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STUDIES ON THE NANOPHYTOPLANKTON OF THE FIRTH OF CLYDE

A thesis submitted to the University of Glasgow

for the degree of Doctor of Philosophy

in the Faculty of Science

by

FIONA JACKSON HANNAH

April, 1979

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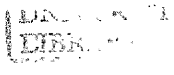

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DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise cited or acknowledged and that the thesis is of my own composition. The research was carried out within the period October 1975 - September 1978. This dissertation has not in whole or in any part been previously presented for any other degree.

Signed Fiona J. Hannah

FIONA J. HANNAH

DATE: 2nd April 1979

SUMMARY

The significance of the nanophytoplankton in the Firth of Clyde was assessed during the period January 1976 to May 1978 by estimating its contribution to the total chlorophyll and productivity of the area. Its significance both temporally and spatially were investigated.

The nanophytoplankton in the Firth of Clyde is made up predominantly of small flagellates of maximum cell dimension less than 10 μm, many being in the size range 2-5 μm. It includes organisms from most algal classes with the exception that the Diatomaceae is poorly represented. One to two cell chains of Skeletonema costatum are included in this group and also small single cells of a Chaetoceros spp. which were occasionally observed.

Weekly (followed by fortnightly) samples were collected from a midchannel station in the Fairlie Channel to assess the seasonal significance of the nanophytoplankton. Nutrient analyses, particle size distributions and microscopic examination of the samples were carried out as well as chlorophyll and productivity determinations. To assess how representative the chosen sampling station was of the Fairlie Channel as a whole, several grid surveys were carried out in which the chlorophyll levels from 16 stations covering an area of 0.75 km^2 were compared. Although on three out of six occasions significant differences were observed between stations, these being mainly found when inshore stations were compared with those in mid-channel, the main sampling station did not differ significantly from the other stations, and the results from this station reflected the seasonal changes which occurred in the Channel.

The seasonal patterns of the total phytoplankton and nutrients in the Fairlie Channel were similar to those observed in the past. In terms of total chlorophyll a and productivity, higher levels were recorded in 1976 than in 1977. The total chlorophyll a in 1976 reached values of above 10 mg m^{-3} during the spring diatom increase in April and also in July when the maximum fixation rate of 66.6 mg carbon $m^{-3}h^{-1}$ was recorded. In 1977 maximum values of chlorophyll (7.8 mg m^{-3}) and fixation (55.7 mg C $m^{-3}h^{-1}$) were observed during an autumnal bloom in September.

While the contribution of the netplankton (predominantly diatoms) was high during bloom conditions in spring and summer, over an annual cycle the nanophytoplankton in the upper 10 metres of the water column contributed at least 50% of the activity. During 1976 and 1977, the average % contribution of the nanophytoplankton to the productivity was 50% and its contribution to the chlorophyll was 60%. Figures of up to 100% contribution of the nanophytoplankton to the biomass and productivity have been recorded.

The nanophytoplankton formed a more stable component of the phytoplankton fluctuating in terms of chlorophyll and productivity less dramatically over the year than the netplankton. The relative importance of the two fractions of the phytoplankton showed a marked seasonality.

The nanophytoplankton was highly significant during late autumn, winter and early spring forming the major part of the biomass at these times. Following the spring diatom increase, the phytoplankton was made up almost exclusively of nanophytoplankton in 1976, while in 1977 it was of slightly less significance. During summer

the contribution of the nanophytoplankton to the biomass and productivity was approximately equal to that of the netplankton.

Sampling was extended to other areas of the Firth to assess the spatial distribution of the nanophytoplankton and its significance. In the Inner Firth Area, the observed contribution of the nanophytoplankton to the total chlorophyll ranged from 20-98%. Higher netplankton values at stations situated near the estuary in comparison with those found lower down in the Firth were the main cause of variations in the total chlorophyll over the area since the nanophytoplankton varied less dramatically. In Loch Long and the Gareloch, the nanophytoplankton contributed 11-62% of the chlorophyll and 13-77% of the productivity during a period of investigation in August 1976.

In a separate study of two rockpools on Great Cumbrae Island, it was found that the nanophytoplankton was very productive in this type of extreme environment, producing high levels of fixation (maximum recorded rate of 189 mg C $m^{-3}h^{-1}$) in the early months of 1976 when production in the sea was at a minimum. In these pools, the average contribution of the nanophytoplankton was 83% to the total chlorophyll and 86% to the productivity.

The significance of the nanophytoplankton in relation to the rest of the ecosystem in the Firth of Clyde is discussed.

CHAPTER 1

INTRODUCTION

The plankton community is made up of species covering a wide range of size and shape. Field studies have traditionally considered the plant component, the phytoplankton, as a homogeneous unit, emphasizing the role of diatoms and dinoflagellates in primary production and often ignoring the possible contribution made by the other photosynthetic organisms. This traditional approach relied predominantly on net samples to assess populations and biomass. Lohmann (1903) drew attention to the fact that an unknown proportion of the biomass was lost by this method since many cells were too small to be retained by the nets used and he collectively referred to these cells as the "nannoplankton."[1]

Since many factors which regulate population dynamics have been shown to be related to cell size, the phytoplankton is now frequently divided into two size classes depending on whether the cells are retained by fine plankton nets (netplankton) or pass through the nets (nanoplankton[1]). The response of two size fractions can then be studied in relation to changes in their environment with the aim of achieving a better understanding of species succession and the varying patterns of phytoplankton production.

Several schemes have been proposed for the size classification of the phytoplankton. Strickland (1960) proposed a scheme in which netplankton represented cells of maximum dimensions 500-50 μm; nanoplankton cells of 50-10 μm, while cells with a maximum cell dimension of

1. Both the original form of spelling (nannoplankton) and the more modern form in line with S.I. nomenclature (nanoplankton) are found in the literature. Restricting the term to photosynthetic organisms, Holligan and Harbour (1977) used the term nanophytoplankton and this terminology has been adopted in the present study.

less than 10 μm were considered as ultraplankton. The work in this thesis is, however, based on the scheme proposed by Dussart (1965) in which the nanoplankton is considered to consist of cells with a maximum dimension of between 2 and 20 μm while the netplankton includes cells within the size range 20-200 μm. No distinction is made here between nanoplankton and ultraplankton.

The study of preserved phytoplankton samples indicate that, although a proportion of the nanoplankton may be diatoms, the majority consists of small flagellates belonging to several different algal classes (Beers, Reid & Stewart, 1975; Throndsen, 1976). These organisms are difficult, in many cases impossible, to preserve (Bernard, Rampi and Zattera, 1967). In some areas the nanoplankton has been reported to be composed primarily of small diatoms (Yentsch and Ryther, 1959; Kristiansen, 1971) and Collier and Murphy (1962) isolated several genera of diatoms in the nanoplankton size range. Some individuals were observed to have a diameter of 0.75 μm while a species of Chaetoceros measured 1.5 x 3.0 μm on the apical and pervalvar axes respectively.

The difficulty of preserving nanoplankton organisms together with their small size, has meant that the systematics of this group are poorly understood and developed in comparison with larger planktonic algae. A large number of species were, however, isolated and described in considerable detail at the beginning of this century by Schiller (1913a, 1913b, 1925), Conrad (1926a, 1926b), Pascher (1925, 1927) and others. The electron microscope, together with the development of single cell isolations and culture techniques has allowed the ultrastructure and systematics of some of these organisms, many being found in British coastal waters, to be thoroughly investigated (e.g. Parke,

Manton and Clarke, 1955, 1959; Parke, Boalch, Jowett and Harbour, 1978; Green, 1975, 1976; Hibberd, 1976; Leadbeater, 1972, 1974; Manton and Leadbeater, 1974; Manton, 1959, 1977, 1978).

Although Lohmann drew attention to the "nannoplankton" in 1903, their importance was not verified until much later. Steeman Nielsen (1938), Atkins (1945), Harvey (1950), Knight-Jones and Walne (1951) and Wood and Davies (1956) demonstrated in several ways that much of the phytoplankton population was too small to be retained by plankton nets. Obtaining an accurate estimate of the nanoplankton contribution to the phytoplankton biomass and productivity was difficult at first due to the lack of suitable methods.

Ballantine (1953) assessed the six methods available at that time for estimating the nanoplankton component and concluded that cell counts of water samples concentrated by centrifugation gave the most reliable results. The introduction of chlorophyll determinations (Richards and Thomson, 1952) as a method of assessing standing stocks and the carbon 14 method for measuring primary productivity (Steeman Nielsen, 1952) provided relatively easy and more accurate methods of assessing the size fractions of phytoplankton populations and consequently the number of studies on the nanoplankton has risen substantially since the 1950's when these techniques were introduced, and information is now available from many different parts of the world.

Studies by Lund (1961) and Findenegg (1965) of freshwater lakes in England and Switzerland found that nanoplankton-dominated populations were characteristic of oligotrophic lakes where overall production was low. Findenegg (1965) also noted that, in general, the nanoplankton assimilated more carbon per unit biomass than did

larger diatoms or blue-green algae - a fact previously noted by Rodhe (1958). In the eutrophic lake situation, the nanoplankton is less important but still appears to make a significant contribution to the biomass and productivity. Kalff (1972) found that cells of size less than 64 μm contributed 9-99% of the standing crop and approximately 75% of the productivity in a eutrophic lake in Quebec, Canada while cells of less than 20 μm contributed 50% of the productivity. Gelin (1975), in a study of a Swedish lake, also found that 50% of the productivity of the lake was accounted for by the less than 20 μm fraction of the phytoplankton.

In the marine environment, the contribution of the nanoplankton to the total organic production in tropical waters has been documented by Steeman Nielsen and Jensen (1957), Teixeira (1963), Saijo (1964), Sumitra Vijayaraghawan, Joseph and Balachandran (1974), Pant, Bhargava and Goswami (1976), Malone (1971a) and Beers, Reid and Stewart (1975). Temperate waters have been investigated by Yentsch and Ryther (1959), Holmes and Anderson (1961), Gilmartin (1964), Malone (1971b), McCarthy Taylor and Loftus (1974), Garrison (1976) and Revelente and Gilmartin (1976).

The importance of the nanoplankton in colder waters has been less well documented although studies have been carried out by Digby (1953), Kawamura (1960), Reynolds (1973), Fay (1973) and Throndsen and Heimdal (1976). In the Barents Sea, Reynolds (1973) has shown that over 90% of the phytoplankton biomass is made up of nanoplankton organisms. Fay (1973) found that although the nanoplankton contribution in Antarctic waters was lower than that in the tropics or temperate regions, it was still the most abundant size fraction of the phytoplankton.

TABLE 1

CONTRIBUTION OF THE NANOPLANKTON TO TOTAL PHYTOPLANKTON STANDING CROP AND PRODUCTIVITY IN DIFFERENT LOCATIONS. VALUES ARE EXPRESSED AS PERCENTAGE OF THE TOTAL PHYTOPLANKTON

IA. TROPICAL WATERS

LOCATION	LATITUDE	NANOPLANKTON SIZE MAXIMUM	NANOPLANKTON % OF TOTAL			SOURCE
			NO. OF CELLS	STANDING CROP CHLOROPHYLL A	PRODUCTION C^{14} UPTAKE	
Temperate & tropical waters		50 µm			94% oceanic stations 82% coastal	Steeman, Nielsen & Jensen, 1957
Equatorial Atlantic	0°	65 µm	77.8%		90%	Teixeira, 1963
Indian Ocean	10°N-20°S	110 µm 5 µm			95% 22-49%	Saijo, 1964
Indian Coastal Waters - Cochin	10°N	50 µm	4-58%	50-93%	36-94%	Sumitra Vijayaraghava et al, 1974
Indian Coastal Waters - Porto Novo Waters	~ 12°N	20 µm		33-100%		Ramadhas et al, 1975
Goa Waters India	15°N	60 µm	> 90%	> 90%	> 90%	Pant et al, 1976
Tropical Pacific	5°N-25°N	22 µm		66-100%	80-100%	Malone, 1971
Peru Current	10°S-10°N	22 µm		80-96%	87-99%	Malone, 1971
North Pacific Gyre	28°N	20 µm	99%			Beers et al 1975

TABLE IB TEMPERATE WATERS

LOCATION	LATITUDE	NANOPLANKTON SIZE MAXIMUM	NANOPLANKTON % OF TOTAL NO. OF CELLS	STANDING CROP CHLOROPHYLL A	PRODUCTION C^{14} UPTAKE	SOURCE
Vineyard Sound	41°N	65 µm	91%	92%	98%	Yentch & Ryther, 1959
Puget Sound	48°N	35 µm			> 50-90%	Holmes & Anderson 1961
British Columbian fjord	49°N	56 µm			> 90%	Gilmartin, 1964
Monterey Bay	35°-50°N	22 µm		60-90%	60-90%	Malone, 1971a
Monterey Bay	35°-50°N	22 µm		up to 82% (upwelling period - 6%)	up to 95% (upwelling period 7%)	Garrison, 1976
Chesapeake Bay	37°-39°N	35 µm 10 µm		93% 81%	100% 94%	McCarthy et al, 1974
Chesapeake Bay	37°-39°N	10 µm		81-88%	65-75%	Van Valkenbur & Flemer 1974
Narragansett Bay	45°N	20 µm		47%	51%	Durbin et al 1975
Northern Adriatic	45°N	20 µm	74-88%	62-76%		Revelante & Gilmartin 1976

TABLE IC COLDER WATERS

LOCATION	LATITUDE	NANOPLANKTON SIZE MAXIMUM	NANOPLANKTON % OF TOTAL NO. OF CELLS	STANDING CROP CHLOROPHYLL A	PRODUCTION C^{14} UPTAKE	SOURCE
Ocean Weather Station "P" - Pacific	50°N	10 µm		75%		McAllister et al 1960
North Pacific and Bering Sea	45-60°N	110 µm			44-84%	Kawamura, 1960
North Sea - South Bight	51-52°N	50 µm			43%	Mommaerts, 1973
Barents Sea	62-82°N	25 µm		55-90%		Reynolds, 1973
Tromso, Norway	60°N	20 µm 5 µm			7%(Summer) 85%(Winter) 6% (S.) 73% (W.)	Throndsen & Heindal 1976
Antarctic Region	45-79°S	35 µm		73.9%	72.5%	Fay, 1973

The study by Digby (1953) in Greenland is one of the few which have reported a netplankton dominated community.

The results of the above studies in the marine environment are summarised in Table 1. Although it is difficult to directly compare all the studies in Table 1 since mesh sizes of 10-110 μm have been variously used to separate the net- and nanoplankton fractions, several features have emerged. In general the nanoplankton fraction of the phytoplankton often accounts for between 50 to 100% of both the standing stock and primary productivity.

The nanoplankton organisms are found to be dominant in oceanic environments where nutrient concentrations are low and the photic zone is well stratified (Malone, 1971a; Beers et al, 1975) and in areas where the velocities of vertical water movement are high (Semina, 1968, 1972). In neritic waters where nutrient concentrations are generally higher, the netplankton is often more significant (Digby, 1953; Steeman Nielsen and Jensen, 1957; Subrahmanyan and Sarma, 1965; Malone, 1971b). Malone (1971a) found that the mean primary production of the nanoplankton did not differ significantly between oceanic and neritic environments; whereas the netplankton exhibited a marked increase in production in neritic areas. The higher total production associated with neritic water was, therefore, due mainly to the increase of the netplankton.

The nanoplankton appears to form a more stable component of the phytoplankton, being less prone to the large seasonal fluctuations in numbers observed with the netplankton (Yentsch and Ryther, 1959; Teixeira et al, 1967). Gelin (1976) found that a 10-fold variation in the nanoplankton biomass occurred throughout the year in Lake

Vombsjon, Sweden, while a twenty-five-fold variation was observed for the netplankton biomass. Corroborating the seasonal stability of the nanoplankton, Malone (1971a) observed netplankton standing crop and productivity to vary from one order of magnitude less than that of the nanoplankton to one order of magnitude greater during a seasonal period of upwelling. Seasonal variations in nanoplankton biomass have however been reported by Kalff (1972) and Sumitra Vijayaraghavan et al (1974).

The assimilation number (mg C mg chl$a^{-1}h^{-1}$ at light saturation) may be used as an indicator of growth rates of natural phytoplankton populations (Yentsch and Ryther, 1959). Nanoplankton size fractions have usually been found to have a higher assimilation number than netplankton fractions (Saiyo and Takasue, 1965; Malone, 1971; Gelin, 1975) indicating higher growth rates in this fraction, although exceptions to this have been reported. Durbin et al (1974) found no significant differences between the mean assimilation numbers of the different size fractions considered in their study.

The higher nanoplankton growth rates can be related to the high ratio of surface area to volume (A/V ratios) which increases with decreasing cell size. This high A/V ratio in nanoplankton has further ecological implications. Small cells generally have shorter generation times and higher growth rates in a given environment than do larger cells (Findenegg, 1965; Williams, 1964; Eppley and Sloan, 1966; Eppley and Thomas, 1969; Eppley, Rogers and McCarthy, 1969), especially under optimal conditions (Banse, 1976).

Studies on nutrient uptake kinetics have shown that the half saturation constants (Ks) for nitrate and ammonia vary according to cell

size (Eppley et al, 1969). Maximum rates of nutrient uptake (Vm) also increase with increasing cell size (Dugdale, 1967). These results have led to the hypothesis that cells in the netplankton size range with high Vm and Ks values are favoured when nutrients are high (i.e. in neritic and upwelling regions). The converse is true for nanoplankton with low Vm and Ks values; this fraction is dominant when nutrient concentrations are low (i.e. in oceanic conditions). This hypothesis, however, must be considered in the light of evidence which is now accumulating which supports the view that the nutritional history of the phytoplankton populations is as important or more important than cell size in determining nutrient uptake rates (Carpenter and Guillard, 1971; Guillard, Kilham and Jackson, 1973).

High surface area to volume ratios facilitate the suspension of the cells (Munk and Riley, 1952; Smayda and Boleyn, 1966; Smayda, 1970; Eppley, Holmes and Strickland, 1967) so increasing the potential residence time of the nanoplankton in the euphotic zone in stratified conditions. Since sinking rates generally increase as cell size increases (Munk and Riley, 1952) large cells will tend to be concentrated in regions of upward water flow while smaller cells will be distributed along a gradient towards regions of downward water flow (Semina, 1968).

The factors governing the predominance of net- or nanoplankton in a given environment are, at present, under debate. Semina (1968, 1972, 1976[x]) looking at large and medium scale size distributions in the Pacific and the Atlantic Oceans found that the mean cell size in an area was influenced by three main factors, viz., the direction and velocity of vertical water movement; the density gradient in the

[x] Semina, Tarkhova & Truong Ngoc An, 1976

pycnocline and the phosphate concentration. She proposed that the environmental control was predominantly physical. However, Parsons and Takahashi (1973) placed less emphasis on the hydrodynamical aspects and proposed a model which incorporated several additional factors such as 1) the rate of nitrate or ammonia input to the cell, 2) the extinction coefficient of the water, 3) the mixed depth layer, 4) surface light intensity, 5) the sinking rate of the phytoplankton and 6) the upwelling velocity of the water, i.e., their control being related more to physiological parameters than physical. Laws (1975) extended Parsons and Takahashi's model and suggested that, under certain light conditions, the inverse relationship between respiration rate and cell size may cause larger cells to have higher growth rates. Considerations of the two arguments are discussed by Hecky and Kilman (1973).

A further biological factor which will affect the size distribution of the phytoplankton in a particular area will be the distribution and abundances of herbivores which graze selectively on the basis of size. Nanoplankton appear to be the preferred food of many planktonic invertebrate larval stages (Cole, 1936; Bruce, Knights and Parke, 1940; Thorson, 1950) and microzooplankton (Beers and Stewart, 1969; Parsons and Le Brasseur, 1970) while herbivorous copepods have been shown to selectively graze on larger, netplankton cells (Marshall and Orr, 1955; Mullin, 1963; Conover, 1966; Richman and Rodgers, 1969; Richman, Heinle and Huff, 1977). Phytoplankton cell size will have an effect on the efficiency of energy transfer to larger predators since nanoplankton-based food chains appear to require one or two additional energy transfers to reach a given sized

consumer than do net-based food chains (Ryther, 1969; Parsons and Le Brasseur, 1970).

Thus although much information has now been accumulated on the significance of the nanoplankton in many different environments, there are conflicting reports on several aspects of their ecology and the factors which control their distribution are still unclear. Further work in this field is, therefore, of use to help clarify this subject, particularly in temperate, estuarine environments where less work has been done, as pointed out by Durbin et al (1974).

In the coastal waters and seas around Britain there is little quantitative data available on the nanoplankton. Jones and Spencer (1970) found that the bulk of the phytoplankton in the Menai Straits, Anglesey was made up of small diatoms and flagellates. Over the three year study period, the netplankton contributed a mean value of 13% (range 0.04 - 38%) of the total standing crop. In a survey carried out over the summer months at E1, in the English Channel, Holligan and Harbour (1977) found that during midsummer small flagellates were dominant in the surface layers while dinoflagellates produced a sub-surface maximum. Except during and immediately after the spring diatom outburst, cells of less than 10 μm accounted for morethan 50% of the productivity.

Wood, Tett and Edwards (1973) obtained similar results in Loch Etive, a west coast sealoch which lies to the north of the Firth of Clyde. Here the μ-flagellates made a significant contribution to the biomass after the spring bloom but their relative abundance was greatest in autumn and in winter. The study by Mommaerts (1973) in the North Sea which was briefly summarized in Table 1 is relevant to this section.

In the Firth of Clyde itself, while the seasonal cycles of the larger phytoplankton species have been well documented in the works of Marshall and Orr (1924, 1927, 1930 and 1955) and reviewed in detail by Hinton (1974), the seasonal changes in nanoplankton organisms of the area have not been studied in detail. It is, however, one of the few areas in which population estimates of the nanoplankton have been made. Marshall (in Marshall, Nicholls and Orr, 1934 and Nicholls, 1933) assessed the numbers of μ-flagellates present on several occasions in the Firth of Clyde in connection with studies on the biology of Calanus finmarchicus, the most commonly occurring and most important copepod in this area. Although present in large numbers at times, the nanoplankton was found not to be efficiently filtered by C. finmarchicus or its larval stages (Marshall and Orr, 1955, 1956) and was therefore not considered in any more detail.

Occasional references to flagellate populations are found in reports on oyster cultivation experiments at Millport (Miller, 1956). Marshall and Orr (1962) using a total carbohydrate assay found that a May 'bloom' of surface flagellates in Loch Striven caused an appreciable increase in carbohydrate values.

Nanoplankton organisms isolated from various localities around the Firth of Clyde have provided much of the source material used in studies on the physiology of microbial algae by Droop (1955, 1961) and these studies have made major contributions to our knowledge of nanoplankton algae. The seasonal changes of these organisms in the Firth of Clyde have not been studied in detail however.

Another aspect of the local phytoplankton which has not been studied in detail is its primary productivity. Marshall and Boney

(1974), in their review of the current knowledge of the plankton in the Firth of Clyde, pointed out that there has never been a measure of primary productivity in the area using modern methods. Marshall and Orr (1928) carried out *in situ* productivity studies on diatom cultures using the Winkler technique and a short-term study of the productivity of Irvine Bay has been carried out (Johnston, Adams and Dooley, 1971).

The aim of the present work was to complement the previous studies of the phytoplankton in the Firth of Clyde by carrying out a survey of the seasonal changes of the nanophytoplankton and to assess its contribution to the primary productivity of the area. A study of the nanophytoplankton is particularly relevant at this time as there is increasing industrial development along the coastline of the Firth, particularly in the region of the Fairlie Channel and laboratory studies have already shown that certain species of the nanophytoplankton are pollution-sensitive. The knowledge of the seasonal changes of these organisms may be of use in the future to indicate short or long term environmental changes.

CHAPTER 2. METHODS

Throughout this survey the same basic procedures have been used and these will be described in the present chapter. Any variations of these will be described in the relevant sections and any other procedures used in specific cases will be described where appropriate.

2.1. Collection of the samples

Depth samples were collected by means of a 5 litre Van Dorn-type sampler (Hydrobios, West Germany) while surface samples were collected by means of a clean plastic bucket. The samples were transferred to 5 litre carboys, mixed and sub-samples from these were taken for the various analyses.

2.2. Meteorological Data

Data on daily maximum and minimum air temperatures, sea surface temperature and rainfall were obtained from the Marine Station, Millport. To obtain an estimate of sunshine levels (hours of sunshine per day) and of wind speeds and directions, the records from the Prestwick meteorological station were consulted. Prestwick, which lies approximately twenty miles to the south-east of Cumbrae on the Ayrshire coast, is the nearest coastal station known to record these parameters. Barnes (1955) found when comparing the sunshine records of coastal stations in the vicinity of Cumbrae that there was no great variation over the coastal area of the Firth of Clyde and the Prestwick records will therefore provide a reasonable estimate of levels of sunshine

recorded at Cumbrae. Differences in the local topography of the two localities will affect the wind patterns to a certain extent and the wind data from Prestwick can therefore only be taken as an indicator of conditions at Millport.

2.3. Tidal Information

Information on the state of the tide at times of sampling was obtained from the continuous records maintained by the tide gauge (Negretti and Zambra) at Keppel Pier, Millport.

2.4. Temperature and Salinity Determinations

The temperature and salinity of the water samples were recorded *in situ* at the time of sampling by means of a combined salinity and temperature probe (MC5 Mark II supplied by Electronic Switchgear and recommended by the National Institute of Oceanography) and temperature and salinity profiles were constructed.

The calibration of both the thermistor and salinity probes were checked periodically against the temperatures recorded on the reversing thermometers on the water samplers and the salinity against values obtained by the silver nitrate technique for salinity determinations (Strickland and Parsons, 1972).

2.5. Determination of pH

The hydrogen ion concentration (pH) of the water samples was determined with a Phillips PW9404 pH meter immediately on return to the laboratory (usually within 30 minutes of sampling). The electrode

was standardised using two buffer solutions and the temperature of the meter adjusted to that of the samples in the usual manner before use.

2.6. Determination of the Total CO_2 content of the Seawater

The total alkalinity of the samples was measured by the method outlined in Strickland and Parsons (1972). From this and several other measurements (salinity, initial temperature, pH and the temperature at which the pH was measured) the total CO_2 content of the seawater could be calculated in the following way:-

1. Carbonate Alkalinity = Total Alkalinity - A^* (milliequivalents l^{-1})

and

2. Total CO_2 = Carbonate Alkalinity x 12 x Ft^* (mg ^{12}C available l^{-1}).

*A and Ft are both factors which are temperature, salinity and pH dependent and the values of which can be looked up in tables. In the present study an average Ft value of 0.98 was found and the mean total CO_2 content of the water in the Fairlie Channel was 24320.7 $\pm$ 805.4 ($\pm$ 1 S.D.) mg C available l^{-1}.

2.7. Determination of Nutrients

Immediately after collection, subsamples for nutrient analysis were filtered to remove suspended and particulate matter (samples for phosphate, nitrite and nitrate determinations through Whatmans GF/C glassfibre filters and samples for silicate analysis through Millipore membrane filters), and these samples were then immediately frozen for storage until they were analysed. This was usually within a week and not more than one month after collection.

2.7.1. Determination of Orthophosphate Phosphorus

Virtually all methods for the determination of phosphate in natural waters are photometric and most are based on the development of the heteropoly blue formed after the reduction of 12-molybdophosphic acid which forms under well-defined acid conditions. Combined forms of phosphate do not react with the molybdenum (Olsen, 1966); these include both dissolved and particulate organically combined phosphorus and condensed phosphates (such as detergent polyphosphates). Thus the normal analysis measures only inorganic orthophosphate phosphorus. The method used in the present study was that described by Strickland and Parsons (1972) which is based on the method of Murphy and Riley (1962) and involved treating the sample with a single reagent consisting of acidified molybdate, ascorbic acid and antimony.

This procedure has no interference with silicate up to 10 p.p.m. and has a salt error of less than 1%. The final colour is stable for 24 hours and its development is temperature-independent between 15^{o} and $30^{o}C$. The accuracy is $\pm$ 1% at a concentration of 20 $\mu g\ P\ l^{-1}$ (0.64 μg at. l^{-1}) and the minimum limit of detection is 1 $\mu g\ P\ l^{-1}$ (0.03 μg at. l^{-1}). (Olsen, 1966).

After thawing and warming to room temperature each seawater sample was analysed in duplicate, the final colour development being measured at 885 nm. For calibration purposes, each set of analyses was accompanied by standards and blanks analysed in triplicate; the standard being a solution of potassium dihydrogen phosphate ($KH_2\ PO_4$) at a concentration of 3 μg at. l^{-1} and the blanks were distilled water.

2.7.2. Determination of Orthosilicate Silicon

In soluble form, silicon is present in natural waters as silicate or silicic acid. Martin (1972) considers that, at the normal pH of seawater the dissolved form is largely undissociated orthosilicic acid (H_4 Si O_4) and that only a small percentage exists as ions. The method of the determination of silicate in seawater depends on the reaction of the orthosilicic acid with molybdate, producing a silicomolybdate complex which is then usually reduced to a heteropoly blue. Lund (1965) considers that the orthosilicate which is estimated by the standard molybdate method is available to diatoms while the more highly polymerized forms are not. This view is supported by Strickland and Parsons (1972) who state that "the reactive silicate" measured by this method probably gives a meaningful measure of the amount of silicon available to growing plant cells.

The method used in the present study was based on the procedure of Mullin and Riley (1955) as outlined by Strickland and Parsons (1972). With this method, the salt error is small (less than 3% between 25‰ and 35‰) and the colour is stable for at least 3 hours. The precision of the method at 10 µg at Si l^{-1} is better than $\pm$ 2%.

This method involves the reaction of duplicate water samples (25 ml) with acidified ammonium molybdate solution followed after 10 minutes by the addition of a second solution containing oxalic acid, sulphuric acid and a metol-sulphite reductant. The oxalic acid is included to destroy any molybdophosphate formed in the first reaction which would interfere with the final result. The extinction was measured after three hours at 812 nm in a 4 cm cuvette.

Each set of analyses was accompanied by standards and blanks, three of each being carried through the procedure. The standard used was sodium silicofluoride (Na_2SiF_6) at a final concentration of 4 µg at Si l^{-1} and the blanks were silicate-free distilled water.

2.7.3. Determination of nitrate nitrogen

The method used in the present study was that recommended by Strickland and Parsons (1972) and depends on the reduction of nitrate to nitrite and the subsequent colorimetric determination of nitrite by a diazotization method.

The procedure which was developed by Wood, Armstrong and Richards (1967) involves passing the sample treated with a tetrasodium EDTA through a column of copperized cadmium in which the nitrate is quantitatively reduced with the possible reaction being:

$$NO_3^- + Cd + EDTA^{4-} + H_2O \rightarrow Cd\ EDTA^{2-} + 2OH^- + NO_2^-$$

This reaction proceeds under neutral or alkaline conditions and has an efficiency of 99% ± 1%. The copper serves as a cathode in the redox couple and the complexing agent, tetrasodium EDTA sequesters cadmium to prevent the precipitation of Cd(OH)2 and the subsequent loss of efficiency (Martin, 1972).

The columns were made and prepared as specified by Wood et al (1967) and the procedure for analysis followed that outlined in Strickland and Parsons (1972) although in the present study EDTA was retained as the activator and not ammonium chloride as suggested by the above authors. Duplicate blanks (distilled water) and triplicate standards (potassium nitrate solution with a final

concentration of 20 μg at.N l^{-1}) were carried through each set of analyses. After being reduced in the columns the samples were treated as nitrite samples and analysed by the method of Bendschneider and Robinson (1952), their extinction coefficient being measured at 543 nm in 1 cm cuvettes.

2.7.4. The Determination of Nitrite Nitrogen

The determination of nitrite in natural waters is conveniently carried out by a diazotization process. Under acid conditions the nitrite ion reacts with an aromatic amine to form a diazo-compound which is then coupled with a second aromatic amine to form an azo dye. The intensity of the final colour is proportional to the amount of nitrite present. The use of sulphanilamide as the diazotizing agent and N-(1-naphthylethylenediamine dihydrochloride) as the coupling agent was recommended by Bendschneider and Robinson as these give a rapid colour development and good sensitivity and the details of the procedure were taken from Strickland and Parsons (1972).

The calibration of the procedure was checked routinely by analysing standard solutions of sodium nitrite (1.0 μg at. N l^{-1}) with the samples. The extinction values were measured at 543 nm with 4 cm cuvettes.

2.8. Phytoplankton

2.8.1. Fraction of the Samples into Net- and Nano-phytoplankton

To obtain a nanophytoplankton sample for chlorophyll and productivity determinations, water samples were passed through a

nylon net of nominal pore size 20 μm (Nybolt N20/16) to remove the netplankton. The filters were supported in a Millipore filtration unit (Aseptic Filtration System XX1104700) and were backwashed between samples and changed frequently to prevent clogging.

This filtration method did not give an absolute separation as it is possible for a proportion of the netplankton, particularly diatoms with a small cross-sectional area to pass through if orientated towards the mesh in the correct way. One such species is Skeletonema costatum which is the most commonly occurring diatom in the Firth of Clyde and which, although forming long chains of up to 165 μm in length, has an average cross sectional diameter of 8-15 μm.

The efficiency of separation was regularly checked by comparing the particle size distribution of the samples before and after fractionation on a Coulter Counter. A typical plot of the results obtained is shown in Fig. 1. It was found that the 20 μm mesh effectively removed everything above 40 μm and that although the bulk of the cells above 20 μm was screened out, after fractionation they still contributed approximately 5-15% of the total volume of the sample. In terms of actual cell numbers, an example can be given in which the counter was preset to count 20,000 particles. Before filtration there were 334 particles (1.7%) above 20 μm and after, only 6 particles (0.03%) were counted.

A smaller mesh size (10 μm) was tested to try and improve the separation but this was found to give a poorer separation, possibly as this mesh was more easily stretched with consequent distortion of the pores.

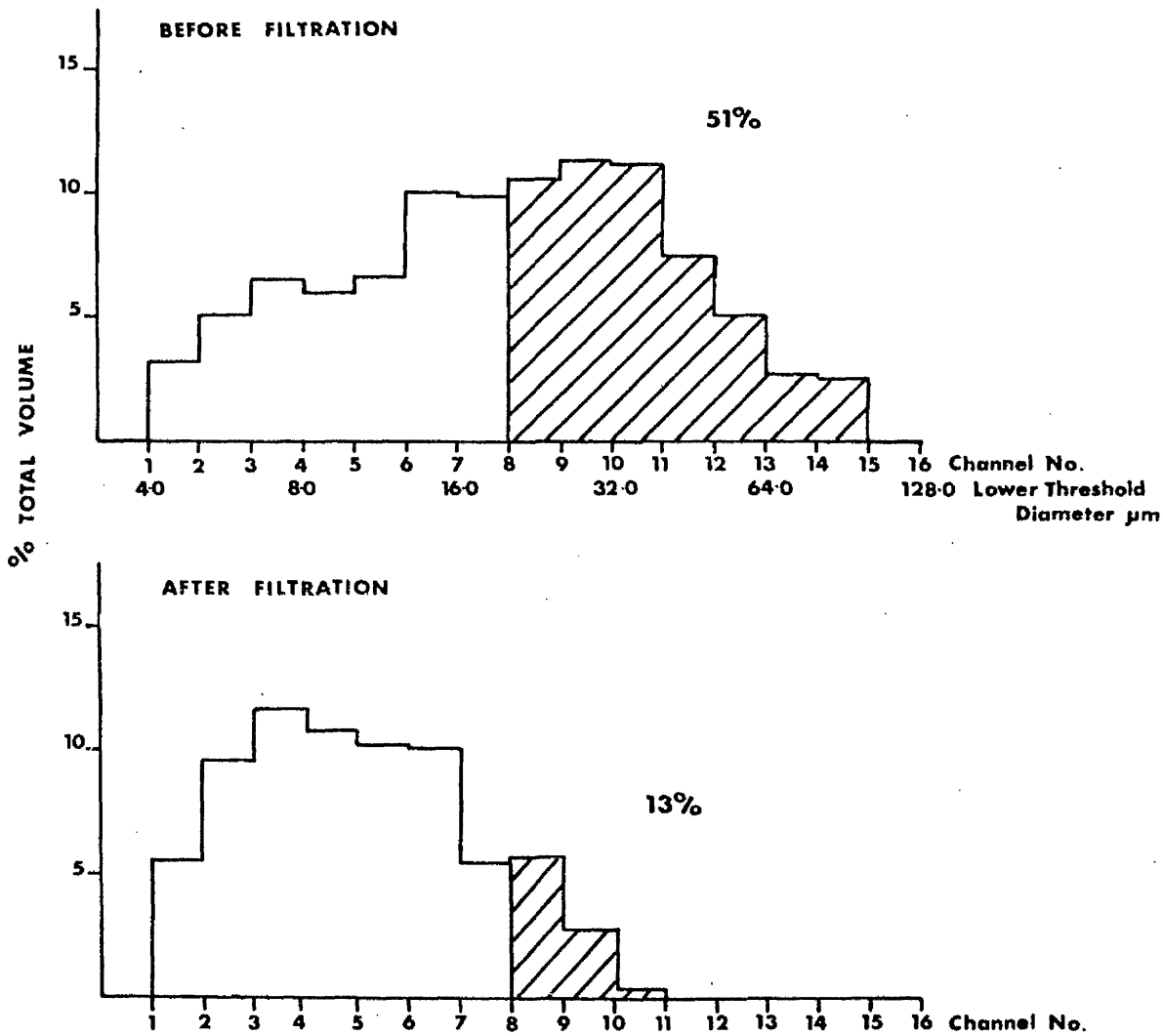


Figure 1. The particle size distribution of a seawater sample before and after filtration through a 20 µm mesh net.

The netplankton contribution to the chlorophyll and productivity levels was estimated by subtraction of the nanophytoplankton fraction from those of the total, unfractionated samples. An alternative method would have been to wash off and quantitatively collect the cells trapped on the mesh but it was considered that this method would be subject to larger handling errors. When the two methods were compared in a productivity determination, the coefficient of variation of the fixation values of the total-nanophytoplankton with the netplankton values as measured by collecting the cells trapped on the 20 μm mesh was 11.47%.

2.8.2. Estimation of Standing Crop - Chlorophyll a determinations

The spectrophotometric and more recently the fluorimetric determination of chlorophyll a as an estimate of standing crop is used extensively in both limnology and oceanography although the use of plant pigments for the quantitative evaluation of the phytoplankton biomass has been criticized by several workers.

The main criticisms have concerned the fact that the amount of chlorophyll per algal cell varies depending on the physiological state of the cell (Lund and Talling, 1957) and that the different classes of algae possess different proportions of photosynthetic pigments and vary in their ease of pigment extraction (Riley, 1940). The presence of detrital chlorophyll will also interfere with the results. Given these limitations, the technique still continues to be used since it is relatively easy and quick to perform, it monitors the seasonal changes which take place in phytoplankton

numbers and serves as an indicator of productive and non-productive regions.

Chlorophyll a levels of fractionated (< 20 μm) and unfractionated (total phytoplankton) samples were measured spectrophotometrically in the present study using the method described in Strickland and Parsons (1972).

1 to 2 litres of a sample were filtered at reduced pressure on to Whatman GF/C glassfibre filters. Before filtration a few drops of Mg CO_3 suspension were added to the sample to prevent acidity and the consequent formation of phaeophytins. The filters were then either stored in darkened desiccators at -20°C or, more usually, extracted immediately in 90% acetone.

The extraction involved the grinding up of the filter in ice-cold acetone by means of a tissue grinder under subdued light conditions. The glass fibre pulp was then quantitatively transferred to centrifuge tubes and the volume of acetone made up to 12 ml, and these were then left in a darkened refrigerator for 24 hours to allow complete extraction. The tubes were then centrifuged for 5 minutes at 5000 r.p.m. to remove debris and fibres and the supernatant was transferred to 4 cm cuvettes. Extinction values were read at 750, 665, 645, 630 and 480 nm.

The chlorophyll a was then calculated from the equations of Parsons and Strickland (1963) which are based on those of Richards with Thomson (1952).

$$\text{Chlorophyll } a \text{ mg m}^{-3} = Ca \left(\frac{v}{V.l} \right) \qquad 1.$$

v = volume (in ml) of acetone used.

V = volume (in litres) of water filtered for extraction.

l = pathlength (in cm) of cuvette.

$$Ca = 11.6\ D_{665} - 1.31\ D_{645} - 0.14\ D_{630} \qquad 2.$$

D_{665}, D_{645} and D_{630} being the extinction values measured at the wavelengths 665, 645 and 630 nm respectively.

When replicate samples were taken from a larger well mixed volume and analysed to check the analytical error of this method, a mean coefficient of variation of 7.58 $\pm$ 5.63% and 11.77 $\pm$ 3.69% ($\pm$ 1 S.D.) was found for the total unfractionated and the nanoplankton samples respectively.

2.8.3. Phaeopigment Determinations

Phaeopigment levels were not routinely measured and the chlorophyll values in the text are not corrected for these (unless specified otherwise).

A check was made, however, when surprisingly high levels were reported for other marine samples (Reynolds, 1977). To measure the phaeopigment levels the samples were carried through the above procedure for chlorophyll analysis. After measuring the extinction values at the different wavelengths, the samples were acidified with 2 drops of 50% hydrochloric acid, mixed, and after a period of 5 minutes to allow the complete breakdown of the chlorophyll a, the extinction values at 750 and 665 nm were remeasured.

The equation used to calculate the phaeopigment levels

is given in Strickland and Parsons (1972) and is based on the original proposed by Lorenzen (1967).

$$\text{Phaeopigments mg m}^{-3} = \frac{26.7\ (1.7[665_a] - 665_o) \times v}{V \times l}$$

665_o = extinction value before acidification (- blank measurement at 750 nm).

665_a = extinction value after acidification (- blank).

v, V and l, as before (equation 1).

2.8.4. Enumeration and Identification of the Phytoplankton

The various methods of counting and identifying the phytoplankton, especially those concerning the nanoplankton, have been discussed by Ballantine (1953), Braarud (1958) and more recently by Reynolds (1973).

The problem remains of finding suitable preservatives and accurate methods for collecting and counting. Methods which are suitable for the larger algae, e.g. the inverted microscope technique, are less suited to the small nanoplankton and these require methods which select against the larger forms, e.g. the haemocytometer (Lund, Kipling and Le Cren, 1958).

It was therefore decided with the time available when carrying out a reasonably intensive weekly sampling programme to aim for only a semi-quantitative estimate of the populations present and to identify the main components of these as far as possible. To do this a combination of methods was used.

a) A subsample of each water sample was routinely fixed in Lugol's Iodine (usually a 250 or 500 ml sample),

allowed to settle for at least two weeks and the supernatant then drawn off to leave a 5 ml slurry of cells. Replicate counts of this were then made in an improved Neubauer haemocytometer. Although the limitations in the use of a haemocytometer are recognized (Lund and Talling, 1975; Lund et al, 1958), it was decided to use this method as it was useful for counting small cells which were the main interest in this survey. A small sample was also mounted directly on a slide and examined at X 1000 magnification under light field for further identification of the fixed cells.

b) Live cells were also examined under oil immersion having first been either concentrated by means of a continuous centrifuge or by filtration on to a membrane filter and the cells thus collected being resuspended in a small volume of seawater (Coles and Knight-Jones, 1949).

c) Raw enrichment cultures of the samples were set up in two different media - Erdschreiber's and Boney's (for ingredients for these media see Appendix 1) and these were then either incubated at 10°C in a light regime of 16 hours light : 8 hours dark, or in continuous light at room temperature. The organisms growing in these were usually examined after approximately 3 weeks and intervals thereafter.

