors.

These perhaps represent three different life-strategies.
a) Maintenance of a residual population within the loch as motile cells. This requires growth rates high enough or behaviour such that the population is not flushed from the loch.

b) Maintenance of a population within the loch by means of a cyst stage. (There is further discussion of this in Chapter 5).

c) Maintenance of a population in the Firth of Lorne or further offshore.

It should be noted that a species from category 3 could easily move into category 2 if it had a cyst stage in its life-cycle or into category 1 if its division rate was fast enough or its habits such that it was not flushed from the loch.

Comparison with other surveys

Western Scotland

Etive is another fjordic sea-loch that opens into the Firth of Lorne. Wood *et al*. (1973) note that during the summer and autumn photosynthetic dinoflagellates (*Scrippsiella trochoidea*, *Heterocapsa triquetra*, *Dinophysis* spp., *Prorocentrum micans* and *Gonyaulax* spp.) made a significant contribution to the total phytoplankton of Loch Etive. Tett (1969, unpubl. obs.) found small, armoured, brown dinoflagellates (SABD) (including *Scrippsiella* spp., *Heterocapsa triquetra*, and small gonyaulacoids), and *Diplopsalis* spp. to be most common from April until August. *Protoperidinium* spp. were present most often between April and August. *Ceratium* spp. increased in August and were common in September. *Prorocentrum* occurred occasionally throughout the year but reached a peak in September and *Dinophysis* spp. were present throughout the year. However, numbers were very low the maximum being of SABD at around 1,000 cells per litre. These surveys indicate that the composition and succession of dinoflagellates is very similar to that of Loch Creran. However, the numbers described for each species are much lower than those found in L. Creran. The similarity between the two lochs is to be expected if it is considered that their source

water will have been similar over their recent history. The lower numbers of dinoflagellates described in Loch Etive may be due to the lower salinities encountered in the surface layers of the loch because of the large amount of fresh water run-off it receives. In general, this run-off causes decreased surface concentrations of nitrate and phosphate (Solórzano and Grantham, 1975).

Dinoflagellates seem only to have occurred sporadically in the small rapidly flushed Loch Ardbhair in Sutherland. Gowen et al. (1983) list taxa present throughout the year. No dinoflagellates were found before June, Ceratium spp. were present at the beginning of June followed later in the month by Protoperidinium divergens and small Protoperidinium spp. No dinoflagellates are listed for the rest of the year, except at the end of September when Ceratium fusus and Gymnodinium spp. occur. The hydrography (detailed by Gowen et al., 1983) is probably the most important factor here. The circulation of L. Ardbhair is controlled by tidal exchange with a flushing rate of only a few days, and so the phytoplankton is dominated by that present in the source water of Eddrachilis Bay. Eddrachilis Bay is generally well mixed and its phytoplankton is probably light limited. It is only when there was stratification in the bay that dinoflagellates occurred in L. Ardbhair.

Marshall and Orr (1927) found the occurrence of dinoflagellates in Loch Striven was irregular and they were never present in large numbers. Increases were coincident with low salinities and a rise in temperature. The most common species during these increases was Heterocapsa triquetra having maximum numbers (41,150 cells per litre) at the head of the loch in October. Other abundant species were Protoperidinium bipes (10,650 cells per litre) at the beginning of April and Diplopsalis spp. at the end of August. Large Protoperidinium spp. were common in net tows from April onwards at the surface

and after November at the bottom having their maximum in August. Ceratium spp. appeared in net samples at the end of July remaining abundant until December. They noted a bloom of H. triquetra in Loch Long.

Tett (1969) collected samples from Keppel pier (Milport). This work gives the most detailed account of dinoflagellate succession available for the area. Summarized in general terms the numbers of dinoflagellates were low in the winter; in the spring the Protoperidinium spp. increased in numbers remaining at abundances of 100 - 1000 per litre during the summer and decreasing in numbers in the autumn. Scrippsiella spp. was present for much of the year, reaching peak densities in July / August (up to 100,000 cells per litre). Dinophysis spp. also increased in spring reaching maximum numbers (around 400 cells per l) in the summer and declining quickly in the autumn. Ceratium spp., and Prorocentrum micans reached their highest densities in the late summer / early autumn (up to 10,000 cells per l of Ceratium longipes, around 15 cells per l of P. micans).

The lochs around the Clyde described by Marshall and Orr (1927) and Tett (1969) are generally nutrient enriched compared to those further north and so greater abundances of cells might be expected under good conditions. The types of species they describe and their succession would appear to be generally similar to that found in Loch Creran albeit with greater abundances of certain species. Gonyaulax spp. do not appear to be as important, but this may be a function of identification problems. In the Clyde Ceratium spp. seem to be more prevalent with Ceratium longipes, a species rarely encountered in this study, important in the late summer / autumn.

Rest of the British Isles

In general surveys from other areas of the British Isles do not seem to be closely related to the patterns observed in Loch Creran. This is probably because most of the sampling areas are more coastal than estuarine and because many (particularly net samples) would have missed small dinoflagellates unless they were present in extremely large numbers (e.g. Scrippsiella spp., Heterocapsa triquetra).

The most interesting comparisons arise from the paper by Holligan, Maddock and Dodge (1980). Samples were collected from all around the British Isles, concentrated on a 10μm sieve and only a qualitative analysis is presented. By use of correspondance analysis four groups of species were defined. The two groups that are relevant to this study are the Scrippsiella group and the Prorocentrum micans group. The Scrippsiella group also contains Heterocapsa triquetra and Gonyaulax triacantha. It is associated with well-mixed water, variable temperatures and possibly low salinities (<34.25‰). The P. micans group contains various Ceratium spp., Dinophysis acuminata, Dinophysis acuta, Gonyaulax grindleyi and Gonyaulax spinifera. It was associated with variable stability conditions and low salinities. The patterns of distribution of these two groups would seem to fit in well with what is observed in Loch Creran.

With regard to the general seasonal cycle of dinoflagellates in British waters there seems to be two patterns. The first consists of a post-spring increase in numbers of Ceratium spp. followed by mixed species in the summer, and finally a further Ceratium bloom in the autumn (Sykes, 1969; Horwood et al., 1982). The second shows a gradual increase in many species from May onwards, with a peak in about July and a gradual decline into the

autumn (Lebour, 1917; Robinson, 1965; Dodge and Hart-Jones, 1974, 1977; Holligan and Harbour, 1977; Maddock et al., 1981; Robinson, 1983). These patterns do not seem to relate to geographic locations.

Most dinoflagellate surveys record a greater variety and abundance of Ceratia than was found in Loch Creran. They also seldom mention Scrippsiella spp. and Heterocapsa triquetra probably because of their small size and the methods of collection. Holligan and Harbour (1977) mention Heterocapsa triquetra occuring from May - July in the English Channel in quite large numbers at its peak (86,000 cells per l). There is no mention of this species in other descriptions of work in the Channel (Lebour, 1917; Maddock et al., 1981). Lebour (1917) does, however, mention other small species for example Protoperidinium bipes. She notes Prorocentrum micans has its peak in September and Ceratium fusus in August. Dodge and Hart-Jones (1974 & 1977) mention Scrippsiella spp. and Heterocapsa triquetra but these occurred in relatively few of their samples in the latter study. At Blyth, Northumberland 1971-72 they occurred in April and August, a timing similar to that in L. Creran. Dinophysis norvegica was also important in their samples. They show dinoflagellate abundance to be closely related to surface water temperatures.

Thus Loch Creran, contains a broadly similar assemblage of species to the rest of the British Isles. Differences are probably due to its enclosed estuarine situation and northern latitude (with relatively cooler temperatures).

The Norwegian fjords

Dramsfjord / Oslofjord (lat. 59.00 N)

Dramsfjord is separated from Oslofjord by a shallow sill. These two fjords were studied in March to December 1951 by Braarud, Føyn and Hasle (1958). They receive a large freshwater input. Cycles in the inner Dramsfjord and Oslofjord were markedly different perhaps because of the differing hydrographic regimes in each. The situation in the outer part of Oslofjord was more similar to that in Creran. There were small peaks of Prorocentrum micans, Gonyaulax polyedra and ceratia in May, and a fairly high level of dinoflagellates throughout the summer months with a second peak of ceratia towards the end of August. The species recorded were very similar to those in L. Creran with possibly a greater importance of Ceratium species. Four common species are discussed as being abundant at certain times of the year. Of these P. micans and G. polyedra had their peak abundances (3,240 and 2,160 cells per litre respectively) in May unlike Creran. Scrippsiella trochoidea had its peak in April / May (1,500 cells per l) and Heterocapsa triquetra in September (12,000 cells per l).

Trondheimsfjord (lat. 63.25 N)

The cycle in Trondheimsfjord was studied during 1963 - 1966 and 1970 - 1971 by Sakshaug (1972) and Sakshaug and Myklestad (1973) and appears very similar to that of L. Creran. There was a bloom of dinoflagellates in April / May with Gonyaulax tamarensis and Scrippsiella trochoidea predominating. A mixed, increasing population ensued over the summer months including many Protoperidinium spp., Gonyaulax spp. and Heterocapsa triquetra. In late summer / Autumn Scrippsiella trochoidea

became important once more along with Prorocentrum micans and Ceratium spp. Sakshaug points out the complete absence of Gonyaulax tamarensis after its May bloom and considers that it is restricted to this time of the year.

Hardangerfjord (lat. 63.10 N)

Hardangerfjord was studied by Braarud (1974 and 1976) and Braarud et al. (1974). The numbers of dinoflagellates were low from October to March and growth started in April with such species as Dinophysis lachmannii (probably Dinophysis acuminata), Gonyaulax tamarensis, Scrippsiella trochoidea and Gonyaulax spinifera and several Protoperidinium species. In June and July there were peaks in numbers of Scrippsiella trochoidea, Gonyaulax spinifera, Gonyaulax grindleyi and towards the end of this period Heterocapsa triquetra and Prorocentrum balticum. Finally during August / September there was an increase in Ceratium spp. and Prorocentrum micans. Apart from the species not found in L. Creran, Hardangerfjord has a very similar dinoflagellate cycle.

The seasonal dinoflagellate cycles found in some Norwegian fjords bear quite a close resemblance to the cycle observed for L. Creran. This similarity is much stronger than that observed in comparison to other British coastal waters. Obviously the hydrographic regime of the fjords is akin to that of the Scottish sea lochs. This would seem to imply that certain of the species common to both situations can exploit these fjordic conditions. This is perhaps worth bearing in mind in the context of toxic blooms for species that are, at the moment, rare or not present in Scottish waters but have been a problem in Norway (e.g. Prorocentrum minimum).

EXPLANATION OF TABLES

All figures are $x10^{-3}$

+ represents 0 - 199 cells per litre, ++ represents 200 - 399 cells per litre, (for explanation see Chapter 2).

A date with an asterisk (*) means that the sample was in the 'very thin' category (less than 20 cells of the dominant species counted, for explanation see Chapter 2).

For Table 4.5 the following abbreviations for sample stations are used:-

U.C. = Upper Creran

Cr.Br. = Creagan bridge

B.P. = Barcaldine Pier

For locations see Figure 4.3

Table 4.1 : Cell numbers per litre Loch Creran 1982

Species / Date	28-4	4-5	11-5	18-5	8-6	15-6	22-6	29-6
Ceratium furca	-	-	-	-	-	-	-	-
C. fusus	-	-	-	-	-	-	-	-
C. lineatum	-	-	-	-	-	-	-	-
C. tripos	-	-	-	-	-	-	-	-
Dinophysis spp.	-	-	-	+	-	+	+	-
D. acuminata	+	-	-	-	+	+	+	+
D. dens	-	-	-	-	-	-	-	-
D. norvegica	-	-	-	+	-	+	-	-
D. pulchellum	-	-	-	-	-	-	-	-
D. punctata	-	-	+	-	-	-	-	-
D. rotundatum	-	+	-	+	-	-	-	-
Diplopsalis spp.	-	+	-	+	-	+	-	-
D. lenticula	-	-	-	-	-	-	-	-
Dissodinium pseudocalani	-	-	-	-	-	-	-	-
Glenodinium spp.	-	-	-	-	-	-	-	-
Gonyaulax spp.	+	-	+	+	-	-	-	-
G. digitale	-	-	-	-	-	-	-	-
G. grindleyi	-	-	-	-	-	-	-	+
G. polyedra	-	-	-	-	-	+	+	-
G. spinifera	-	-	-	+	+	++	-	-
?*G. tamarensis*	-	-	-	-	-	-	-	-
G. verior	-	-	-	-	-	-	-	-
Heterocapsa triquetra	-	-	-	+	-	+	+	-
?*Helgolandinium subgluosum*	-	-	-	-	-	-	+	-
Katodinium rotundatum	-	+	+	-	-	-	+	-
Oblea rotundata	-	-	-	-	-	-	-	-
Prorocentrum gracile	-	-	-	-	-	-	-	-
P. micans	-	+	-	-	+	+	+	+
P. scutellum	-	-	-	-	-	-	-	-
Protoperidinium /*Diplopsalis* spp.	-	-	-	-	-	-	-	-
Protoperidinium spp.	+	+	+	+	+	+	+	+
P. bipes	+	+	+	-	+	0.4	+	-
P. brevipes	-	-	-	-	+	+	+	+
P. cerasus	-	-	+	-	-	-	-	-
P. claudicans	-	-	-	-	-	-	+	-
P. conicum	-	-	-	-	-	-	-	-
P.curtipes	-	-	-	-	-	-	-	+
P. denticulatum	-	-	-	-	-	-	-	-
P. diabolum	-	-	-	-	-	-	-	-
P. divergens	-	-	-	-	-	-	-	+
P. excentricum	-	-	-	-	-	-	-	-
P. leonis	-	-	-	+	-	+	-	+
?*P. minutum*	-	-	-	-	+	-	-	-
P. ovatum	+	-	-	-	-	-	+	-
P. pallidum	+	-	-	-	-	-	-	-
P. pellucidum	-	-	-	-	-	-	-	-
P. pentagonum	-	-	-	+	-	-	+	+
P. pyriforme	-	-	-	-	-	-	-	-
P. steinii	-	-	-	-	-	-	-	+
P. subinerme	+	+	-	+	-	+	-	-
?*P. thorianum*	-	-	-	-	-	-	-	+
Scrippsiella spp.	1.3	0.6	1.5	1.5	0.6	12.4	7.2	0.9
TOT. CELL NOS. ($x10^{-3}$)	1.7	0.9	1.7	1.9	1.0	13.6	7.8	1.6

Table 4.1 cont..

Species / Date	6-7	13-7	20-7	27-7	3-8	10-8	17-8	24-8
Ceratium furca	-	-	-	-	-	-	-	-
C. fusus	-	-	-	-	-	-	+	++
C. lineatum	-	-	-	-	-	-	+	+
C. tripos	+	-	-	-	-	-	-	-
Dinophysis spp.	-	-	-	-	+	+	-	+
D. acuminata	+	-	-	+	++	+	+	+
D. dens	-	-	-	-	-	-	-	-
D. norvegica	-	-	-	-	-	+	+	+
D. pulchellum	-	-	-	-	-	-	-	-
D. punctata	-	-	-	-	+	-	-	-
D. rotundatum	+	-	-	+	-	+	-	+
Diplopsalis spp.	-	+	-	-	+	-	-	-
D. lenticula	-	-	-	-	-	-	-	+
Dissodinium pseudocalani	-	-	-	-	+	-	-	-
Glenodinium spp.	-	-	-	+	+	++	+	-
Gonyaulax spp.	-	-	-	-	+	+	+	-
G. digitale	-	-	-	-	-	-	-	-
G. grindleyi	-	-	-	+	+	-	+	-
G. polyedra	-	+	+	-	+	0.7	++	5.5
G. spinifera	-	-	-	++	+	0.4	-	0.4
?G. tamarensis	-	-	-	-	-	-	-	-
G. verior	-	-	-	-	-	-	-	+
Heterocapsa triquetra	-	+	-	+	++	++	0.6	+
?Helgolandinium subgluosum	-	-	+	-	-	-	-	-
Katodinium rotundatum	-	-	-	-	+	+	-	-
Oblea rotundata	-	-	-	-	+	++	+	+
Prorocentrum gracile	-	-	-	-	-	-	-	+
P. micans	+	-	-	+	+	+	++	0.6
P. scutellum	-	-	-	-	-	+	-	+
Protoperidinium /Diplopsalis spp.	-	-	-	+	+	+	+	-
Protoperidinium spp.	+	+	+	+	-	-	-	+
P. bipes	-	+	++	0.9	++	1.3	1.0	+
P. brevipes	-	-	-	+	+	+	+	+
P. cerasus	-	-	-	-	+	-	+	+
P. claudicans	-	-	-	+	-	-	-	-
P. conicum	-	-	-	-	-	-	-	+
P. curtipes	-	-	-	-	-	-	-	-
P. denticulatum	-	-	-	-	-	-	-	-
P. diabolum	-	-	-	-	+	-	+	-
P. divergens	-	-	-	-	-	-	-	-
P. excentricum	-	-	-	-	-	-	-	-
P. leonis	+	+	+	-	-	-	-	-
?P. minutum	-	-	-	+	-	-	-	-
P. ovatum	+	+	+	+	+	-	+	+
P. pallidum	+	-	-	+	+	-	-	-
P. pellucidum	-	+	-	+	-	-	-	0.9
P. pentagonum	-	-	-	-	-	-	-	-
P. pyriforme	-	-	-	-	-	-	-	-
P. steinii	-	-	-	-	+	+	+	+
P. subinerme	-	-	-	+	-	-	-	-
?P. thorianum	-	-	-	-	-	-	-	-
Scrippsiella spp.	0.4	1.8	1.1	4.0	1.4	2.4	4.4	0.5
TOT. CELL NOS. ($x10^{-3}$)	0.9	2.3	1.6	5.9	3.3	6.4	7.5	9.3

Table 4.1 cont..

Species / Date	31-8	7-9	14-9	21-9	28-9	5-10	2-11	30-11 *
Ceratium furca	-	+	+	+	+	+	+	-
C. fusus	+	++	+	+	+	-	+	-
C. lineatum	+	+	+	+	+	+	+	-
C. tripos	-	-	-	-	-	-	-	-
Dinophysis spp.	+	-	+	-	-	-	-	-
D. acuminata	+	+	-	+	+	+	-	-
D. dens	+	-	-	-	-	-	-	-
D. norvegica	+	-	+	-	-	+	-	-
D. pulchellum	-	-	-	+	-	+	-	-
D. punctata	-	-	-	-	-	-	-	-
D. rotundatum	-	-	-	-	+	-	+	+
Diplopsalis spp.	-	-	++	-	-	-	-	-
D. lenticula	+	+	-	+	+	-	-	-
Dissodinium pseudocalani	-	-	-	-	-	-	-	-
Glenodinium spp.	2.5	-	-	-	-	-	-	-
Gonyaulax spp.	-	+	-	-	-	+	+	-
G. digitale	-	-	+	+	-	-	-	-
G. grindleyi	-	+	-	+	-	-	-	-
G. polyedra	+	7.8	+	-	-	-	-	-
G. spinifera	+	0.6	0.7	++	+	+	++	+
?G. tamarensis	-	-	++	-	-	-	-	-
G. verior	+	++	+	-	-	+	-	-
Heterocapsa triquetra	++	-	1.6	+	+	+	+	+
?Helgolandinium subgluosum	-	-	-	-	-	-	-	-
Katodinium rotundatum	-	-	-	+	-	-	-	+
Oblea rotundata	-	+	-	-	-	-	-	-
Prorocentrum gracile	-	-	-	-	-	-	-	-
P. micans	++	3.1	2.7	0.9	1.5	+	+	+
P. scutellum	-	+	-	-	+	-	-	-
Protoperidinium /Diplopsalis spp.	-	-	-	-	-	-	-	-
Protoperidinium spp.	-	+	++	-	-	-	+	-
P. bipes	-	++	+	+	-	+	+	-
P. brevipes	+	-	+	+	-	+	-	-
P. cerasus	-	+	+	+	+	+	+	-
P. claudicans	-	-	-	-	-	-	-	-
P. conicum	-	-	-	-	-	-	-	-
P. curtipes	-	-	-	-	-	-	-	-
P. denticulatum	-	-	+	-	-	-	-	-
P. diabolum	-	+	+	-	-	-	-	-
P. divergens	-	-	-	-	-	-	-	-
P. excentricum	-	-	-	+	-	-	-	-
P. leonis	-	-	-	-	+	-	-	-
?P. minutum	-	-	-	-	-	-	-	-
P. ovatum	-	-	-	-	-	-	-	-
P. pallidum	-	+	+	-	-	-	-	-
P. pellucidum	-	+	-	-	+	-	-	-
P. pentagonum	-	-	-	-	+	-	-	-
P. pyriforme	-	+	+	-	+	-	-	-
P. steinii	-	++	+	+	+	-	-	-
P. subinerme	-	+	+	-	-	-	-	-
?P. thorianum	-	-	-	-	-	-	-	-
Scrippsiella spp.	0.4	+	++	++	+	+	+	+
TOT. CELL NOS. ($x10^{-3}$)	4.1	13.8	6.9	1.9	2.2	++	0.4	++

Table 4.2 : Counts of cysts and tintinnids, Creran 1982

Date	S. trochoidea cyst	S. ?sweeneyae cyst	G.polyedra cyst	Tintinnids
28-4	-	-	+	+
4-5	-	-	-	0.6
11-5	-	-	-	0.5
18-5	1.2	-	-	1.1
8-6	+	-	-	0.6
15-6	0.5	+	+E	0.8
22-6	-	-	-	++
29-6	+	+	-	+
6-7	-	-	-	0.4
13-7	-	-	-	0.6
20-7	-	-	-	0.4
27-7	0.7	+	-	+
3-8	+	-	-	+
10-8	+	-	-	-
17-8	+	-	-	+
24-8	-	-	+	+
31-8	-	-	-	+
7-9	-	-	-	++
14-9	-	-	-	0.6
21-9	-	-	-	++
28-9	-	-	-	0.9
5-10	-	-	-	++
2-11	-	-	-	+
30-11 *	-	-	-	+

E = empty cyst

Table 4.3 Cell numbers per litre, Loch Creran 1983

Species / Date	25-1	2-2	29-3	8-4	20-4	26-4	3-5	9-5
Ceratium furca	-	-	-	-	-	-	-	-
C. fusus	-	-	-	-	-	-	-	-
C. lineatum	-	-	-	-	-	-	-	-
C. longipes	-	-	-	-	-	-	-	-
Dinophysis spp.	+	-	+	-	-	-	-	+
D. acuminata	-	-	+	-	-	+	+	+
D. acuta	-	-	-	-	-	-	-	-
D. contractum	-	-	-	-	-	-	-	-
D. norvegica	-	-	-	-	+	-	+	+
D. pulchellum	-	-	-	-	-	-	-	-
D. punctata	-	-	+	-	-	-	-	+
D. rotundatum	-	-	-	-	-	-	-	-
Diplopsalis spp.	-	-	-	-	+	-	-	-
D. lenticula	-	-	-	-	+	-	-	-
Dissodium asymmetricum	-	-	-	-	-	-	-	-
Glenodinium spp.	-	-	-	-	-	-	-	-
Gonyaulax spp.	+	-	+	-	+	+	+	++
G. digitale	-	-	-	-	-	-	+	+
G. grindleyi	-	-	-	-	-	-	-	-
G. polyedra	-	-	-	-	+	-	-	+
G. polygramma	-	-	-	-	-	-	-	-
G. spinifera	-	-	+	-	-	+	-	2.3
G. tamarensis	-	-	+	-	+	+	+	3.0
G. triacantha	-	-	+	-	-	-	-	-
G. verior	-	-	-	-	-	-	-	-
Heterocapsa triquetra	-	-	0.5	-	+	++	+	0.8
Katodinium rotundatum	-	-	-	+	+	-	-	-
Prorocentrum spp.	-	-	-	-	-	-	-	-
Oblea rotundata	-	-	-	+	-	-	-	-
P. micans	+	-	+	-	-	-	-	+
P. scutellum	-	-	-	-	-	-	-	-
Protoperidinium /*Diplopsalis* spp.	-	-	-	+	1.0	++	+	++
Protoperidinium spp.	+	-	+	-	-	-	-	-
P. bipes	-	-	+	+	+	+	+	+
P. brevipes	-	-	+	-	-	+	+	++
P. cerasus	-	-	+	+	+	+	+	+
P. claudicans	-	-	-	+	-	-	-	-
P. conicoides	-	-	-	-	-	-	-	-
P. denticulatum	-	-	-	-	-	-	-	+
P. depressum	-	-	-	-	-	+	-	-
P. diabolum	-	-	-	-	0.6	++	-	-
P. excentricum	-	-	-	-	-	-	-	-
P. leonis	-	-	-	-	-	+	-	-
P. minutum	-	-	-	-	-	-	-	++
P. mite	-	-	-	-	-	-	-	-
P. oblongum	-	-	-	-	-	-	-	-
P. ovatum	-	-	+	+	-	+	-	+
P. pallidum	-	-	-	-	-	-	-	+
P. pellucidum	-	-	-	-	++	+	+	+
P. pentagonum	-	-	-	-	-	+	+	+
P. pyriforme	-	-	-	-	+	-	-	+
P. steinii	-	-	-	-	-	+	-	-
P. subinerme	-	-	-	-	-	-	-	-
P. thorianum	-	-	-	-	-	-	-	-
Scrippsiella spp.	+	0.4	6.8	0.6	0.6	3.7	1.8	12.3
TOT. CELL NOS. ($x10^{-3}$)	++	0.4	8.0	0.9	2.9	5.4	2.3	20.4

Table 4.3 cont..

Species / Date	18-5	24-5	1-6	7-6	14-6	21-6	28-6
Ceratium furca	-	-	-	-	-	-	-
C. fusus	-	-	-	-	-	-	+
C. lineatum	+	-	-	-	+	-	-
C. longipes	-	-	-	-	-	-	-
Dinophysis spp.	+	-	+	-	-	-	+
D. acuminata	++	+	++	-	-	+	+
D. acuta	-	-	-	-	-	-	-
D. contractum	-	-	-	-	-	-	-
D. norvegica	+	-	-	-	+	-	-
D. pulchellum	-	-	-	-	-	-	-
D. punctata	-	-	-	-	-	-	-
D. rotundatum	-	-	+	-	-	-	-
Diplopsalis spp.	-	-	-	-	-	-	-
D. lenticula	+	+	-	-	-	-	-
Dissodium asymmetricum	-	-	-	-	-	-	-
Glenodinium spp.	5.7	0.9	+	+	+	-	+
Gonyaulax spp.	-	+	-	+	-	-	-
G. digitale	+	-	-	-	-	+	-
G. grindleyi	+	-	-	-	-	-	-
G. polyedra	-	-	-	-	-	+	+
G. polygramma	-	-	-	-	-	-	-
G. spinifera	5.2	0.5	0.5	+	0.5	++	+
G. tamarensis	14.6	+	+	-	-	-	-
G. triacantha	+	-	+	-	-	-	-
G. verior	-	-	-	-	-	-	-
Heterocapsa triquetra	3.7	++	++	+	++	+	+
Katodinium rotundatum	-	-	-	+	+	-	+
Oblea rotundata	++	+	+	-	-	+	+
Prorocentrum spp.	-	-	-	-	-	-	-
P. micans	+	-	-	-	+	-	-
P. scutellum	-	-	-	-	-	-	-
Protoperidinium /Diplopsalis spp.	0.4	++	+	+	+	++	++
Protoperidinium spp.	-	-	-	-	-	-	-
P. bipes	+	0.6	+	+	+	0.6	++
P. brevipes	0.7	+	++	+	-	+	++
P. cerasus	+	+	-	+	+	+	-
P. claudicans	-	+	-	-	-	-	-
P. conicoides	-	-	-	-	-	-	-
P. denticulatum	-	-	-	-	-	-	-
P. depressum	-	-	-	-	-	-	-
P. diabolum	+	+	-	-	-	+	-
P. excentricum	-	-	-	-	-	-	-
P. leonis	+	+	-	-	+	-	+
P. minutum	-	-	-	-	+	-	-
P. mite	-	-	-	-	-	-	-
P. oblongum	-	-	-	-	-	-	-
P. ovatum	+	+	+	-	+	+	-
P. pallidum	-	-	-	-	-	-	-
P. pellucidum	-	-	-	-	-	-	-
P. pentagonum	+	+	-	-	-	-	-
P. pyriforme	+	+	-	-	-	-	-
P. steinii	-	-	-	-	-	-	-
P. subinerme	-	-	-	-	-	-	-
P. thorianum	-	-	-	-	-	-	-
Scrippsiella spp.	15.5	0.6	2.1	0.5	3.5	6.8	20.3
TOT. CELL NOS. ($x10^{-3}$)	47.5	3.7	4.0	1.0	4.9	8.3	21.5

Table 4.3 cont..

Species / Date	5-7	15-7	19-7	26-7	2-8	11-8	17-8	23-8
Ceratium furca	+	+	-	-	+	-	+	0.6
C. fusus	-	-	+	-	-	-	+	-
C. lineatum	+	+	+	+	-	+	+	++
C. longipes	-	-	-	-	-	-	-	-
Dinophysis spp.	+	++	+	+	+	+	+	++
D. acuminata	+	++	+	+	+	+	+	0.6
D. acuta	-	-	-	+	-	-	-	-
D. contractum	-	-	+	-	-	-	-	-
D. norvegica	-	+	-	+	+	++	+	++
D. pulchellum	-	-	+	-	+	-	-	-
D. punctata	-	-	+	+	-	-	-	-
D. rotundatum	+	-	+	+	+	-	+	+
Diplopsalis spp.	-	+	-	-	+	-	-	-
D. lenticula	+	-	+	-	-	+	+	+
Dissodium asymmetricum	-	-	-	-	-	-	-	-
Glenodinium spp.	-	2.6	+	+	+	0.5	0.5	+
Gonyaulax spp.	-	-	+	-	+	+	+	-
G. digitale	-	-	-	-	+	-	-	-
G. grindleyi	-	-	-	-	+	+	+	+
G. polyedra	-	++	+	+	-	-	++	98.4
G. polygramma	-	-	-	-	-	-	-	-
G. spinifera	-	++	++	+	+	0.4	+	0.7
G. tamarensis	-	-	-	+	+	-	+	-
G. triacantha	-	-	-	-	-	-	-	-
G. verior	-	-	-	+	+	-	+	-
Heterocapsa triquetra	+	+	+	+	+	+	+	+
Katodinium rotundatum	-	+	-	-	+	-	-	-
Oblea rotundata	-	-	-	-	-	-	++	+
Prorocentrum spp.	-	-	-	-	-	-	-	-
P. micans	-	+	+	+	+	+	+	0.4
P. scutellum	-	-	-	-	-	-	-	++
Protoperidinium /Diplopsalis spp.	+	-	+	+	+	+	+	++
Protoperidinium spp.	-	+	+	+	-	-	-	+
P. bipes	0.4	+	+	+	+	1.0	0.9	+
P. brevipes	-	+	+	++	+	+	+	0.5
P. cerasus	-	-	-	+	-	+	+	+
P. claudicans	-	-	-	-	-	+	+	-
P. conicoides	-	-	-	-	-	-	-	+
P. denticulatum	-	-	-	-	-	-	-	-
P. depressum	-	-	-	-	+	-	-	-
P. diabolum	-	-	-	-	-	-	-	-
P. excentricum	-	-	-	-	-	-	-	-
P. leonis	+	-	-	+	+	-	+	-
P. minutum	+	-	+	-	+	-	+	+
P. mite	-	-	-	-	-	-	+	+
P. oblongum	-	-	-	-	-	-	+	+
P. ovatum	+	+	+	-	-	-	+	-
P. pallidum	-	-	-	-	-	-	-	-
P. pellucidum	-	-	-	-	+	-	-	-
P. pentagonum	-	-	+	-	-	-	+	-
P. pyriforme	-	-	-	-	+	-	-	-
P. steinii	-	-	-	+	-	-	+	+
P. subinerme	-	-	+	-	-	-	-	-
P. thorianum	-	-	-	-	+	-	-	-
Scrippsiella spp.	3.8	23.3	5.9	13.1	4.7	4.7	2.6	7.8
TOT. CELL NOS. ($x10^{-3}$)	4.8	27.8	7.0	15.6	5.3	7.2	5.8	111.3

Table 4.3 cont..

Species / Date	31-8	5-9	9-9	14-9	23-9	28-9	4-10	13-10
Ceratium furca	2.5	+	1.6	1.1	2.3	3.1	15.4	10.4
C. fusus	0.6	+	+	+	++	0.4	1.0	+
C. lineatum	1.3	+	1.2	+	3.9	0.9	2.8	++
C. longipes	+	-	-	-	-	-	-	-
Dinophysis spp.	++	+	+	+	+	+	+	+
D. acuminata	++	+	+	+	+	+	+	+
D. acuta	-	-	-	-	-	-	-	-
D. contractum	-	-	-	-	-	-	-	-
D. norvegica	+	+	+	+	+	+	+	-
D. pulchellum	+	-	+	-	-	-	-	+
D. punctata	-	-	-	-	-	-	-	-
D. rotundatum	+	+	-	+	+	+	+	-
Diplopsalis spp.	-	-	+	+	-	+	+	-
D. lenticula	+	+	+	+	+	-	+	-
Dissodium asymmetricum	-	-	-	+	-	-	+	-
Glenodinium spp.	+	0.5	+	-	-	-	-	-
Gonyaulax spp.	-	-	-	-	-	-	-	+
G. digitale	+	-	-	-	-	-	-	-
G. grindleyi	0.5	+	+	++	+	+	+	-
G. polyedra	96.2	4.2	97.5	5.7	6.9	0.8	+	++
G. polygramma	+	-	-	-	-	-	-	-
G. spinifera	2.1	++	1.5	4.5	++	0.6	0.9	1.3
G. tamarensis	-	+	-	-	-	-	-	-
G. triacantha	-	-	-	-	+	-	-	-
G. verior	++	+	++	++	0.8	++	+	-
Heterocapsa triquetra	+	+	+	+	+	+	-	+
Katodinium rotundatum	-	-	-	-	-	-	-	-
Oblea rotundata	0.7	+	+	+	1.8	+	+	-
Prorocentrum spp.	+	+	+	-	-	-	-	-
P. micans	0.8	0.5	1.2	5.9	9.8	2.7	4.0	1.8
P. scutellum	0.5	+	++	+	+	+	0.8	+
Protoperidinium /Diplopsalis spp.	++	+	+	1.2	++	+	0.6	-
Protoperidinium spp.	+	+	+	-	+	-	+	-
P. bipes	+	+	-	+	+	+	+	-
P. brevipes	0.6	+	0.6	1.2	0.7	++	++	+
P. cerasus	+	+	+	++	+	+	+	+
P. claudicans	+	+	-	-	-	-	-	-
P. conicoides	-	-	-	-	-	-	-	-
P. denticulatum	-	-	-	-	-	-	-	-
P. depressum	+	-	-	-	-	-	-	-
P. diabolum	-	-	-	-	-	-	-	-
P. excentricum	+	-	-	-	-	-	-	-
P. leonis	+	-	+	+	+	+	+	+
P. minutum	+	+	-	-	+	+	-	-
P. mite	+	-	+	+	-	-	-	-
P. oblongum	+	-	-	-	-	+	-	-
P. ovatum	+	-	+	-	+	-	+	-
P. pallidum	-	-	+	-	-	-	-	-
P. pellucidum	-	-	-	-	+	+	-	-
P. pentagonum	-	-	-	-	+	-	+	-
P. pyriforme	-	-	-	-	+	-	-	-
P. steinii	+	+	+	+	+	+	+	-
P. subinerme	+	+	+	+	+	-	+	-
P. thorianum	-	-	-	-	+	-	-	-
Scrippsiella spp.	1.1	1.5	0.5	0.7	1.0	0.5	++	0.7
TOT. CELL NOS ($x10^{-3}$)	131.5	8.5	106.7	24.8	30.4	10.5	27.0	15.4

Table 4.3 cont..

Species / Date	18-10	27-10	2-11
Ceratium furca	+	2.7	3.4
C. fusus	-	-	+
C. lineatum	+	+	++
C. longipes	-	-	-
Dinophysis spp.	+	-	+
D. acuminata	+	-	+
D. acuta	-	-	-
D. contractum	-	-	-
D. norvegica	-	-	+
D. pulchellum	-	-	-
D. punctata	-	-	-
D. rotundatum	-	-	+
Diplopsalis spp.	-	-	-
D. lenticula	-	-	-
Dissodium asymmetricum	-	-	-
Glenodinium spp.	-	-	-
Gonyaulax spp.	+	-	-
G. digitale	-	-	-
G. grindleyi	-	-	-
G. polyedra	+	-	+
G. polygramma	-	-	-
G. spinifera	0.7	+	+
G. tamarensis	-	-	-
G. triacantha	-	-	-
G. verior	-	-	-
Heterocapsa triquetra	0.6	+	+
Katodinium rotundatum	-	-	-
Oblea rotundata	-	-	-
Prorocentrum spp.	-	-	-
P. micans	2.0	1.0	0.4
P. scutellum	-	-	+
Protoperidinium /Diplopsalis spp.	+	+	+
Protoperidinium spp.	-	-	-
P. bipes	-	+	-
P. brevipes	+	+	+
P. cerasus	+	-	+
P. claudicans	-	-	-
P. conicoides	-	-	-
P. denticulatum	-	-	-
P. depressum	-	-	-
P. diabolum	-	-	-
P. excentricum	-	-	-
P. leonis	-	-	-
P. minutum	-	-	-
P. mite	-	-	-
P. oblongum	+	-	-
P. ovatum	-	-	-
P. pallidum	-	-	-
P. pellucidum	-	-	-
P. pentagonum	-	-	-
P. pyriforme	+	-	-
P. steinii	-	-	-
P. subinerme	+	-	-
P. thorianum	-	-	-
Scrippsiella spp.	0.5	+	+
TOT. CELL NOS ($x10^{-3}$)	4.5	4.0	4.6

Table 4.4 : Counts of cysts and tintinnids, Creran 1983

Date	Brown	G.Poly	S.troch	S.swee	Br.rd	Grind	spinif	tintin
25-1	-	-	-	-	-	-	-	+
2-2	-	-	-	-	-	-	-	+
29-3	-	-	-	+	-	-	-	++
8-4	-	-	-	-	-	-	-	+
20-4	-	-	-	-	-	-	-	+
26-4	-	-	-	-	-	-	-	+
3-5	-	-	-	-	-	-	-	+
9-5	-	-	0.6	++	+	-	-	3.0
18-5	-	-	-	-	-	-	-	4.2
24-5	-	-	-	-	-	-	-	1.6*
1-6	-	-	-	-	-	-	-	++*
7-6	-	-	-	-	-	-	-	++
14-6	-	+	++	++	-	-	+	++*
21-6	-	-	-	-	-	-	-	++
28-6	+	-	+	-	-	-	+	0.6
5-7	-	-	-	-	-	-	-	0.5
15-7	-	-	-	-	-	-	-	++
19-7	-	-	+	-	-	-	-	0.5
26-7	-	-	+	-	-	-	-	1.0
2-8	+	-	+	-	-	-	-	++
11-8	-	-	-	-	-	-	-	+
17-8	-	-	-	-	-	-	-	+
23-8	-	-	-	-	-	-	-	-
31-8	-	+	+	-	-	+	-	+
5-9	-	+	+	+E	-	+	-	+
9-9	-	++	-	-	-	-	-	+
14-9	-	++	-	-	+	+	-	+
23-9	-	+/+E	-	-	-	+	-	0.5
28-9	-	+	-	-	-	-	-	+
4-10	-	-	-	-	+	-	+	+
13-10	-	-	-	-	-	-	-	++
18-10	-	-	-	-	-	-	-	++
27-10	-	-	-	-	-	-	-	+
2-11	-	-	-	-	-	-	-	1.1

E = empty cysts * = tintinnid cysts present
brown = ?*Epidinium shagrinum* G.poly = *Gonyaulax polyedra* cysts
S.troch = *Scrippsiella trochoidea* cysts S.swee = *S. ?sweeneyae* cysts Br.rd = Round, brown cysts Grind = *Gonyaulax grindleyi* cysts spinif = *spiniferites* cysts Tintin = tintinnids

Table 4.5 Numbers of cells per litre during G. tamarensis bloom, Creran 1983

Species / Sample	U.C. I176	CrBr I177	B.P. I175	C3a I178	CrBr I180	B.P. I179
?*Amphidoma*	+	-	-	-	-	-
Ceratium lineatum	-	+	+	-	-	-
Dinophysis spp.	+	-	+	-	-	-
D. acuminata	+	-	++	+	+	+
D. norvegica	+	-	+	+	-	-
?*D. ovum*	+	-	-	-	-	-
D. punctata	-	+	-	-	-	-
D. rotundatum	+	-	-	+	+	-
Diplopsalis lenticula	-	-	+	-	-	+
Glenodinium spp.	39.8	15.2	5.7	14.9	0.5	0.9
Gonyaulax spp.	+	-	-	-	-	+
G. digitale	+	+	+	+	-	-
G. grindleyi	-	-	+	-	-	-
G. polygramma	+	-	-	+	-	-
G. spinifera	4.5	3.0	5.2	4.2	1.3	0.5
G. tamarensis	16.5	9.3	14.6	14.6	0.5	+
G. triacantha	+	++	+	++	+	-
G. verior	-	+	-	-	-	-
Heterocapsa triquetra	4.1	4.8	3.7	3.3	0.9	++
Oblea rotundata	+	+	++	+	+	+
Prorocentrum micans	+	+	+	+	+	-
Protoperidinium /*Diplopsalis* spp.	0.7	++	0.4	+	+	++
P. bipes	+	+	+	+	0.6	0.6
P. brevipes	1.6	1.2	0.7	1.4	0.4	+
P. cerasus	+	+	+	+	-	+
P. claudicans	-	-	-	-	-	+
P. depressum	-	-	-	-	+	-
P. diabolum	-	+	+	+	+	+
P. leonis	-	+	+	-	+	+
P. ovatum	-	+	+	-	+	+
P. pentagonum	-	+	+	-	+	+
P. pyriforme	-	-	+	-	+	+
P. steinii	-	+	-	-	-	-
Scrippsiella spp.	10.2	7.3	15.5	7.2	1.8	0.6
TOT. CELL NOS ($x10^{-3}$)	78.3	42.2	47.5	46.6	6.7	3.7
S. ?*sweeneyae* cyst	-	-	-	-	+	-
S. trochoidea cyst	-	+	-	+	-	-
Tintinnid	0.9	2.3	4.2	3.5	0.9	1.6

Table 4.6 Distribution of cells with depth

Species / Date / Depth	9-9 0m	9-9 2m	9-9 4m	9-9 8m	9-9 18m
Ceratium furca	+	1.6	4.5	1.8	0.4
C. fusus	+	+	0.5	++	+
C. lineatum	+	1.3	5.1	1.0	+
Dinophysis spp.	+	+	++	+	+
D. acuminata	+	+	+	+	+
D. norvegica	+	+	+	+	-
D. pulchellum	-	+	-	-	-
D. rotundatum	-	-	+	-	+
Diplopsalis spp.	-	+	-	+	-
D. lenticula	-	+	+	-	+
Dissodium asymmetricum	-	-	-	+	+
Glenodinium spp.	+	+	-	-	+
Gonyaulax grindleyi	+	+	+	+	+
G. polyedra	11.4	97.5	148.0	42.0	25.0
G. spinifera	++	1.5	2.7	1.1	0.5
G. triacantha	-	-	-	-	+
G. verior	+	++	++	++	+
Heterocapsa triquetra	+	+	-	-	-
Oblea rotundata	+	+	++	+	+
Prorocentrum spp.	-	+	-	+	-
P. micans	0.4	1.2	1.3	0.7	0.5
P. scutellum	+	++	0.6	++	+
Protoperidinium /*Diplopsalis* spp.	+	+	++	+	+
Protoperidinium spp.	-	+	+	-	-
P. bipes	+	-	-	-	-
P. brevipes	0.5	0.6	0.8	1.0	1.1
P. cerasus	+	+	++	+	+
P. denticulatum	-	-	-	+	-
P. diabolum	-	-	-	+	-
P. excentricum	-	-	+	-	-
P. leonis	-	+	+	-	-
P. minutum	-	-	+	-	-
P. mite	+	+	+	-	-
P. oblongum	-	-	-	-	-
P. ovatum	-	+	-	-	+
P. pallidum	-	+	-	-	-
P. pellucidum	-	-	-	-	-
P. pentagonum	-	-	-	-	-
P. pyriforme	-	-	-	-	-
P. steinii	-	+	+	+	+
P. subinerme	-	+	+	+	+
Scrippsiella spp.	1.2	0.5	0.6	+	+
TOT. CELL NOS. ($x10^{-3}$)	14.8	106.7	166.1	49.6	28.9

Table 4.6 cont..

