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The distribution and biodegradation of urea in costal waters

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THE DISTRIBUTION AND BIODEGRADATION OF

UREA IN COASTAL WATERS

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ABSTRACT

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The biodegradation of urea by phototrophic and heterotrophic micro organisms and the urea sea water concentration were investigated in relation to the microbial population, inorganic sources of nitrogen and the hydrography of the Elbe estuary and Southern German Bight during three cruises (HGL Cruises) from the end of July to the end of September 1976.

During the HGL cruises and a preliminary investigation in Beaumaris Bay and the Menai Strait, no evidence was found to suggest that land derived urea was an important contributor to sea water urea concentration. In situ production seems likely to be a major source of urea.

Urea contributes an ecologically significant amount to the 'total nitrogen' (ammonium, nitrate, nitrite and urea-N) in the Elbe estuary and S. German Bight. Urea-N concentrations in the latter water, although showing greater spacial variation than the inorganic nitrogen, often exceeded the concentrations of the inorganic nitrogen. Urea concentrations were highest during periods of greatest biological activity (Cruise HGL I: July-August) and decreased as the year advanced.

Both phototrophic and heterotrophic micro organisms are important in the biodegradation of urea and rates of degradation were highest during the time of highest biological activity (Cruise HGL I: July-August), phototrophic urea degradation predominating in the Elbe estuary while heterotrophic degradation generally predominated in offshore waters. A complex relationship may exist between the urea producers (possibly zooplankton) and urea degraders as well as between the phototrophic and heterotrophic micro organisms.

Distinct water regimes (the Elbe, Coastal and North Sea regimes) of different physical characteristics, often separated by frontal regions were encountered on the HGL cruises. The distribution of the micro organisms and sea water urea concentrations were related to the hydrography and these in turn affected the distribution of rates of urea biodegradation.

Urea assimilation indices indicated that in the stratified

North Sea regime, containing low inorganic nitrogen, bacteria were more effective urea degraders than phytoplankton.

Cellular ATP:cellular C ratios may be a useful indicator of physiological activity and environmental stress. Urea assimilation indices and cellular ATP: cellular C ratios may indicate that the micro organisms in the Elbe estuary are under greater environmental stress than those in the more offshore waters of the North sea regim e.

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GENERAL INTRODUCTION

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GENERAL INTRODUCTION

The availability of nitrogen has long been recognised as important to phytoplankton growth in the marine environment (Harvey, 1940; Ryther and Dunstan, 1971).

Until quite recently most estimates of available nitrogen have only included inorganic nitrogen present as ammonia, nitrate and nitrite. However, in the last decade more attention has been paid to the distribution and utilization of various organic nitrogen compounds in the marine environment (eg. North and Stephens, 1971; Remsen, 1971; McCarthy, 1972(a); McCarthy, 1972(b); McCarthy and Kamykowski, 1972; Wheeler et al., 1974; Antia et al., 1975; North, 1975). Urea has taken a leading role as far as this development is concerned, partly because of the claim of early research workers (Eppley et al., 1971; Remsen, 1971 and McCarthy, 1972(a)) that urea comprises a significant percentage of the 'available' nitrogen (ammonia, nitrate, nitrite and urea), sometimes as much as 79% (Steinmann, 1976), and partly because of the comparative ease of the methods of measuring the urea concentration (Newell, et al., 1967; McCarthy, 1970 and Emmet, 1969) and the measurement of urea utilization using the readily available ^{14}C - method.

Although concentrations of urea have been as low as undetectable (McCarthy, 1970) and as high as 8.60, 9.04, 9.14 and 11.20 μg atom urea - N L^{-1} (Swain, 1973; Steinmann, 1976; Pineda, 1973 and Remsen, 1971 respectively) there seems to be no obvious distribution pattern. Indeed, the most characteristic feature concerning the distribution of urea seems to be the great variability, when compared to the distribution of inorganic nitrogen compounds, between different sampling areas, within a given sampling area and from one month to another (Remsen, 1971; Remsen, et al., 1974; McCarthy and Kamykowski, 1972 and Savidge & Hutley, 1977). To get a closer understanding about the distribution of urea it might first be necessary to examine its possible sources.

The majority of nitrogen excreted by ureotelic animals (mammals and elasmobranch fish) is in the form of urea and produced via the ornithine cycle (Baldwin, 1964). Elasmobranchs and marine mammals would therefore contribute directly to the sea water concentration of urea while terrestrial mammals may make a contribution via land runoff, and in the case of man through domestic sewage discharges (Emmet, 1969 and Remsen, et al., 1974). Man-made soil fertilizers may also influence the urea concentration in coastal waters.

Ammonotelic animals such as teleost fish (Scheer and Ramimurthi, 1968 and McCarthy and Whitledge, 1972) and zooplankton (Corner and Newell, 1967 and Dagg, et.al. 1980) may also excrete ecologically significant amounts of urea. Crustaceans also excrete dissolved amino acids, notably arginine (Smith and Young, 1955), which can be utilized by bacteria and converted to urea (Webb and Johannes, 1969).

Uric acid excreted by uricotelic animals such as birds may enter the sea water particularly in localised coastal waters. Uric acid can be broken down by algae (Mckee, 1962) and bacteria (Steinmann, 1976) and urea produced from it.

Heterotrophic microbial action on particulate and detrital material eventually often leads to the production of urea.

Fish, zooplankton and phytoplankton have long been known to occur in schools, patches and layers. The considerable fluctuations in the distribution of urea may therefore reflect the spatial patchiness of the urea producers. Such a relationship between urea and the biota has been proposed when high urea concentrations were associated with high chlorophyll a concentrations (Remsen, 1971), high zooplankton numbers and schools of fish (McCarthy and Kamykowski, 1972 and McCarthy and Whitledge, 1972).

The distribution of urea will not only depend on the rate of production but will also be influenced by the rate of degradation by the micro organisms capable of utilizing it.

Since Harvey's work (1940) on unicellular algal cultures, which indicated that they could utilize and grow on urea as a sole nitrogen source, other workers have produced much

evidence that green algae, blue-green algae, diatoms and dinoflagellates can utilize urea as a nitrogen source (Syrett, 1962; Guillard, 1963; Hayward, 1965 and Carpenter et.al., 1972(a)). Indeed, there is some evidence that some unicellular algae show preference to urea rather than some of the inorganic nitrogen compounds (McCarthy et.al., 1977 and Antia et.al., 1975).

Some yeasts and unicellular algae have another urea-degrading enzyme system other than urease, that is, ATP: urea amidolyase (UAL-ase) which has been described by Roon and Levenberg (1968), elaborated on by Adams (1971), Thompson and Muenster (1974) and Whitney & Cooper (1972) and the overall reaction neatly summarized by Syrett and Leftley (1976) (also see Section 2.5).