2.8.5. Primary Productivity Measurements

Primary production in aquatic environments is measured most accurately at present by techniques which monitor the changes in the O_2 and CO_2 content of the water as photosynthesis (and/or respiration) takes place, and usually involves the enclosure of a small sample of the natural community in light and dark bottles and exposing these to natural or simulated natural light conditions.

The comparative simplicity of the procedure for measuring carbon-14 uptake and, above all, its sensitivity, has led to the widespread use of radiocarbon for measuring primary productivity in both seas and lakes, and in most circumstances it has now replaced the O_2 method which was first used by Gaarder and Gran (1927) which is less sensitive and more prone to experimental error.

The main drawback of the ^{14}C method, which was introduced by Steeman Nielsen (1952), is that the interpretation of the results obtained is not simple. Problems of interpretation arise since there is the possibility that

a) some of the respired CO_2 is reassimilated

b) the dark fixation may not be fully corrected for in the dark bottle measurements

c) an unknown quantity of the fixed carbon may be lost as extracellular products (this can be as much as 35% of the total fixed in oligotrophic areas (Fogg, Nalewajko and Watt, 1965).

The possibility of photorespiration occurring and the levels of this in unicellular algae have not yet been well researched

and this could be a further source of error.

Strickland (1960) in his review of measuring production in marine phytoplankton concluded that experiments with carbon-14 do not measure gross productivity but a value between gross and net and that this value is probably nearer the net productivity value than the gross.

Bottle Effects

The usefulness of results obtained from enclosed samples depends on the accuracy with which they reflect the natural environment and several bottle effects have been observed. These include the difference in turbulence and light climate within the bottles, and the existence of a solid substrate inside the bottle.

The light climate of the cells within the bottle will be altered since the absorption of light by glass is considerably greater than that by most lake or sea waters (Soeder and Talling, 1974). Within the bottles, the cells are restricted to one level in the light zone whereas in nature, the phytoplankton are presumably not confined to a single depth but are continually mixed through a layer of variable thickness and are exposed to a range of light intensities.

Turbulence and gross circulation patterns will not only affect the supply of light to the cells but also the nutrients reaching the cells and the sedimentation rate. The existence of a solid substrate might cause a build up of plankton or bacterial growth on the walls of the bottles and Verdwin (1960) suggested

that damage may occur when delicate flagellates swim into the glass surface. Lewis (1974) found that varying the ratio of substrate area to volume did not significantly affect the carbon-14 uptake during short incubations and suggested that the error from this source was small.

Errors from containment have generally not been considered significant in physiological studies but a recent study by Venrick, Beers and Heimbokel (1977) showed that with longer incubation periods of up to 24 hours, both physiological changes and changes in species abundance occurred, and they suggested that the changes in the crop during incubation could be sufficient to account for much of the heterogeneity in productivity estimates. Cassie (1962) had previously examined the variability of time zero cell counts and concluded that the variability of the phytoplankton standing crop contributed only slightly to that of the productivity.

The aim in the present study was to use the technique to compare the rates of photosynthesis as measured by carbon-14 uptake of the nanophytoplankton and the total phytoplankton when both are under the same environmental conditions.

Outline of Procedure Used for Measuring Primary Productivity

The phytoplankton productivity was measured by the method of Steeman Nielsen (1952) as described by Strickland and Parsons (1972).

Four light and two dark 125 ml biochemical oxygen demand (BOD) bottles of actual volume 129.8 $\pm$ 0.5 ml were filled with water from each depth sampled (surface 1, 5 and 10 metres). Each bottle was inoculated with 1-5 µCi of labelled sodium bicarbonate (1 µCi = 2.22×10^6 DPM) depending on the expected fixation levels by means of an automatic syringe (10 ml Repette syringe - Jencons). The radioactive

$Na\ H^{14}\ CO_3$ was obtained from the Radiochemical Centre, Amersham, in 1 ml quantities of 50 $\mu Ci\ ml^{-1}$ in sterile vials and these were diluted to the required concentration immediately before use with a sodium chloride dilution solution (5% w/v analar NaCl in distilled H_2O with 0.3 g anhydrous $NaCO_3$ and 0.2 g NaOH added per litre).

After inoculation the bottles were well stoppered, mixed, the dark bottles had aluminium foil placed round their stoppers to prevent any light penetration at the neck, and then all the samples were resuspended at their original sampling depths. Care was taken to protect the samples from excessive light during collection and preparation. Dark bottles were included for all sampling depths as controls to check that there was no significant dark fixation of carbon-14.

To suspend the samples <u>in situ</u> a float consisting of a lifebuoy with a thin wooden spar strapped across it was moored on station. Two lines were attached to either end of the spar, away from the possible shading effect of the buoy, and these had attached, at the required depths, perspex holders each designed to hold three sampling bottles in a horizontal position to allow maximum exposure of the bottles to the available light at each depth. The design of the holders was taken from Schindler and Holmgren (1971) and the design is illustrated in Plate 1.

The bottles were incubated under natural light and temperature conditions for 6 hours from 0900 to 1300 hours. After incubation the samples were placed in a dark box to prevent any further fixation and returned immediately to the laboratory for processing.

In the laboratory, 100 ml samples from 2 light and 1 dark

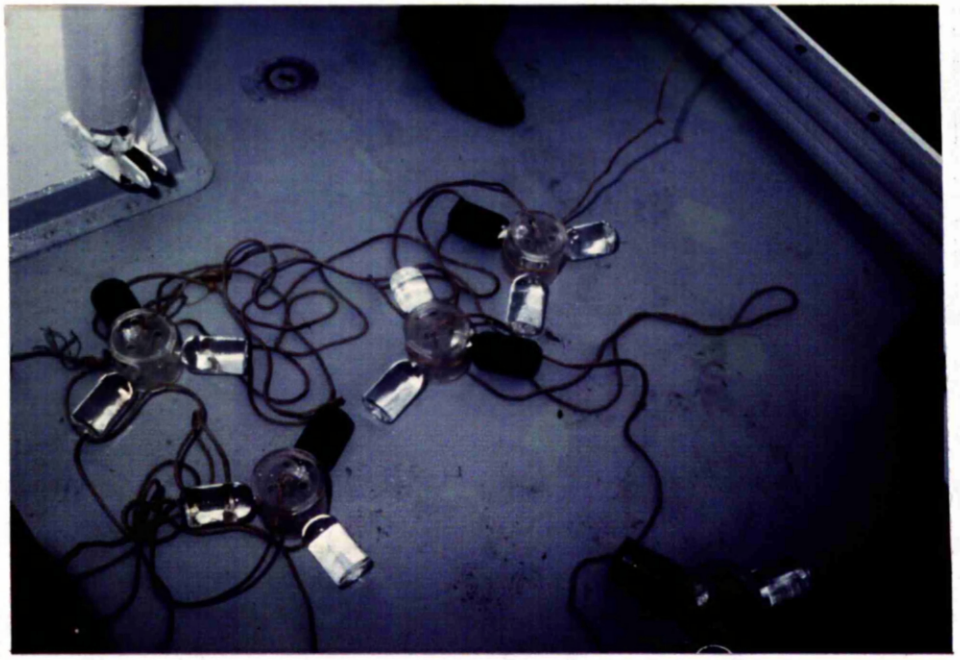


Plate 1 illustrates the perspex bottle holders used in the "in-situ" fixation experiments.

bottle per depth were filtered directly on to 27 mm Millipore HA filters (0.45 ± 0.02 μm pore size) using pressure of less than 150 mm Hg, while the remaining 2 light and 1 dark bottles were similarly filtered following prefiltration through a 20 μm mesh to remove the netplankton.

Non-biological adsorption of ^{14}C on to the filters had been reported by Williams, Holm Hansen and Berman (1972), Nalewajko and Lean (1972) and Berman (1973). Preliminary trials in which control water samples were added to 3 ml of chloroform and filtered immediately after the addition of radioactive bicarbonate showed that this error could be reduced by a) Prewetting the filter before filtration with filtered sea-water and b) After filtration washing the filter with 25 ml of filtered sea-water and then fuming the filter over HCl (see Table 2).

TABLE 2. Treatment of filters and the effect on the CPM - Non-biological adsorption on the filters

Treatment	Average CPM (± 1 S.D.)
1) Sample filtered without treatment	1040.0 ± 140.9
2) Filter prewet with filtered seawater	670.7 ± 20.1
3) After filtering, filter washed with 25 ml of filtered seawater	187.3 ± 2.9
4) Filter prewet and filter washed with 25 ml filtered seawater	151.5 ± 19.1
5) After filtering, filter washed with 25 ml 0.001N HCl	139.0 ± 63.4
6) Prewet filter and washed with 25 ml 0.001N HCl	82.0 ± 19.3
7) Filter prewet with filtered seawater and filter fumed over HCl	46.7 ± 10.8

A certain amount of activity still remained after this treatment, possibly due to contamination in the original stock, and this had to be taken into account when calculating the results.

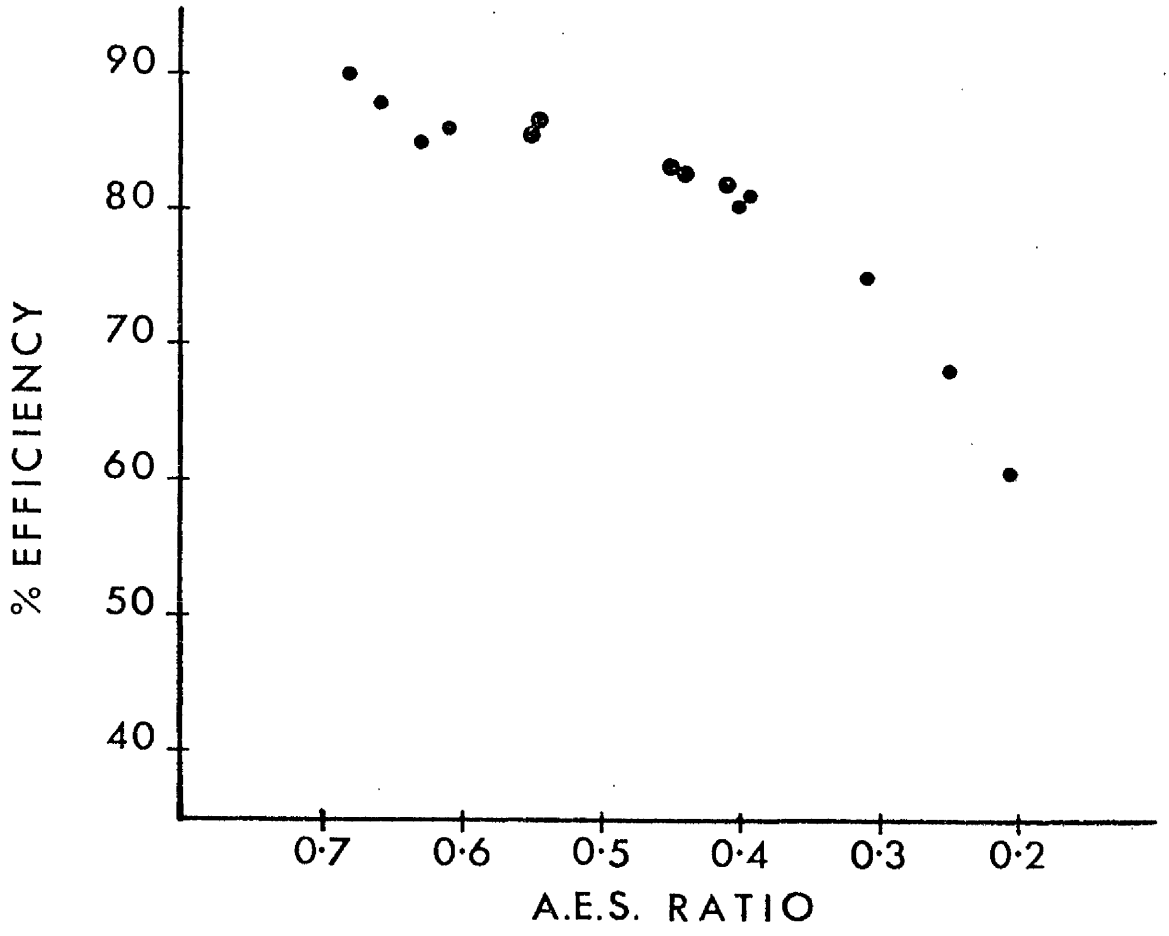


Figure 2. Calibration curve of chlorophyll-quenched hexadecane standards used to calculate the efficiency of the scintillation counting.

The above procedure of washing, fuming etc., was followed for each sample and after fuming the damp filters were transferred to scintillation vials containing 10 ml of Unisolve scintillation fluid (Koch-Light Laboratories Ltd). The scintillation vials were then left for 24 hours in the dark at a low temperature to allow the filter to be completely dissolved and then the vials were counted on a Packard Tricarb scintillation counter.

The efficiency of counting was determined using the external standard channels ratio method with a series of quenched standards of ^{14}C-labelled hexadecane of known activity. The efficiency was normally checked every six months and a new calibration curve constructed (Fig. 2 shows an example). The efficiencies with Unisolve scintillation fluid were normally in the region of 80-85%.

The ^{14}C-measured photosynthesis was calculated using the following equation.

$$P = \frac{^{14}C \text{ uptake} \times ^{12}C \text{ availability} \times 128.8 \times 1.06}{^{14}C \text{ added} \times E \times V \times T}$$

P = Photosynthetic production in mg C $m^{-3}h^{-1}$

^{14}C uptake = CPM = mean light-dark bottle values

128.8 = Volume of incubation bottles (ml).

1.06 = Isotope correction factor.

E = Scintillation counting efficiency.

V = Vol. of sample filtered from incubation bottle (ml).

T = Incubation time (in hours).

^{12}C availability = total CO_2 content of water - see 2.6.

A mean coefficient of variation between duplicate light bottle counts of the total and nanophytoplankton fractions was $4.86 \pm 3.76\%$ and $4.56 \pm 4.28\%$ respectively.

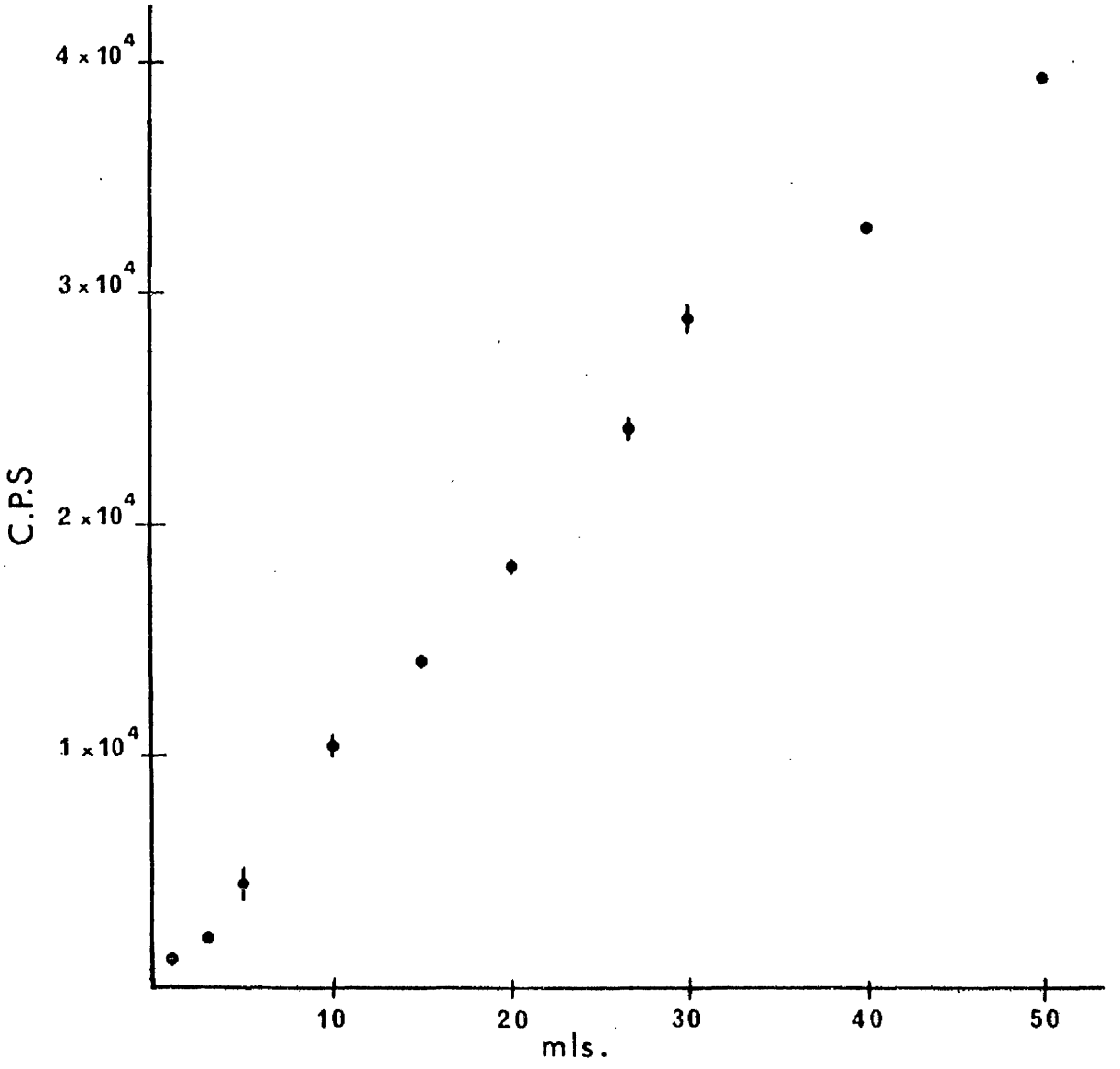


Figure 3. Graph showing the relationship between the volume of labelled sample filtered in a carbon-14 productivity experiment and the resultant count.

$r = 0.98 \quad (p < 0.01)$

Arthur and Rigler (1967) and Schindler and Holmgren (1971) reported large filtration errors with the carbon-14 technique; the latter found increased loss in samples which were abundant in nanoplankton. This effect was investigated by incubating a culture of Dunaliella primolecta with labelled sodium bicarbonate and then filtering a range of volumes from this in the usual way. The results are plotted in Fig 3 and reveal no significant loss of radioactivity with increasing volumes of sample filtered ($r = 0.98$) and the error from this effect was therefore not considered to be significant in the present study.

The levels of extracellular release were checked periodically following the method of Fogg (1974).

2.9. Determination of Particle Size Distributions/Coulter Counter

The electronic particle counter (Coulter Counter) was originally designed for counting blood cells, but has since found use in the study of particle size distributions of suspended matter in aquatic environments. The principal of the instrument is based on the fact that cells are poor electrical conductors when compared with the saline solution in which they are suspended. As a small volume of water containing particles is drawn through a small aperture which has a voltage maintained across it, each particle passing through displaces its own volume of seawater and causes a drop in voltage (due to the increased aperture impedence), which is directly proportional to the particle volume. The resulting impulses are automatically counted and recorded.

The application of the Coulter counter to determine phytoplankton biomass in natural populations has been investigated by

Mulligan and Kingsbury (1968), Evans and McGill (1970), Parsons (1969) and Zeitzschel (1977) and significant correlations have been found between the biomass determined by the Coulter Counter and by other standard techniques such as visual analysis, chlorophyll a, carbon content and particulate nitrogen. As an example, Zeitzschel (1977) found that particle volume was significantly correlated ($P < 0.01$) with phytoplankton carbon ($r = 0.893$), chlorophyll a ($r = 0.856$), and particulate nitrogen ($r = 0.840$).

Poorer correlations will, however, be expected in areas where a larger proportion of the seston is made up of silt, fine sand or bacteria i.e., in areas subject to freshwater run-off. Evans and McGill (1970) found when comparing chlorophyll values and calculated algal volumes with particle volumes measured with the Coulter Counter from reservoir samples that a linear relationship was found only above a total particle volume of 0.8×10^6 μm^3 ml^{-1}.

Used in conjunction with other methods, particularly microscopical examination of the samples, the Coulter counter appears to be able to provide rapid valid results.

The number and volume of particles in unpreserved water samples were estimated by means of a Coulter counter model TAII (the use of which was kindly provided by the Sedimentary Pollution Unit, Millport) within 1 to 3 hours of collection.

Particles of 3.17 - 101.6 μm diameter (particle diameter referred to is that of a sphere with the same volume as the particle measured) were counted in 16 channels using a 280 μm orifice. The counter was calibrated according to the procedure in the instruction manual (Coulter Electronics Limited, 1976) using Ragweed pollen grains of known diameter (18.49 μm).

In the Coulter model TAII the thresholds which divide the 16 channels are spaced at two to one vol. ratios and so the thresholds correspond to a $3\sqrt{2}$ diameter spacing i.e., every 4th channel is twice the diameter of the 1st. Sheldon and Parsons (1967) showed that, for measurements of particulate matter in the sea, the plot of particle diameter on this type of logarithmic scale against particle counts expressed as volume (or biomass) gave the most informative arrangement of data.

Counts from channel 1 were not normally included in the results as "background noise" from the instrument interfered with counts in this channel but the loss of small cells of < 3.2 μm would introduce a small error. Coincidence levels were automatically monitored by the instrument and if above 5%, the sample was diluted before counting. Samples were counted for a preset time or volume and the number of particles in each channel was automatically counted. From this, the total number of particles ml^{-1} and the total particle volume (TPV) ml^{-1} were recorded for each sample.

$$\text{TPV } (\mu m^3 \times 10^6 \text{ ml}^{-1}) = \Sigma \Delta N.V.$$

ΔN = particle No. recorded in each channel.

V = minimum particle volume in each channel.

When the total particle volumes were compared with the chlorophyll a values for the samples, the correlation coefficients ranged from r = 0.12 - 0.87.

CHAPTER 3

DESCRIPTION OF THE STUDY AREA

The Clyde Sea area, which lies between latitudes $55^{o}5'$ to $56^{o}17'$ North and longitude $4^{o}30'$ to $5^{o}40'$ West, was first described in detail by Mill (1889) who carried out a comprehensive physical survey of the area. A summary of the main features of this region is given below.

By its widest definition the area consists of the estuary of the River Clyde, which is joined by a number of other rivers, the Leven which flows from Loch Lomond being particularly important and the area to the seaward which is divided into deep basins on either side of Arran and a wide plateau or sill to the south. The limit of the area is taken as a line running south-east from the tip of the Mull of Kintyre to the Ayrshire coast. It also includes a complex of long, narrow sealochs to the north. The Clyde Sea Area thus defined has a connected water area of 1160 square miles, a volume of approximately 100 km^3 and a catchment area of 3350 square miles in extent.

The bathymetry of the Clyde Sea Area is mainly a function of glacial scouring which occurred during Pleistocene times. Overdeeped hollows cut into solid rock are common in Kilbrannan Sound, off north-east Arran and in Loch Fyne and other sea lochs. These hollows have only been partly filled with glacial, post-glacial and recent sediments and still remain as depressions, followed for the most part by modern channels (Deegan, 1974).

Tidal conditions and general hydrography of the area have been discussed by Mill (1901), Barnes and Goodley (1961), Allen (1966) and Collar (1974).

Because of its width and depth, the Firth of Clyde is not a typical estuary and in many respects can be regarded as a shallow sea. In comparison with other estuaries, the tidal ranges are relatively small. Allen (1966) found that they are largely semidiurnal although a diurnal influence of up to 10% of the range may be apparent at times. At Cumbrae, the mean spring range is 2.92 metres (9.6 feet) and the neap range is 1.76 metres (5.8 feet). This becomes amplified as it passes up the Firth reaching a spring range of 4.11 metres (13.5 feet) in Glasgow. The delay of high water from the outer to inner Firth is only 17 minutes (Mill, 1889).

The tidal currents in the Clyde Area are generally weak with the exception of certain channels where the local topography causes increased flow rates. Barnes and Goodley (1961) found a spring rate for the main tidal streams of 1.5 to 2.0 knots. Mill (1901) noted that currents increased or decreased to a marked degree according to the direction and strength of the wind. This effect was also noted by Dooley & Steele (1969) in nearshore coastal waters, off the Ayrshire coast, which responded very rapidly to changes in the wind. Offshore, however, they found that the water movement was more complex with the flow being part of the large scale wind-induced circulation of the Firth.

The most recent data, available from Steele, McIntyre, Johnston, Baxter, Topping and Dooley (1973) showed that the estuarine circulation is barely detectable from current measurements. The estuarine inflow was detected along the eastern shores of the Firth where the water appears to originate from the Irish Sea. Except in this narrow strip the salinity of the surface water is relatively low and constant over

the whole Firth to the estuary. Measurements indicate that this upper water flows slowly southward above the depth of the strong pycnocline at about 15 m with the amount of freshwater in this layer rarely exceeding 2%. Although currents in the Clyde Sea Area are slight, the retention time of water is not long as spatial scales are small and the estimated residence time of water in the area is approximately one month (Steele et al, 1973).

As stated by Hinton (1974) there is no published data available for circulatory patterns in the Fairlie Channel, but from a general concensus of opinion, it appears that there is an anti-clockwise circulation of surface water within the Channel. This results in a continued southward flow of water at Keppel Pier throughout the tidal cycle, with the exception of a short period around low tide, when the direction changes to northward.

The climatology of the area has been reviewed by Mill (1889) and Barnes (1955). In the latter review, it was stated that the temperature trends are typical of a north temperate zone and that the rainfall is typical of a wet oceanic climate. The prevailing winds in this area are usually from the southwest quadrant, except for March and May when the north-easterlies predominate.

Except in the estuary, where stratified layers of freshwater on top of salt water often occur (Allen, 1966), temperature and salinity usually vary only gradually in the area. Mill (1889) found the highest mean salinity value of 34.2% in the north channel, falling to around 33% at the Cumbraes. Within narrow channels the salinity of surface waters was apt to be lowered by spells of wet weather or heavy rain storms but this reduction in salinity was not found at any depth.

Both Mill (1889) and Barnes (1955) showed a clear reduction in salinity in the Clyde Sea Area during the winter months, reaching a minimum value of 31.26% at Millport in January. Maximum surface values were recorded in summer between July and September. Barnes (1955) found a maximum value of 32.98% at Millport in June. Both authors correlated salinity changes with changes in the pattern of seasonal rainfall.

Early studies on the chemical nature of the water mass in the Clyde Sea Area involved a study of carbonate and sulphate levels by Mill (1889) and a seasonal survey of the dissolved phosphate, the pH and the percentage saturation of oxygen in Loch Striven by Marshall and Orr (1927). Following these early works on the chemistry of the Clyde, little attention was given to such studies until recent years when new impetus was given by the increasing emphasis on water pollution.

A detailed survey of the dissolved phosphate, silicate and nitrate levels in the Fairlie Channel was carried out by Hinton (1974). Sampling twice daily over a period of one year, Hinton (1974) found that the winter maximum values for the three nutrients (phosphate - 1.6 μg at.P l^{-1}, silicate - 14.95 μg at.S l^{-1} and nitrate - 23.7 μg at. N l^{-1}) exceeded those recorded for any other coastal region, while summer minimum values, although low, never reached undetectable levels.

It has been found that generally, in the Firth of Clyde the background winter nitrate level is 25% higher than that of the North Sea and that this is due to nutrient addition from the River Clyde and the Irish Sea (Steele et al, 1973).

The nitrate enrichment of the region of the Firth in the vicinity of Irvine Bay was studied by Johnston et al (1974) for a

short period during April. The lowest nitrate values were found along the eastern coastline of Kintyre (5-9 μg at. N l^{-1}) while in the upper Firth levels were markedly higher to the west of Cumbrae (12-14) than to the east (10.5-12 μg at. N l^{-1}). Within Irvine Bay itself, localized nitrate values exceeding 30 μg at. N l^{-1} were found on occasions.

Nutrient levels, including ammonia levels, throughout the Clyde Sea Area are monitored at regular intervals by the Clyde River Purification Board and a summary of their results over the period 1974-1975 are published in a baseline report (CRPB, 1976).

3.2. SAMPLING PROGRAMME

The University Marine Biological Station which is situated in the southeast corner of the Isle of Cumbrae (latitude 55°57', longitude 4°46' W Fig. 4) provided a convenient base for the main part of the field work carried out in this survey and the use of the Marine Station's research boats, RV's Leander and Evadne, were kindly made available for sampling.

The major part of the sampling programme was carried out in the Fairlie Channel which separates Great Cumbrae from the mainland. This channel is one of two deep channels which run up either side of the Great Cumbrae. It has a maximum depth of 35 metres between Keppel Pier (Marine Station pier) and the limit of the Hunterston sands (the Perch) and the width of the deep channel is approximately 1.4 km (Fig. 5).

This area was chosen for sampling since it was convenient, with only a small boat time requirement and usually only a minimal delay between collection and processing of the samples on returning to the Marine Station. In addition the area around Hunterston has become increasingly important in recent years as a site of industrial development. The deep water facilities and the availability of sea-water for cooling purposes has resulted in the development of two nuclear power stations with a third planned, the British Steel Corporation development of an ore terminal and direct ore reduction plants and an adjacent site has been developed by a consortium (Andoc) as a construction site for concrete oil platforms. An intensive survey of the larger phytoplankton forms in this channel had previously

Figure 4. Map of the Inner Firth Region of the Clyde Sea Area. The numbers shown indicate sampling stations used by the Sedimentary Pollution Unit, Millport (Station 3, which is not indicated lies south of Garroch Head just outwith the southernmost region of the map). The main coastal industrial developments are indicated (▲).

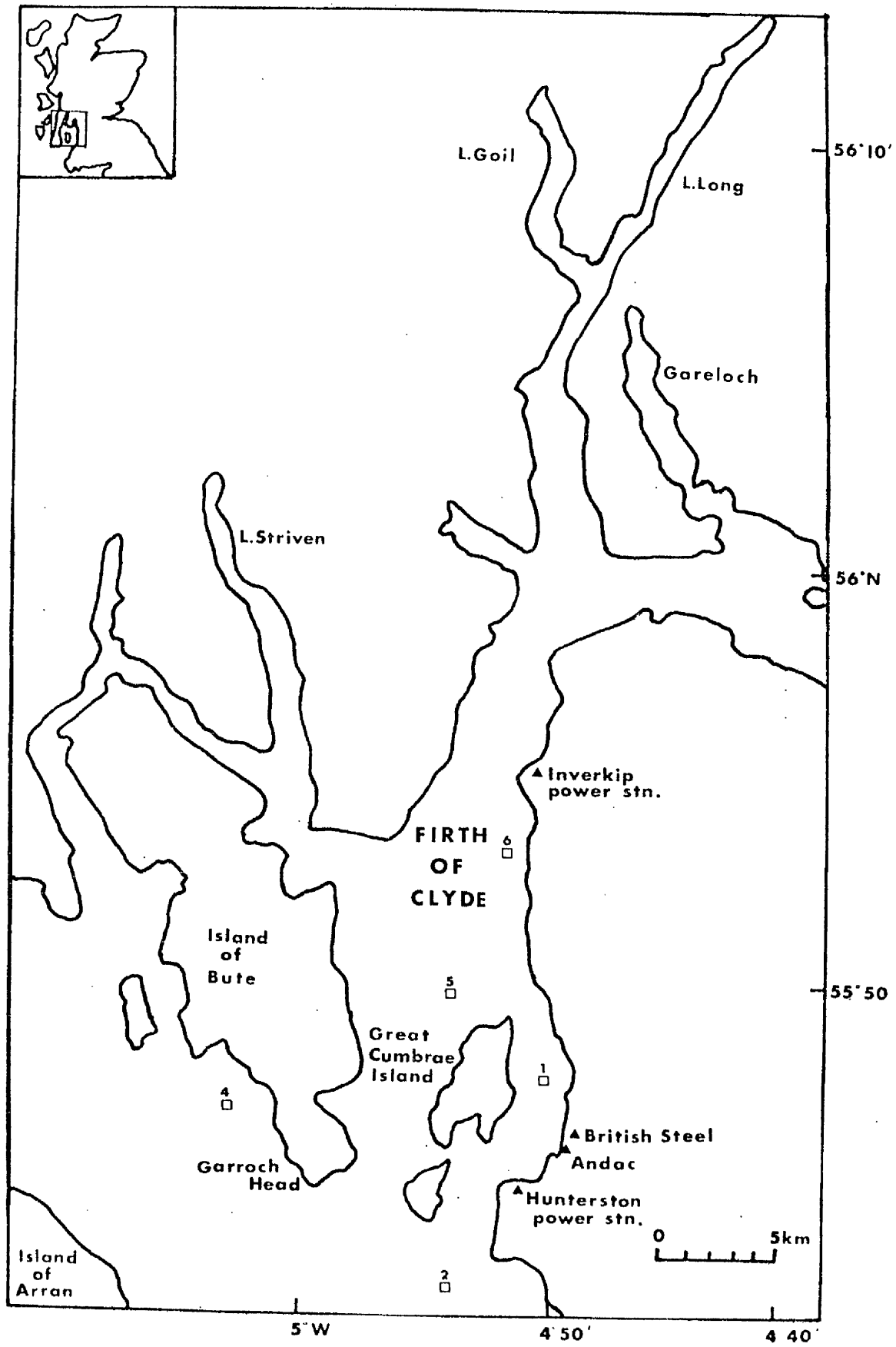
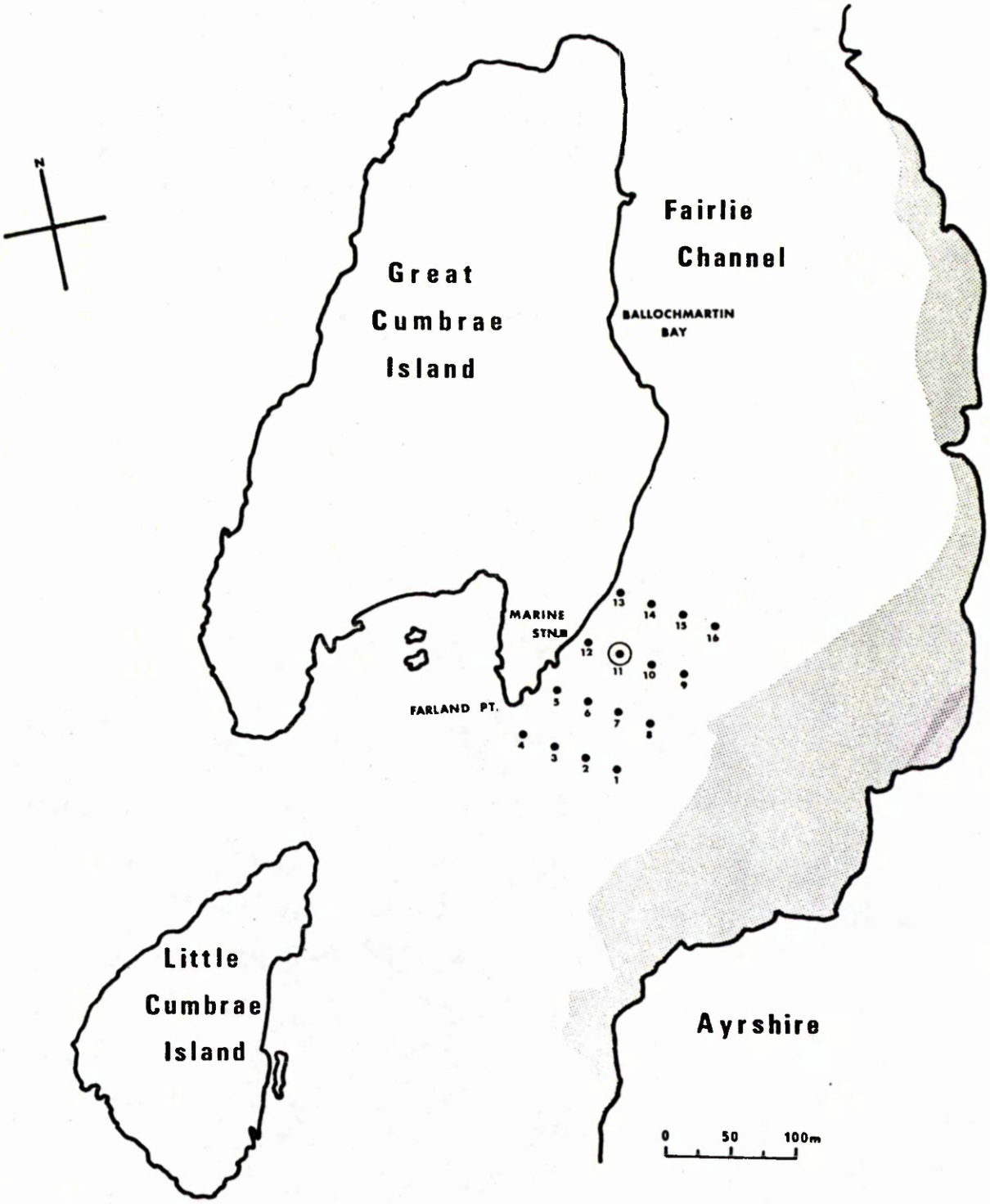

L.Goil
L.Long
56°10'
Gareloch
L.Striven
56°N
Inverkip
power stn.
FIRTH
OF
CLYDE
6
Island
of
Bute
5
55°50
Great
Cumbrae
Island
1
4
British Steel
Andac
Garroch
Head
Hunterston
power stn.
0
5km
Island
of
Arran
2
5°W
4°50'
4°40'

Figure 5. A detailed map of the Fairlie Channel showing the position of the main sampling station (Station 11) and the positions of the grid stations. The stippled area represents Huntersston and Fairlie Sands.


N
Great
Cumbrae
Island
Fairlie
Channel
BALLOCHMARTIN
BAY
MARINE
STN.
FARLAND PT.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Little
Cumbrae
Island
Ayrshire
0
50
100m

been carried out by Hinton (1974) and for comparative purposes it was considered useful to sample in the same area.

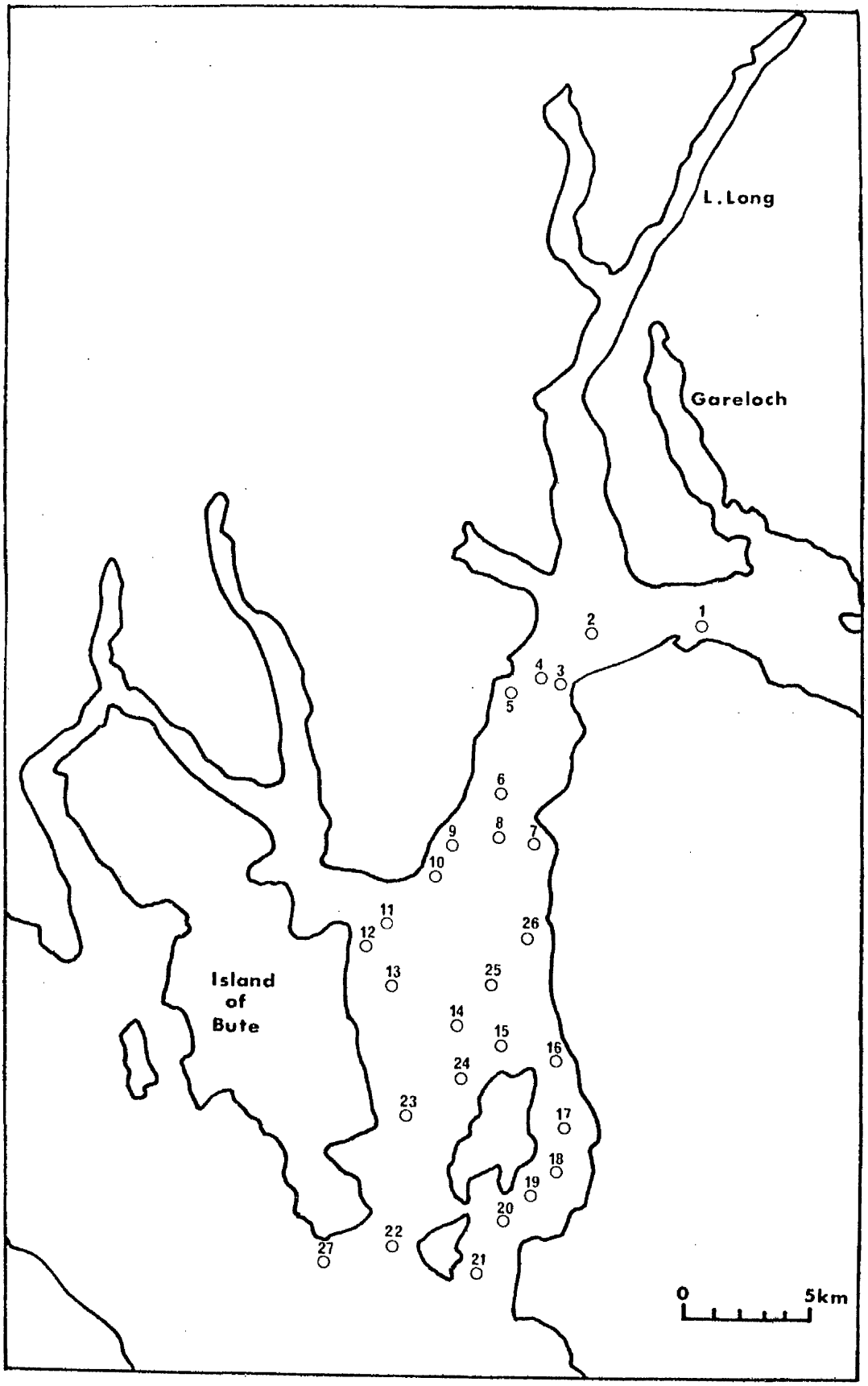
The field work was divided into four sections:-

1) The first part of the study was undertaken to determine if there was a nanophytoplankton population present in the Firth and, if present, if its significance varied seasonally. To do this, weekly samples were collected from a deep, mid-channel station (station 11, Figure 5) in the Fairlie Channel from February 1976 to December 1976. Samples were not collected during August of this year as no boat was available for sampling. Water samples were collected from the surface, 1, 5 and 10 metres and the samples for productivity measurements were incubated on station. If, however, the weather was particularly unfavourable, the samples were incubated in Ballochmartin Bay (Figure 5) in a more sheltered position.

   Sampling at this station was continued for a second year (January 1977 to December 1977) and into the spring period of 1978, but apart from selected periods (i.e., spring outburst or periods of expected high nanophytoplankton production) the sampling period was reduced to two to three week intervals.

2) Six grid surveys were carried out at different periods during the course of the field work to check on the reliability of the results obtained from the single sampling station and to obtain a more detailed knowledge of conditions in the Fairlie Channel. Samples were collected at 1 metre depth from the sixteen stations illustrated in Figure 5. The grid was designed to include the normal sampling station, station 11. It covered an area of 0.75 km^2 and the distance between the stations lying across the channel was

Figure 6. The positions of the Clyde River Purification Board's sampling stations.


L. Long
Gareloch
Island of Bute
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
0
5km

200 m while those lying in a north-south direction down the channel were 425 m apart. The samples were collected within a two hour period and the state of the tide at the time of sampling varied between grids. Chlorophyll levels, the particle size distribution and the species composition of the stations were compared.