Species / Date / Depth	14-9 0m	14-9 2m	14-9 4m	14-9 8m	14-9 12m	14-9 18m	28-9 2m	28-9 19m
Ceratium furca	+	1.1	0.8	++	-	+	3.1	-
C. fusus	+	+	0.8	+	+	+	0.4	-
C. lineatum	-	+	1.9	++	-	+	0.9	-
Dinophysis spp.	-	+	++	-	+	-	+	-
D. acuminata	+	+	+	+	-	-	+	-
D. norvegica	-	+	+	+	+	+	+	-
D. pulchellum	-	-	-	-	-	-	-	+
D. rotundatum	-	+	+	+	-	+	+	-
Diplopsalis spp.	-	+	-	+	-	+	+	-
D. lenticula	-	+	+	+	-	+	-	-
Dissodium asymmetricum	-	+	+	-	-	-	-	-
Glenodinium spp.	+	-	-	-	-	-	-	-
Gonyaulax grindleyi	-	++	++	+	-	+	+	-
G. polyedra	0.7	5.7	25.6	13.6	3.8	2.8	0.8	-
G. spinifera	0.4	4.5	8.6	1.4	++	+	0.5	-
G. triacantha	-	-	-	-	-	-	-	-
G. verior	-	++	0.9	+	+	-	++	-
Heterocapsa triquetra	+	+	+	+	-	+	+	+
Oblea rotundata	+	+	0.8	++	+	-	+	-
Prorocentrum spp.	-	-	+	-	+	-	-	-
P. micans	++	5.9	3.8	0.7	+	+	2.7	-
P. scutellum	-	+	++	++	+	-	+	-
Protoperidinium /*Diplopsalis* spp.	+	1.2	0.7	0.4	+	+	+	-
Protoperidinium spp.	-	-	-	-	-	-	-	-
P. bipes	+	+	+	-	+	-	+	+
P. brevipes	1.5	1.2	1.8	1.6	0.8	1.8	++	0.5
P. cerasus	++	++	++	++	+	+	+	+
P. denticulatum	-	-	-	-	-	-	-	-
P. diabolum	-	-	+	-	-	-	-	-
P. excentricum	-	-	-	-	-	-	-	-
P. leonis	-	+	+	+	+	+	+	-
P. minutum	-	-	-	-	+	-	+	-
P. mite	-	+	+	-	-	-	-	-
P. oblongum	-	-	-	-	-	-	+	-
P. ovatum	-	-	-	+	-	-	-	-
P. pallidum	-	-	-	-	-	-	-	-
P. pellucidum	-	-	-	-	-	-	+	-
P. pentagonum	-	-	-	+	-	-	-	-
P. pyriforme	-	-	+	-	-	-	-	-
P. steinii	+	+	+	+	+	+	+	+
P. subinerme	-	+	+	+	+	-	-	-
Scrippsiella spp.	1.1	0.7	+	++	+	+	0.5	+
TOT. CELL NOS. ($x10^3$)	4.6	24.8	47.8	20.1	5.6	5.7	10.5	0.9

CHAPTER 5

SEASONAL ASPECTS OF DINOFLAGELLATE CYSTS IN LOCH CRERAN

INTRODUCTION

This chapter will cover the stages of encystment and excystment of the dinoflagellate life-cycle so far as they can be observed in the sea-loch environment. During this study laboratory experiments have only been carried out on excystment and these are reported in Chapter 8.

It seems likely that the dinoflagellate resting cyst is a hypnozygote involved in the dinoflagellate sexual cycle. Only recently has the importance of sexual reproduction in dinoflagellates been realised, with the work of von Stosch and more recently Pfeister (on freshwater species). So far three types of cycle have been described. In some species the zygote is motile throughout (planozygote) and no cyst is formed (e.g. Ceratium horridum; von Stosch, 1972). In other species this zygote loses motility and forms a temporary resting cyst (e.g. Helgolandinium subglobosum; von Stosch, 1972). In the final group of species the zygote forms a resting cyst (hypnozygote) with a resistant wall (e.g. Gonyaulax monilata; Walker and Steidinger, 1979). Dale (1976) first suggested that resting cysts and fossil cysts were hypnozygotes. He reports observations consistant with this for Peridinium faeroense (Dale, 1977) and other dinoflagellates he has excysted (Dale, 1983). Further work on stages leading up to encystment is required to clarify this picture.

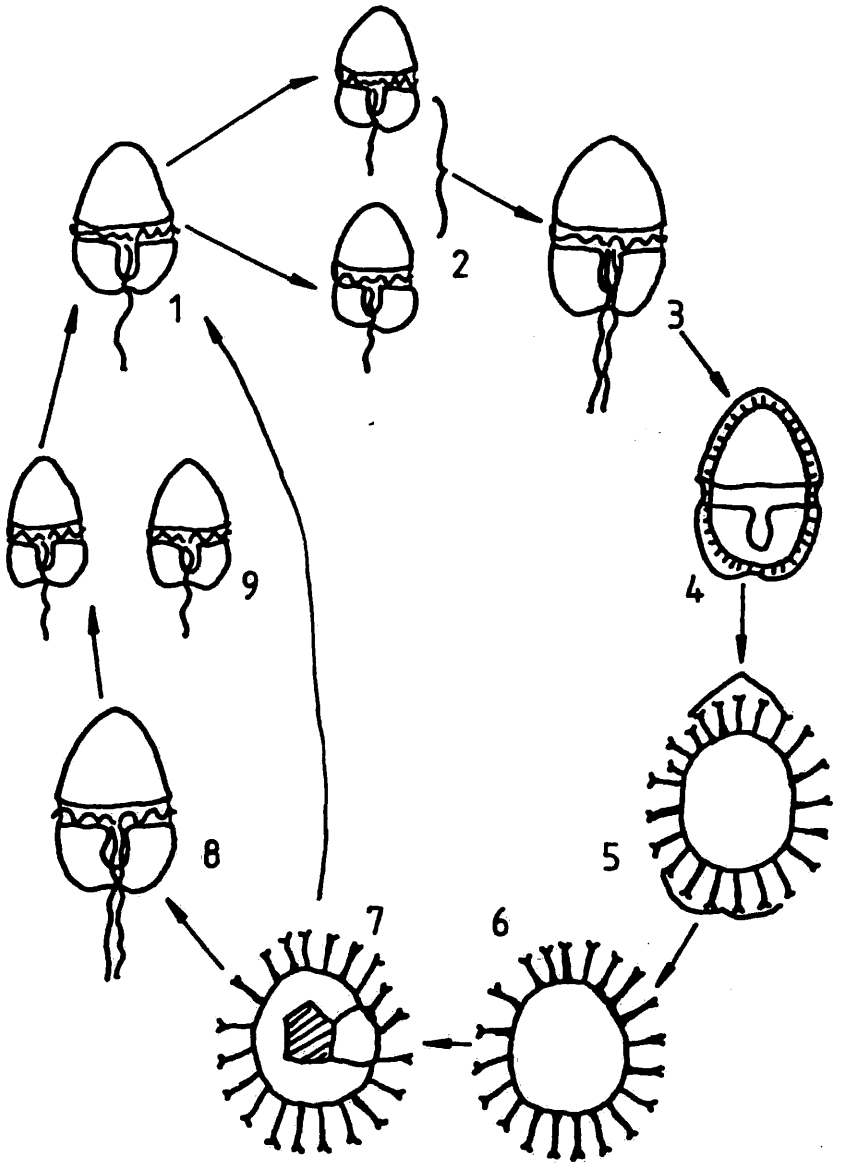
Occasional observations of natural encystment by palynologists such as Evitt and Davidson (1964) led to the development of the "contractional growth" hypothesis for cyst formation. This implies complete formation of the cyst

(including any processes) inside the intact theca. This idea was developed in the geological literature to the extent of being the basis of a simple cyst classification into proximate cysts (formed close inside the walls of the parental theca) and chorate cysts (formed well away from the walls of the parental theca). Observations on modern encysting populations have not supported this theory (Nordli, 1951; Bibby and Dodge, 1972; Chapman et al., 1982 and Dale, 1983). Observations in this study also support the contention that the cyst body does not contract as its processes lengthen, rather that these help to break up the theca as the cyst expands (Pl. 5.1, fig.1).

After their observations of the hatching of dinoflagellate cysts Wall and Dale (1968a) produced a scheme of the dinoflagellate life-cycle including a cyst stage. This was elaborated by Dale (1983) and is reproduced in Figure 5.1.

Most studies of the mechanism of encystment have relied on light microscope observations (e.g. Walker and Steidinger, 1979). In general the planozygote seems to lose motility, the cyst wall may thicken and the cytoplasm accumulates peripheral lipid globules and more centralized pigmented globules. As the cyst matures globules may become smaller and the cytoplasm darkens (or loses pigmentation in some cases) and pulls away from the cell wall. There have been few electron microscopical studies of this process. This is probably because of difficulties with fixing and staining such a resistant body and also lack of easily available material. Electron microscope studies by Bibby and Dodge (1972) and Chapman et al. (1982) also suggest that there is some reorganisation of cell contents. This involves build-up of storage products (e.g. starch, lipids); reduction of other cell components (e.g. chloroplasts) and formation of a resistant wall.

Figure 5.1: Schematic diagram of dinoflagellate sexual cycle, after Dale (1983)



Motile planktonic vegetative stage (1), producing gametes (2) pairs of which fuse to give planozygote (3). This eventually loses motility and cyst formation begins (4) and may proceed (5) by expansion rather than contraction of cyst, producing resting cyst (hypnozygote) (6). Excystment (7) may produce a planozygote comparable with (3), which by reduction division (9) reestablishes planktonic vegetative stage (1), or in other species the reduction division is completed during encystment, allowing direct reestablishment of stage (1). (Based largely on work by von Stosch)

Detailed observations of encystment in the natural environment are scarce. This is probably because of the short period of cyst production, the rapid sinking of cysts and because the proportion of cysts to cells can be very small (e.g. 1:500 for Gonyaulax digitale; Dale, 1976). The first detailed report was that of Nordli (1951). He observed an encysting population of Gonyaulax polyedra in late September in Drøbak Sound, Oslofjord. The dinoflagellate population described (not unlike that of Loch Creran at this time of year) was dominated by Ceratium furca (171,000 cells per l) and G. polyedra (159,200 cells per l) with numerous Prorocentrum micans also present. To determine cyst distribution, samples were collected from a number of stations and at a number of depths. Nordli found that percentage cyst occurrence increased down to the thermocline and that few cysts were found below this.

Wall and Dale (1968a) show annual graphs of cysts and cells of three species (Gonyaulax digitale, G. grindleyi and Protoperidinium oblongum). They conclude that cyst formation takes place towards the end or after a period of exponential growth. More recently Anderson, Chisholm and Watras (1983) followed the decline of Gonyaulax tamarensis blooms in salt ponds with a corresponding rapid increase of new cysts in the surface layer of the sediments. In the two years documented the recruitment of cysts to the sediments was markedly different and seemed to be dependent on population size of the motile cells.

Dale (1983) discusses seasonal patterns of cyst formation. He describes two well-defined patterns of cyst formation:-

1. Cyst formation in late spring / early summer after the species reaches maximum abundance in the spring (e.g. Peridinium faeroense; Dale, 1977b)

2. Cyst formation in the late summer / autumn after species reaches maximum abundances in the summer (e.g. Gonyaulax polyedra; Nordli, 1951; Gonyaulax digitale; Wall and Dale, 1968a)

He also tentatively describes a further two categories:-

3. Species with two annual peaks of abundance, with cyst formation after each peak (usually spring and autumn) (e.g. Gonyaulax tamarensis; Anderson and Morel, 1979)

4. Species with sporadic abundances and cyst formation spread over spring, summer and autumn (e.g. Scrippsiella trochoidea; Dale, 1983)

What induces cyst formation? Early workers assumed that it was in response to unfavourable conditions. However, laboratory observations (Wall et al., 1970; Morey-Gaines and Ruse, 1980) and recent research by Anderson et al. (1983) suggests that this is not the case. Populations of Gonyaulax tamarensis observed in salt-ponds became encysted in apparently ideal growth conditions without any obvious environmental stimulus. This suggests that encystment may just be a routine stage in the life-cycle. If cysts are hypnozygotes then to answer this question it may be more appropriate to look at the factors influencing sexual reproduction. What advantages cyst production may confer are discussed in Chapter 8.

After a mandatory dormancy period (also discussed in Chapter 8) cysts are capable of returning to the motile thecate stage. If indeed there are any environmental triggers it is not clear what they are. Laboratory stimulated excystment has frequently been observed, mostly for the purpose of establishing cyst-theca relationships and this process is described in Chapter 8. Studies of excystment in the environment are rare. Anderson et al. (1983) noted the importance of excystment in providing an

inoculum for future growth of Gonyaulax tamarensis populations. They followed G. tamarensis excystment by observation of planomeiocytes (recently excysted cells) in the water column. They also note that a large population of viable cysts remained in the bottom sediments and were available for future years.

The most detailed study of excystment in situ is that of Heaney, Chapman and Morison (1983) on the freshwater dinoflagellate Ceratium hirundinella. They followed the changes in the benthic cyst population (the appearence of empty cysts) and monitered the appearence of pre-ceratium (recently excysted) cells in the water column. Their findings provide strong evidence that excystment delivered the inoculum for the summer growth of the population. Their calculations show that a very small proportion of the encysted population (<0.5%) was required to give a suitable inoculum.

Similar calculations have been carried out for the marine environment by Steidinger and Haddad (1981) for an unspecified red tide dinoflagellate. They state that "Theoretically, cyst density in the sediments can be as low as 4 cysts cm^{2} to seed a $2km^{2}$ area with a 10m depth to a cell density of 24,576 cells $litre^{-1}$ (division rate of 0.5 day^{-1}, 14 days to develop, 50% motility sucess)." There appears, however to be a major error in their calculation since the given parameters predict a final concentration of 2,193 cells per litre.

Reid (1972b) sampled sediments on a seasonal basis to see if there was any change in the palynological assemblage through the year at Neston on the Dee estuary. He found little variation in the dinoflagellate cyst assemblage although he does note an increase in the number of cysts with protoplasm (particularly of Impletosphaeridium insolitum) in the autumn. Any new additions to the sediment appeared to be quickly mixed into the existing assemblage.

To examine the process of encystment and excystment water samples and sediment samples were taken on a regular basis from Loch Creran. It was felt that the enclosed sea-loch situation was a suitable place to examine the cycles between sediment and water column.

METHODS

Water column

Methods used for water column sampling are described in Chapter 2. The data discussed in this Chapter are that obtained during 1982-83 in Loch Creran. Samples were taken weekly at 2m between late spring and autumn and monthly during the winter. During the *Gonyaulax polyedra* bloom in 1983 samples were taken from a number of depths.

Sediments

In 1983 regular sediment sampling was carried out at station C5 (Fig. 4.3) in Loch Creran as described in Chapter 2. The first sample was a 5cm core taken in February and was formalin preserved. Two-weekly sampling was carried out from the beginning of April. Initially 5cm cores were taken and stored at 4°C. However, it was decided that to make detection more sensitive it would be more appropriate to examine just the top surface of cores. Accordingly 1cm cores were taken from the beginning of May. To ensure there was no problem with anomalous hatching of cysts due to removal from the environment, half of these 1cm core samples were preserved in formalin. Sampling continued in this fashion until the end of October. Counts of mud samples were made as described in Chapter 2. The most numerous cyst type in Loch Creran sediments in the size range counted was that of *Gonyaulax polyedra* (*Lingulodinium machaerophorum*). These were the most easily counted cysts

because of their size, the presence of a red pigmented body and the ease of identification. Therefore to follow the seasonal cycle counts were made of the 1cm cores exclusively of G. polyedra and between 150 and 200 cysts were counted per sample. Scrippsiella cysts were not counted because of their small size which meant that a proportion of them were washed through the sieves.

RESULTS

Water column

Counts of motile thecate cells are given in Chapter 4. Tables are also given in Chapter 4 of cyst numbers in the plankton samples (Tables 4.2 and 4.4). In addition Table 5.1 shows cyst distribution with depth at the time of the Gonyaulax polyedra bloom. As can be seen from the tables, cysts of Scrippsiella spp. and G. polyedra were the most frequently encountered in the water column during 1982-83. Graphs of their occurrences are given in Figures 5.2 - 5.5. Graphs of the distribution with depth are given in Figure 5.6.

The occurrence of Scrippsiella cysts throughout the year was sporadic and was not clearly linked with numbers of thecate motile stages present (Figs. 5.2 - 5.3). This is perhaps because of the heterogeneity of this group (see Chapter 3). Two types of cysts were recognised in the water samples, those of Scrippsiella trochoidea (Pl. 5.1, fig.1) and those of Scrippsiella ?sweeneyi (Pl. 5.1, fig.2).

On the other hand the occurrence of Gonyaulax polyedra cysts (Lingulodinium machaerophorum) clearly happened after a period of exponential growth of the thecate stages. Cysts were present throughout the water column. Their abundance increased with depth peaking below the halocline (below the maximum abundance of

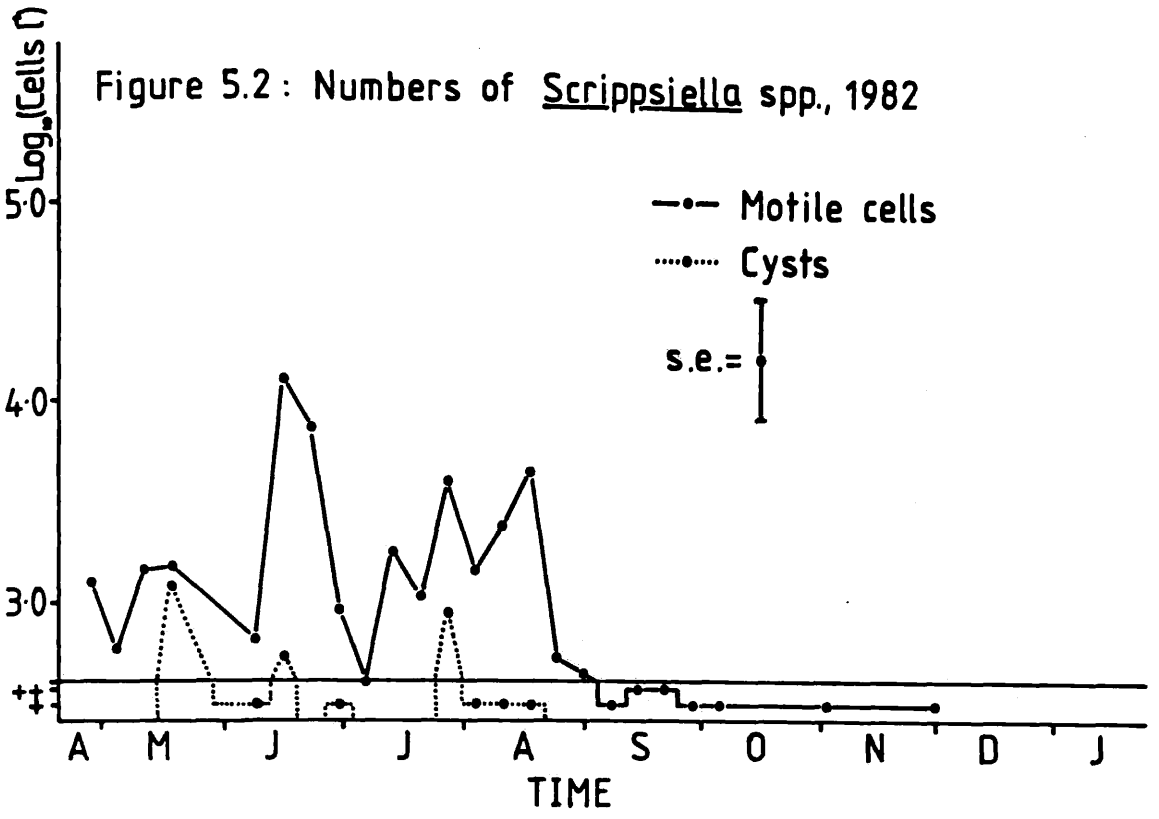


Figure 5.2 : Numbers of Scrippsiella spp., 1982

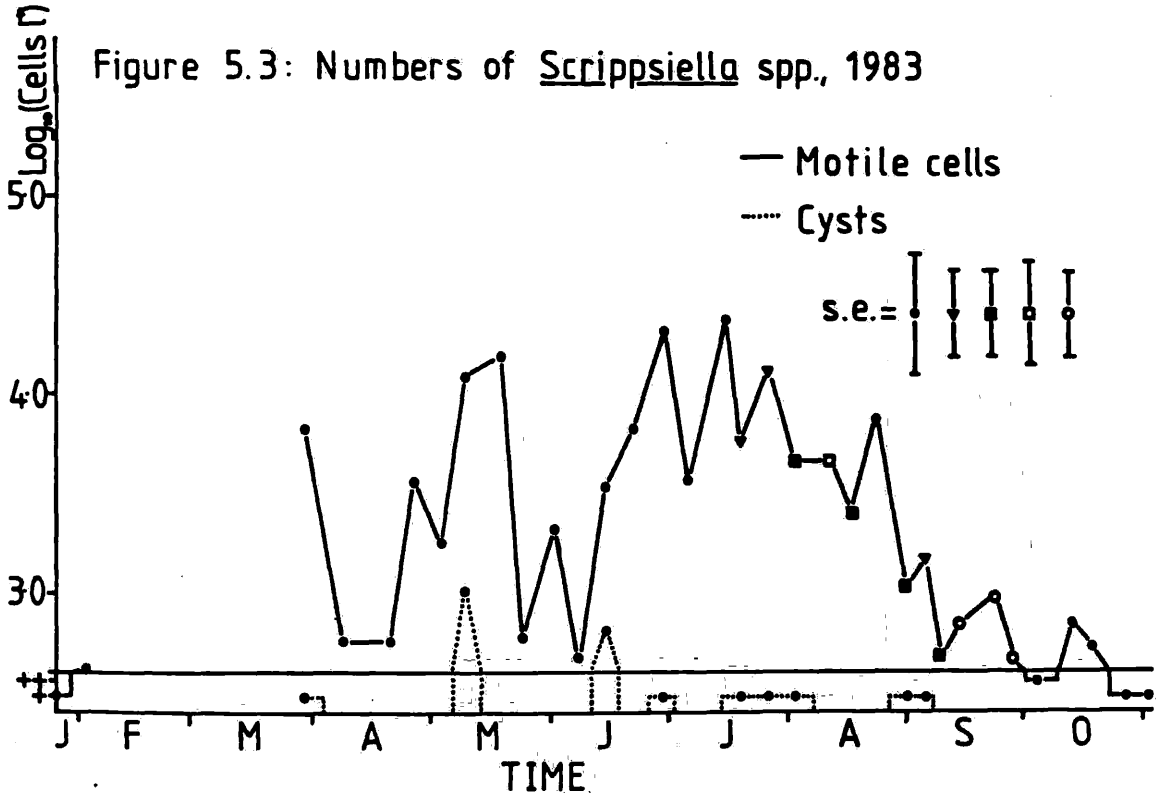
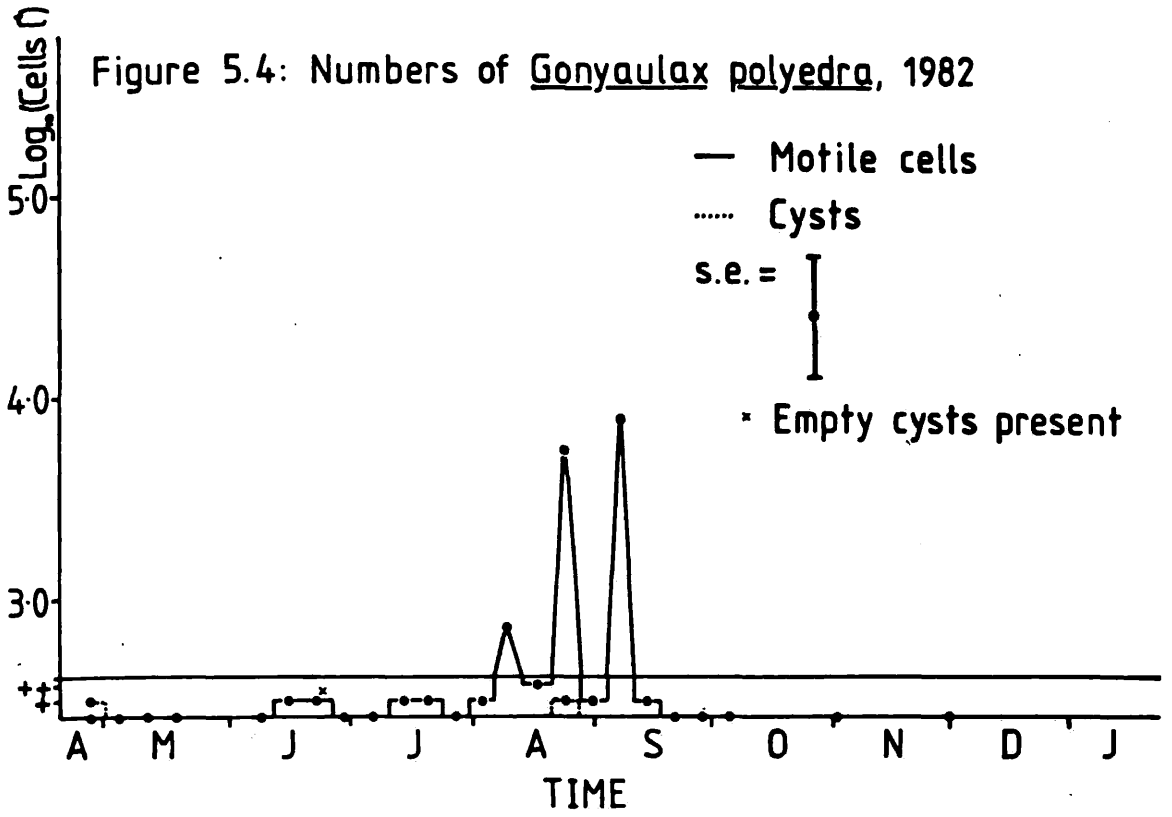


Figure 5.3: Numbers of Scrippsiella spp., 1983


Log10(Cells l-1)
5·0
4·0
3·0
Figure 5.4: Numbers of Gonyaulax polyedra, 1982
— Motile cells
..... Cysts
s.e. =
* Empty cysts present
A M J J A S O N D J
TIME

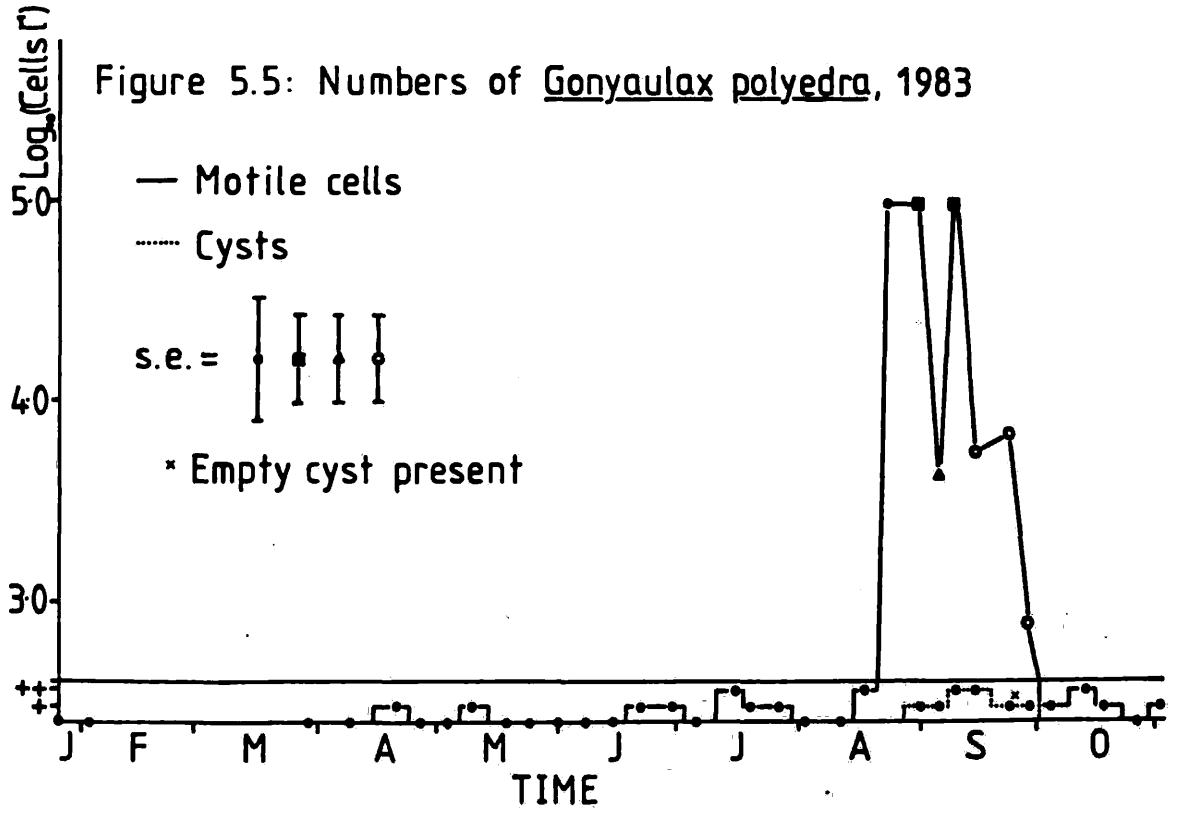

Log10(Cells l-1)
5·0
4·0
3·0
Figure 5.5: Numbers of Gonyaulax polyedra, 1983
— Motile cells
..... Cysts
s.e. =
* Empty cyst present
J F M A M J J A S O
TIME

Table 5.1 : Distribution of cysts with depth during Gonyaulax polyedra bloom

Date	Depth	Full G. polyedra cysts	Empty G. polyedra cysts	Round brown	G. grindleyi cysts
9-9	0	+	-	-	+
	2	++	-	-	-
	4	+	-	-	+
	8	0.5	-	-	-
	18	0.5	-	-	+
14-9	0	+	-	+	-
	2	++	-	+	+
	4	0.9	+	-	-
	8	1.8	+	-	-
	12	1.7	+	-	+
	18	0.7	+	-	+
28-9	2	+	-	-	-
	19	-	-	-	-

PLATE 5.1

All figures are S.E.M.s

Fig.1 : Side view of a recently encysted *Scrippsiella trochoidea* cell, cyst 30 µm across; Loch Creran water sample.

Fig.2 : View of two recently encysted *Scrippsiella* ?*sweeneyae* cells, cysts 31 µm across; Loch Creran water sample.

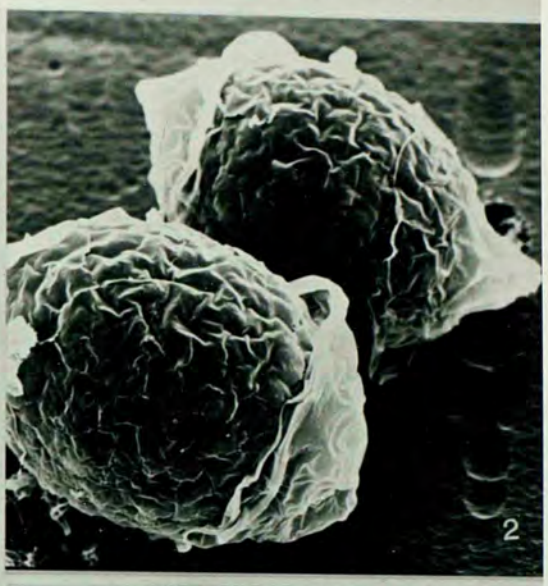
Fig.3 : *Lingulodinium machaerophorum* (*Gonyaulax polyedra*), showing little evidence of spines, 40 µm across; Loch Creran water sample (9/9/83).

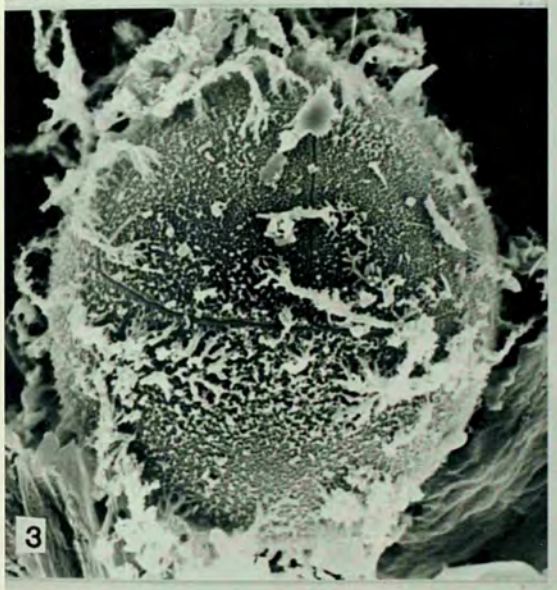
Fig.4 : *Lingulodinium machaerophorum* (*Gonyaulax polyedra*), with spines of moderate length, 41 µm across (excluding spines), Loch Creran water sample (9/9/83).

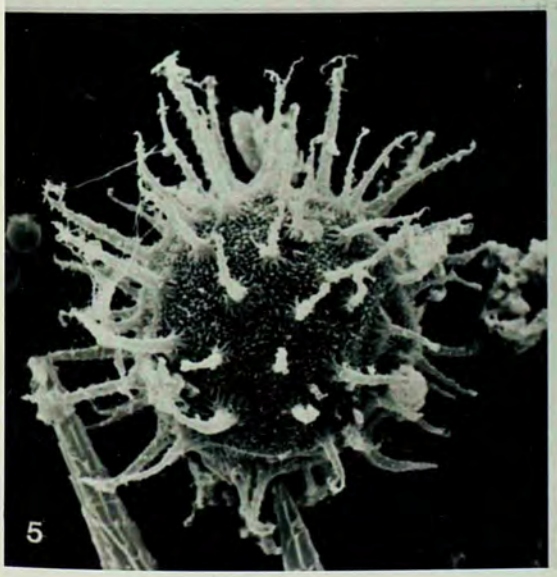
Fig.5 : *Lingulodinium machaerophorum* (*Gonyaulax polyedra*), with long and curly spines, 39 µm across (excluding spines), Loch Creran water sample (9/9/83).

Fig.6 : Detail of spines of *Lingulodinium machaerophorum* (*Gonyaulax polyedra*) shown in Fig.5, x 3024; Loch Creran water sample (9/9/83).

Plate 5.1







thecate stages) (Fig. 5.6). The spine length of the cysts formed varied from 1µm to 20 µm (Pl. 5.1, figs.3-6) although most were around 12µm in length. Wall, Dale and Harada (1973) describe clavate spines on Lingulodinium machaerophorum cysts formed in low salinity environments. These were not observed in this study.

Gonyaulax grindleyi (Operculodinium centrocarpum) was the most frequent of the other cysts occasionally encountered. It was found in late August / September of 1983 during and after the peak in numbers of the thecate stage at the end of August. In 1983 round, brown cysts and 'spiniferites'-type (see Chapter 3) cysts were also seen.

Tintinnid cysts were noted in samples after their peak in numbers at the end of May / begining of June although they were not enumerated.

Sediments

Figure 5.7 shows the percentage empty cysts in the 1cm samples. As can be seen in this figure the counts made on the unpreserved sediment all show greater percentages of empty cysts than were found in the preserved sediment. All the counts were carried out at Royal Holloway College after samples had been transported from Scotland. It is possible that in transit they were subjected to an increase in temperature and some hatching may have taken place.

Both curves have roughly the same shape. There were always empty cysts present in the sediments probably from previous years. There was a small increase in the numbers of empty cysts at the end of June although this could have been sample variation rather than evidence of excystment. The most noticeable change was during September when the percentage of empty cysts dropped

Figure 5.6: Distribution with depth of *Gonyaulax polyedra*, 1983

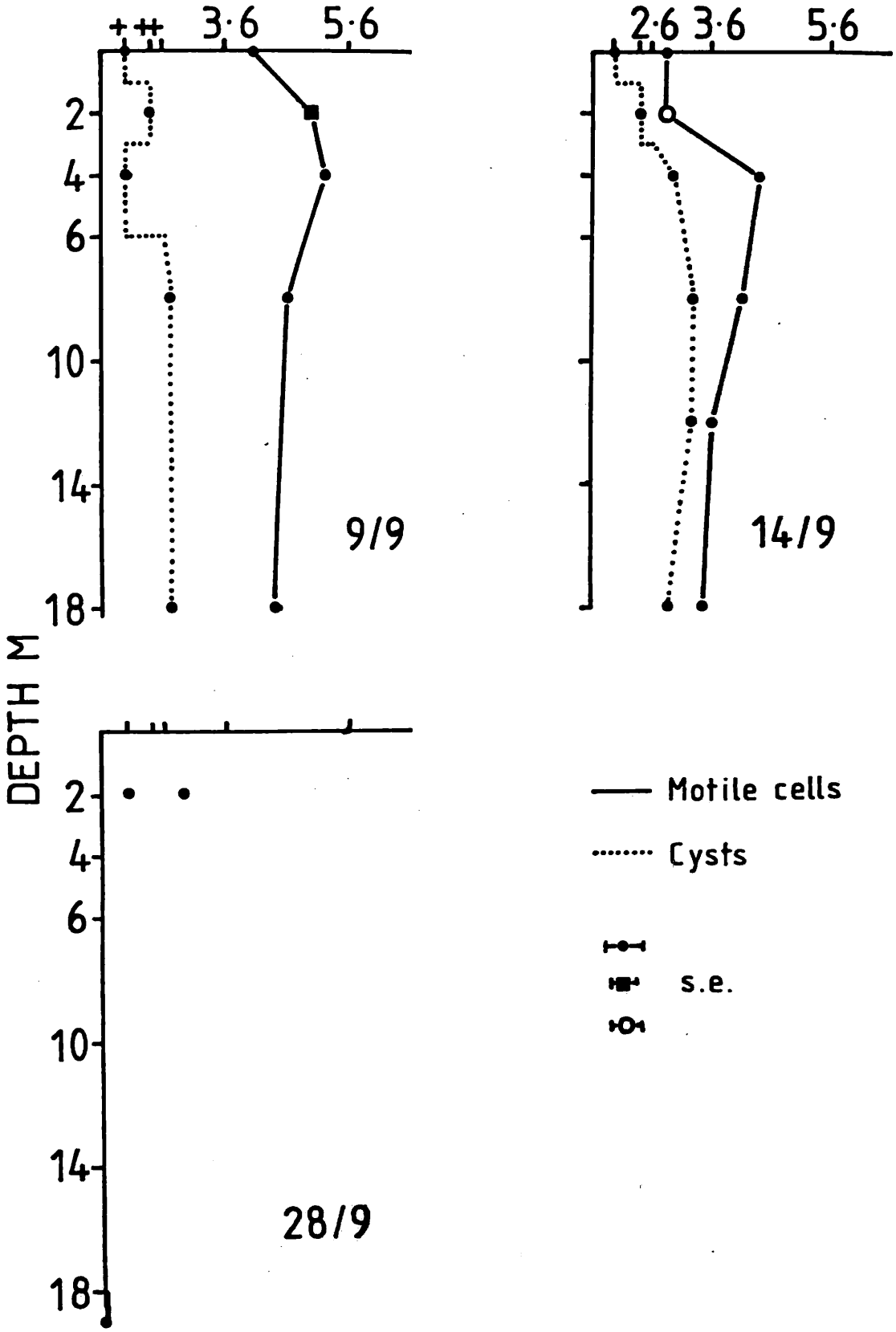
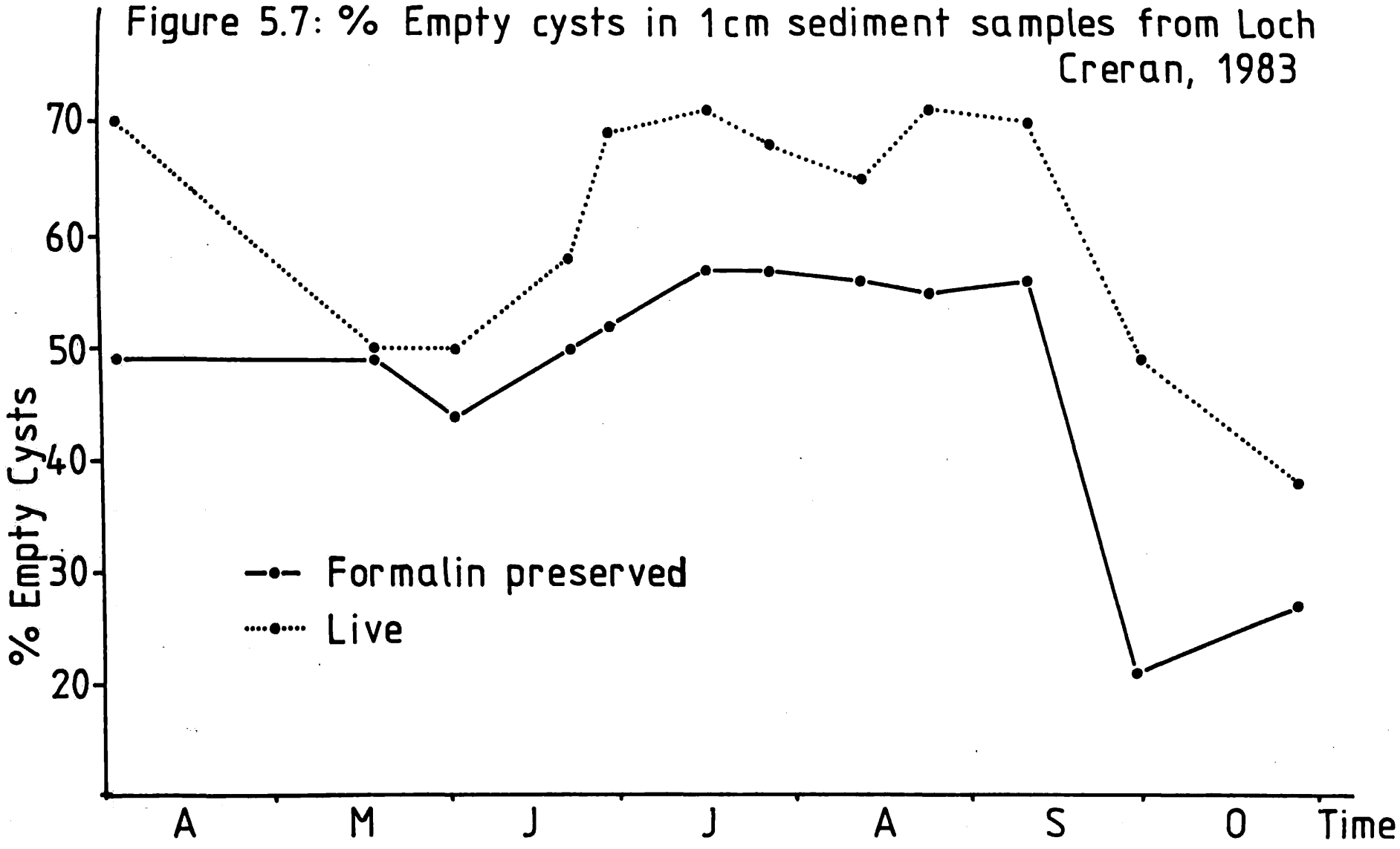


Figure 5.7: % Empty cysts in 1cm sediment samples from Loch Creran, 1983



dramatically, because of recruitment of newly formed cysts to the sediment. These were noticeable because of their brightly pigmented red spot and lack of debris collected around the spines. Their cytoplasm had not darkened as in more mature cysts.

DISCUSSION

It was not possible to follow a full cycle of events for the Scrippsiella spp. because of the difficulties of assessing their numbers in the sediments. In addition the taxonomic difficulties in separating the thecate cells into species (see Chapter 3) mean that cyst formation cannot be related to species numbers. This group provides an excellent example of how sometimes cysts are more easily defined than their motile stages. Encystment of two species (on the basis of cyst types Scrippsiella trochoidea and Scrippsiella ?sweeneyae) was noted occasionally in spring, summer and autumn of both years. These species would fit into Dale's (1983) category of species with sporadic abundances and cyst formation spread over spring, summer and autumn. This confirms the species he cites as an example of this (Scrippsiella trochoidea). Although Peridinium faeroense has been found in water samples no cysts of this type (Impletosphaeridium bifurcatum) were noted, probably due to sieving procedures.

It was possible in 1983 to follow the alternation of cyst and motile stage for Gonyaulax polyedra. During the summer there appeared to be some excystment as thecate motile cells appeared in the plankton (Figs. 5.4 - 5.5) and this can perhaps also be seen in the slight increase in the percentage empty cysts found in the sediments in June and July (Fig. 5.7.). Finally, conditions in late August seemed to favour the fast development of the population so that the autumnal bloom of this species occurred. As mentioned in the introduction of this chapter

calculations can be made of numbers of cysts per unit area required to produce a suitable inoculum. One such calculation follows here. Using numbers of G. polyedra when maximum measured on 9-9-1983:-

Number of cells = 50,630 l^{-1} (averaged over the water column with the average weighted according to the volume of the loch in each depth segment)

This number of cells developed over about 29 days (none were observed on the 11-8-1983 sampling trip).

Prézelin and Sweeney (1978) record the maximum specific growth rate (μ) of G. polyedra to be 0.3 day^{-1}

Using this data it follows that the inoculum needs to have been:

$$\frac{N_t}{N_o} = e^{\mu t}$$

where N_o and N_t are the numbers of cells at time 0 and time t respectively

$$N_o = N_t \times e^{-\mu t}$$

$$50,630 \times e^{-29 \times 0.3} \text{ cells } l^{-1}$$
$$= 8.43 \text{ cells per } l^{-1}$$

The mean volume of Creran (from Tyler, 1983)

$$= 182.86 \times 10^9 \ l^{-1}$$

The mean area of Creran at MHWS (from Tyler, 1983)

$$= 15.19 \times 10^{10} \ cm^2$$

Therefore $\frac{8.43 \times 182.86 \times 10^{9}}{15.19 \times 10^{10}}$ cells cm^{-2} needed

$= 10.15$ cells cm^{-2}

If one assumes that only 50% of the cysts hatch successfully (Steidinger and Haddad, 1981) then:

20.31 cysts cm^{-2} required to start this bloom.

In April there were on average 91,904 cysts (with protoplasm) in a 5cm sediment core of area 25.07 cm^{2}. Therefore in 1 cubic cm there was:-

$$\frac{91904}{5 \times 25.07} \text{ cysts}$$

so there were about 733 cysts cm^{-3}

It follows that only 2.8% of cysts are required to have hatched.