Investigations on the assimilation of urea in sea water have indicated that urea is an important source of nitrogen for the microbes (McCarthy, 1972; Remsen et.al., 1974; Mitamura and Saijo, 1975; Webb and Haas, 1976 and Savidge & Hutley, 1977). It has been generally acclaimed by these investigators that phytoplankton play a more dominant role in the degradation of urea than bacteria although Remsen et.al. (1974) claim that bacteria play a more dominant role in the open oceans whilst the role of phytoplankton is greater in coastal waters. Rates of urea assimilation or degradation tend to vary considerably depending on location, depth and time of year. However, these variations seem to relate to the distribution and photosynthetic activity of the phytoplankton (Remsen, et.al., 1972 and 1974; Mitamura & Saijo, 1975; Webb and Haas, 1976 and Savidge & Hutley, 1977).

Although much effort has been expended in the investigation of urea degrading bacteria in soils (eg. Gibson, 1935; Conrad, 1942; Roberge and Knowles, 1967 and Paulson & Kurtz, 1969) little attention has been shown to urease bacteria in sea water. Some investigations have, however, indicated that urea degrading bacteria are present (Bavendamm, 1932) and some attempt has been made in their enumeration; Zobell and Feltam (1935) found 1-10 ureolytic bacteria per ml. off the coast of California; Remsen et.al. (1972 and 1974) found 4-1600 per ml. in waters between the Canary and Madeira Islands and Steinmann (1976) found a winter maximum of 2500

per ml. in the Baltic Sea. These few investigations, however, give little idea of the distribution of urea degrading bacteria in the marine biotope and certainly no indication of the rate of heterotrophic degradation of urea.

Since this work was first began in 1975, interest in the distribution and biodegradation of urea has increased. However, despite this increased research activity, no pattern in the detailed distribution of urea and its assimilation has to light, although the evidence that urea may be an important nitrogen source for phytoplankton has increased. The heterotrophic assimilation of urea has often been ignored or when investigated found to be insignificant. This study therefore aims to elaborate on the distribution of urea and its significance in relation to the inorganic nitrogen compounds. The effect of terrestrially produced urea on its concentration in coastal and estuarine waters is also investigated by examining two areas receiving a large input of domestic sewage - the Menai Strait and the Elbe estuary and Southern German Bight. This investigation also attempts to compare heterotrophic and phototrophic urea assimilation and relate them to the microbiology of the water.

There are a few slight indications from investigations by Remsen (1971), Remsen et.al. (1974) and Dagg et.al. (1980) on the distribution of urea, that high urea concentrations are in some way associated with the hydrography; some of the highest concentrations being associated with upwelling, surface slicks, windrows and estuarine plumes. During the course of this investigation the importance of the hydrography on the micro-organisms and on the distribution and biodegradation of urea is demonstrated and implicates that a hydrographical survey should be an integral part of an investigation such as the one attempted here.

SECTION 2

MATERIALS AND METHODS

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MATERIALS AND METHODS

2.1 General Protocol

When the research vessel reached a station, the following procedure was adopted. Subsamples for nutrient analysis, biomass and urea utilization measurements were taken from a sample collected with a sterile 2.5 l glass bottle attached to a Johnson-Zobell (J-Z) microbiological sampler. A 50 ml. portion of the sample was immediately frozen for nutrient analysis. Samples for the enumeration of bacteria were preserved in a sterile 25 ml Universal bottle containing 1 ml of 0.5% V/V formalin. One-hundred to 1000 ml of the sample was filtered for chlorophyll analysis. One hundred ml aliquots were added asceptically to three 250 ml Erlenmeyer flasks for the determination of urea utilization. The remainder of the sample was filtered through a sterile 200 µm pore size nylon filter to remove all but the smallest zooplankton and concentration by filtration of the remaining cells carried out for the determination of microbial adenosine triphosphate (ATP). The filters were immediately extracted in boiling tris buffer and the extracts frozen.

Salinity and temperature were determined from samples taken by oceanographic sea water samplers with attached reversing thermometers. Hydrographical bottle casts were made immediately after the J-Z sampler cast.

Unless stated otherwise, sea water samples using J-Z samplers were taken at a depth of 10 m (± 2 m due to poor weather conditions).

Measurements were not carried out in replicate because of practical reasons of insufficient man power, ship space, materials and time. However, on Cruise HGL I, continuous recordings from a Turner fluorimeter and discrete samples from the J-Z samplers showed the same distribution of chlorophyll a suggesting that discrete sampling at least for the phytoplankton satisfactorily represented the overall distribution.

2.2 Physical Measurements

Salinity samples were collected by reversing Nansen samplers and analysed on an Autolab salinometer with a quoted accuracy of $\pm$ 0.003 °/oo.

Temperature measurements were made using duplicate protected deep-sea reversing thermometers attached to the Nansen bottles and accurate to $\pm$ 0.01°C. Continuous vertical temperature profiles were made with a bathythermograph with quoted accuracy of 0.1°C and 1 m. Owing to the unavailability of this instrument this was not implemented at all stations.

A Secchi disc was deployed on Cruise HGL III to give an estimate of total suspended matter, the extinction depth being read to the nearest tenth of a meter.

Density in the form of Sigma t was calculated from temperature and salinity from an algorithm supplied by the Woods Hole Oceanographic Institute.

V bar ($\bar{V}$), a stratification parameter was calculated from surface-bottom density difference, after Simpson et.al. (1977).

Infra-red satellite images were taken from the NOAA 5 satellite and supplied by Brush and Bayliss, Dundee Satellite Receiving Centre.

2.3 Nutrient Measurements

As a means of examining thé significance of urea for microbial nutrition it was necessary to measure other nitrogen sources already accepted as important, such as inorganic nitrogen, present as nitrate, nitrite and ammonium.

Samples for nutrient analysis, taken from the J-Z samplers, were poured into screw capped polyethylene bottles, sealed in a plastic bag and stored at -20°C until analysis.

2.3.1 Ammonium Measurements

Difficulties were found with the Solorzano (1969) method of ammonium estimation in sea water. Blank absorbancies were high and erratic and the intensity of the blue indophenol colour reaction

for standard ammonium solutions varied from batch to batch of analysis. Liddicoat et al. (1975) found similar difficulties and produced another method for the determination of ammonium in sea water. This method was investigated and was found to produce stable, reproducable blanks and no day to day variation in the blue indophenol colour. This method was therefore adopted for the determination of ammonium in the waters investigated in Section 3.

However, owing to the length of time required to prepare and carry out this manual method, albeit simple, an automated method by Pugh and Chubb (1974) was adopted for the larger investigations carried out in the Southern German Bight.

2.3.2 Urea Measurements

Urea concentrations in sea water were determined by the urease method (McCarthy, 1970) in which the urea is hydrolysed by urease to ammonium and the concentration of ammonium determined by the method of Solorzano (1969). However, difficulties mentioned above concerning the Solorzano method resulted in the application of the urease method to the method of Liddicoat et al. (1975) for the determination of the hydrolysed urea-ammonium. This manual method was deployed in the preliminary investigation in the Menai Strait and Beaumaris Bay.

For the same reasons stated for the ammonium method the urease method was used in conjunction with Pugh and Chubb's automated ammonium method for the determination of urea in samples taken in the Southern German Bight. Thus the McCarthy method of hydrolysis of urea by urease to ammonium was carried out manually and the determination of ammonium by the automated method.