3) By accompanying the Clyde River Purification Board on several of their sampling trips of the Inner Firth and the Sedimentary Pollution Unit from the Marine Station on several of their collection trips, the sampling programme of the present study was extended to cover a much wider area of the Firth of Clyde.

At regular intervals (usually monthly) the Clyde River Purification Board carry out surveys of the nutrient levels in the Inner Firth collecting samples from the stations shown in Fig. 6 and listed in Table 3, and the samples from these stations were collected at 1 metre depth on five occasions during the period December 1977 to May 1978. From these samples, the chlorophyll *a* levels of the total and the nanophytoplankton fraction were measured. Sub-samples were fixed in Lugol's Iodine and raw enrichment cultures were set up.

Samples were also collected on four occasions at the sampling stations used by the Sedimentary Pollution Unit for their zooplankton work. These stations are illustrated in Figure 4 and detailed in Table 4 below.

Table 3. List of the Clyde River Purification Board's Sampling Stations in the Inner Firth with map references and Decca coordinates (for use with ship's "Decca" Navigator System)

Station & No.	Latitude	Longitude	Decca Coordinates
1. CMT8	55° 57.7'N	4° 50.0'W	N/A
2. North Cloch	55° 57.7'N	4° 52.5'W	D 20.1 B 67.2
3. Cloch Point	55° 56.55'N	4° 52.8'W	D 20.0 B 63.4
4. CMT7	55° 56.85'N	4° 53.65'W	D 20.8 B 63.5
5. Gantocks	55° 56.32'N	4° 55.2'W	D 22.0 B 60.0
6. CMT6	55° 53.7'N	4° 55.25'W	D 21.4 B 50.0
7. Wemyss Bay	55° 52.45'N	4° 53.95'W	D 20.0 A 78.0
8. UIFM 1	55° 52.23'N	4° 55.2'W	D 21.0 A 76.0
9. UIFM 2	55° 52.1'N	4° 56.7'W	D 22.3 A 74.0
10. Toward Point	55° 51.9'N	4° 58.0'W	D 23.5 A 72.0
11. Ent. Rth. Sd. (Entrance Rothesay Sound)	55° 50.3'N	4° 59.4'W	E 0.8 A 65.0
12. Ascog	55° 49.6'N	4° 59.65'W	E 1.0 A 63.0
13. CMT5	55° 49.2'N	4° 58.67'W	D 23.5 A 61.5
14. MIF 1	55° 48.6'N	4° 56.75'W	D 21.5 A 61.0
15. MIF 2	55° 48.1'N	4° 54.8'W	D 19.5 A 61.0
16. Largs	55° 47.7'N	4° 52.2'W	D 18.0 A 61.0
17. CMT4	55° 45.8'N	4° 52.7'W	D 17.0 A 53.8
18. Hunterston 1	55° 44.15'N	4° 55.3'W	D 19.0 J 75.0
19. Hunterston 2	55° 44.55'N	4° 54.1'W	D 18.0 J 78.0
20. Hunterston 3	55° 44.92'N	4° 52.95'W	D 17.0 A 50.0
21. Largs Ch.	55° 43.0'N	4° 55.6'W	D 19.0 J 70.0
22. Main Ch.	55° 43.5'N	4° 58.95'W	D 22.5 J 69.5
23. CMT3	55° 46.18'N	4° 58.9'W	D 23.0 A 50.0
24. Mountstuart	55° 48.0'N	4° 58.0'W	D 22.5 A 57.8
25. Ex 1.	55° 50.0'N	4° 56.4'W	D 21.5 A 66.7
26. Skelmorlie	55° 51.05'N	4° 54.0'W	D 19.7 A 72.8
27. Garroch Head (CMT2)*			E 1.6 J 64.9

TABLE 4 Positions of the Sedimentary Pollution Unit's Sampling Stations

Station	Latitude	Longitude	Decca Cordinates	
1) Hunterston.	55°47'N	4°50'W	D 17.5	A 51.5
2) Portencross	55°43.5'N	4°53'W	D 18.9	J 64.8
3) Garroch Head*	55°41'N	4°59'W	E 0.00	I 74.7
4) Stravanan Bay	55°47'N	5°02'W	E 5.1	J 70.1
5) Midchannel Stn.	55°49.5'N	4°54'W	D 22.5	A 53.3
6) Skelmorlie	55°53.5'	4°51'W	D 20.8	A 71.6

*The stations in Table 3 and 4 at Garroch Head are in the area used by Glasgow Corporation for the dumping of sewage sludge. Approximately 1-1.5 megatonnes of sludge is dumped annually. Within the area of dumping, the deep water movements are minimal and so the effects of this huge organic loading is restricted to a small area of the sea bed - about 15-20 km. Surveys carried out in the area show that there is an increase in the concentration of organic matter and heavy metals in the sediments of the dumping ground and a decrease in the diversity of marine life (CRPB, 1976).

The nanophytoplankton biomass and productivity of two adjoining sea lochs, Loch Long and the Gareloch, were compared during a period of study in August 1976.

4) In addition to the survey of the temporal changes in Fairlie Channel, a concurrent survey was carried out in two littoral rockpools in the vicinity of the Marine Station, Cumbrae. Chlorophyll, productivity and nutrient levels were measured in these and compared with the adjacent levels in the sea. These pools were sampled weekly from February 1976 till May 1976 when one of the pools dried out and it was decided to then concentrate on the work in the Fairlie Channel.

A log of all the field trips undertaken is given in Appendix 2.

CHAPTER 4. SEASONAL VARIATIONS IN THE OCCURRENCE AND CONTRIBUTION TO PRODUCTIVITY OF THE NANOPHYTOPLANKTON IN THE FAIRLIE CHANNEL

The results discussed in this section are based on those obtained from the water samples collected at station 11 during the period February 1976 to December 1977. The spring period of 1978 was also investigated and the results from this period although not included in the figures, will be discussed where appropriate.

4.1. Environmental Factors

4.1.1. Weather

The local weather conditions during 1976 and 1977 are summarized in Figures 7 to 10. The sea surface temperature at Keppel Pier (Fig 7a) reached a winter minimum (7.59°C) in March 1976. Following this, the sea temperature rose progressively to reach maximum levels during July and August of 14.8°C and 14.6°C respectively. The decrease in sea temperature following the summer maximum was more gradual than the increase in spring, reaching a winter minimum in February 1977 (6.99°C). The highest mean monthly sea surface temperature in 1977 was 14.0°C in August.

The sea surface temperature followed closely the changes in maximum and minimum recorded air temperatures (Fig 7b). The mean monthly maximum and minimum values for these in 1976 and 1977 and the months in which these occurred are given in Table 5 which also includes the values recorded for the period 1949-1953 (Barnes, 1955). More extreme temperatures were recorded in 1976/77 than in the period 1949-53.

Fig 7(c) gives the mean monthly values for the hours of sunshine recorded per day (at Prestwick). In 1976 the low winter

Figure 7. Climatological data.

a) Monthly mean sea surface temperature at Keppel Pier.

b) Monthly mean maximum and minimum air temperatures.

c) Monthly mean sunshine levels.

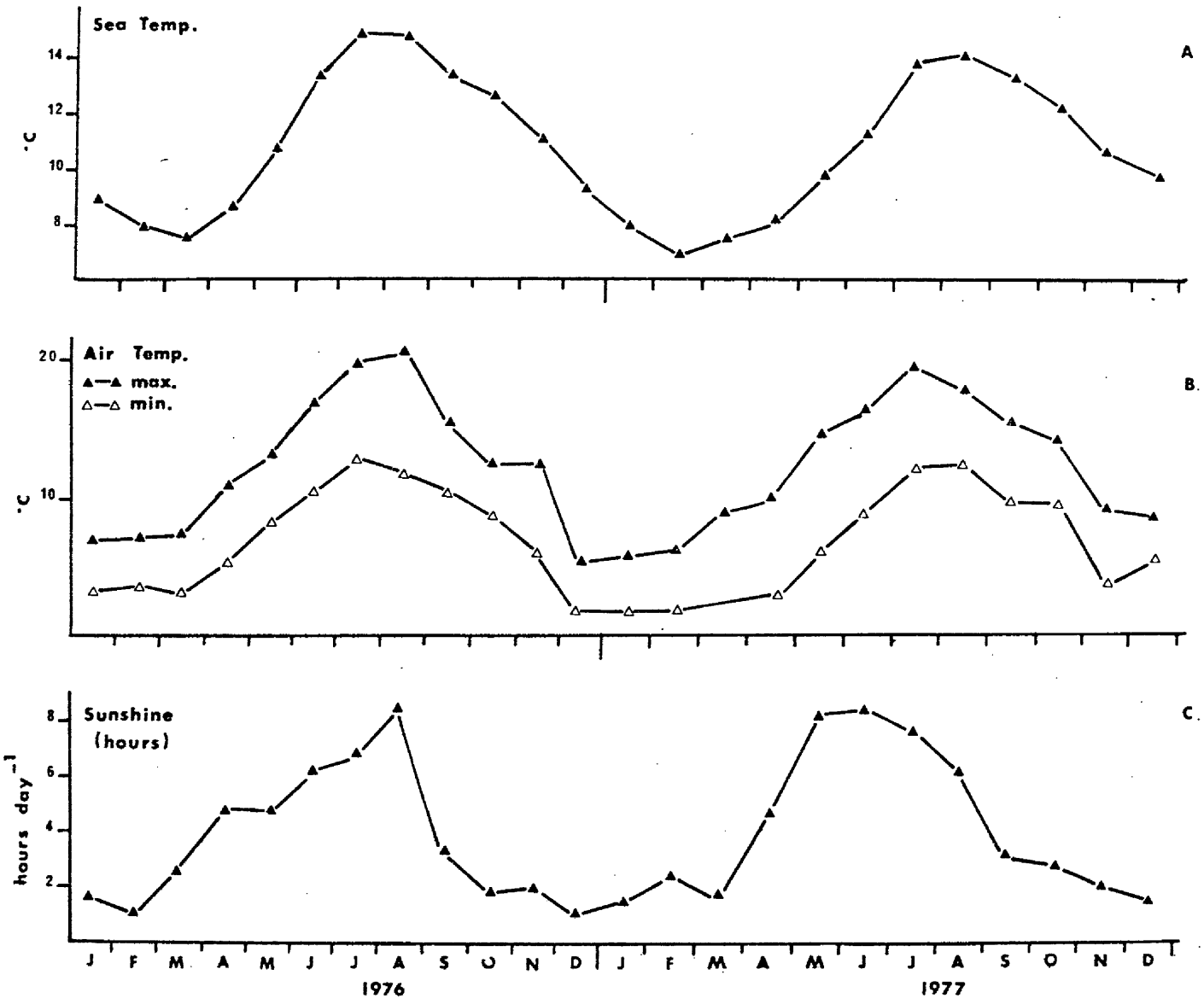
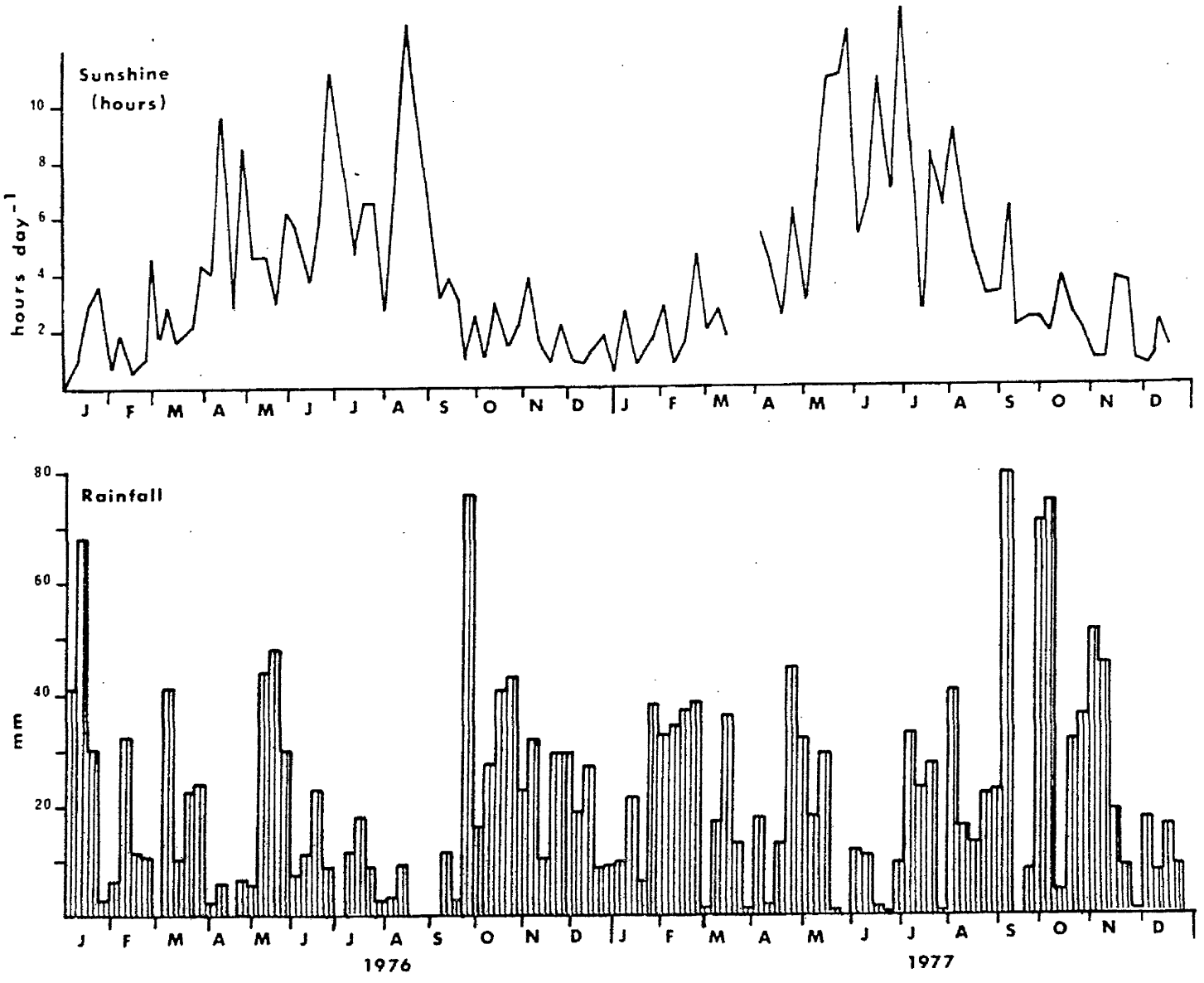

Sea Temp.
A
°C
14
12
10
8
Air Temp.
▲—▲ max.
△—△ min.
B.
°C
20
10
Sunshine
(hours)
C.
hours day⁻¹
8
6
4
2
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977

Figure 8 a) Weekly average levels of sunshine per day.

b) Weekly total rainfall levels in mm.


Sunshine
(hours)
hours day^{-1}
10
8
6
4
2
J F M A M J J A S O N D J F M A M J J A S O N D
Rainfall
mm
80
60
40
20
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977

levels gradually increased to a peak in August (8.58 h day^{-1}). In 1977, however, the maximum sunshine levels were in May (8.29 h day^{-1}) and June (8.44 h day^{-1}) with decreasing levels over July and August.

Table 5. Mean monthly maximum and minimum air temperatures at Millport

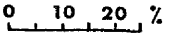
	MAXIMUM	MINIMUM
1976	20.4 (August)	3.0 (March)
1977	19.3 (July)	1.8 (January)
1949-53	14.1 (July)	4.3 (February)

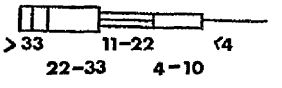
The weekly average sunshine levels (Fig 8a) were also of interest as the productivity experiments were carried out once a week. The values varied considerably from week to week and large day to day fluctuations were also found. Over the two year period, approximately 50% of the sampling days recorded above weekly average values and 50% had below average sunshine (40 days with higher than average values : 43 below).

The rainfall levels were plotted as weekly total values in mm (Fig 8b). 1976 was a comparatively dry year (total rainfall = 952.4 mm) when compared with 1977 (1147.6 mm) and 1949-53 (1143 mm). The wettest and driest months occurred at different times in the two years. In 1976, January was the wettest month (142.39 mm) and August was the driest with 12.7 mm. The wettest month in 1977, however, was in September (158.4 mm) while May, as the driest, recorded 48.4 mm.

Figures 9 and 10 summarize the wind data (for Prestwick) for the early spring and summer periods of 1976 and 1977 (August 1976 was not included as no sampling was carried out during this month). Barnes (1955) found that with the exception of March and May

Figure 9. Summary of monthly wind speeds and direction. Early spring and summer 1976.

Scale of frequency : 

Scale of force : 

1976

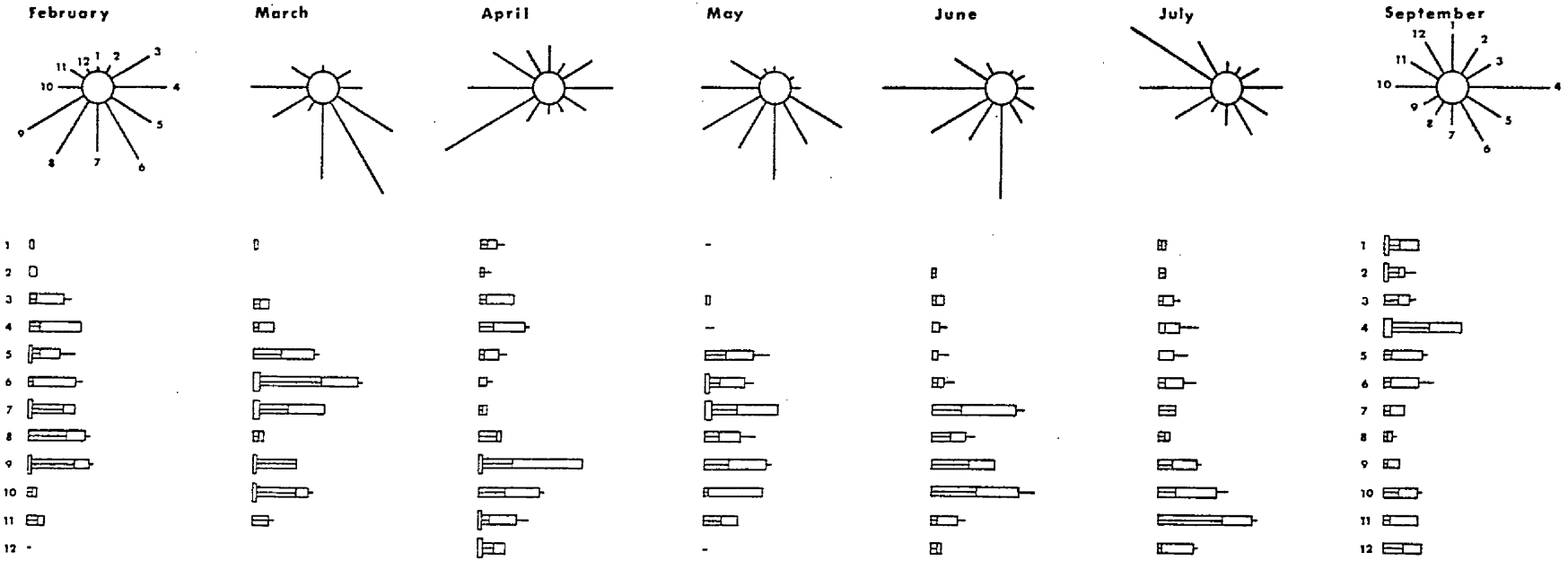
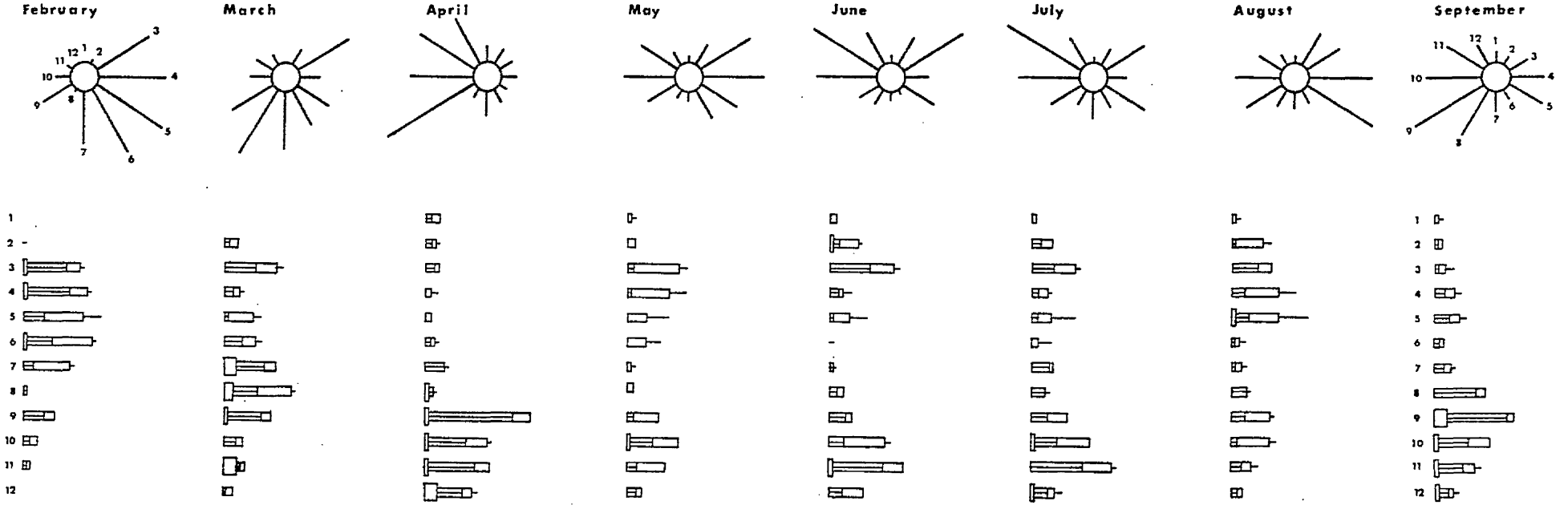


Figure 10. Wind data. Spring and Summer 1977.

Scale for frequency and force :

see Fig. 9.

1977



the most frequent winds at Millport were always from the Southwest quadrant while in March and May a high proportion were from the north-east. The present results did not follow this pattern. In the months considered, the wind was in the south-west quadrant for only 18-19% of the time while during March and May the wind was from the north-east for 2% of the time in 1976 and 18% in 1977.

The results would suggest that either the winds differed quite significantly from the normal during 1976/77 or that the wind patterns at Prestwick differed from those at Millport, although since the winter months were not taken into account, direct comparison with figures for 1949-53 (Barnes, 1955) cannot be made.

Accepting the reservation that the direction of the prevailing winds may perhaps vary between Millport and Prestwick, the wind speeds during 1976 and 1977 (at Prestwick) were compared to see if differences occurred between the two years. The main differences were found during March and April; in March 1977 there was a higher proportion of wind speeds above 22 knots (9.6%) than in the previous year (4.8%) and during April 1977, 66.4% of the wind speeds were above 11 knots, of these 6.5% were above 22 knots while the corresponding figures for 1976 were 32.4% and 2.4% respectively.

4.1.2. Hydrography

In midchannel, at station 11, the water column was well mixed throughout most of the year with the exception of short periods during the summer months (Figure 11). In 1976 slight stratification was observed in July. During August when no records could be obtained, the weather was particularly sunny (Fig 7c) and dry (Fig 8b)

Figure 11. Temperature-depth profile at Station 11, Fairlie Channel. 1976-1977.

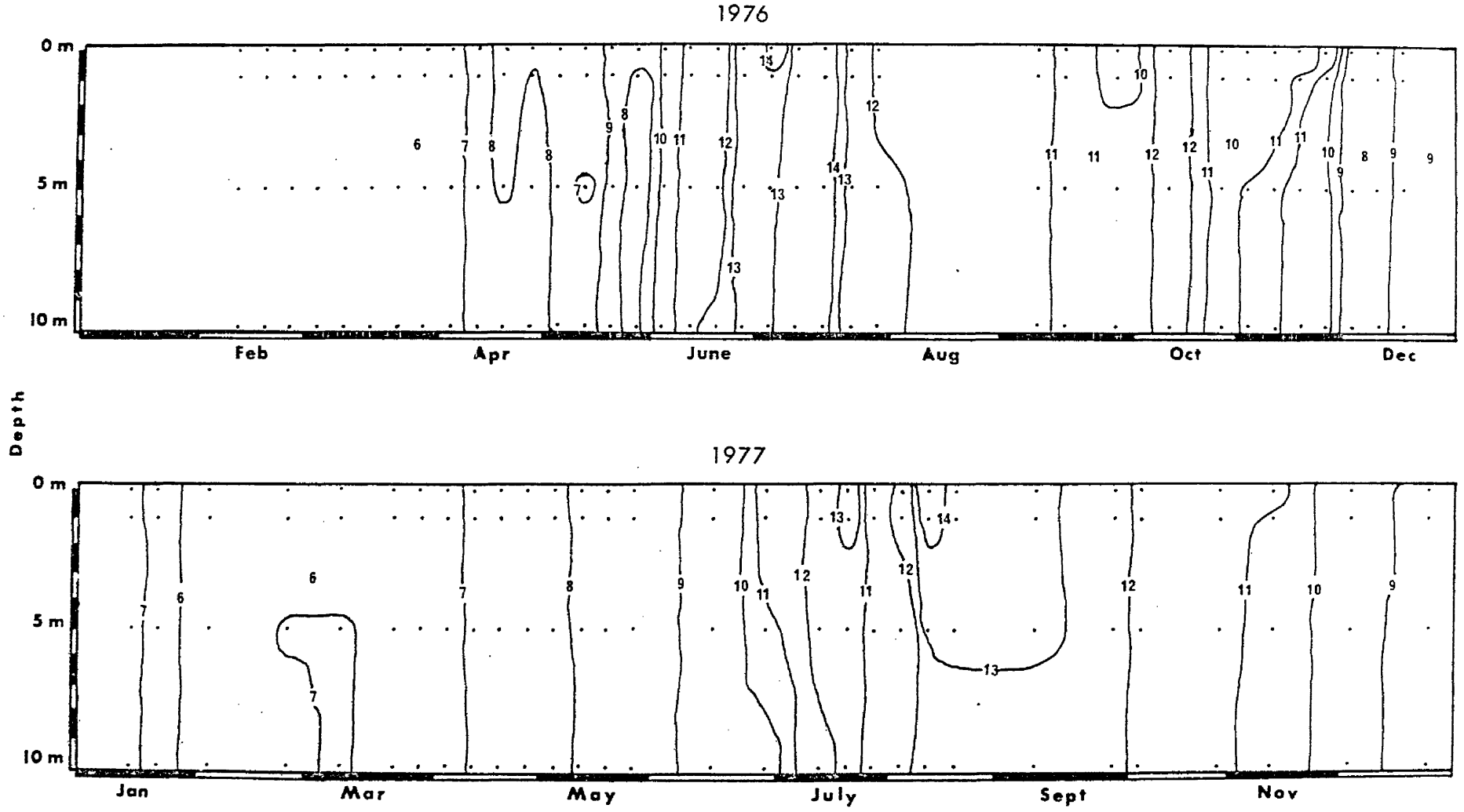

1976
0 m
5 m
10 m
Feb
Apr
June
Aug
Oct
Dec
Depth
1977
0 m
5 m
10 m
Jan
Mar
May
July
Sept
Nov

Figure 12. Salinity-depth profile at Station 11, Fairlie Channel. 1976-1977.

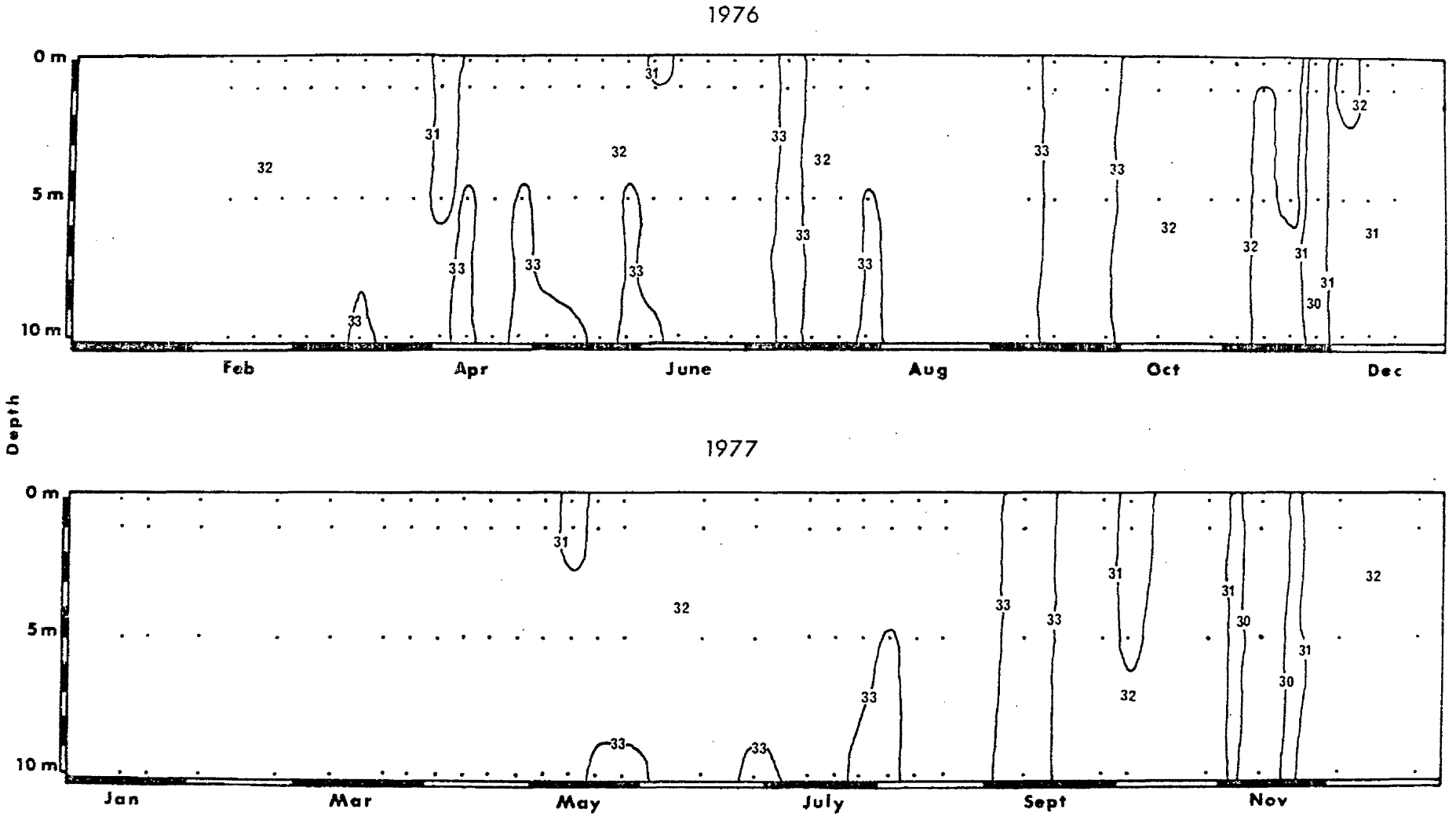
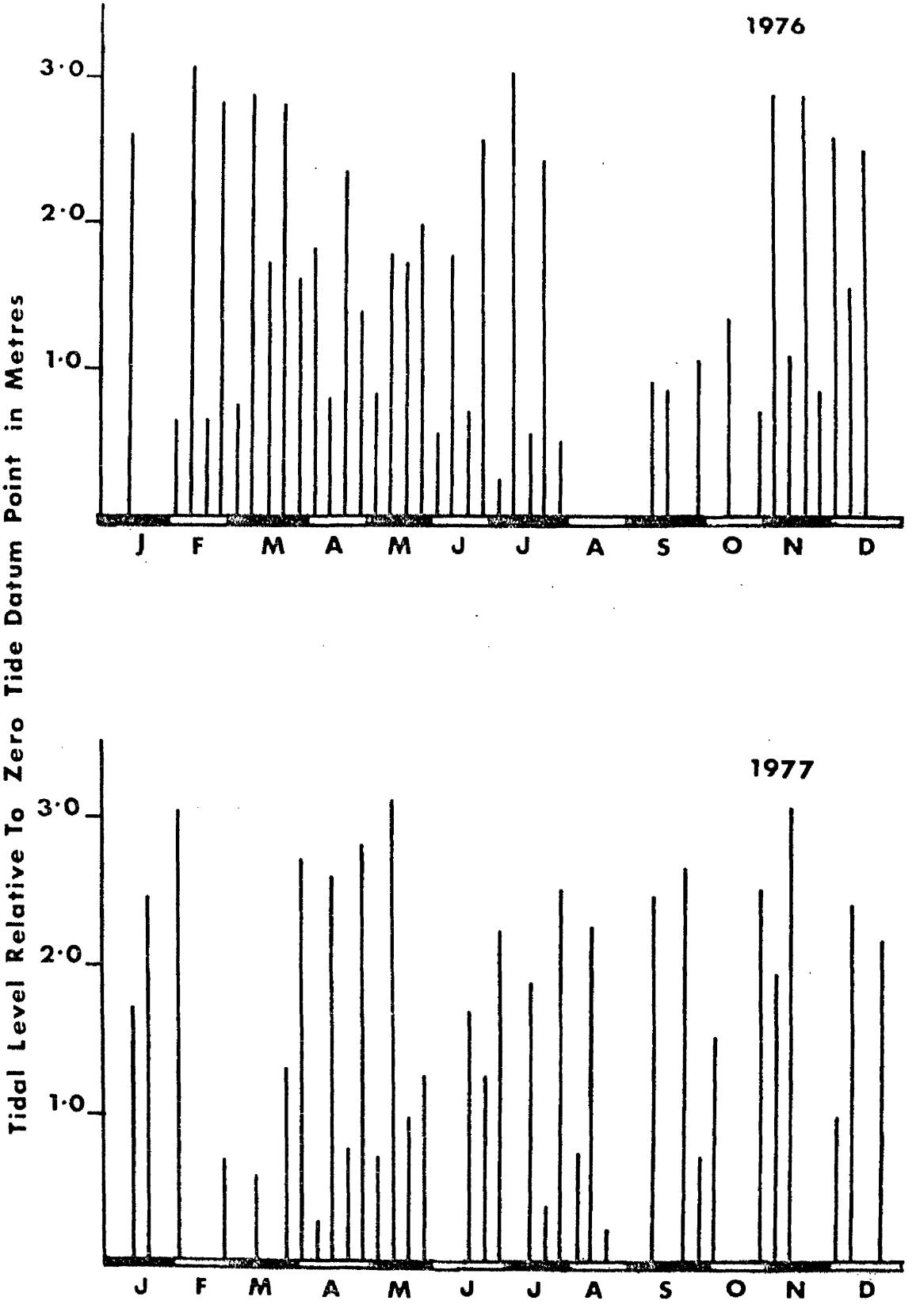

1976
0 m
5 m
10 m
Depth
Feb
Apr
June
Aug
Oct
Dec
1977
0 m
5 m
10 m
Jan
Mar
May
July
Sept
Nov

Figure 13. Tide levels at times of sampling.


1976
3·0
2·0
1·0
J F M A M J J A S O N D
1977
3·0
2·0
1·0
J F M A M J J A S O N D
Tidal Level Relative To Zero Tide Datum Point in Metres

and it is likely that stratification occurred during this period. Both Loch Long and Gareloch were found to be stratified at this time. Thermocline development was observed during late June and August 1977. The minimum and maximum recorded surface temperature at Station 11 during 1976 were 6.4°C (March 25) and 14.8°C (July 15) and in 1977 the lowest recorded surface temperature was 5.9°C (February 24) and the highest was 14.2°C (August 11).

A depth-time diagram of salinity (‰) values is shown in Figure 12. The surface salinity values fluctuated between a minimum of 31.2‰ (April 8) and a maximum of 33.3‰ (Sept 15) in 1976 and minimum and maximum values of 30.2 (Nov 10) and 33.0‰ (Sept 8) in 1977. The reduction in salinity values due to freshwater run-off was normally only observed down to a maximum depth of 10 metres in the Fairlie Channel. The salinity values recorded may have been affected by the state of the tide at time of sampling (Barnes and Goodley, 1958) and these are shown in Figure 13.

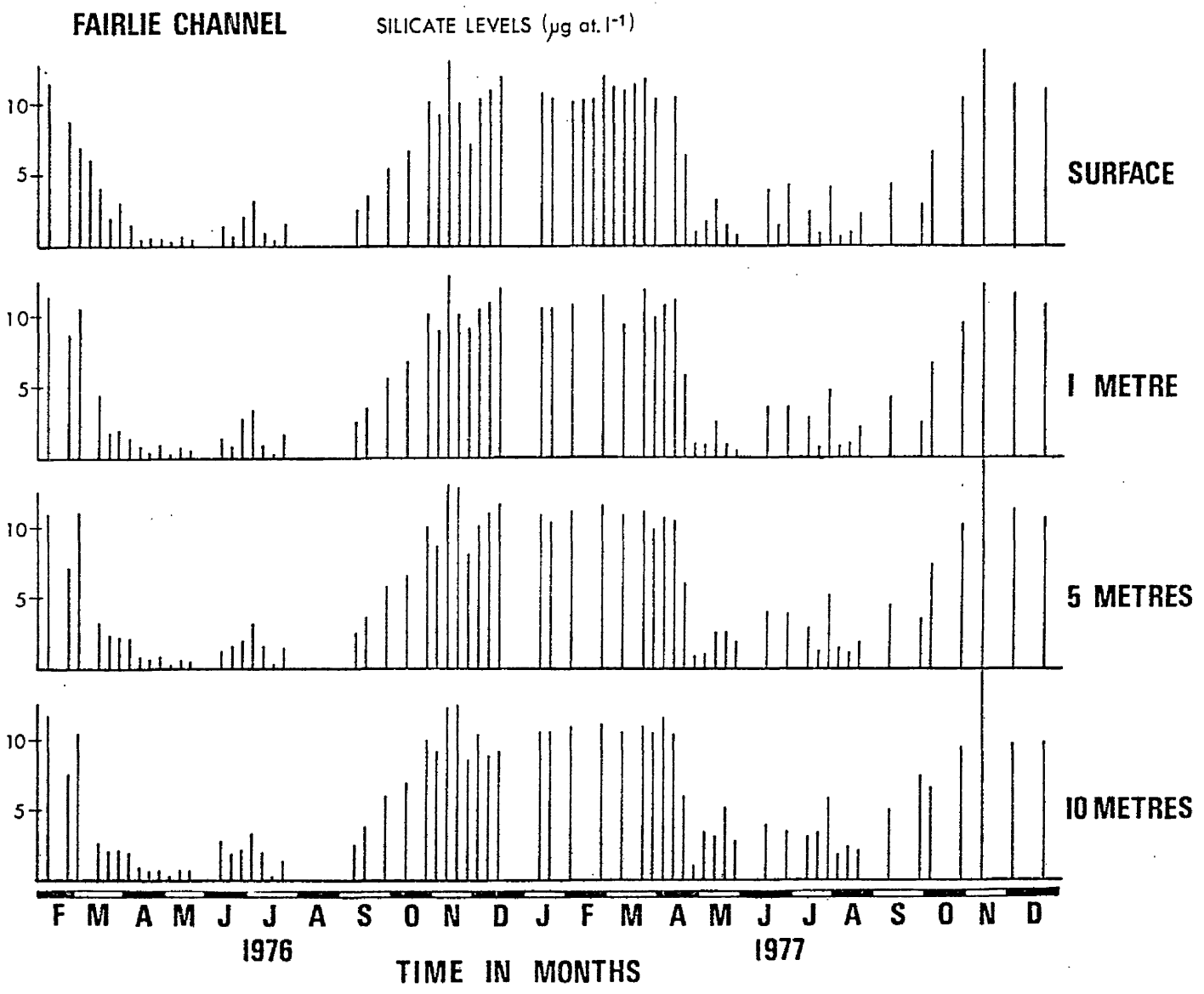
4.1.3. Nutrients

The results of the nutrient analyses (silicate, nitrate and phosphate) are summarized in Figures 14, 15 and 16. The minimum and maximum recorded levels are tabulated in Table 6 and compared with those found by Hinton (1974) for the same area in 1973.

Table 6. Maximum and minimum recorded nutrient values (in μg at. l^{-1})

	1976		1977		1973 (Hinton, 1974)	
	Max.	Min.	Max.	Min.	Max.	Min.
Phosphate	1.76	0.12	1.32	0.31	1.60	0.20
Silicate	11.5	0.26	12.33	0.8	13.4	0.40
Nitrate	20.0	0.75	21.9	1.24	23.7	4.00 (1973) < 0.5 (1972)

Figure 14. Seasonal changes in the silicate ($\mu g\ at.l^{-1}$) levels at the surface, 1 metre, 5 metre and 10 metre depths. Station 11, 1976-1977.


FAIRLIE CHANNEL
SILICATE LEVELS (μg at. l⁻¹)
10
5
SURFACE
1 METRE
5 METRES
10 METRES
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

The levels found were similar to those obtained by Hinton (1974) although the minimum values recorded for all three nutrients in 1977 were higher than those found in either the previous year or in 1974. When comparing the nutrient levels found in the Firth of Clyde with those from other coastal areas, Hinton (1974) found that the concentrations of the nutrients in the Fairlie Channel were higher than those recorded for any other area.