This amount of hatching is unlikely to be observable in the sediment samples given sampling error. The detection of new empty cysts is made more difficult by the presence of a high number of empty cysts in the sediments. The gonyaulacioid cysts in particular seem to be very resistant to decay and so accumulate in the sediments. The fossil record is evidence of their persistance. The results of the calculation implies that many cysts are left each year even if there is a bloom of the species. As dicussed by Heaney et al. (1983) it also means that if there is a failure of, or little encystment in one year there is still a reservoir of cysts available for the following year. Marine cysts stored in the laboratory have been shown to have a life-span of at least 16.5 years (Steidinger & Haddad, 1981). There is little information available about factors apart from

excystment which remove viable cysts from the sediments. Such factors are likely to be consumption, degeneration and attack by parasites and fungi. Chapman (1981) working on Ceratium hirundinella notes that temporary cysts present in the lake sediments were suceptible to decay and attack by a chitrid fungus. She also notes predation of cysts by an amoeban organism. In this study some Scrippsiella ?sweeneyae cysts have occasionally been observed with fungi attacking them. Cysts are also subject to ingestion by certain types of shellfish as is shown by investigations of causes of their toxicity (Yentsch and Mague, 1979). It is not clear whether they are digested. Some estimates of these processes would help in the prediction of the potential of the cyst reservoir.

In Creran in 1982 and 1983 the encystment of Gonyaulax polyedra started at the time of maximum numbers of motile cells. Figure 5.6 shows the number of cysts increases down the water column an effect also noted by Nordli (1951). This is probably because of the effects of sinking. Ageing G. polyedra cells sink faster than healthy cells (Smayda and Bienfang, 1983) so even if cyst formation starts high up in the water column some sinking would have taken place by its completion. Perhaps this can be seen where the maximum number of cysts is present below the maximum number of thecate cells. Light microscopy shows that cysts sink quickly. The recruitment of new cysts to the sediments can clearly be seen in Figure 5.7. The top few centimetres of sediment is not stable and after storms it will probably be mixed with deeper layers returning the ratio of full and empty cysts to about 50%.

Cysts behave as fine sediment particles and therefore will have a tendency to accumulate within the low turbulent energy basins of sea-lochs or fjords (Dale, 1976). As Gonyaulax polyedra cysts have fast sinking rates this will increase the likelihood of their retention within the loch. It can be seen

that if a species is introduced to a sea-loch, and if it has a cyst stage then if conditions are not too severe, the species is likely to become a permanent member of the dinoflagellate assemblage. From the point of view of mariculture therefore it is important that transportation of shellfish is carefully controlled to prevent movement of sediment. Shellfish should also be cleaned (gut contents emptied) because they ingest cysts. It should also be remembered that the composition of the dinoflagellate population in a loch could drastically change over a short time if water movement brought in a cyst-forming bloom species.

Clearly the benthic resting cyst is extremely important in the life-cycle of certain dinoflagellates and merits more attention from ecologists.

CHAPTER 6

DISTRIBUTION OF MOTILE DINOFLAGELLATES ON THE SCOTTISH WEST COAST

INTRODUCTION

"It is an arresting point that a prevalent feature of the phytoplankton is its unpredictability." (Hulburt, 1983).

Hulburt goes on to discuss the unpredictability of phytoplankton in terms of predicting concentrations of given species. It has more generally been hypothesized (Margalef, 1978) and observed (Pingree *et al.*, 1978) that diatoms predominate in mixed waters with high nutrient concentrations and that as water column stability increases and nutrient concentrations decrease dinoflagellates become dominant. Margalef points to ideal categories ("life-forms") of phytoplankton corresponding to "certain recurrent patterns of selective factors". He choses the principal factors as those related to the supply of external energy (i.e. nutrients and decaying turbulence). Organisms adapted to high nutrient concentrations may also be adapted to a high turbulence, for example the diatoms. In contrast, organisms adapted to low nutrient concentrations may also be adapted to low turbulence, as in the case of many motile dinoflagellates. Margalef *et al.* (1979) also note that, in general and unlike other dinoflagellates, red tide dinoflagellates may require high nutrient concentrations for growth.

Much of Margalef's work assumes steady state conditions. These sort of conditions are unlikely to be experienced by water bodies circulating in Scottish west coast sea-lochs, whose flushing times are of the order of a few days. These conditions might, however, be observed in the larger frontal regions of the Firths and Sounds. Nevertheless data from the Scottish west coast

is in general agreement with the hypothesis that greater diatom biomass is found in mixed waters and a greater dinoflagellate biomass is found in weakly stratified and stratified water (Gowen, 1984). In addition, fjord exchange is important and the species composition of the source water can be a major factor in determining the species composition within a sea-loch (Gowen et al., 1983).

Gowen (1984) outlines three possible origins for phytoplankton blooms in sea-lochs: Firstly, the introduction of a bloom from outside a sea-loch; secondly, the introduction of an inoculum from outside a sea-loch which if conditions are suitable forms a bloom within the sea-loch; and thirdly, growth of a species normally present within a sea-loch. A knowledge of hydrographic parameters (which determine the likely stability of the water column in particular areas and the possibilities for exchange of waters between lochs and sea) allows an assessment of the likelihood of blooms within different sea-lochs. The species composition of these blooms is unspecified; part of the aim of the present study was the hope that from investigations of dinoflagellate distribution would come additional knowledge of the occurrence of particular notorious species which might help to define the 'risk' of toxic blooms at particular sites.

Blooms of phytoplankton, frequently referred to as red tides (because of water discolouration), are known to have occurred since ancient times (see for example Exodus Ch.7 v 20-21). There are also legends associated with toxicity of shellfish at certain times of the year (see for example Yasumoto et al., 1978). Documented examples of blooms and fish mortalities are available from at least the early nineteenth century (for references see Rounsefell and Nelson, 1966; Hurst, 1975; Maclean, 1979 and Wyatt, 1979). These happenings are world wide occurrences (see for example Sweeney, 1976) and such is their economic importance

that much research effort has been directed to investigating the causative organisms (reviewed by Steidinger, 1983), their toxicity (reviewed by Shimizu, 1978) and their ecology (see for example Steidinger and Haddad, 1981).

Such blooms are not always toxic (producing toxins with restricted targets) or harmful (causing other ill effects) and neither does a bloom need to occur for toxic effects to be noticable. The toxic effects fall into two categories: direct toxicity to marine organisms; and indirect toxicity to man (for example paralytic shellfish poisoning (PSP), caused by the consumption of shellfish which have ingested toxic cells). In Scottish waters the former might cause problems with farmed fish and the latter with shellfish farming. Many members of the Pyrrophyta have been accused of toxicity (Halstead, 1965) but evidence is often only circumstantial. It is complicated by the fact that gill clogging by cells, high nocturnal oxygen demand of blooms and oxygen depletion due to decay of blooms may also cause the death of marine organisms. Consideration will be given here to the following potentially toxic dinoflagellates found in western Scottish waters. In the appendix to this chapter the evidence for their toxicity is summarized and discussed.

Dinophysis acuminata Claparede and Lachmann
Gonyaulax polyedra Stein
Gonyaulax tamarensis Lebour
Gyrodinium aureolum Hulburt
Prorocentrum lima (Ehrenberg) Dodge
Prorocentrum micans Ehrenberg
Prorocentrum minimum (Pavillard) Schiller

Gowen (1984) summarizes known mortalities of farmed fish associated with phytoplankton blooms on the Scottish west coast. There have been no reported incidents in this region of shellfish toxicity of the type associated with phytoplankton blooms.

It is worth noting that of all the species described above only one, (Gyrodinium aureolum), has so far been certainly associated with an incident on the Scottish west coast. There have been other incidents involving major fish losses (e.g. in Loch Striven 1979: Tett ed., 1980) but for which algae other than dinoflagellates have been blamed.

Some general information about the distribution of dinoflagellates on the Scottish west coast is available from Dodge (1981); Holligan, Maddock and Dodge (1980) and the continuous plankton recorder survey (see for example Robinson, 1965). More detailed information is available in Tett (1969); Marshall and Orr (1927) and much unpublished data held by the S.M.B.A.

The infomation gained in studying the wider distribution of motile dinoflagellates provides an insight into two aspects of this study in that it

a) Allows comparison with Loch Creran.
b) Reports the distribution of toxic species.

METHODS

Samples for the distribution investigation were collected on cruises during the summers of 1982 and 1983 listed in Table 6.1. Data relating to general distributions were also obtained from the seasonal sampling of Loch Creran already described (see Chapter 4) and from day trips made to several lochs close to Oban (Loch Etive, Loch Spelve, and Loch Melfort) for the purpose of cyst collection.

TABLE 6.1

Ship	Dates	Area	Report/Chief Scientist
Calanus (1/82)	12/5 - 14/5/82	Clyde	Dr R. Gowen (S.M.B.A.)
Shackleton (4/82)	22/5 - 4/6/82	Scottish shelf	Hill, 1983
Calanus (2/82)	5/7 - 23/7/82	Sound of Jura	Jones *et al.*, 1984
		Northern lochs	Dr R. Gowen (S.M.B.A.)
		Firth of Lorne	Grantham *et al.*, 1983
Calanus (3/82)	21/9 - 23/9/82	Loch Sunart	Dr K. Jones (S.M.B.A.)
Calanus (1/83)	28/6 - 14/7/83	Sound of Jura	Jones *et al.*, 1984
		Firth of Lorne	Oatham, 1983
		Loch Sunart	J.M. Lewis

Samples were collected as described in Chapter 2 except for the Shackleton cruise (4/82) when 2 litre samples were taken using a pump from the depth of maximum *in vivo* fluorescence. Samples were filtered and treated in the standard way. Hydrographic data were collected at all stations, and sediment samples at many. Counts of samples were made as described in Chapter 2. In the case of samples from the Shackleton cruise, which contained few dinoflagellates, the complete sample was centrifuged and counts of at least 200 cells made, results for each species being recorded as percentage presence.

RESULTS

Hydrographic data collected is described in the reports listed in Table 6.1 or can be obtained from the chief scientist of each cruise and will only be referred to in a general way here. Excluding the counts of seasonal samples described and listed in Chapter 4 something over 200 sample counts have been made. Results of the counts will be deposited in the S.M.B.A. and Royal Holloway College libraries and only certain features described here. A far more detailed analysis may be possible but it was beyond the scope of this project to attempt it. Figure 6.1 shows the main features of the sampling area covered, and a full list of species is given in Table 6.2.

Maps are given summarizing the occurrence of numerically dominant species in Figures 6.2 - 6.7. The numerically dominant species were taken to be all those species present in numbers greater than 400 cells per litre in the majority of samples from a particular area. Areas were decided on the basis of the similarity of numbers and dominant species in the individual samples. In the case of the Shackleton samples the distribution map was based on the three species with the highest percentage presence in each sample.

General distribution of thecate dinoflagellates

Calanus 1/82 - Firth of Clyde

This short cruise took place in May 1982. Samples were taken from around Arran (see Chapter 7) but all contained few dinoflagellates, falling into the "very thin" category where less than 20 cells of the dominant species were counted. Cells of *Scrippsiella* spp. were the most abundant with a maximum of 260 cells per litre.

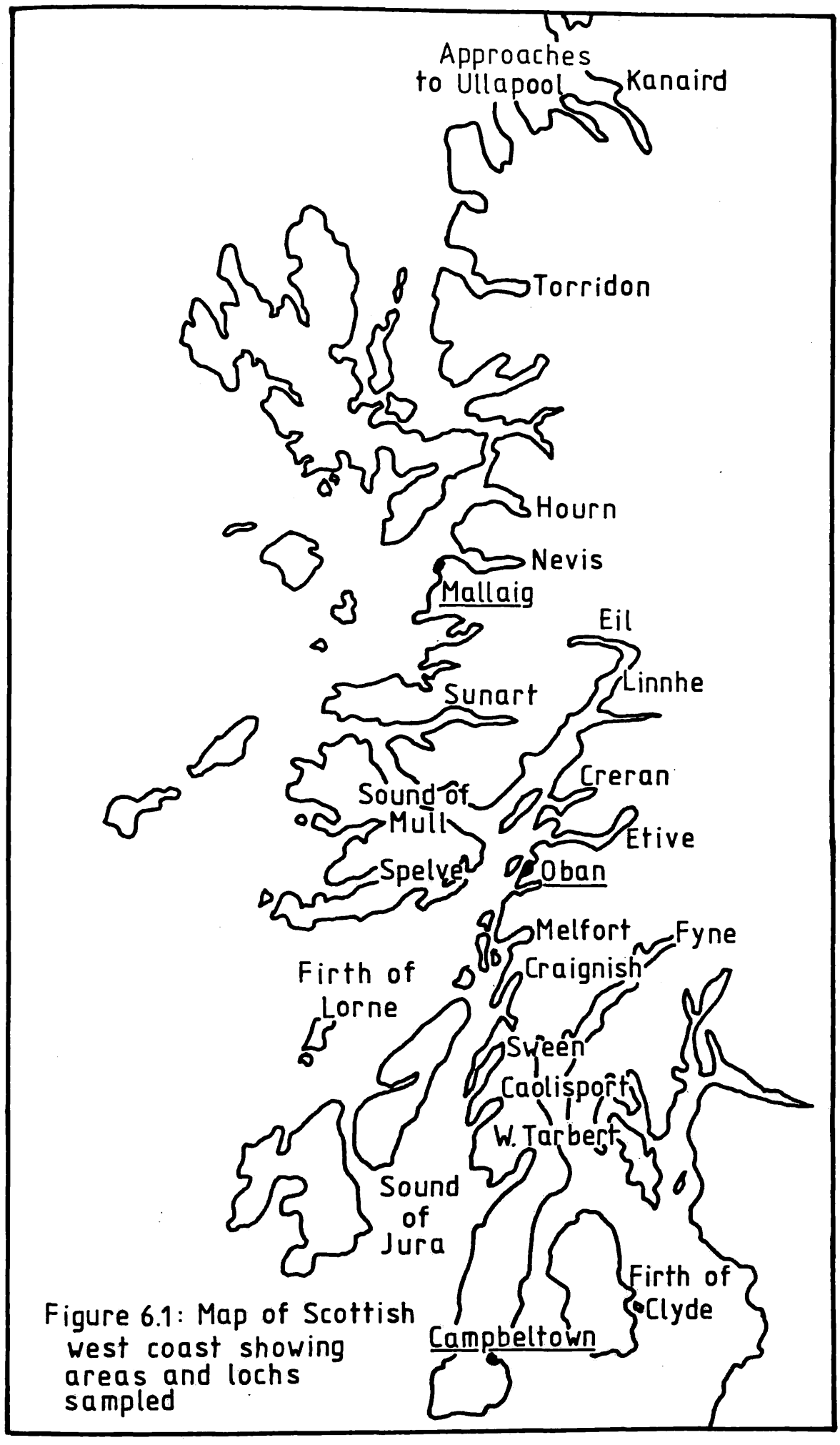


Figure 6.1: Map of Scottish west coast showing areas and lochs sampled

TABLE 6.2 : SPECIES FOUND DURING THIS STUDY

Amphidoma caudata
Ceratium arietinum
C. compressum
C. furca
C. fusus
C. hexacanthum
C. horridum
C. lineatum
C. longipes
C. macroceros
C. tripos
Dinophysis acuminata
D. acuta
D. contractum
D. dens
D. hastata
D. norvegica
D. nasutum
D. ovum
D. pulchellum
D. punctata
D. recurva
D. rotundatum
Diplopsalis lenticula
Dissodium asymmetricum
Dissodinium pseudocalani
Glenodinium sp.
Gonyaulax digitale
G. grindleyi
G. polyedra
G. polygramma
G. spinifera
G. tamarensis
G. triacantha
G. verior
Helgolandinium subglobosum
Heterocapsa triquetra
Katodinium rotundatum
Oblea rotundata
Prorocentrum balticum
P. compressum
P. gracile
P. micans
P. scutellum
Protoperidinium bipes
P. brevipes
P. cerasus
P. claudicans
P. conicoides
P. conicum
P. curvipes
P. curtipes
P. denticulatum
P. depressum
P. diabolum
P. divergens
P. excentricum
P. granii
P. leonis
P. minutum
P. mite
P. oblongum
P. ovatum
P. pallidum
P. pellucidum
P. pentagonum
P. pyriforme
P. steinii
P. subinerme
P. thorianum
Scrippsiella faeroense
Scrippsiella ?sweeneyae
Scrippsiella trochoidea

Shackleton 4/82 - Scottish shelf

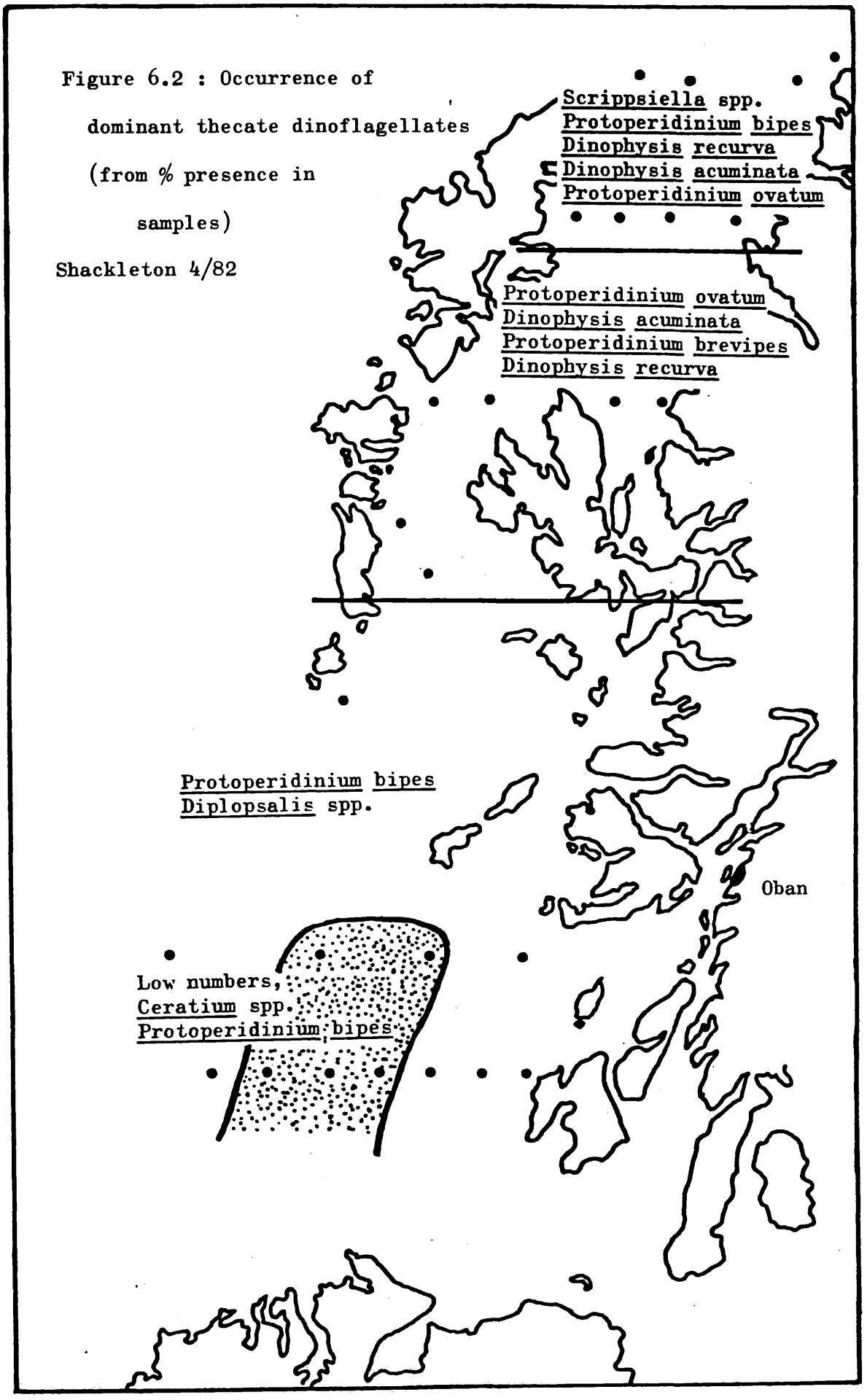
This cruise was part of a wider study of tidal mixing around islands in shelf seas. Samples were collected to ascertain the distribution of species further offshore than could normally be sampled. The occurrence of numerically dominant thecate dinoflagellates is summarized in Figure 6.2 Many other species were recorded (50 species in total) including 7 species of Ceratium, more than are usually found inshore. The rare species Amphidoma caudata was also found although it was not recorded from this area by Dodge (1981).

Calanus 2/82 - Sound of Jura, Northern lochs, and Firth of Lorne

This cruise covered three separate areas during July 1982 and the distribution of numerically dominant thecate dinoflagellates in each area is summarized in Figures 6.3 - 6.5. Taking all three areas together the most prevalent dinoflagellates were Scrippsiella spp. and Heterocapsa triquetra. Other common dinoflagellates were Prorocentrum micans, Gonyaulax spinifera and Ceratium lineatum. In general the highest numbers of dinoflagellates were to be found within the sea-lochs (and exceptionally, in Eddrachillis bay). The populations within the sea-lochs seemed quite variable but frequently sea-lochs in close proximity (e.g. Loch Melfort and Loch Craignish) had similar populations. Over 50 different species were recorded, the areas outside the sea-lochs (the Firths and Sounds) being the poorest in species and the sea-lochs the richest.

Figure 6.2 : Occurrence of dominant thecate dinoflagellates (from % presence in samples)

Shackleton 4/82



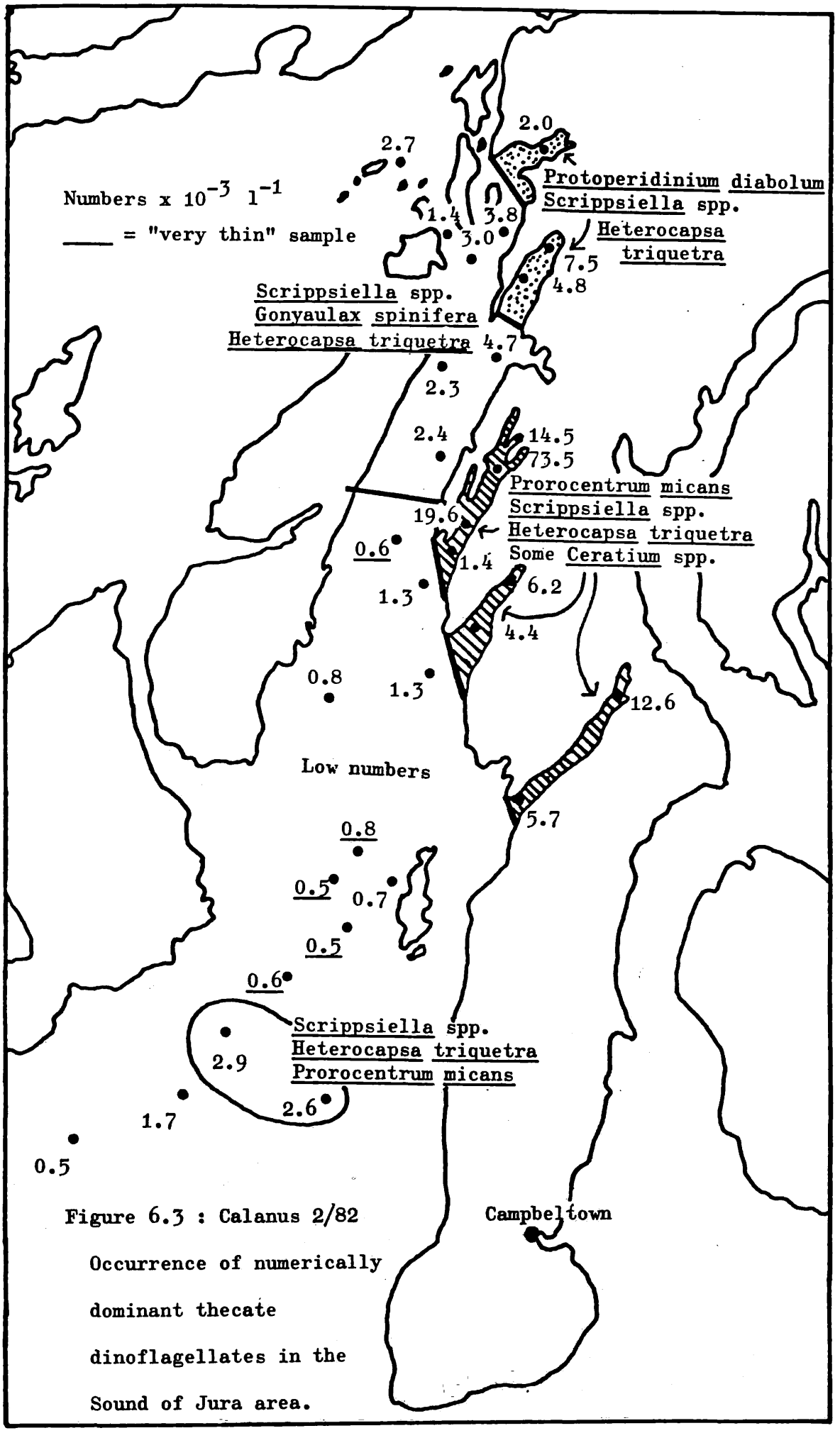


Figure 6.3 : Calanus 2/82

Occurrence of numerically dominant thecate dinoflagellates in the Sound of Jura area.

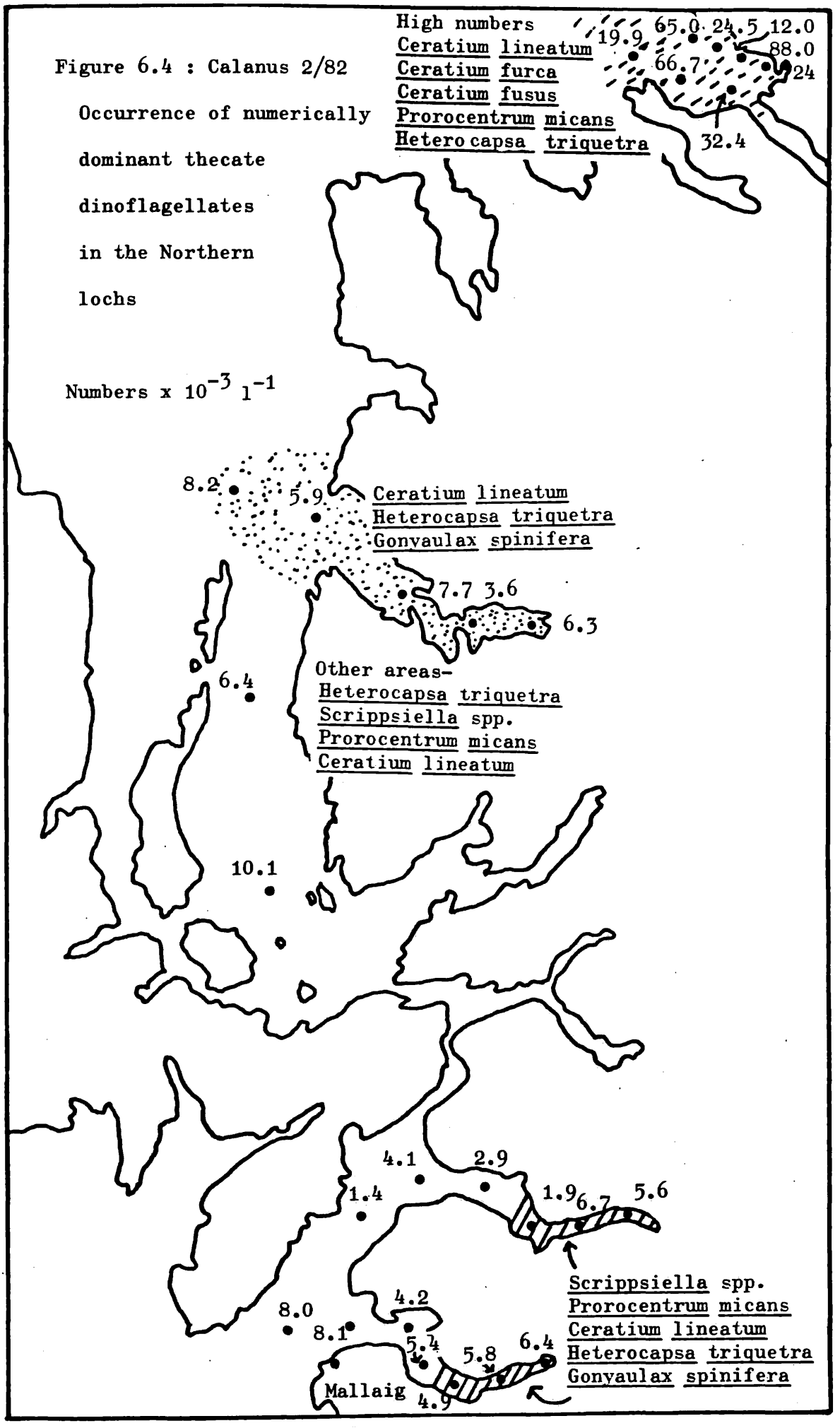


Figure 6.4 : Calanus 2/82

Occurrence of numerically dominant thecate dinoflagellates in the Northern lochs

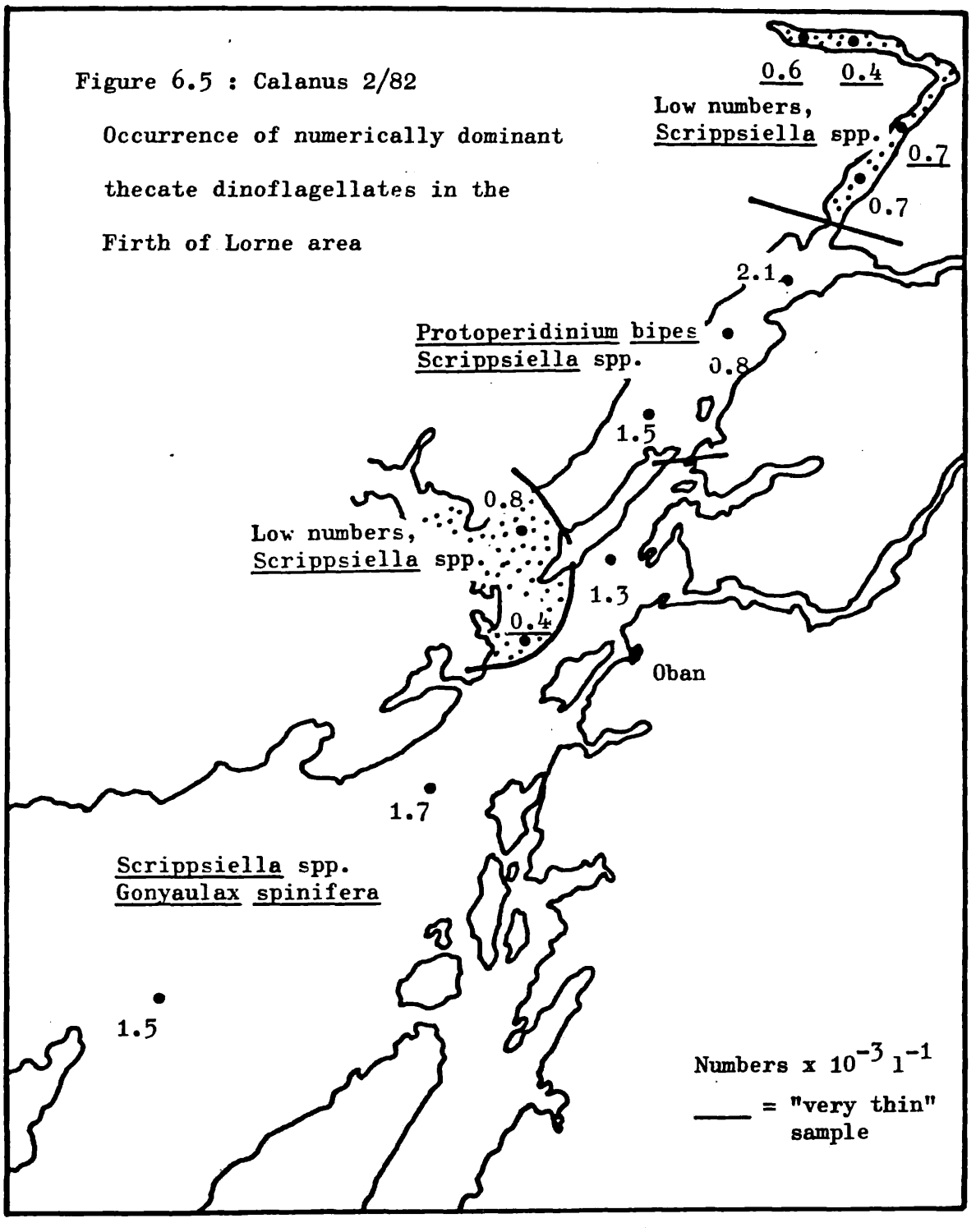


Figure 6.5 : Calanus 2/82

Occurrence of numerically dominant thecate dinoflagellates in the Firth of Lorne area

Calanus 3/82 - Loch Sunart

This cruise was in late September 1982, when there were few dinoflagellates present in the loch. The most common species was *Prorocentrum micans*. Other common species were *Scrippsiella* spp. and *Heterocapsa triquetra*.

Calanus 1/83 - Sound of Jura, Firth of lorne, and Loch Sunart

This cruise covered several areas of the coast in June / July 1983. The distributions of numerically dominant dinoflagellates in the areas of the Sound of Jura and the Firth of Lorne are described in Figures 6.6 - 6.7. As in the previous year thecate dinoflagellates were found to be abundant in the sea-lochs. The entrances to both the sound of Jura and the Firth of Lorne also contained high numbers of thecate dinoflagellates. The most common species were *Scrippsiella* spp., *Heterocapsa triquetra*, and *Gonyaulax spinifera*. About 50 different species were encountered. The central portions of the Sound of Jura and the Firth of Lorne were the poorest in species.

Loch Sunart contained a rich population of dinoflagellates the numerically dominant species being *Scrippsiella* spp., *Gonyaulax spinifera*, *Heterocapsa triquetra* and *Prorocentrum micans*.

Potentially toxic species

As can be seen from Chapter 4 the composition of the dinoflagellate population within a sea-loch can vary greatly during the year. This must be remembered when looking at the distribution data reported here which is based on single cruises

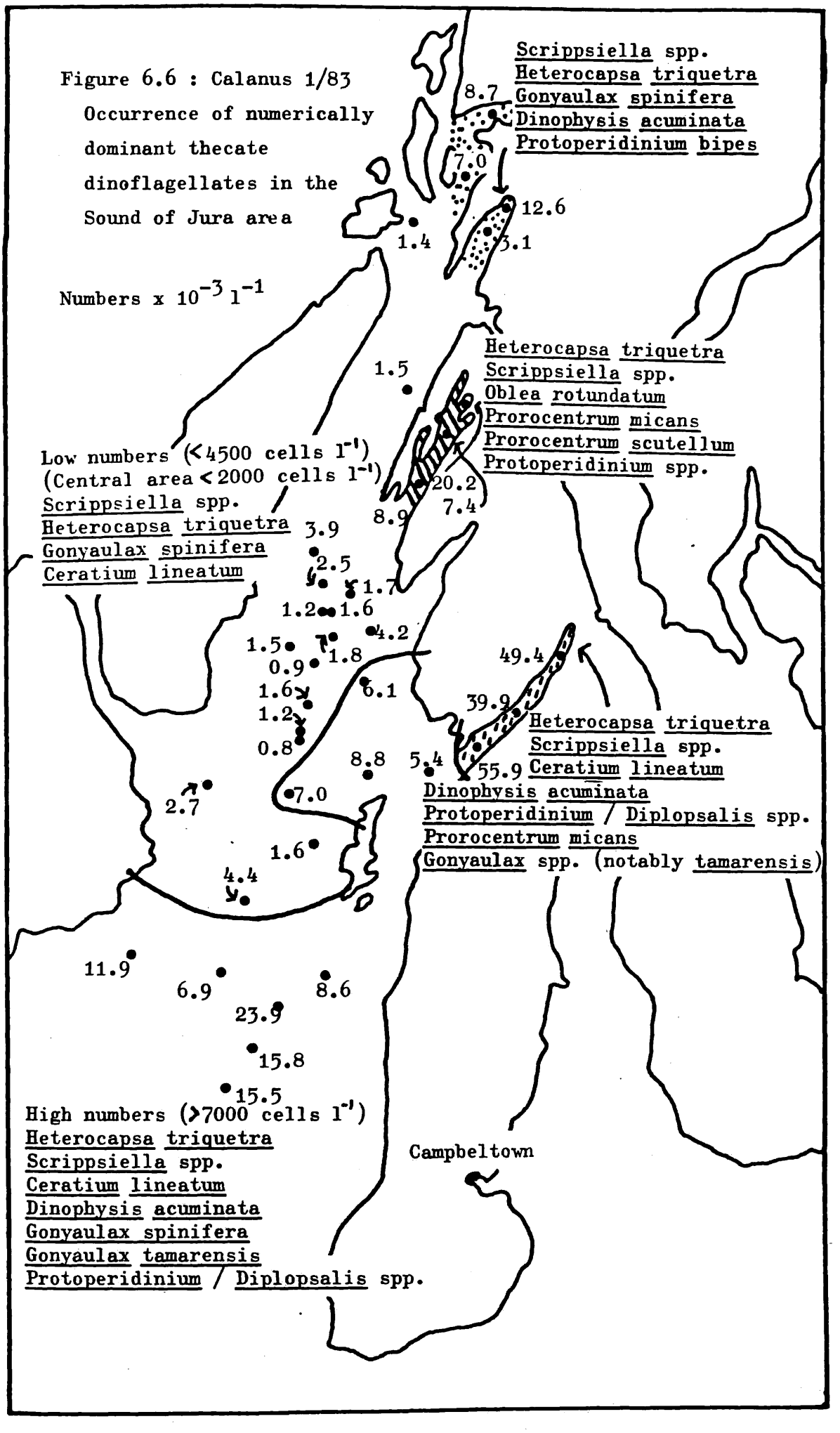


Figure 6.6 : Calanus 1/83
Occurrence of numerically dominant thecate dinoflagellates in the Sound of Jura area

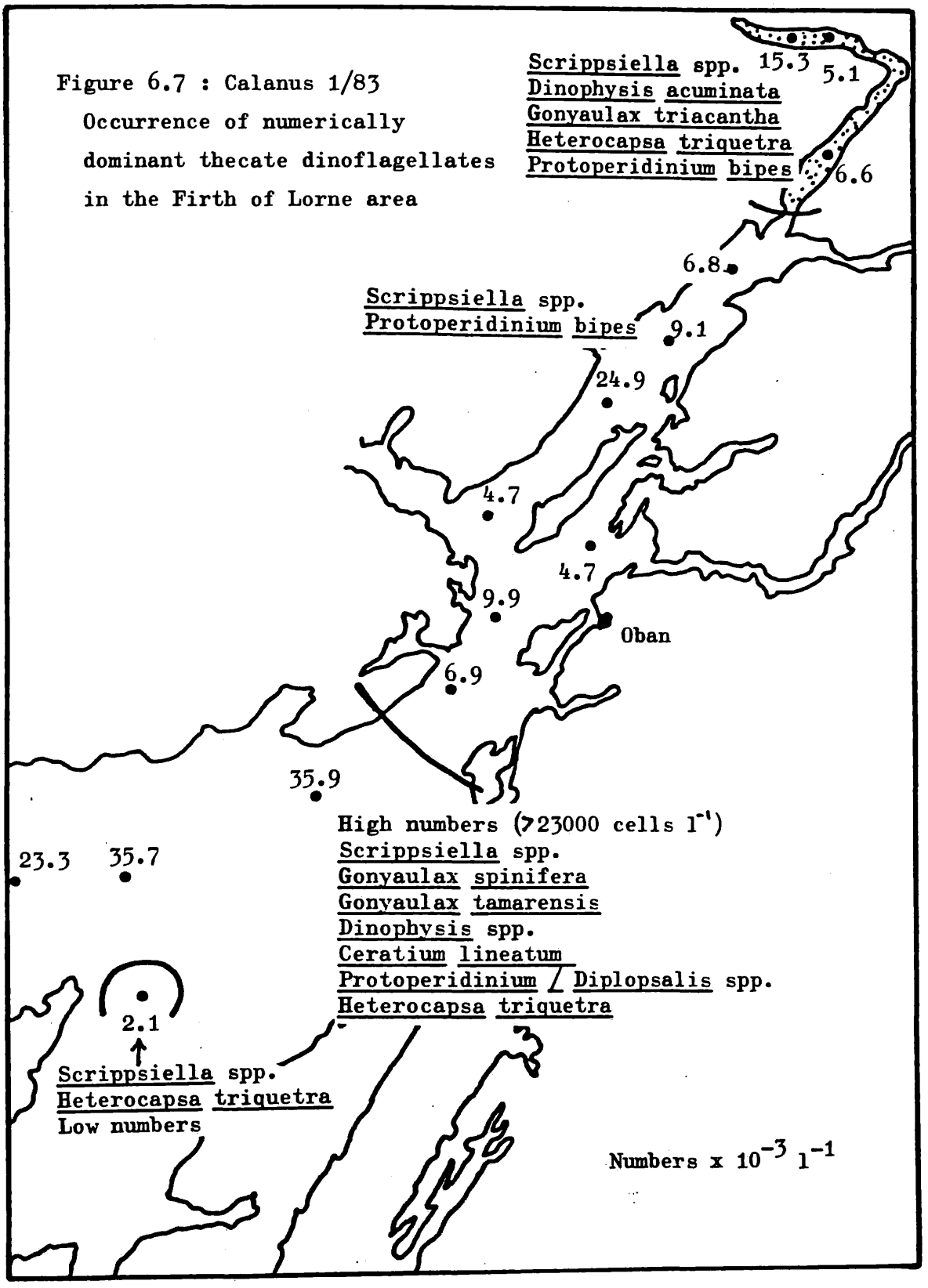


Figure 6.7 : Calanus 1/83
Occurrence of numerically dominant thecate dinoflagellates in the Firth of Lorne area

and therefore shows just a glimpse of the whole picture. Nevertheless, the main cruises were at times of the year when a good population of dinoflagellates would be expected.

With regard to the toxic species listed in the introduction Prorocentrum minimum has not been found in this survey although this tiny alga is easily missed. Gyrodinium aureolum is a naked dinoflagellate and therefore would have been found only in the live samples. It was found once in Loch Creran in May 1982. Prorocentrum lima is a coastal benthic dinoflagellate and its habitat was not sampled in this study. Dinophysis acuminata and Prorocentrum micans were considered in Chapter 4 to be regular members of the phytoplankton in Loch Creran. They were both found in all the lochs sampled in the distributional study. The highest numbers (56,700 cells per l) of P. micans were found in 1982 in Loch Sween. High numbers were also found in West Loch Tarbert (1982), Loch Nevis (1982), Eddrachillis Bay (1982), Loch Sween (1983), and Loch Sunart (1983). The highest numbers (3,400 cells per litre) of Dinophysis acuminata were found in West Loch Tarbert in 1983. Gonyaulax grindleyi and Gonyaulax polyedra were found to be occasional members of the Loch Creran phytoplankton, probably remaining resident in the loch by means of a cyst stage (see Chapters 4 and 5). Both species were occasionally present in water samples from the areas investigated but might well have been more widespread. Further information on their distribution can be obtained from the cyst counts discussed in Chapter 7.

Gonyaulax tamarensis was not found in this study in 1982 but Figure 6.8 shows its occurrence as recorded in 1983. During the occurrence of G. tamarensis in Loch Creran in 1983 mussels were collected from the loch and sent for bioassay to MAFF at Burnham-on-Crouch where no toxicity was detected. This is possibly because it was a non-toxic variety of this complex of species or, if conditioning is important, conditions did not favour toxin production (see Appendix to this Chapter).