The difference between the total ammonium concentration (that is, urea-ammonium plus in situ ammonium) and the in situ ammonium concentration gives the ammonium derived from urea.

2.3.3 Nitrate and nitrite measurements

Nitrate- and nitrite nitrogen were determined by the automated method of Pugh and Chubb (1974).

2.3.4 'Total nitrogen'

'Total nitrogen' was calculated from the sum of urea-N, ammonium-N, nitrate-N and nitrite-N. It should be noted that other sources of nitrogen, i.e. organic compounds such as amino acids have not been included in the term 'total nitrogen'.

2.4 Biomass Measurements

2.4.1 Chlorophyll a Measurements

Chlorophyll a was determined by the method recommended by the SCOR-UNESCO Working Group on Photosynthetic Pigments (1966) using 0.45 µm pore size Sartorius membrane filters for concentrating the cells, and an Ultra-Turrax homogenisor for disrupting them so aiding the release of pigments into the extraction solvent (90% acetone). Optical densities were measured with an Elko II spectrophotometer at the appropriate wavelengths and the SCOR-UNESCO (1966) equation used to determine the concentration of chlorophyll a in the sea water sample.

2.4.2 Enumeration of bacteria

A number of techniques for studies of bacteria by incident light fluorescence have been developed since Strugger (1948) examined soil bacteria with Acridine Orange (Francisco et.al. 1973; Zimmermann and Mayer-Reil, 1974). Investigations of the efficiency and errors in direct counts by epifluorescence microscopy showed the necessity for not even the smallest change in the method and for the use of 0.2 µm membrane filters (Jones and Simon, 1975).

The method described here, using the fluorochrome Acridine Orange, was developed at this laboratory by

Dr. N. Burton (unpublished) and found to be suitable for direct counting of marine bacteria in both the sea water and sediment.

Counts were made using a Leitz Ortholux microscope with incident ultra violet (UV) light Ploem fluorescence vertical illuminator with a beam splitting mirror (TK 495) combined with a suppression filter (K 495). The light source was a 200 W mercury vapour high-pressure lamp (HBO 200) and the following filter combinations used. A 4 mm. BG 38 interference heat filter with a 3 mm. and/or (depending on the intensity of background fluorescence) a 5 mm. BG 12 filter to excluding background fluorescence. The image was viewed through a K 530 barrier filter. Bacteria were counted through a 10 x Periplan GF eye-piece and a 90 x fluorite oil immersion objective Pv Apo oel (aperture 1.15) at a total magnification of 900 x.

Unipore polycarbonate membrane filters of 0.2 μm pore size and 47 mm. diameter (Bio-Rad laboratories) were stained overnight in a 0.2% solution of Lanasyn Brilliant Black (Sandoz) with 4% formalin. The filters were rinsed in sterile filtered distilled water just prior to use and mounted moist on a millipore filter holder XX10 047 30 producing an effective filter area of 9.625×10^8 μm^2.

Both Lanasyn Brilliant Black and Acridine Orange (AO) solutions and the distilled water were filtered through 0.2/u pore size filters. One to 10 ml. of the 25 ml preserved sample was placed in a Universal bottle. This was made up to a constant volume of 10 ml with filtered distilled water and 0.25 ml of 0.1% AO (G.T. Gurr Ltd.) in distilled water added and allowed to stain for 5 min. The AO contained 1% formalin to prevent growth of possible contaminants. The preparation was poured onto the polycarbonate filter and the bottle rinsed twice with 10 ml of filtered distilled water and then filtered at a constant pressure of 60 mm Hg. Immediately after

filtration the membrane was removed and a section of the filter placed, whilst still moist, on a drop of commercial liquid paraffin (British Pharmacopoeia) on a microscope slide. Another drop was placed on the top of the filter, covered with a coverslip and the bacteria counted immediately. Prior to counting, each filter was examined for fluorescent fading and even distribution of bacteria on the membrane.

Control counts were carried out, in which the sample was replaced by filtered distilled water and treated as above. The fluorescent bacterial-size particles were counted and subtracted from the sample counts. Control counts did not form a significant proportion of the sample counts and were constant between membrane filters.

Differences between counts taken from the periphery and the centre of the filter did not appear to be significant within the limits of the analysis carried out.

All luminous green-yellow objects (bar those of irregular shape or blurred image) of bacterial size, including very small luminous "coccoid" images (< 0.3 μm diameter) were counted. These minute images are probably small rods and vibroi$\S$ of $0.2\,\mu$m diameter and $0.5\,\mu$m in length as described by Watson et.al. (1977) using a transmission electron microscope. The "coccoid" appearance is due to a fluorescent "halo" effect.

A minimum of 400 cells were counted per sample using a microscope grid with a measured area of $6773\,\mu m^2$. Assuming a Poisson distribution a $\pm$ 10% variation of the mean count per field will give 95% confidence limits according to the schedules of statistical precision produced by Cassells (1965).

Using the effective filter area and the bacterial numbers per area counted under the microscope the number of bacteria per litre sea water can be calculated.

Approximately 200 cells from each sample were classified into different classes depending on their morphology and size:

	Diameter (/um)	Length (/um)	Volume (/um^3) calculated from median size
a) Cocci	0.2-1.2(0.7)*		0.18
b) Cocci	1.2-1.8(1.5)*		1.75
c) Rods	0.2	0.4-1.2(0.8)*	0.03
d) Rods	0.5	1.2-2.4(1.8)*	0.29
e) Vibrois	0.2	0.4-1.8(1.1)*	0.03

* ( )* = median diameter or length in the size class

The volumes were calculated by approximating the bacterial cell to geometrical shapes of spheres or cylinders. For each sample the percentage of the size classes was estimated. From these values, the volume of the size classes and the total number of bacteria in the sample the total volume of the bacterial population per litre sea water was estimated.

2.4.3 ATP Determinations

The determination of ATP in the microbial populations of sea water is a valuable indicator of the metabolic activity of the population, although it does not define the nature of the population. The method described here is a modification of the method of Holm Hansen and Booth (1966) who first measured ATP concentrations in sea water.

The measurement of ATP is based on the use of the firefly lantern reaction: the ATP provides the energy source for a light-emitting oxidation of a substrate, luciferin, under the influence of an enzyme luciferase. Briefly the steps shown below in the firefly bio-luminescence reaction results in light emission (McElroy, 1960; Plant et.al., 1968).

$$E + LH_2 + ATP \underset{}{\overset{Mg^{2+}}{\rightleftharpoons}} E - LH_2 - AMP + PPi$$

$$E\text{-}LH_2 - AMP + O_2 \longrightarrow \text{oxyluciferin} + E + CO_2 + AMP + \text{light}$$

Where E is the luciferase, LH_2 is reduced luciferin, ATP is adenosine triphosphate, AMP is adenosine monophosphate and PPi is pyrophosphate. For more detailed information see McElroy & Deluca (1978).