Dissolved Silica (Fig 14)

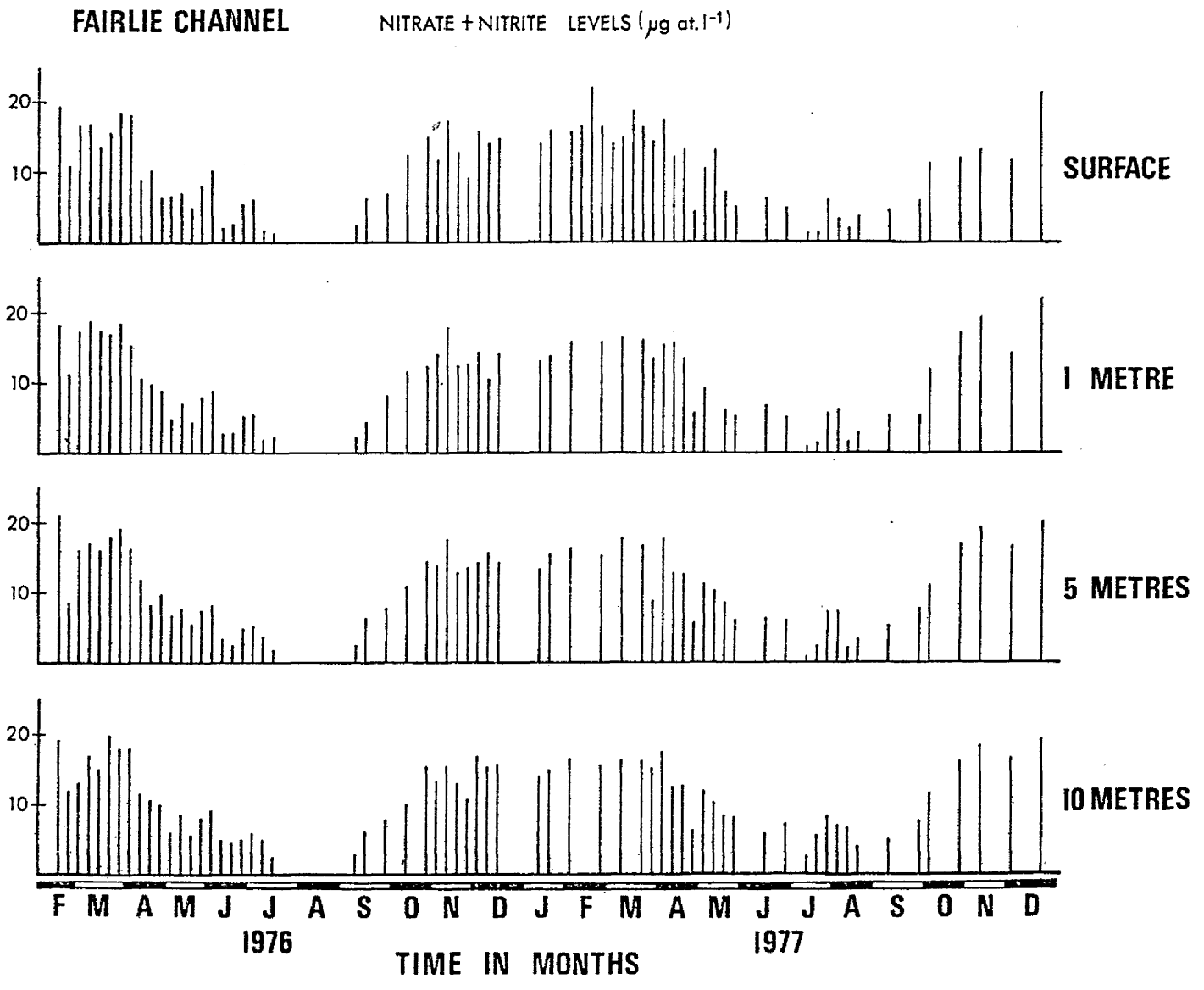
During the winter months from November until early March, the silicate at all depths was high ranging from 6.90 to 13.1 μg at. Si l^{-1}. During the time of the spring diatom increase the silicate levels declined rapidly. During March 1976 the silicate decreased from 6.9 μg at. l^{-1} to 3.14 μg at. l^{-1} and during April, after the main period of the bloom, was further reduced to 0.42 μg at. l^{-1} reaching a minimum value of 0.21 μg at. l^{-1} on May 5. Levels remained low over summer and then gradually increased from September onwards.

In 1977, silicate remained high until mid-April when it declined from 6.30 μg at. l^{-1} (April 21) to 0.95 μg at. l^{-1} within a week. The chlorophyll *a* values recorded on April 21 were the highest of the spring period. During the summer months, silicate remained higher than that recorded in the previous year, but since the interval between sampling had been increased, lower levels could have been missed.

Nitrate (Fig 15)

The decrease in nitrate during the spring outburst from the high winter values was more gradual than that of silicate in both

Figure 15. Seasonal changes in the combined nitrate plus nitrite levels ($\mu g\ at.l^{-1}$) at the sampling depths. Station 11, 1976-1977.


FAIRLIE CHANNEL
NITRATE + NITRITE LEVELS (μg at.l⁻¹)
20
10
SURFACE
1 METRE
5 METRES
10 METRES
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

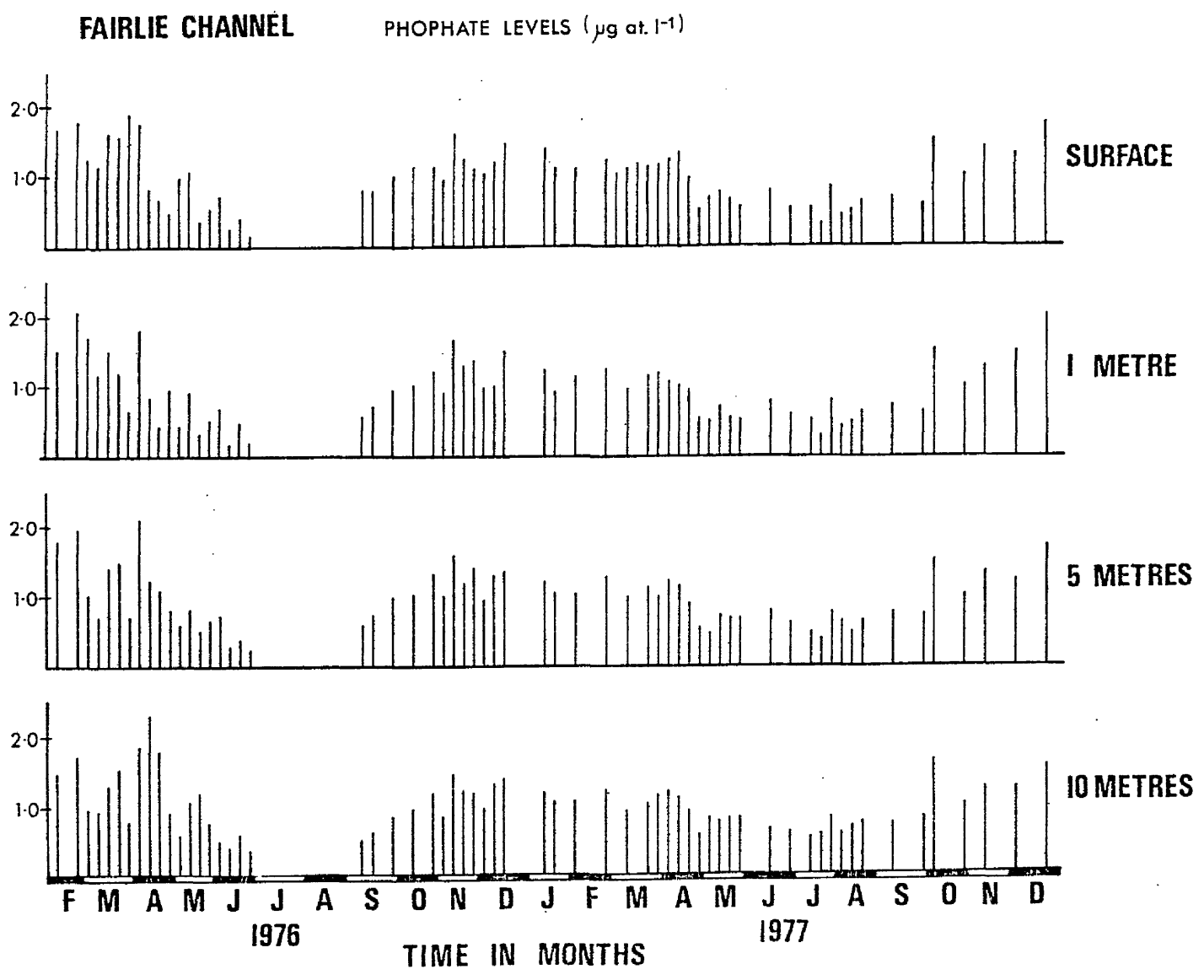
years. In 1976, the high winter levels did not start to decrease until April 8, falling from 17.9 μg at. l^{-1} to 4.75 μg at. l^{-1} in mid-May. The levels increased briefly at the end of May (following a period of strong winds on May 24). Following this, nitrate was low, reaching a minimum of 0.75 μg at. l^{-1} in mid-July. From September, nitrate increased and a maximum value of 21.9 μg at. l^{-1} was recorded on February 17. After the spring diatom increase in 1977, nitrate dropped from 13.3 μg at. l^{-1} (April 21) to 4.5 μg at. l^{-1} (April 28) but then increased until May 12, after which the levels gradually decreased to reach a minimum of 1.24 μg at. l^{-1} on July 21.

The nitrate levels in the present study were similar to those recorded by Hinton in 1973 (4 μg at. l^{-1} during the vernal diatom increase) and not the lower values observed in 1972 (0.5 μg at. l^{-1} in April).

Phosphate (Fig 16)

The observed winter levels of phosphate were normally above 1 μg at.Pl^{-1}. During the spring diatom increase in early April 1976, phosphate dropped from 1.78 μg at.l^{-1} (April 8) to 0.80 (April 15). The levels continued to decrease until April 29 when there was a slight increase. This occurred before the observed increases in silicate and nitrate. Phosphate then gradually decreased and a minimum value of 0.12 μg at. l^{-1} was recorded on June 24. Levels rose during autumn and remained high over winter. The decrease in phosphate during the spring increase of 1977 was not pronounced, dropping from 0.97 μg at. l^{-1} (April 21) to 0.51 μg at. l^{-1} (April 28) and the levels remained around this value for most of the summer with a recorded minimum of 0.31 μg at. l^{-1} on July 21.

Figure 16. Seasonal changes in phosphate levels ($\mu g\ at.l^{-1}$) at Station 11, 1976-1977.


FAIRLIE CHANNEL
PHOPHATE LEVELS (µg at. l-1)
2·0
1·0
SURFACE
1 METRE
5 METRES
10 METRES
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

The maximum and minimum values quoted above are those of the surface samples. The between depth differences over the upper 10 metres were low for most of the year. During the summer months, however, higher nutrients were usually found at 5 and 10 metres and minimum values were often found at 1 metre coinciding with the chlorophyll a maximum.

4.2.1. Standing Crop

The seasonal patterns in total chlorophyll a distribution and the contribution to this of the nanophytoplankton for the surface, 1, 5 and 10 metres in the Fairlie Channel are shown in Fig 17. As the spread of values observed was large ranging from low, barely detectable winter levels to values above 10 mg chlorophyll a m^{-3} at times, the results are also summarized diagramatically on a logarithmic scale, shown in Fig 18.

The classical pattern of seasonal variation in phytoplankton biomass in the open sea and deep fresh-water lakes in temperate regions is that of a spring increase followed by a reduction in activity during the summer, a small autumnal increase and low winter levels (Fogg, 1975). The sequence in the Firth of Clyde however, deviates from this in that successive peaks of chlorophyll a were recorded throughout summer.

Following the spring increase in chlorophyll a in 1976, which at the surface reached a maximum of 10.0 mg chl a m^{-3} (April 12), four subsequent peaks in chlorophyll were observed between May and July. Each peak was of increasing magnitude with that on July 29 being comparable with the spring increase. The chlorophyll distribution during August 1976 was not determined. No distinct

Figure 17. Seasonal changes in the total and the nanophytoplankton chlorophyll *a* at the surface, 1 metre, 5 metres and 10 metres. Station 11, 1976-1977 (mg chlorophyll *a* m^{-3}).

Net chlorophyll -------

Nanophytoplankton chlorophyll ——

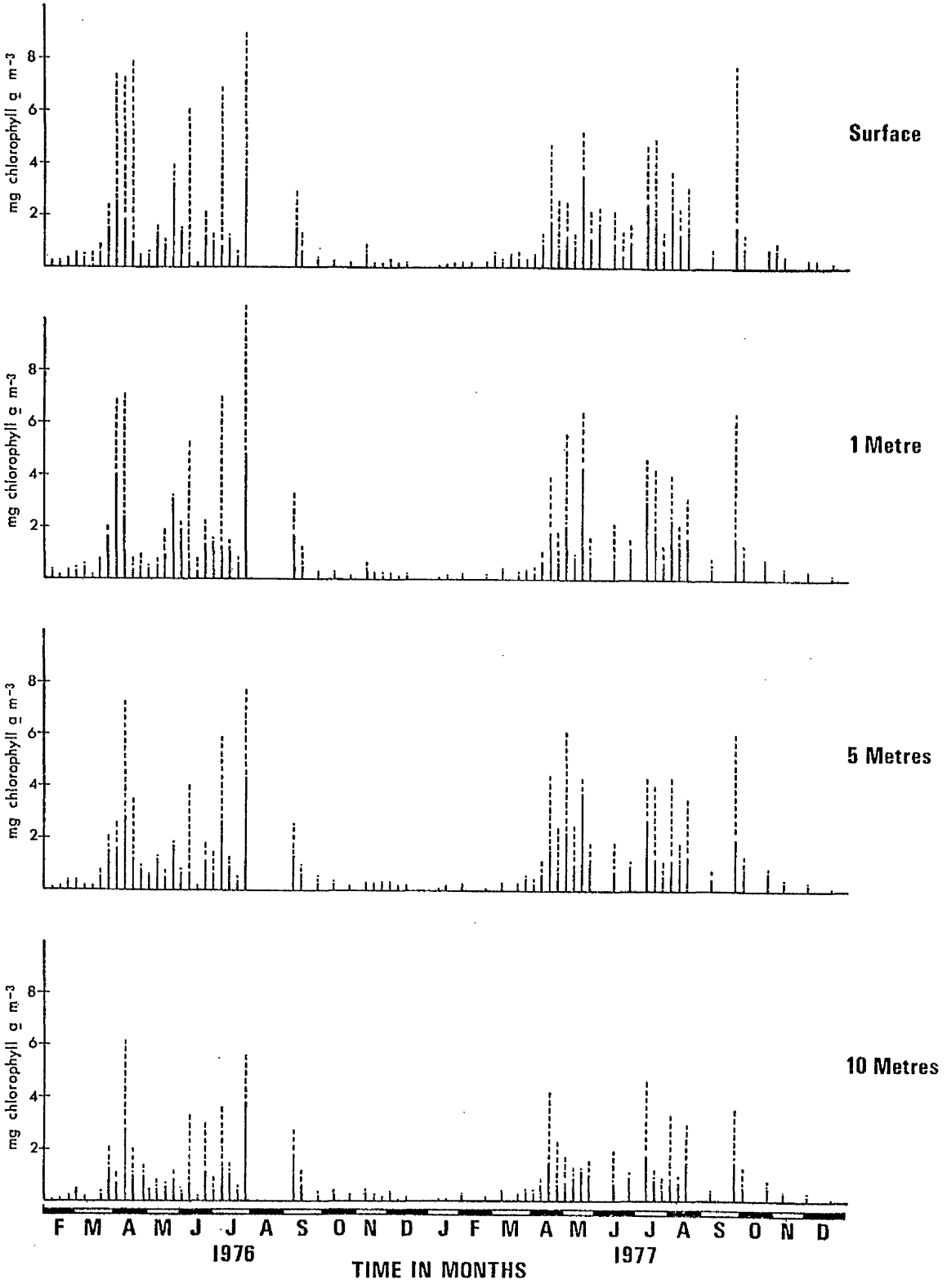
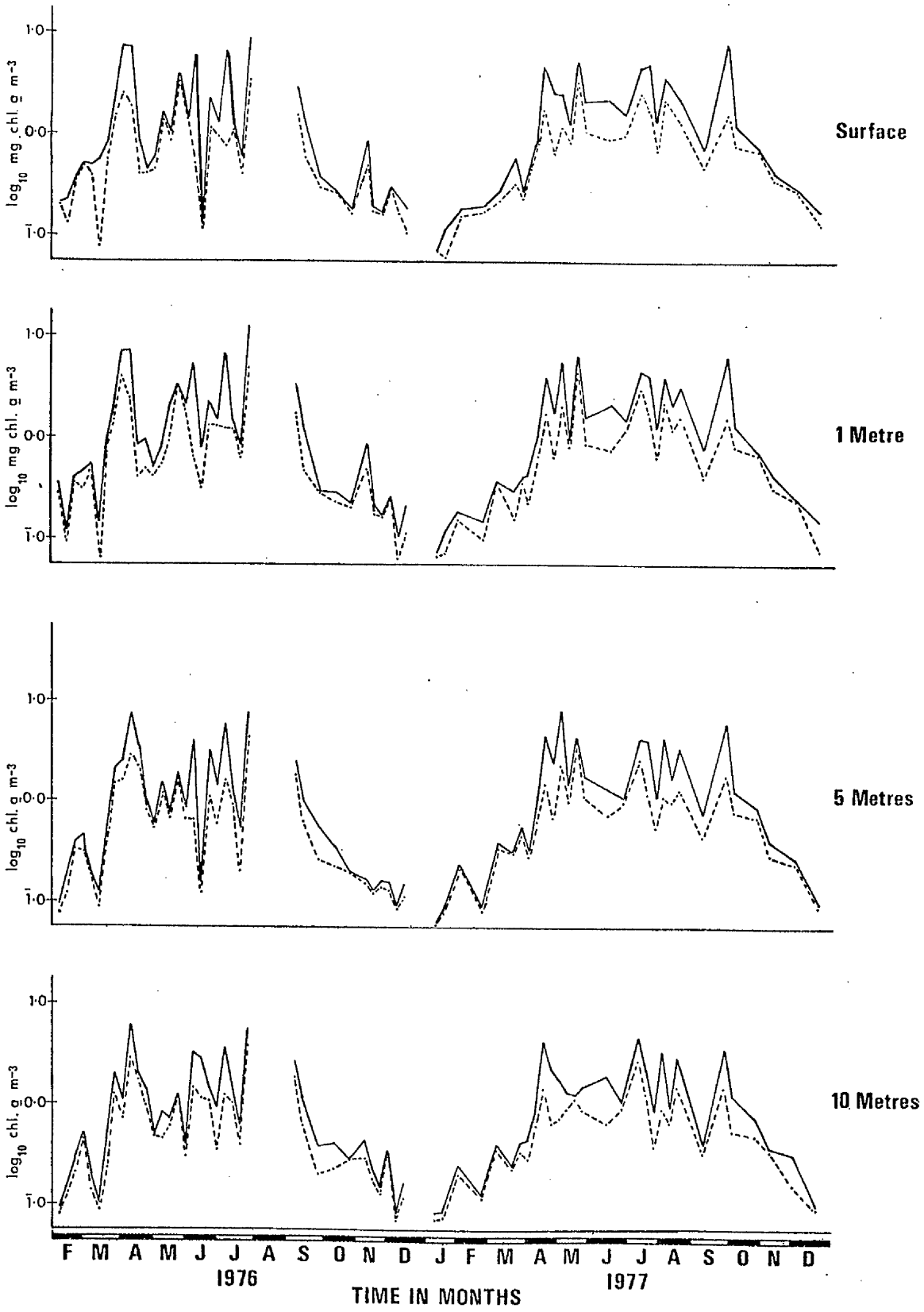

mg chlorophyll a m-3
2
4
6
8
Surface
1 Metre
5 Metres
10 Metres
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

Figure 18. Seasonal changes in the total and nanophytoplankton chlorophyll a at Station 11 during 1976-1977 represented on a logarithmic scale.

Total ————————

Nanophytoplankton – – – – –


1·0
0·0
$\bar{1}$·0
$\log_{10}$ mg chl. g m^{-3}
Surface
1 Metre
5 Metres
10 Metres
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

autumnal peak was observed in 1976. After mid-September the chlorophyll levels remained low with an average surface value of 0.27 mg m^{-3} for September to December.

In 1977, a similar overall seasonal pattern was observed although the maximum recorded levels were lower than those observed in 1976 (Table 7). An autumnal peak was measured on September 22, 1977 in which the chlorophyll values were the highest obtained for that year (surface = 7.8 mg m^{-3}) exceeding those observed in spring, which is unusual.

Fluctuating high and low levels of chlorophyll during the summer appear to be typical of the Firth of Clyde (Marshall and Orr, 1934; Hinton, 1974). In these previous studies, it was generally found that the magnitude of the spring increase was greatest with later pulses becoming successively smaller until July but this was not the case in 1976. In 1977, however, the samples showed a decline in peak heights following the spring maximum. Hinton (1974) obtained a maximum chlorophyll *a* value of 8.3 mg chl *a* m^{-3} (March 23, 1973). This lay between the spring maxima recorded in the present study (1976 - 10.0 mg m^{-3}; 1977 - 6.4 mg m^{-3} and 1978 - 5.86 mg m^{-3}) and occurred at an earlier date.

In Loch Etive, Wood *et al* (1973) found a similar pattern of seasonal distribution of chlorophyll with fluctuations about a moderately high average level from April to July and a decline in August and September.

As a result of the water column remaining mixed for most of the year the between depth variations in total chlorophyll were usually quite small. The maximum quantities obtained were normally found

Table 7 Maximum recorded values of chlorophyll a and carbon fixation in the net- and nanophytoplankton fractions and the total unfractionated samples

a) Chlorophyll a mg chlorophyll a m^{-3}

	1976			1977		
Depth	Total	Net-	Nano-	Total	Net-	Nano-
Surface	10.00	6.98	4.88	7.81	6.23	3.37
1 Metre	10.51	8.24	4.85	6.43	4.81	4.39
5 Metres	7.70	4.43	4.31	6.10	4.09	3.72
10 Metres	6.10	3.30	3.79	4.63	2.75	2.75

b) Carbon Fixation mg Carbon $m^{-3}h^{-1}$

	1976			1977		
Depth	Total	Net-	Nano-	Total	Net-	Nano-
Surface	66.64	60.31	28.04	55.70	50.31	13.08
1 Metre	63.97	58.68	25.38	52.98	47.67	14.85
5 Metres	47.71	46.06	12.89	30.07	27.23	10.85
10 Metres	12.37	12.28	4.98	5.28	4.63	3.15

at the surface or 1 metre depth whilst those at 10 metres were smallest.

Figures 17 and 18 both show that the nanophytoplankton made up a significant part of the total biomass in terms of chlorophyll *a* and that their relative importance varied at different times of the year. The mean annual contribution of the nanophytoplankton was remarkably constant between the two years and over the depths investigated, representing between 61 - 72% of the total chlorophyll (Table 8).

During the winter months when the total phytoplankton biomass was low, the nanophytoplankton made the major contribution, on occasions representing 100% of population at certain depths. During periods of low measured chlorophyll the contribution of the nanophytoplankton is more clearly seen in the logarithmic data (Fig 18). At these times, the lines representing the total chlorophyll and nanophytoplankton chlorophyll *a* are often virtually superimposed on one another. In the winter period before the spring increase, the nanophytoplankton contributed 75.4 $\pm$ 10.8% ($\pm$ 95% confidence limits) in 1976 and 82.3 $\pm$ 4.9% in 1977 to the total chlorophyll *a*. With the improved light conditions in spring, both the net- and the nanophytoplankton fractions increased. The greater increase however was in the net fraction and the relative contribution of the nanophytoplankton consequently decreased to 44.4 $\pm$ 8.4% and 37.6 $\pm$ 4.5% in 1976 and 1977 respectively during the spring outburst.

Following the waning of the spring increase in 1976 the nanophytoplankton became the dominant fraction again providing low levels of chlorophyll for several weeks but then giving rise to a peak

Table 8. Mean annual fraction of the total chlorophyll a and carbon fixation contributed by the nanophytoplankton (mean value ± 95% confidence limits)

a) Chlorophyll

Depth	1976	1977
Surface	0.65 ± 0.09	0.61 ± 0.07
1 Metre	0.66 ± 0.09	0.65 ± 0.07
5 Metres	0.72 ± 0.07	0.66 ± 0.08
10 Metres	0.65 ± 0.06	0.67 ± 0.07

b) Productivity

Depth	1976	1977
Surface	0.55 ± 0.10	0.50 ± 0.09
1 Metre	0.52 ± 0.09	0.52 ± 0.09
5 Metres	0.54 ± 0.11	0.48 ± 0.10
10 Metres	0.43 ± 0.10	0.45 ± 0.10

on May 27 which was composed predominantly of nanophytoplankton (87% of the total). The increase at this time in the number of nanophytoplankton organisms was observed only in the surface layers with elevated chlorophyll levels in the surface and 1 metre samples whilst at 5 and 10 metres, the quantities measured were as in previous weeks.

During June and July 1976, with the exception of the period at the end of July, the nanophytoplankton chlorophyll remained fairly constant at 1 mg m^{-3} whilst the changes in total chlorophyll were due mainly to rapid increases in netplankton biomass (June 10, July 8).

Very high levels of total chlorophyll were recorded on July 29 with 9.0, 10.5, 7.7 and 5.7 mg m^{-3} at the surface, 1, 5 and 10 metre depths respectively. This peak was composed of both net- and nanophytoplankton with the percentage contribution of the nanophytoplankton increasing with depth from 38% at the surface to 67% at 10 metres.

Chlorophyll decreased during September and for the remaining months of the year, was less than 0.5 mg m^{-3} with the nanophytoplankton being the major contributor. During October to December 1976 the average contribution of the nanophytoplankton was 83.7 $\pm$ 6.07%. In 1977, the fluctuations in total chlorophyll were less dramatic than in 1976 and this was mainly due to smaller increases observed in the netplankton fraction than in the previous year, with the exception of the autumnal pulse.

A small nanophytoplankton-dominated peak following the decline of the spring diatom outburst was again observed in 1977 (May 19). During the summer months (June to August) the nanophytoplankton made an average contribution of 50.9 $\pm$ 5.4% to the total chlorophyll and after the autumnal peak, became the major contributors again.

Although the maximum recorded values for the nanophytoplankton (Table 7) were fairly constant between depths, it was usually found that on a particular sampling day the highest chlorophyll levels associated with the nanophytoplankton were in the upper metres.

4.2.2. Phaeopigment levels

These were checked during the autumn period of 1977 and the spring of 1978 and it was found that these made up a substantial part of the plant pigment content of the water, the phaeopigments being often twice as high as the chlorophyll *a* levels (Table 9).

Table 9. Average chlorophyll *a* and phaeopigment levels 0-10 metres

Date	Chl *a*	Phaeopigment	Date	Chl *a*	Phaeopigment
8. IX.77	0.43	0.41	30.III.78	0.27	0.91
22. IX.77	3.07	4.98	6. IV.78	0.22	0.53
4. X.77	0.26	0.80	12. IV.78	2.32	3.77
16.III.78	0.26	0.25	20. IV.78	2.59	5.05
20.III.78	0.20	0.50	27. IV.78	1.06	3.27
23.III.78	0.51	0.76	11. V.78	0.30	0.77

Results from this indicate that the chlorophyll values discussed in the previous section may have been overestimated as these were not corrected for phaeopigments but as both the total and the nanophytoplankton fraction would be similarly affected, the ratios of the corrected and uncorrected values would be similar.

Figure 19. Carbon fixation rates at Station 11 during 1976 and 1977. Carbon fixation was measured in the total and nanophytoplankton fraction by ^{14}C uptake and expressed as mg carbon $m^{-3}h^{-1}$.

Net plankton ------

Nanophytoplankton ——

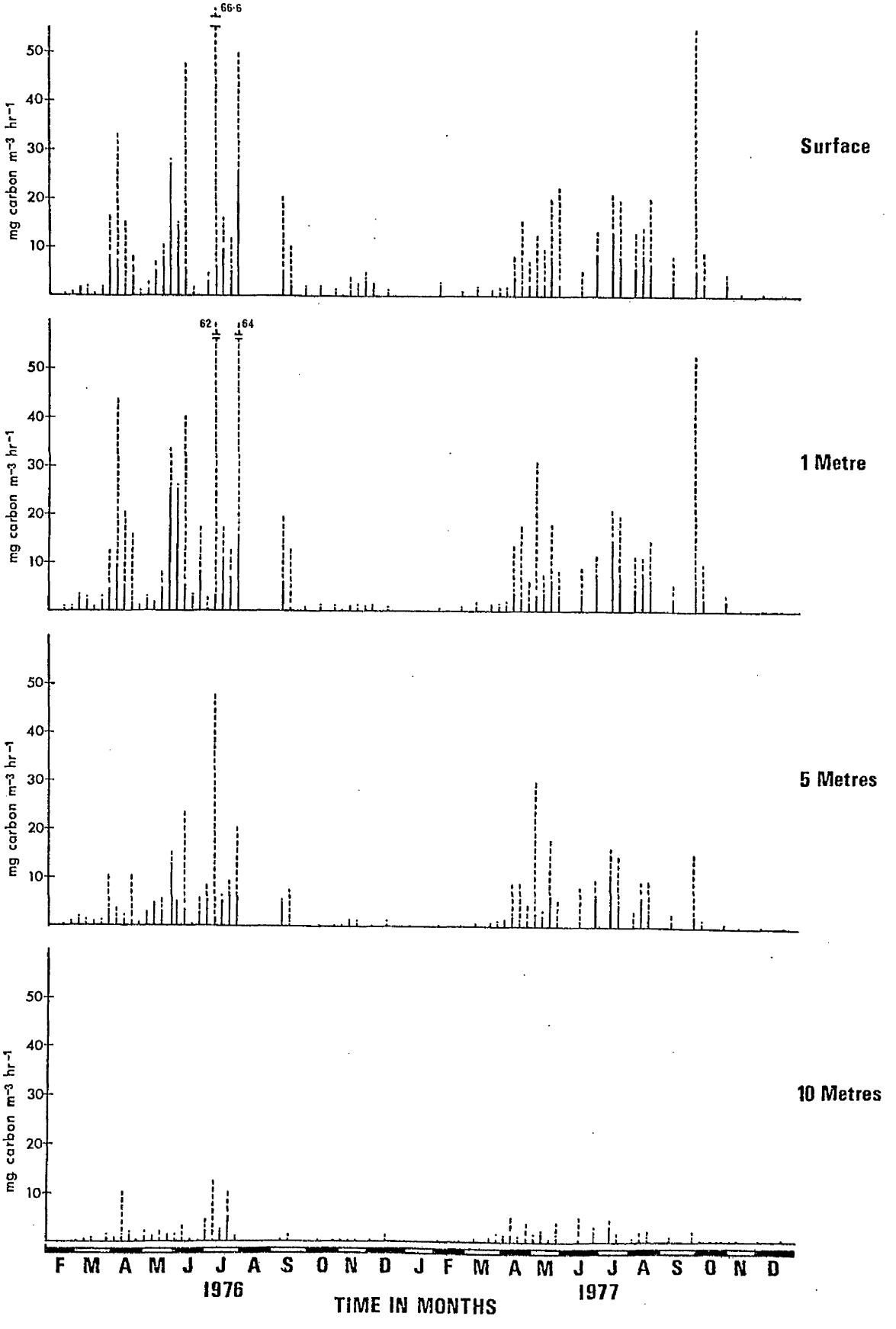
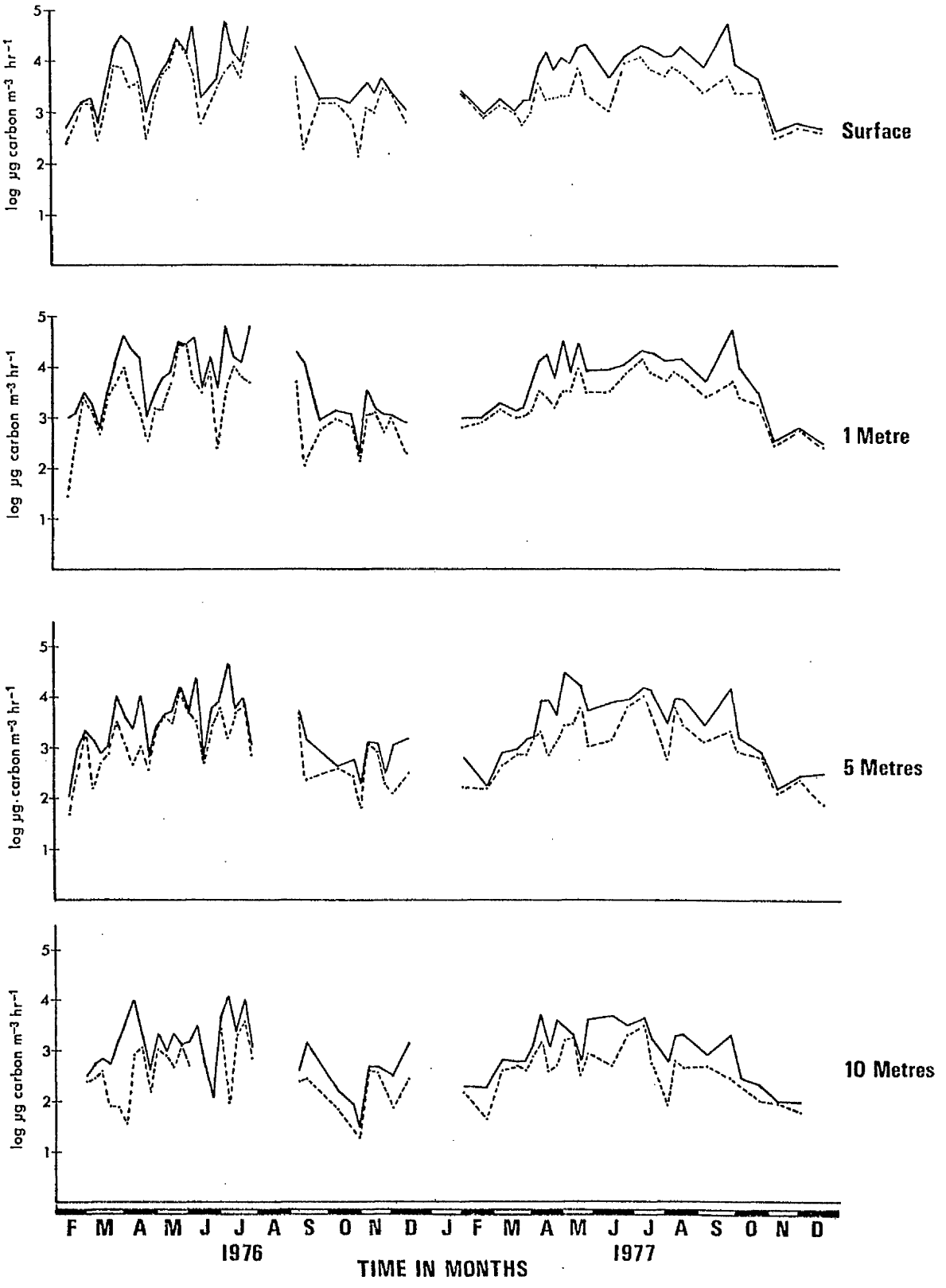

66·6
62
64
mg carbon m⁻³ hr⁻¹
10
20
30
40
50
Surface
1 Metre
5 Metres
10 Metres
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

Figure 20. ^{14}C-fixation rates of total and nanophytoplankton at Station 11 during 1976 and 1977 represented on a logarithmic scale.

Total ————————

Nanophytoplankton - - - - -


log µg carbon m⁻³ hr⁻¹
Surface
1 Metre
5 Metres
10 Metres
F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
TIME IN MONTHS

4.3. Carbon fixation

The changes in chlorophyll a levels were closely paralleled by the changes in carbon fixation as shown in Figures 19 and 20. The average annual contribution of the nanophytoplankton to the total fixation was slightly lower than its contribution to the total chlorophyll, ranging from between 43 to 55% (Table 8).

As with the chlorophyll content, the relative importance of the nanophytoplankton in assimilation varied at different times of the year (Table 10).

Table 10. Percentage contribution of the nanophytoplankton to the total assimilation at different times of the year

(Mean value ± 95% confidence limits)

	1976	1977
Winter - Early Spring	63.5 ± 14.8%	66.1 ± 8.3%
Spring Increase	21.6 ± 8.9%	16.1 ± 9.3%
Summer	46.1 ± 10.3%	43.8 ± 7.3%
Autumn-Winter	65.9 ± 10.3%	72.1 ± 9.8%

After the decline of the spring increase in 1976, the nanophytoplankton assimilated 88.9% and 98% of the total carbon fixed on May 27 and June 3 respectively. High fixation values in the nanophytoplankton fraction were not observed after the spring increase in 1977, however, although there was an increase in chlorophyll.

The maximum recorded fixation value for each fraction of

the phytoplankton at each sampling depth is given in Table 7. The highest fixation rates were recorded during July 1976. The first peak in early July reached a maximum of 66 mg carbon $m^{-3}h^{-1}$ in the surface layer and was produced predominantly by netplankton. High fixation levels were also recorded on July 29 when a maximum level of 64.0 mg carbon $m^{-3}h^{-1}$ was measured at 1 metre. At the time of this peak, 41.5% of the fixation was due to the nanophytoplankton. In 1977, the only comparable high fixation was during the autumn pulse when 55.7 and 53.0 mg carbon $m^{-3}h^{-1}$ were fixed in the surface and 1 metre samples. Minimum fixation levels were found during winter when less than 1 mg carbon $m^{-3}h^{-1}$ were found on occasions at the surface with lower levels at the depth below.

When the depth distribution of productivity was considered, it was noted that on many occasions during spring and summer there was inhibition of surface samples with maximum fixation at 1 metre despite equal or higher chlorophyll levels from the surface samples. The fixation at 10 metres was greatly reduced from that at the surface. On occasions during autumn and winter, assimilation at 10 metres was zero or just above, this depth being approximately at the compensation point at these times (28.10.76, 22.12.77).

Dark fixation was normally low representing only a few percent of the light fixation but during a period in January 1977, the dark fixation levels were so high, comparable with or exceeding those of the light fixation that light and dark fixation were calculated separately. The high light fixation levels at this time were surprising in themselves as chlorophyll was barely detectable and the ambient light intensity was low.

Table 11. Dark and light fixation levels, January 13, 1977

(mg carbon $m^{-3}h^{-1}$)

	TOTAL		< 20 μm	
	LIGHT	DARK	LIGHT	DARK
Surface	6.45	6.00	4.48	-
1 Metre	5.76	2.80	3.35	2.54
5 Metres	6.62	9.20	3.68	2.88
10 Metres	4.38	1.85	3.30	2.59

One possible explanation for the observed high light - independent assimilation is that the carbon-14 was absorbed by detritus which formed a large part of the particulate matter at this time of year or alternatively that the high fixation was due to bacterial uptake. If the high fixation had been solely due to bacteria, it would have been expected that the total and the less than 20 μm fraction would have similar values as the bacteria would not be retained by the net and this was not observed, although this hypothesis is complicated by the possibility of bacteria adhering to detritus. The use of antibiotics or autoradiography would be of value in an investigation of this effect. High dark fixation levels in marine samples had previously been reported by Morris, Yentsch and Yentsch (1971) and Taguchi and Platt (1977).

A good correlation was found between the total chlorophyll a at 1 metre and the levels of carbon fixation recorded at this depth (eg. $r=0.84$; $p < 0.1$) while the correlation between the nanophyto-

plankton chlorophyll and assimilation at this depth was lower (eg. $r = 0.67$; $p < 0.1$) but still significant. The lower correlation is possibly due, in part, to errors introduced during fractionation. Larger volumes were involved in measuring chlorophyll (1-2 litres) than in productivity (100 ml) and this could increase the likelihood of netplankton cells being washed through the mesh and included as nanophytoplankton which would lead to an overestimation of the nanophytoplankton chlorophyll a.

4.4. Coulter Counter - Particle Size Distributions

Microscopic examination showed that usually a high percentage of the particulate matter was made up of non-living detritus and organic material and this was reflected in the particle size distributions which were typically low and evenly distributed between the size classes when the majority of the material was detrital (e.g. samples from March 20 and 23 shown in Fig 21). Increases in phytoplankton numbers could, however, be identified as an increase above the normal levels in particular size classes (e.g. April 12, Fig 22). The correlation between total particle volume (as estimated by the Coulter Counter) and the chlorophyll a varied but was normally significant. The best correlation was found when samples collected with the Sedimentary Pollution Unit, Millport were analysed, $r = 0.85$ ($p < 0.001$) while the correlation coefficient for the samples collected at Station 11 over the two year period was 0.45 ($p < 0.001$).

4.5. Phytoplankton Composition and related factors

4.5.1. Winter - Spring 1976

This period was characterized by low light levels, high

nutrients and low phytoplankton biomass and productivity. The nanophytoplankton was the major contributor at this time and was composed mainly of small (< 5 μm) flagellates, cryptomonads and prasinophytes.

4.5.2. Spring 1976

The spring diatom increase was dominated by Skeletonema costatum with Thalassiosira nordenskioldii and Nitzschia seriata also being found in considerable numbers. Chlorophyll concentrations and productivity began to rise rapidly between March 25 and March 31. Maximum assimilation was recorded on April 8 (44.0 mg carbon $m^{-3}h^{-1}$) and maximum chlorophyll four days later on April 12 (10.51 mg m^{-3}). After this, both the chlorophyll and productivity began to decrease and this was preceded by a reduction in nutrients between March 31 and April 12. Silicate was reduced from 3.14 to 0.35 μg at. Si l^{-1}, nitrate from 18.42 to 8.21 μg at. NO_3^- l^{-1} and phosphate from 2.29 to 1.17 μg at. l^{-1}. The phosphate and nitrate continued to decrease until April 29 while the silicate remained fairly constant at approximately 0.4 μg at. l^{-1} during this time.

During May, the nanophytoplankton was again dominant representing 70-90% of the biomass and 50-100% of the productivity. The levels of nanophytoplankton reached a peak on May 27 (representing 81% of the total surface chlorophyll which was 3.96 mg m^{-3} and 100% of the fixation - 27.26 mg carbon m^{-3} h^{-1}). During this period short chains of Skeletonema (1-4 cells long) formed part of the nanophytoplankton but the majority was composed of small flagellates, prasinophytes, haptophytes (in size ranges 3-4 μm, 6-8 μm and 10-12 μm), cryptomonads and chrysophytes, particularly Apedinella spinifera.

The nutrient levels remained low throughout May but a slight increase was recorded on May 27. This followed a period of strong winds which would have caused some mixing of the water column and replenishment of nutrients.

4.5.3. Summer 1976

An increase in the numbers of diatoms was observed on June 10 with a concurrent increase in chlorophyll (6.04 mg m^{-3}) and productivity (47.8 mg carbon $m^{-3}h^{-1}$). This followed a period of sunny weather and slightly increased nutrients. The nitrate concentration dropped sharply from 10.6 µg at l^{-1} on June 3 to 2.0 µg at l^{-1} on June 10 with smaller changes in the other nutrients. Skeletonema had been succeeded by a Chaetoceros spp.as the dominant diatom in the surface and at 1 metre but was the most common species at 5 and 10 metres.

In the period between this diatom increase and the following, a mixed population was observed. The nanophytoplankton represented a considerable proportion of the biomass and productivity and was composed mainly of small (< 5 µm) flagellates, cryptomonads and small dinoflagellates. Rhizosolenia deliculata began to appear in numbers from June 24 while several dinoflagellate species were observed on July 1. These included Ceratium furca, C. tripos and Dinophysis spp. Dinoflagellate cysts had been observed in the preceding weeks.

On July 9 very high levels of productivity (66.6 mg carbon $m^{-3}h^{-1}$) and chlorophyll (7.0 mg chl a m^{-3}) were observed and these were due to a large increase in diatom numbers. These were predominantly Thalassiosira spp. with Chaetoceros spp., R. deliculata and Guinardia flaccida also common. In the period before this

outburst, the weather had been very sunny (Fig 8a) and there had been an increase in nitrate and silicate.

In the following period during mid-July, the diatoms were almost totally succeeded by dinoflagellates both small non-thecate species and larger species such as Dinophysis acuta which was common, Peridinium spps., Ceratium fusus and C. tripos and also by small (<5 μm) flagellates. Chlorophyll values at this time ranged from 0.5 to 1.5 mg m^{-3}.

On July 29 high fixation rates with high chlorophyll levels were recorded in both the net- and the nanophytoplankton fractions despite the day being overcast. The surface levels of fixation and chlorophyll for the net- and nano-fractions respectively were 24.2 mg carbon $m^{-3}h^{-1}$, 5.58 mg chl a m^{-3} and 26.18 mg carbon $m^{-3}h^{-1}$ and 3.43 mg chl a m^{-3}. Large numbers of Ceratulina pelagica were observed, also Chaetoceros spp., Thalassiosira spp. and Rhizosolenia deliculata and these made up the main part of the netplankton. The nanophytoplankton was made up of small unidentifiable flagellates.