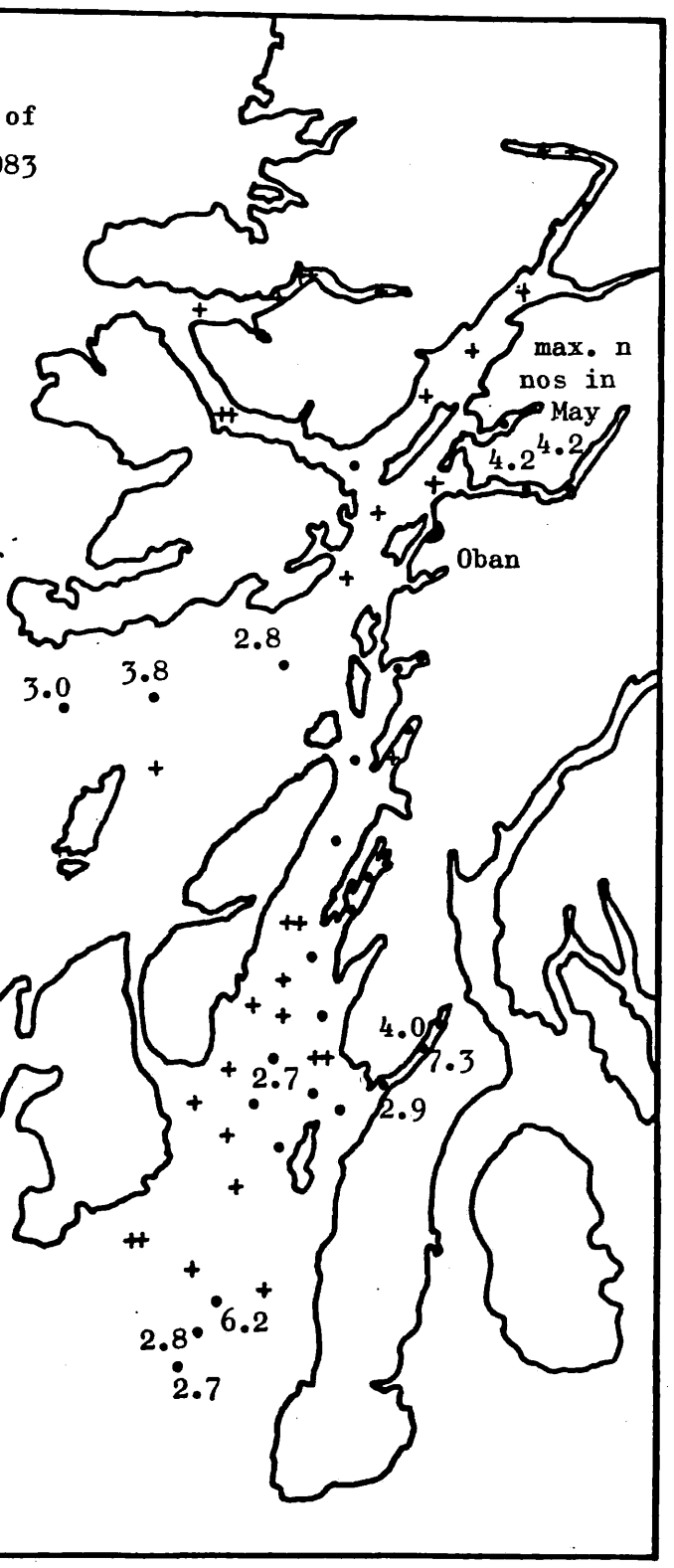
Figure 6.8 : Distribution of *Gonyaulax tamarensis*, 1983

Numbers x 10^{-3} l^{-1}

+ = 0-199 cells l^{-1}

++ = 200-399 cells l^{-1}

All sampling carried out on Calanus 1/83 except for Loch Creran.



DISCUSSION

The most frequently found dinoflagellate species in this study were Scrippsiella spp. and Heterocapsa triquetra. Other common species were Prorocentrum micans, Protoperidinium bipes, Gonyaulax spinifera, Dinophysis acuminata and Ceratium lineatum. 72 species were found in total from the water samples counted, these are listed in Table 6.2. This is a considerable variety even given possible taxonomic errors, especially as this area is not regarded as being rich in dinoflagellates. This variety exceeds that of Dodge and Hart-Jones (1974, 1977) who found totals of 53 and 61 species in their seasonal study on the north-east coast of Britain, an area probably richer in dinoflagellates than the west coast of Scotland. This shows the advantage of the collection and counting methods used in this study which involve a combination of filtration and settlement, yielding both large and small rare species.

The survey of dinoflagellates by Dodge (1981) did not cover the Scottish west coast in as much detail as this study although it did show the presence of 76 species (including naked species). This study extends the known distribution of some thecate species covered in that survey. Observations by Tett (1969) from Millport on the Firth of Clyde show the large Ceratium species (for example tripos) are more important in this area than they are further north where they were seldom observed except well offshore.

In general the highest numbers of dinoflagellates were to be found in the sea-lochs. In 1983 high numbers were also observed at the entrance to the Firth of Lorne and the entrance to the Sound of Jura. Most of the sea-lochs sampled during summers 1982 and 1983 appear to have been stratified. Part of the Sound of Jura was stratified with respect to temperature in 1982 and 1983

(Jones et al., 1984). The region of highest stability was in the centre of the sound to the west of Loch Caolisport. In 1983 the highest numbers of dinoflagellates were observed to the south of this region in an area of transitional stability. In 1982 in the Sound of Jura only low numbers of thecate dinoflagellates were observed although increased numbers were noted in the areas of transitional stability. Jones et al. (1984) note that much of the increase in numbers of dinoflagellates in this area in 1982 was due to naked species.

Gowen (1984), with data from Scottish coastal waters, shows that a weakly stratified water column supports a higher phytoplankton biomass than either a well mixed or stratified water column. The hypothesis of Margalef (1978) that dinoflagellates dominate in more stable water columns (weakly and strongly stratified water columns) thus seems to hold true for Scottish coastal waters.

In the Firth of Lorne in 1983 the four outermost stations sampled seem to represent a transitional area between a thermally stratified water column out to sea and a salinity stratified water column further inshore (Oatham, 1983). In this transitional area, as in the Sound of Jura in 1983, high numbers of thecate dinoflagellates were found. High numbers were also found in the stratified Lochs Eil and Linnhe. The rest of the Firth of Lorne had lower numbers than these areas. In both the Firth of Lorne and the Sound of Jura (and indeed in Loch Creran) many more thecate dinoflagellates were found in 1983 than 1982.

Comparing the lochs sampled on the summer cruises Loch Creran shows the importance of 'source' water. In 1982 during the July cruises the total numbers of thecate dinoflagellates per litre in Loch Creran were between 900 and 2300 and these were dominated by Scrippsiella spp. Most of the lochs visited (with the exception of Lochs Eil and Melfort) had greater numbers and

variety of dinoflagellates present at this time, although Scrippsiella spp. was common elsewhere. The population in Loch Creran was in keeping with the generally low numbers in the Firth of Lorne and the other loch sampled in the Firth of Lorne, Loch Linnhe / Eil. In 1983 during the June - July cruise the total number of thecate dinoflagellates per litre in Loch Creran were between 4,800 and 27,800, again dominated by Scrippsiella spp. with Protoperidinium bipes common. This again reflects the numbers and species present in the Firth of Lorne. Numbers were more similar in this year to other southern west coast sea-lochs but the variety of species present in other lochs was greater.

The only dinoflagellates occurring in Scottish coastal waters for which there is clear evidence of toxicity are Gyrodinium aureolum and Gonyaulax tamarensis. The former was only seen once in this study (Loch Creran, May 1982). The distribution of Gonyaulax tamarensis appears to have been widespread in 1983. Some varieties of this species complex form cysts (see Chapter 3) and although none have been found to date, it is possible that they are present in such low numbers that they have been missed. If cysts were formed this organism could become a recurring feature of the phytoplankton of the Scottish west coast. The other risk to farmed fish is that of non-toxic phytoplankton blooms causing gill clogging or deoxygenation of the water. Clearly in Scottish coastal waters there are many species of dinoflagellates that have previously been recorded as forming blooms under suitable conditions. The reader is referred to Gowen (1984) for a discussion of the likelihood of phytoplankton blooms on the Scottish west coast.

With regard to aquaculture the other area of possible anxiety is that of shellfish farming. At the moment this is a relatively minor activity in Scottish west coast sea-lochs. However, as a clean and sheltered environment the sea-lochs provide an ideal site for shellfish farming. There are a number

of species that are potentially a problem here; Dinophysis acuminata, Prorocentrum micans, Gonyaulax tamarensis and Gonyaulax polyedra. These species appear to have a widespread distribution and routine monitering at certain times of the year may be advisable.

APPENDIX TO CHAPTER 6

POTENTIALLY TOXIC DINOFLAGELLATES OCCURING ON THE SCOTTISH WEST COAST

For the purposes of this appendix these species are divided into the categories used by Ayres, Seaton and Tett (1982):-

Species toxic to marine organisms and indirectly to man

Gonyaulax tamarensis Lebour

This species (or group of species - see Chapter 3) is a source of the toxins in molluscs responsible for Paralytic Shellfish Poisoning (PSP) in man. Passage of the toxin through marine food chains may also cause deaths in higher trophic levels (White, 1982). *G. tamarensis* has affected shellfisheries in many parts of the world including the North-east coast of Britain where toxins have been found to be present in shellfish annually since 1968 (Ayres *et al.*, 1982). In a survey of all the major shellfisheries in England and Wales Ayres and Callum (1978) found toxicity only on the North-east coast of England. Toxicity has also been reported from the Scottish North Sea coast (Conn and Farrard, 1970). There is evidence that mussels may become toxic due to continued exposure to low numbers of *G. tamarensis* cells (<1000 cells per litre). Examination of *Mytilus* gut contents (Ayres and Cullum, 1978) and water samples (Yentsch and Mague, 1979) suggests that cysts may be important in this respect. Cysts of the *G. tamarensis* complex have been shown to be more toxic than their thecate stages (Dale, Yentsch and Hurst, 1978; Oshima *et al.*, 1982). There is well documented evidence for this organism's toxicity, however, it appears to be a species complex and some forms / varieties appear to be non-toxic. There is also

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evidence that toxin content increases with increasing salinity (White, 1978). This species has been recorded from the Scottish west coast (Dodge, 1981). In this study G. tamarensis was found to be widespread (from the entrance to the Sound of Jura to Loch Sunart) in 1983.

Prorocentrum minimum (Pavillard) Schiller

Although this species has not been recorded from Scottish waters it occurs in Norwegian waters and because of the similarity of these situations (see Chapter 4) it was felt worthy of mention here. Toxins are again passed to man through shellfish (venerupin poisoning, Okaichi and Imatomi, 1979). Tangen (1983) describes a possible incidence of venerupin poisoning in Norway from Oslofjord mussels harvested at the time of a bloom of P. minimum. Schmidt and Loeblich (1979) detected no paralytic shellfish poison in this species. This small species could easily be overlooked or confused with the other small species Prorocentrum balticum or Mesoporos perforatus.

Species associated with gastro-enteric disorders in man

Dinophysis acuminata Claparéde and Lachmann

There have been a number of incidences of diarrhetic mussel poisoning in Dutch coastal areas since 1961 (Kat, 1983). The dominant dinoflagellates at the time of the outbreaks were Prorocentrum spp. (including P. micans and P. minimum) and these were implicated as the likely causative organisms (Kat, 1979). Further investigations into an incident in 1981 showed that the toxin responsible was a Dinophysis - type toxin. This incident was preceded by a bloom of D. acuminata (considerable numbers of this species being found in the mussels digestive tracts) and D. acuminata is now considered to be the most likely source of the toxin (Kat, 1983a). Further work with cultures is required

to confirm this. Only the largest blooms of >20,000 cells per litre seemed to be followed by mussel poisoning. This species has been recorded from the Scottish west coast (Dodge, 1981). In this study it was found in all the sea-lochs sampled.

Prorocentrum micans Ehrenberg

As explained in the previous paragraph this species was initially implicated in Dutch incidents of gastro-enteric disorders. Tests at the time elicited no ill effects in mice (Kat, 1979) and it seems more likely that Dinophysis acuminata was responsible for these incidences. A survey for PSP in Irish waters found some traces of toxicity associated with blooms of P. micans (Dunne and Parker, 1981). In this study it was found in all the sea-lochs sampled.

Species toxic to marine organisms or to mice in laboratory tests

Gonyaulax polyedra Stein

Red tides of G. polyedra are a common occurrence in certain parts of the United States (see for example Sweeney, 1976). They have occasionally been associated with mortalities of marine organisms (see for example Kofoid, 1911). In 1962 Schradie and Bliss reported tests on mice with extracts from laboratory cultures which showed the presence of toxins similar to those responsible for PSP as isolated from Gonyaulax catenella. The crude extract seemed to be less toxic than the purified extract, and thus the toxin was perhaps inhibited by some other extract constituent. Oguri, Soule, Juge and Abbott (1975) report that extracts from cultures were toxic to fish and that cells harvested from red tides showed a wide range of toxicity. They consider oxygen depletion to be the most likely cause of fish deaths in the sea and mention observations of gill clogging and subsequent death of Mytilus. Sweeney (1975) could detect no

toxicity in cultures or cells from red tides and indeed Patton *et al*. (1967) examined the value of a red tide (principally composed of *G. polyedra*) as food for rats. Most recently Schmidt and Loeblich (1979a) found little evidence of toxicity in a number of *G. polyedra* cultures tested although some extracts did cause sluggishness in mice tested.

There might be several reasons for these variable results. Crude extracts might contain a toxin-inhibitory substance as discussed by Schradie and Bliss and perhaps witnessed by the sub-lethal effects found by Schmidt and Loeblich. There is also some evidence that cellular conditioning may influence toxin production (see under *Gyrodinium aureolum*) in which case the conditions of growth before tests would become very important.

There was a bloom of *G. polyedra* in 1978 in Bantry Bay (Ireland) but no associated evidence of mortalities or trace of PSP toxins were found (Cross and Southgate, 1981; Dunne and Parker, 1981). *G. polyedra* is recorded from several sites on the Scottish west coast (Dodge, 1981). In this study *G. polyedra* was found occasionally in water samples. Reference to the presence of *Lingulodinium machaerophorum* (its cyst) in sediment samples, however, seems to show its distribution to be widespread in this area.

Gyrodinium aureolum Hulburt

This species has been associated with mortalities of wild and cultivated marine organisms throughout Northern Europe (see for example Tangen, 1977; Boalch and others, 1979; Ottway *et al*., 1979; and Jones *et al*., 1982). Some of the resultant mortalities have probably been due to oxygen depletion (see for example Helm *et al*., 1974). There is, however, laboratory evidence of toxic effects of *G. aureolum* on *Mytilus edulis* (Widdows *et al*., 1979) and rainbow trout (Roberts *et al*., 1983). In addition there is some preliminary evidence to suggest that culture conditions may

affect the toxicity of this alga (Turner *et al* ., 1984), findings which may explain some of the apparently contradictory toxicity results obtained for this and other dinoflagellate species.

G. aureolum has been associated with the mortality of pond-reared salmon on the Scottish west coast in 1980 (Jones *et al*., 1982). Since that time it has been observed only occasionally and in low numbers in Scottish waters (Gowen, 1984).

Prorocentrum lima (Ehrenberg) Dodge

Prorocentrum lima has been implicated in ciguateric poisoning (Steidinger, 1983) the incidence of which is so far restricted to the tropics. Laboratory experiments reveal the presence of a number of toxins all lethal to mice (Murakami, *et al*., 1982). This species is not found in the plankton but is typical of sandy and muddy shores (Dodge, 1982). It has been found at a number of Scottish west coast sites (Dodge, 1981; Dodge, unpub. obs.).

Species associated with mass mortalities of fish and / or invertebrates

Ayres *et al*. (1982) include a large number of species in this category of which the following occur in Scottish waters:-

Ceratium furca (Ehrenberg) Claparède and Lachmann
Ceratium tripos (O.F. Müller) Nitzsch
Gonyaulax grindleyi Reinecke
Gymnodinium splendens Lebour
Heterocapsa triquetra (Ehrenberg) Stein
Polykrikos schwartzii Bütschli
Protoperidinium depressum (Baillie) Balech
Scrippsiella trochoidea (Stein) Loeblich III

The original description of Gonyaulax grindleyi Reinecke comes from a bloom off the west coast of South Africa, and Reinecke (1967) mentioned that a paralytic toxin was found in shellfish collected from areas affected by this bloom. De Villiers (1975) describes the recovery of a population of white sand mussels after a mass mortality caused by a bloom of G. grindleyi but it is not clear whether these effects were due to oxygen depletion or to toxicity. Schmidt and Loeblich (1979a) found no paralytic shellfish poison in cultures of this species. G. grindleyi has been found at a number of Scottish west coast sites (Dodge, 1981). In this study it was found in a number of sea-lochs.

The rest of the species on this list have probably only been associated with mortalities of organisms due to indirect effects (e.g. oxygen depletion by Ceratium tripos, Mahoney and Steimle, 1979) or co-occurrence with a genuinely toxic species. Ayres et al. give no references to substantiate their inclusion in this list. Most are common neritic dinoflagellates and their lack of prominence in the toxicity literature suggests they are not a serious problem.

CHAPTER 7

DISTRIBUTION OF DINOFLAGELLATE CYSTS ON THE SCOTTISH WEST COAST

INTRODUCTION

As microfossils dinoflagellate cysts are a potentially important palaeoecological tool (Harland, 1982). Studies of the distribution of their modern counterparts in recent sediments, as related to present day environmental factors have therefore been made in a number of areas by palynologists (North Atlantic, Williams, 1971; South West Africa, Davey and Rogers, 1975; Trondheimsfjord, Dale, 1976; Northeastern Japan, Matsuoka, 1976; Brittany, Morzadec-Kerfourn, 1977). The most extensive of such studies is that of Wall, Dale, Lohmann and Smith (1977) covering the North and South Atlantic oceans and adjacent seas. Of particular pertinence to this study is the work of Reid on intertidal sediments from around the United Kingdom (Reid, 1972a,b, 1974, 1975 and 1977) and that of Harland on recent sediments from around the United kingdom and the North Atlantic (Harland, 1977 and 1983).

These studies have shown that particular cyst assemblages can often be related to environmental factors. These influences were summarized by Reid and Harland (1977) as

a) latitude (encompassing such variables as solar radiation, temperature and climate);

b) water depth (typified in offshore / onshore differentiation);

c) water masses (having different hydrographic regimes); and

d) sedimentary factors (for example selective concentration).

Wall et al. (1977) expanded these ideas and proposed an ecological classification for extant cyst species. The development of these species groups was further justified by interpreting different water masses as unique hydrographic niches each with their own stability, predictability and severity characteristics. Wall et al. concluded that living fossilizable dinoflagellate cysts were adaptations to the unstable (unpredictable) marine climates of shallow waters typical of continental margins and oceanic archipelagos. However, within this pattern some individual species tended to be adapted to stable sectors of the environment and such localized species were of the greatest interest with regard to palaeoecology.

The other main body of work about cyst distribution are those studies concerned with the role of cysts in dinoflagellate bloom initiation. Early studies showed that cysts were potentially important in the initiation of blooms (Steidinger, 1975; Anderson and Wall, 1978). Since then the distribution of cysts of bloom species (especially Gonyaulax tamarensis / excavata) has been extensively studied (Lewis et al., 1979; White and Lewis, 1982; Anderson, Kulis, Orphanos and Ceurvels, 1982; Anderson, Auberey, Tyler, and Coats, 1982; Thayer, et al., 1983). Distribution of these bloom species seems to be heavily influenced by hydrographic processes both in initial areas of deposition (for example frontal convergences) and later (by selective concentration after deposition by currents) (Tyler Coats and Anderson, 1982; White and Lewis, 1982). Work has also been carried out on the distribution of cysts within the sediments which shows that there are significant subsurface accumulations of cysts of bloom species (Anderson, Aubrey, Tyler and Coats, 1982).

Few of either of these types of studies have included simultaneous examination of the water column and the sediments. Where this has been done often it has only served to highlight

the apparent differences between the dinoflagellate population present in the water column and that present in the sediments (for example Davey and Rogers, 1975; Reid, 1972a; and Matsuoka, 1976). The reasons for this are threefold. Firstly, few of the marine motile dinoflagellates appear to produce cysts (most cyst producing species being confined to the genera Protoperidinium and Gonyaulax). Secondly, the water column samples represent very small intervals of time whereas the sediments provide information integrated over a large period of time. Thirdly, selective transport processes may result in the concentration of cysts in areas distant from regions of initial deposition. These three processes often result in the apparent over representation of certain species in the sediments (Dale, 1976). An extra problem for palaeoecologists is that variable preservation of cysts may further selectively distort the fossilized dinoflagellate population.

Despite these problems the integrated information that can be provided by analysis of cysts from recent sediment samples is a useful addition to plankton surveys. It can provide information on the distribution of species difficult to identify in their motile stages (see Chapter 3) as well as information on species not present at the time of the year the water sampling took place or even during several previous years (Dale, 1983). Dale (1976) found that at least 5 years of plankton records were needed to compare water and sediment samples. The use of sediment sampling to supplement a limited programme of plankton sampling may provide information on dinoflagellates more efficiently than a long programme of plankton sampling alone.

MATERIALS AND METHODS

Samples were collected and counted as described in Chapter 2. As far as possible between 100 and 200 cysts were counted in each sample. Sometimes because of paucity of cysts this was not

practicable and such samples are marked accordingly. The top 5 cm of sediment was sampled; in one case 1 cm sections of a core were taken down to 5 cm with an additional 5 - 10 cm deep sample to assess the distribution of cysts within the sediment.

RESULTS

Some 57 sites were sampled, several of these on more than one occasion: thus, excluding the seasonal investigations described in Chapter 5, 72 samples have been counted. Results of these counts will be deposited in the S.M.B.A. and Royal Holloway College libraries and only certain features described here. A list of species found is given in Table 7.1. Certain groups of species were counted as one, details of species included in these groups being given in Chapter 3.

Table 7.1 : Cyst species and groups found during this study

?*Epidinium shagrinum*	
Lingulodinium machaerophorum	*Gonyaulax polyedra*
Operculodinium centrocarpum	*Gonyaulax grindleyi*
Polykrikos spp.	
?*Protoperidinium minutum*	
Quinquecuspis concretum	*Protoperidinium leonis*
Round, brown cysts	
Scrippsiella ? *sweeneyi*	
Scrippsiella spp.	
Selenopemphix sp	*Protoperidinium conicum*
Spiniferites spp.	
Stelladinium stellatum	*Protoperidinium compressum*
Trinovantedinium capitatum	*Protoperidinium pentagonum*
Votadinium calvum	*Protoperidinium oblongum*
Votadinium spinosum	*Protoperidinium claudicans*
Xandarodinium xanthum	*Protoperidinium divaricatum*

Cysts were counted as being 'empty' or 'full'. No attempt was made to ascertain the viability of those cysts that had not hatched. For the purposes of this distributional survey 'empty' and 'full' counts were added together. On the whole the percentage of full cysts was greatest within the sea-lochs (mean 60%) and less in the Firths and Sounds (mean 35%) although these figures were somewhat variable.

The results discussed here are the latest (and hence most accurate) counts, where a site was visited on more than one occasion, and for station C5 in Loch Creran an average based on 10 separate samples.

Figure 7.1 shows the total numbers of cysts per gram dry weight of sediment. The number of cysts present in Scottish west coast sediments seems to vary greatly. On the whole the highest numbers of cysts were found within the sea-lochs (for example West Loch Tarbert and Loch Creran) rather than in the Firths and Sounds, but, some lochs (for example Etive and Eil) had very low numbers of cysts per gram dry weight of sediment.

Figures 7.2 to 7.7 show the distribution of the cyst types found to occur in significant numbers in this study. Of the cysts in the size fraction examined the most numerous species was Lingulodinium machaerophorum (Gonyaulax polyedra). Figure 7.2 shows its distribution. This species was found at all sites sampled and was present in greatest numbers within the sea-lochs, notably West Loch Tarbert and Loch Creran. In considering overall dominance it must, however, be remembered that a considerable number of Scrippsiella cysts were lost through the fine sieve and thus that the distribution of this group shown in Figure 7.3 understates the abundance of what appears to be a very common species on the Scottish West Coast.

Figure 7.1 : Total numbers of cysts per gram dry weight of sediment

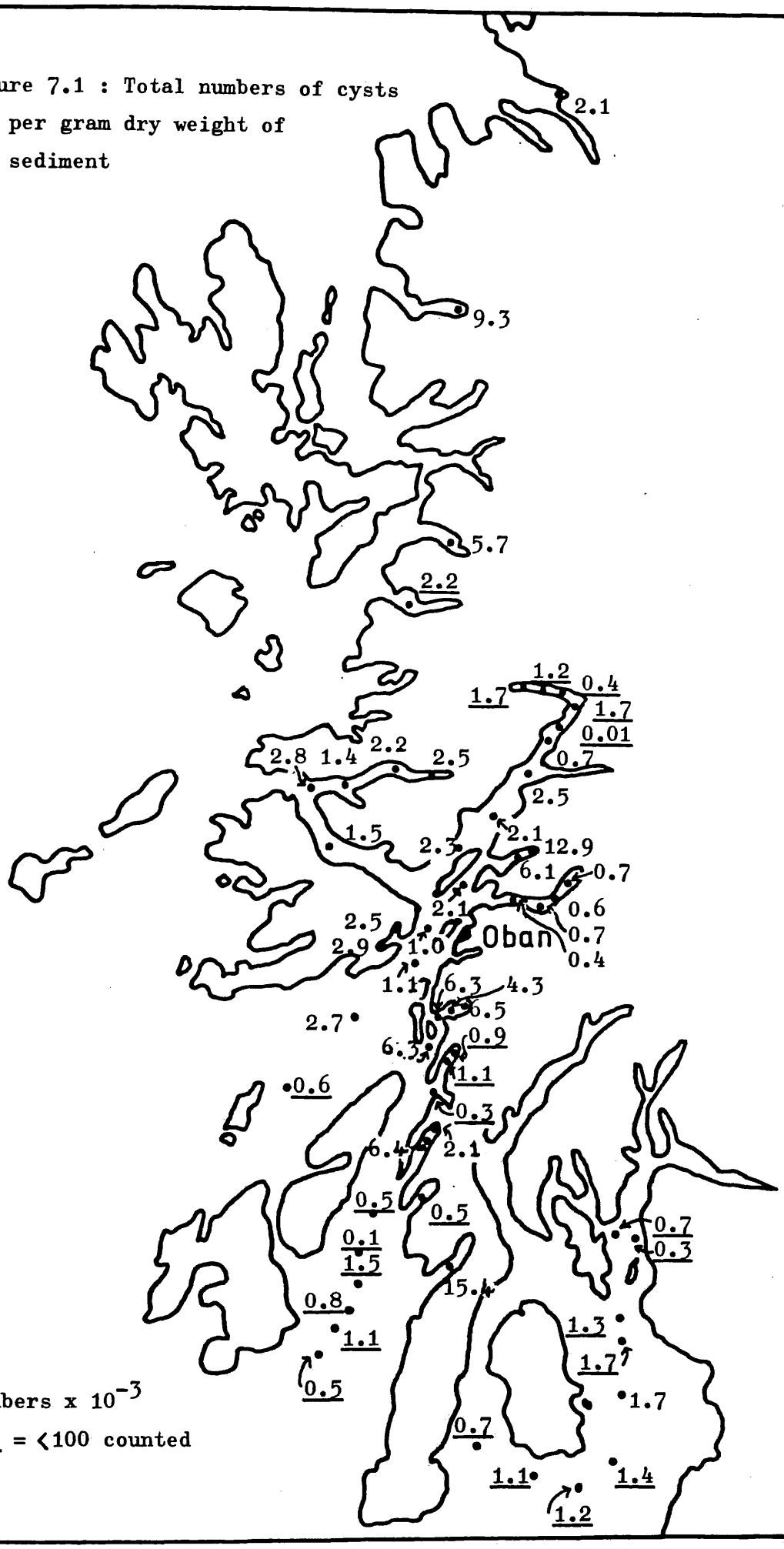


Figure 7.2 : Numbers of Lingulodinium machaerophorum per gram dry weight of sediment

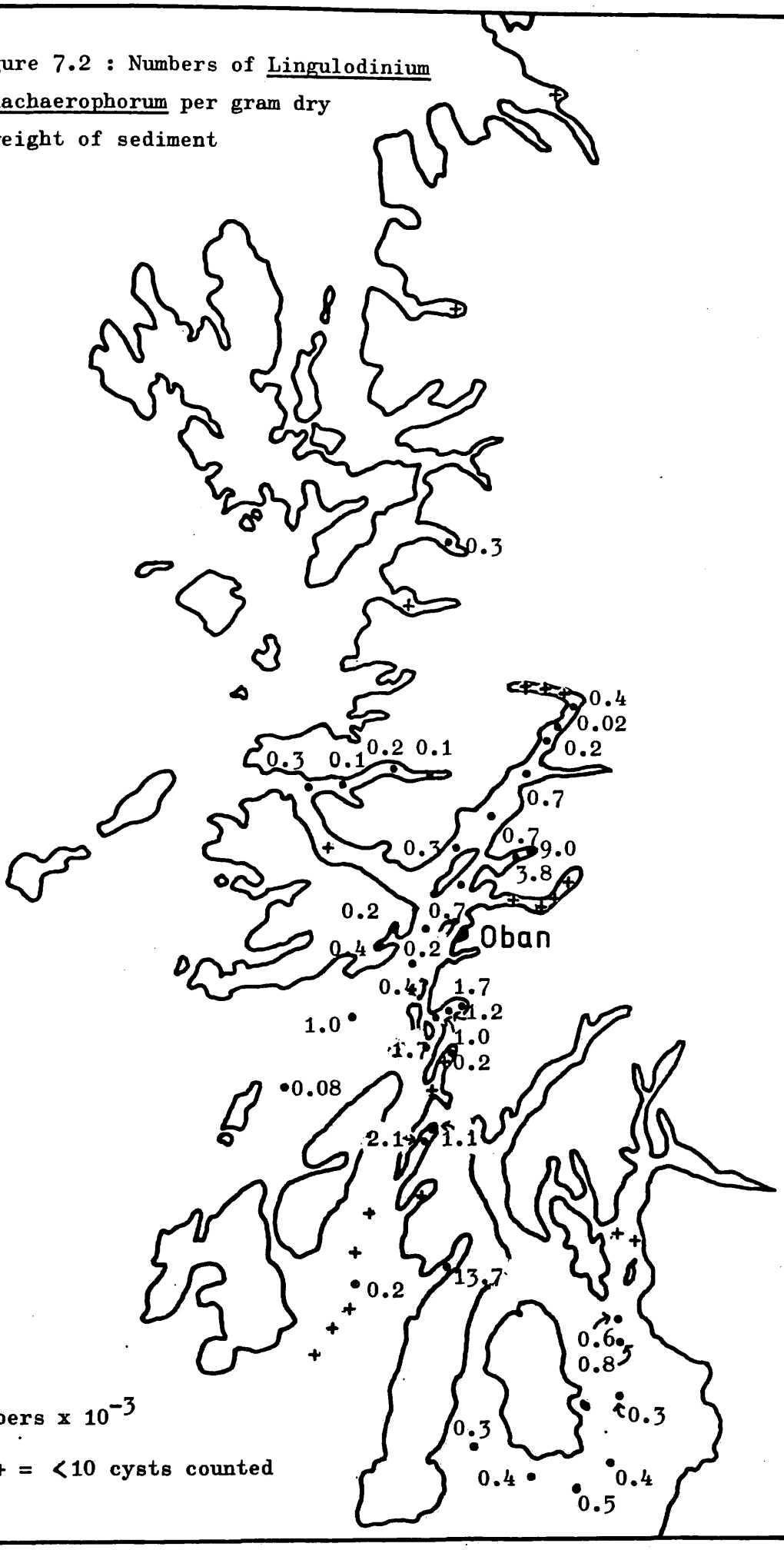


Figure 7.3 : Numbers of Scrippsiella spp. cysts per gram dry weight of sediment

Figure 7.4 : Numbers of Round, brown cysts per gram dry weight of sediment

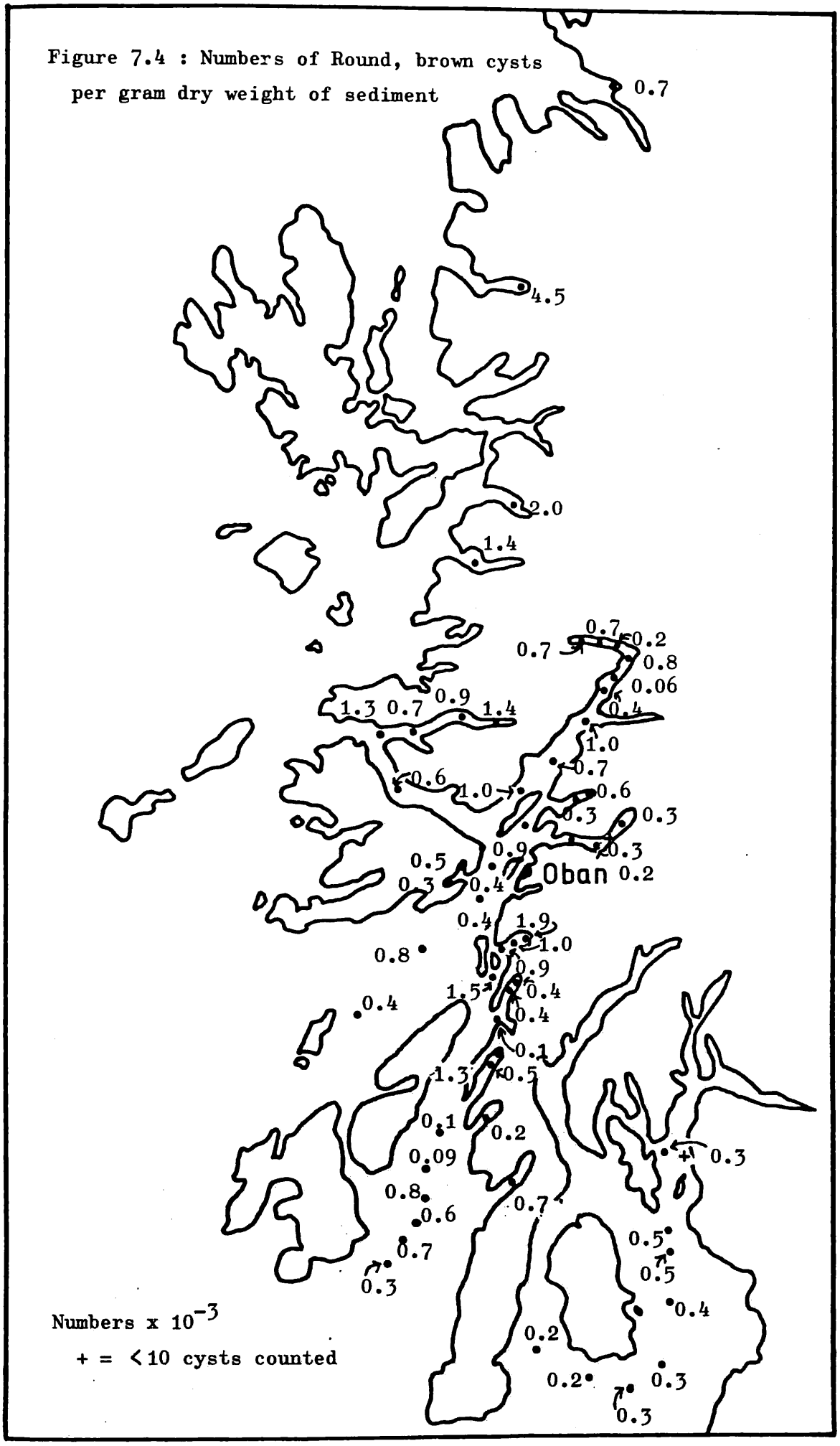


Figure 7.5: Numbers of Spiniferites spp. per gram dry weight of sediment

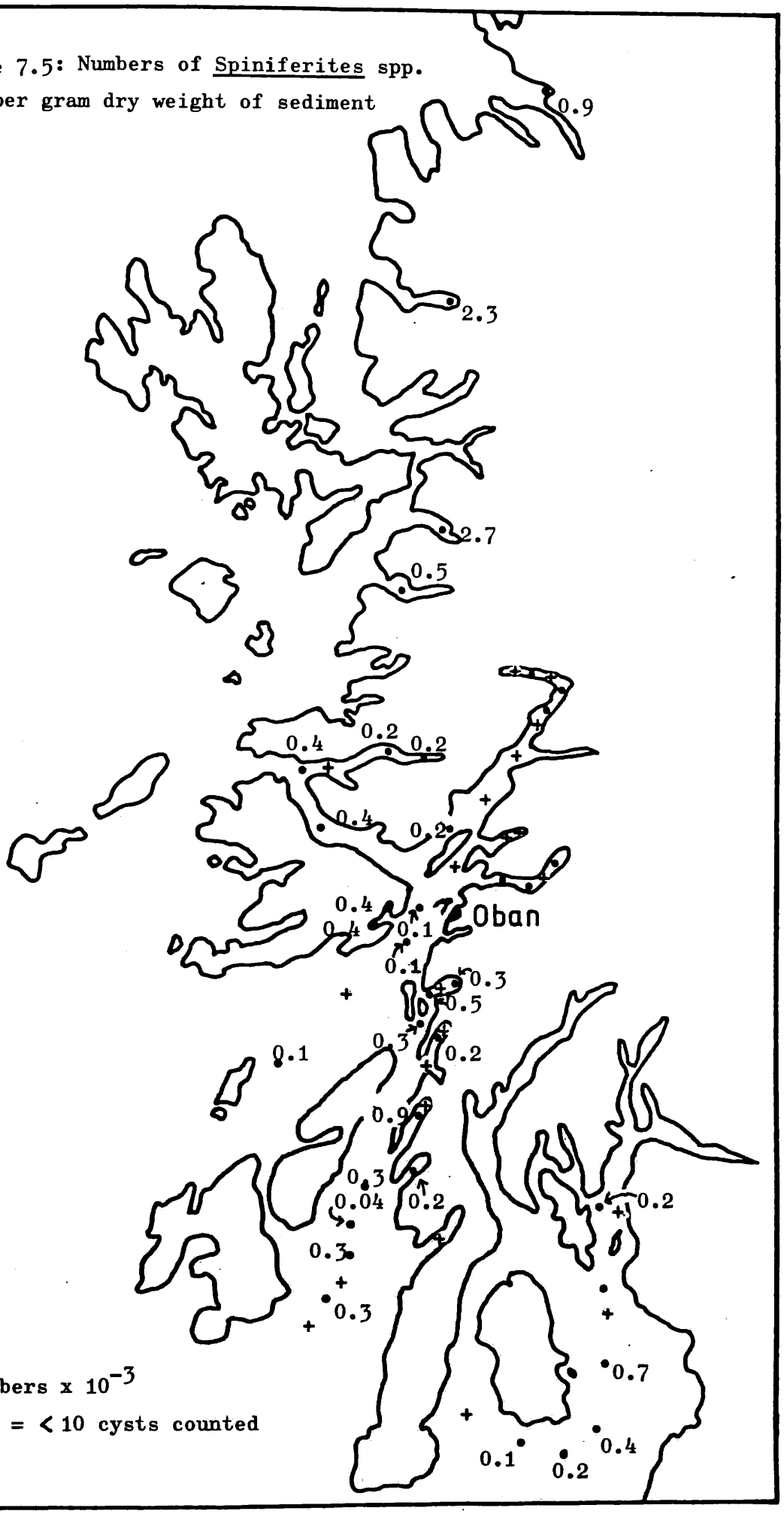
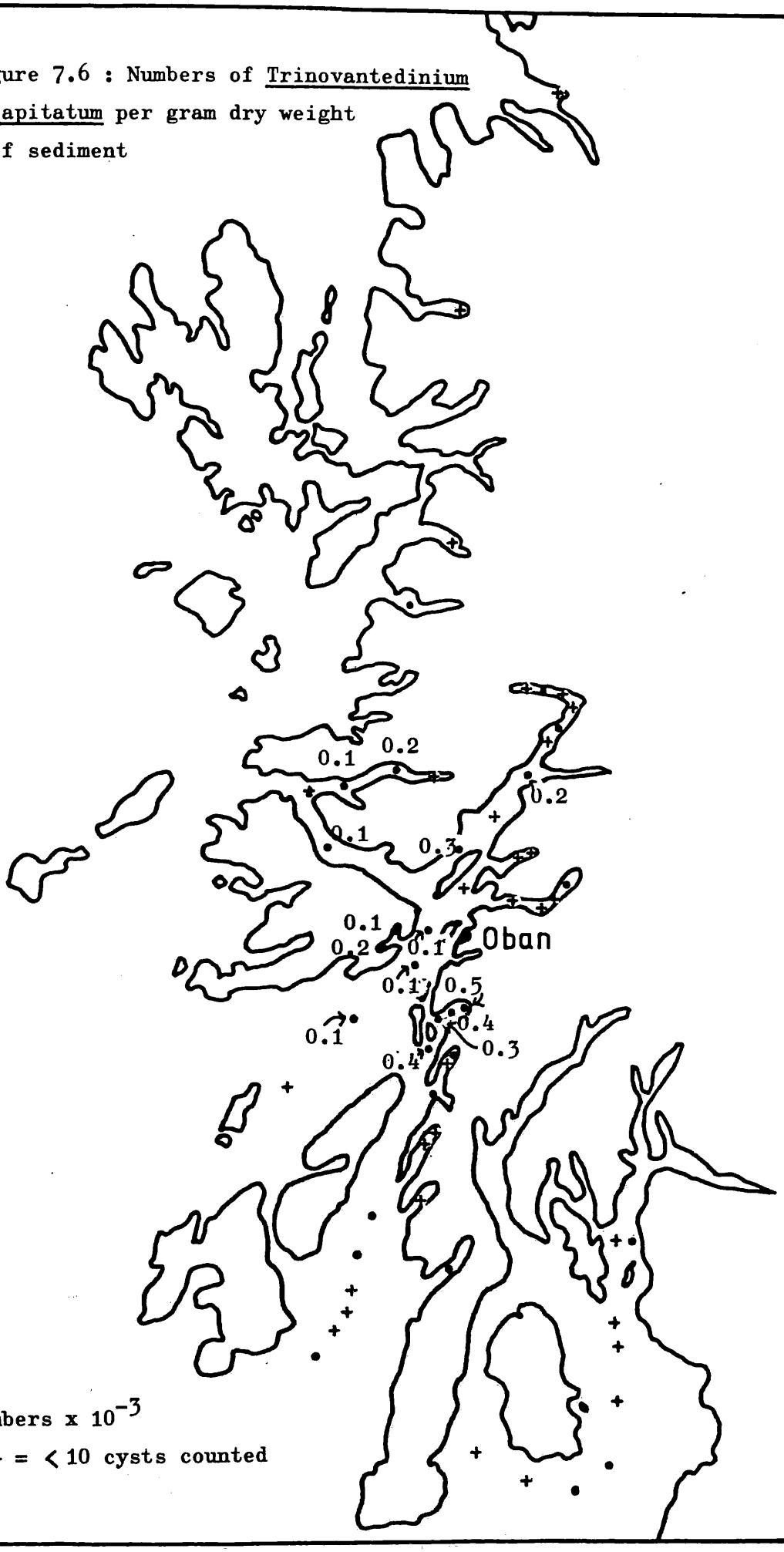


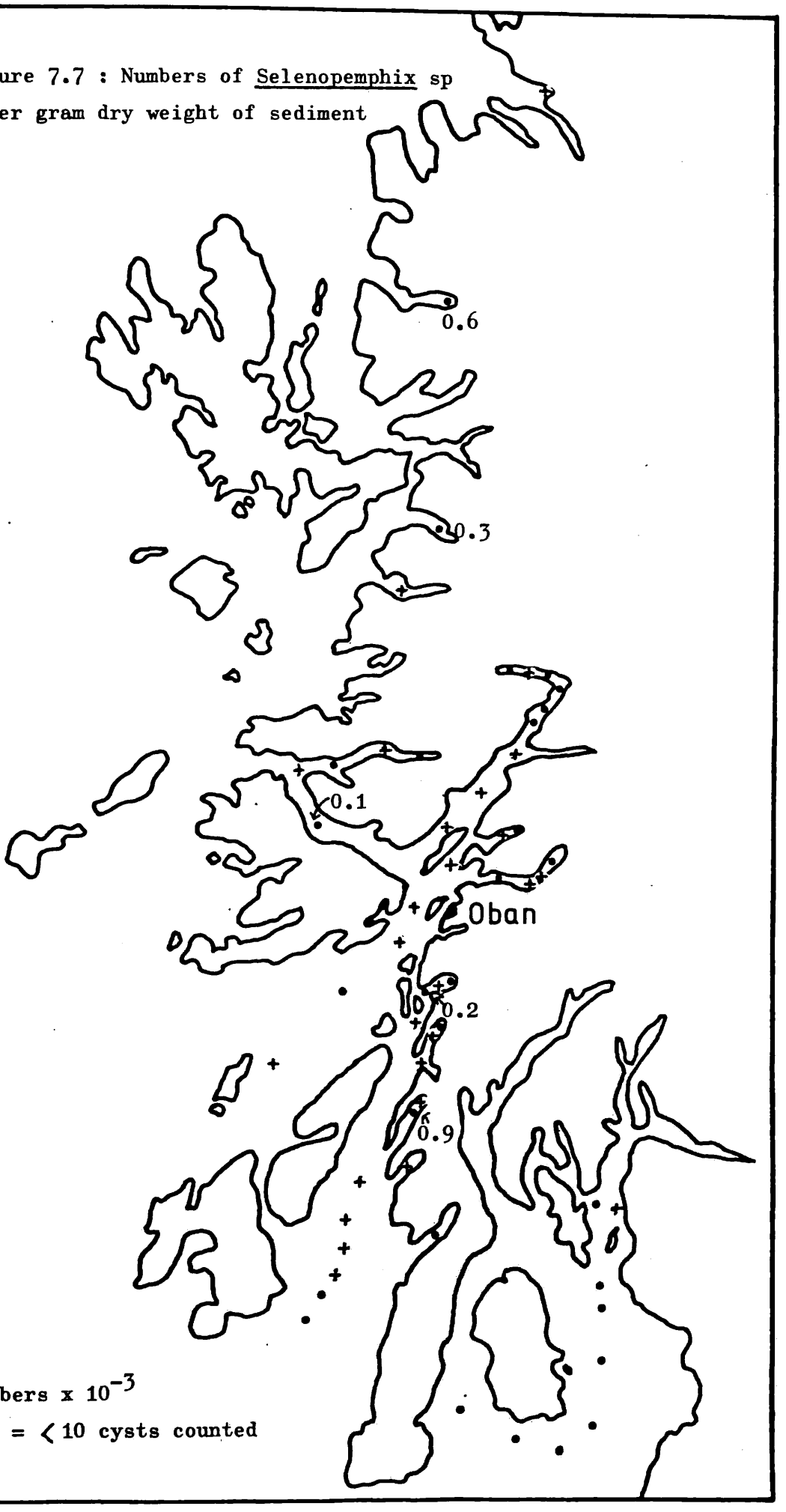
Figure 7.6 : Numbers of Trinovantedinium capitatum per gram dry weight of sediment



Numbers x 10^{-3}

+ = < 10 cysts counted

Figure 7.7 : Numbers of Selenopemphix sp per gram dry weight of sediment



Numbers x 10^{-3}

+ = < 10 cysts counted

The next most numerous group were Round, brown cysts (described in Fig. 7.4). Again these were present in greatest numbers within the sea-lochs notably Loch Melfort and Loch Torridon. Spiniferites species (Fig. 7.5) and Trinovantedinium capitatum (Protoperidinium pentagonum) (Fig. 7.6) also appear to be widespread although they were present in fairly low numbers. Selenopemphix (Protoperidinium conicum) (Fig. 7.7) was present in low numbers in most samples taken except for those from the southern part of the study area (notably the Firth of Clyde).