Biometer

A Dupont 760 Luminescence Biometer was used to measure the amount of light produced by the firefly reaction. Upon addition of firefly reagents, luciferin and luciferase, a flash of light occurs which is detected by a photomultiplier tube. The signal is converted to a digital readout which is proportional to the maximum intensity of the flash. The peak intensity of the light flash is directly proportional to the concentration of ATP. The biometer was calibrated, as described in the Dupont Manual, for each batch of reaction mixture to a freshly prepared ATP standard (1×10^8 fg ml^{-1}) so that varying sensitivity from batch to batch of enzyme would not be a source of error. The linearity of the calibration was checked by plotting ATP readout against standard ATP concentration (1×10^6, 1×10^7, 1×10^8, and 1×10^9 fg ml^{-1}) before and after a series of analysis. The inherent light of each luciferin-luciferase batch was measured before analysis of the sample.

Preparation of the enzyme

Initially the Dupont reagent kit was used, and is composed of a highly purified luciferase, the substrate luciferin and buffer salt tablets containing MOPS and $MgSO_4$. The reagent kit, although extremely sensitive, with low inherent light, proved to be extremely expensive. Jones and Simon (1977) published a method for increasing the sensitivity of a cheaper firefly reagent by adding extra luciferin, protein and EDTA, the latter two chelate interfering ions. The reconstituted firefly lantern preparation proved to have a low inherent light and to be sensitive enough for use in sea water analysis and was therefore adopted in preference to the Dupont reagent kit.

Preparation of solutions

Low Response Water (LR water): distilled deionised water was acidified (1 drop of concentrated HCl per litre), autoclaved and when cool neutralized with diluted NaOH and resterilized by autoclaving. It was stored at 5°C for up to 3 days. This treatment results in water containing a low concentration of ATP.

Tris Buffer: A 0.02M Tris-(hydroxymethyl) - methylamine (BDH Chemicals, Aristrar grade) solution was made up in LR water at pH 7.75. The solution was sterilized by autoclaving and 5 ml aliquots dispensed into clean, sterile Universal bottles and resterilized by autoclaving. This solution was used as the ATP extractant.

Mops Buffer: A 0.01M 3-(N-Morpholino) propanesulphonic acid (BDH Chemicals or Boehringer and Mannheim) solution in LR water, pH 7.4, was sterilized by autoclaving and stored at -20°C or at 5°C for up to 3 days.

ATP Solutions: Standards of 1×10^6, 1×10^7, 1×10^8 and 1×10^9 fg ml^{-1} of crystalline adenosine 5' triphosphate-disodium salt (BDH Chemicals or Boehringer and Mannheim) were made up in MOPS buffer. If the standards were not used immediately they were frozen in polyethylene containers at -20°C.

Preparation of Glassware

All glassware was soaked in a detergent solution (Decon 90), rinsed three times with 2N HCl, deionised water, MOPS buffer to neutralize any remaining acid and finally twice in LR water.

Extraction

A known volume (100-500 ml) of the sample from the J-Z bottles, having been prefiltered through a 200 μm mesh to remove all but the smallest zooplankton, was filtered through a 0.45 μ pore size 47 mm diameter Millipore membrane filter under a pressure of 250 mm Hg. This is necessary both for the concentration of the cells and the removal of NaCl which inhibits the

firefly reaction. After filtration the membrane filter was immediately plunged into a Universal bottle containing 5 ml boiling Tris buffer and boiling point maintained by heating on a sand bath. After 5 min. the filter was removed and extracted a second time. The two extracts were combined and stored on solid CO_2 until analysis. As controls on the method, samples of the extraction buffer were heated at 100°C for 5 min. and stored as above, and ATP concentrations subsequently analysed and the value subtracted from the ATP concentration of the extracted sample. Standard ATP solutions were added as "spikes" to a number of subsamples and treated in the same manner as a sample and the recovery efficiency calculated and found to be 37%. A correction factor of 2.7 was applied to each ATP measurement. It should be noted that internal standards or "spikes" were not carried out on each sample and that one recovery efficiency has been applied to all samples.

Analysis

No difference was found between injecting the sample into the firefly reagents or the firefly reagents into the sample as long as the sample to enzyme ratio was 2:1. For ease of use a cuvette containing 100 µl of the extracted sample was placed in the biometer facing the photomultiplier tube and 50 µl enzyme was injected through the light tight septa into the sample and the readout noted. To insure a constant mixing ratio in the cuvette the enzyme was injected with a 50 µl Hamilton syringe (style 705N, point style #3) mounted on a mechanical injector (Shandon-Reprojector, SAA-1350).

The concentration of microbial ATP in the sea water was calculated from the ATP readout on the biometer (corrected for inherent light of the enzyme, ATP background concentration in the extractant and recovery efficiency of the method), the volume of the extract and the volume of sea water filtered.

2.4.4 Estimation of Microbial Carbon

An attempt was made to compare the biomass of plant and bacterial populations. Since all microbial biomass is expressed in units which are not directly comparable, such as /ug chl a l^{-1}, /ug ATP l^{-1} and cells l^{-1}, the plant and bacterial biomass are expressed in terms of /ug C l^{-1} using various conversion factors from the literature:

Phototrophic carbon = Chlorophyll a x 30 (Strickland, 1965) .....(A)

Total microbial carbon = Microbial ATP x 250 (Holm Hansen, 1969) .....(B)

Heterotrophic carbon = Total microbial carbon (B) - phototrophic carbon (A) .....(C)

Bacterial carbon = Bacterial cell volume (/um^3 l^{-1} sea water) as calculated from direct counts x 1×10^{-7} which was calculated from cell density of 1.1 g cm^{-3} (Lamanna et.al. 1973) and dry weight:wet weight ratio 0.2 and C: dry weight ratio 0.5 (Luria, 1960) .....(D)

Total microbial carbon = Phototrophic carbon (A) + bacterial carbon (D) .....(E)

All units, unless otherwise stated, are in /ug C l^{-1}. For Cruises HGL I and II only microbial biomass (A), (B) and (C) have been calculated. However, for Cruise HGL III all the above methods of calculating biomass, (A) - (E), have been used. To prevent confusion all terms of biomass in Cruise HGL III will therefore be labelled with the appropriate letter to indicate their origin eg. total microbial carbon (E).