4.5.4. Autumn 1976

When sampling was recommenced in September the population was made up of Leptocylindricus danicus chains with Chaetoceros spp., small non-thecate dinoflagellates (<15 μm) and small flagellates. The fixation and chlorophyll levels (surface values - 20.6 mg carbon $m^{-3}h^{-1}$ and 2.97 mg chl m^{-3}) were reasonably high on September 9 but decreased after this date. By the end of September the chlorophyll content of the samples was below 0.5 mg m^{-3} with the nanophytoplankton being the major contributors of this. Small (< 5 μm) flagellates, cryptomonads, Katodinium rotundata and other small non-thecate dinoflagellates were observed at this time.

4.5.5. Winter 1976/77

After a small increase in chlorophyll and fixation on November 11, coinciding with a period of sunny weather there was a period of very low activity over the winter months extending to the end of March 1977. With the exception of the period in November when the numbers of Skeletonema increased, the nanophytoplankton consisting of small flagellates was the main contributor to the winter levels of chlorophyll and fixation as in the previous year.

4.5.6. Spring 1977

The spring diatom increase was later in commencing than in the previous year. Chlorophyll levels remained at approximately 0.5 mg m^{-3} until April 14 when the surface value rose to 1.25 mg m^{-3} with a further increase to 4.76 mg m^{-3} on April 21 when the total surface fixation was 15.5 mg carbon $m^{-3}h^{-1}$. There were several climatological factors which could have contributed to this delay. Sea surface temperatures over February and March 1977 (7.01 and 7.37°C respectively) were lower than those found in the previous year (7.99 and 7.75°C). The levels of sunshine in March 1977 were lower than in the previous March (1.28 h day^{-1} compared with 2.59 h day^{-1}). An important factor was probably the fact that the strong winds experienced in March and April 1977 (Fig 10) possibly delayed the required degree of stabilization necessary in the water column which permitted increased growth to occur.

The maximum recorded levels of chlorophyll and fixation were lower during the spring increase in 1977 than in the previous year and instead of a sharp increase and decline over a short period, the increased levels persisted into May, with slight oscillations in values occurring. The minimum nutrients were recorded on April 28 (0.95 µg at.Si l^{-1}, 0.95 µg at.PO_3 l^{-1} and 4.52 µg at.NO_3 l^{-1}).

In the weeks preceding the spring diatom increase, the phytoplankton was dominated by small flagellates, cryptomonads, prasinophytes and other small (< 5 μm) flagellates. Skeletonema began to appear regularly in the samples from April 6 while Thalassiosira was first observed on April 14. During the peak in diatom numbers Skeletonema was dominant as in the previous year. Thalassiosira spp. ranked next in abundance while Chaetoceros spp. and N. seriatia were also common. Colonies of Phaeocystis pouchetii were observed during the bloom.

Skeletonema remained common throughout May with the proportions of short, 1-2 cell chains and longer chains with larger cells varying from week to week. Thalassiosira spp and Chaetoceros spp were observed in small numbers. The remainder of the population was made up of small flagellates and small thecate (< 20 μm) and non-thecate (< 15 μm) dinoflagellates.

4.5.7. Summer 1977

During June the populations observed were generally mixed. Thalassiosira spp. succeeded Skeletonema as the most common diatom and Chaetoceros spp. were also more common. Also observed were Nitzschia closterium, N. seriata, Leptocylindricus danicus, Peridinium spp. and small flagellates which included prasinophytes, chlorophytes and haptophytes. Chlorophyll and productivity were generally low ranging from 1-2 mg chl m^{-3} and 5-13 mg carbon $m^{-3}h^{-1}$ with the exception of an observed increase on June 8 (chlorophyll - 4.83 mg m^{-3}). The percentage contribution of the nanophytoplankton to the fixation increased between June 15 (22%) and June 30 (65.7%) and over this

period Chlamydomonas bullosa was observed to be common.

Apart from slightly reduced levels on July 28, productivity and biomass was generally high throughout July and August with the nanophytoplankton contributing approximately 50%. On July 14, large numbers of P. pouchetii were recorded together with other small (<5 μm) flagellates. The most commonly observed diatoms during this period were Chaetoceros spp. and N. seriata, Skeletonema and Thalassiosira spp. being of lesser importance. Fewer species and also fewer numbers of dinoflagellates were recorded during the summer of 1977 than in the previous year. Dinophysis spp was observed occasionally and Peridinium spp (including P. triquietra) and Katodinium rotundata were quite common.

4.5.8. Autumn - Winter 1977

A striking autumnal increase was recorded on September 22 (surface chlorophyll and fixation being 7.8 mg m^{-3} and 55.7 mg C $m^{-3}h^{-1}$ respectively) and this was composed predominantly of cells of N. seriata although several other diatom species were recorded, eg. Skeletonema, Thalassiosira spp., Rhizosolenia spp. and also Eucampia zoodiacus. By October 4 the nutrient levels had increased, the water temperature was dropping, there was decreasing phytoplankton activity in terms of biomass and productivity but the relative importance of the nanophytoplankton was increasing to its high winter level.

4.5.9. Spring 1978

The progression of the spring diatom increase in 1978 is shown in terms of the particle size distribution of the samples in Figures 21 and 21a (note the expanded scales on April 12 and April 20). The total chlorophyll remained below 1 mg m^{-3} until April 12 and the

Figure 21. Particle size spectra of water samples collected in the period before the spring diatom increase 1978.

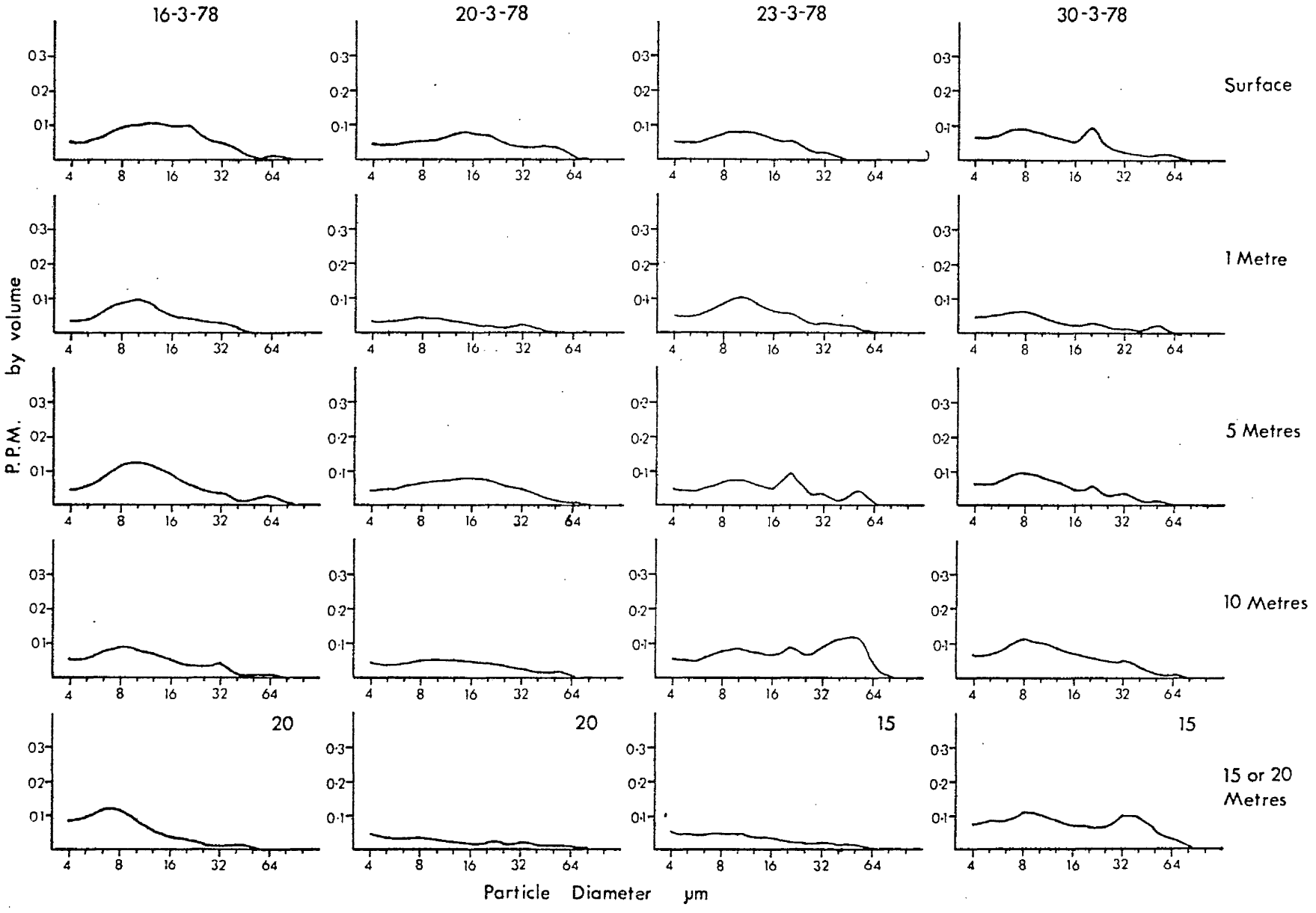
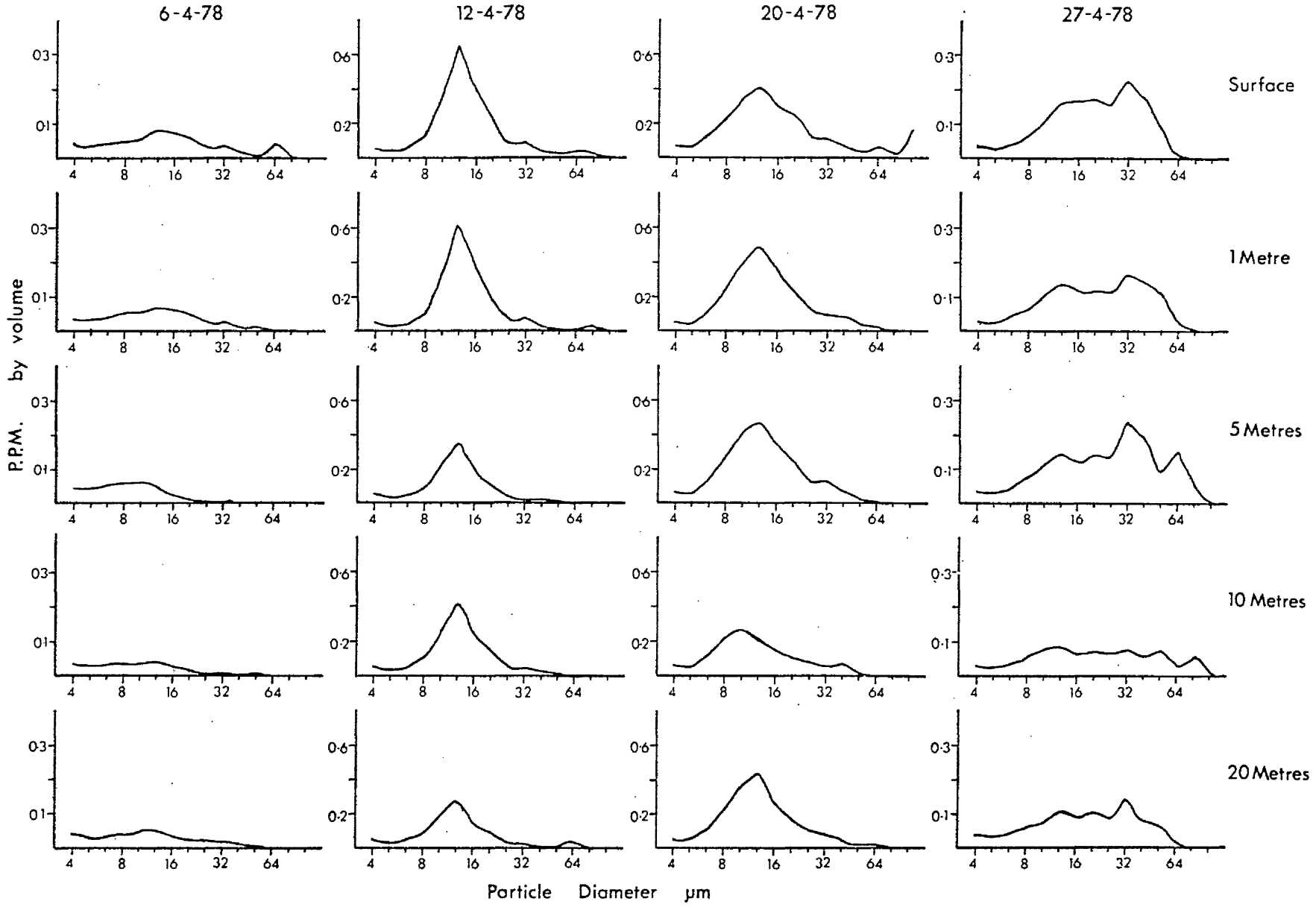

16-3-78
20-3-78
23-3-78
30-3-78
Surface
1 Metre
5 Metres
10 Metres
15 or 20 Metres
20
20
15
15
P.P.M. by volume
Particle Diameter µm

Figure 21a. Particle size spectra of water samples collected before (6-4-78) and during the spring increase 1978.
(Note that the vertical scale has been expanded on April 12 and April 20).


6-4-78
12-4-78
20-4-78
27-4-78
Surface
1 Metre
5 Metres
10 Metres
20 Metres
P.P.M. by volume
Particle Diameter µm

particle size distributions during this time were low and flat, being slightly displaced to the left indicating a predominance of small particles.

The climax of the spring diatom increase probably occurred between sampling dates as similar high values of chlorophyll and productivity were found on April 12 and 20 (chlorophyll - 5.86 mg m^{-3} and 5.86 mg m^{-3}, productivity 48.7 mg c $m^{-3}h^{-1}$ and 46.4 mg c $m^{-3}h^{-1}$). Skeletonema was virtually totally dominant on April 12 and long chains of this represent a peak on the particle size distribution at 12.8 μm diameter. On April 20 Skeletonema chains were shorter and there were increased numbers of other species (Thalassiosira and Chaetoceros spp) producing a flatter particle size peak with increased numbers of particles on either side of 12.8 μm diameter.

The particle size distributions had changed by April 27 reflecting a change in the population - very long chains of Thalassiosira were observed with fewer Skeletonema. By May 11 chlorophyll and productivity were low. Nanophytoplanktonic organisms were virtually all that were observed and contributed 99% of the biomass (the maximum total observed was 0.86 mg m^{-3}) and 94% of the productivity (4.78 mg C $m^{-3}h^{-1}$ maximum total).

In the period prior to the bloom in 1978, an organism which appeared to be very similar to that described by Smayda (1973) as an ebridian, possibly Ebria tripartita was observed attached to Skeletonema chains on several occasions (Plate 2). The chains contained living cells to one side of this organism while on the other the cytoplasmic contents had been removed and the cells were empty suggesting active predation. As a quantitative estimate of these organisms was not

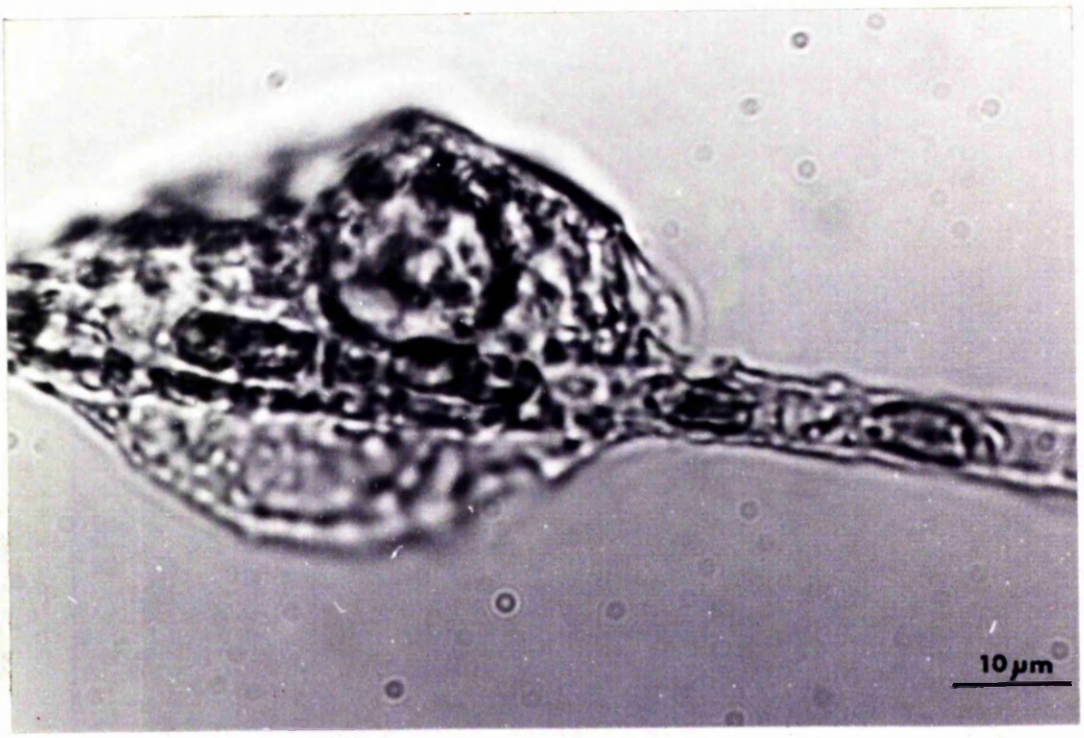


Plate 2. A photomicrograph showing an Ebridian-like organism attached to a Skeletonema chain, April 1978.

obtained, however, it was difficult to assess its importance in limiting the increase of Skeletonema.

Discussion

The physical conditions found in the Fairlie Channel in the present survey appear to have changed little from those recorded in the past. The weather and salinity data were similar to those recorded by Barnes (1955) for 1949-53 with the exception that temperatures were more extreme during 1976-1977.

Nutrient levels were comparable to those found by Hinton (1974). In 1977, the decrease in nutrients following the spring diatom increase and the following summer, was not as dramatic as in 1976 or in 1973 (Hinton, 1974). For example, phosphate decreased from 0.97 to 0.51 μg at. l^{-1} during the first part of the spring bloom and remained around this level over the summer period with a minimum recorded value of 0.31 μg at. l^{-1} on July 21. These higher minimum nutrients together with the lower maximum chlorophyll a and productivity for 1976 suggest that the phytoplankton did not reach their maximum growth potential given the available nutrients during this period with some other factor (possibly light or grazing pressure) having a stronger influence on their growth.

The seasonal pattern of phytoplankton succession and growth observed during 1976 and 1977 also appeared to be fairly typical although the spring diatom increases in mid and late April in 1976 and 1977 respectively were slightly later than those recorded in the past. Marshall and Orr (1930) compared the timing, composition and magnitude of the spring increase in successive years and showed that, in general, the increase occurred within a week of March 20.

The total chlorophyll a levels recorded during the different seasons were of similar magnitude to those found by Hinton (1974) and also the Clyde River Purification Board at their Main Channel station (CRPB, 1976). Hinton (1974) recorded the presence of successive pulses of phytoplankton following the first spring peak (maximum chlorophyll - 8.3 mg m^{-3}), each being smaller than the preceding. The spring peak of 1976 (maximum - 10.0 mg chl a m^{-3}) was similarly followed by a series of pulses although, while the first subsequent peak was reduced, the succeeding pulses then increased in magnitude with the final recorded peak at the end of July having a similar chlorophyll maximum (10.5 mg chl a m^{-3}) to that of the initial spring peak. In 1977, the peaks decreased in size following the spring maximum (6.4 mg chl a m^{-3}) until September when a large diatom pulse (max. 7.8 mg m^{-3}) was observed. Low winter levels were found in all surveys.

Productivity in the Firth of Clyde was measured on a long term basis for the first time in this survey. Johnston, Adams and Dooley (1971) had previously carried out a three-day survey in the Firth during April 1970 and found that the carbon-14 productivity was around 1 mg C^{14} per m^3 per hour. This level of fixation was found in the present survey just before and also immediately after the collapse of the spring bloom.

The maximum observed levels of fixation were 66.6 mg C m^{-3} h^{-1} in July 1976 and 55.7 mg C m^{-3} h^{-1} in September 1977. The general pattern of carbon fixation in the upper 10 metres of the water column was similar to that measured by Wood et al (1978) in Loch Etive although the maximum fixation level per depth was higher

in the Fairlie Channel. This could be a consequence of the lower sampling frequency in Loch Etive resulting in peaks of productivity being missed.

In the past, it has been assumed that diatoms were mainly responsible for the productivity of the Firth of Clyde. Marshall and Orr (1927) found that the changes in chemical factors coincided with changes in diatom numbers and these were therefore assumed to be the most important producers in the Firth.

The present study has shown, however, that while the contribution of the netplankton is high during bloom conditions, over the annual cycle the nanophytoplankton, composed mainly of small flagellates, contributed at least 50% to the chlorophyll and productivity. Over the two year period the average % contribution of the nanophytoplankton to the productivity in the upper 10 metres of the water column was 50% while its contribution to the chlorophyll was 66%. Figures of up to 100% contribution of the nanophytoplankton to the biomass and productivity have been recorded at times.

Marshall, Nicholls and Orr (1934) and Nicholls (1933) had previously noted that minute flagellates occurred in large numbers during summer at Keppel and in Loch Striven. The significance of these flagellates, however, was doubted since many appeared to be colourless and also since their presence in large numbers had no effect on the survival of a second abortive brood of Calanus. The graph of diatom and flagellate numbers in the surface samples collected at Keppel from March to September 1932 (Nicholls, 1933) is very similar to that of the net- and nanophytoplankton chlorophyll levels in 1976 in the present survey, with peaks of flagellates occurring after peaks of diatoms.

The biomass and productivity of both fractions of the phytoplankton varied seasonally. In winter, the low light intensity and the mixed, turbulent water column combine to produce unfavourable conditions for photosynthesis although the nanophytoplankton would appear to be able to utilize the low light intensities more effectively than the netplankton since they form the major part of low biomass present at this time.

During spring and summer both fractions increased, the nanophytoplankton gradually while large scale variations in total biomass and productivity were due to changes in the netplankton. The nanophytoplankton tended to form a reasonably stable background level on which peaks of activity of netplankton were superimposed. During June and July 1976 (with the exception of the end period) the nanophytoplankton chlorophyll *a* remained around 1 mg chl *a* m^{-3} while peaks of netplankton activity increased the total chlorophyll *a* to 6.04 and 7.00 mg chl *a* m^{-3} on two occasions.

The relative constancy of the nanophytoplankton in comparison with the netplankton has been observed in several situations. Marshall (1947) observed that μ-flagellate numbers varied greatly in Loch Craiglin but that there was no great increase at any one time as there was with diatoms nor was there any time of the year when they were very scarce. Lännergren and Skjoldal (1975) found that in contrast to the large fluctuation of diatoms, the numbers of flagellates and monads increased rather slowly and regularly and did not seem to be influenced by the variations in nutrient contents in a Norwegian fjord.

In more open waters, Boalch, Harbour and Butler (1978) found that flagellates were present throughout the year at El in the English Channel. Since the flagellates did not show such marked seasonal fluctuations as the larger species they did not alter the seasonal picture but just raised the whole graph of cell numbers by about one-fifth. In the Californian Current Malone (1971a), observed little seasonal variation in the nanoplankton (22 μm) productivity but observed large changes in netplankton productivity which were associated with upwelling.

In the Firth of Clyde, the relative importance of the net- and nanophytoplankton fractions of the phytoplankton showed a marked seasonality. During late autumn, winter and early spring, the major part of the phytoplankton biomass is composed of nano-phytoplankton and it is highly significant at this time of year.

Bulter, Corner and Marshall (1970) have shown that overwintering populations of Calanus in the Firth of Clyde must be feeding during winter. Although the nanophytoplankton have been found in general to be a poor food source for Calanus (Marshall and Orr, 1955) these organisms may provide the only available food source during this period. There is some evidence that C. finmarchicus can modify its feeding patterns to match the available food material and that it will filter small particles (Gamble, 1978). In the Strait of Georgia, Parsons, Le Brasseur, Fulton and Kennedy (1969) found that at certain times the μ-flagellates augmented the total biomass and were at times grazed effectively by Pseudocalanus minutus. This occurred during February when the copepods were surviving on subsistence levels of

food while at other times the flagellates were selectively avoided when diatom concentrations were adequate during May.

High numbers of μ-flagellates had previously been found in Loch Craiglin in the winter months (Marshall, 1947) and in Loch Etive where the μ-flagellates were observed to make an important contribution to the biomass, their relative abundance was greatest in autumn and winter (Wood et al, 1973). Mommaerts (1974) found that the nanoplankton (< 50 μm) was dominant everywhere in winter and also just after the spring bloom.

In the Fairlie Channel an increase in nanophytoplankton significance was also observed after the spring diatom increase. Following the rapid decrease in diatom numbers, there was a period of a few weeks of low biomass and productivity which was dominated by nanophytoplankton, mainly small flagellates but also single and two-cell chains of Skeletonema, until May 27 when the nanophytoplankton produced a peak of chlorophyll (3.96 mg m^{-3}, 87% of which was contributed by the nanophytoplankton) and productivity (27.3 mg C m^{-3} h^{-1} - 89% being nanoplankton produced). Levels of nutrients during the post spring bloom period were low. The increase in nanophytoplankton following the spring increase in 1977 was less pronounced.

During the summer months the nanophytoplankton was of approximately equal significance as the netplankton. While the nanoplankton tended to maintain fairly constant levels of fixation and biomass, peaks of netplankton activity occurred usually following, or concomittant with, periods of increased nutrients and sunny weather.

The biomass and activity of the net- and nanoplankton (< 30 μm) during the spring bloom in Lindåspollene, a land-locked Norwegian fjord has been studied by Skjoldal and Lännergren (1978). The netplankton contributed on average 48% to the total chlorophyll and only 7% to the total carbon assimilation. It was observed that the netplankton only grew actively in the first phase of the bloom and that the nanoplankton, predominantly small monads and flagellates in the size range 2-5 μm, predominated later, apparently due to low nutrient concentrations. As in the Firth of Clyde, Skeletonema costatum dominated the spring bloom but the chain lengths were shorter than those found in the Firth. During the early part of the bloom, chains were three to four cells long with one to two cell chains becoming numerous later. In the Firth, chains of up to fifteen to twenty cells long were observed during the peak of the bloom while short chains became common towards the end. Skeletonema towards the end of the bloom contributed to the nanophytoplankton as well as the net.

Pingree, Holligan, Mordell and Head (1976) found that, in terms of carbon fixation in the Celtic Sea and at station E1, in the English Channel, the relative importance of the nanophytoplankton (< 5 μm) was $> 70\%$ before and after the spring bloom and fell to $< 10\%$ during, although in absolute terms, production by the nanophytoplankton also increased during the bloom.

As the thermocline developed at E1 during the summer of 1976, the concentrations of inorganic nutrients at the surface reached their lowest values by midsummer since upward transport was inhibited by the physical and biological properties of the

thermocline and during this period small flagellates were the dominant phytoplankton in the surface waters with dinoflagellates forming a chlorophyll maximum in the thermocline (Holligan and Harbour, 1977).

Thus a pattern of the seasonal significance of the nanophytoplankton in the waters in and around Britain appears to be emerging. When conditions appear to be suboptimal in terms of light, nutrients or both, the nanophytoplankton increase in significance in terms of biomass and productivity. The netplankton, however, show rapid increases in growth when conditions are favourable. The effect of selective grazing by herbivores will also influence the significance of a particular fraction of the phytoplankton at a given time.

Chapter 5. DISCUSSION ON THE FACTORS AFFECTING THE VALIDITY OF THE RESULTS FROM THE FAIRLIE CHANNEL

The choice of sampling methods and programme for any ecological study have a direct influence on the results obtained. In the design of a sampling programme for phytoplankton, account has to be taken of the relatively short time scales over which changes in populations can occur, the possible influence of tides in an estuarine or coastal environment and the problem of overdispersion or patchy distribution of the organisms. This may range from the small scale variations arising from slight changes in the microstructure of the environment as described by Cassie (1959, 1962) which can result in variations in samples collected only 10 cm apart, to the large scale patches up to 10 miles in diameter described by Bainbridge (1957).

Due to the limitations of the time and work involved, the main sampling programme in the present study was restricted to one station, with collections made at regular depths and at regular time intervals. Several investigations (Barnes and Marshall, 1951; Hasle, 1954; Cassie, 1962; Platt, Dickie and Trites, 1970; Platt and Filion, 1973; Platt, 1975) have considered the errors due to spatial heterogeneity incurred in this type of survey using a single station and have assessed the validity of the results and the conclusions drawn. Although in most cases significant differences were observed, even with station densities as high as 10 per 0.0625 sq. miles (Platt, Dickie & Trites, 1970), it was found that measurements from one station reflected the temporal changes and gave an adequate assessment of the annual production.

The aim of the work described in this chapter was to check

both on the possible sources of error and their magnitude, in relation to the present study and to assess the reliability of the results obtained in indicating the seasonal trends in productivity and in the importance of the nanophytoplankton.

5.1. Consideration of the spatial heterogeneity within the Fairlie Channel

To investigate this, six grid surveys were carried out, the details of which are given in chapter 3. By sampling at different times of the year it was hoped to cover as wide a range of conditions and levels of phytoplankton biomass as possible. Chlorophyll *a* was used as an index of phytoplankton biomass since this was one of the main parameters used to compare the nanophytoplankton with the total. The chlorophyll values are given in Table 12 while the results of two-way analysis of variance of these are given in Tables 13 and 14.

When the differences found between the levels of total and nanophytoplankton chlorophyll *a* at the different stations were compared with the differences found between the sampling dates, the latter was observed to be highly significant for both the total ($F_{5,74} = 184.35$, $P < 0.01$) and the nanophytoplankton ($F_{5,74} = 134.155$, $P < 0.01$) while the differences between the stations were not significant.

It was important to assess how representative the main sampling station (11) was when compared with the other fifteen. This was done by carrying out a student's t-test, comparing the mean value of station 11 with the mean of the rest. The standard error was computed from $(RMS)\left(\frac{1}{6} + \frac{1}{15x6}\right)$ (RMS = residual mean squares, obtained from the anovas in Table 13). The values obtained were not

Table 12 : Chlorophyll *a* values for grid surveys (upper figure gives total chl *a*, lower - value for nanophytoplankton and figure in brackets is ratio of the two)

GRID 1		23 JUNE 1977	
1.02	2.21	2.43	1.60
0.37	0.46	0.63	0.32
(.37)	(.21)	(.26)	(.20)
2.37	1.43	1.93	2.17
0.68	0.42	0.70	0.65
(.29)	(.30)	(.37)	(.31)
1.96	1.72	2.98	0.92
0.72	0.70	0.80	0.60
(.37)	(.41)	(.27)	(.64)
1.85	1.42	0.76	1.05
0.84	0.50	0.48	0.61
(.54)	(.36)	(.64)	(.58)

GRID 2		29 SEPTEMBER 1977	
2.84	2.06	1.82	2.29
1.27	0.91	0.82	1.05
(.45)	(.44)	(.45)	(.46)
2.24	1.83	1.91	2.14
0.89	0.81	0.85	1.28
(.40)	(.44)	(.44)	(.60)
1.96	2.26	1.99	2.70
1.21	0.95	1.03	1.48
(.62)	(.42)	(.52)	(.54)
1.98	1.98	1.94	2.50
1.70	1.24	1.46	1.47
(.86)	(.67)	(.76)	(.59)

GRID 3		3 NOVEMBER 1977	
0.89	1.00	1.11	1.31
0.81	0.96	0.90	1.02
(.91)	(.97)	(.81)	(.78)
0.87	0.89	1.06	1.30
0.64	0.67	0.60	0.94
(.74)	(.75)	(.57)	(.73)
0.91	0.91	0.96	1.36
0.62	0.65	0.79	0.99
(.68)	(.72)	(.82)	(.73)
0.97	1.57	1.35	1.73
0.87	0.83	0.91	1.11
(.90)	(.53)	(.68)	(.64)

GRID 4		9 DECEMBER 1977	
0.24	0.22	0.31	0.22
0.20	0.12	0.12	0.22
(.84)	(.57)	(.40)	(1.00)
0.23	0.24	0.26	0.23
0.20	0.20	0.27	0.19
(.87)	(.87)	(1.04)	(.82)
0.36	0.22	0.27	0.17
0.24	0.16	0.26	0.16
(.67)	(.74)	(.98)	(.96)
0.45	0.26	0.38	0.29
0.40	0.15	0.29	0.19
(.88)	(.60)	(.75)	(.66)

GRID 5		27 FEBRUARY 1978	
0.22	0.25	0.32	0.23
0.20	0.23	0.30	0.20
(.91)	(.92)	(.95)	(.87)
0.31	0.19	0.33	0.24
0.25	0.19	0.30	0.24
(.81)	(1.0)	(.90)	(1.0)
0.14	0.19	0.34	0.17
0.12	0.18	0.24	0.17
(.83)	(.92)	(.71)	(1.0)
0.23	0.24	0.25	0.21
0.22	0.19	0.21	0.20
(.96)	(.80)	(.87)	0.94)

GRID 6		21 APRIL 1978	
3.56	4.68	3.17	3.30
1.99	2.57	1.76	1.61
(.56)	(.55)	(.56)	(.49)
3.69	3.46	3.16	3.67
1.60	1.82	1.65	1.65
(.43)	(.53)	(.52)	(.45)
3.33	3.52	2.98	4.05
1.75	1.88	2.02	1.96
(.53)	(.53)	(.68)	(.48)
3.34	4.15	3.07	3.70
1.89	3.06	1.34	1.94
(.57)	(.74)	(.44)	(.52)

Table 13

a) Two-way analysis of variance of the total chlorophyll a values for grid stations against time

	sum of squares (ss)	Degrees of freedom (df)	Mean Square (M.S.)	Variance Ratio (F)	
Between stations	1.141	15	0.016	0.553	
Between dates	126.619	5	25.3238	184.35	***
Residual	10.165	74	0.137		
Total	137.925	94			

b) Two-way analysis of variance of the nanophytoplankton chlorophyll a for the grid stations against time

	ss	df	M.S.	F	
Between stations	0.810	15	0.054	1.091	
Between dates	33.197	5	6.639	134.155	***
Residual	3.662	74	0.049		
Total	37.669	94			

* significant at the 5% level

** significant at the 1% level

*** significant at the 0.1% level.

Table 14 : Two-way analysis of variance of individual grids comparing chlorophyll values from the vertical rows of stations with the horizontal rows

GRID 1. Total chlorophyll a

	ss	df	MS	F
Rows	1.216	3	0.405	0.955
Columns	0.715	3	0.238	0.562
Residual	3.819	9	0.424	
Total	5.750	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.14	3	0.05	2.74
Columns	0.06	3	0.02	1.19
Residual	0.15	9	0.02	
Total	0.35	15		

GRID 2. Total Chlorophyll a

	ss	df	MS	F
Rows	0.134	3	0.045	0.56
Columns	0.539	3	0.180	2.25
Residual	0.719	9	0.080	
Total	1.392	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.63	3	0.21	9.90**
Columns	0.34	3	0.11	5.33*
Residual	0.19	9	0.02	
Total	1.16	15		

GRID 3. Total Chlorophyll a

	ss	df	MS	F
Rows	0.390	3	0.130	8.44**
Columns	0.545	3	0.182	11.834**
Residual	0.139	9	0.015	
Total	1.073	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.15	3	0.05	11.11**
Columns	0.19	3	0.06	14.12***
Residual	0.04	9	0.004	
Total	0.38	15		

GRID 4. Total Chlorophyll a

	ss	df	MS	F
Rows	0.018	3	0.058	1.545
Columns	0.028	3	0.009	2.433
Residual	0.034	9	0.004	
Total	0.079	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.02	3	0.007	1.58
Columns	0.02	3	0.007	2.27
Residual	0.03	9	0.003	
Total	0.07	15		

GRID 5. Total Chlorophyll a

	ss	df	MS	F
Rows	0.01	3	0.003	1.31
Columns	0.03	3	0.01	4.32*
Residual	0.02	9	0.002	
Total	0.06	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.01	3	0.003	3.85
Columns	0.01	3	0.003	4.30*
Residual	0.01	9	0.001	
Total	0.03	15		

Table 14 contd

GRID 6. Total Chlorophyll a

	ss	df	MS	F
Rows	0.10	3	0.003	0.24
Columns	1.56	3	0.52	3.63
Residual	1.29	9	0.14	
Total	2.96	15		

Nanophytoplankton chlorophyll a

	ss	df	MS	F
Rows	0.32	3	0.11	0.83
Columns	1.00	3	0.33	2.59
Residual	1.16	9	0.13	
Total	2.48	15		

significant indicating that the two groups were similar.

(T_{total} = 1.5, d.f. = 75, 0.2 > P > 0.1; T_{nano} = 1.21, d.f. = 75, 0.4 > P > 0.2).

The individual grids were then considered in detail with the stations being grouped for analysis in rows and columns. The results of the two-way analysis of variance of these are given in Table 14 and show that in three of the six grids, significant differences between the total, nanophytoplankton chlorophyll or both were present. In these the differences were further analysed to find out which particular stations varied from the rest.

Table 15. Summary of results of the analyses of the grids

A. No significant differences observed between stations

A.1. June 23, 1977 (thermocline below 5 metres)

A.2. December 9, 1977 (thoroughly mixed water conditions)

A.3. April 21, 1978 (during spring diatom increase).

B. Significant differences observed

B.1. September 29, 1977 (thoroughly mixed water conditions)

B.1.i. No significant differences observed between total chlorophyll *a* values

B.1.ii. With values for nanophytoplankton, the columns of stations adjacent to the shores differed significantly (5% level) from the two rows in midchannel ($F_{1,14}$ = 5.50).

B.1.iii. Also the most southerly row of stations differed significantly (5%) from the other rows with respect to nanophytoplankton chlorophyll *a* values ($F_{1,14}$ = 7.81).

B.2. November 3, 1977 (following a period of very wet weather, the freshwater influence extending to 15 m with salinities at 1 metre in range 29.5 - 30.1‰).

B.2.i. The two columns of stations nearest the Ayrshire coast differed significantly (5%) from the other two columns with respect to total chlorophyll ($F_{1,14} = 6.86$). Also for total chlorophyll values, the most southerly row of stations differed from the rest (5% level, $F_{1,14} = 7.81$). Considering the nanophytoplankton values, the column of stations adjacent to the Ayrshire coast differed significantly (1%) from the other three columns ($F_{1,14} = 12.86$) while the two central rows of stations differed significantly (5%) from the one above and one below ($F_{1,14} = 8.48$).

B.3. February 27, 1978 (mixed conditions)

B.3.i. With the total chlorophyll a, one column (2nd column in from the Ayrshire coast) differed significantly (1%) from the rest ($F_{1,14} = 14.00$).

B.3.ii. This column of stations also differed from the rest with respect to the nanophytoplankton chlorophyll a levels ($F_{1,14} = 9.43$, 1% level of significance).

Consideration of the individual grids showed that significant differences between stations can occur in the Fiarlie Channel, with stations sampled at a density of 16 per 0.78 km^2 but that the differences did not always occur. It was observed that mixed conditions did not guarantee a homogeneous population.

The degree of influence of physical and/or biological

factors on these inhomogeneities is difficult to assess but several points can be made. It is suggested that the differences which arose in the November survey were mainly due to the physical factor of the freshwater run-off. Slightly lower salinities were observed down the Ayrshire coast and the bottom stations and these had higher chlorophyll a levels but this would not explain why the upper and lower rows of stations had higher nanophytoplankton chlorophyll a levels than the central rows.

Microscopic examination of preserved samples from these grids showed that large populations of Chlorella spp. localized at particular stations could be partly responsible for some of the differences observed e.g. in Grid 2 (September 1977) large numbers of Chlorella spp were observed at station 4 with lesser numbers at station 3 and other stations along the Cumbrae coastline. In this grid, the stations in the columns nearest the shore-lines and the bottom row of stations differed significantly from the rest in terms of nanophytoplankton.

Distinct populations of Chlorella spp were quite regularly observed at station 4 (grids 1, 2, 4 & 6) while another station which was distinctive in often having different populations of organisms from the surrounding stations was station 7. In grid 5 (February 1978) the large numbers of Chlorella spp at station 7 and to a lesser extent those present at the stations lying directly north of station 7 (i.e. stations 10 and 15), could have been responsible for the significant difference which was observed between the column containing these stations and the rest.

The localized populations at stations 1 and 7 suggest a

shore or possible current effect in this area but station 11 remained apart from these and appeared to be representative of the changes which occurred in the midchannel.

5.2. Consideration of the effect of tides

The timing of the incubation of the productivity samples was kept constant to allow for a six hour incubation period between 0900 - 1500 hours, whilst the state of the tide at the time of sampling varied between sampling dates. To try and assess if this had any effect on the results, the data accumulated over the two year period were grouped into four classes; those samples collected at high tide $\pm$ 1 hour, those collected at low tide $\pm$ 1 hour and those in the two intervening periods between high and low tide and vice versa. When the ratios of the nanophytoplankton chlorophyll a to the total chlorophyll a and productivity in these groups were analysed by means of a one-way analysis of variance (Table 16), no significant differences were found, suggesting that over a long term study, no persistently high or low ratios were found at a particular state of the tide. This suggests a minimal effect of tides on the overall results.

Table 16. One-way analysis of variance of nanophytoplankton chlorophyll a and the total chlorophyll a and productivity ratios with respect to tides

	Chlorophyll a				Productivity			
	ss	d.f.	M.S.	F.	ss	d.f.	M.S.	F
Between tide groups	0.08	3	0.03	0.44	0.12	3	0.04	0.51
Residual	3.79	62	0.061		4.40	57	0.08	
Total	3.87	65			4.56	60		

5.3. Consideration of diurnal variation

Chlorophyll 'a' fluorescence (Lorenzen, 1966) was continuously monitored over a 30 hour period during August 2-3 1978 by means of a flow-through door fluorimeter (Turner, mark III) to investigate this phenomenon. Although a continuously pumped sample from midchannel would have been preferred, the requirement of a steady power supply necessitated this experiment being set up on Keppel Pier, inshore of the main sampling station.