Of the other cyst species mentioned in Table 7.1 Stelladinium stellatum (Protoperidinium compressum) and Xandarodinium xanthum (Protoperidinium divaricatum) were the most rare. The other species occurred sporadically in many parts of the sampling area.

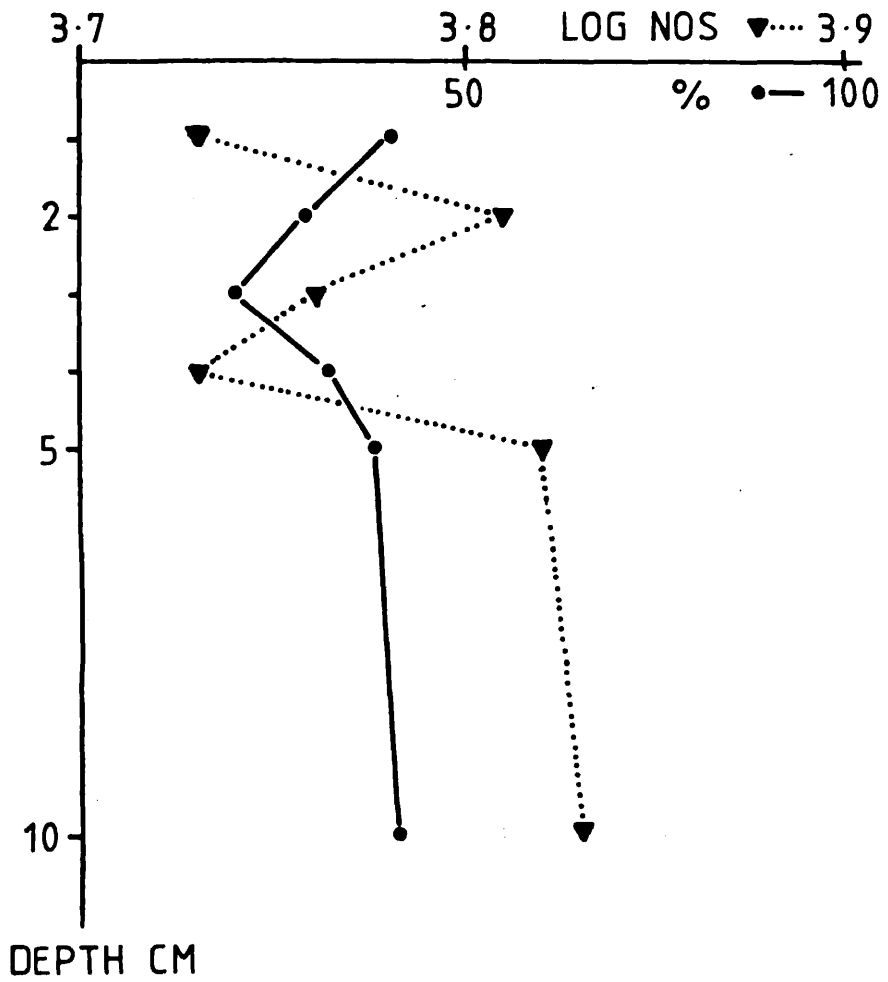
Figure 7.8 shows a graph of the distribution of cysts with depth in the one core in which this was studied. The species composition remained fairly constant down the core and although the total number of cysts did fluctuate by 30% this variation was not thought significant. The percentage of full cysts did decrease slightly in the top 4 cm of the core but reverted to the sediment-surface value below 5 cm.

DISCUSSION

The numbers of cysts per gram dry weight of sediment varies greatly in the area studied. Values of 373 to 15,431 (mean 3,630 based on 28 samples) have been found in the sea-lochs studied. This compares with 3,416 to 16,106 (mean 10,032 based on 4 samples) given by Wall et al. (1977) for fjords in southern Norway. Considering the probable underestimation of cyst numbers in this study these figures by Wall et al. compare well with those from most of the Scottish lochs studied with the exception of the few lochs (Eil, Etive, Craignish and Caolisport) where

Figure 7.8 : Distribution of cysts down core from Loch Melfort

Cyst distribution shown as Log numbers per gram dry weight of sediment, and % of full cysts.



numbers were low. The numbers of cysts per gram dry weight of sediment in the Firths and Sounds was lower (89 to 2,694; mean 1,204 based on 27 samples) also in keeping with figures given by Wall et al. (1977). Considerable local variation was encountered in these nearshore sediments as has been noted by other authors (for example Wall et al., 1977). The high cyst densities in the sea-lochs is probably due to a combination of high local production of cysts (as documented for Loch Creran, see Chapter 5) and the sediment-trapping nature of sea-lochs (Dale, 1976). So why do some sea-lochs have comparatively low numbers of cysts? Several relevant factors have been suggested by other workers (for example Balch et al., 1983)

a) Low production of cysts because of few parental motile cells;

b) a high sedimentation rate within the sea-loch effectively diluting the numbers of cysts found;

c) Poor depositional environment with fine sediments and cysts washed out of the loch by a high flushing rate.

Loch Etive is a long sea-loch with deep basins, it has a comparatively poor motile dinoflagellate population throughout the year (Tett, unpubl. data). In addition it has a high catchment area and a large freshwater input which brings in much terrestrial debris (Ansell, 1974). So although it is a good depositional environment for fine grained particles all the other factors are likely to combine to give a poor dinoflagellate cyst population in the sediments. Loch Eil, however, seems to have a normal sea-loch motile dinoflagellate population (from the few water samples examined in this study), but probably has a high sedimentation rate and this may explain its poor dinoflagellate cyst population. Loch Caolisport is a small shallow sea-loch with a relatively deep entrance sill (20m) (Milne, 1972) and

although its motile dinoflagellate population seemed normal on the one occasion it was sampled it seems likely that the loch is well flushed. Loch Craignish has a low flushing (Gowen, 1984) but the motile dinoflagellate population was low on the occasions it was visited. There is little further data available about the latter two lochs and so it is difficult to assess the factors at work.

Some studies (Tyler et al., 1982; Balch et al., 1983) have noted the concentration of cysts at frontal boundaries. This effect was not observed in this study in the section taken across the frontal regions in the Sound of Jura but since these fronts appear quite variable in position (Jones et al., 1984) they may not result in a marked delineation at the sea-bed.

The species recorded in this study are broadly similar to those described by Harland (1977, 1983) in Scottish coastal waters. Much of the sampling for his studies was, however, further offshore than most of the samples taken in this study, and some differences in the proportions of species are apparent. Most noticable are the small numbers of Operculodinium centrocarpum (Gonyaulax grindleyi) found in this study. However, in offshore areas where direct comparisons can be made (for example the Sound of Jura and boreholes 75/40 and 75/43 of Harland, 1977) comparatively few cysts were found and counts may not have been truly representative, indeed Harland's results showed considerable local variability. Samples in this study were from the top 5cm of a core unlike the palynological samples which start deeper and this may cause further differences.

Reid (1975) places the west coast of Scotland in his group 4. A group where assemblages were dominated by Spiniferites spp., Peridinium cysts and cysts of unknown affinity (Impletosphaeridium sp, probably Scrippsiella cysts) with Lingulodinium machaerophorum (Gonyaulax polyedra),

Bitectadodinium tepikiense (Gonyaulax spinifera), Operculodinium centrocarpum (Gonyaulax grindleyi), Diplopeltopsis cysts and Polykrikos cysts also present. More specifically he created a sub-group 4a covering some northern lochs and this was dominated by cysts of unknown affinity (Impletosphaeridium sp, probably Scrippsiella cysts) and Spiniferites spp. with B. tepikiense (G. spinifera), O. centrocarpum (G. grindleyi) and Peridinium cysts also present. Again this broadly agrees with species described here considering that Scrippsiella cysts were probably more numerous than shown in Fig. 7.3. Investigating a large number of lochs has, however, shown that against the background of Scrippsiella cysts there is variability in the sea-loch cyst assemblage. This is especially noticable where the population is dominated by L. machaerophorum (G. polyedra) (for example in Loch Creran and West Loch Tarbert). This seems analagous to the situation described by Reid (1974, 1975) for deep embayments off the west coast of Ireland where L. machaerophorum also dominated the assemblages. Such sea-lochs and embayments are potential seed beds for dinoflagellate blooms and may cause the inoculation of other coastal waters.

Figure 7.8 shows that, at least in the core examined in detail, there is a considerable sub-surface population of dinoflagellate cysts. This is in agreement with the findings of Anderson, Aubrey, Tyler and Coats (1982). The viability of sub-surface cysts was shown by their hatching from the 5cm slice of the core used in the incubation experiments (see Chapter 8). The consistency of the cyst population down to 10 cm suggests that some mixing may take place to this depth in Loch Melfort. Investigations in other Scottish sea-lochs suggest that sediment reworking and resuspension are an important processess in these environments (Ansell, 1974; Stanley et al., 1981). Resuspension has been postulated as an important mechanism of inoculating

overlying waters with a seed population of excysted dinoflagellates (Balch et al., 1983). It is clear that any study of living dinoflagellate cysts should take into account these sub-surface populations whose longevity requires further investigation.

Comparison of the cyst population with the motile dinoflagellate population is difficult. Cysts in the sediment may have accumulated for several years, and there are few areas for which a sufficient time series of water column data is available for comparison with sediment data. Such data are available for Loch Creran and Table 7.2 gives the mean cyst counts from 10 separate 5 cm samples from station C5 in Loch Creran, for comparison with the water column data in Chapter 4. The latter shows a wide range of motile dinoflagellate species present in the water column, many of which are not represented in the cyst assemblage. Most notable among these are members of the genera Prorocentrum, Dinophysis and Ceratium. In addition there also appears to be some over representation of certain species (for example Gonyaulax polyedra (Lingulodinium machaerophorum)) in the sediments. Such apparent anomalies have been noted by other authors (e.g. Dale, 1976). Striking also is the fact that the cyst assemblage reveals species (for example Stelladinium stellatum, Protoperidinium compressum) that have not been recorded in the planktonic phase.

Comparison between the cyst populations of Loch Melfort and Loch Creran as shown in Table 7.2 suggests that there may be overall differences in their motile populations. Loch Melfort having a much greater population of Protoperidinium cysts than Loch Creran. This topic may be worthy of further investigation as it might reveal information on determinants of species composition.

Table 7.2 : Cyst counts from Loch Creran and Loch Melfort

Species	Loch Creran	Loch Melfort
?*E. shagrinum*	107	255
L. machaerophorum	3798	1670
O. centrocarpum	+	-
Polykrikos	+	+
Q. concretum	-	+
Round, brown	309	1855
S. ?sweeneyi	1159	1090
Scrippsiella spp.	304	348
Selenopemphix	+	-
Spiniferites spp.	+	255
S. stellatum	+	+
T. capitatum	+	533
V. calvum	+	+
V. spinosum	+	+

Information on the current deposition of dinoflagellate cysts is useful to the palaeoecologists, allowing comparison of current assemblages deposited under known climatic conditions with fossil assemblages. As mentioned in the introduction to this chapter, factors such as selective transportation and preservability of cysts distort the fossil record, and the present study has provided some information relevant to the assessment of this distortion. Observations during this study suggest that once excysted many of the Round, brown cysts are easily broken down and would probably not be preserved in the fossil record.

The cyst record may also be of use to mariculture. At present assessment of the likelihood of phytoplankton blooms requires knowledge of the hydrographic regime combined with knowledge of the phytoplankton population (the latter needing a

long time series of data). It is possible that the integrated record from dinoflagellate cysts may provide valuable additional information at a lower cost than extensive phytoplankton surveys. Clearly, therefore, relations between the cyst population and the motile dinoflagellate population are worthy of more detailed investigation.

CHAPTER 8

CYST-THECA RELATIONSHIPS

INTRODUCTION

If the cyst assemblage in the bottom sediments is to be correlated with the plankton (i.e. the assemblage of motile thecate dinoflagellates) then the relationship between the various cysts and their motile stages needs to be determined. Approximately 170 distinctive cyst morphotypes have been found in recent sediments and many of these have live contents (Dale, 1983). Investigation of new regions frequently yields new cyst types so it is possible that there are many cyst types yet to be discovered. Of the known cyst types about 50 have been correlated with their thecate motile stages (see Table 2 in Dale, 1983).

The earliest observations of dinoflagellate cysts were probably made by Ehrenberg in the early nineteenth century (Dale, 1983). He found the cysts in thin flakes of Cretaceous flints although he mistook them for fossilized motile stages. During the first half of this century the geological interest in these microfossils (hystrichospheres) greatly expanded when their potential as stratigraphic markers was realised. Their relationship to living dinoflagellates remained unnoticed and they were presumed to be motile plankton that became extinct sometime after the Tertiary. The only clues to their modern counterparts were occasional descriptions in the phytoplankton literature: observations of cysts in the plankton were made during phytoplankton surveys by Paulsen (1908), Gran and Braarud (1935), Nordli (1951) and Grøntved (1952). Relationships were inferred either by the presence of the cyst within the dinoflagellate thecate stage or because parts of the theca were left behind on the cyst. Relationships were thus established for

Protoperidinium conicoides, Gonyaulax tamarensis (Gran and Braarud, 1935) and Gonyaulax polyedra (Nordli, 1951). Braarud also noted formation of cysts in some of his cultures of Heterocapsa triquetra (Braarud and Pappas, 1951) and Scrippsiella trochoidea (Braarud, 1958). The only experimental work on cysts and their hatching was that carried out on cysts of the freshwater Ceratium hirundinella by Huber and Nipkow (1922 and 1923).

More recently Evitt examining the morphological features of hystrichospheres noted their characteristic openings (archeopyles) and their 'reflected' dinoflagellate features and suggested they were dinoflagellate cysts (Evitt, 1961). At around the same time modern hystrichospheres were being discovered by palynologists in recent sediments and in sediment traps (see for example Erdtmann, 1954). The interest of palynologists was aroused and throughout the 1960's and early 1970's Wall and Dale carried out extensive incubation experiments establishing the role of the resting cyst in the life cycle of dinoflagellates beyond doubt.

It was this history of parallel investigations that has encumbered the researcher working with modern dinoflagellates and their cysts with a dual nomenclature. This will be discussed later, and throughout this chapter names of both stages of the life cycle will be given where possible.

Cysts have traditionally been linked with their motile stages by incubation experiments. For marine organisms the encystment of thecate motile cells whilst in culture seems largely fortuitous. Braarud (1958) reported that cooling and darkness did not seem to induce encystment in Scrippsiella trochoidea and related it instead to overcrowding in the cultures. However, Turpin et al. (1978) and Walker and

Steidinger (1979) induced encystment of Gonyaulax tamarensis and Gonyaulax monilata respectively by depletion of nitrogen. For many freshwater organisms the depletion of nitrogen has been used to stimulate sexual activity and encystment (see for example von Stosch, 1972; Pfiester, 1975, 1976, and 1977). Current culturing techniques do not appear suitable for many marine dinoflagellates (notably the Protoperidiniales) and so cyst incubation experiments are a simpler way of establishing relationships. This type of experiment was first reported by Wall (1965) and Wall and Dale (1966). In 1968 they published the results of extensive incubation experiments covering over 30 species which they had successfully germinated. Since that time reports of incubation experiments have been confined to single species (Pyrodinium bahamense, Wall and Dale, 1969; Pyrophacus horologium, Wall and Dale, 1971; Protoperidinium minutum, Fukuyo, et al., 1977; Protoperidinium divaricatum, Matsuoka, et al., 1982) or a small group of species (calcareous cysts, Wall and Dale, 1968b and Dale, 1977b). With few biologists seemingly interested in these relationships the work has been carried out by palaeontologists in a comparatively small number of locations (America, Norway, and Japan) and no incubation work has hitherto been carried out in the United Kingdom.

The most extensive biological study of living cysts has been made by the groups investigating the role of cysts in bloom formation (red tides). This work and that of Huber and Nipkow (1922, 1923) provides the only systematic investigation into what causes excystment and the 'dormancy' period required before excystment can take place. Anderson (1980) shows that the length of this dormancy period is dependent on the temperature at which the cysts are kept. Cysts of Gonyaulax tamarensis stored at 22°C had a mandatory dormancy period of about one month, or four months kept at 5°C. Pfiester (1975) reports similar results for the freshwater Peridinium cinctum.

Excystment is usually triggered in the laboratory by raising the temperature above the normal environmental temperature the cysts are exposed to in winter (for example by increasing the cyst temperature from 5°C to 18°C). Other factors (light regime, nutrient and chelator concentrations) have been found to be ineffective (Anderson and Wall, 1978). Perhaps this temperature change simulates the change experienced by cysts passing from winter to summer. Time taken for excystment also seems to be temperature dependent. Huber and Nipkow (1922) showed excystment was completed within 36 hours at optimum temperature but was slower at lower temperatures. Dale (1983) discusses this phenomenon and suggests that the need for 'stimulation' to cause excystment is perhaps misleading. He postulates that if dormancy is completed at a suitable temperature, excystment will follow as a natural consequence (for example Gonyaulax tamarensis after 8 weeks at 17°C; Turpin et al., 1978).

Excystment has been described for a number of marine species (Gonyaulax digitale, Wall, 1965; Gonyaulax spinifera, Wall and Dale, 1968a; Gonyaulax tamarensis, Anderson and Wall, 1968). The cyst contents are described as first withdrawing from the wall and then after the archeopyle opens the protoplast moving through it with an amoeboid-like motion. The longitudinal flagellum is formed shortly after excystment and the transverse flagellum is formed later. This stage is described as the gymnodinioid stage as it takes some time for the theca to be formed. More detailed description of excystment in Ceratium hirundinella is given by Chapman et al. (1981) using electron microscopy.

METHODS

Sediment samples were collected and prepared as described in Chapter 2. Individual cysts were picked out using a micropipette and placed in small incubation chambers (Wall and Dale, 1968a)

(Fig. 8.1.) or 5cm watch glasses enclosed in petri dishes. The medium used for incubation was f/50 (Guillard and Ryther, 1962). The cysts were kept at 20°C and if they had not germinated within 5 days the experiment was abandoned.

After excystment, cyst and hatched cell were observed and photographed under the light microscope and then preserved in formalin in small containers for S.E.M., for which the cyst and cell pairs were again individually picked out and prepared as described in Chapter 2.

RESULTS

The actual hatching of a motile cell was never observed. It was noticed, however, that before hatching the cyst contents withdrew from the cell wall. Frequently a light area would appear across the middle of the contents in an area approximating to the cingulum of the motile cell. After excystment the gymnodinioid stage generally took only a few hours to form a recognisable theca.

The *Protoperidinium* species listed in Table 8.1 have been successfully hatched. Many of the cyst-theca relationships (shown by * in Table 8.1) repeat the discoveries of Wall and Dale (1968). Hatching the cysts of *P.minutum* and *P.divaricatum* confirmed the findings of Fukuyo *et al*. (1977) and Matsuoka *et al*. (1982). In addition the species listed in Table 8.2 were hatched. Although many species of *Gonyaulax* have been incubated successfully, particularly from the *Spiniferites* group of cysts (Wall and Dale, 1968a), only *G. polyedra* was successfully incubated in this study. *Spiniferites* cysts are not common in

Figure 8.1 : Single cell incubation chamber after Wall & Dale (1968a)

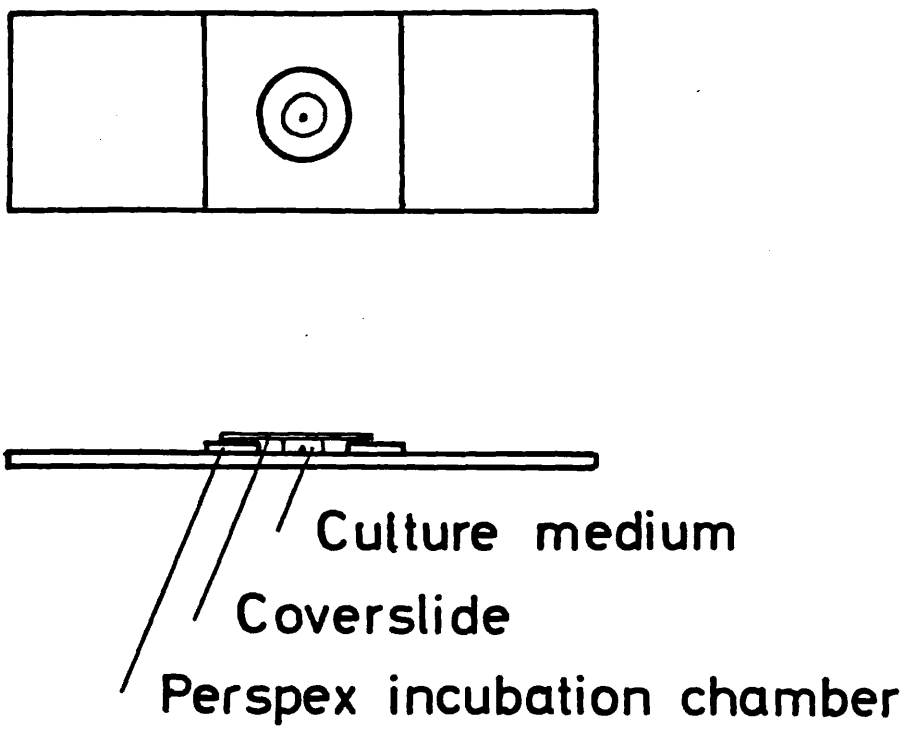


Table 8.1 Protoperidinium species germinated

Thecate stage	Palaeontological name for cyst
* Protoperidinium avellana (Meunier) Balech	Brigantedinium cariacoense (Wall) Reid
* P. claudicans (Paulsen) Balech	Votadinium spinosum Reid
* P. conicoides (Paulsen) Balech	Brigantedinium simplex Reid
* P. conicum (Gran) Balech	Selenopemphix Benedek
* P. denticulatum (Gran & Braarud) Balech	
P. divaricatum (Meunier) Parke & Dodge	Xandarodinium xanthum Reid
P. excentricum (Paulsen) Balech	
P. ?hangoei (Schiller) comb.nov.	
* P. leonis (Pavillard) Balech	Quinquecuspis concretum (Reid) Harland
?P. minutum (Kofoid) Loeblich III	
* P. oblongum (Aurivillius) Parke & Dodge	Votadinium calvum Reid
* P. pentagonum (Gran) Balech	Trinovantedinium capitatum Reid
P. subinerme (Paulsen) Loeblich III	
P. thorianum (Paulsen) Balech	
P. ?thulesense (Balech) Balech	

Table 8.2 Species other than *Protoperidinium* germinated

Thecate stage	Palaeontological name for cyst
Gonyaulax polyedra Stein	*Lingulodinium machaerophorum* (Deflandre & Cookson) Wall
Diplopsalis lenticula Bergh	
Zygabikodinium lenticulatum (Paulsen) Loeblich & Loeblich III	*Dubridinium caperatum* Reid
Scrippsiella ?sweeneyae Balech ex Loeblich III	

sea lochs and may be in poorer condition than those of other, more common species. Novel hatchings were those of Protoperidinium ?hangoei, Protoperidinium thorianum, Protoperidinium ?thulesense and Scrippsiella ?sweeneyae.

In many cases the cyst germinated but the naked protoplast did not properly form its thecal plates (Pl. 8.2, fig.2). It seems that the type of sea water used was important in this respect. Several different types of sea water were tried including deep and surface water from the loch in which the cores were taken. Sea water from Dunstaffnage Bay near Oban was found to be the most suitable for germination. Possibly the quality of the sea water with regard to cyst hatching varies with the time of the year. As f/50 medium provides only a small addition of nutrients the sea water used needs to fulfil most of the requirements of the newly excysted protoplast. Dunstaffnage Bay contains a sewage outfall and a high algal biomass and its sea water may thus contain more dissolved organic material than that of the sea lochs. These problems require further investigation.

All the hatched cells contained numerous small bodies which were probably storage products. Some cysts contain many small red bodies or a single pigmented body (for example Protoperidinium conicum, Gonyaulax polyedra). These are contained within the motile cell on excystment. Wall and Dale (1968b) note that in the case of the division of Scrippsiella sweeneyae these were passed on to one of the daughter cells and thereafter lost. A similar process was noted for Scrippsiella ?sweeneyae in this study. Cells were seldom allowed to survive long enough to divide but it was noticed that in some cases (for example P. conicum) the red bodies seemed to diffuse throughout the cell giving it the characteristic 'pink' colour often noted in Protoperidinium species. When cells were allowed to die of natural causes their survival time was between a few hours and six days.

In most cases the operculum remained attached to the archeopyle of the cyst and this point of attachment is shown by broken lines around the archeopyle in Figures 8.2 - 8.6. It is not known if the point of attachment is a consistant feature but in the cysts germinated in this study it appeared to be. In the wild this attachment probably does not last long and the operculum is lost or falls inside the cyst (Pl. 8.9, fig.4.).

Descriptions of species incubated

Phylum : Pyrrophyta Pascher
Class : Dinophyceae Fritsch
Order : Peridiniales Haeckel
Family : Peridiniaceae Ehrenberg
Genus : *Diplopsalis* Bergh

Diplopsalis lenticula Bergh

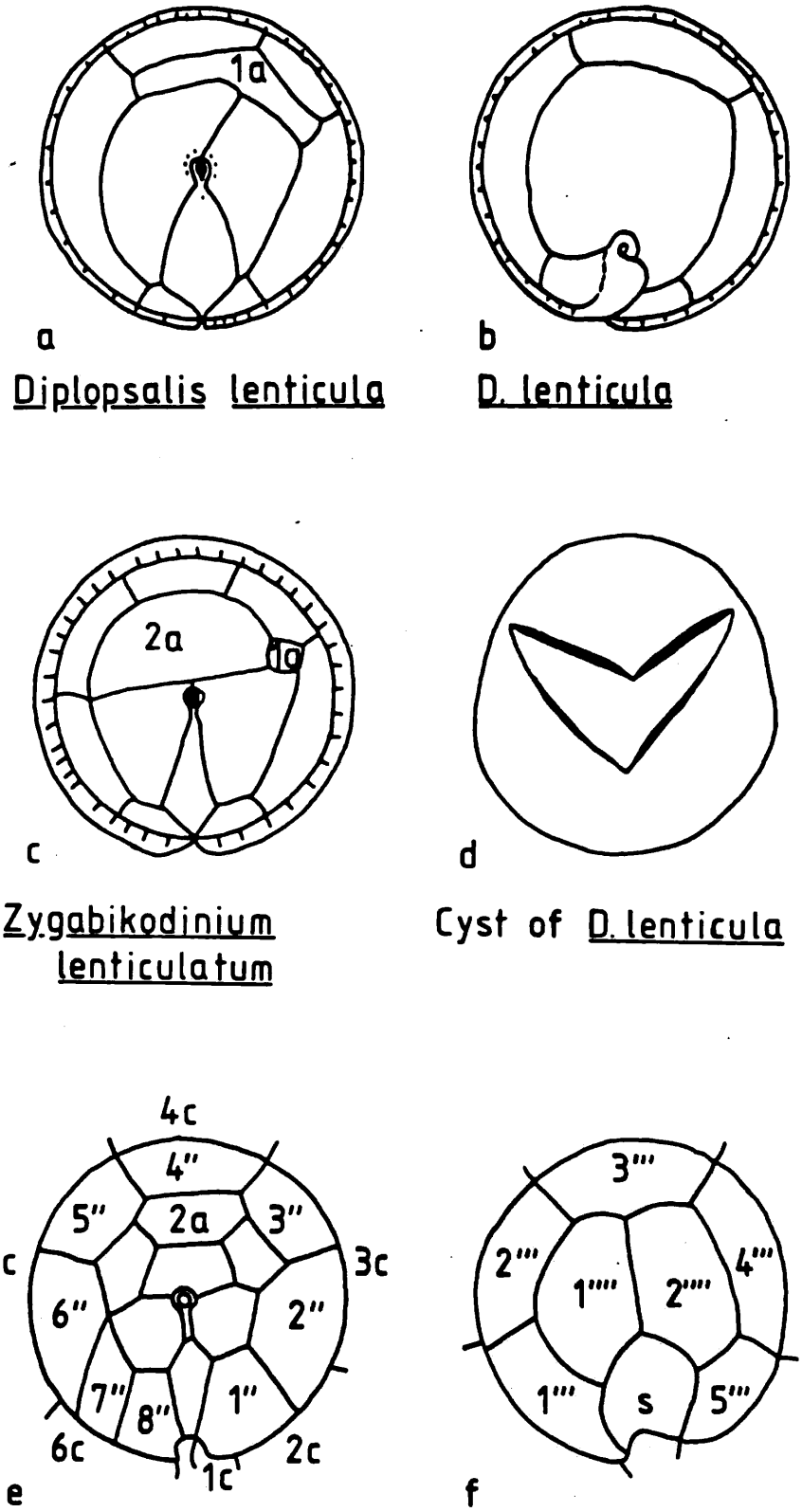
Fig. 8.2, a-b,&d; Pl. 8.1, figs.1-4

Size:- theca 30-33μm long, 38-49μm wide
cyst ~ 45-50μm across

Cysts

Cysts were round and light brown. The archeopyle was a V-shaped slit in the delicate cyst wall (Pl. 8.1, fig.1). This sometimes resulted in the rolling back of the archeopyle edges (Fig. 8.2, d). Although Wall and Dale (1968a) also hatched this species from a similar cyst, the archeopyle they describe is slightly different from that obtained here. In their experiments the archeopyle was equatorially elongate and hexagonal in shape appearing to correspond to the mid-dorsal intercalary plate of the theca.

Figure 8.2



Diplopsalis lenticula

D. lenticula

Zygabikodinium lenticulatum

Cyst of D. lenticula

Scrippsiella ?sweeneyae

S. ?sweeneyae

Thecae

Five thecae were incubated. These were ovoid in shape, showing polar compression. They had a small apical projection and a large sulcal wing (Pl. 8.1, fig.2). The 'diplopsalis group' consists of small cells very similar in shape and consequently difficult to distinguish. The confusing taxonomic literature was reviewed and revised by Dodge and Hermes (1981). According to that classification the thecae described here are Diplopsalis lenticula. The thecal plates are exactly the same as those described by Wall and Dale (1968a) (Pl. 8.1, figs.3-4; Fig. 8.2, a-b). It is possible that there may be some regional differences in the cyst type.

Genus : Zygabikodinium Loeblich & Loeblich III

Zygabikodinium lenticulatum (Paulsen) Loeblich & Loeblich III

Fig. 8.2, c; Pl. 8.1, figs.5-6; Pl. 8.2, figs.1-2

Size:- theca ~40-50μm wide
cyst ~45-60μm across, ~35-50μm high

Cysts

The cysts were slightly oblate, brown and often showed some reflected tabulation in the form of a paracingulum and parasulcus (Pl. 8.1, fig.5). The surface of the cyst was sometimes wrinkled. It had an inner cyst body (Pl. 8.1, fig.6). Reid (1977) named these cysts Dubridinium caperatum and commented on the occasional presence of the parental theca. In this study parental theca were found to be present around cysts examined from the sediment (Pl. 8.2, fig.2).

PLATE 8.1

All figures are S.E.M.s

Fig. 1 : Side view, showing the acheopyle, of a hatched *Diplopsalis lenticula* cyst, approximately 43 µm across, Loch Melfort.

Fig. 2 : Ventral view of an excysted thecate cell of *Diplopsalis lenticula*, 42 µm across, Loch Melfort, (same cell as shown in Fig. 4).

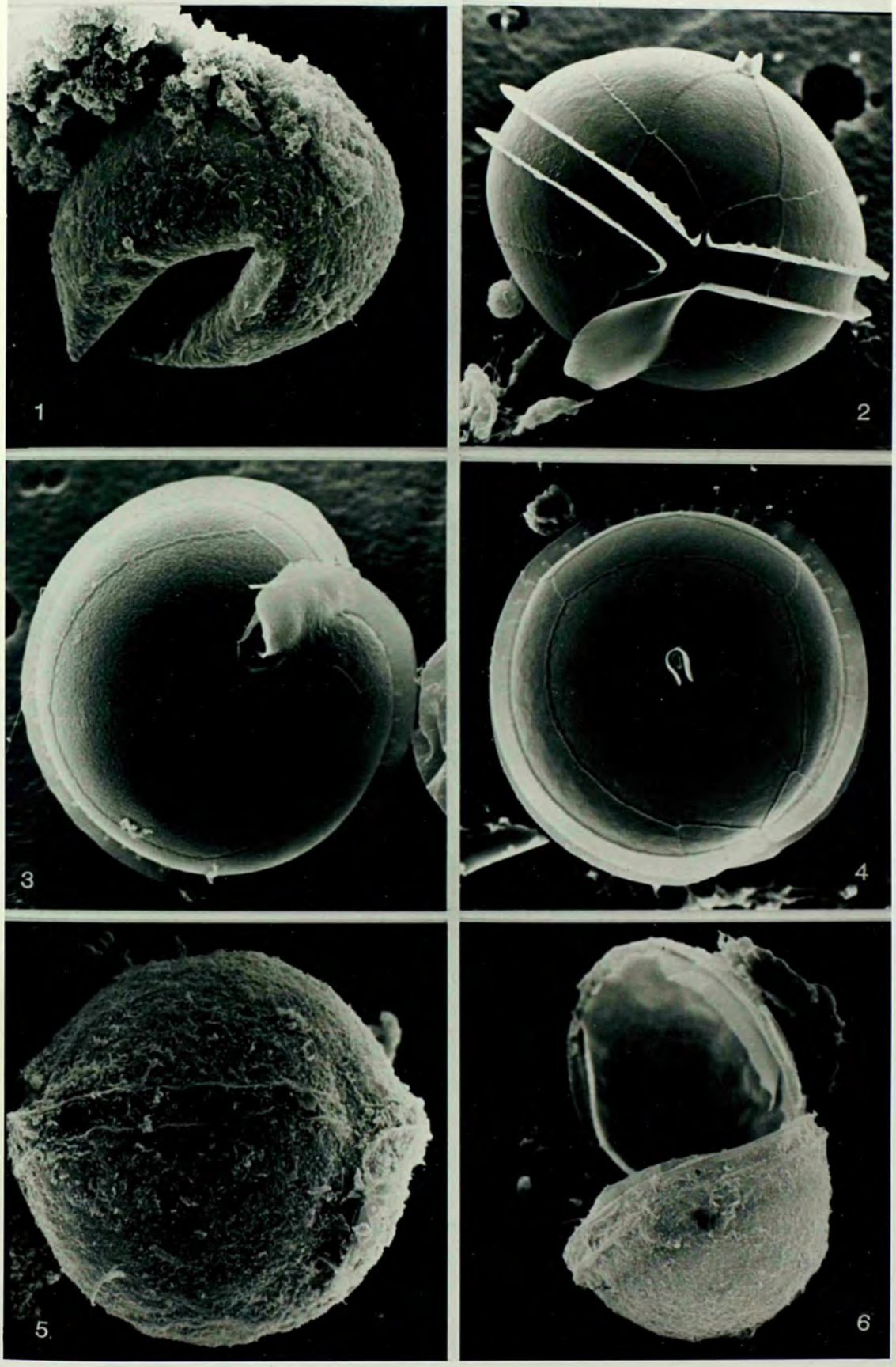
Fig. 3 : Antapical view of an excysted thecate cell of *Diplopsalis lenticula*, 46 µm across, Loch Melfort.

Fig. 4 : Apical view of an excysted thecate cell of *Diplopsalis lenticula*, 42 µm across, Loch Melfort, (same cell as shown in Fig. 2).

Fig. 5 : Side view (showing paracingulum and parasulcus) of hatched *Zygabikodinium lenticulatum* cyst (*Dubridinium caperatum*), approximately 51 µm across, Loch Melfort.

Fig. 6 : *Zygabikodinium lenticulatum* cyst (*Dubridinium caperatum*), showing inner wall, from Loch Creran sediment.

Plate 8.1



Thecae

Six thecae were hatched. They seemed more delicate than those of Diplopsalis lenticula and only one preserved sufficiently well for S.E.M. This enabled the determination of the antapical plate pattern (Pl. 8.2, fig.1) but not the apical configuration. It is felt, however, that there was sufficient evidence from thecae enclosing cysts and the literature (Wall and Dale, 1968a; Reid, 1977) to ascribe this species to Zygabikodinium lenticulatum. The motile thecate stage is globular and can only be distinguished from the previous species by its extra intercalary plate. The first intercalary plate is very tiny (Fig. 8.2, c).

Genus : Scrippsiella Balech ex Loeblich III

Scrippsiella ?sweeneyae Balech ex Loeblich III

Fig. 8.2, e-f; Pl. 8.2, figs.3-6; Pl. 8.3, figs.1-6

Size:- Thecae:- 22-38 µm long, 18-30 µm wide
Cysts:- 61-68 µm long, 40-43 µm across

Cysts

The cysts were somewhat egg-shaped, had a granulate surface and contained a red body. They had a calcareous outer layer composed of crystals of a substance dissolved by hydrochloric acid presumed to be Calcium carbonate. Two forms of this outer layer were found in this study using S.E.M. (Pl. 8.2, figs.3-4). In one the crystals appeared to be lying flat and in the other they seemed to be clustered together lying on their edges. Similar variations in orientation were found by Keupp (1981)

PLATE 8.2

All figures are S.E.M.s

Fig. 1 : Antapical view of excysted thecate cell of Zygabikodinium lenticulatum, 47 µm across, Loch Melfort.

Fig. 2 : View of girdle of Zygabikodinium lenticulatum cyst enclosed by parental theca, x 3,439.

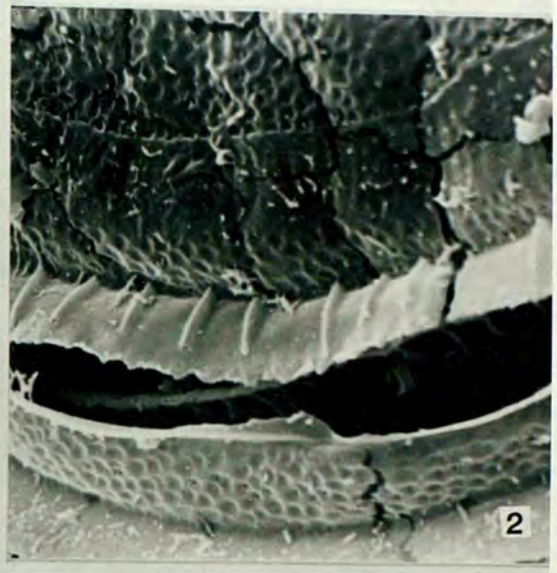
Fig. 3 : Hatched Scrippsiella ?sweeneyae cyst, the opercular piece has closed back on to the cyst but is just visible at the apex of the cyst, 42 µm across (at widest part).

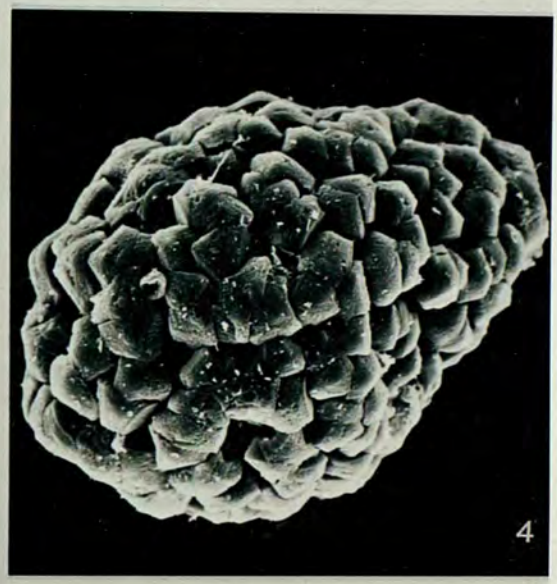
Fig. 4 : Scrippsiella ?sweeneyae cyst, showing alternative ornamentation to that in Fig. 3, 36 µm across (at widest part), Loch Melfort.

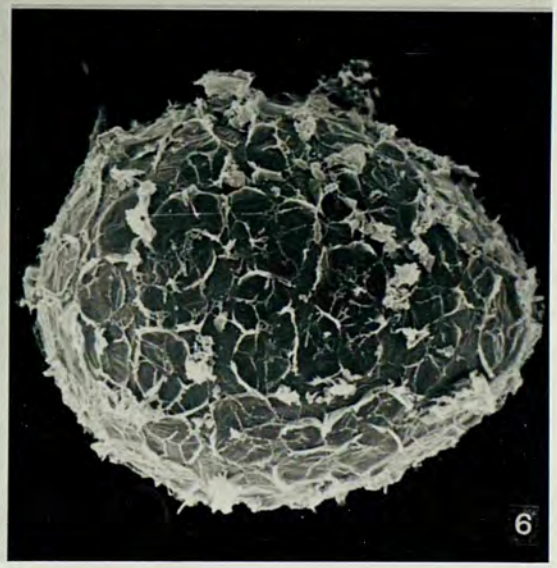
Fig. 5 : View of archeopyle of hatched Scrippsiella ? sweeneyae cyst showing membrane beneath calcareous ornamentation, x 3,273.

Fig. 6 : Side view of Scrippsiella ?sweeneyae cyst treated with HCl to show organic membrane, no paratabulation visible, 40 µm long.

Plate 8.2







working on calcareous cysts of the Boreal lower Cretaceous. These differences are possibly due to different concentrations of Calcium carbonate in the water column at the time of mineralisation (Keupp pers. comm.).

The inner layer of the cyst seemed to be organic and survived a gentle acid treatment. It can be seen inside the calcareous layer of the hatched cyst in Pl. 8.2, fig.5. Dale (1983) shows photographs of this cyst type which he describes as an unidentified calcareous dinoflagellate. He also dissolved away the outer calcareous layer and stained with Trypan blue to reveal possible traces of paratabulation. In this study cysts with their outer layer dissolved were examined under the S.E.M. for possible traces of paratabulation but none were apparent (Pl. 8.2, fig.6). The apical archeopyle was a simple split around the apex of the cyst, and the large opercular piece(s) remained attached to the cyst (Pl. 8.3 fig.1).

Wall and Dale (1968b) describe nine types of calcareous cysts, six of which were isolated from recent sediments. None of these appear to be the cyst described here. The cyst from which they hatched Scrippsiella sweeneyae, however, appears to be related, the outer calcareous layer being composed of rounded ridges with some degree of paratabulation. From the palynological literature the most closely related group of cysts appears to be that of Obliquipithonella loeblichi (Boli) Keupp (Keupp pers. comm.). [Pithonella loeblichi (Boli) is figured by Keupp (1981) but it is included in his new genus Obliquipithonella (Keupp and Mutterlose, 1984).] Futher more detailed examination particularly of the inside of the cyst is required to confirm this relationship.

Thecae

These cysts did not hatch successfully in the chambers used for incubation experiments. The naked protoplast remained rounded and moved across the chamber by exuding gelatinous sheaths (periplasts) (Pl. 8.3, fig.2). These appear to be the same as those described by Braarud (1958) and Wall and Dale (1968a) for Scrippsiella trochoidea and Kayser (1976) for Scrippsiella faeroense Balech et Soares (= Scrippsiella trochoidea, Dale, 1977b). The latter was caused by the addition of mercuric acetate and this behaviour would seem to be in response to adverse conditions. Hatching success rate was, however, very good in watch glasses (which hold more sea water than the chambers) and many of the excysted cells formed a girdle and were clearly recognisable as Scrippsiella spp. Some problems were found in the fixation of cells for the S.E.M. Apparently few cells had properly formed thecal plates and many cells were picked out and scanned with no plate patterns being discernable. This is probably because of the method of division of this group. The theca breaks and is shed and the naked protoplasm divides by constriction. Smooth thecal surfaces would thus be characteristic of newly formed cells (see for example Kalley and Bisalputra, 1970). Plate 8.3, fig.3 shows a typical excysted cell, from this study, that is just beginning to form its girdle plates. To overcome this problem, excysted motile cells from one hatching experiment were used to start a small culture. Many cells from this culture were S.E.M.ed but only a few provided clear pictures of thecal tabulation.

The cell had a rounded hypotheca with a somewhat larger conical epitheca (Pl. 8.3, fig.4). It swam rapidly with a rotating motion occasionally touching its apex to the base of its container. It had a large nucleus contained in the centre of the cell towards the hypotheca. Cells that had recently excysted

PLATE 8.3

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Light micrograph of hatched cyst of Scrippsiella ?sweeneyae showing archeopyle, 40 µm across (at widest part), Loch Creran.

Fig. 2 : Light micrograph of excysted Scrippsiella ?sweeneyae cell without properly formed thecal plates, showing discarded periplasts, Loch Creran.