The reliability and usefulness of the ATP method of estimating biomass depends on the following assumptions some of which have undergone severe questioning since this work was started.(1) ATP is a constituent of all living cells. There is no evidence to the contrary. (2) There are no significant changes in cellular ATP from the time the water sampler closes to the time it reaches the deck of the ship. An assumption which has not yet been tested. (3) During filtration and extraction processes there is no significant

alteration or breakdown of the cellular ATP content. An assumption which is supported by Hamilton and Holm-Hansen (1967) but severely questioned by other workers (eg. Jones and Simon, 1977; Afghan et.al. 1977). (4) Extraction efficiency from the cells is 100% or at least constant from cell to cell, species to species and sample to sample of sea water. The measurement of ATP is indirect and therefore absolute values and variations in extraction efficiencies unestimatable. (5) ATP is not found in dead cells nor associated with non-living detrital material. An assumption supported by Holm-Hansen and Booth (1966) but evidence to the contrary is prevalent (eg. Afghan et.al., 1977). Indeed, Ernst and Goerke (1974) used $CaCO_3$ to absorb ATP extracted from sediments. (6) Microbial cells of different species contain a relatively constant ratio of cellular ATP:cellular carbon. (7) The cellular ATP content of any one species does not vary greatly with changing environmental conditions nor with age. Evidence contrary to the latter two assumptions (eg. Hamilton and Holm-Hansen, 1967; Brezonik and Patterson, 1972; Brezonik et.al. 1975) renders the use of estimating biomass from ATP and particularly heterotrophic biomass (which involves an additional conversion factor for phototrophic carbon) in natural waters questionable. Jassby (1975) evaluated ATP estimations of bacterial biomass in the presence of phytoplankton using the difference between carbon obtained from total microbial ATP and the phytoplankton carbon calculated from phyto-plankton counts using laboratory determined conversion factors. He found that systematic errors in the methods used to determine phytoplankton and total carbon could be of sufficient magnitude to render accurate estimates of bacterial carbon impossible with the exception of the situation where heterotrophic biomass is dominant.

Although the error involved in calculating phytoplankton carbon from chlorophyll a may be less than from phytoplankton numbers some degree of scepticism should be placed on heterotrophic carbon (C), particularly when phytoplankton biomass is great.

2.5 Measurements of urea utilization and turnover

Two enzymes which degrade urea have been described by Leftley and Syrett (1973):-

a) Urease which catalyses the hydrolytic cleavage of urea:-

$$CO(NH_2)_2 + H_2O \longrightarrow CO_2 + 2\ NH_3$$

b) ATP Urea amidolyase (UAL ase) which catalyses the ATP-dependent degradation of urea. UAL ase appears to be two separate enzymes; urea carboxylase and allophanate hydrolase which catalyse the reactions:-

$$\text{Urea} + \text{ATP} + HCO_3^- \underset{\text{urea carboxylase}}{\overset{Mg^{2+}\ K^+}{\rightleftharpoons}} \text{allophanate} + \text{ADP} + \text{Pi}$$

$$\text{allophanate} \xrightarrow[\text{allophanate hydrolase}]{} 2\ NH_3 + 2CO_2$$

Both urease and UAL ase catalyse the degradation of urea to ammonium and CO_2. Therefore, if the carbon in urea is labelled with ^{14}C, then enzymic hydrolysis will release $^{14}CO_2$ which can be collected and measured. Thus, the following method, similar to that described by Remsen et.al. (1972) was used to measure urea utilization in the sea water.

One-hundred-ml subsamples were taken aseptically from the J-Z samplers and placed in three sterile, 250 ml, wide necked Erlenmeyer flasks; a light, dark and control flask. Activity in the control flask was terminated immediately by adding 0.5 ml formalin. Then 0.05 ml urea solution (0.05 ml contained 0.1 μmole urea with 0.5 μCi ^{14}C urea) was added to each of the flasks, which were then sealed with parafilm and incubated at ship temperature (about 20°C). Light flasks were incubated at 800 lux (0.01 langleys min^{-1}). After 8 hrs. activity in light and dark flasks was terminated as above and a scintillation vial containing an accordion-folded piece of filter paper (8 x 2 cm) moistened with 0.5 ml 2-phenylethalamine (Ega Chemie) was suspended

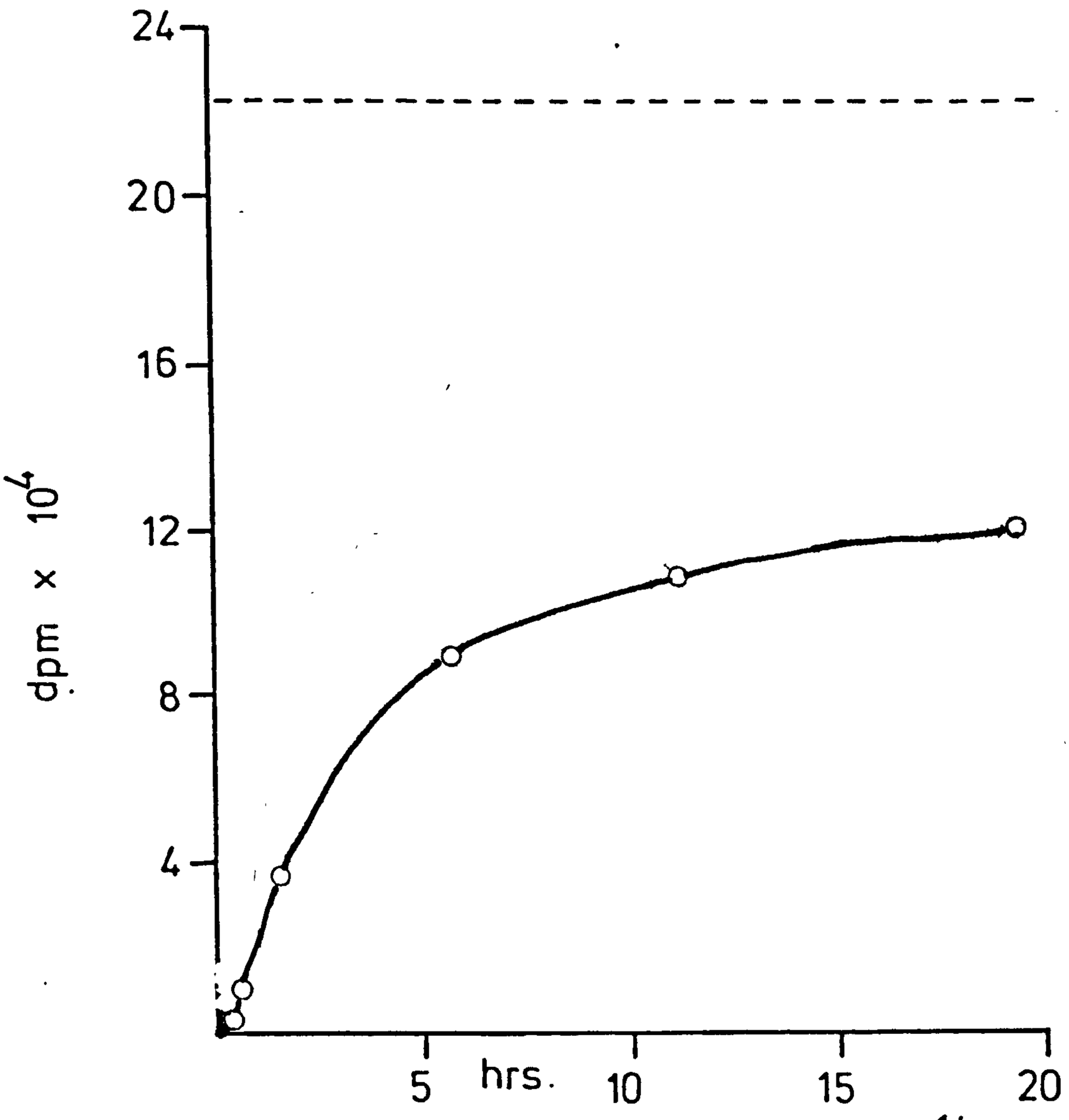

figure 2.1: Absorption of $^{14}CO_2$ onto 2-phenylethalamine.