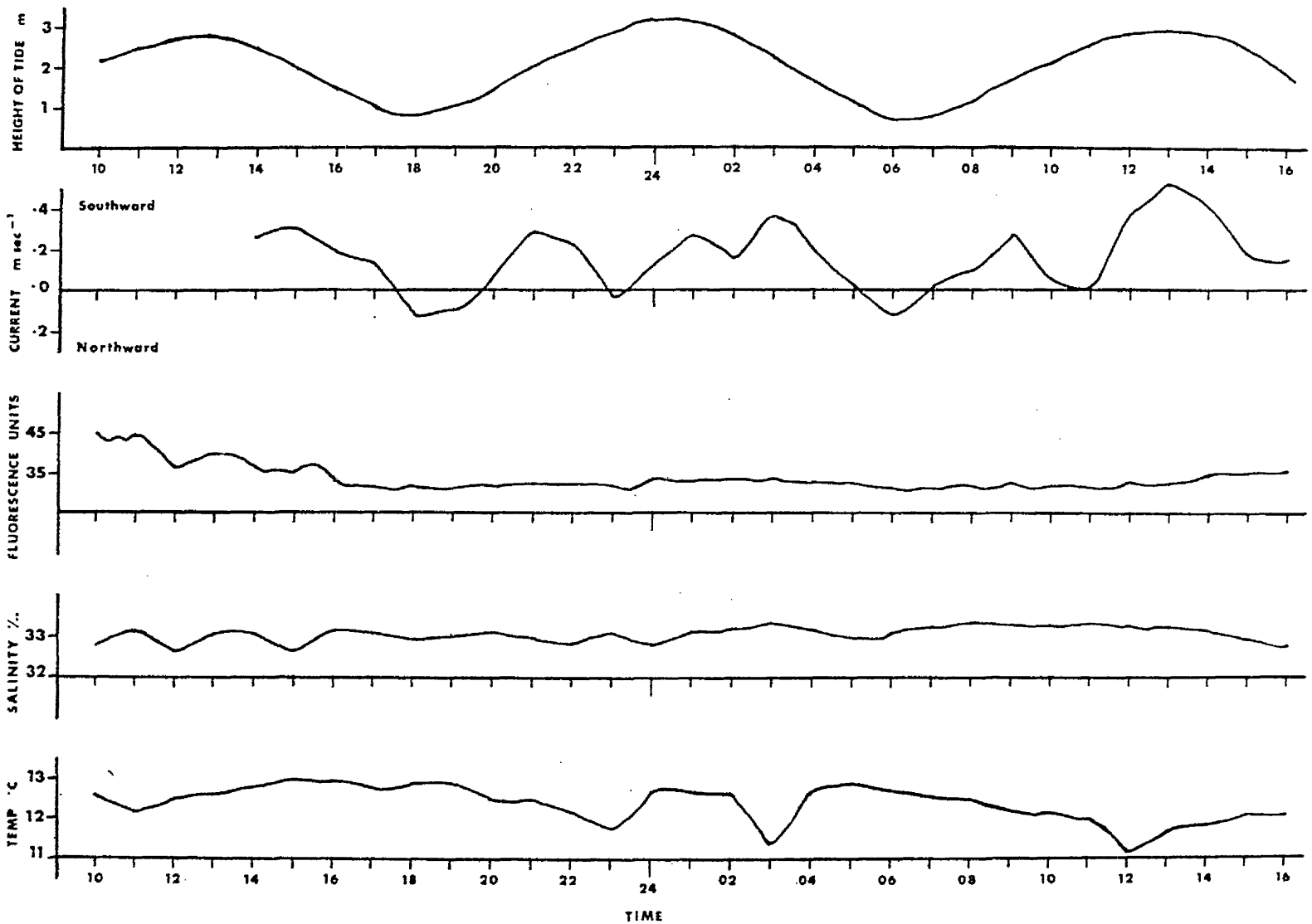
Methods

Water was continuously pumped from one meter below the surface by means of a submersible pump (Flygt) at a flow rate of 0.75 l min^{-1} and this was passed through the fluorimeter. Throughout the experiment this was set on its most sensitive scale (x 30). As the fluorimeter was being used primarily to monitor any changes which were occurring in the chlorophyll levels, the results were expressed as fluorescent units. Discrete samples were also collected, every two hours. These were divided into a total and nanophytoplankton fraction, extracted and analysed spectrophotometrically to measure the chlorophyll *a* (mg m^{-3}) in both fractions.

Meter readings of salinity, temperature, current speed and direction were taken at hourly intervals. Every six hours, samples were collected and frozen for subsequent nutrient analyses and samples were also fixed in Lugol's Iodine at regular intervals to check the species present and any changes in populations which occurred. One of the possible anticipated problems of using Keppel Pier was that at low tide, in particular, there was the possibility of the disturbance

Figure 22. Investigation of diurnal/tidal variations. Results from 30 hour sampling period August 2/3, 1978.

Keppel Pier 30 Hour Sampling Period August 2/3 1978



and suspension of benthic micro-algae and of detritus in the water mass which would interfere with the results. One of the main purposes of collecting the fixed samples was to record the incidence of benthic micro-algae.

Results

These are summarized in Fig 22 and Table 17. The current readings showed that with the exception of a short period around low tide, the current at Keppel Pier flowed continuously southward with speeds ranging from 0.1 m sec^{-1} to 0.53 m sec^{-1}. The level of fluorescence in the samples, after an initial period of fluctuation between 35-45 units remained steady at a lower level of approximately 28 units. These levels recorded on the most sensitive scale of the fluorimeter indicated low levels of chlorophyll in the Channel at this time; the values of chlorophyll for the discrete samples measured spectrophotometrically are in agreement with this. The chlorophyll levels for the total and nanophytoplankton are given in Table 17. Both show low mean values, 0.32 and 0.28 mg m^{-3} respectively with only slight variations. The range for the total values was 0.27-0.38 mg m^{-3} while that for the nanophytoplankton was 0.22-0.37 mg m^{-3}. Over the period investigated, the average contribution of the nanophytoplankton to the total chlorophyll was 87% but a slight decrease in the percentage contribution was observed between August 2nd and August 3rd.

The organisms present in the samples which had been collected and preserved were predominantly planktonic, Rhizosolenia delicatula, occasional Skeletonema chains, small thecate dinoflagellates and small

Table 17. Results of the various analyses carried out during the 30 hour sampling period, August 2/3, 1978

		Time (in hours)											
		10.00	12.00	14.00	16.00	18.00	20.00	22.00	24.00	02.00	04.00	06.00	08.00
Chlorophyll a (mgm^{-3})	Total	0.27	0.28	0.38	0.29	0.37	0.31	0.29	0.37	0.32	0.31	0.34	0.27
	Nano-	0.27	0.26	0.37	0.29	0.36	0.28	0.27	0.29	0.24	0.25	0.25	0.22
Ratio Nano/Total		1.00	0.91	0.95	1.00	0.96	0.90	0.94	0.80	0.76	0.82	0.74	0.82
Nutrients (μg at l^{-1})	Phosphate	0.68			0.70			0.71			0.67		
	Silicate	3.29			3.46			3.68			3.50		
	Nitrate	3.63			3.30			3.14			3.19		
Total Particle Volume $\mu m^3 \times 10^3\ ml^{-1}$					594.7	248.6	611.9	333.4	446.6	420.8	217.0	231.7	307.3

(< 5 μm) flagellates being mainly observed. Between 1800 and 2200 hours, occasional cells of Licmorphora and Grammatophora spp.were observed indicating some mixing with the benthos at low tide but observations of these were rare and it was considered that this mixing would not affect the chlorophyll results to a great extent. The sampling took place during a period of neap tides and this effect of bottom mixing at low tide would have been more substantial during low spring tides.

Of the other parameters studied, the nutrients showed very little change over the sampling period; the salinity fluctuated slightly at the beginning but remained fairly constant at approximately 33‰, the temperature over most of the period was around 12.6°C with four distinctive falls being observed. Three occurred in the period (1-2 hours) before high tide while the fourth at 0300 shows no correlation with any other measured parameter. The total particle volumes varied between samples and showed no consistent trends or obvious correlation with other factors.

Although the value of this study was limited in that samples were collected only from one depth and not throughout the water column and since it was carried out inshore instead of midchannel, it did indicate that during this period in August 1978 when the levels of chlorophyll and consequently phytoplankton biomass were low no diurnal or tidal fluctuation were apparent and that the levels of chlorophyll and nutrients remained very constant. At times of more active growth, more variation would be expected and it is possible that rhythms would then become apparent.

Some evidence of a diurnal fluctuation of the pycnocline has

already been shown in the Fairlie Channel by Hinton (1974). This affected the nutrient levels which showed maximal values in the early morning with a second peak in the afternoon. Results from the present study on chlorophyll levels differed from those of Hinton (1974) who found that large variations could be expected within a time period of two hours. The chlorophyll levels were higher (3-5 mg chl *a* m^{-3}) during this period which coincided with the decline of a diatom bloom and during a bloom period, the fluctuations would be expected to be more dramatic.

Chapter 6. The Relative Importance of the Nanophytoplankton throughout the Firth of Clyde

The survey of the Fairlie Channel provided detailed information on the distribution and abundance of the nanophytoplankton in this area but since this represents only a small part of the Firth in general, it was considered necessary to extend the sampling area to cover a wider section of the Firth to check that the results from the Fairlie Channel were typical of the area as a whole.

Sedimentary Pollution Unit (Millport) Sampling Stations

The programme was initially extended by sampling the five or six sampling stations in the Inner Firth used by the Sedimentary Pollution Unit. The positions of these stations are shown in Fig 23. Surface samples (0-0.5 m) were collected and used to estimate chlorophyll and nutrient levels, to study the particle size distributions of the seston and the organisms present in fixed, live and cultured samples.

The results from the four sampling cruises are given in Tables 18 and 19. The first cruise was on July 15, 1977 when high total chlorophyll *a* levels were observed at all stations sampled with the exception of Garroch Head. The populations at Skelmorlie and the Main Channel were almost totally dominated by a *Phaeocystis* bloom. *Phaeocystis* was, however, less numerous at Portencross and Hunterston where the populations included small flagellates and small non-thecate dinoflagellates, while at Garroch Head the majority of the organisms observed were small (< 5 µm) flagellates. Nutrients were not measured on this occasion.

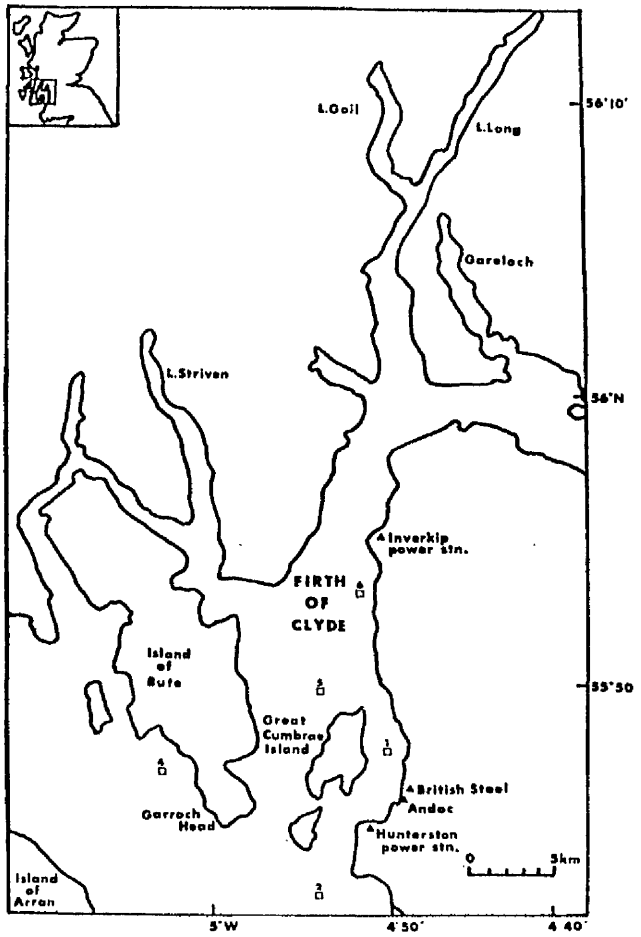
The second cruise on September 13 preceded the autumnal diatom increase which was observed around September 22. The highest

Figure 23.

A. Map of Inner Firth of Clyde with the Sedimentary Pollution Unit Sampling Stations indicated.
1 - Hunterston, 2 - Portencross, 3 - Garroch Head (not indicated on the map as it lies just outwith the southern-most part of the map), 4 - Stravanen, 5 - Main Channel, 6 - Skelmorlie.

B. Map of the same area, now indicating the Clyde River Purification Board Sampling Stations.

A


L.Goil
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Gareloch
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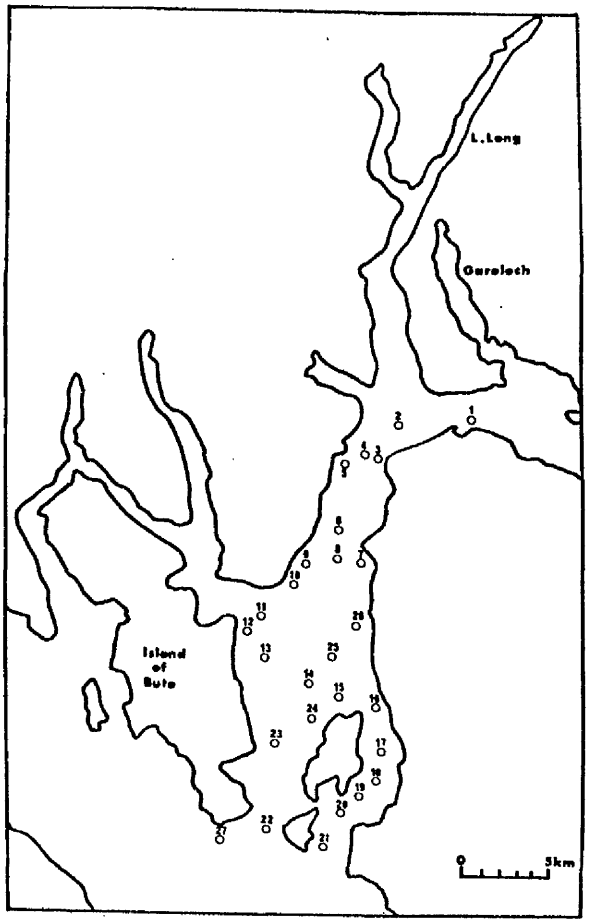
FIRTH OF CLYDE
Island of Bute
Great Cumbrae Island
British Steel Andoc
Garroch Head
Hunterston power stn.
Island of Arran
0
5km
56°10'
56°N
55°50
5°W
4°50'
4°40'

B


L.Long
Gareloch
Island of Bute
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5km

Table 18. Chlorophyll a levels and the ratios of the nanophytoplankton chlorophyll a/total at the Sedimentary Pollution Unit Sampling Stations July - November 1977

(Values quoted in mg chl a m^{-3})

		Garroch	Portencross	Hunterston	Main Channel	Skelmorlie	Stravanen
15.7.77	Total	0.23	2.66	3.01	3.51	6.66	
	Nanoplankton	0.14	1.10	1.35	0.71	2.00	
	Ratio	0.60	0.41	0.45	0.20	0.30	
13.9.77	Total	0.97	1.37	2.55	2.59	2.69	2.45
	Nanoplankton	0.68	0.53	0.87	1.05	1.03	1.22
	Ratio	0.71	0.39	0.34	0.41	0.38	0.50
11.10.77	Total	0.64	0.52	0.35	0.64	0.28	
	Nanoplankton	0.59	0.43	0.32	0.34	0.17	
	Ratio	0.92	0.84	0.92	0.53	0.59	
20.10.77	Total	0.28	0.40	0.69	0.42	0.58	0.62
	Nanoplankton	0.24	0.36	0.50	0.35	0.39	0.61
	Ratio	0.85	0.90	0.72	0.83	0.67	0.98

nutrient levels were recorded at Skelmorlie (phosphate - 2.41 μg at. l^{-1}) followed by the Main Channel Station while the stations situated lower down the Firth had similar lower values (e.g. Hunterston - phosphate 0.88 μg at. l^{-1}, nitrate 5.45 μg at. l^{-1} and silicate 4.41 μg at. l^{-1}). With the exception of Garroch Head and Stravanen the ratios of nanophytoplankton/total chlorophyll *a* were similar although the total chlorophyll *a* at Portencross was approximately half that of the other three. At these stations a mixed population of diatoms (of several species) and small flagellates were observed. At Stravanen the nanophytoplankton contributed a higher percentage (51%) of chlorophyll and it was also observed at this station that there were fewer diatoms present with *Chaetoceros* spp. being the most common. At Garroch Head few diatoms were observed and this was reflected in the low chlorophyll level of 0.97 mg chl *a* m^{-3}, 71% of which was made up of nanophytoplankton which consisted of cryptomonads and other small flagellates.

On the following cruise on October 11, the chlorophyll levels were considerably reduced; Skelmorlie had the lowest value of 0.28 mg chl *a* m^{-3} while maximum chlorophyll was observed at Garroch Head and Main Channel (0.64 mg chl *a* m^{-3}). The percentage contribution of the nanophytoplankton had increased throughout the area although at Skelmorlie (59%) and Main Channel (53%) the percentages were lower than at the other stations where they were above 80%. Nutrients had increased at all stations with the exception of Skelmorlie where levels were lower than those recorded in September and Main Channel where there was little change.

The following week (October 20) the total levels were further reduced and the overall percentage contribution of the nanophytoplankton had increased (82.5% mean $\pm$ 11.4%).

Table 19. Nutrient levels observed at the Sedimentary Pollution Unit Stations, July - November 1977

(Values are in µg at. of nutrient l^{-1})

		Garroch	Portencross	Hunterston	Main Channel	Skelmorlie	Stravanen
	Phosphate	0.81	0.85	0.88	1.50	2.41	0.70
13.9.77	Silicate	5.29	5.21	4.41	7.15	12.06	4.09
	Nitrate	7.03	5.10	5.45	12.52	20.92	4.68
	Phosphate	0.93	1.25	1.41	1.35	1.32	-
11.10.77	Silicate	6.39	10.56	8.78	7.38	9.06	-
	Nitrate	8.58	12.04	14.47	15.59	15.73	-
	Phosphate	0.93	1.29	1.42	1.10	1.32	1.33
20.10.77	Silicate	6.51	10.91	10.25	10.06	10.54	10.36
	Nitrate	9.70	16.65	15.18	11.93	14.32	15.50

Conclusions

Over the summer and autumn period studied, the average contribution of the nanophytoplankton to the chlorophyll in the area of the Inner Firth sampled was 61% ($\pm$ 24%). Considerable variation was apparent throughout the area however. Although only surveyed twice, the conditions and the phytoplankton populations at Stravanen appeared to be distinct from those in the Main Channel and the situation at Garroch Head also seems to be quite distinctive. There appears to be a general trend moving down the Firth from more estuarine to more open water conditions of lower chlorophyll and nutrient levels but with increasing importance of the nanophytoplankton component.

Clyde River Purification Board Sampling Stations (Inner Firth)

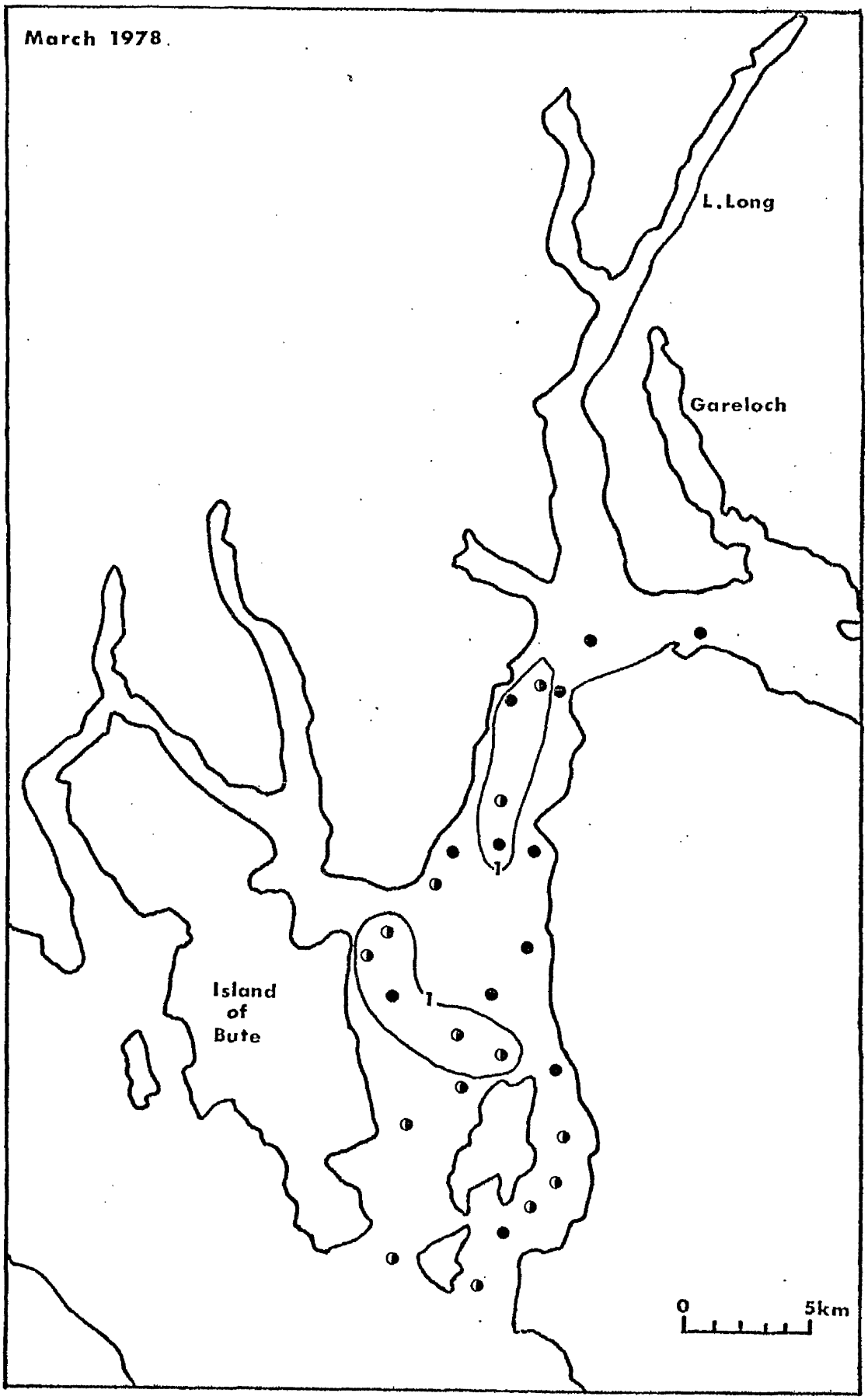
Extending the work in the Inner Firth, five sampling cruises were made with the Clyde River Purification Board during winter 1977 - spring 1978. A total of twenty six stations were sampled covering the area of the Inner Firth from Gourock to just south of the Little Cumbrae (Fig 23). The samples were collected by means of a water sampler from 1 metre depth and were used to estimate the total and the nanophytoplankton chlorophyll. Fixed and cultured subsamples were examined microscopically.

Results

During November and January the levels of total and nanophytoplankton chlorophyll at all stations were low. The average values of these and their ratio for each cruise are given in Table 20. In November the mean total chlorophyll was 0.24 mgm^{-3} (max - 0.35,

Figure 24. Total chlorophyll *a* distribution in Inner Firth on March 21, 1978 during a CRPB cruise. The chlorophyll levels with the exception of those in the two areas outlined were below 1 mg chl *a* m^{-3}.

- ◑ Stations at which the nanophytoplankton represented over 50% of the chlorophyll
- ● Stations at which the nanophytoplankton represented over 75% of the chlorophyll.


March 1978.
L. Long
Gareloch
Island
of
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1
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min - 0.17) while in January the mean total value was 0.17 mg chl *a* m^{-3} (max - 0.31 and min - 0.11). The differences between stations appeared to be inconsistent with no obvious patterns. During these two winter cruises the percentage contribution of the nanophytoplankton was high (89.4% and 89.9%).

The total chlorophyll *a* distribution for March 21 is summarized in Fig 24. Stations at which the nanophytoplankton represented over 50% of the chlorophyll *a* are indicated by a darkened half circle while those over 75% are indicated with a completely darkened circle.

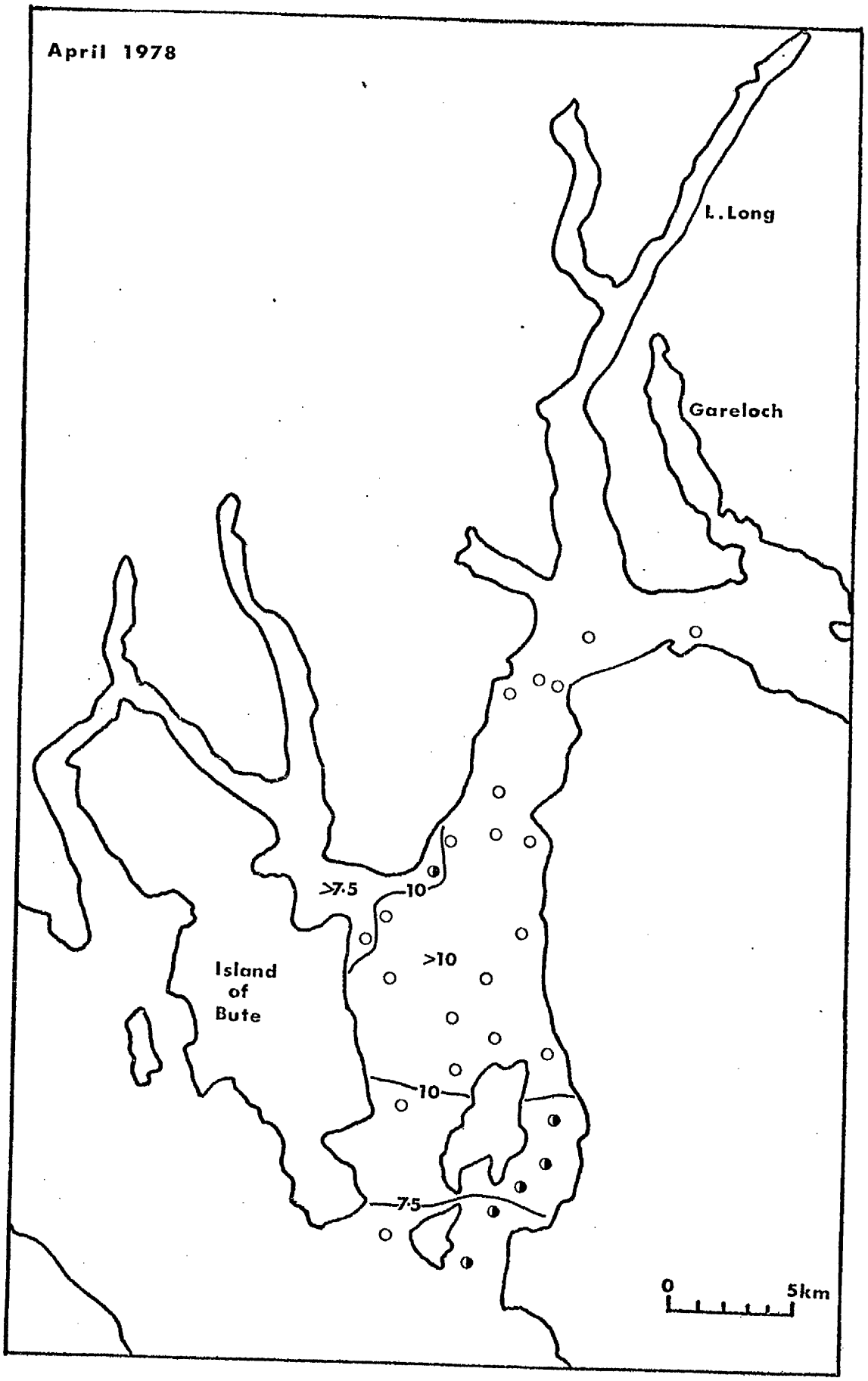
Table 20. Average chlorophyll *a* values for the CRPB cruises

	Chlorophyll *a* mgm^{-3}		
Cruise	Total	Nanophytoplankton	Ratio
22 November 1977	0.24 ± 0.06	0.21 ± 0.05	0.89 ± 0.15
19 January 1978	0.17 ± 0.05	0.15 ± 0.05	0.90 ± 0.19
21 March 1978	0.88 ± 0.18	0.66 ± 0.15	0.75 ± 0.12
18 April 1978	10.57 ± 2.58	4.33 ± 0.82	0.44 ± 0.09
31 May 1978	7.23 ± 6.33	1.26 ± 1.18	0.26 ± 0.19

The nanophytoplankton contributed at least 50% of the chlorophyll at all the stations and at a large proportion of these (mainly in the upper reaches) its contribution rose above 75%. At this time the chlorophyll levels were slowly beginning to rise after the winter minimum and in the two areas outlined the total chlorophyll was above 1 mg m^{-3}. The values for total chlorophyll ranged from 0.51 to 1.20 mg m^{-3}. A mixed population of organisms was observed at this time being made up predominantly of small flagellates although *Skeletonema* chains of 8 to 10 cells were quite common, and to a lesser extent, a *Thalassiosira* spp.

Figure 25. Total chlorophyll a distribution in the Inner Firth, April 18, 1978. (mg chl a m^{-3}).

- ◑ Stations at which the nanophytoplankton represented over 50% of the chlorophyll.
- ● Stations at which the nanophytoplankton represented over 75% of the chlorophyll.


April 1978
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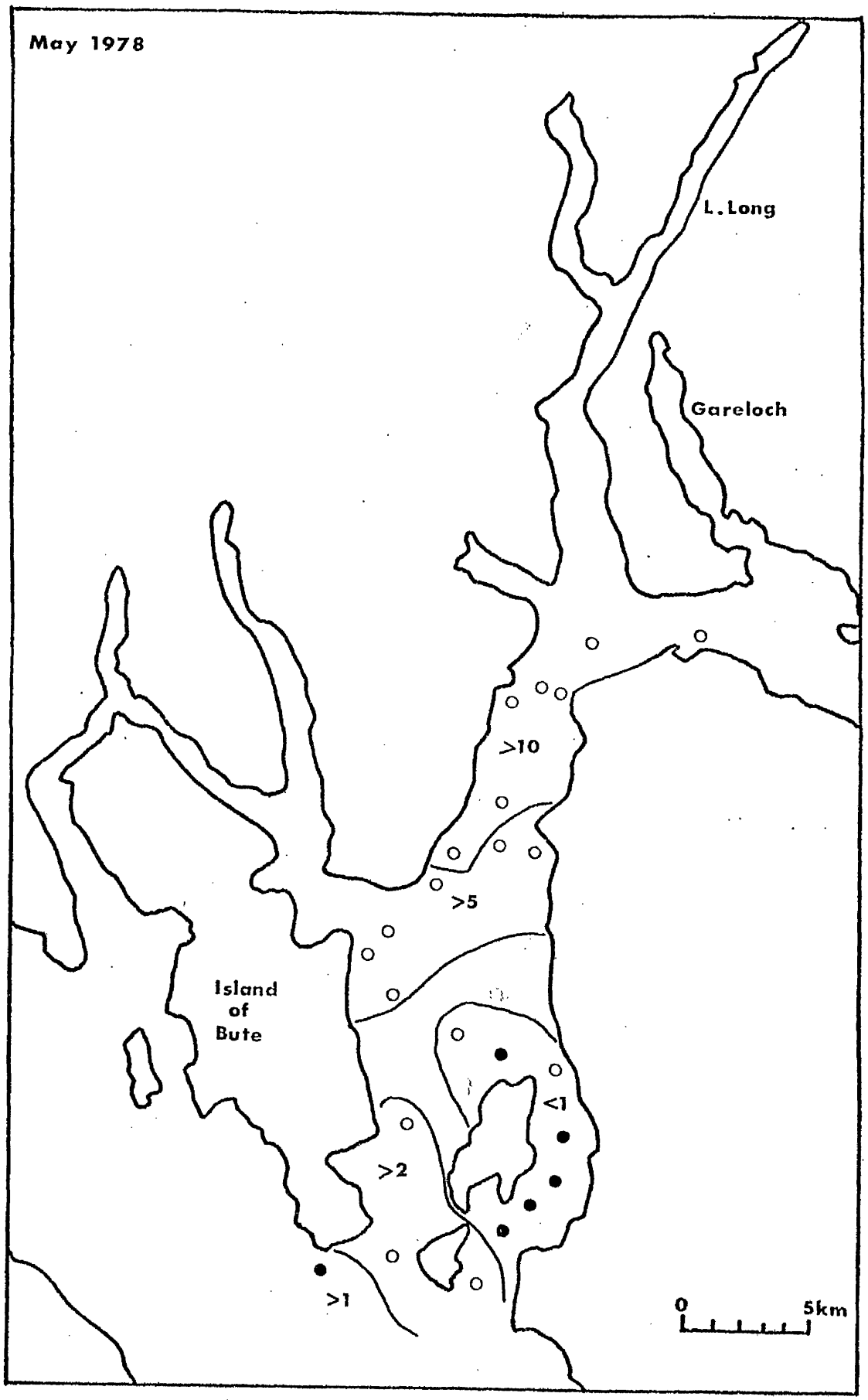
Gareloch
>7.5
10
>10
Island
of
Bute
10
7.5
0
5km

Figure 26. Total chlorophyll *a* distribution in the Inner Firth, May 31, 1978. (mg chl *a* m^{-3})

- ◑ Stations at which the nanophytoplankton represented over 50% of the chlorophyll
- ● Stations at which the nanophytoplankton represented over 75% of the chlorophyll.

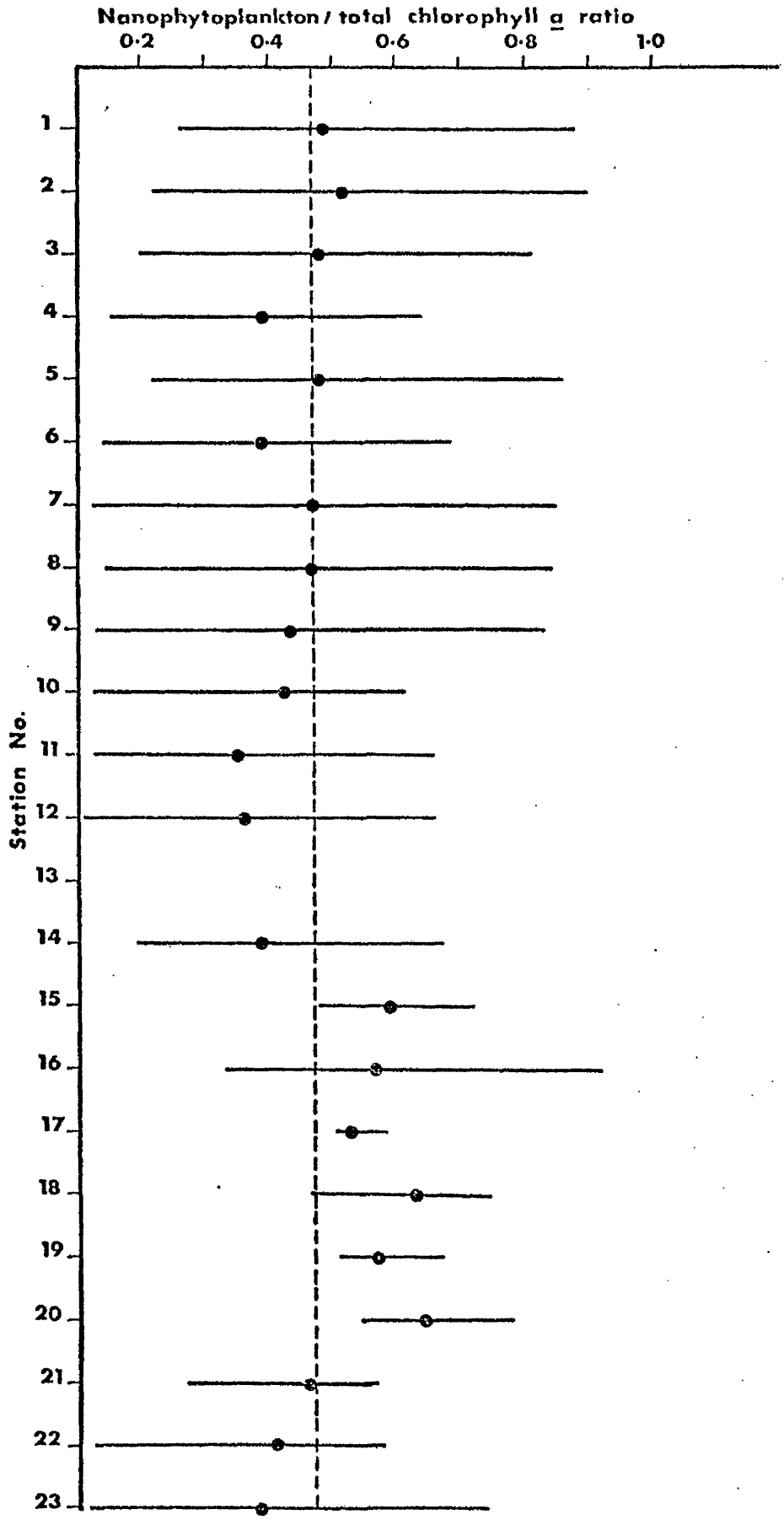

May 1978
L. Long
Gareloch
>10
>5
Island
of
Bute
<1
>2
>1
0
5km

On April 18 (Fig 25), chlorophyll (total) levels were above 10 mg m^{-3} in a large part of the upper firth. In the region of Great Cumbrae the chlorophyll was between 7.5 and 10 mg m^{-3} while south of the Great Cumbrae the levels were between 5 and 7.5 mg m^{-3}. At the majority of the stations the nanophytoplankton represented less than 50% (average 44%) of the chlorophyll. With the exception of station 10, the stations where the nanophytoplankton contribution was above 50% were localized in the region of the Fairlie Channel. These samples were collected towards the end of the spring diatom increase when the chlorophyll maxima were situated at approximately 10 metres depth (CRPB pers. comm.). The Skeletonema chain lengths were shorter (5-8 cells long) and single Skeletonema cells were common.

During May (Fig 26) the contribution of the nanophytoplankton had decreased to an average value of 28.6% with only a few stations where its contribution was above 50%; these again, as in April, were in the region of the Fairlie Channel.

Large variations in the total chlorophyll were observed between stations ranging from 0.71 (station 18) to 20.61 mg m^{-3} (station 2) and also in the nanophytoplankton values which ranged from 0.15 (station 23) to 4.51 mg m^{-3} (station 2). The highest levels were found in the upper reaches with decreasing concentrations towards the lower, more southerly part of the Inner Firth (Fig 26). In this lower region the chlorophyll maximum was subsurface (approximately 10 metres - CRPB pers. comm.) suggesting that the diatom outburst had just passed its peak in this region while at station 4 the chlorophyll maximum was still near the surface suggesting that the bloom was still in progress, possibly since higher nutrients are available in this area. A species of Thalassiosira was dominant at this time.

Figure 27. Geographical variation in the significance of the nanophytoplankton chlorophyll a in the Inner Firth. CRPB spring cruises 1978. Mean value and range plotted.


Nanophytoplankton / total chlorophyll a ratio
0·2
0·4
0·6
0·8
1·0
Station No.
1
2
3
4
5
6
7
8
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Conclusions

The winter cruises (November and January) confirmed the result found in the main study and that found in the previous section which was that the nanophytoplankton is the dominant contributor to the biomass and productivity at this time of year (average 89.6 $\pm$ 17% contribution).

The spring cruises showed varying degrees of significance of the nanophytoplankton from March (75% $\pm$ 12%) to May (26% $\pm$ 19%) when the nanophytoplankton were of minor importance.

When the results from the spring cruises were analysed by station (Fig 27) it was found that stations 15-20 (i.e. those lying around Great Cumbrae to the east) had a significantly higher ratio of nanophytoplankton/total chlorophyll than the rest of the stations ($t = 3.18$, $0.01 > p > 0.002$, d.f. = 64).

This result is of direct significance to the main study suggesting that the results from the Fairlie Channel are in general slightly higher than those encountered in other areas of the Inner Firth. The reason for the increased significance of the nanophytoplankton is uncertain but it is possible that these stations could be influenced by inward water currents moving up the estuary from the Outer Firth and are therefore possibly more indicative of marine, open water conditions than stations which are influenced by the increased nutrient levels flowing down from the estuary. More detailed information on the circulation patterns of the currents in the area would be necessary to verify this.

The observed changes in the ratio of nanophytoplankton to total chlorophyll were found to be due mainly to variations in the levels of netplankton with high values for these observed towards the estuary

and decreasing levels moving seawards. The corresponding levels of nanophytoplankton changed much less dramatically.

Sea Lochs - Loch Long and Gareloch

The Firth of Clyde in addition to the estuary, the inner and outer firths also includes a complex of seven long narrow fjord-type sea lochs which branch from its northern shores into the mountains of Argyll and Dunbartonshire. Two of these lochs, Loch Long and the Gareloch, were sampled during August 1976 and the nanophytoplankton contribution to the total biomass and productivity of these was assessed. The two lochs, some of the physical characters of which are given in Table 21, show several contrasts despite their close proximity.

Table 21. Physical Characters of Loch Long and the Gareloch

	Gareloch	Loch Long
Length	18 km	27 km
Depth	50 m (North basin) 20 m (South basin)	100 m
Coastline length	31 km	60 km
Total volume	0.21 km^3	1.29 km^3
Intertidal volume	0.05 km^3	0.10 km^3
Catchment area	38.6 km^2	119.7 km^2

The Gareloch is a shorter loch, its maximum depth (50 m) is only half that of Loch Long while its shoreline is more densely populated and with more industry. The sewage load into the Gareloch is over four times that of Loch Long in terms of biological oxygen demand and suspended solids (CRPB, 1976).

Samples were collected from the two lochs over a two-day

period; one loch was visited on the first day and the second on the following. Two visits were made to each loch. All samples were subsurface and were collected from a series of midchannel stations down the length of the lochs. The samples were returned to the laboratory for processing. Chlorophyll (total and nanophytoplankton) and nutrient levels were measured. Carbon fixation was also measured, with the samples incubated under white fluorescent light (1491 $\mu W\ cm^{-2}$) at $12^{o}C$. Temperature and oxygen profiles were taken during sampling.

Results

The temperature and oxygen data on the Gareloch showed that a thermocline developed in the north basin (south basin was not sampled) between August 3 and August 12 and was situated at approximately 7 metres. The thermocline was obvious at the head of the loch but became less so towards the spit which separates the north and south basins where the rapid currents would cause mixing and the breakdown of the thermocline. On Loch Long, however, a slightly deeper thermocline (10 metres) was present on both sampling days.

Within a loch on a particular sampling day, quite large differences were found between stations in terms of chlorophyll and productivity but for the purpose of comparing the two lochs the values were averaged and tabulated in Table 22 where data from Millport from the preceding week is included for comparison. The differences between stations were, however, taken into account when t-tests were carried out to determine if the differences between the lochs were significant.

Gareloch had very high nutrient levels for that particular time of year when nutrients in the sea are often almost undetectable.

Table 22. Summary of Results from Sealoch Sampling, August 1976

Date	Loch	Nutrients (µg at l^{-1})			Chlorophyll A mg mg m^{-3}			Productivity (mg C $m^{-3} hr^{-1}$)		
		Phosphate	Silicate	Nitrate	Total	Nanoplankton	Ratio	Total	Nanoplankton	Ratio
29.7.76	Millport	0.33(i)	1.20	1.36	9.00	3.43	0.38	50.39(ii)	26.18	0.52
3.8.76	Gareloch	1.39 ± 0.10	2.38 ± 0.62	8.08 ± 2.02	10.51 ± 3.94	2.03 ± 0.98	0.15 ± 0.05	57.34 ± 26.88	10.41 ± 3.38	0.22 ± 0.13
4.8.76	Loch Long	0.10 ± 0.02	0.59 ± 0.38	0.73 ± 0.28	5.31 ± 1.05	2.22 ± 0.77	0.41 ± 0.07	23.12 ± 10.88	11.68 ± 4.75	0.54 ± 0.16
11.8.76	Loch Long	0.40 ± 0.19	0.46 ± 0.17	1.08 ± 0.42	0.84 ± 0.19	0.41 ± 0.18	0.44 ± 0.108	5.06 ± 1.56	3.03 ± 1.46	0.59 ± 0.17
12.8.76	Gareloch	1.39 ± 0.38	1.79 ± 1.14	5.38 ± 3.92	3.200 ± 1.10	0.84 ± 0.14	0.28 ± 0.07	11.92 ± 5.52	7.46 ± 3.98	0.63 ± 0.13

(i) Figures quoted = Mean ± 1 S.D.