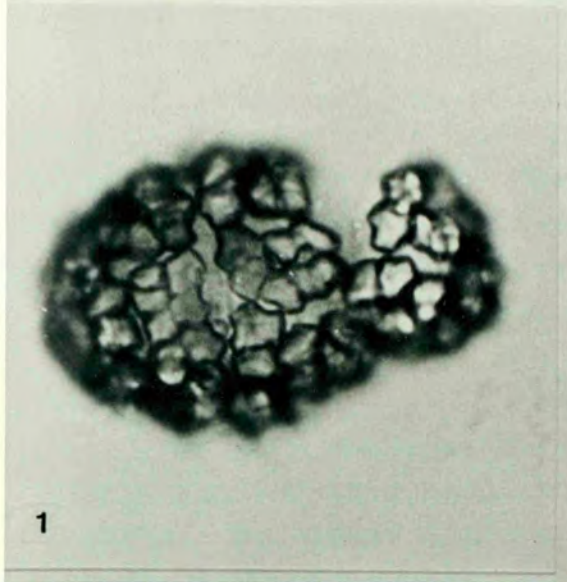
Fig. 3 : Side view of excysted cell of Scrippsiella ?sweeneyae with girdle just becoming visible, 23 µm long, Loch Creran.

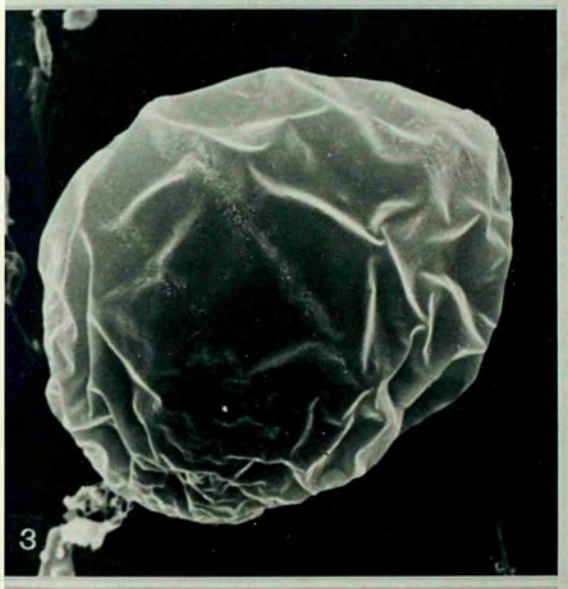
Fig. 4 : Ventral view of thecate cell of Scrippsiella ?sweeneyae from culture started with cysts from Loch Creran, 23 µm across (same cell as shown in Fig. 6).

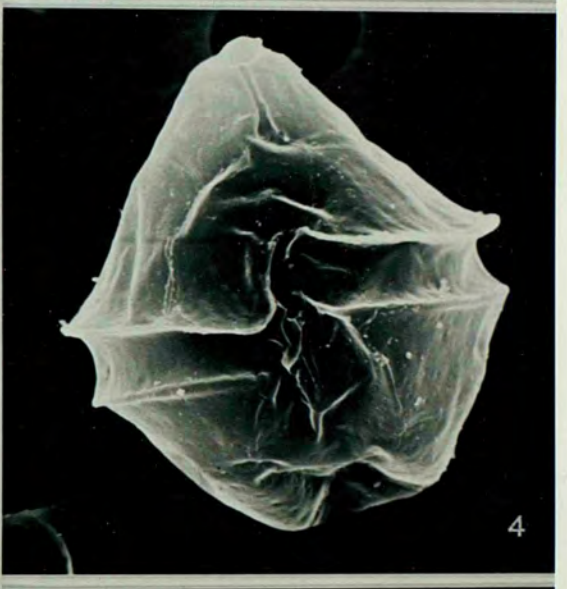
Fig. 5 : Antapical view of thecate cell of Scrippsiella ?sweeneyae from culture started with cysts from Loch Creran, 22 µm across.

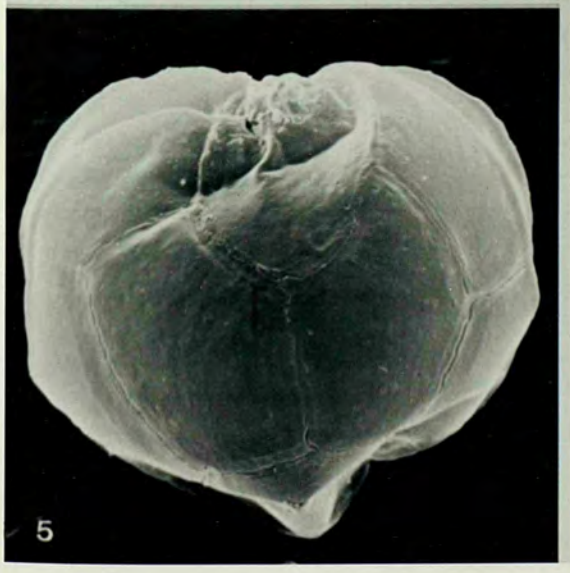
Fig. 6 : Apical view of thecate cell of Scrippsiella ?sweeneyae from culture started with cysts from Loch Creran, 23 µm across (same cell as shown in Fig.4).

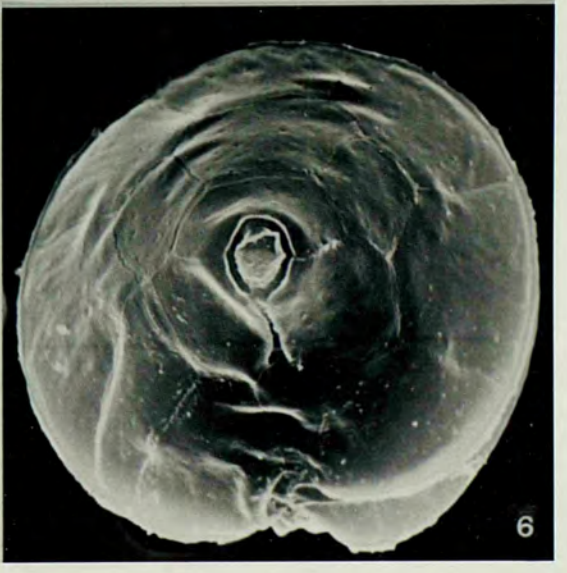
Plate 8.3











also contained the red body that had been seen in the cyst. The girdle was excavated and displaced by about one girdle width and thus one antapical lobe was larger than the other. The thecal plates were smooth with randomly scattered simple trichocyst pores.

The plate tabulation was typical for the Scrippsiella group (Fig. 8.2, e-f; Pl. 8.3, figs.5-6). The cell having six cingular plates. The number of precingular plates in the Scrippsiella group has been found to be variable (S. sweeneyae, 4"- 7", Balech, 1959; S. hexapraecingula, 6", Horiguchi and Chihara, 1983). In this study only one cell was found on which the seventh precingular plate (7") was clearly visible and it was divided to form an eighth Precingular (8") (Pl. 8.3, fig.6). In all other details the species described here appears to be similar to S. sweeneyae as described by Balech (1959) who does mention the occurrence of abberrant forms in his cultures. The S. sweeneyae of Wall and Dale (1968b) is different to the species described here in its cyst type, the asymmetry of the antapical plates and the third post cingular (3''') plate, which in their hatched cells did not contact the left antapical plate (1''''). However, they also mention variations in plate tabulation.

The taxonomy of the Scrippsiella species is extremely confused (see Chapter 3). The thecate motile stages are all apparently similar (for example it is difficult to distinguish between the motile stages of S. trochoidea and S. sweeneyae) but their cyst types are quite different - possibly giving an easier taxonomic guide. Further work with especial emphasis on comparison of the many cultures available and including cyst studies is required to elucidate this problem.

Genus : Protoperidinium Bergh emend Balech
sub-genus : Archaeperidinium (Jörgensen) Balech

Protoperidinium avellana (Meunier) Balech

Fig. 8.3, a-b; Pl. 8.4, figs.1, 3 & 4

Size:- theca 50-55μm long, 45-50μm wide
cyst 50-55μm across

Cysts

The cysts were spherical, smooth-walled and dark brown. They had a distinct curved hexagonal archeopyle (Pl. 8.4, fig.1). The operculum remained attached at the short side of the archeopyle and was related to the second intercalary (2a) paraplate (Fig. 8.3, a-b). This cyst is known under the name Brigantedinium cariacoense (Wall) Reid.

Thecae

Seven of these delicate thecae were germinated. The rounded cells had little thecal ornamentation (Pl. 8.4, fig.4). The girdle was left handed, excavated and striated (Pl. 8.4, fig.3).

Protoperidinium denticulatum (Gran & Braarud) Balech

Fig. 8.3, g-i; Pl. 8.4, fig.4

Size:- theca (single cell) 35μm long 50μm across
cyst ~50μm across

PLATE 8.4

All figures are S.E.M.s unless otherwise stated

Fig. 1 : *Protoperidinium avellana* cyst (*Brigantedinium cariacoense*) showing archeopyle.

Fig. 2 : Light micrograph of excysted thecate cells of *Protoperidinium denticulatum*, 35 µm across, Loch Melfort.

Fig. 3 : Ventral view of excysted thecate cell of *Protoperidinium avellana*, 50 µm across, Loch Melfort, (see also Fig. 4).

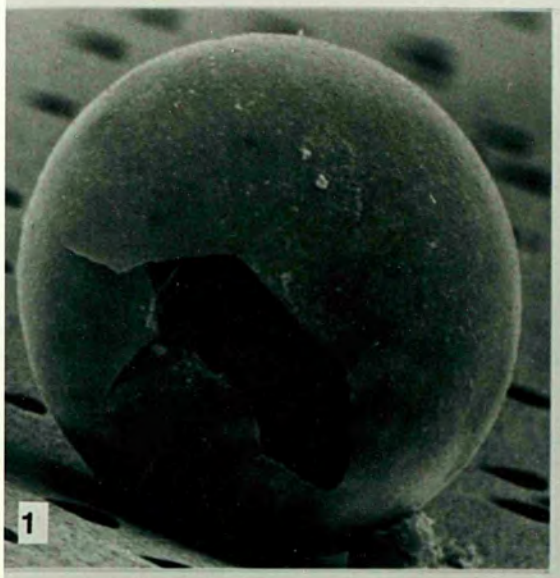
Fig. 4 : Detail of surface patterning of *Protoperidinium avellana* cell shown in Fig. 3, x 6,300.

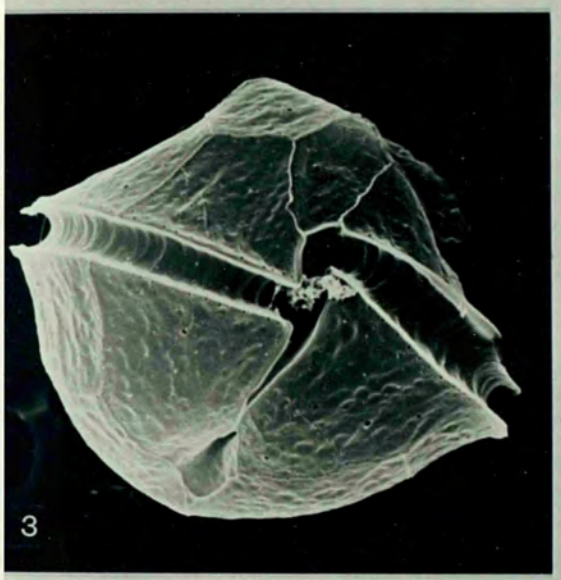
Fig. 5 : Detail of ornamentation of *Protoperidinium excentricum* cell shown in Fig. 7, x 12,271.

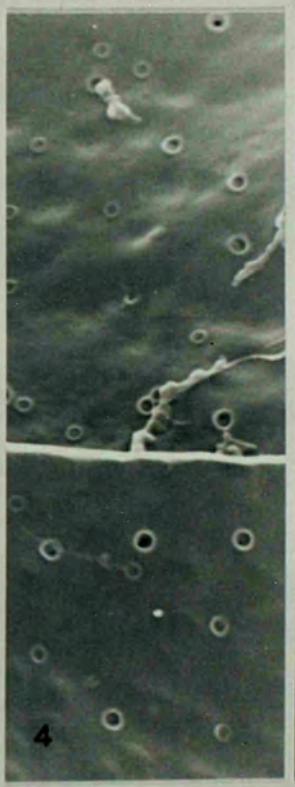
Fig. 6 : Light micrograph of hatched cyst of *Protoperidinium excentricum*, approximately 50 µm across, Loch Melfort.

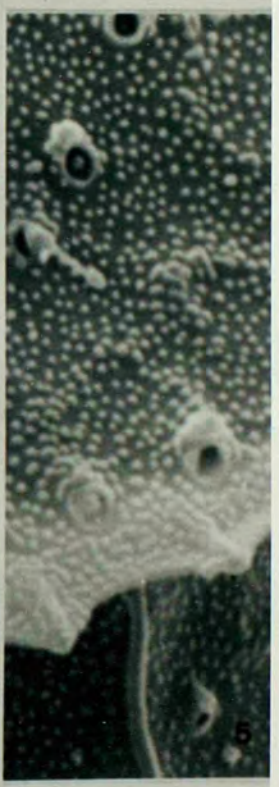
Fig. 7 : Dorsal / lateral view of excysted thecate cell of *Protoperidinium excentricum*, 56 µm across, Loch Melfort, (see also Fig. 5).

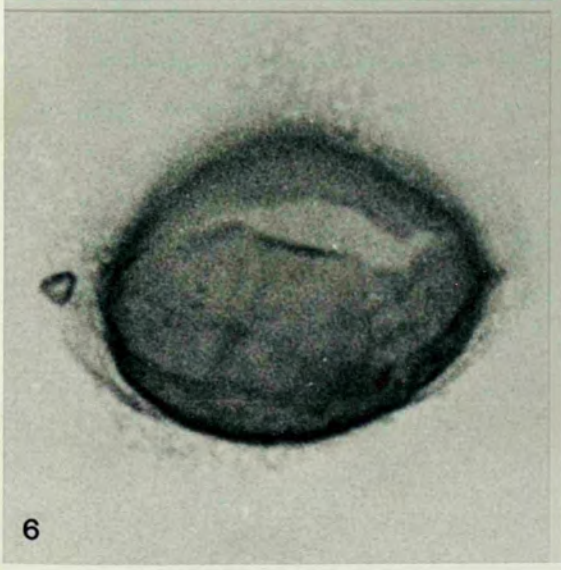
Plate 8.4

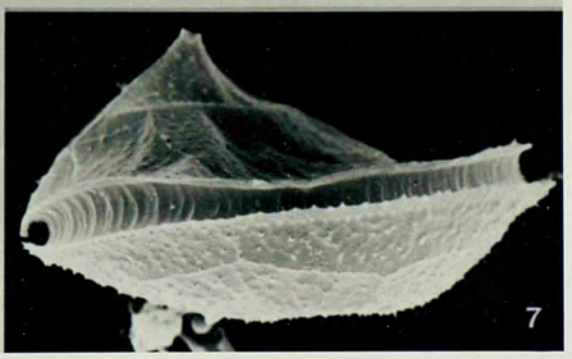












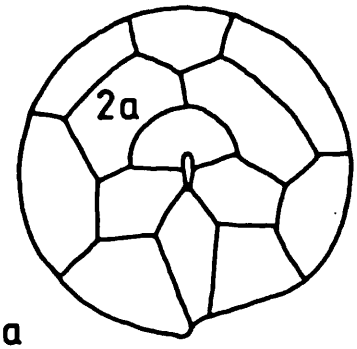
Cysts

Cysts were spherical smooth and brown and were very similar to the cysts produced by the other archaeperidiniums. The archeopyle is usually described as 2a but in the one cyst germinated in this study the archeopyle appeared to be more closely related to the 1a plate of the P. denticulatum cell (Fig. 8.3, g-h). Dale (1983) Figs. 21 & 22 also shows this.

Thecae

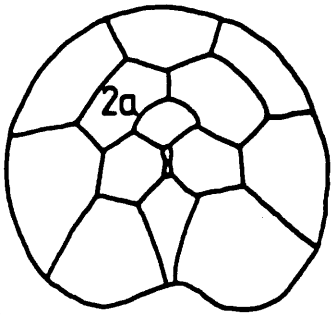
Only one cyst was successfully germinated in this study and the motile thecate stage burst before fixation for the S.E.M. The cells of this species have a characteristically flattened side and sometimes swim around in pairs (Pl. 8.4, fig.2). It was thought that these pairs had adjoining hypothecae (Dodge 1982). However, recent scanning microscope studies show that pairs are joined hypotheca to epitheca (Fig. 8.3, i). Abé (1981) has described the cell with the flattened epitheca as a separate species P. hemisphaericum. A number of interesting questions arise ; does just a single cell of the pair hatch from the cyst or do the cells excyst in pairs? If a single cell excysts which type? (P. denticulatum or P. hemisphaericum). When the cells disrupted in the incubation chamber only one thecal skeleton remained. It is possible therefore that only one cell excysted and that in this case although a second cell had been formed it had not had time to form its thecal plates. If only one cell excysts it could be possible that there is more than one type of cyst (one for P. denticulatum and one for P. hemisphericum) or perhaps only one cell type encysts. More study of the excystment of this species should answer these questions. If both cells hatch from the same type of cyst this will pose some interesting genetic and evolutionary questions.

Figure 8.3



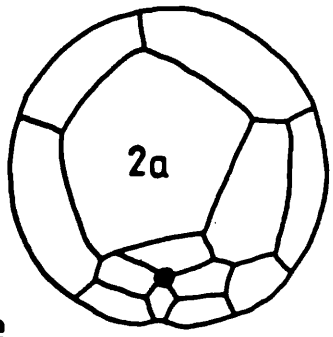
a

Protoperidinium avellana



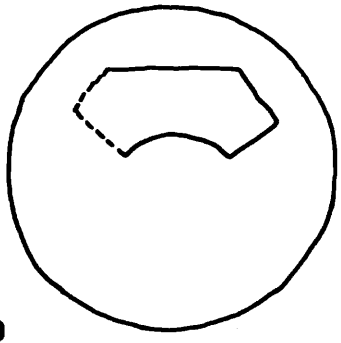
c

Protoperidinium thorianum



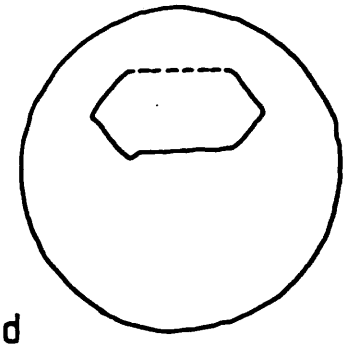
e

Protoperidinium excentricum



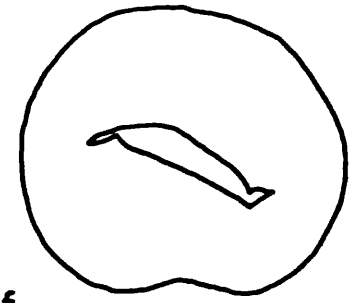
b

Cyst of P. avellana



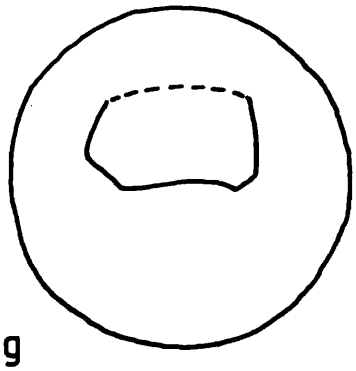
d

Cyst of P. thorianum



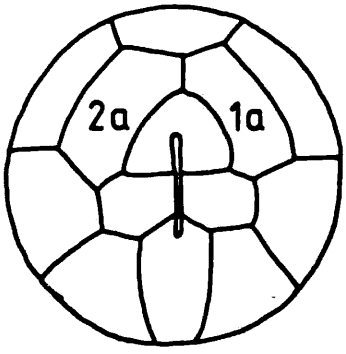
f

Cyst of P. excentricum



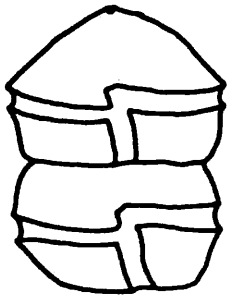
g

Protoperidinium denticulatum cyst



h

P. denticulatum



i

P. denticulatum

Protoperidinium excentricum (Paulsen) Balech

Fig. 8.3, e-f; Pl. 8.4, figs.5-7

Size:- thecae 30μm long 59μm wide
cysts 50μm across

Cysts

The cysts are smooth-walled, pale brown and slightly dorsoventrally flattened. They have an indented parasulcus and are sometimes distinct in the sediment due to being enclosed by the parental theca. Both of the cysts incubated in this study had old thecae present. The archeopyle was an indistinct zig-zag split (Fig. 8.3, f; Pl. 8.4, fig.6) somewhat reminiscent of the ?Protoperidinium cyst described by Harland (1982 - Pl.38, figs.10-12.). It did not appear to be related to any paraplate boundaries (Fig. 8.3, e). This cyst does not have a palynological description but is probably grouped with the other round, brown cysts of peridiniacean or glenodiniacean affinities.

Thecae

Two of the characteristically flattened thecae were germinated (Pl. 8.4, fig.7.). They had an unusual arrangement of apical plates (Fig. 8.3, e). The theca was finely reticulated and the girdle was bordered by short spines (Pl. 8.4, fig.5). The irregular flattening caused the cells to swim in a very distinct manner with the apical pore uppermost and the body swinging from side to side.

?*Protoperidinium minutum* (Kofoid) Loeblich III

Size:- thecae ~40μm across
cyst ~40μm across

Cysts

The cyst incubated in this study was spherical and appeared to be covered in short spines. Like many other spiny cysts much debris had accumulated about the test so the structure was a little obscured. The operculum remained attached to the test so it was difficult to determine the archeopyle shape. It did not appear to resemble the cyst described by Wall and Dale (1968a) for this species but was similar to that described by Fukuyo *et al*. (1977).

Thecae

Only one cyst of this type was sucessfully hatched and only a brief examination was possible before it ruptured. The gross morphological characteristics were those of *P. minutum*. It was a globular cell with a ventral sulcal list. Further work including S.E.M. is needed to confirm this cyst-theca relationship.

Protoperidinium thorianum (Paulsen) Balech

Fig. 8.3, c-d; Pl. 8.5, figs.1-2

Size:- thecae 50-60μm across
cysts 50-55μm across

Cysts

The cysts were spherical, smooth-walled and dark brown. The operculum, although similar in shape to that of Protoperidinium avellana; was not curved and was attached to the archeopyle along the long side (Fig. 8.3,d). Again this is a round, brown cyst that has probably not been described separately. It is most similar to the cysts of Protoperidinium denticulatum.

Thecae

Three thecae were germinated. They were very similar to P. avellana having two intercalary plates and a left handed, striated, excavated girdle (Fig. 8.3, c; Pl. 8.5, fig.1). They were characterised by their papillate thecal plate surface (Pl. 8.5, fig.2) and their slightly larger size. As the only difference between the cell types of P. avellana and P. thorianum appears to be the papillate surface and because the thecal structure of some species varies with age this may be a somewhat dubious species distinction. However, the cells of both species were all examined at a similar 'age' after hatching so differences in thecal patterning are likely to be significant.

sub-genus : Orthoperidinium

This will be sub-divided according to the configuration of the 2a plate. In the orthoperidinium the 2a plate contacts the other two intercalary plates. If it also contacts the third apical (3') and the fourth precingular (4"), it is described as 'quadra'. If in addition to the 3' and the 4" it touches the third or the fifth precingular (3" / 5") it is described as 'penta'. If it touches all these plates (3', 3", 4", 5") it is described as 'hexa'.

PLATE 8.5

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Lateral view of excysted thecate cell of *Protoperidinium thorianum*, 54 µm across, Loch Creran.

Fig. 2 : Detail of surface patterning of theca of an excysted *Protoperidinium thorianum* cell, x 6,900.

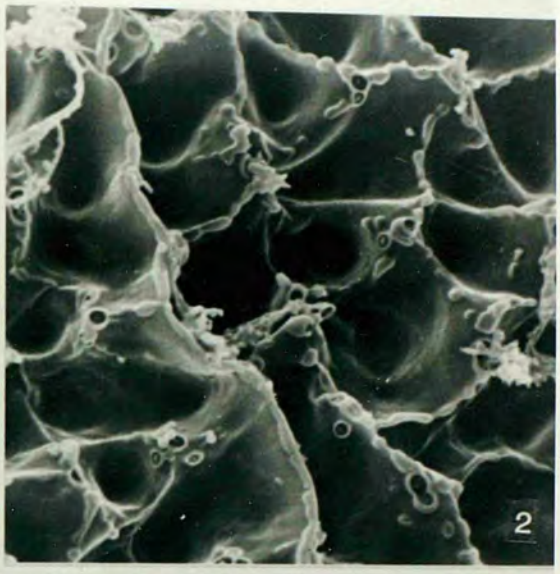
Fig. 3 : *Protoperidinium claudicans* cyst (*Votadinium spinosum*), 59 um across (at widest part).

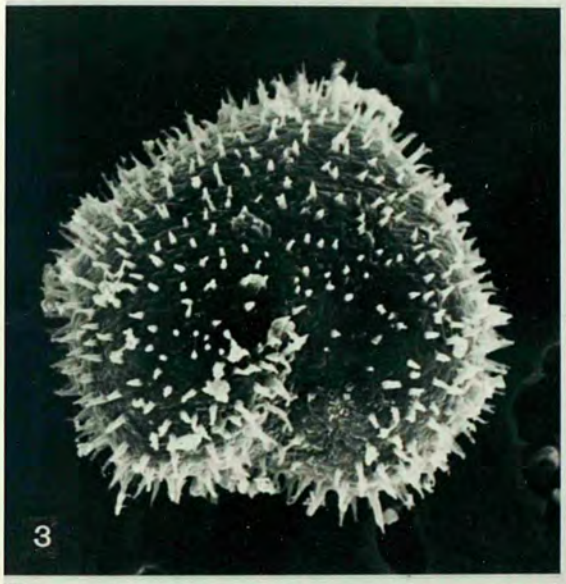
Fig. 4 : *Protoperidinium claudicans* cyst (*Votadinium spinosum*) showing debris collected on it, 63 µm across, Loch Creran.

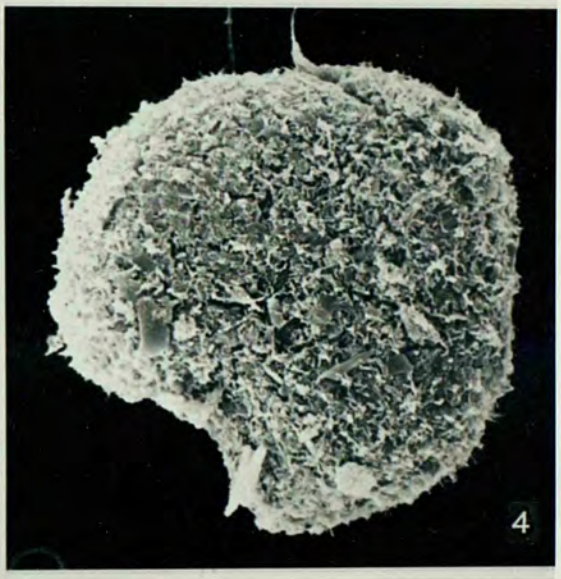
Fig. 5 : Apical view of hatched *Protoperidinium claudicans* cyst (*Votadinium spinosum*), Loch Creran, (same cell as shown in Fig. 6).

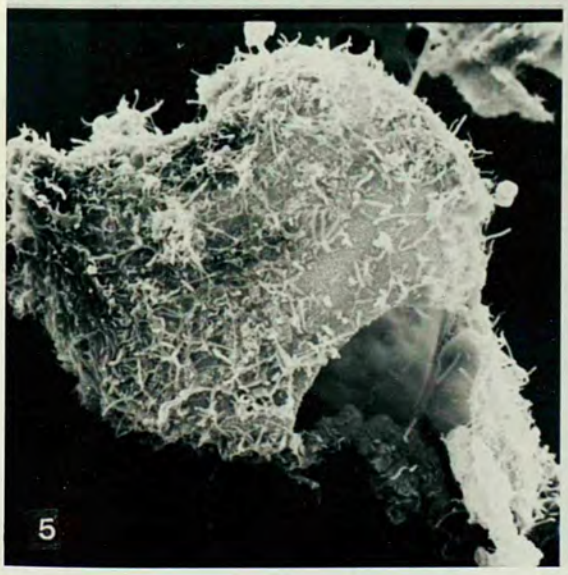
Fig. 6 : Light micrograph of *Protoperidinium claudicans* cyst (*Votadinium spinosum*), showing archeopyle, approximately 65 µm across, Loch Creran, (same cell as shown in Fig. 5).

Plate 8.5









2a plate quadra

Protoperidinium claudicans (Paulsen) Balech

Fig. 8.4, a-c; Pl. 8.5, figs.3-6; Pl. 8.6, figs.1-2

Size:- thecae 55-80μm long 48-56μm wide
cyst 50-65μm across

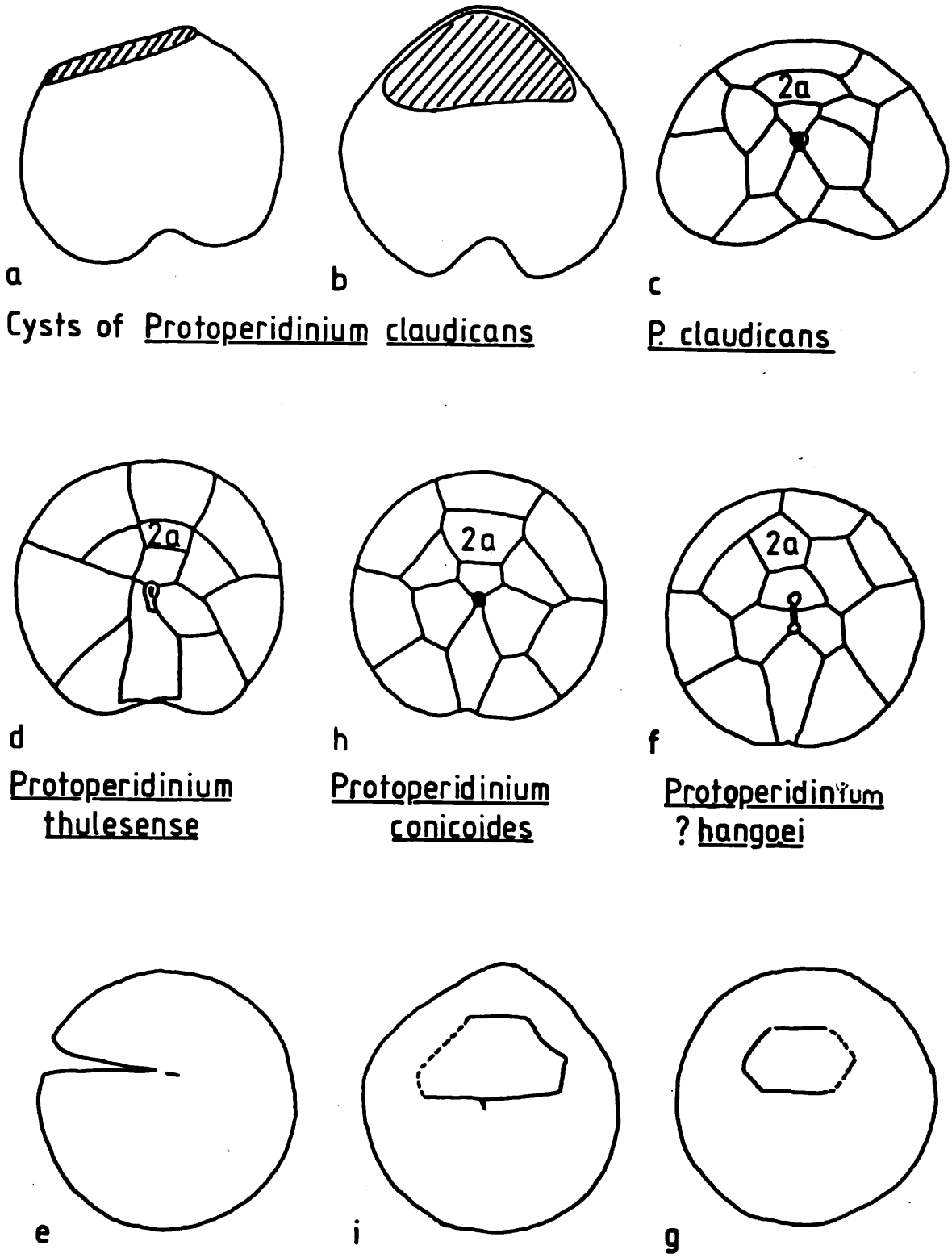
Cysts

The cysts were heart-shaped and dorso-ventrally compressed. The surface was covered in short pointed spines (Pl. 8.5, fig.3). Occasionally these were not visible because of an accumulation of debris around them (Pl. 8.5, fig.4). The archeopyle was quite large and was sometimes of the intercalary type. It sometimes had a tendency to truncate the cyst (Fig. 8.4, a-b; Pl. 8.5, figs.5-6). It is usually described as representing the loss of the 2a paraplate. These cysts are included in Reid's (1977) genus Votadinium.

Thecae

Numerous thecae of this species were successfully hatched. The cells were dorso-ventrally flattened with an apical horn and two antapical horns (the right one usually being longer than the left) (Pl. 8.6, figs.1-2). This species has been described as having a quadra or penta 2a plate (Harland 1982). All the cells hatched in this study that were examined on the S.E.M. had a penta configuration (Fig. 8.4, c; Pl. 8.6 fig.2). This cell is similar to Protoperidinium oblongum.

Figure 8.4


a
b
c
2a
Cysts of Protoperidinium claudicans
P. claudicans
d
h
f
2a
2a
2a
Protoperidinium thulesense
Protoperidinium conicoides
Protoperidinium ? hangoei
e
i
g
P. thulesense cyst
P. conicoides cyst
?P. hangoei cyst

Protoperidinium oblongum (Aurivillius) Parke & Dodge

Pl. 8.6, figs.3-6; Pl. 8.7, figs.1-4

Size:- theca 77-119μm long 50-66μm wide
cyst 61-85μm long 58-69μm across

Cysts

The cyst form was quite variable, which may indicate that a species complex is involved. They were smooth-walled, brown and varied in shape from rhombo-chordate (Pl. 8.6, fig.3) to pyriform (Pl. 8.6, fig.4). There was dorso-ventral compression. The archeopyle sometimes truncated the apex of the cyst and at other times appeared intercalary (Pl. 8.6, fig.5). This is very similar to the archeopyle formation of Protoperidinium claudicans. The smaller rhombic cysts appeared to have no paratabulation (Pl. 8.6, fig.3) whereas the larger cysts had a raised paracingulum and an indented parasulcus containing reflected flagellar pores (Pl. 8.6, fig.6). In the larger cysts the wall was covered with the pitting noted by Reid (1977) (Pl. 8.6, figs.4 & 6). The cysts were full of small globules some of which were coloured crimson (Pl. 8.7, fig.1). This cyst type is also included in Reid's (1977) genus Votadinium.

Thecae

Many thecae were successfully hatched. They had a long apical horn and two long sub-equal antapical horns (Pl. 8.7, fig.2). Occasionally damaged specimens were hatched where the cell shape was not properly formed (for example cells with one antapical horn, cells with square antapical horns). Several varieties have been described for this species by Dangeard (1927) having different dorsal epithecal plate arrangements. It is also similar to other Protoperidinium species, the smaller specimens

PLATE 8.6

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Light micrograph showing ventral view of excysted thecate cell of *Protoperidinium claudicans*, from cyst shown in Pl. 8.5, figs. 5-6, approximately 60 µm across, Loch Creran.

Fig. 2 : Dorsal view of excysted thecate cell of *Protoperidinium claudicans*, approximately 50 µm across.

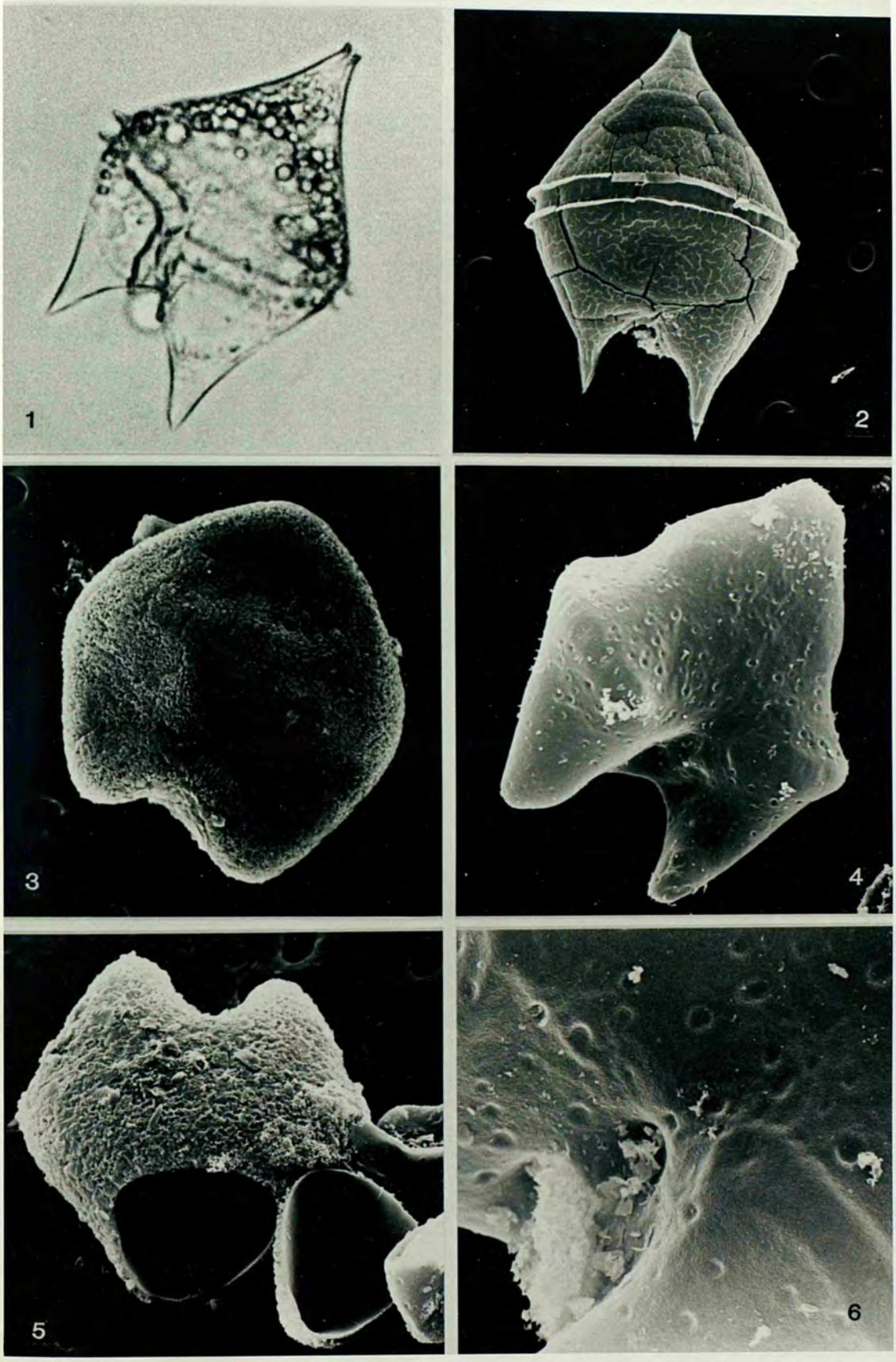
Fig. 3 : *Protoperidinium oblongum* cyst (*Votadinium calvum*), 66 µm across.

Fig. 4 : Ventral view of a hatched *Protoperidinium oblongum* cyst (*Votadinium calvum*), approximately 73 µm long.

Fig. 5 : Apical view of a hatched *Protoperidinium oblongum* cyst (*Votadinium calvum*), approximately 65 µm across.

Fig. 6 : Detail of sulcal region of hatched *Protoperidinium oblongum* cyst (*Votadinium calvum*), x 6,900.

Plate 8.6



being akin to P. claudicans and the larger specimens to Protoperidinium oceanicum. These species are largely distinguished by size and shape. Wall and Dale (1968a) discuss the variation in thecal type and mention obtaining the different Dangeard varieties, but did not relate these to particular cyst types. Two different varieties with quadra and penta 2a plates were obtained in this study (Pl. 8.7, figs.3 & 4), and appear to relate to the Danegard varieties P. oblongum var symmetricum and var inequale. Distinctions between cysts were not made during S.E.M. work so correlations between cyst types and thecal varieties were not possible. Further critical work is needed to distinguish the varieties and their cyst types in this species complex.

Protoperidinium ?thulesense (Balech) Balech

Fig. 8.4, d-e; Pl. 8.7 figs.5-6

Size:- theca 46µm long 44µm wide
cyst 40µm across

Cysts

The cyst was light brown and spherical. It was very like the cysts of D. lenticula. The archeopyle was a slit and appeared to follow the girdle it divided the cyst unequally (Fig. 8.4, e; Pl. 8.7, fig.5). A S.E.M. of the front of the cyst showed that the archeopyle (with its split at the back of the cyst) also reflected the slightly offset girdle. Even after hatching this cyst could easily be confused with other round brown cysts of Diplopsalis affinities.

PLATE 8.7

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Light micrograph of Protoperidnium oblongum cyst (Votadinium calvum) showing cyst contents, approximately 70 µm long, Loch Creran.

Fig. 2 : Ventral view of excysted thecate cell of Protoperidinium oblongum, 119 µm long.

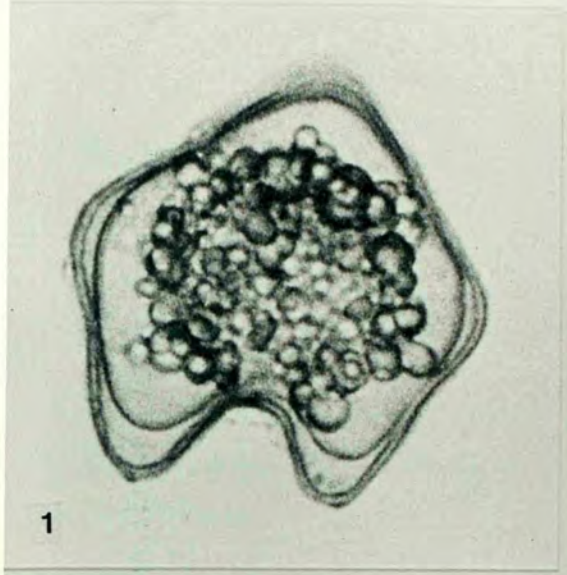
Fig. 3 : Dorsal view of excysted thecate cell of Protoperidinium oblongum (note five sided 2a plate), 110 µm long.

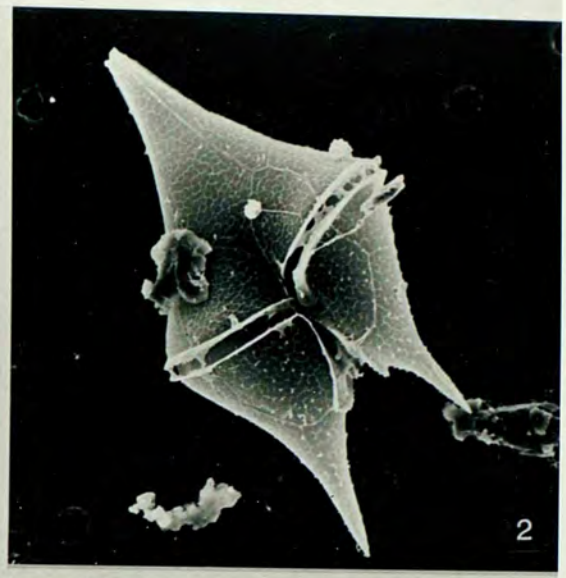
Fig. 4 : Dorsal view of excysted thecate cell of Protoperidinium oblongum (note four sided 2a plate), approximately 80 µm long.

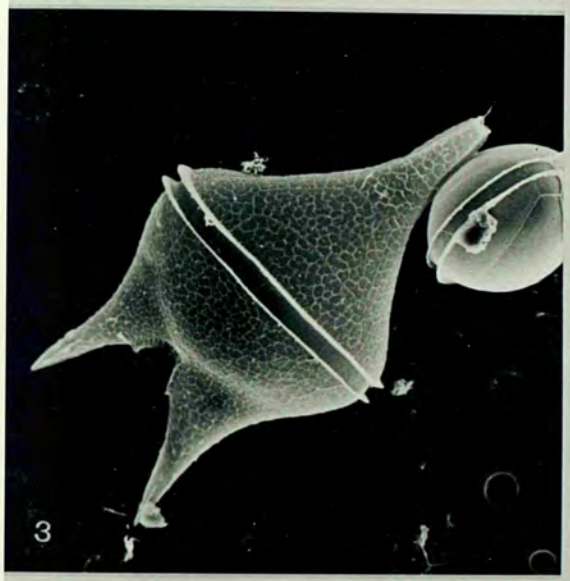
Fig. 5 : Side view of Protoperidinium ?thulesense, 35 µm across, Loch Creran.

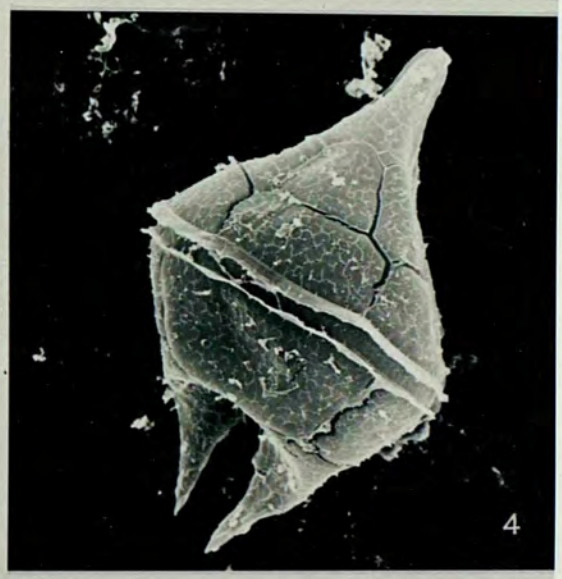
Fig. 6 : Light micrograph showing median section of Protoperidinium ?thulesense, 44 µm across, Loch Creran.