----- dpm of $NaH^{14}CO_3$ added.

—o— dpm of $^{14}CO_2$ recovered

in each flask as a CO_2 trap and the sample acidified with 0.4 ml 1N HCl and the flasks immediately sealed. The flasks were left standing for 20 hr. for maximal absorption of CO_2 (Fig. 2.1) produced by the hydrolysis of urea and released to the air on acidification of the water. The CO_2 released in this manner will contain $^{14}CO_2$ from the labelled urea. The scintillation vials were removed and 15 ml Aquasol scintillation fluid added.

The micro organisms from each flask were recovered by filtering onto a 0.45 μm pore size, 47 mm diameter Millipore membrane filter, rinsed with sterile sea water and the filter placed in a scintillation vial containing 15 ml Aquasol to determine the ^{14}C incorporated within the cells.

All scintillation vials were allowed to stand in the dark for 24 hrs. for chemiluminescence to subside, prior to counting on a BF Betascint 5000 (for samples taken in the Southern German Bight) or a ICN Tracerlab (for the preliminary studies) scintillation counter.

Efficiency of CO_2 capture using NaH $^{14}CO_3$ was determined over the complete range of CO_2 levels encountered and found to be 52% ($\pm$ 1%). Counting efficiency was determined by a channels ratio technique for both the vials containing the filter paper and 2-phenylethalamine and those containing the Millipore membrane filter. In order to determine the counting efficiency of the former, flasks without labelled urea were treated as for a sample; the vials containing the filter paper and 2-phenylethalamine removed and Aquasol plus a known number of disintergrations per minute (dpm) of standard C^{14} hexadecane (Radio-chemical Centre, Amersham) added.

Counting efficiency for the latter, that is, the vials containing the membrane filter was determined by filtering different aliquots (25-200 mls) of unlabelled sea water through Millipore membrane filters which were then placed in scintillation vials containing Aquasol and a known number of dpm of standard C^{14} hexadecane.

All vials were counted in two channels on the scintillation counter, Channel 1 covered almost all the

whole of the C^{14} pulse height spectrum and Channel 2 the high energy end of the spectrum (scintillation counter settings : Channel 1; threshold 25, Windrow 400; Channel 2; threshold 100, Windrow 400). The channels ratio (cpm channel 1 / cpm channel 2), efficiency in channel 1 and correction factor which is applied to counts per minute (cpm) to give dpm were calculated for both sets of vials. The correction factor for counting efficiency for the filter paper and 2-phenylethalamine is 1.2 and the correction factor for efficiency of CO_2 absorption is 1.9, giving an overall correction factor of 2.4. The correction factor for the vials containing the Millipore membrane filter is 1.3. Background counts were also determined and the appropriate corrections made.

Uptake in dpm (d) was calculated by:

$$d = \left(C_s - C_c\right)F$$

where C_s is the cpm for the sample in Channel 1, C_c is the cpm for the control and F is the appropriate correction factor.

The turnover time (T) for the ^{14}C - urea added to each flask was calculated after Dietz et.al. (1977)

$$T = \frac{A_d.t}{U_d}$$

where A_d is the dpm added, t is the incubation duration in hours and U_d is the net uptake in dpm (from $^{14}CO_2$ evolved and uptake of ^{14}C into the cells). This assumes that the reaction velocity is constant.

The rate of urea assimilation (v) was calculated after Parsons and Strickland (1962)

$$v = \frac{U_d.(S + A)}{A_d.t}$$

where S is the <u>in situ</u> concentration of urea and A is the concentration of added urea. The isotope discrimination factor is ignored. In contrast to T as determined by the Dietz formula above, here v is dependent upon the <u>in situ</u> substrate concentration.

Urea uptake and utilization by phytoplankton is light dependent (Webb and Haas, 1976; Mitamura and Saijo, 1975)