(ii) Millport samples incubated *in situ*; loch samples incubated in laboratory at 12°C, under a light intensity of 1491 µW cm^{-2}.

Maximum values for phosphate, nitrate and silicate were 1.75, 9.96 and 2.93 μg at. l^{-1} respectively. In contrast the levels in Loch Long were low, the levels being more comparable with those found at Millport in the previous week with the exception of silicate which was lower in Loch Long (mean values were 0.59 (week 1) and 0.46 μg at. Si l^{-1} (week 2)).

On August 4, the nanophytoplankton was found to contribute 41 ± 7% to the total chlorophyll *a* in Loch Long and 54 ± 16% to the estimated productivity. Although the mean levels of nanophytoplankton chlorophyll and productivity in the two lochs at this time did not differ significantly ($t_{chl} = 0.324$, $t_{prod} = 0.45$, d.f. = 7), the average contribution of the nanophytoplankton in the Gareloch was only 15 ± 5% (chlorophyll) and 22 ± 13% (productivity). This difference was due to increased netplankton activity in the Gareloch producing higher total chlorophyll and productivity levels which differed significantly from those in Loch Long ($t_{chi} = 2.83$, $t_{prod} = 2.52$, d.f. = 7).

During the first week of sampling the maximum recorded chlorophyll and carbon fixation in water samples from the Gareloch was 14.4 mg chl *a* m^{-3} and 91.95 mg carbon $m^{-3}h^{-1}$. The weather during this period was particularly warm and sunny.

On the second visit in the following week the total levels of both chlorophyll and C-fixation were reduced in both lochs. The maximum figures for chlorophyll and productivity in Loch Long were 1.1 mg chl *a* m^{-3} and 7.02 mg carbon $m^{-3}h^{-1}$ and for the Gareloch the respective figures were 4.2 mg chl *a* m^{-3} and 17.5 mg carbon $m^{-3}h^{-1}$. Although the total levels had decreased the contribution of the

nanophytoplankton to chlorophyll and productivity in Loch Long was similar to that found in previous week (44 $\pm$ 10% and 59 $\pm$ 17% respectively). In the Gareloch, the importance of the nanophytoplankton had increased, contributing 28 $\pm$ 7% to the total chlorophyll and 63% to the productivity.

Comparing the results of the second week, it was found that, while both the total and the nanophytoplankton chlorophyll levels varied significantly between the two lochs, no significant differences were observed with respect to productivity (Chlorophyll $t_{total} = 3.68$, $t_{nano} = 3.47$, d.f. = 5; Productivity $t_{total} = 2.09$, $t_{nano} = 1.84$, d.f. = 5).

Conclusions

As in other areas of the Firth, the contribution of the nanophytoplankton was significant. Within the two lochs it contributed 11-62% of the chlorophyll and 13-77% to the productivity.

In Loch Long while the total chlorophyll dropped from an average value of 2.22 to 0.41 mg m^{-3} between sampling dates, the percentage contribution of the nanophytoplankton remained fairly constant around 40-45%. Similarly, the high level of productivity (23.12 mg carbon $m^{-3}h^{-1}$) in the first week dropped to 5.06 mg C $m^{-3}h^{-1}$ in the second but the contribution of the nanophytoplankton to the total was 50-60% on both occasions.

In the Gareloch, the significance of the nanophytoplankton was more variable and also lower than that found in Loch Long. The average contribution of the nanophytoplankton rose from 15 to 28% of the chlorophyll and 22 to 63% to the productivity between sampling dates.

While the population in Loch Long is presumed to be relatively stable since the transfer of water between this loch and the main firth is minimal, Gareloch is influenced by incursions of water from the main channel and rapid changes in phytoplankton populations may result from this. The increased activity of the netplankton in the Gareloch is possibly due to a mild pollution effect caused by the high nutrients which coupled with the nanophytoplankton gave high levels of chlorophyll and productivity in this loch. It was noted that as the water column stabilized and a thermocline developed in the Gareloch, the nanophytoplankton became more significant.

Chapter 7 : ROCKPOOL SURVEY

Introduction

Rockpools form small naturally enclosed ecosystems and consequently have been the focus of several ecological studies. The advantages of studying rockpools include their small size, poor and characteristic flora and fauna and the possibility of reproducing the whole system in the laboratory. However, they show great biogeochemical instability which is a major reason for their specific biological conditions.

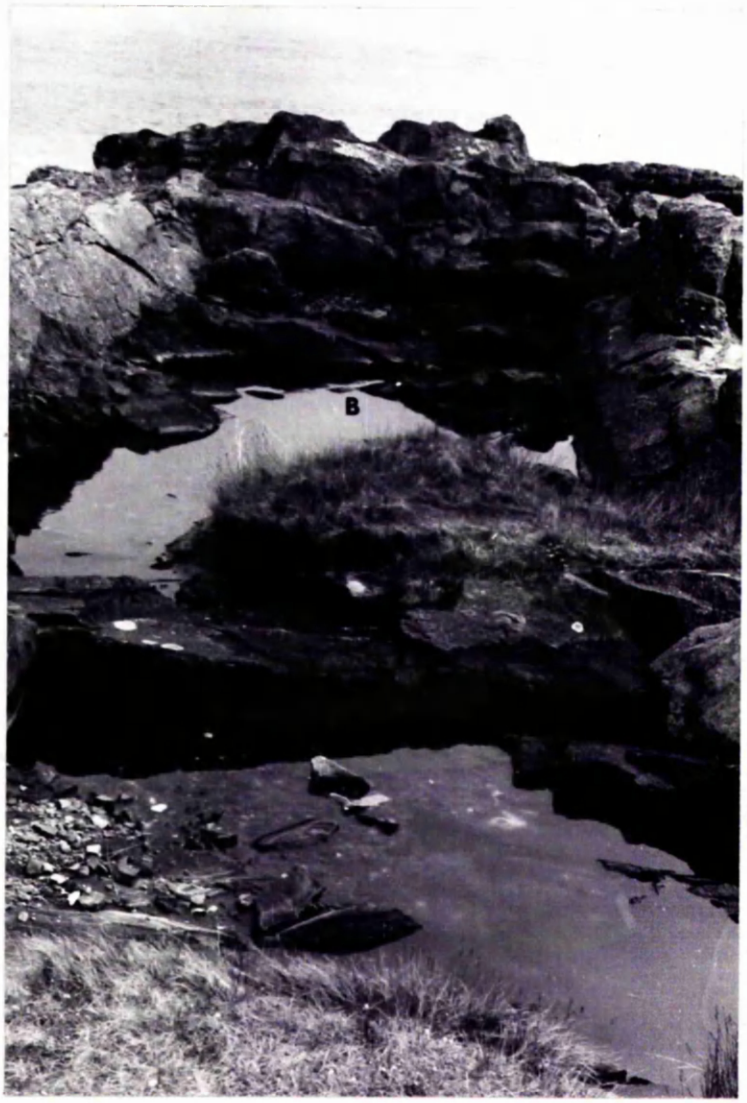
Several studies on the microflora of rockpools have been carried out in the past in relation to species identification and autecological aspects (Conrad, 1927; Carter, 1937; Droop, 1953, 1955 and Bourrelly, 1958a,b) and in relation to more general ecological studies (Vacelet 1959, 1969; Chretiennot, 1971; Saugestad, 1971). From these it appears that rockpools seem to offer conditions which lead to the dominance of small flagellates (Hulbert, 1956; Chretiennot, 1971) and they were usually found to be rich in nanophytoplankton.

Rockpools therefore provided a possible source of nanophytoplankton in the area of study. Droop (1953) had previously surveyed a number of supralittoral pools on Cumbrae and isolated several new species of flagellates from these. The intention of the study was to examine the biomass and productivity in two rockpools in the vicinity of the marine station and to compare these with the surface levels obtained from the nearby survey in the Fairlie Channel. The productivity of the rockpools was of interest as no previous reports of natural fixation rates in this environment have been found.

Plate 3. The situation of the rockpools used in the sampling programme.

3.1. Pool A is indicated by arrow (A) while the arrow in the foreground of the picture indicates the approximate position of Pool B in relation to A. Pool B lies just to the right of the edge of the picture.

3.2. Plate shows Pool B with the sea in the background. Samples were normally collected in the lower part of the pool, which at the time of taking the photograph, had dried out.


B

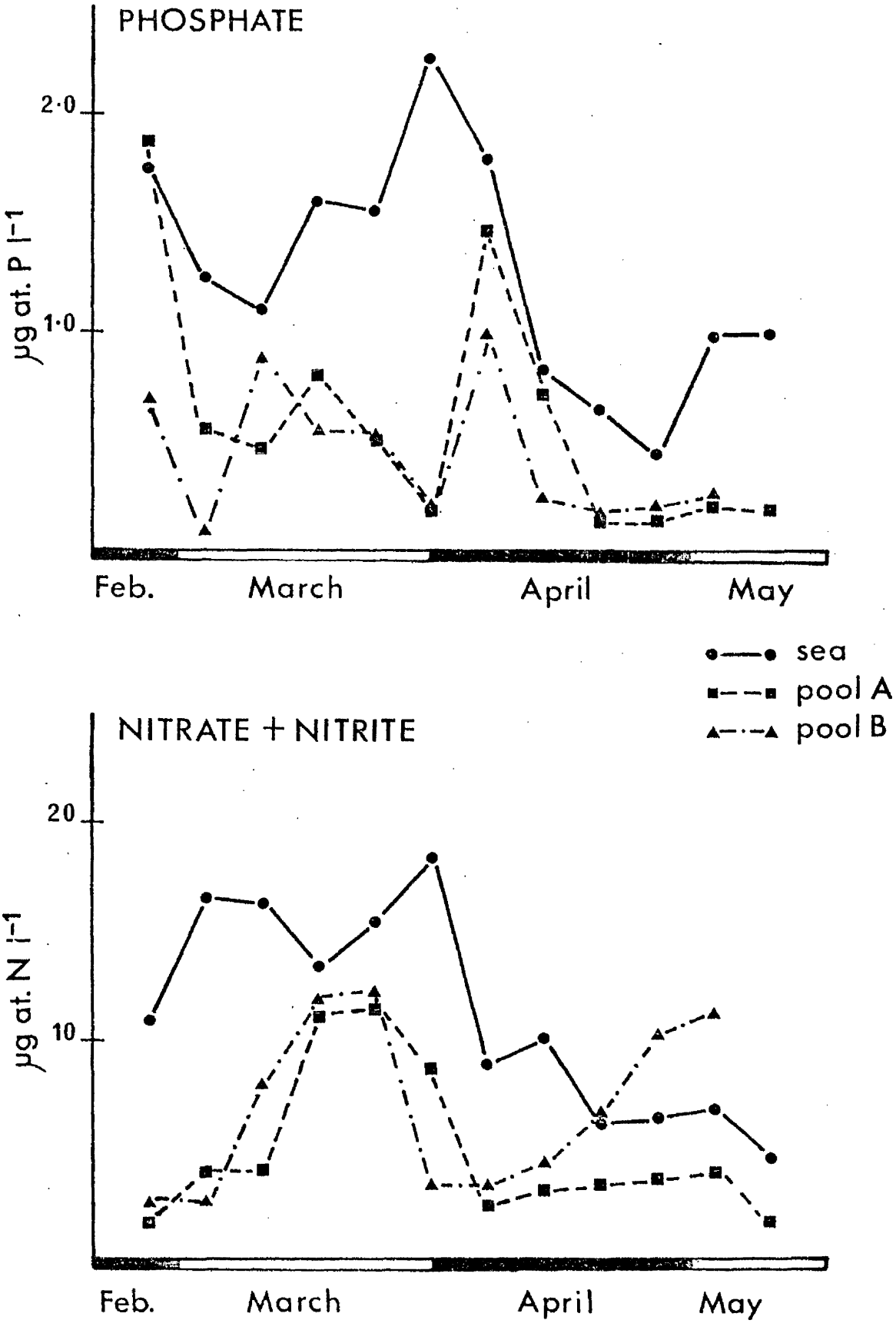
Description of Rockpools

Both pools were situated on Keppel Bight, directly below the Marine Station specimen supply department. They were above the mean spring high water mark and according to Droop's (1953) modified classification of Levander's (1900) would be considered as brackish or Type III pools. Type III pools are usually those with salinity above 1‰ and without macrovegetation. These pools are often discoloured with sediments in the deepest parts, as were the pools studied.

Pool A, whose position is indicated in Plate 3, was very high up on the shore with one side bounded by vegetation (marsh-type). It measured 3 metres by 1 metre and had a maximum depth was 0.5 m. It was sandstone-based and had low salinity (∿1‰). Unless at very high spring tides with south-westerly winds, it would have little contact with the sea but was possibly influenced by salt water run off from the specimen supply department. The phytoplankton populations observed reflected the fresh water conditions. Commonly observed species were Brachiomonas submarina, Scenedesmus spp., Trachelomonas spp., Chlamydomonas pusillata, Phacus spp., Euglena spp., Nannochloris oculata and blue-green algae.

Pool B whose position is also shown on Plate 3 with the sea behind, lay below and to one side of Pool A on a basalt outcrop just above the mean spring high water mark. The salinity of this pool was more variable and over the study period ranged between 9-15‰. It was a smaller pool (1 m x 2.5 m) with a maximum depth of 0.25 metres. The phytoplankton observed in Pool B included Oxyrrhis marina, Hemiselmis virescens, other Cryptomonads, Pyramimonas spp., Chlamydomonas spp., small dinoflagellates and also several diatom species on occasions - small Chaetoceros spp. and Phaeodactylum tricornutum.

Figure 28 : Nutrient (phosphate, nitrate + nitrite) levels in rockpools A and B on Keppel Bight, Great Cumbrae over the period mid-February to May 1976 compared with the adjacent levels in the sea (surface samples).
Both phosphate and nitrate + nitrite are expressed in $\mu g\ at.l^{-1}$.


PHOSPHATE
2·0
1·0
µg at. P l-1
Feb.
March
April
May
sea
pool A
pool B
NITRATE + NITRITE
20
10
µg at. N l-1
Feb.
March
April
May

These pools were sampled for a few months during 1976 (end of January until mid-May) and the methods used to analyse these samples were those used in the main survey (see Chapter 2).

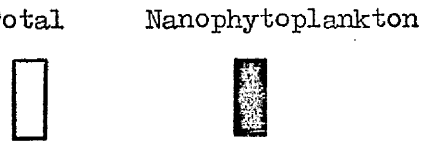
Results

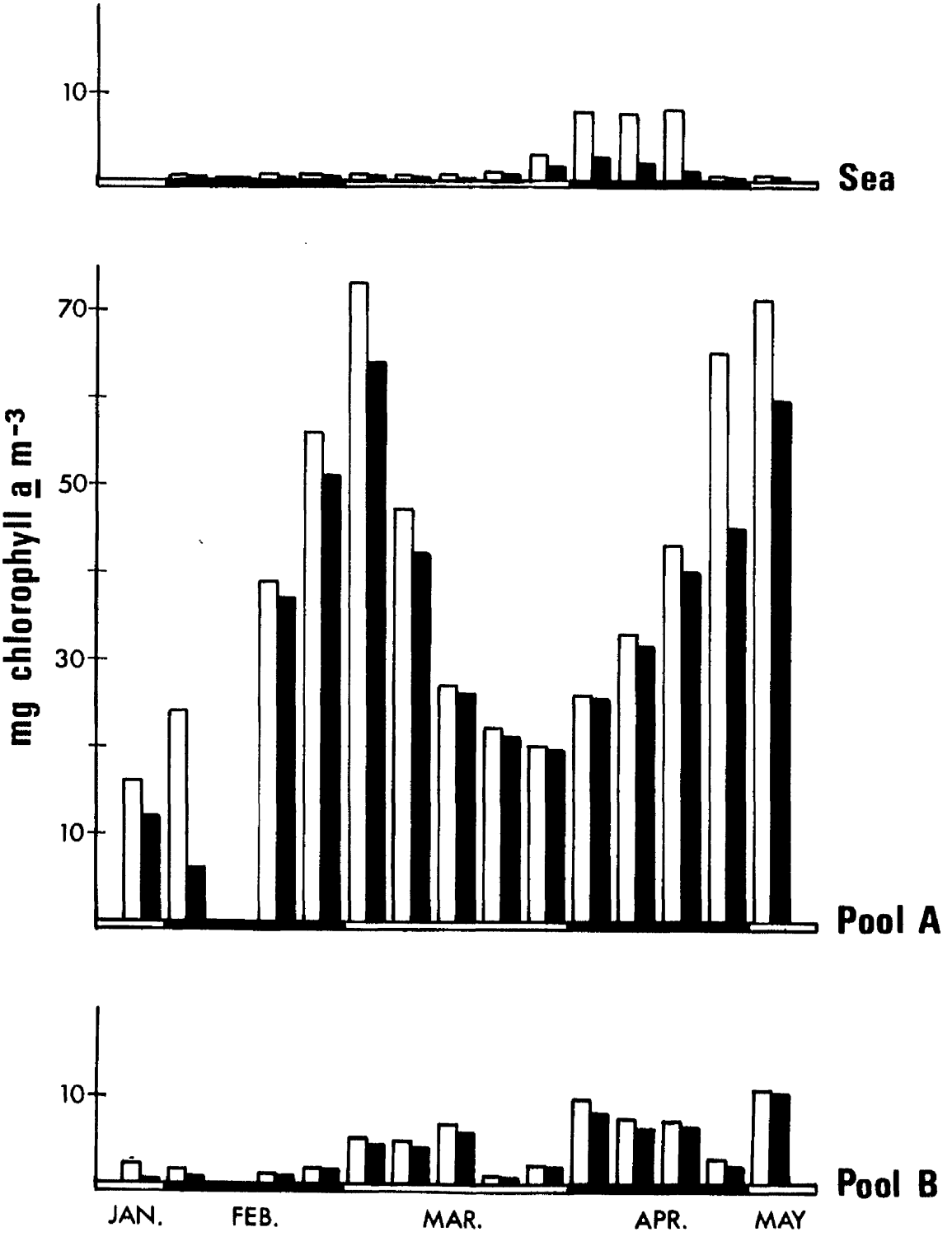
The nutrient levels in the pools with the exception of silicate were measured and the results are compared with the sea surface values in Fig 28. The phosphate contents of both pools were of similar magnitude and lower than that found in the sea. The results for nitrate + nitrite were similar with the exception of the period towards the end of April when the nitrate + nitrite level in Pool B rose above that in the sea. In general, an inverse relationship between the nutrients studied in the rockpools was observed; when phosphate was high, nitrate and nitrite were low.

Despite the lower nutrients, these pools, in particular Pool A, supported higher standing crops of phytoplankton (Fig 29 - chlorophyll values) over the winter and spring months measured and were more productive (Fig 30) than the sea. The contribution of the nano-phytoplankton in the rockpools to these parameters was high. In several instances, fixation values for the nanophytoplankton exceeded those for the total production and these were possibly due to handling errors. For Pools A and B respectively, the mean percentage contribution of the nanophytoplankton to the chlorophyll was 86% and 80% and to the productivity 90% and 79%.

Pool A sustained very high levels of chlorophyll. The maximum total value of 73 mg chl a m^{-3} was recorded on March 5 while the minimum, on January 29 was 18.1 mg m^{-3}. At this time the level of chlorophyll in the sea was just at the limit of detection. The

Figure 29 : Comparison of chlorophyll *a* levels in rockpools A and B and the adjacent sea surface. Chlorophyll *a* values are expressed in mg m^{-3}.




10
Sea
70
50
30
10
mg chlorophyll a m-3
Pool A
10
Pool B
JAN.
FEB.
MAR.
APR.
MAY

productivity in A was particularly high at the beginning of March and May coinciding with chlorophyll maxima and sunny weather. Despite the high chlorophyll levels at other times productivity was not excessively high and fixation per mg chl a at ambient light intensities was low. The mean value was 1.26 while in Pool B, on average, 3.54 mg carbon was fixed per mg chl a $m^{-3}h^{-1}$.

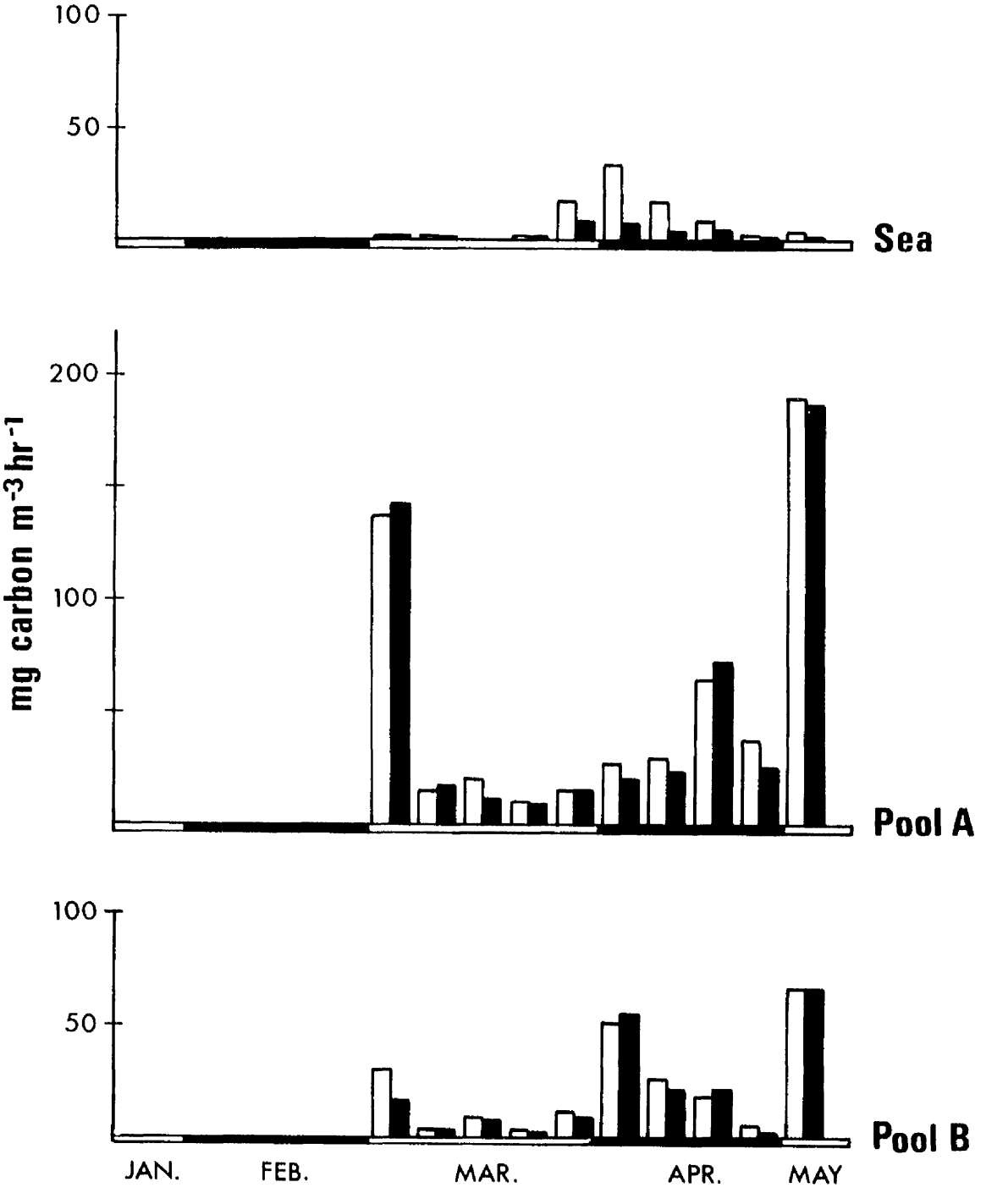
In Pool B, chlorophyll and productivity were lower and more comparable with the sea. The levels in Pool B however exceeded those in the sea except during the period of the spring increase when the total chlorophyll and productivity were similar. The species composition differed, however, and while the levels in the sea were due to an increase in netplanktonic diatoms, the nanophytoplankton was the major source of chlorophyll in Pool B. During the spring bloom period, a concurrent small diatom increase was observed in Pool B when the numbers of a small Chaetoceros spp. (approximately 10-12 μm x 5 μm) increased from March 31 until April 22 when these were succeeded by large numbers of cryptomonads.

Discussion

This short term survey illustrated the potential of the nanophytoplankton to survive and contribute high levels of biomass and productivity in the extreme environment of the rockpools, exceeding those in the more stable nearby sea environment.

The very high density of organisms in Pool A possible led to the shading of cells and this could have been an important factor in the low assimilation rates observed. Other possible contributory factors include nutrient competition and the possible build up of soluble inhibitory products excreted from the cells. Findenegg (1965)

Figure 30 : Comparison of the productivity levels in the rockpools A and B and the sea as measured by the carbon-14 technique. The fixation levels are expressed in mg carbon $m^{-3}h^{-1}$.


100
50
Sea
200
100
mg carbon m-3 hr-1
Pool A
100
50
Pool B
JAN.
FEB.
MAR.
APR.
MAY

in the freshwater lake environment had previously observed that increasing population density diminished the relative assimilation rate.

Pool B was subject to more variable conditions and had more contact with the sea. In this pool again the nanophytoplanktonic flagellates predominated and fixation rates and biomass were above those of the sea.

Over winter the major growth-limiting factor in the sea is insufficient light, with the ambient light intensities being low and the circulating organisms not remaining near the top of the water column long enough to obtain sufficient light energy for active growth. In the rockpool situation, however, active growth is possible as the organisms, particularly the motile forms, are in a shallow, stable environment where they can utilize the available light energy.

The predominance of nanophytoplankton in these rockpools is also possibly related to this feature of stability as this will favour small motile forms, non-motile forms such as diatoms possibly sinking and settling out before they have time to reproduce. The predominance of nanophytoplankton could also be due to physiological factors as Throndsen (1976) has shown that the ability to overcome sudden changes in the environment (e.g. changes in salinity) was pronounced in several species of small marine flagellates examined.

CHAPTER 8

A SURVEY OF THE NANOPHYTOPLANKTON SPECIES FROM LOCALITIES UNDER INVESTIGATION

The aim of this chapter is to draw up a preliminary list of the nanophytoplankton found in the Firth of Clyde and to give an indication of those taxa which were the most common. A thorough investigation of the systematics of this group would require the use of transmission electron microscopy to study both whole cell mounts and sectioned cells since most species, as distinct from genera, can only be accurately identified at these levels of magnification. A taxonomic study was not the main aim of the present investigation but it was thought of value to include a summary of the information obtained from the examination of the preserved, live and cultured material with the light microscope although identification was only possible to the genus in many cases.

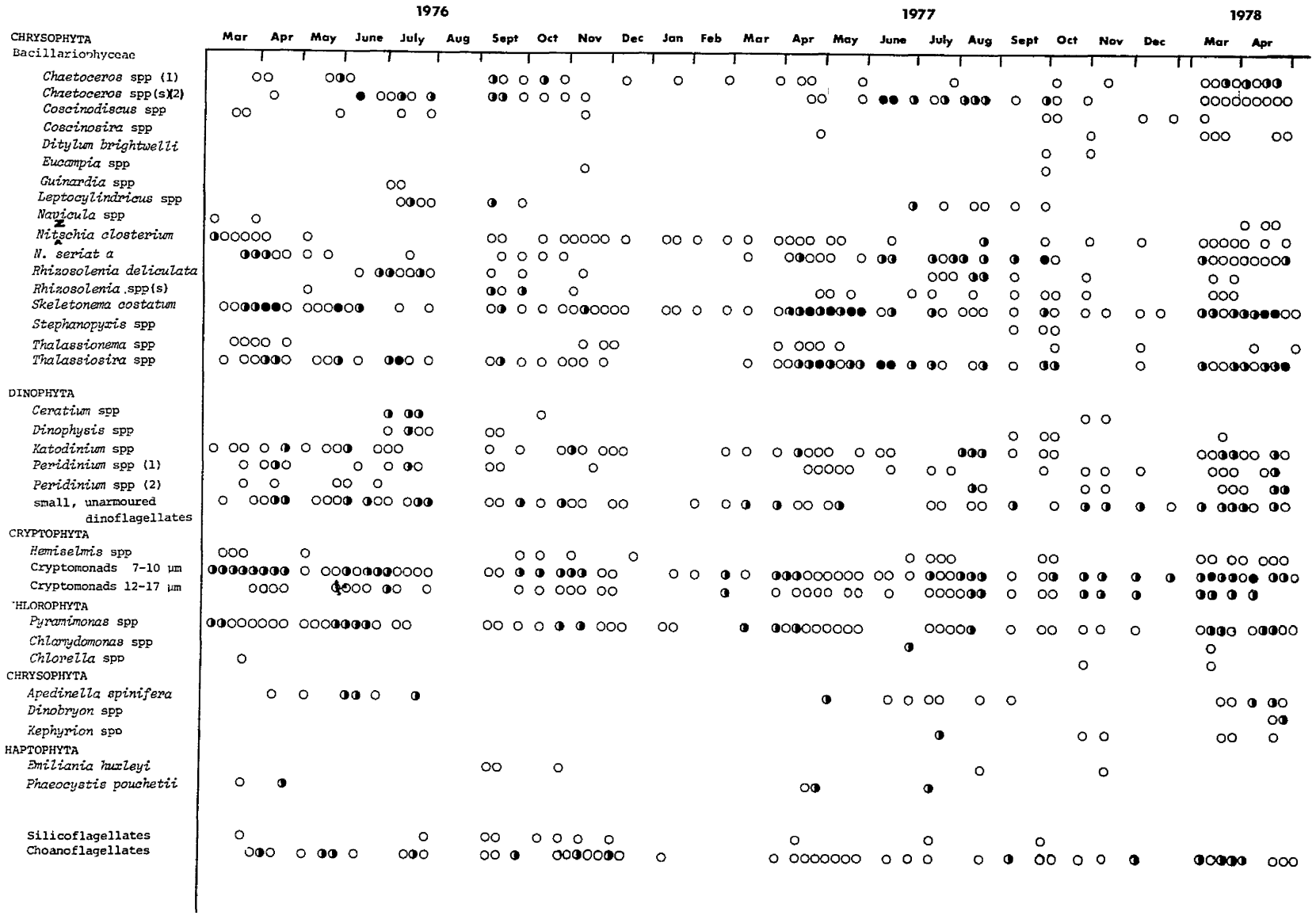
The samples fixed in Lugol's Iodine were of most use in identifying the larger, less delicate netplankton. The seasonal occurrence of these is summarized in Fig. 31. Since these are all well documented species and since those of importance in the present study have previously been discussed in Chapter 4, the netplankton will not be considered further. Fig. 31 also contains a summary of the seasonal occurrence of several genera included in the nanophytoplankton which remained identifiable in the preserved samples. In most cases, however, the small flagellates could only be recorded as "μ-flagellates" in specific size ranges, as so little detail could be observed. The majority of these cells were less than 10 μm in maximum cell dimension, often in the size range 2-5 μm.

Figure 31. The seasonal occurrence of the most commonly observed phytoplankton in the Fairlie Channel.

- ● very common
- ◑ common
- o observed.

Note 1: Chaetoceros spp (1) includes the single Chaetoceros cells usually in the size range 5-10 μm while Chaetoceros spp (2) includes all the larger, chain-forming species.

Note 2: Peridinium spp (1) groups together all the larger Peridinian cells (usually greater than 30 μm) with conspicuous spines while Peridinium spp (2) is made up of smaller cells (usually ≤25 μm) and includes P. triquetra and similar species.


1976
1977
1978
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
Mar
Apr
CHRYSOPHYTA
Bacillariophyceae
Chaetoceros spp (1)
Chaetoceros spp(s)(2)
Coscinodiscus spp
Coscinosira spp
Ditylum brightwelli
Eucampia spp
Guinardia spp
Leptocylindricus spp
Navicula spp
Nitzschia closterium
N. seriata
Rhizosolenia deliculata
Rhizosolenia spp(s)
Skeletonema costatum
Stephanopyxis spp
Thalassionema spp
Thalassiosira spp
DINOPHYTA
Ceratium spp
Dinophysis spp
Katodinium spp
Peridinium spp (1)
Peridinium spp (2)
small, unarmoured dinoflagellates
CRYPTOPHYTA
Hemiselmis spp
Cryptomonads 7-10 µm
Cryptomonads 12-17 µm
CHLOROPHYTA
Pyramimonas spp
Chlamydomonas spp
Chlorella spp
CHRYSOPHYTA
Apedinella spinifera
Dinobryon spp
Kephyrion spp
HAPTOPHYTA
Emiliania huxleyi
Phaeocystis pouchetii
Silicoflagellates
Choanoflagellates

The advantage of examining live cells obtained from either concentrated water samples or from raw enrichment cultures was that several distinguishing features could be observed which were not easily examined in preserved samples, if at all. These features included:

a. The organisms predominant state, i.e. motile, non-motile, amoeboid or colonial.

b. The size and shape of the cell.

c. The number of flagella and their behaviour, i.e. homo- or hetero-dynamic.

d. The position of insertion of the flagella.

e. The presence or absence of a haptonema and its behaviour, i.e. coiling or non-coiling.

f. The location number, shape and colour of the chromatophores.

g. The distribution and abundance of leucosin and other inclusion bodies.

h. The swimming characteristics of the organism.

One of the main problems found in examining live cells was that many of the organisms soon started to contract and disintegrate in the light with the heat of the microscope lamp.

It was possible to positively identify two different species from some preliminary work carried out using the electron microscope. To observe the organisms as whole cell mounts, the cells in culture were fixed in 2% osmium tetroxide in cacodylate buffer, washed several times in distilled water and mounted on carbon coated formvar grids. These grids were then shadowed with chromium and observed in a Philips EM300 transmission electronmicroscope (60 kV). The help and advice of Dr. J.H. Freer in this work is gratefully acknowledged.

The following list is limited by the selectivity of the culture technique and the inexperience in identification with the result that the most commonly occurring easily identifiable forms are mainly described. Many less common forms remain to be isolated and identified. The genera listed below are arranged according to the system of Parke and Dixon (1976). For the Euglenophyta, the classification of Butcher (1961) was used.

CRYPTOPHYTA.

CRYPTOPHYCEAE.

Hemiselmidaceae.

Cells of Hemiselmis spp. could be identified in the preserved samples and their seasonal distribution is summarized in Fig. 31 . H. rufescens Parke grew up regularly in culture and H. virescens Droop was observed in cultures isolated from the rockpool samples (Pool B) and very occasionally in seawater samples (e.g. from samples isolated on 21-3-78 and 31-5-78). The type strain of H. virescens was originally isolated from Great Cumbrae Island by Droop (1955).

Cryptomonadaceae.

Like Hemiselmis spp., this group of organisms remained recognizable in the preserved samples by their obvious "bean" or "comma" shape with laterally inserted flagella. As it was difficult to distinguish between different species these were grouped initially according to size in Fig. 31. Both size groups (7-10 μm and 13-17 μm in length) were observed throughout the year, the smaller organisms being the more common.

These small cryptomonads were normally 6-7.5 μm x 5 μm in size and had a very characteristic wedge shape with a wide truncate apex, tapering posteriorly to a pointed antapex which curved towards the ventral

Plate 4. Illustrating some of cryptomonads found in the Firth of Clyde.

A. Rhodomonas lacustris (Iodine fixed)

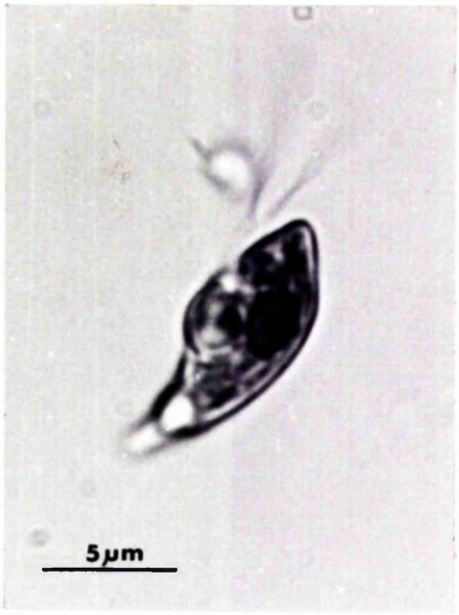
B. Cryptomonas reticulata (live cell)

C. Hemiselmis spp. isolated from rockpool (Iodine fixed)

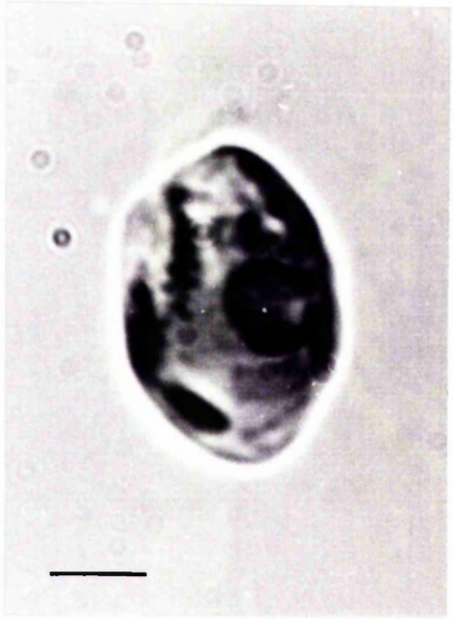
D. Hemiselmis spp. with other small bean-shaped cryptomonad.

All scale lines represent 5µm.

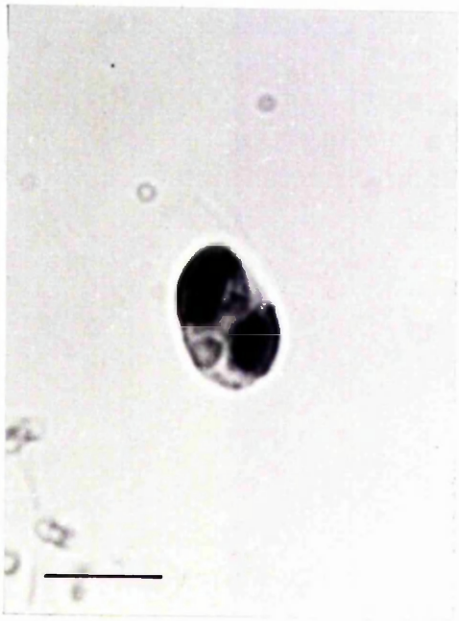
A



B



C



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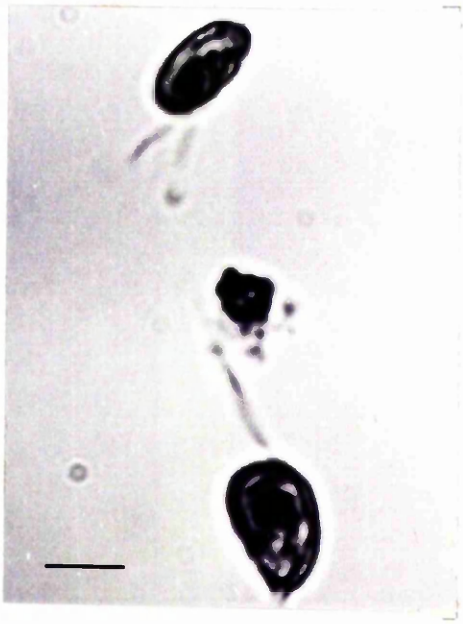


side (side in which flagella were inserted). A refractive granule (or granules) was often present at the base of the cell and a pyrenoid with a surrounding starch sheath was visible in the fixed cells lying in an approximately central position. Although not listed in the marine checklist of algae (Parke and Dixon, 1976), these cells correspond well with the description of Rhodomonas lacustris Pascher and Ruttner (Javornický, 1967, 1976).

In the larger size group of cells, Cryptomonas acuta Butcher was quite commonly observed. Also observed was C. reticulata Lucas (from Cloch Point isolated on 21.3.78 and from Fairlie Channel isolated on 20.4.78) and two other unidentified species. Plate 4 shows photomicrographs of several of the observed types of Cryptomonads.

DINOPHYTA.

Small, non-thecate dinoflagellates in the size range 10-20 μm were a regular, often common component, of the nanophytoplankton but were found to be very difficult to identify. Katodinium rotundata Lohmann (Plate 5) could, however, be distinguished and occurred quite commonly throughout the year (see Fig. 3I)

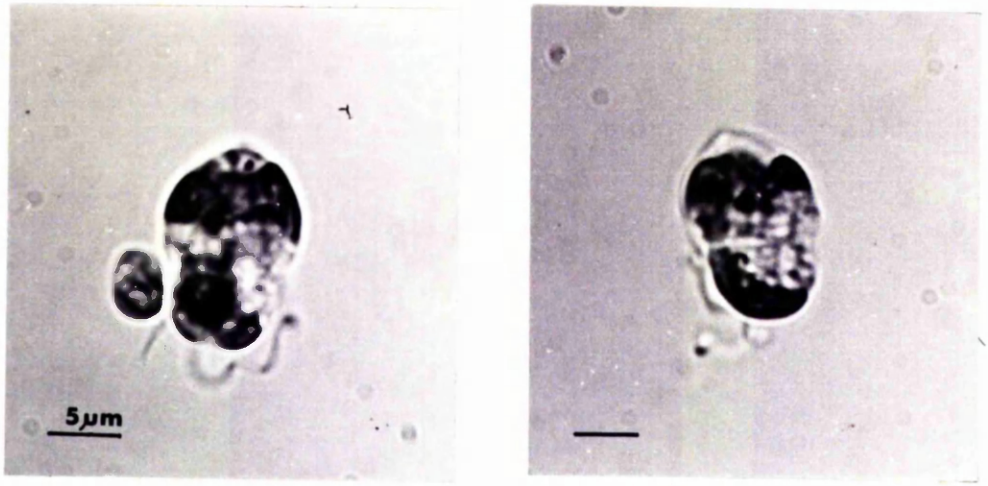
Only a few dinoflagellates were observed growing up in culture and these only occasionally: Prorocentrum micans Ehrenberg (isolated on 15.7.77, 4.8.77, 13.9.77 and 29.9.77); Gymnodinium spp. (isolated on 27.2.77, 14.7.77, 3.11.77); Gyrodinium estuariale Hulbert (isolated on 14.7.77); Katodinium rotundata (isolated on 14.7.77, 19.1.78, 27.2.78, 31.5.78) and Scrippsiella trochoidea Stein (isolated on 21.7.77, 28.7.77, 4.8.77 and 11.10.77).