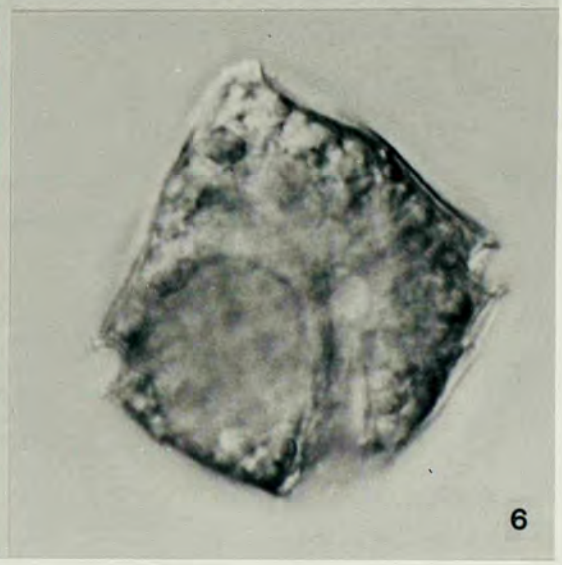
Plate 8.7











Thecae

One thecate motile stage was sucessfully hatched. It had a number of distinctive features. The epitheca was longer than the hypotheca (Pl. 8.7, fig.6). It had a very unusually shaped first apical plate (Fig. 8.4, d) and the 2a plate is quadra. The cell also had an excavated girdle with no lists which is slightly offset (about half a girdle width). This cell has not previously been hatched.

2a plate penta

Protoperidinium ?hangoei (Schiller) comb. nov.

Basionym: Peridinium hangoei Schiller 1937 p.135 fig.129,a-d

Fig. 8.4, f-g; Pl. 8.8, figs.1-2

Size:- thecae 35µm wide
cysts 38µm across

Cysts

The cysts were smooth-walled, brown and spherical and the hexagonal operculum remained attached to one of the short sides of the archeopyle (Fig. 8.4, g). This cyst type is so similar in appearence to those of P.punctulatum and various other round brown cysts that it has probably not been described as a separate cyst species.

Thecae

Two thecae were germinated. These were rounded with a slightly angular epitheca and an apical pore which extended into the third apical plate. The theca had three similarly sized

PLATE 8.8

All figures are S.E.M.s

Fig. 1 : Apical view of excysted thecate cell of Protoperidinium ?hangoei, 35 µm across, Loch Melfort, (same cell as shown in Fig. 2).

Fig. 2 : Apical view of excysted thecate cell of Protoperidinium ?hangoei, showing five sided 2a plate; 35 µm across, Loch Melfort, (same cell as shown in Fig. 1).

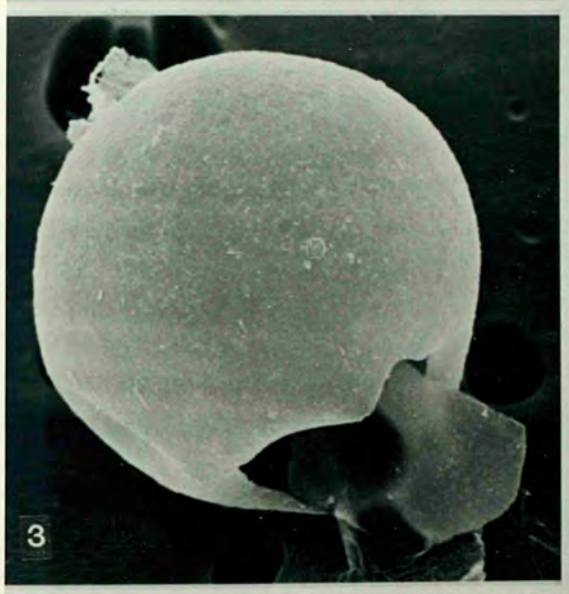
Fig. 3 : Dorsal view of hatched Protoperidinium conicoides cyst (Brigantedinium simplex) showing opercular piece tucked inside the archeopyle, approximately 43 µm across, Loch Creran.

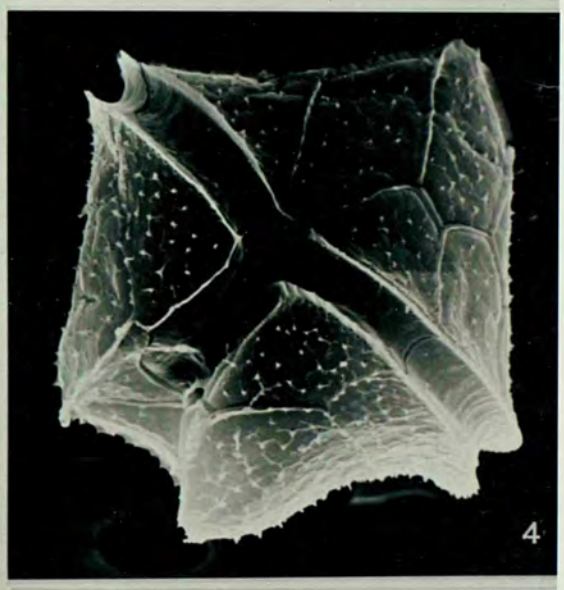
Fig. 4 : Ventral view of excysted thecate cell of Protoperidinium conicoides, 54 µm across, Loch Creran.

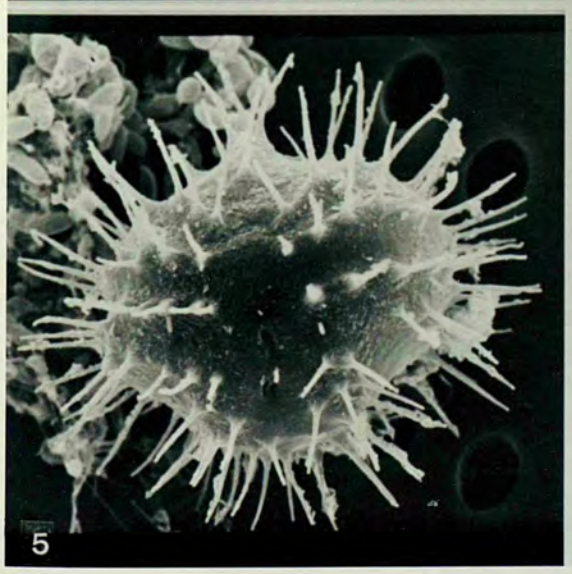
Fig. 5 : Ventral view of Protoperidinium conicum cyst (Selenopemphix), approximately 41 µm across (excluding spines), from Loch Sween sediment sample.

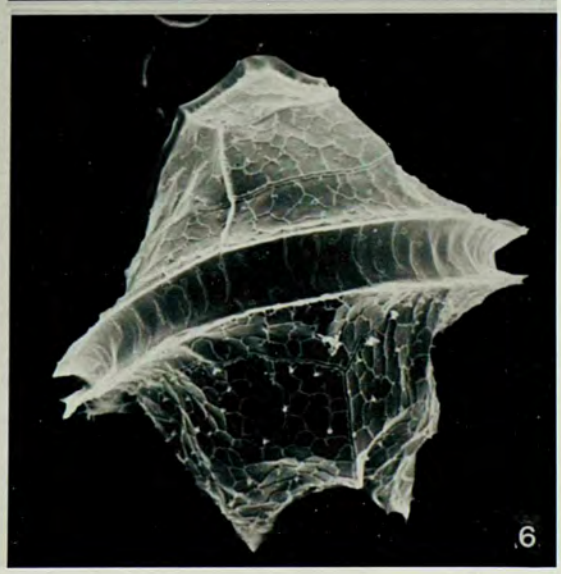
Fig. 6 : Dorsal view of excysted thecate cell of Protoperidnium conicum, approximately 36 µm across.

Plate 8.8









intercalary plates, the second of which was "penta" (Fig. 8.4, f; Pl. 8.8, fig.2). The girdle was striated and excavated with small lists. The sulcus was bordered on one side by a small wing. The thecal affinity of this cell was difficult to decide. It has provisionally been ascribed to P.hangoei largely because of the plate patterning, albeit the original description was drawn in mirror image (Lindemann, 1924). There are, however, a number of differences. The scanning micrograph of the excysted motile stage (Pl. 8.8, fig.1 & 2) shows the theca to have some relief whereas previous descriptions of P.hangoei by light microscopy have shown it as smooth walled. P.hangoei is also drawn as being rounded but the epitheca of our specimens was slightly angular.

2a plate hexa

Protoperidinium conicoides (Paulsen) Balech

Fig. 8.4, h-i; Pl. 8.8, figs.3-4

Size:- thecae 54µm long 54µm wide
cysts 50µm across

Cysts

The cysts were smooth-walled, dark brown and almost spherical. All the cysts germinated of this type had a domed apex and some also had an indented parasulcus with reflected flagellar pores (Pl. 8.8, fig.3). The archeopyle was six sided and appeared to reflect the 2a plate (fig.4, h-i). This cyst was described by Reid (1977) as Brigantedinium simplex and used as his type species for Brigantedinium.

Thecae

Three recognisable thecae were germinated. These were rhombic in dorsoventral view and had a deeply excavated sulcus with a characteristic twist on the left below the girdle (Pl. 8.8, fig.4). Germination has not previously been achieved with this species although Wall and Dale (1968a) established a link between this cyst type and P.conicoides by examining specimens from the plankton.

Protoperidinium conicum (Gran) Balech

Fig. 8.5, a; Pl. 8.8, figs.5-6

Size:- theca 37µm long 37µm across
cyst 38µm long 43µm across (the body) spines ~10µm long

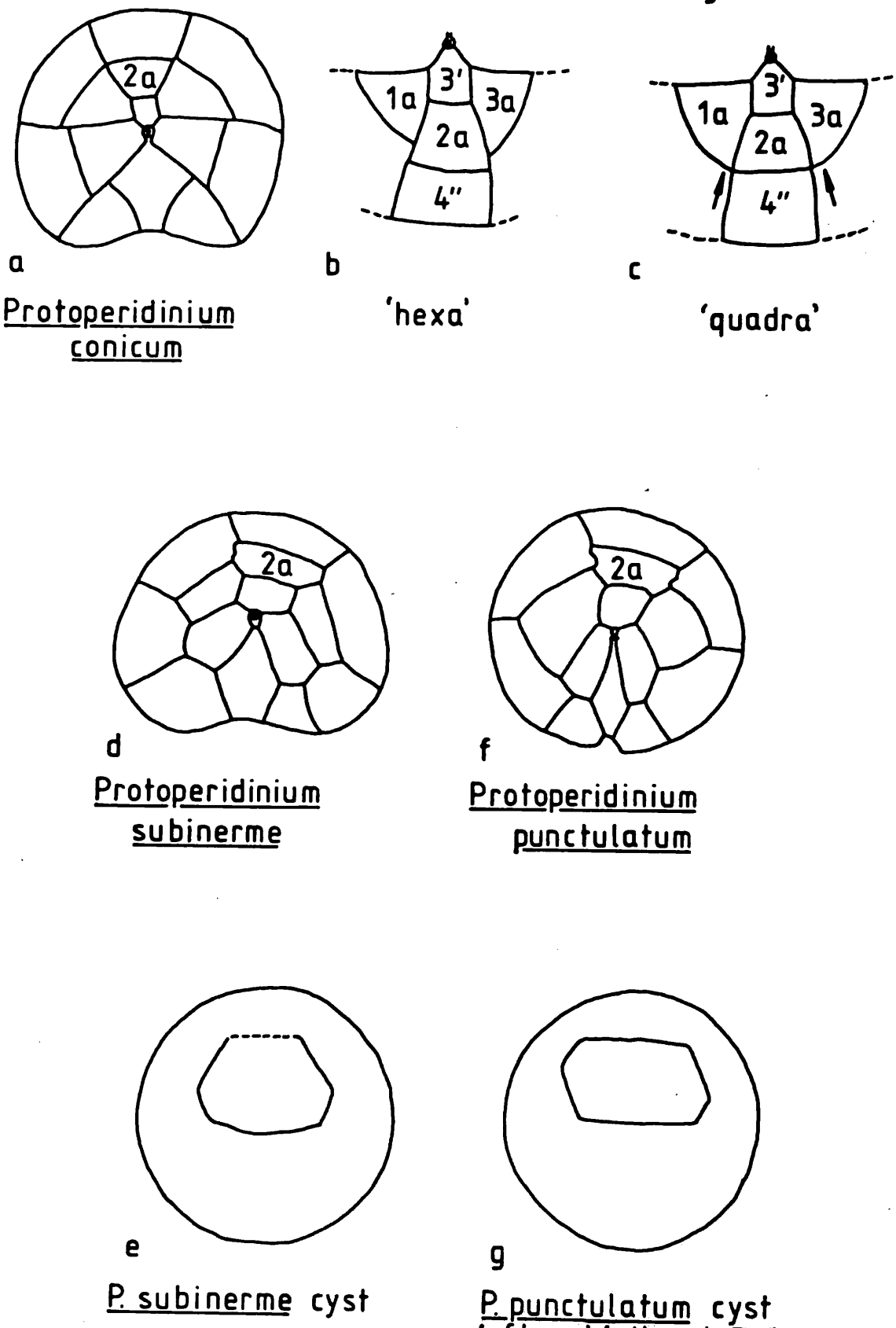
Cysts

The cysts showed polar compression and were spiny, the spines reflecting some degree of paratabulation. The girdle was especially obvious (Pl. 8.8, fig.5). There were also reflected flagellar pores in the parasulcal region of the cyst. The cysts were full of small globules sometimes coloured brilliant red. The archeopyle is described as probably being 2a (Harland, 1982). It has been described in the cyst genus Multispinula Bradford but this is a junior synonym of Selenopemphix Benedek (Harland, 1982).

Thecae

Four motile thecate stages were hatched. Each had the characteristic raised straight sutures between the apical and precingular series of plates (Pl. 8.8, fig.6). Newly excysted cells also contained the red bodies that had been observable in

Figure 8.5


2a
a
Protoperidinium conicum
1a
3'
3a
2a
4"
b
'hexa'
1a
3'
3a
2a
4"
c
'quadra'
2a
d
Protoperidinium subinerme
2a
f
Protoperidinium punctulatum
e
P. subinerme cyst
g
P. punctulatum cyst
(after Wall and Dale, 1968a)

the cyst. After a few days these dispersed within the cell giving it the characteristic pink colour often noted in the Protoperidiniales. The cell is usually described as having an ortho-hexa plate arrangement. The original description by Gran (1902) figures it as quadra or hexa and Wall and Dale (1968) noted both qudra and hexa forms. Both the excysted thecae studied on the S.E.M. had a quadra 2a plate (Fig. 8.5, a; Pl. 8.8 fig.6). The plate arrangement is such that it appears easy for there to be "slippage" from a quadra to a hexa configuration (Fig. 8.5, b-c) Because of this and the distinctive cyst type these cells are clearly P. conicum

Protoperidinium divaricatum (Meunier) Parke and Dodge

Pl. 8.9, figs.1-3

Size:- theca 38µm long 38µm across
cyst ~50µm across

Cysts

Only one cyst of this type has been found in this study of the sea-loch sediments. The cyst was covered with a variety of processes (Reid, 1977). It had a concave ventral area and a convex dorsal area. The archeopyle in this case appeared to be trapezoidal (Pl. 8.9, fig.1). The cyst has been described as Xandarodinium xanthum (Reid, 1977).

Thecae

Only one cyst was hatched. There was some problem in identifying the thecate motile stage but the cyst-theca relationship was felt to be the same as that described by Matsuoka et al. (1982), suggesting that the motile cell was P. divaricatum. The thecate stage was smooth walled and had two

PLATE 8.9

All figures are S.E.M.s unless otherwise stated

Fig. 1 : Light micrograph of cyst of Protoperidinium divaricatum (Xandarodinium xanthum), approximately 70 µm across, Loch Melfort.

Fig. 2 : Light micrograph of excysted thecate cell of Protoperidinium divaricatum (from cyst in Fig. 1), approximately 40 µm across, Loch Melfort, (see also Fig. 3).

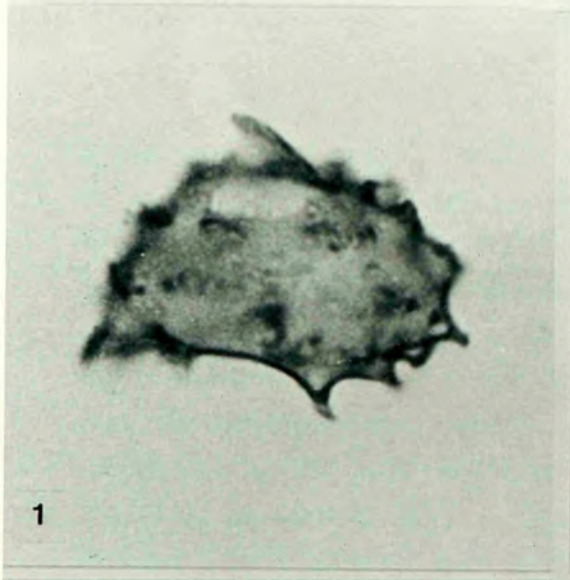
Fig. 3 : Ventral view of excysted thecate cell of Protoperidinium divaricatum shown in Fig. 2, approximately 40 µm across, Loch Melfort.

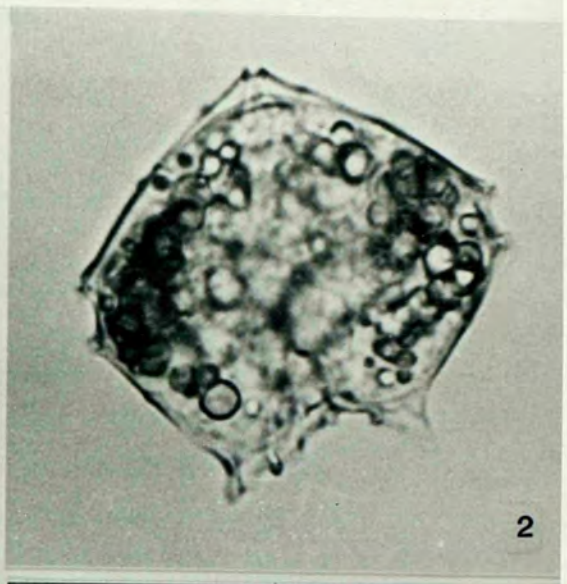
Fig. 4 : Dorsal view of hatched cyst of Protoperidinium leonis (Quinquecuspis concretum), 63 µm across, Loch Melfort.

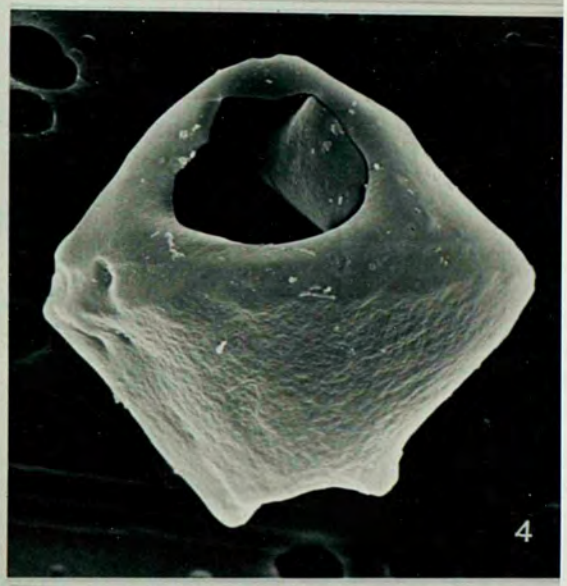
Fig. 5 : Dorsal view of Protoepridinium leonis cyst (Quinquecuspis concretum) showing archeopyle, from sediment sample, 65 µm across.

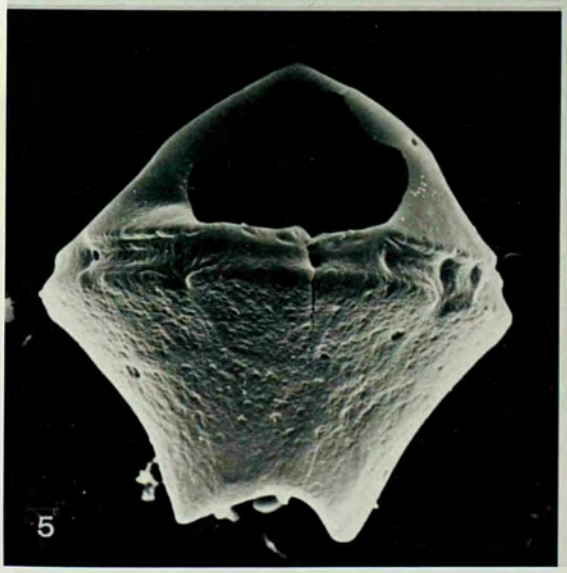
Fig. 6 : Ventral view of Protoperidinium leonis cyst (Quinquecuspis concretum) showing reflected tabulation, 65 µm across, Loch Spelve.

Plate 8.9









conspicuous, divergent, hollow antapical horns (Pl. 8.9, fig.2). It had a deeply indented sulcus and an excavated girdle with small lists (Pl. 8.9, fig.3). It differed from Matsuokas' description in having a quadra 2a plate but this was probably due to "slippage" (Fig. 8.5, b-c). This thecate dinoflagellate is not commonly identified as being present around the British Isles (see for example Dodge, 1982). Reid (1977) found the cyst to be common along the south coast of the Southern North Sea and along the English Channel coast. It is probable that it is usually confused with other species such as Protoperidinium mite and Protoperidinium brevipes.

Protoperidinium leonis (Pavillard) Balech

Pl. 8.9, figs.4-6; Pl. 8.10, figs.1-2

Size:- thecae 60µm long 60µm wide
cysts 65µm long 65µm wide

Cysts

The cysts were pentagonal, smooth-walled and brown. They often had a raised paracingulum and an excavated parasulcus containing reflected flagellar pores (Pl. 8.9, fig.6). Apparent pores in the cyst wall, especially around the paracingulum, have been observed occasionally using the S.E.M. (Pl. 8.9, fig.5). It is not clear whether these were artifacts of the preparation technique or if they are functional in any way. These cysts have been ascribed to various cyst genera but Harland (1982) considers they should reside in Quinquecuspis. The archeopyle of this cyst has previously been considered to represent the loss of the 2a paraplate. Evitt (1967) considered it to be a fine example of an enlarged 2a archeopyle. Some doubt was expressed by Harland (1977) who postulated the involvement of the third apical paraplate. Pl. 8.9, figs.4-5 clearly show the archeopyle is not

PLATE 8.10

All figures are S.E.M.s

Fig. 1 : Dorsal view of thecate cell of Protoperidinium leonis hatched from cyst shown in Pl. 8.9, fig.4, 59 µm across, Loch Melfort.

Fig. 2 : Detail of surface patterning of excysted Protoperidinium leonis theca, x 9,000.

Fig. 3 : Capitate spine of Protoperidinium pentagonum cyst (Trinovantedinium capitatum) as shown in Fig. 4, x 27,000.

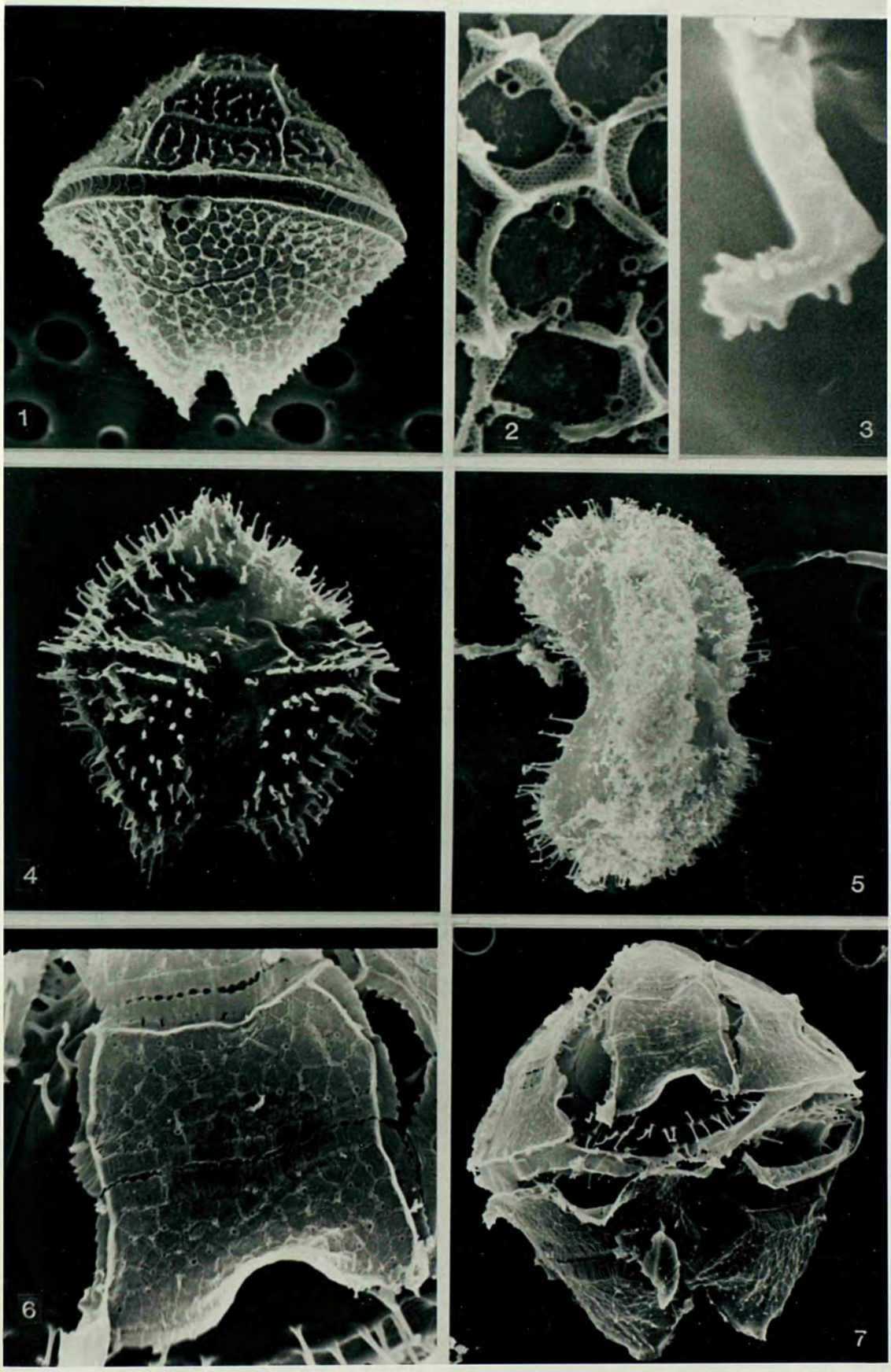
Fig. 4 : Ventral view of Protoperidinium pentagonum cyst (Trinovantedinium capitatum), 59 µm across (excluding spines), Loch Melfort.

Fig. 5 : Apical view of Protoperidinium pentagonum cyst (Trinovantedinium capitatum), 52 µm across (excluding spines), Loch Spelve.

Fig. 6 : Detail of archeopyle and associated thecal plates of Protoperidinium pentagonum cyst / theca shown in Fig. 7, x 2,550, Loch Creran water sample.

Fig. 7 : Dorsal view of theca of Protoperidinium pentagonum enclosing a cyst, 65 µm across, picked from a plankton sample taken in Loch Creran in early July.

Plate 8.10



simple in shape and seems to represent the loss of more than one paraplate. Its proximity to the paracingulum, and comparison with the thecate stage (Pl. 8.10, fig.1), suggests the additional loss of the fourth precingular (4") paraplate (for further discussion see under P.pentagonum).

Thecae

The theca was covered with a characteristic pattern of ridges and spines enclosing a "netted" pattern and pores (Pl. 8.10, fig.2). This is also seen in P. leonis thecae from the plankton (Dodge and Saunders, unpubl.). The hypotheca extended to two hollow horns with a solid spine on each. As noted by several authors (Wall and Dale, 1968a and Harland, 1982) there is much variation in this cyst type and a species complex may exist. However, only one theca has been germinated and positively identified so far.

Protoperididinium pentagonum (Gran) Balech

Pl. 8.10, figs.3-7; Pl. 8.11, figs.1-2

Size:- thecae 70µm long 60µm wide
cysts 65µm long 60µm wide

Cysts

The cysts were colourless, pentagonal and ornamented with capitate spines (Pl. 8.10, fig.3). The spines formed a paracingulum and delineated an indented parasulcus which frequently contained reflected flagellar pores (Pl. 8.10 fig.4). In apical view the cysts often reflected the unusual 'banana' shaped profile of the thecate stage (Pl. 8.10, fig.5). They are of the type Trinovantedinium capitatum Reid. The archeopyle was hexagonal and although it is usually described as intercalary,

PLATE 8.11

All figures are S.E.M.s

Fig. 1 : Antapical / ventral view of excysted thecate cell of Protoperidinium pentagonum, 58 µm across, (same cell as shown in Fig. 2).

Fig. 2 : Antapical view of excysted thecate cell of Protoperidinium pentagonum, 58 µm across, (same cell as shown in Fig. 1).

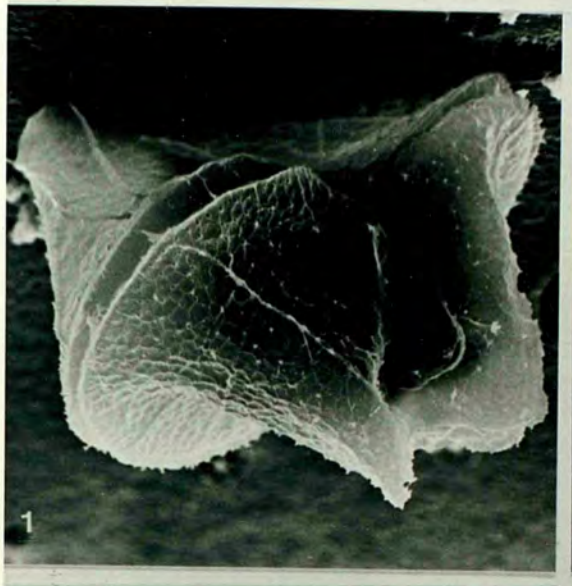
Fig. 3 : Apical view of excysted thecate cell of Protoperidinium subinerme, 55 µm across, Loch Melfort, (same cell as shown in Figs. 4 & 6).

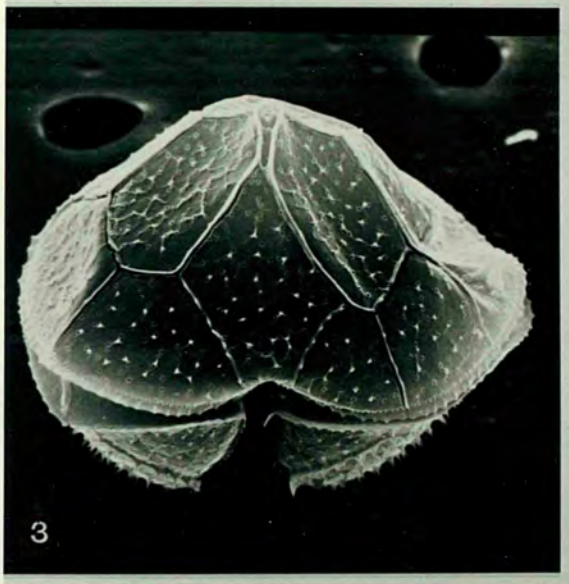
Fig. 4 : Detail of right hypothecal lobe of cell shown in Fig. 3, x 5,347.

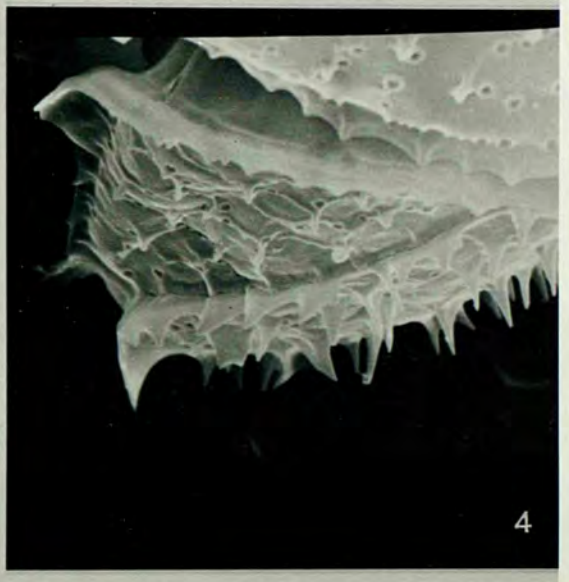
Fig. 5 : Ventral view of Protoperidinium punctulatum, 61 µm across, Kerbihan beach, courtesy of R. Saunders.

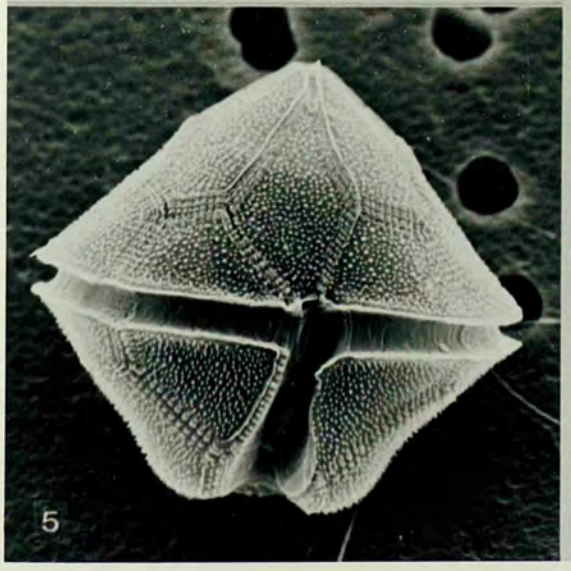
Fig. 6 : Apical view of excysted thecate cell of Protoperidinium subinerme, 55 µm across, Loch Melfort, (same cell as shown in Figs. 3 & 4).

Plate 8.11









S.E.M.'s of a specimen picked from the plankton with its theca attached showed clearly that the archeopyle represents the loss of the 2a and the 4" paraplates (Pl. 8.10, figs.6-7). The cyst was somewhat variable in form.

Thecae

Many thecae were hatched. Some resembled P.pentagonum but as Abé (1981) points out this is a little-studied species and can easily be confused with Peridinium bidentatum Abé, P.expansum, Abé and P.sinuosum (Lemmerman) Jørgensen. There were slight variations in this cyst type so it is felt that more than one species may have been involved, as implied by Wall and Dale (1968). P. pentagonum is characterised by a flattened antapex, slightly displaced girdle, a short sulcus and distinct ridges between apex and girdle. The cell is usually broader than tall with two solid antapical spines. It has a distinct concave ventral region (Pl. 8.11, figs.1-2). Some of the thecae germinated in this study did not, and the cell in Pl. 8.10, fig.7 does not, appear to be P.pentagonum. More critical work is required to elucidate this situation.

Protoperidinium subinerme (Paulsen) Loeblich III

Fig. 8.5, d-e; Pl. 8.11, figs.3-6

Size:- theca 55µm across
cyst 50µm across

Cysts

The cysts were smooth, spherical and dark brown. They had a fairly large hexagonal operculum which remained attached to the long side of the archeopyle (Fig. 8.5, e) and appeared to be most closely related to the 2a paraplate (Fig. 8.5, d). They were

quite unlike the cyst already described for P.subinerme by Wall and Dale (1968a) (Selenopemphix nephroides Benedek) which has not been found in Scottish sea-loch sediments in this study. It was not mentioned by Reid in his survey of U.K. sediments and did not appear to occur around the British Isles in Harland's survey of North Atlantic dinoflagellates (Harland, 1983) although P.subinerme is relatively common around the British Isles (Dodge, 1981). Unfortunately no comparative work has been possible. Perhaps there is more than one variety of P.subinerme or a species complex with more than one cyst type involved.

Thecae

One theca was germinated and was initially thought, after light microscopy, to be Protoperidinium punctulatum. Examination by S.E.M., however, showed the theca to be P.subinerme. The two species are very similar, but P.subinerme has a distinctly spiny surface and there are spines at the base of the sulcus (Pl. 8.11, figs.3-4) unlike P.punctulatum which has small rounded protrusions all over the surface of the theca (Dodge and Saunders, unpubl., Pl.11, fig.5). The plate patterns in P.subinerme are quite variable, and in this case the 2a plate was "hexa" (Pl. 8.11, fig.6).

Family : Gonyaulacacae Lindemann

Genus : Gonyaulax Deising

Gonyaulax polyedra Stein

Pl. 8.12, figs.1-5

Size:- theca ~47µm long 44µm across

cyst ~46µm across spines 1-12µm long (occasionally more)

PLATE 8.12

All figures are S.E.M.s

Fig. 1 : Lingulodinium machaerophorum (cyst of Gonyaulax polyedra), 37 µm across (excluding spines), Loch Creran.

Fig. 2 : Detail of spine of Lingulodinium machaerophorum (cyst of Gonyaulax polyedra), showing spine structure and surface detail, x 4,350, Loch Creran.

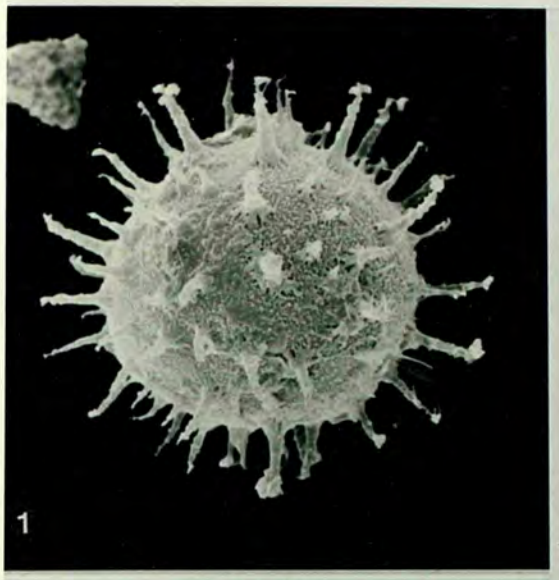
Fig. 3 : Lingulodinium machaerophorum (cyst of Gonyaulax polyedra), showing archeopyle, approximately 41 µm across (excluding spines), Loch Creran sediment.

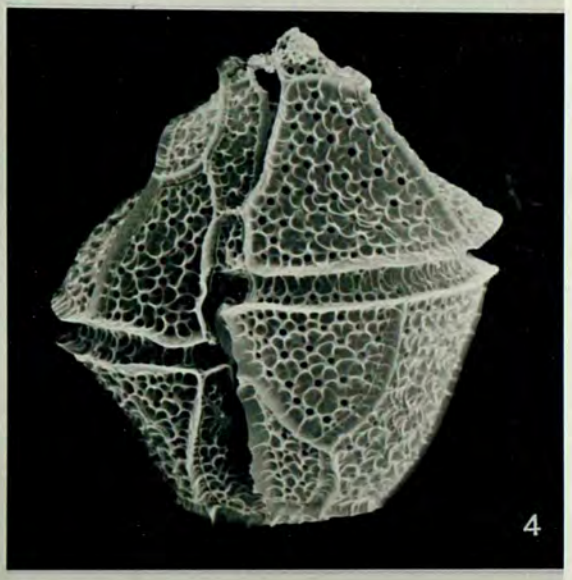
Fig. 4 : Ventral view of excysted thecate cell of Gonyaulax polyedra, 47 µm long, Loch Creran.

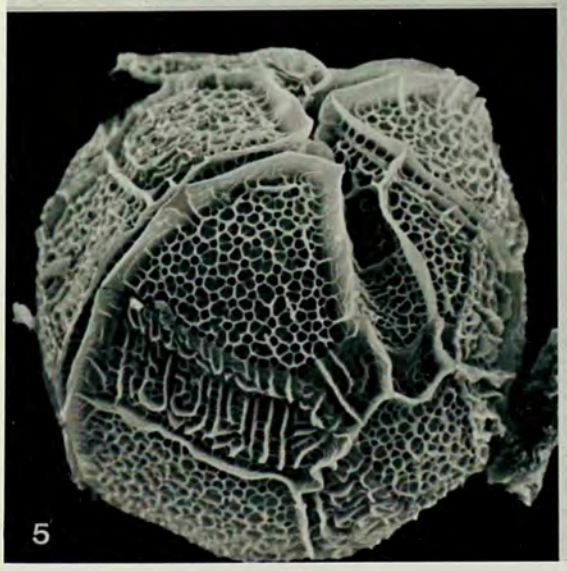
Fig. 5 : Antapical view of excysted thecate cell of Gonyaulax polyedra, showing 'rounding-off' of the cell, approximately 53 µm across, Loch Creran.

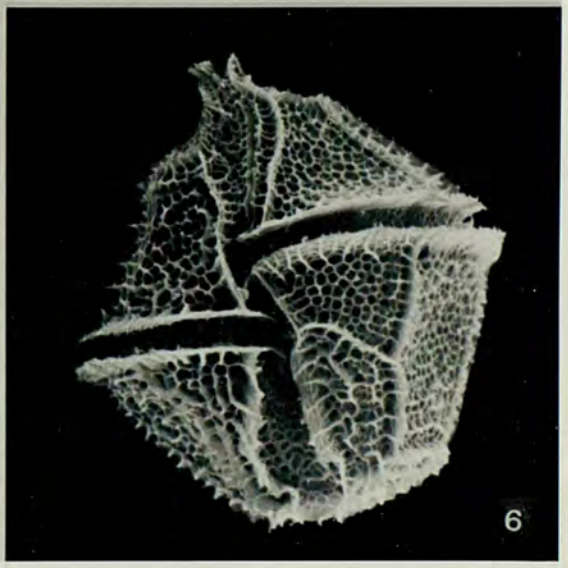
Fig. 6 : Ventral view of thecate cell of Gonyaulax polyedra from the plankton, 50 µm long, Loch Creran.

Plate 8.12









Cysts

The cysts were easily recognised in the sediments because they contain a prominent red body. They were spherical with a microgranular surface bearing numerous spines (Pl. 8.12, figs.1-2), which were variable in length (see Chapter 5). The archeopyle of this cyst was also very variable and was difficult to discern in the incubation experiments as the opercular pieces remained attached. It is described as relating to the loss of between one and five paraplates (Wall and Dale, 1968a) (Pl. 8.12, fig.3). In these incubation experiments between one and three paraplates appeared to be lost. The palynological name for this cyst is Lingulodinium machaerophorum (Deflandre & Cookson) Wall. Several other similar species have been described (for example Morzadec-Kerfourn, 1966) but these are probably all one species (Reid, 1974).

Thecae

Numerous thecae were hatched. They give rise to angular cells with distinct ridges along the plate sutures. The girdle was slightly displaced (1-2 girdle widths) (Pl. 8.12, fig.4). The hatched cells contained the red body present in the cyst. When left after hatching cells tended to gradually round off (Pl. 8.12 fig.5) and after 5 days they would often shed their thecae and form spherical temporary resting stages. Occasionally the hatched cells would divide in the incubation chamber. Cells were hatched from cysts with many different spine lengths but the thecae all appeared morphologically similar under the light microscope. There has been some work to suggest that spine length may be related to salinity or some other environmental variable (Wall, 1967). Further work involving the establishment of clonal cultures from the hatching of certain cysts could be carried out to see whether there were varieties of this species adapted to different environmental conditions.

DISCUSSION

The scanning micrographs of excysted thecate motile stages show them to be identical with their counterparts in the plankton (for example Gonyaulax polyedra Pl. 8.12, figs.4-5). The S.E.M. has proved an invaluable tool in this work allowing detailed examination of the few specimens usually available of each species. The pictures thus obtained show plate patterns clearly.

When there is little or no paratabulation on the cysts it is only possible to speculate on the relationship of the archeopyle to specific paraplates. Clues provided by the examination of the Protoperidinium pentagonum cyst with its parental thecate stage present suggest that what has been regarded as a simple archeopyle may involve the loss of two paraplates. S.E.M.'s of Protoperidinium leonis cysts suggest similarly that more than one paraplate is involved (Pl. 8.9, figs.4-5). It is felt that in both cases the 2a and the 4" paraplates are responsible.

Round brown cysts have long been a taxonomic problem. Ten Protoperidinium species have now been described as having such cysts. Before incubation or chemical treatment these cysts are indistinguishable and could also be confused with Diplopsalis cysts. After germination there is still confusion as many of the thecate stages have similar intercalary plates and hence similar archeopyles - for example the archaeperidiniums P.avellana, P.denticulatum and P.thorianum. During the present study observations of empty recent brown spherical cysts from the sediments show that damage can cause them to have more than one opening in the cyst wall. Specimens are also indistinguishable if they are crushed or not in a favourable orientation. It is possible that they may be distinguished by size but further critical research is needed to confirm this. They may, however,

need to be separated only if the species concerned are ecologically different. Most of the species germinated in this study have been obtained from one sea-loch so they all survived in approximately the same environmental conditions.

The taxonomic problems are not only confined to dinoflagellate cysts. Identification of motile thecate stages can also cause many problems. Frequently this is because of the poor descriptions in the literature based on light microscope observations. For many species the plate patterns have been inadequately described. In addition there is evidence of plate variations within species. This is particularly noticable in the 2a plate. Where thecae are similar apart from these minor variations, and derive from the same distinctive cyst type they should clearly ascribe to the same species.

Differences in cyst types may also help to resolve some of the problems associated with 'species complexes', such as those of Protoperidinium pentagonum and Protoperidinium oblongum. Here the more easily distinguished cysts may improve the understanding of the thecate taxonomy. This has already proved to be the case for the small orthoperidinioid dinoflagellates. Here small differences in the thecate tabulation are reflected in major differences in cyst types (Dale, 1977b & 1978). This may also prove to be the case with the Gonyaulax spinifera group of species. Five very different cyst types (9 cyst species) all produce thecate stages attributable to this group (Dale, 1983). Detailed S.E.M. study of the gonyaulacoids (Dodge and Saunders, unpubl.) shows that there may be several species involved in the G. spinifera group and work including cyst incubation studies could show there is a case for 'species splitting'. A taxonomy that combines the results of cyst and thecate studies and thus encompasses the whole of the dinoflagellate life-cycle is likely to be more 'natural' and hence more relevant to ecology. It must be remembered, however, that to the phytoplankton ecologist, to

whom only the thecate stage is available in water samples, the 'species complex' is a useful concept. Perhaps taxonomists who need to classify organisms to species level for the purposes of phylogeny should bear this in mind and at the same time note groups of closely related species as 'species complexes'. Many thecate stages are difficult to distinguish by light microscopy and further splitting just leads to more errors in identification or even an unwillingness to try. Terms such as "Gonyaulax spinifera group" or "Protoperidinium oblongum group" may give sufficiently detailed information for the ecologist and are a considerable improvement on Gonyaulax sp., Protoperidinium sp. or even dinoflagellate sp. As more evidence comes to light about the sexual cycles of dinoflagellates these 'species complexes' may turn out to have a natural source.

Nomenclature within the Dinophyceae as a whole remains a difficulty. The dual classification system is particularly cumbersome and sometimes leads to confusion. As the taxonomy of the group is refined with life-cycle observations so a single system of nomenclature should evolve. Harland (1982) for example showed that cyst and thecate nomenclature within the genus Protoperidinium is compatible. The cyst-theca relations described in this study fit into his scheme:- e.g. Protoperidinium (Archaeperidinium section Fucusphaeridinium) thorianum and Protoperidinium (Protoperidinium sect. Asymmetropedinium) hangoei. However, there is possible confusion over P.subinerme. As it is described in this paper it fits best with sub-genus Protoperidinium sect. Brigantedinium, along with P.conicoides. It will be noted that their thecal morphologies are very similar. However, the cyst described for P.subinerme by Wall and Dale (1968a) has been assigned to sub-genus Protoperidinium sect. Selenopemphix. Harland referred to Xandarodinium xanthum in the 1982 paper but because of insufficient evidence was unable to place it in his scheme. Now with the work of Matsuoka et al. (1982) and the present observations it seems possible that

X.xanthum should be placed in the Selenopemphix section of Harland's scheme or more likely in a new section of its own. Protoperidinium thulesense with its slit archeopyle and quadra 2a plate would need a new section in order to fit into this scheme.

Dale (1983) notes that in temperate environments many dinoflagellates spend more time as benthic resting cysts than as motile plankton. Not all marine dinoflagellates appear to produce resting cysts. The ability seems to be concentrated in the Peridiniales and Gonyaulacales. Certain naked species also have resting cysts (Gymnodinium, Wall and Dale, 1968a; Polykrikos, Dale, 1976; Morey-Gaines & Ruse, 1980; Gyrodinium, Dale, 1983). Work by von Stosch (1972) comparing the sexual cycles of Ceratium cornutum (freshwater) and C. horridum (marine) showed that the freshwater species formed a resting cyst whilst the marine species formed only a temporary cyst. Despite searches for them no cysts have been found for the Prorocentrales, Dinophysales or the marine ceratia. Although Steidinger (1983) believes that certain toxic benthic Prorocentrum species may have such cysts. So what is the function of cysts in the dinoflagellate life cycle? What 'survival strategy' do they represent?

Dale (1983) suggests four possible functions: their role in the sexual cycle; protection during the parts of the year unsuitable for the thecate motile stage; propagation of species in extending climatic ranges which they can tolerate and dispersion or transport allowing invasion of new areas. To this list should be added maintenance of populations in areas where they have invaded. In the sea-lochs, for example, thecate stages would be washed out each year and would have to rely on hydrographic good fortune to re-establish themselves each year in a particular loch. Rapid sinking of cysts could cause them to be retained within a loch giving them an opportunity to re-colonise

the loch annually if conditions are suitable. It would seem as discussed in Chapter 4 that both stategies are employed by the dinoflagellates. The former by such species as Ceratium furca and the latter by such species as Gonyaulax polyedra.

As pointed out by Dale (1983) the survival strategy should be considered as a 'life strategy' combining both thecate and resting stages. It seems likely that there is more than one stategy being employed by the cyst- forming dinoflagellates. The difference between the rare Protoperidinium species and the bloom forming Gonyaulax and Scrippsiella species is quite marked. The Protoperidinium strategy includes heterotrophy, limited numbers and cyst formation whereas the photosynthetic gonyaulacoids have a tendency to dominate the phytoplankton population and produce large numbers of cysts. Perhaps the Protoperidinium species with their few cysts rely on good viability whereas the gonyaulacoids require only a small proportion of a large number of cysts germinating for their yearly maintenance. Further clues to this puzzle might be obtained by research into the contents of both types of cysts and their viability.

CHAPTER 9

SUMMARY AND CONCLUSIONS

The ecology and taxonomy of dinoflagellates was investigated in 1982 and 1983 in sea-lochs and coastal waters of north-western Scotland, in order to provide a better understanding of conditions leading to blooms harmful to mariculture. Because such blooms are rare the ecology of all common thecate dinoflagellates was studied, particular attention being paid to the cyst stage and its role in bloom initiation. Sampling was carried out on both a seasonal and distributional basis. As well as collecting water samples, temperature, salinity and chlorophyll concentrations were routinely determined. Sediment samples were taken using a Craib corer. When required the taxonomy of the thecate dinoflagellates was investigated using the scanning electron microscope.

Regular sampling for motile dinoflagellates was carried out from April 1982 to October 1983 in Creran, a small fjordic sea-loch on the Scottish west coast near Oban. The first peak of dinoflagellate numbers occurred in May or June as sea temperatures increased. At this time Scrippsiella spp. were the most common dinoflagellates, accompanied in 1983 by Gonyaulax tamarensis. During July and August there was a mixed population of dinoflagellates, including Scrippsiella spp., Heterocapsa triquetra, Protoperidinium spp. and Diplopsalis spp. Numbers of Scrippsiella declined sharply at the end of August possibly due to increased flushing of the surface layers by the autumnal increase in river flow. The decrease in mean salinity and increase in salinity stratification preceded an autumn succession of Gonyaulax polyedra, Prorocentrum micans and Ceratium species.

Possibly because it is itself a small fjord (a partially mixed estuary with a restricted entrance) the seasonal cycle observed in Loch Creran was more similar to those in Norwegian

fjords than to cycles in other British waters. It was hypothesized that there were three main patterns of seasonal distribution in Creran, each stemming from a different life strategy:

1. Species present in the loch as motile cells all year round although sometimes only in concentrations of a few cells per litre (for example Dinophysis acuminata and Prorocentrum micans).

2. Species present in the loch all year, found in the water column during the summer and overwintering as cysts in the sediment (for example Scrippsiella spp. and Gonyaulax polyedra).

3. Species which are brought into the loch as its contents exchange with the Firth of Lorne (for example Protoperidinium depressum and Ceratium furca).

Regular sampling for dinoflagellate cysts in the sediment of Creran was carried out during 1983. Of the many forms present Lingulodinium machaerophorum (Gonyaulax polyedra) formed an average 67% of cysts passing a 64μm but retained by a 38μm sieve, and its seasonal cycle was therefore chosen for detailed analysis. On average about 50% of its cysts were empty. At the end of June a slight increase in the percentage of empty cysts in the sediment was accompanied by the appearance of a few motile cells in the water column. Cyst formation of Gonyaulax polyedra was noted in water column samples after a period of exponential growth of the motile cells in both 1982 and 1983. This was accompanied by a marked decrease in the percentage of empty cysts in the surface sediments. In 1983 cysts were observed to be present throughout the water column with peak abundances below the halocline. Cysts appeared to sink rapidly, which may help in their retention within the loch. Calculations suggest that 20

cysts cm^{-2} (that is 2.8% of the encysted population) were required to 'seed' the bloom observed in 1983. This 'seed bed' seems likely to ensure that Gonyaulax polyedra will remain an important component of the Creran phytoplankton.

The distribution of motile dinoflagellates and their cysts on the west coast of Scotland was investigated on cruises of R.V. Calanus in 1982 and 1983. 72 species of motile thecate dinoflagellates were found. The most common species were in rough order of abundance, Scrippsiella spp., Heterocapsa triquetra, Prorocentrum micans, Protoperidinium bipes, Gonyaulax spinifera, Dinophysis acuminata and Ceratium lineatum. The greatest numbers and variety of species were found in water columns of intermediate and strong stratification. Of potentially toxic species Gonyaulax tamarensis was found to be widespread between the entrance to the Sound of Jura and Loch Sunart in 1983.

Cysts also varied in their distribution, with higher numbers found in sea-lochs (373 - 15,431 per g dry weight sediment) than in the more open Firths and Sounds (89 - 2,694 per g dry weight sediment). Scrippsiella cysts were widely distributed, but there was some variation in the species composition of the cyst assemblage: there was for example a group of lochs (including Creran and West Loch Tarbert) where the 38 - 64μm cyst assemblage was dominated by Lingulodinium machaerophorum (Gonyaulax polyedra). Considerable populations of cysts were found down to 10 cm below the sediment surface and viable cysts were found at 5cm. Comparison of water column and sediment data showed that a considerable portion of the motile dinoflagellate population (including species of Prorocentrum, Dinophysis and Ceratium) was not represented in the sediments whereas other species (for example Gonyaulax polyedra) were over-represented. Interestingly,

some species were present as cysts but were not observed in the plankton. Further work on the relationship between the cyst population and the motile dinoflagellate population is suggested, such work should include studies on the viability and longevity of cysts.

Work in the laboratory on the hatching of dinoflagellate cysts using the scanning electron microscope to elucidate details of thecate taxonomy led to the discovery of some new cyst - theca relationships for example, Protoperidinium subinerme and Protoperidinium thorianum. Such work has great value in further clarifying the taxonomy of the dinoflagellates and is discussed in this context.

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R.H.B.N.C.

ABBREVIATIONS

General

H.I.D.B. Highlands and Islands Development Board

M.A.F.F. Ministry of Agriculture Fisheries and Food

S.E.M. Scanning Electron Microscope

S.M.B.A. Scottish Marine Biological Association

Statistical

c.v. Coefficient of variation

df Degrees of freedom

s.d. Standard deviation

s.e. Standard error

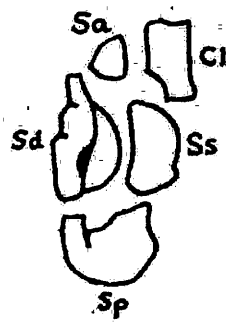
var. variance

EXPLANATION OF TERMS

'meta' : A term referring to a five-sided first apical plate in Protoperidinium and related genera (see for example Pl. 3.2 fig.1).

Trichocyst pore : Small round opening in the theca of armoured dinoflagellates allowing the ejection of sticky threads (trichocysts).

Sp : One of the small sulcal plates of thecate dinoflagellates - see diagram below (after Dale, 1977b).



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Cyst-theca relationships in some *Protoperidinium* species (Peridiniales) from Scottish sea lochs

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ABSTRACT–Recent dinoflagellate cysts were collected from Scottish west coast sealoch sediments and germinated to establish cyst-theca relationships. Fourteen different *Protoperidinium* species have been germinated and studied using the scanning electron microscope. New cyst-theca relationships are described for *Protoperidinium subinerme, P. thorianum* and ?*P. hangoei*.

The archeopyle of the *P. excentricum* cyst is described for the first time. The archeopyles of the cysts of *P. pentagonum (Trinovantedinium capitatum)* and *P. leonis (Quinquecuspis concretum)* have previously been described as representing the loss of the second intercalary paraplate, but are here considered to represent the loss of this paraplate and also the fourth precingular paraplate.

INTRODUCTION

Dinoflagellates have long been known to form cysts. The phenomenon was described as early as 1908 by Paulsen and received occasional mention in the phycological literature during the first half of the twentieth century. Detailed investigation was, however, not carried out until the 1960s with the pioneering work of Evitt & Davidson (1964) and Wall & Dale (1968). Since then, most of the work on modern marine dinoflagellate cysts and their thecate stages has been concentrated on the bloom-forming *Gonyaulax* species (e.g. Anderson & Morel 1979).

Reid (1974, 1977), described the distribution of some modern dinoflagellate cysts around the British Isles as found in surface scrapes of intertidal sediments. A recent review by Dale (1983) in indicating some applications of cyst research to living dinoflagellate studies, pointed to the usefulness of the integrated nature of a sediment sample. As part of a study of the ecology and taxonomy of marine planktonic dinoflagellates in Scottish west coast sea lochs, the dinoflagellate cysts present in the sediments of the lochs were investigated. Many of the cysts were successfully germinated and have given new information on the relationships between cysts and the planktonic stages.

METHODS

Sediments were collected from Lochs Creran and Melfort (Fig. 1) in April. Sediment sampling was carried out using a Craib corer (Craib, 1965) which gives relatively undisturbed cores of sediment and overlying water. The overlying water and the top 5 cm of sediment were taken and stored at 4°C for later study.

For germination of cysts, a small amount of sediment (0.5–0.75 g) was "sonicated" gently in seawater then passed through 63 μm mesh and retained on 38 μm mesh sieves. The material collected on the 38 μm sieve was then washed off into a small amount of culture medium to be used for the incubation experiment and then poured into a gridded petri dish. It was examined under a light microscope and individual cysts picked out using a micropipette and placed in small incubation chambers (Wall & Dale, 1968) or 5 cm watch glasses enclosed in petri dishes. The medium used for incubation was F/50 (Guillard & Ryther, 1962). The cysts were kept at 20°C and if they had not germinated within 5 days the experiment was abandoned.

After excystment, cyst and hatched cell were observed and photographed under the light microscope and then preserved in formalin in small containers for Scanning Electron Microscopy (S.E.M.). For S.E.M., the cyst and cell pairs were again individually picked out and mounted on Nuclepore filters. These were dehydrated in an acetone sequence and dried in a critical point drier using carbon dioxide. After splutter coating with gold-palladium, cysts and germinated cells were examined in a JEOL 25S S.E.M.

RESULTS

The *Protoperidinium* species listed in Table 1 have been successfully incubated. Many of these (shown by * in Table 1) repeat the discoveries of Wall & Dale (1968). The cysts incubated of *P. minutum* and *P. divaricatum* confirm the findings of Fukuyo *et al.*, 1977 and Matsuoka *et al.*, 1983.

In many cases, the cyst germinated but the naked

protoplast did not properly form its thecal plates. It seemed that the type of seawater used was important in this respect and it was found that seawater from Dunstaffnage Bay near Oban was the most suitable for germination. All the thecae hatched contained numerous small bodies which were probably storage products. In most cases, the operculum remained attached to the archeopyle of the cyst and this point of attachment is shown by broken lines around the archeopyle in Fig. 2. It is not known if the point of attachment is a consistent feature but in the cysts germinated in this study, it appeared to be. In the wild, this attachment probably does not last long and the operculum is lost or falls inside the cyst (Pl. 2, fig. 3).

DESCRIPTIONS OF SPECIES THAT ARE OF SPECIAL INTEREST

Protoperidinium avellana (Meunier) Balech
(Pl. 1, figs. 1, 2; Fig. 2 a, b)

Dimensions. Theca: 50–55 μm long, 45–50 μm wide; cyst: 50–55 μm across.

Cysts. The cysts are spherical, smooth-walled and dark brown. They have a distinct curved hexagonal archeopyle. The operculum remains attached at the short side of the archeopyle and is related to the second intercalary (2A) paraplate (Fig. 2, a, b). This cyst is known under the name *Brigantedinium cariacoense* (Wall) Reid.

Thecae. Seven of these delicate thecae were germinated. The rounded cells have little thecal ornamentation (Pl. 1, fig. 2.). The girdle is left handed, excavated and striated (Pl. 1, fig. 1.).

Protoperidinium conicoides (Paulsen) Balech
(Pl. 1, fig. 5; Fig. 2 e, f)

Dimensions. Thecae: 54 μm long 54 μm wide; cysts: 50 μm across.

Cysts. The cysts are smooth-walled, dark brown and almost spherical. All the cysts germinated of this type had a domed apex and some also had an indented parasulcus with reflected flagellar pores. The archeopyle is six sided and appears to reflect the 2A plate (Fig. 2. e, f). This cyst was described by Reid (1977) as *Brigantedinium simplex* and used as his type species for *Brigantedinium*.

Thecae. Two recognisable thecae were germinated. These were rhombic in dorsoventral view and had a deeply excavated sulcus with a characteristic twist on the left below the girdle (Pl. 1, fig. 5.). Germination has not previously been achieved with this species although Wall & Dale (1968) established a link between this cyst type and *P. conicoides* by examining specimens from the plankton.

Protoperidinium excentricum (Paulsen) Balech
(Pl. 1, fig. 6; Fig. 2g, h)

Dimensions. Thecae: 30 μm long 59 μm wide; cysts: 50 μm across.

Cysts. The cysts are smooth-walled, pale brown and slightly dorsoventrally flattened. They have an indented parasulcus and are sometimes distinctive in the sediment due to being enclosed by the parental theca. Both of the cysts incubated in this study had old thecae present. The archeopyle is an indistinct zig-zag split (Fig. 2h) somewhat reminiscent of the ?*Protoperidinium* cyst

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Explanation of Plate 1

Fig. 1. Ventral view of excysted thecate cell of *P. avellana*; 50 μm across (Loch Melfort).

Fig. 2. Detail of surface patterning of *P. avellana*; cell shown in fig. 1 (×4140).

Fig. 3. Detail of surface patterning of theca of an excysted *P. thorianum* cell; ×4140 (Loch Melfort).

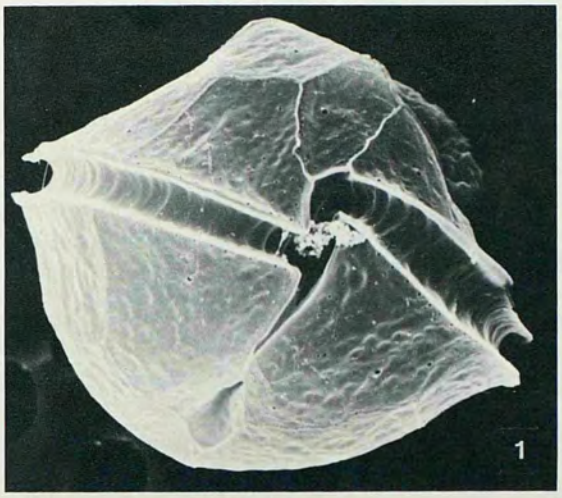
Fig. 4. Lateral view of excysted thecate cell of *P. thorianum*; 54 μm across (Loch Creran).

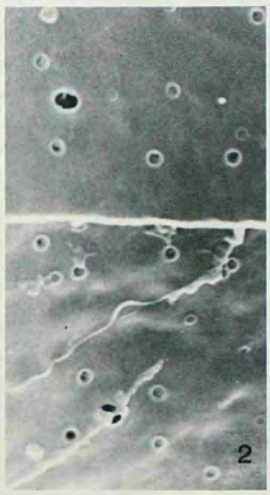
Fig. 5. Ventral view of excysted thecate cell of *P. conicoides*; 54 μm across (Loch Creran).

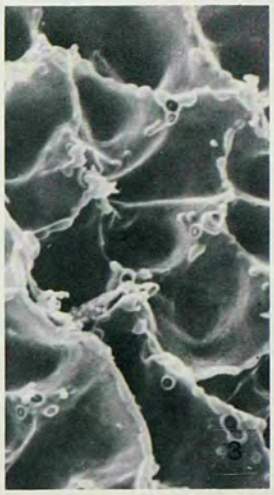
Fig. 6. Dorsal/lateral view of excysted thecate cell of *P. excentricum*; 59 μm across (Loch Melfort).

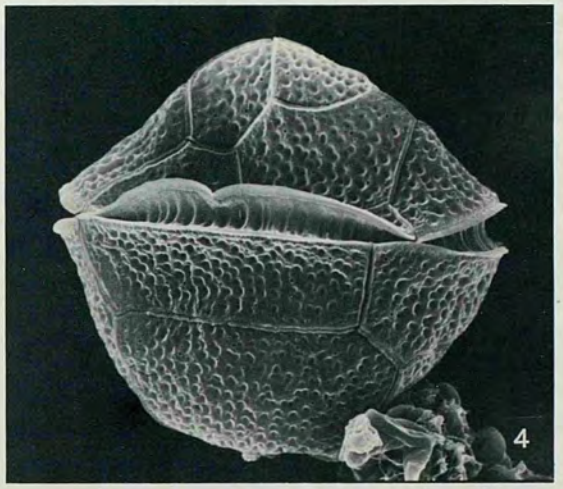
Fig. 7. Epithecal view of excysted thecate cell of ?*P. hangoei* showing five sided 2A plate; 35 μm across (Loch Melfort).

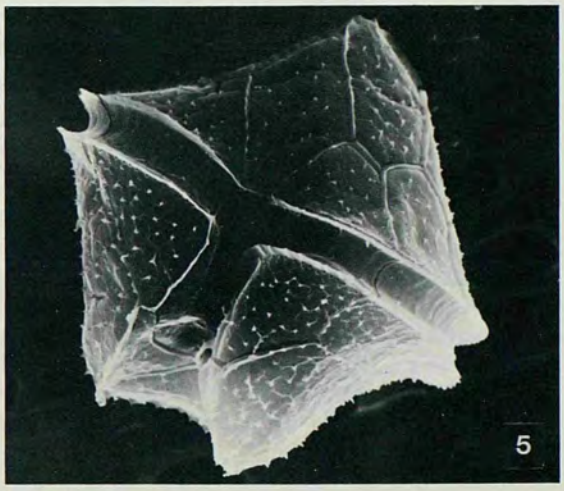
Some *Protoperidinium* species from Scottish sea lochs

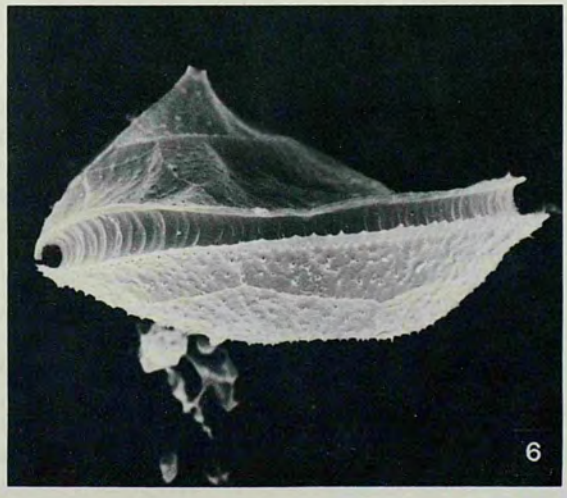












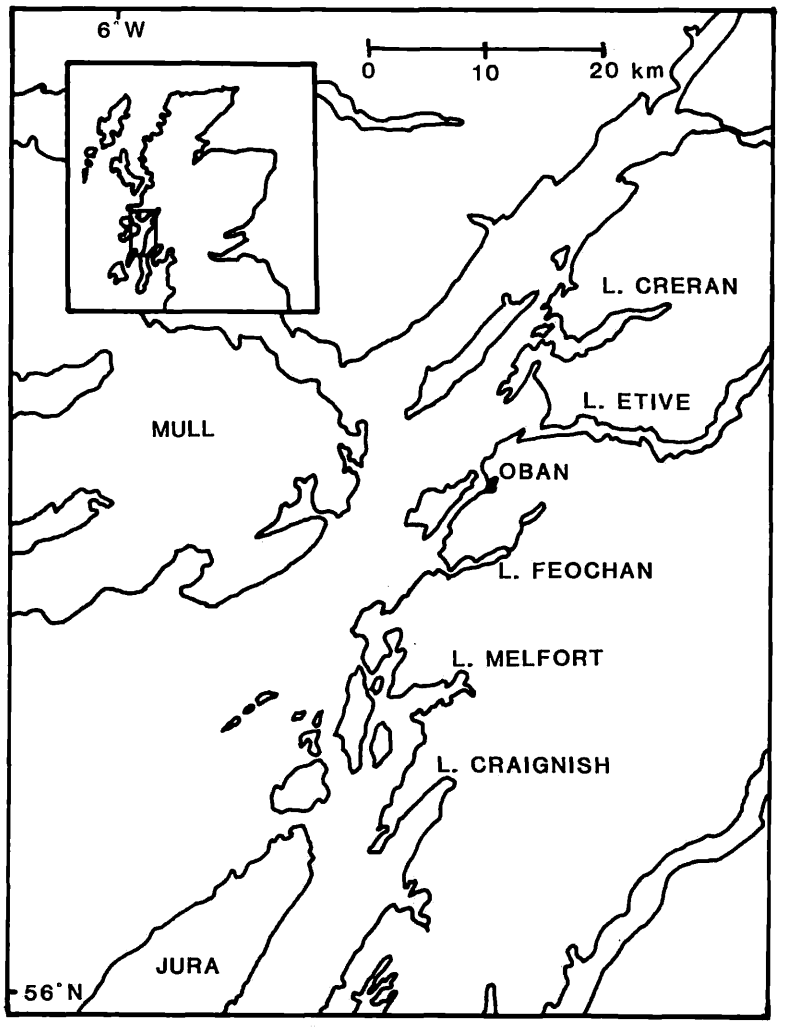


Fig. 1. Map showing location of Lochs sampled.

described by Harland (1982, Pl. 38, figs. 10–12.). It does not appear to be related to any paraplate boundaries (Fig. 2g). This cyst does not have a palynological description but is probably grouped with the other round, brown cysts of peridiniacean or glenodiniacean affinities.

Thecae. Two of the characteristically flattened thecae were germinated (Pl. 1, fig. 6.).

Protoperidinium ?hangoei (Schiller) comb. nov.
(Pl. 1, fig. 7; Fig. 2i, j)

Basionym: *Peridinium hangoei* Schiller 1937 p. 135 fig. 129, a-d

Dimensions. Thecae: 35 μm wide; cysts: 38 μm across.

Cysts. The cysts are smooth-walled, brown and spherical. The hexagonal operculum remains attached to one of the short sides of the archeopyle (Fig. 2j). This cyst type is so similar in appearance to those of *P. punctulatum* and various other round brown cysts that it has probably not been described as a separate cyst species.

Thecae. Two thecae were germinated. These were rounded with a slightly angular epitheca and an apical pore which extends into the third apical plate. The theca is distinguished by its three intercalary plates, the second of which is "penta" (Pl. 1, fig. 7.). The girdle is striated and excavated with small lists. The sulcus is bordered on one side by a small wing. The thecal affinity of this cell was difficult to decide. It has provisionally been ascribed to *P. hangoei* largely because of the plate patterning,

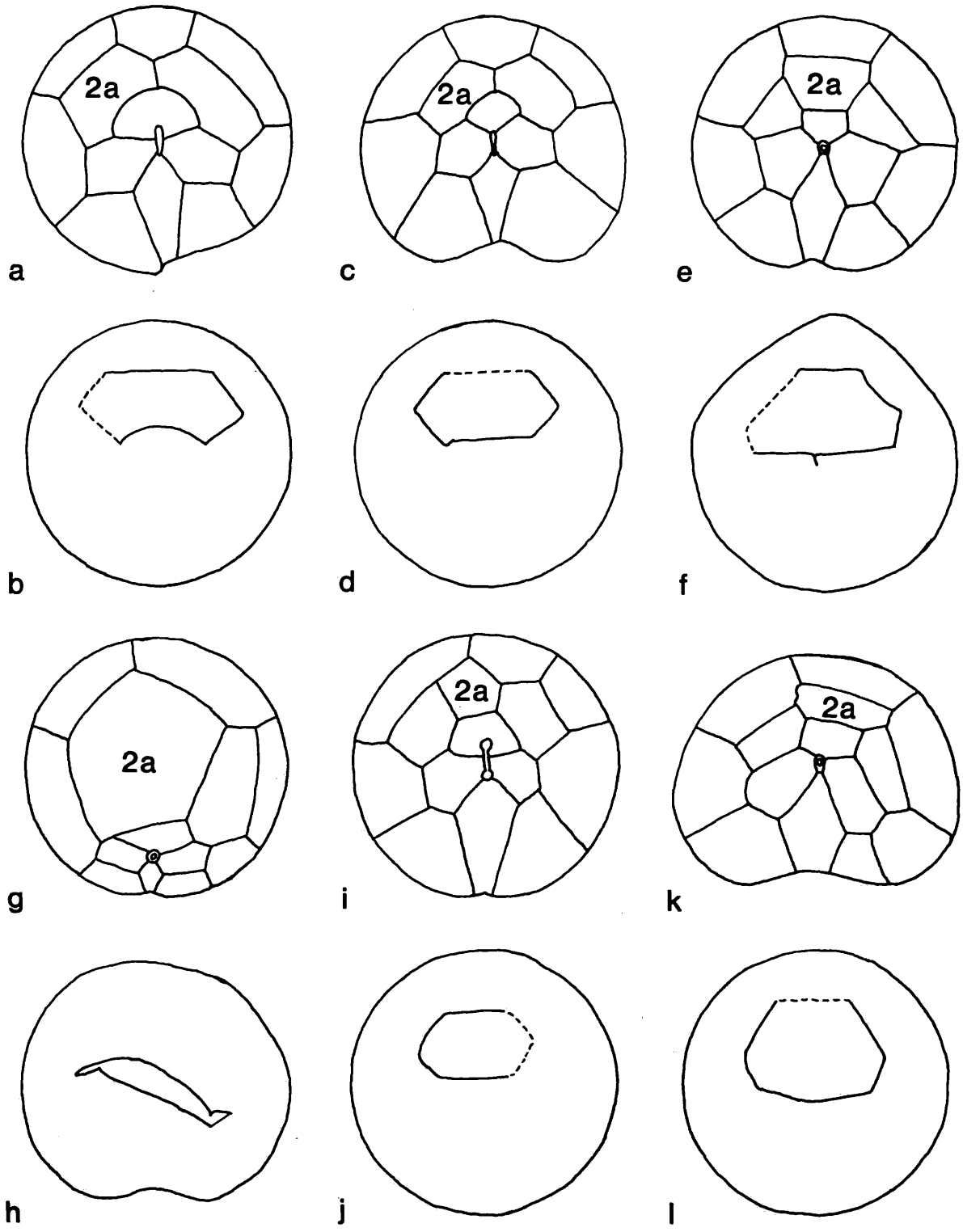


Fig. 2. Broken lines around the archeopyle denote point of attachment of operculum: a, Epithecal tabulation of *P. avellana*; b, Cyst of *P. avellana*; c, Epithecal tabulation of *P. thorianum*; d, Cyst of *P. thorianum*; e, Epithecal tabulation of *P. conicoides*; f, Cyst of *P. conicoides*; g, Epithecal tabulation of *P. excentricum*; h, Cyst of *P. excentricum*; i, Epithecal tabulation of *?P. hangoei*; j, Cyst of *?P. hangoei*; k, Epithecal tabulation of *P. subinerme*; l, Cyst of *P. subinerme*.

Table 1. *Protoperidinium* species germinated

Thecate stage	Palaeontological name for cyst
**Protoperidinium avellana* (Meunier) Balech	*Brigantedinium cariacoense* (Wall) Reid
**P. claudicans* (Paulsen) Balech	*Votadinium spinosum* Reid
**P. conicoides* (Paulsen) Balech	*Brigantedinium simplex* Reid
**P. conicum* (Gran) Balech	*Selenopemphix* sp. Benedek
**P. denticulatum* (Gran & Braarud) Balech	
P. divaricatum (Meunier) Parke & Dodge	*Xandarodinium xanthum* Reid
P. excentricum (Paulsen) Balech	
?*P. hangoei* (Schiller) comb. nov.	
**P. leonis* (Pavillard) Balech	*Quinquecuspis concretum* (Reid) Harland
P. minutum (Kofoid) Loeblich III	
**P. oblongum* (Aurivillius) Parke & Dodge	*Votadinium calvum* Reid
**P. pentagonum* (Gran) Balech	*Trinovantedinium capitatum* Reid
P. subinerme (Paulsen) Loeblich III	
P. thorianum (Paulsen) Balech	

albeit the original description was drawn in mirror image (Lindemann, 1924). There are, however, a number of differences. The scanning micrograph of the excysted motile stage (Pl. 1, fig. 7.) shows the theca to have some relief whereas previous descriptions of *P. hangoei* by light microscopy have shown it as smooth walled. *P. hangoei* is also drawn as being rounded but the epitheca of our specimens was slightly angular.

Protoperidinium leonis (Pavillard) Balech
(Pl. 2, figs. 3, 4, 6)

Dimensions. Thecae: 60 μm long, 60 μm wide; cysts: 65 μm long, 65 μm wide.

Cysts. The cysts are pentagonal, smooth-walled and brown. They have been described in various cyst genera but Harland (1982) considers they should reside in *Quinquecuspis*. The archeopyle of this cyst has previously been considered to represent the loss of the 2A paraplate. Evitt (1967) considered it to be a fine example of an enlarged 2A archeopyle. Some doubt was expressed by Harland (1977) who postulated the involvement of the third apical paraplate. Pl. 2, fig. 3. clearly shows that the archeopyle is not simple in shape and seems to represent the loss of more than one paraplate. Its proximity to the paracingulum, and comparison with the thecate stage (Pl. 2, fig. 6.), suggests the additional loss of the fourth precingular (4″) paraplate (for further discussion see under *P. pentagonum*).

Thecae. The theca is covered with a characteristic patterning of ridges and spines enclosing a "netted" pattern and pores (Pl. 2, fig. 4). This is also seen in *P. leonis* thecae from the plankton (Dodge & Saunders, unpubl.). The hypotheca extends to two hollow horns with a solid spine on each. As noted by several authors (Wall & Dale 1968; and Harland, 1982) there is much variation in this cyst type and a species complex may exist. However, only one theca has been germinated and positively identified so far.

Protoperidinium pentagonum (Gran) Balech
(Pl. 2, figs. 1, 2, 5)

Dimensions. Thecae: 70 μm long, 60 μm wide; cysts: 65 μm long, 60 μm wide.

Cysts. The cysts are colourless, pentagonal and ornamented with capitate spines (Pl. 2, fig. 5). They are of the type *Trinovantedinium capitatum* (Reid). The archeopyle is hexagonal and is usually described as intercalary, however, S.E.M. illustrations of a specimen picked from the plankton with its theca attached showed clearly that the archeopyle represents the loss of the 2A and the 4″ paraplates (Pl. 2, figs. 1, 2).

Thecae. Many thecae were hatched. Some of these resembled *P. pentagonum* but as Abé (1981) points out this is a little-studied species and can easily be confused with such species as *Peridinium bidentatum* Abé, *P. expansum* Abé and *P. sinuosum* (Lemmerman) Jorgensen. There were slight variations in this cyst type so it is felt that more than one species may be involved here, as implied by Wall & Dale (1968). Some of the thecae germinated in this study and the cell in Pl. 2, fig. 1 did not appear to be *P. pentagonum*. More critical work is required to elucidate this situation.

Protoperidinium subinerme (Paulsen) Loeblich III
(Pl. 2, fig. 7; Fig. 2k, l)

Dimensions. Thecae: 55 μm across; cyst: 50 μm across.

Cysts. The cysts are smooth, spherical and dark brown. They have a fairly large hexagonal operculum which remains attached to the long side of the archeopyle (Fig. 2l) and appears to be most closely related to the 2A paraplate (Fig. 2k). These are quite unlike the cyst already described for *P. subinerme* by Wall & Dale (1968) (*Selenopemphix nephroides* Benedek). This cyst type has not been found by us in Scottish sea loch sediments. It was not mentioned by Reid in his survey of U.K. sediments and did not appear to occur around the British Isles in Harland's survey of North Atlantic dinoflagellates (Harland, 1983) although *P. subinerme* is relatively common around the British Isles (Dodge, 1981). Unfortunately, no comparative work has been possible. Perhaps there is more than one variety of *P. subinerme* or a species complex with more than one cyst type involved.

Thecae. One theca was germinated and was initially thought, after light microscopy to be *P. punctulatum*. Examination by S.E.M., however, showed the theca to be *P. subinerme*. The two species are very similar but *P. subinerme* has a distinctly spiny surface and there are spines at the base of the sulcus (Pl. 2, fig. 7) unlike *P. punctulatum* which has small rounded protrusions all over the surface of the theca (Dodge and Saunders unpubl.). The plate patterns in *P. subinerme* are quite variable, and in this case the 2A plate was "hexa".

Protoperidinium thorianum (Paulsen) Balech
(Pl. 1, figs. 3, 4; Fig. 2c, d)

Dimensions. Thecae: 50–60 μm across; cysts: 50–55 μm across.

Cysts. The cysts are spherical, smooth-walled and dark brown. The operculum, although similar in shape to that of *P. avellana*; is not curved and is attached to the archeopyle along the long side (Fig. 2d). Again it is a round, brown cyst that has probably not been described separately. It is most similar to the cysts of *P. denticulatum*.

Thecae. Three thecae were germinated. They were very similar to *P. avellana*, having two intercalary plates and a left handed, striated, excavated girdle (Fig. 2c; Pl. 1, fig. 4.). They are characterised by their papillate thecal plate surface (Pl. 1, fig. 3).

DISCUSSION

The scanning micrographs of excysted thecate motile stages show them to be identical with their counterparts in the plankton. The S.E.M. has proved an invaluable tool in this work allowing detailed examination of the few specimens usually available of each species.

When there is little or no paratabulation on the cysts it is only possible to speculate on the relationship of the archeopyle to specific paraplates. Clues provided by the examination of the *P. pentagonum* cyst with its parental thecate stage present suggest that what has been regarded as a simple archeopyle may involve two paraplates. S.E.M. illustrations of *P. leonis* cysts suggest similarly that more than one paraplate is involved. It is felt that in both cases the 2A and the 4″ paraplates are responsible.

Round brown cysts have long been a taxonomic problem. Nine *Protoperidinium* species have now been described as having such cysts. Before incubation or chemical treatment these cysts are indistinguishable and could also be confused with *Diplopsalis* cysts. After

germination there is still confusion as many of the thecate stages have similar 2A plates and hence similar archeopyles – for example the archaeperidiniums *P. avellana, P. denticulatum* and *P.thorianum*. Observations of recent empty brown spherical cysts from the sediments show that damage can cause them to have more than one opening in the cyst wall. Specimens are also indistinguishable if they are crushed or not in a favourable orientation. It is possible that they may be distinguished by size but further critical research would be needed to confirm this. They may, however, need to be separated only if the species concerned are ecologically different. Most of the species germinated in this study have been obtained from one sea loch so they all survived in approximately the same environmental conditions.

The taxonomic problems are not only confined to cysts: plate variations in the motile thecate dinoflagellates can cause some taxonomic problems. The 2A plate often seems to vary. For example, in the Wall & Dale, 1968 paper *P. conicum* is described as having a quadrate or hexagonal 2A plate and is figured as being "hexa". Two thecae incubated in this study had a "quadra" 2A plate. As all the motile cells come from the same distinctive cyst type *(Selenopemphix)* they should clearly belong to the same species. Conversely, many different cysts give rise to the *Gonyaulax spinifera* group and here perhaps there is a case for further taxonomic splitting of the thecate stages.

Differences in cyst types may also help to resolve some of the problems associated with 'species complexes', such as those of *P. pentagonum* and *P. oblongum*. Here, the more easily distinguished cysts may improve the understanding of the thecate taxonomy. Nevertheless, 'species complex' may be a more useful concept to the ecologist.

Harland (1982) showed that cyst and thecate nomenclature within the genus *Protoperidinium* is compatible. The new cyst-theca relations described fit into his scheme:– e.g. *Protoperidinium* (*Archaeperidinium* section *Fucusphaeridinium*) *thorianum* and *Protoperidinium* (*Protoperidinium* section *Asymmetropedinium*) *hangoei*. However, there is possible confusion over *P. subinerme*. As it is described in this paper, it fits best with *Protoperidinium* (*Protoperidinium* section *Brigantedinium*), along with *P. conicoides*. It will be noted that their thecal morphologies are very similar. However, the cyst described for *P. subinerme* by Wall & Dale (1968) has been assigned to *Protoperidinium* (*Protoperidinium* section *Selenopemphix*). Harland referred to *Xandarodinium xanthum* in the 1982 paper but because of insufficient evidence was unable to place it in his scheme. Now, with the work of Matsuoka *et al.* (1983) and this paper, it seems possible that *X. xanthum* should be placed in the *Selenopemphix* section of Harland's scheme or more likely in a new secton of its own.

We are still far from obtaining a complete overall perspective of the relationship between *Protoperidinium* species and their cysts but it is clear that the taxonomy of the planktonic dinoflagellates should be studied with regard to both cyst and thecate stages to give a more natural classification.

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Explanation of Plate 2

Fig. 1. Dorsal view of theca of *P. pentagonum* enclosing a cyst which was picked from a plankton sample taken in L. Creran in early July; 65 μm across.

Fig. 2. Detail of the archeopyle and associated thecal plates of cyst/theca shown in fig. 1 (×2600).

Fig. 3. A germinated cyst of *P. leonis*, 63 μm across (Loch Melfort).

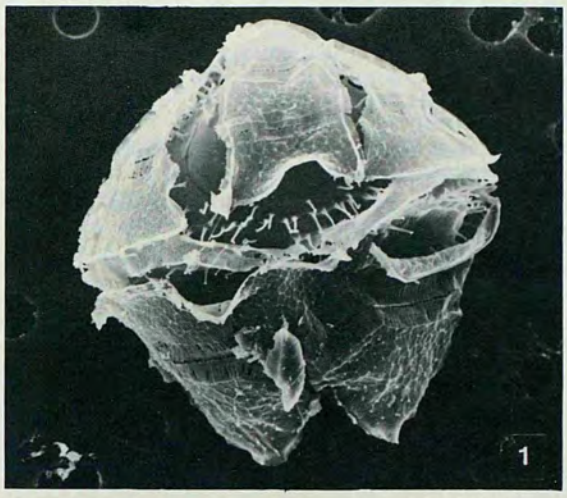
Fig. 4. Detail of surface patterning of excysted *P. leonis* theca (×9000).

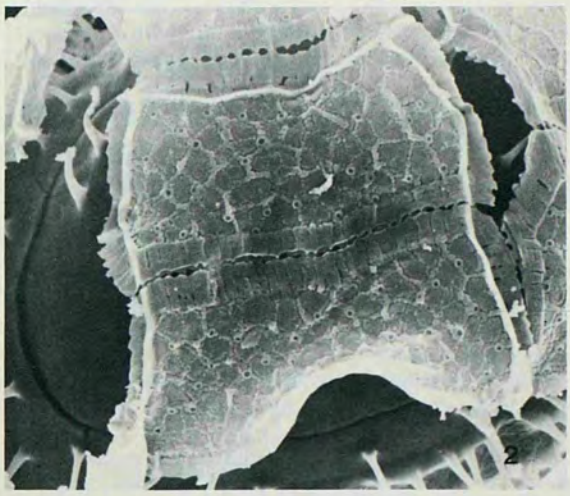
Fig. 5. Capitate spine of *P. pentagonum* cyst shown in fig. 1 (×26,000).

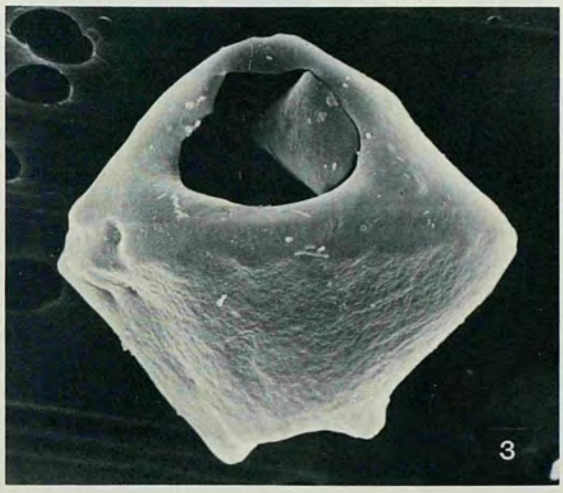
Fig. 6. Dorsal view of thecate cell of *P. leonis* germinated from cyst shown in fig. 3; 59 μm across.

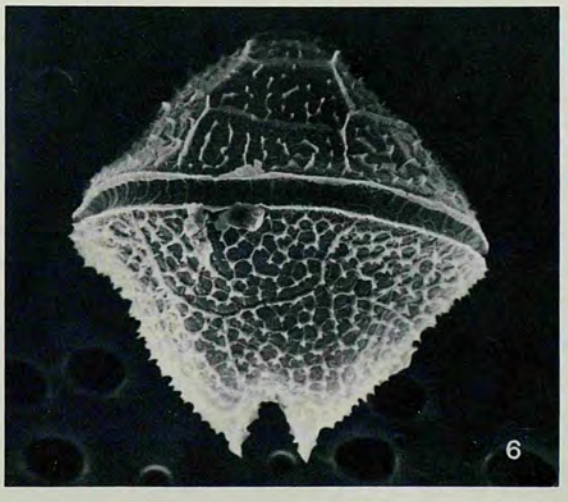
Fig. 7. Apical view of excysted thecate cell of *P. subinerme*; 55 μm across (Loch Melfort).

Some *Protoperidinium* species from Scottish sea lochs









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