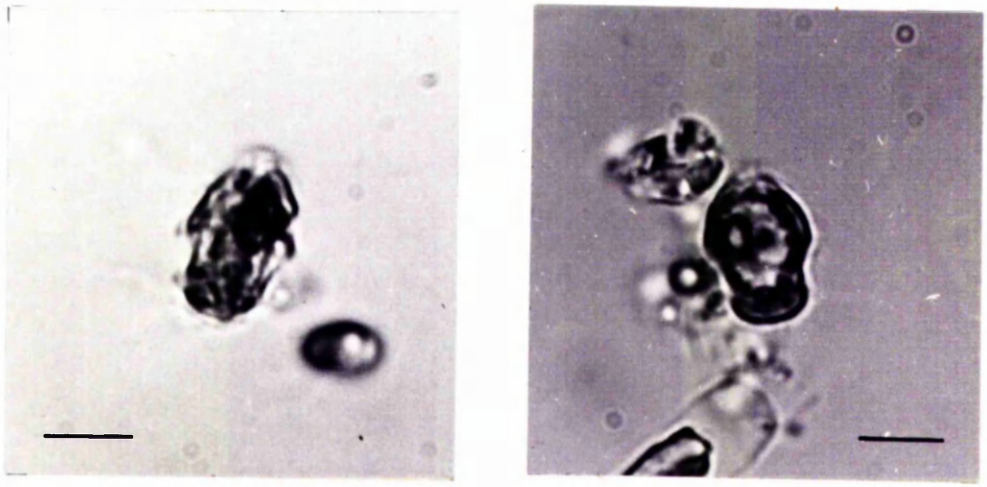
Plate 5A. Illustrating cells of Katodinium rotundata

B. Two species of Chrysochromulina with characteristic saddle shape.

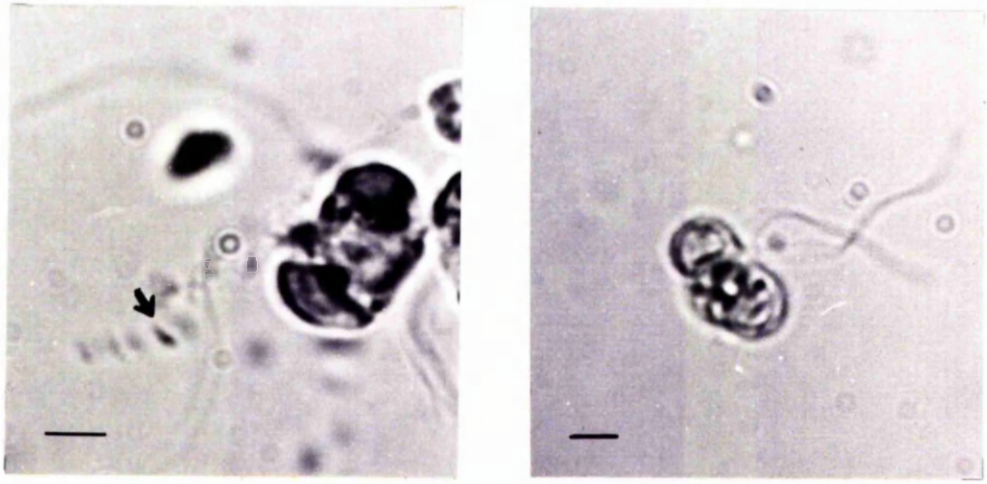
Haptonema indicated by an arrow in 5.B.1.
All scale lines represent 5μm.

A





B



HAPTOPHYTA

HAPTOPHYCEAE

Isochrysidales

Dicrateria inornata Parke grew up regularly in cultures from samples taken throughout most of the year with the exception of the summer months (June - October) when it was not observed. It was not possible to identify Dicrateria in the fixed samples.

Emiliania huxleyi Hay et Mohler in Hay, Mohler, Roth, Schmidt et Boudreaux occurred in the preserved samples in small numbers in September, October 1976 and in August, September and November 1977, and was observed on one occasion in culture (isolated on 27.2.77). The seasonal occurrence of this species in the Fairlie Channel had previously been studied by Hinton (1974) who recorded a maximum of Coccolithus (E. huxleyi = Coccolithus huxleyi) cells in July 1973 (2.8×10^5 cell l^{-1}). The appearance of this species appears to be sporadic as it was not found in any great numbers in 1972 (Hinton, 1974).

PRYMNESIALES

Prymnesiaceae

The genus Chrysochromulina Lackey occurred regularly in the cultured samples collected throughout the Inner Firth. Positive identification of species in this genus is difficult without the use of an electronmicroscope to observe the scale patterns on the surface of the cells, with the exception of two species where the presence of visible spines allowed the positive identification of C. ericina Parke and Manton (isolated on 11.5.78) and C. pringsheimii Parke and Manton (isolated on 31.5.78).

Plate 6. Electronmicrograph of whole cell mount of Chrysochromulina strobilus.

Layers of scales surround the organism and these are of two types, both seen in the lower right hand corner.

Final magnification - 22661.

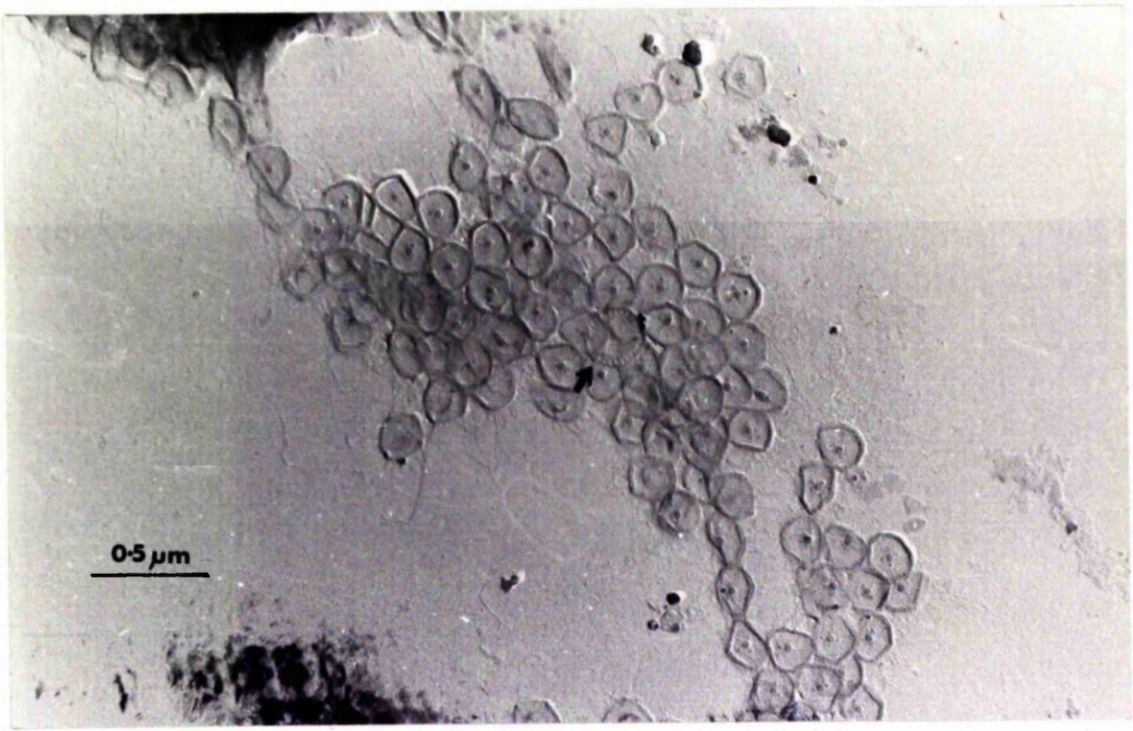


Plate 7. Scales of Chrysochromulina strobilus.
Majority of scales are of the rimmed basket type with one example of the flat plate-like scales indicated by an arrow.
Final magnification - 44,204.

A commonly encountered form had a characteristic saddle-shape (Plate 5B) but this form is found in several Chrysochromulina spp. (C. ephippum Parke and Manton, C. alifera Parke and Manton, C. strobilus Parke and Manton and the closely related species C. camella Leadbeater and Manton and C. cymbium Leadbeater and Manton). C. strobilus was positively identified on one occasion in a culture isolated on 29.9.77 from electron micrographs (Plate 6 & 7) of fixed cells of this species which were compared with those published by Parke, Manton and Clarke (1959) and Leadbeater and Manton (1969a). The dimensions of the two types of scales observed are given below with the values obtained by Leadbeater and Manton (1969a) for C. strobilus given in brackets.

Type of Scale	Size
Flat, plate-like scales	0.29 x 0.26 µm (0.24-0.40 µm long x 0.14 - 0.20 µm wide)
Rimmed basket scales	0.24 x 0.19 µm (0.15-0.20 µm wide).

Other species of Chrysochromulina were also observed.

Prymnesium parvum Carter was observed in the fixed samples, occurring in small numbers during March and April of 1977 and 1978. This species was, however, not observed growing in culture.

Phaeocystaceae.

Phaeocystis pouchetii Lagerheim was found to be common towards the end of April in all three years studied. It also occurred in large numbers in mid-July 1977. In culture, it appeared in the motile phase in samples collected on 22.11.77 and in the motile and colonial phase in samples collected on 19.1.78 and 27.2.78. Hinton (1974) found that Phaeocystis produced a small pulse in early March 1973 which preceded the spring diatom outburst in the Fairlie Channel.

Plate 8A. Pavlova gyrans (Haptophyta)

A group of live cells.

B. Kephyrion spp. (Chrysophyta)

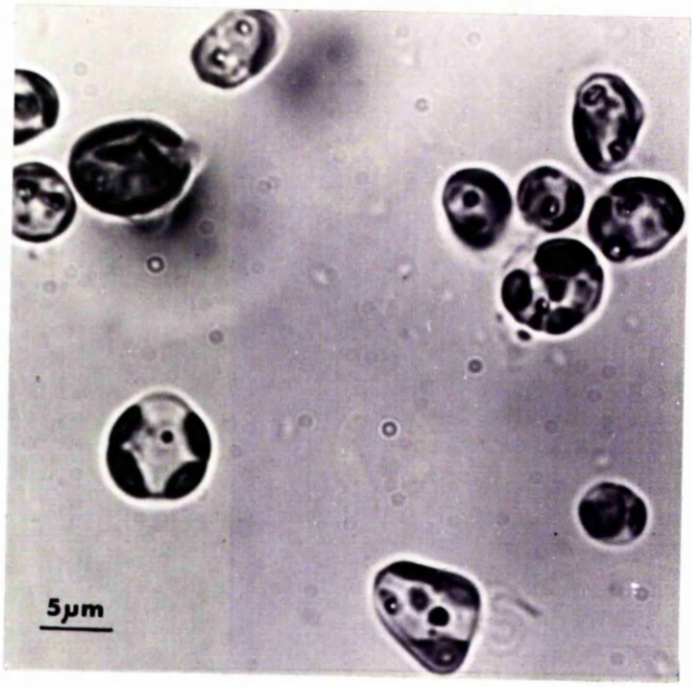
Live cells with flagellum.

C. Calycomonas spp. (Chrysophyta)

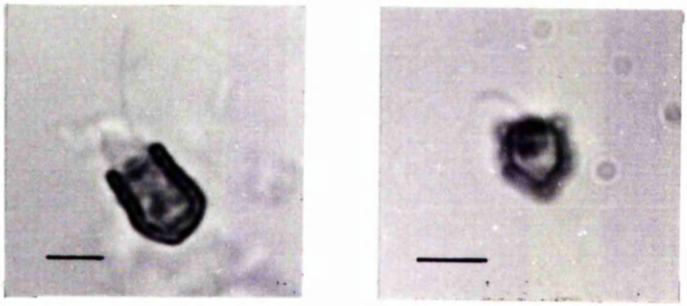
Live cell with a thicker walled lorica than those found in Kephyrion spp.

All scale lines represent 5 µm.

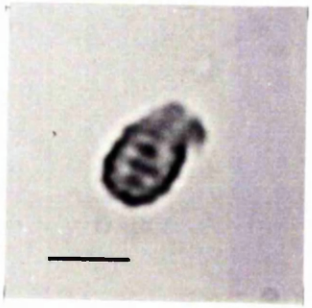
A



B



C



PAVLOVALES.

Pavlovaceae.

A Pavlova species which was identified as P. gyrans Butcher became established periodically in cultures (isolated on 17.8.76 from Garloch and on 23.3.77 and 30.6.77 from Fairlie Channel). Plate 8 A shows cells from the culture isolated on June 30th. Only the longer flagellum was clearly visible with the shorter flagellum being seen only occasionally. A stigma was visible just below the position of the flagellar insertion.

CHRYSOPHYTA.

CHRYSOPHYCEAE.

OCHROMONADALES.

Ochromonadaceae.

Olithodiscus luteus Carter was recognized by its shape and number of yellow/brown chloroplasts. It occurred quite commonly in the samples, mainly in the fixed samples and occasionally in culture.

Dinobryaceae.

Living cells of a Dinobryon spp. were observed during late April and May of 1978 in samples from the Fairlie Channel and also from the dumping ground south of Garroch Head and were quite common. Dinobryon is normally considered as a freshwater genus although three species are mentioned in the marine checklist of algae (Parke and Dixon, 1976).

CHROMULINALES.

Chrysococcaceae.

The loricas of Kephyrion spp. appeared periodically in the preserved samples and live cells with a visible flagellum were also

Plate 9. Cells of Apedinella spinifera.

a) Fixed cell caught in debris alongside a Skeletonema chain. This cell illustrates the two central pyrenoids with surrounding chromatophores.

b) Fixed cell showing surrounding layer of mucilage.

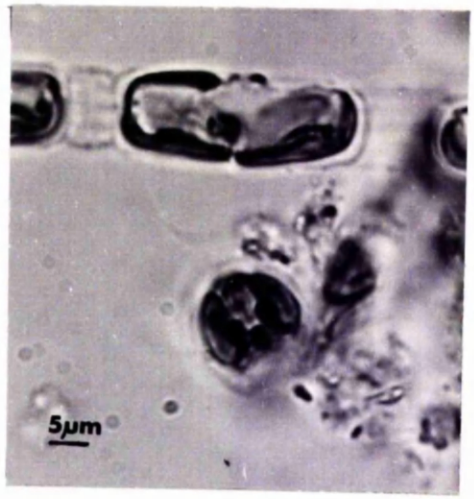
c) Flagellum observed arising from apical depression in the organism.

d) Lateral and terminal spines visible in this cell.

e) Another cell showing terminal long spines and apical depression.

All scale lines represent 5 μm.

a



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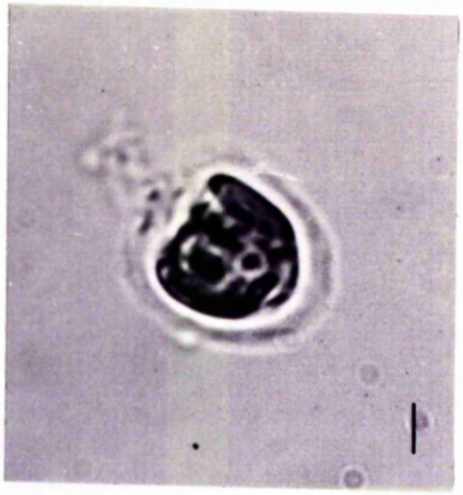

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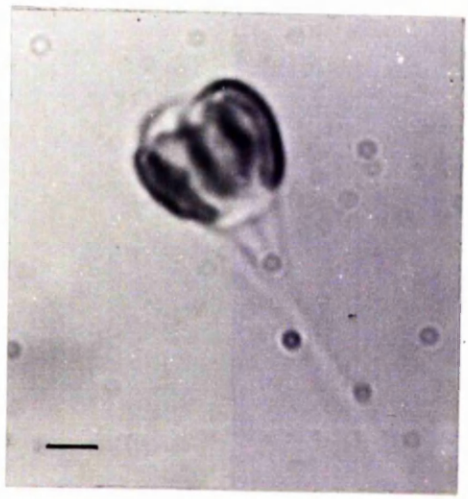

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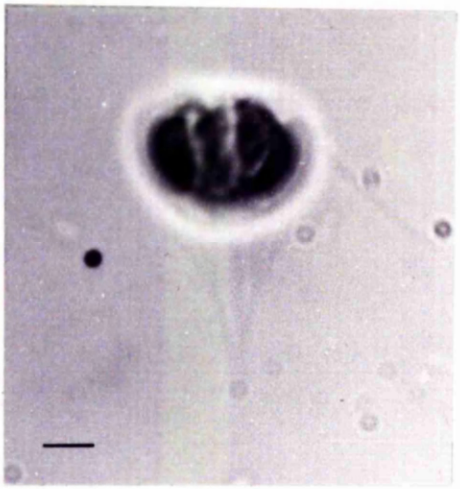

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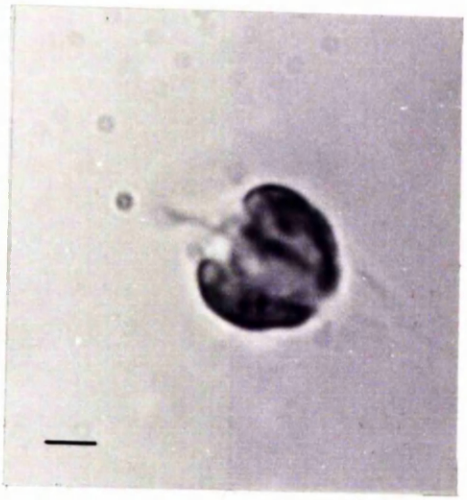


occasionally observed in the seawater samples (14.4.78) and in samples from the rockpools (Pool B, 11.5.78). Examples of these are shown in Plate 8B.

In a previous study of the seasonal occurrence of Kephyrion spp. in the Firth of Clyde, Hinton (1974) found that these organisms appeared in quantity in May, 1972 and 1973 (maximum number of cells recorded in May 1973 was 2.74×10^5 cells l^{-1}).

The thicker walled loricae of Calycomonas spp. were also observed on occasions (Plate 8C).

Pedinellaceae.

The seasonal observations of Apedinella spinifera Throndsen (Plate 9) are recorded in Fig. 31. In each of the three years studied, it was found that A. spinifera appeared in the fixed and cultured samples around the time of the spring diatom outburst (usually just after). It remained in the phytoplankton throughout the early summer months, often present in considerable numbers and was observed quite regularly in 1977 until November. Plate 9 illustrates the position of the spines and the single flagellum appearing from an apical cell depression in the live cells while the chromatophores each with a median pyrenoid on its inner surface are shown in the fixed cells.

Pseudopedinella pyriformis Carter occurred regularly in culture throughout the year (e.g. isolated on 2.6.77, 14.7.77, 29.9.77, 22.11.77, 27.2.78, 21.3.78, 31.5.78). These organisms were very delicate and disintegrated rapidly but their form and movement were very distinctive when observed.

BACILLARIOPHYCEAE.

Diatoms as a group were poorly represented in the nano-phytoplankton of the Firth of Clyde. Single and two to three cell chains of Skeletonema costatum Greve fall within the size range of the nanophytoplankton and would thus at times make up a part of this fraction although normally considered a netplankton species. The very short chains of Skeletonema were usually found at the end of a period of rapid growth, when cell numbers were decreasing.

Small single cells of Chaetoceros spp, section Simplica, were found in small numbers throughout the year. The average size of these cells was 5-15 μm by 5-10 μm.

EUGLENOPHYTA.

EUGLENOPHYCEAE.

Euglenaceae.

Eutreptia scotia Butcher was identified on occasion growing in a culture obtained from one of the rockpools (Pool A on 17.11.75). Eutrepiella spp. was observed in preserved samples collected on several of the sampling trips with the Clyde River Purification Board (December 1977, February and March 1978) and cells were obtained in culture from the March samples. Cells of Eutrepiella spp. were also observed in the Fairlie Channel (isolated on 18.8.77, 9.12.77, 27.2.78).

CHLOROPHYTA.

PRASINOPHYCEAE.

PTEROSPERMATALES.

Nephroselmidaceae.

Bipedinomonas rotunda Carter grew up frequently in culture.

The cultured cells tended to be slightly smaller (approximately 5 μm) than those described by Butcher (1959) which were 6-8 μm but the pyrenoid with its surrounding starch sheath was clearly visible.

B. pyriformis Carter was observed in a culture set up on 17.8.76 from a sample collected in the Gareloch.

Mantoniella squamata Manton and Parke occurred less commonly than Micromonas pusilla (see below) which is quite similar and was observed in culture on only one occasion (isolated on 8.7.76).

Micromonas pusilla (Butcher) Manton and Parke partially retained its shape and its flagellum on fixing in Lugol's Iodine and at X 1000 magnification this species could just be identified by its small size, its starch surrounded pyrenoid and its single flagellum and was commonly found. It occurred in vast numbers when established in culture (isolated on 24.6.76).

Pterospermataceae.

The non-motile, phycoma phase of this group was not observed possibly as a result of the technique used to concentrate the fixed samples. Any phycomas present would possibly have been discarded with the supernatant drawn off from the sedimented cells.

On several occasions (27.7.76, 22.9.77, 21.3.78, 27.4.78 and 31.5.78) motile cells with the characteristic four very long flagella and the pyrenoid with surrounding starch typical of this group were observed. No distinction could be made between the motile phases of Pachysphaera and Pterosperma spp.

A check was made of the lunar phase when each of the observations was made as lunar periodicity in the switch from the motile to the non-motile phase of Pterosperma has been previously reported, with the

Plate 10. Cells of *Pyramimonas* spp.

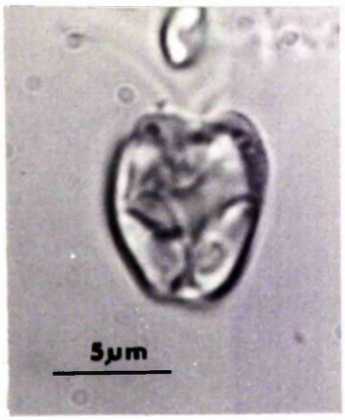
1 - 4. *Pyramimonas obovata*.

5 - 7. *P. grossii*.

(Plates 1 and 5 are of live cells, the remainder are fixed in Iodine).

All scale lines represent 5 µm.

1



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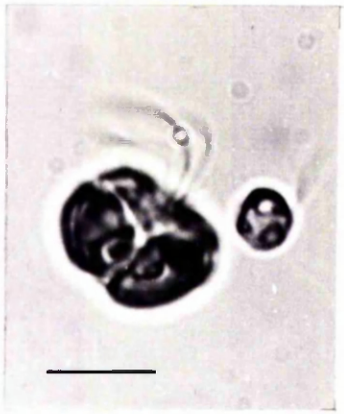

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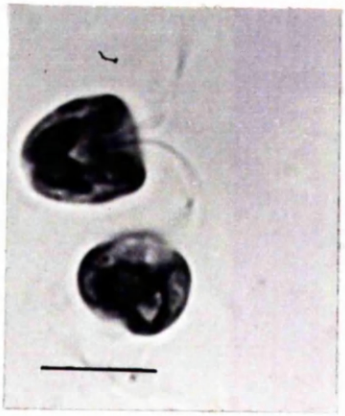

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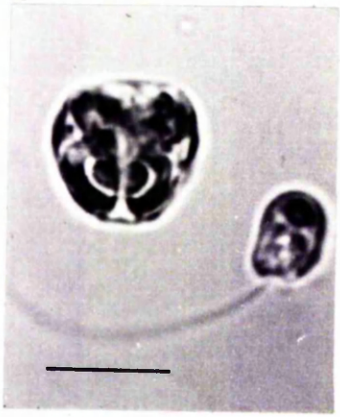

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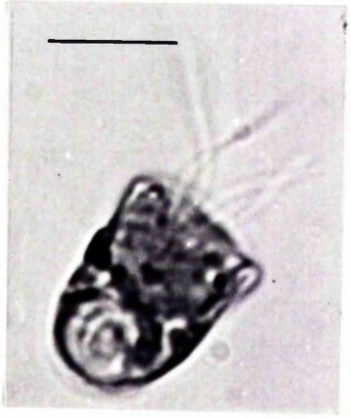

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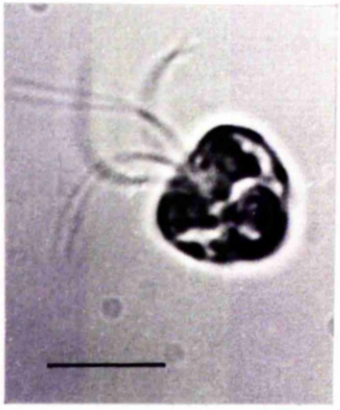

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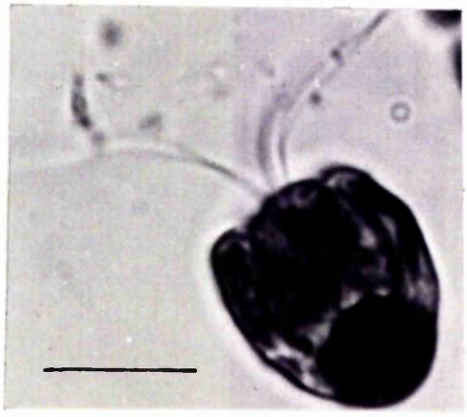


motile cells being released in the period of two to three days on either side of a new or full moon (Parke, Boalch, Jowett and Harbour, 1978). A correlation was found on two occasions. The occurrence on 27.7.76 was on the day of a new moon while that on 21.3.78 was within three days of a full moon.

PYRAMIMONADALES.

Pyramimonadaceae.

Cells of Pyramimonas spp. were a common component of the nanophytoplankton throughout the year (Fig. 31). Many of the cells observed were part of a group of small (< 10 μm), closely related species of Pyramimonas which can only with difficulty be distinguished by light microscopy. P. amylifera Conrad was identified on one occasion (isolated on 13.5.76 from Fairlie Channel) by its larger size and eight flagella.

Many of the cells contained a very distinctive pyrenoid with two large wedge shaped starch grains (e.g. Plate 10) and these appear to closely resemble the description of P. disomata Butcher. The problem of differentiating between this species, P. obovata Carter and P. orientalis Butcher has always been present in the past but it is now thought that these are possibly conspecific (Belcher, Pennick and Clarke, 1974) and these authors unite the three species under the name P. obovata.

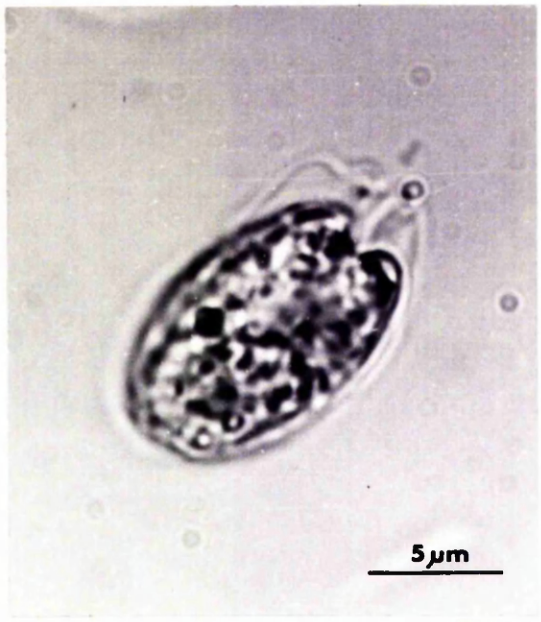
A Pyramimonas spp. isolated from the Fairlie Channel on 2.6.77 was examined as a whole cell mount under the electronmicroscope and the body scales observed corresponded with those of P. grossii Parke (Manton, Parke and Oates, 1963; Leadbeater, 1972). Plate 10 shows examples of P. grossii and P. obovata.

Plate 11a. Single cell of Platymonas suecica together with an example of a dividing stage of this species.

b. Chlamydomonas bullosa with a dividing cell containing four daughter cells in the top of the picture. (Large cryptomonad lying beside the dividing stage).

All scale lines repesent 5 μm.

a



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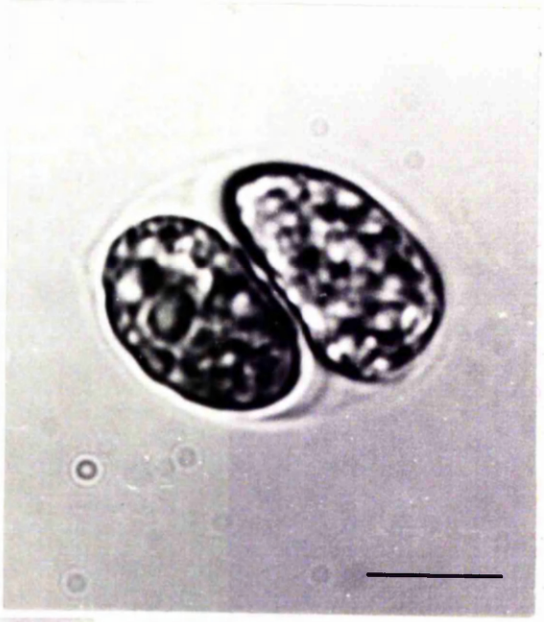

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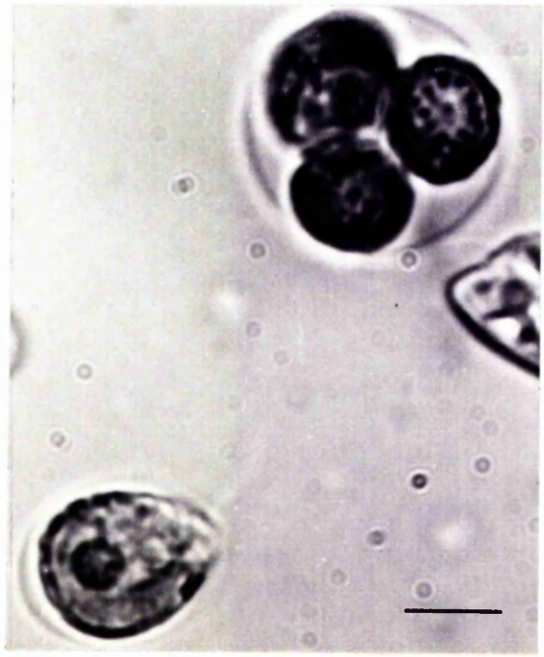

PRASINOCLADALES

Prasinocladaceae.

Platymonas suecica Kylin (Plate 11a) was observed in a culture isolated from Fairlie Channel on 3.6.77. A second Platymonas spp. was observed in considerable numbers in the preserved samples from a grid survey on 9.12.77.

VOLVOCALES.

Dunaliellaceae.

Dunaliella primolecta Butcher was identified in a culture isolated from the Fairlie Channel on 29.3.77.

Chlamydomonadaceae.

Brachiomonas submarina Bohlin was commonly found in the two rockpools sampled on Cumbrae and was obtained in culture from a sample collected in the Fairlie Channel on 25.3.76 and also from the Gareloch (17.8.77). This is generally considered to be a brackish water species. Chlamydomonas bullosa Butcher was very common in the preserved samples of the grid survey of 22.6.77. It was also observed in a culture of a sample collected from Cloch Point (Stn. 3, Fig. 3) on 21.3.78. Plate 11b shows one of these cells, together with a dividing cell containing four daughter cells.

CHLOROCOCCALES.

Oocystaceae.

Chlorella spp. grew up regularly in cultures - C. marina Butcher (isolated on 22.6.77, 29.9.77 and 18.3.76), C. ovalis Butcher (isolated on 12.2.76, 8.7.76, 17.2.77), C. salina Kufferath (isolated 17.8.76) and C. stigmatophora Butcher (isolated on 3.11.77, 9.12.77, 27.2.78).

ULOTRICHALES.

Stichococcus bacillus Nägeli grew up frequently in cultures obtained from seawater samples (e.g. isolated on 18.3.76, 12.7.77, 7.4.77, 2.6.77, 14.7.77, 18.8.77).

Discussion

The species and genera described above were found throughout the study area i.e. the Inner Firth and the two sea lochs, Loch Long and the Gareloch. The available information from earlier studies shows that the species found in coastal waters have a wide distribution (cf Hulburt, 1965; Throndsen, 1969, 1976 and Leadbeater, 1972) and most of the recorded species are probably cosmopolitan.

The main component of the nanophytoplankton was made up of small phytoflagellates. These belonged to several classes. The most commonly occurring of these were Haptophyceae, Chrysophyceae, Prasinophyceae, Cryptophyceae and Dinophyceae. An accurate assessment of the importance of the different classes and species based on cell numbers is difficult to make as cell volume varies by a factor of 500 from the smallest to the largest species common in coastal waters (Throndsen, 1969, Table IV). A better judgement would be based on their biomass standing stock and productivity. Autoradiography has recently been used to determine the fixation rates of individual phytoplankton species in a given environment (Knoechel and Kalff, 1976) and this would seem to be a promising approach to this problem.

The species observed in the present study were generally indicative of a nearshore, estuarine environment.

Chapter 9. Concluding Discussion

As in other areas (Table 1) it has been found that the nanophytoplankton make a significant contribution to the biomass (66%) and productivity (50%) of the phytoplankton in the Fairlie Channel over an annual cycle. These percentages fall within the range of those reported in other studies of temperate waters. Durbin et al (1975) estimated that the <20 μm fraction of the phytoplankton contributed 47% of the chlorophyll and 51% of the productivity of Narragansett Bay, North America.

The nanophytoplankton in the Firth of Clyde is made up predominantly of small flagellates of maximum cell dimension less than 10 μm and representing most algal classes, i.e. representatives of the Haptophyceae, Chrysophyceae, Prasinophyceae, Chlorophyceae, Cryptophyceae and small members of the Dinophyceae (predominantly non-thecate). The nanophytoplankton was observed to form a more stable component of the phytoplankton fluctuating in terms of total chlorophyll and productivity less dramatically than the netplankton.

The significance of the nanophytoplankton was not restricted to the Fairlie Channel although when compared with the rest of the Inner Firth, its importance in this area appeared slightly higher. In the Inner Firth, the contribution of the nanophytoplankton to the total chlorophyll ranged from 20-98% and in the sea lochs, Loch Long and Gareloch, its contribution to the chlorophyll and productivity of these lochs ranged from 11-62% and 13-77% respectively. In the rather extreme environment of the rockpools on Great Cumbrae Island, the nanophytoplankton was very productive, producing high levels of fixation (maximum recorded value - 189 mg C m^{-3} h^{-1}) in the early

months of the year when production in the sea was at a minimum.

Although the nanophytoplankton has been found to make up a significant fraction of the phytoplankton, the question regarding its importance to the rest of the ecosystem in the Firth of Clyde still remains.

The main food chain in the area involves the transfer of energy from the phytoplankton to Calanus finmarchicus which in turn provides food for herring. It has been shown by Marshall (1924) and Marshall and Orr (1952, 1955, 1956) that the main food source of Calanus is diatoms. It was found, using ^{32}P-labelled cultures, that cells of <10 µm were filtered less efficiently than larger cells and that several small organisms in the 2-5 µm range were hardly eaten at all (Marshall and Orr, 1955). Marshall (1924) also found that flagellates were not common in the gut contents of Calanus. Raymont and Gross (1942), however, have shown that Calanus finmarchicus was able to survive on very small (1-3 µm diam) phytoplankton although its survival was greatly improved by the presence of larger diatoms.

Calanus does not appear to utilize the nanophytoplankton to any great extent but, as mentioned in a previous discussion, Calanus, in nature when larger food sources are unavailable, can alter its feeding behaviour to filter smaller organisms (Gamble, 1978).

The nanophytoplankton may provide a food source for the nauplii and adults of the smaller species of copepods which are found, in lesser numbers than Calanus, in the Firth. When investigating the gut contents of Microcalanus spp. and Oithona spp. Marshall (1949) rarely found recognizable remains which suggested that these species may have been feeding on small flagellates. In the Strait of

Georgia, British Columbia, Parsons and LeBrasseur (1970) found that the nanoplankton formed an essential food source for the smallest zooplankton investigated (nauplii and also adults of Oithona spp. and Pseudocalanus minutus) and that these small microzooplankton in turn were essential for the survival of larval fish.

The nanophytoplankton may be used indirectly by Calanus via an intermediate stage involving microzooplankton (small copepods, invertebrate larval stages and protozoans). In the north-eastern Pacific Ocean, Beers and Stewart (1969) found that the main grazers of nanoplankton were protozoans. These were more abundant in terms of number and biomass in coastal than in stable oceanic areas but their relative importance to the total zooplankton community was not as great in coastal situations (Beers and Stewart, 1969).

Little is known about the quantitative significance of the protozoans in the Clyde but ciliated protozoans including tintinnids were commonly observed in the fixed samples during this study. If nanophytoplankton grazers are predominantly protozoans with short generation times (doubling times of 12-24 hours have been recorded for species of tintinnids by Gold (1973) and Heinbokel (1978)), the coupling between primary production and grazing would be much closer for nanophytoplankton based food chains than for netplankton based ones in which the grazers are crustaceans with longer generation times. This close coupling between primary and secondary producers would tend to prevent any rapid fluctuations in numbers of nanophytoplankton and would help to explain the observed relative stability of the nanophytoplankton in the Firth.

Even though only present as a minor fraction of the faunal

biomass of an area, protozoans may be important in the nutrient regeneration of that area since it has been found that small marine animals release nutrients into the water per unit weight of animal faster than do larger animals (Johannes, 1968) as well as providing an alternative food source for Calanus.

Much of the recent speculation concerning the role of the microzooplankton as an intermediate between the nanophytoplankton and the larger copepods has considered the effect which this "extra link" would have in reducing the ultimate yield of exploitable resources from a given level of primary production (Beers and Stewart, 1969; Ryther, 1969; Landry, 1977). The significance of such a loss will be dependent on a number of factors, one of these being the efficiency with which the material ingested by the microzooplankton is utilized for growth. It has been found by Heinbokel (1978) that tintinnids may achieve gross growth efficiencies exceeding 50% over a broad range of food concentration.

The importance of the nanophytoplankton - microzooplankton component of the food chain in a less direct role has been suggested by Steele and Frost (1977) who formulated a model system which takes into account the fact that the interaction between phytoplankton and herbivores appears to be as dependent on the size composition of the trophic levels as on the total biomass of these levels.

In a system such as the Firth of Clyde the model proposes that the presence of Pseudocalanus or possibly other small copepods is essential for the survival of Calanus. Following a period of intensive diatom grazing by Calanus, the available nutrients would accumulate in the small phytoplankton which cannot be effectively

grazed by the larger copepod. The nanophytoplankton would consequently increase ultimately leading to the decrease and removal of Calanus if a population of smaller copepods were not present to control the growth of the small organisms and so reducing the competition with diatoms.

A baseline study of the nanophytoplankton in relation to the total phytoplankton in the Firth of Clyde was also considered of importance because of the increasing industrial development taking place in this area. Controlled ecosystem pollution experiments in which pollutants (copper and also hydrocarbons) were artificially added to a system, have shown that the major effect is to change the size composition of the phytoplankton usually towards a dominance by μ-flagellates (Thomas and Seibert, 1977; Menzel, 1977; Gamble, Davies and Steele, 1977) with little change in the total levels of chlorophyll and productivity following a brief recovery period of a few days (Menzel, 1977; Thomas, Holm-Hansen, Seibert, Azam, Hodson and Takahashi, 1977).

Pavoni (1963) in a study of European lakes found that the percentage biomass of nanoplankton in oligotrophic and also hypertrophic lakes was higher than in eutrophic lakes which suggests that there is a close relationship between extreme environmental conditions and the percentage nanoplankton. The more extreme the environmental conditions are, the greater is the percentage nanoplankton in relation to netplankton.

The nanophytoplankton thus forms a highly active component of the community and its presence appears to be essential for the stability of the coastal ecosystem. If, in the future the stability

of the Firth is disrupted by some form of pollution, it is expected that the significance of the nanophytoplankton will become even greater than at present.

Appendix 1. Culture Media

A. Boney's Medium

To 1 litre of pasteurized seawater were added

1) 60 ml of solution A, which contained:

50 ml 0.4% $NaNO_3$ in distilled water and

2 ml of each of the following:

1.47 g/l	$MnSO_4.4H_2O$
0.0023 g/l	$CuSO_4.5H_2O$
0.064 g/l	$CoCl_2.6H_2O$
0.23 g/l	$Na_2MoO_4.2H_2O$
0.005 g/l	$LiCl \cdot H_2O$

2) 2 ml of solution B, which contained:

4.98 g/l	$ZnSO_4.7H_2O$

3) 15 ml of solution C, which contained:

2.6 g/l	Tetrasodium salt of EDTA
0.12 g/l	$FeSO_4.7H_2O$

4) 1.5 ml of solution D, which contained:

15 g/l	$Na_2HPO_4.12H_2O$.

Each solution was autoclaved separately and stored in a refrigerator until use. The solutions were added to the pasteurized seawater using sterile techniques.

B. Erdschreiber's Medium

Pasteurized seawater	900 ml
Soil extract	50 ml
Sodium nitrate ($NaNO_3$)	0.2 g in 50 ml distilled H_2O
Disodium dihydrogen phosphate ($Na_2HPO_4.12H_2O$)	0.03 g in 50 ml distilled H_2O.

The soil extract was prepared by air drying a sample of garden soil. This was then crushed and passed through a fine sieve to remove stones. The sieved material was autoclaved with twice its volume of supernatant water, the autoclaved mixture left for several days for the soil to sediment and the supernatant then decanted into clean glassware and stored in a refrigerator until use.

The solutions of sodium nitrate, sodium phosphate and soil extract were autoclaved separately before adding to the pasteurized sea water.

Appendix 2

Log of Field Trips

"In Situ" Productivity Measurements with Chlorophyll & Nutrient Analysis

15. 1.76	9. 9.76	12. 5.77
5. 2.76	15. 9.76	19. 5.77
12. 2.76	29. 9.76	25. 5.77
19. 2.76	14.10.76	15. 6.77
26. 2.76	28.10.76	30. 6.77
5. 3.76	4.11.76	14. 7.77
12. 3.76	11.11.76	21. 7.77
17. 3.76	18.11.76	28. 7.77
25. 3.76	25.11.76	4. 8.77
31. 3.76	2.12.76	11. 8.77
8. 4.76	9.12.76	18. 8.77
12. 4.76	16.12.76	8. 9.77
13. 4.76	13. 1.77	22. 9.77
14. 4.76	20. 1.77	4.10.77
15. 4.76	3. 2.77	27.10.77
22. 4.76	24. 2.77	10.11.77
29. 4.76	10. 3.77	2.12.77
5. 5.76	21. 3.77	22.12.77
13. 5.76	28. 3.77	16. 3.78
20. 5.76	29. 3.77	20. 3.78
27. 5.76	30. 3.77	23. 3.78
3. 6.76	1. 4.77	30. 3.78
10. 6.76	6. 4.77	6. 4.78
17. 6.76	7. 4.77	12. 4.78
24. 6.76	14. 4.77	27. 4.78
1. 7.76	15. 4.77	11. 5.78
8. 7.76	21. 4.77	
15. 7.76	28. 4.77	
24. 7.76	5. 5.77	
29. 7.76	12. 5.77	

Grid Surveys

23. 6.77

29. 9.77

3.11.77

9.12.77

27. 2.77

21. 4.77

Sedimentary Pollution Unit Sampling Trips

15. 7.77

13. 9.77

11.10.77

20.10.77

Clyde River Purification Board - Inner Firth

22.11.77

19. 1.78

21. 3.78

18. 4.78

31. 5.78

Gareloch and Loch Long

Gareloch	Loch Long
3. 8.76	4. 8.76
12. 8.76	11. 8.76
17. 8.76	
18. 8.76	

Others

27.1.77 Transect of Fairlie Channel

10.2.77 " " " "

17.2.77 Transect of Fairlie Channel and Tidal Cycle

3.3.77 " " " " " " "

17.3.77 " " " " " " "

22.3.77 Tidal Cycle

20.5.77 " "

2.6.77 " " and 3 stations sampled.

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