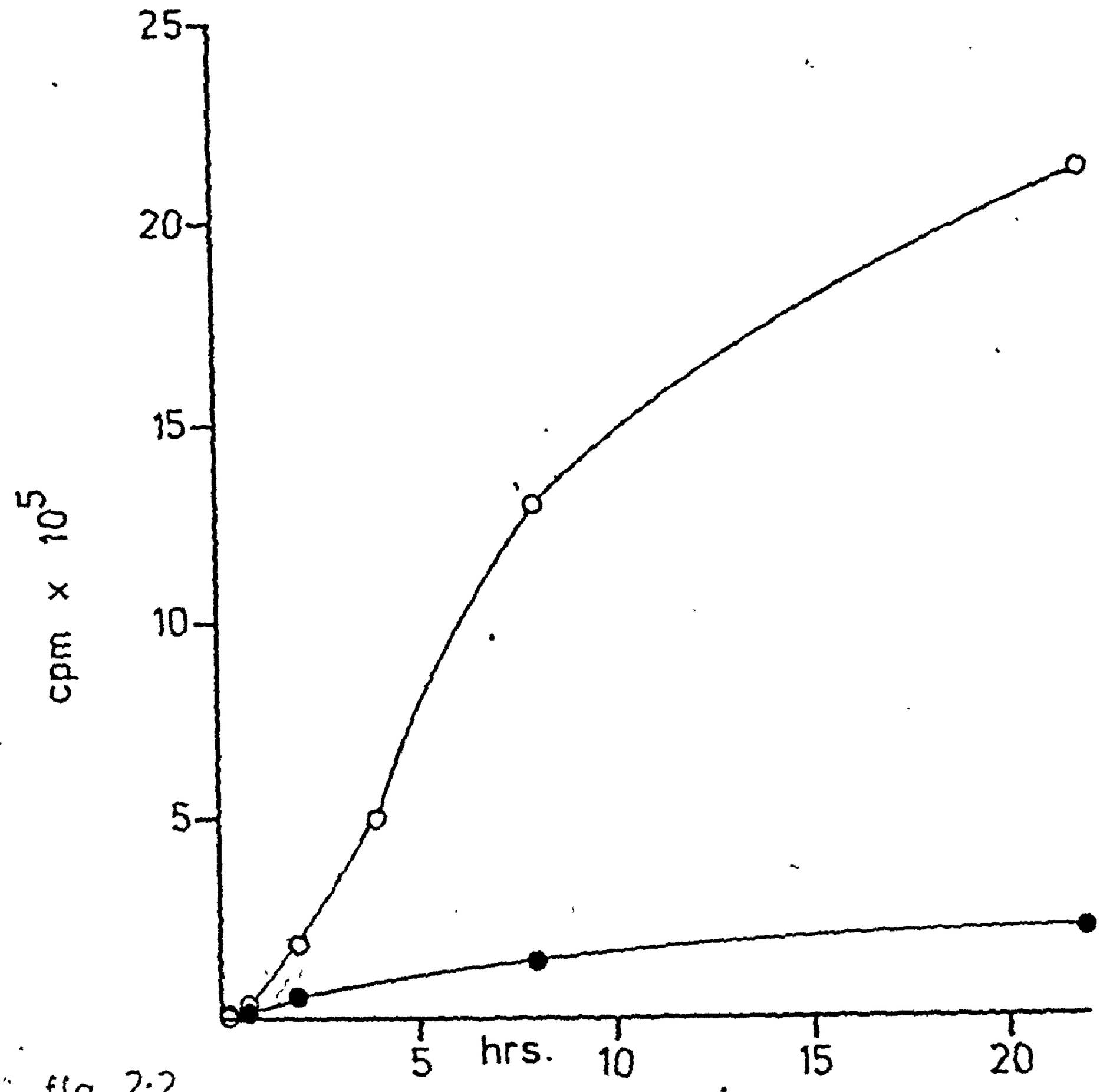

fig. 2·2

Total Uptake of ^{14}C-urea by

Skeletonema costatum

—o— uptake in light

—●— uptake in dark

and therefore the urea utilization in the dark is due mainly to heterotrophic activity of bacteria. This was confirmed for Skeletonema costatum which obviously requires light for the uptake of urea (Fig. 2.2). The small amount of uptake in the dark can be attributed to the algal culture not being completely axenic. Urea utilization in the light is therefore assumed to be a combination of phototrophic and heterotrophic activity. Phototrophic urea utilization was calculated by subtracting the rate of utilization in the dark from that in the light. If the process of urea utilization does not turn off as rapidly as photosynthesis does in the dark there may be a small amount of urea uptake by the phytoplankton. If this occurs the estimates of phototrophic urea utilization may be minimal while urea utilization by the heterotrophs may be maximal.

Urea assimilation indices (nmol urea hr^{-1} /ugC^{-1}), or the ratio of assimilation rate : cellular carbon have been calculated in the following ways:-

Phototrophic urea assimilation index (A) = Phototrophic urea assimilation rate/phototrophic carbon (A)

Total urea assimilation index (B) = Total urea assimilation rate/total microbial carbon (B)

Heterotrophic urea assimilation index (C) = Heterotrophic urea assimilation rate/Heterotrophic carbon (C)

Heterotrophic urea assimilation index (D) = Heterotrophic urea assimilation rate/bacterial carbon (D)

Total urea assimilation index (E) = Total urea assimilation rate/Total microbial carbon (E)

For Cruises HGL I and II only urea assimilation indices (A), (B) and (C) have been calculated. However, for Cruise HGL III all indices, (A) - (E), have been calculated and to prevent confusion will be labelled with the appropriate letter indicating their origin. For example, total urea assimilation index (E).

SECTION 3

PRELIMINARY INVESTIGATIONS

SECTION 3

PRELIMINARY INVESTIGATIONS

3.1 Results and Discussion

Man, on average, excretes 25 g. urea per day and is a prime source of urea as are most of the terrestrial vertebrates. It therefore seems reasonable to assume that a considerable amount of this urea reaches the sea by crude sewage discharges (Remsen et.al., 1974). This enrichment of urea of coastal waters could be important ecologically as marine and estuarine bacteria (Zobell, 1946 and Steinmann, 1976) and phytoplankton (Ryther, 1954; Droop, 1960; Syrett, 1962; Remsen et al., 1974; Mitamura and Saijo, 1975; Webb and Haas, 1976) have been shown to utilize urea as a source of nitrogen.

To investigate the importance of land derived urea in the marine environment the Menai Strait was an appropriate area to study as it has a large untreated domestic sewage input and little input of industrial waste (Table 3.1). To simplify the problem of investigating the multiple sewage sources of the Menai Strait, Beaumaris Bay was chosen for the initial investigation because it was relatively accessible and it had one untreated domestic sewer discharging its contents below the low water mark (LWM) in the North Eastern section of the Menai Strait (Fig. 3.1).

During sampling it was possible to see the fresh water from the sewer coming to the surface of the more dense sea water. When there was little wind action a plume of fresh water could be seen flowing in the direction of the tidal current towards Puffin Island where mixing and dispersion finally occurred.

Results for the stations marked on Figure 3.1 are given in Table 3.2. Urea concentrations are surprisingly low and there is a tendency for the urea concentration to increase with increased distance away from the sewer out-fall. This could be due to:

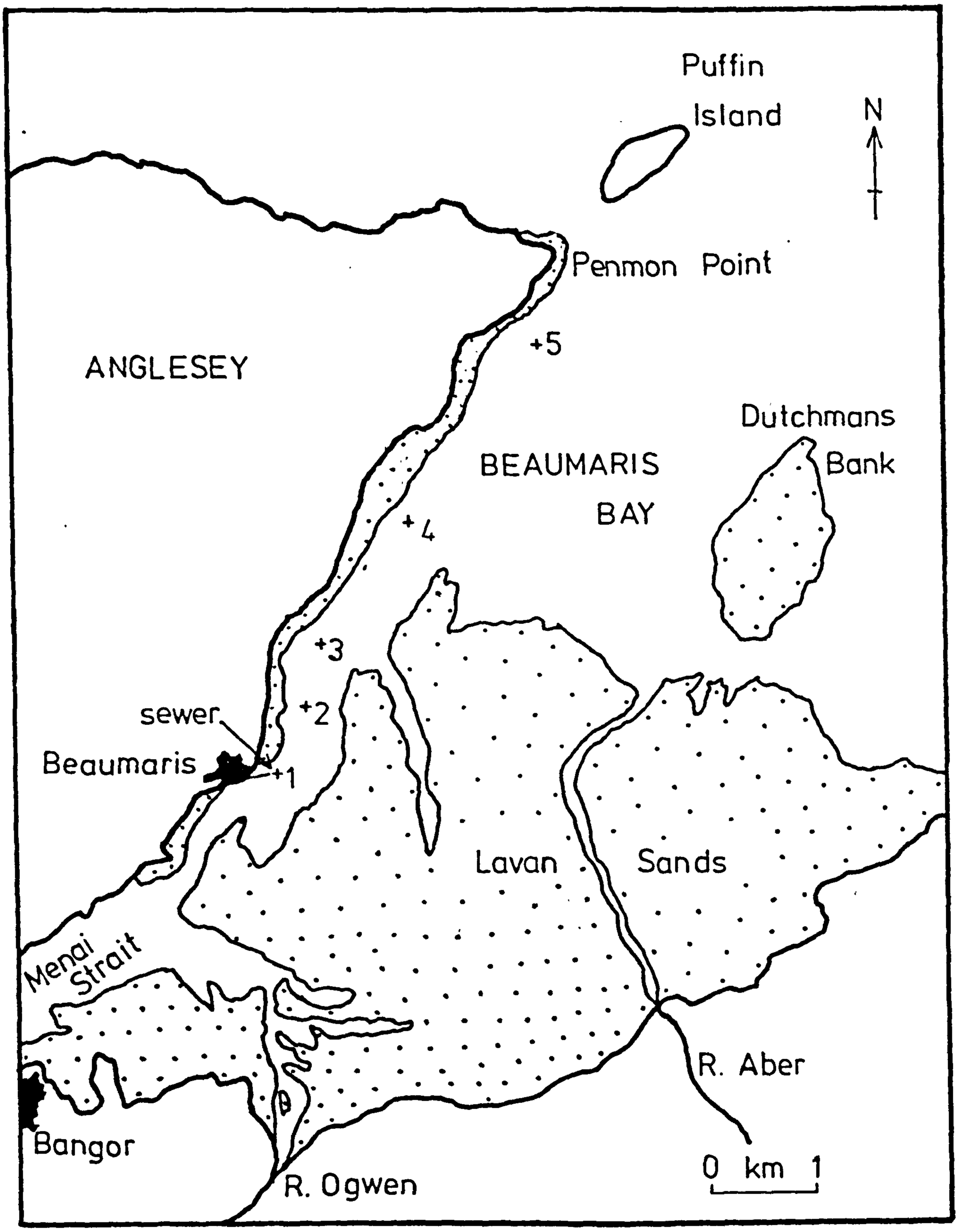

fig. 31 : BEAUMARIS BAY + station position

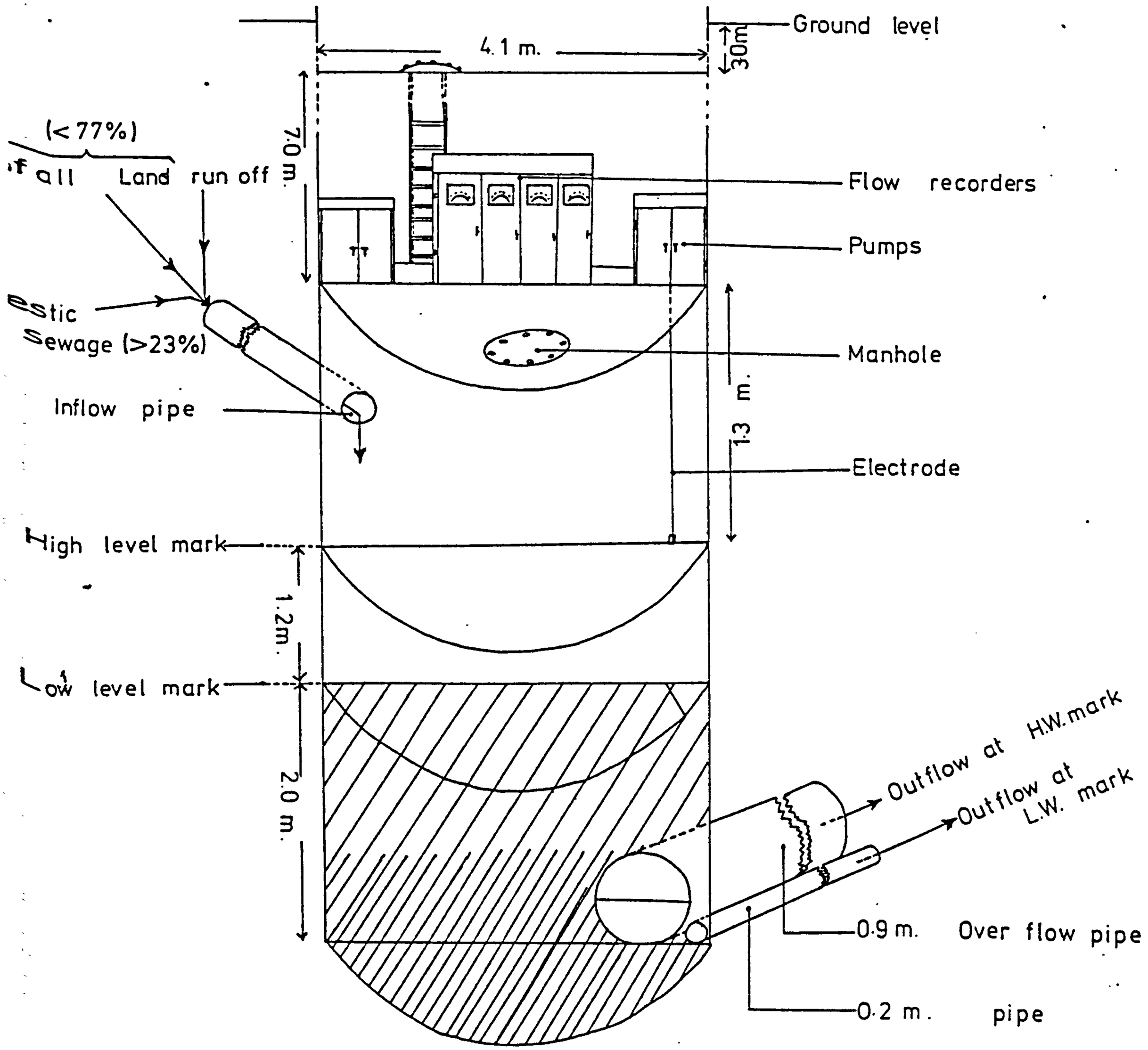

figure 3.2 : Castle pumping station, Beaumaris.

a) sampling error; that is, the sampling did not coincide with discharging of sewage. This occurs once every 5 mins. on a wet day and once every 15 mins. on a dry day.
b) desorption of urea in sea water if it was absorbed to organic matter in the sewage.
c) dilution or inhibition of ureases in the sewage by the sea water.

To eliminate the possibility of sampling error samples were taken of the water overlying the end of the sewer pipe (Station 1 on Figure 3.1) during a 5 hr. period. The results (Table 3.3) again show low urea concentrations.

Sewage collected from the Castle pumping station in Beaumaris (Figure 3.2) was incubated with ^{14}C-urea. Results in Table 3.4 show that an insignificant amount of urea is absorbed onto organic matter. In order to explain these results it is possible to speculate on the amount of urea entering the sewer system and its retention time in the system before entering the sea water. The expected concentration of urea in the Castle pumping station, calculated from the population of Beaumaris and pumping rates in wet (WWF) and dry (DWF) weather flow are shown in Table 3.5. If there was no assimilation of urea within the sewer system urea concentrations would lie between 500 and 2000 μ mol l^{-1}. When the sewage is discharged into the sea water of Beaumaris Bay a certain amount of dilution would be expected. However, the density difference between the fresh water and sea water, to some extent, inhibits the dilution of sewage resulting in the formation of fresh water plumes flowing in the direction of tidal current. The concentrations of urea in the water above the end of the discharge pipe (Table 3.3) were so low (0-1.2 μ mol urea l^{-1}) that dilution alone cannot be the explanation.

Finally, the concentration of urea in sewage taken from the Castle pumping station was measured (Table 3.4) and found to be far lower than the 'expected' concentration. The sewage was incubated with ^{14}C urea and the turnover time and assimilation rate determined (Table 3.4). These

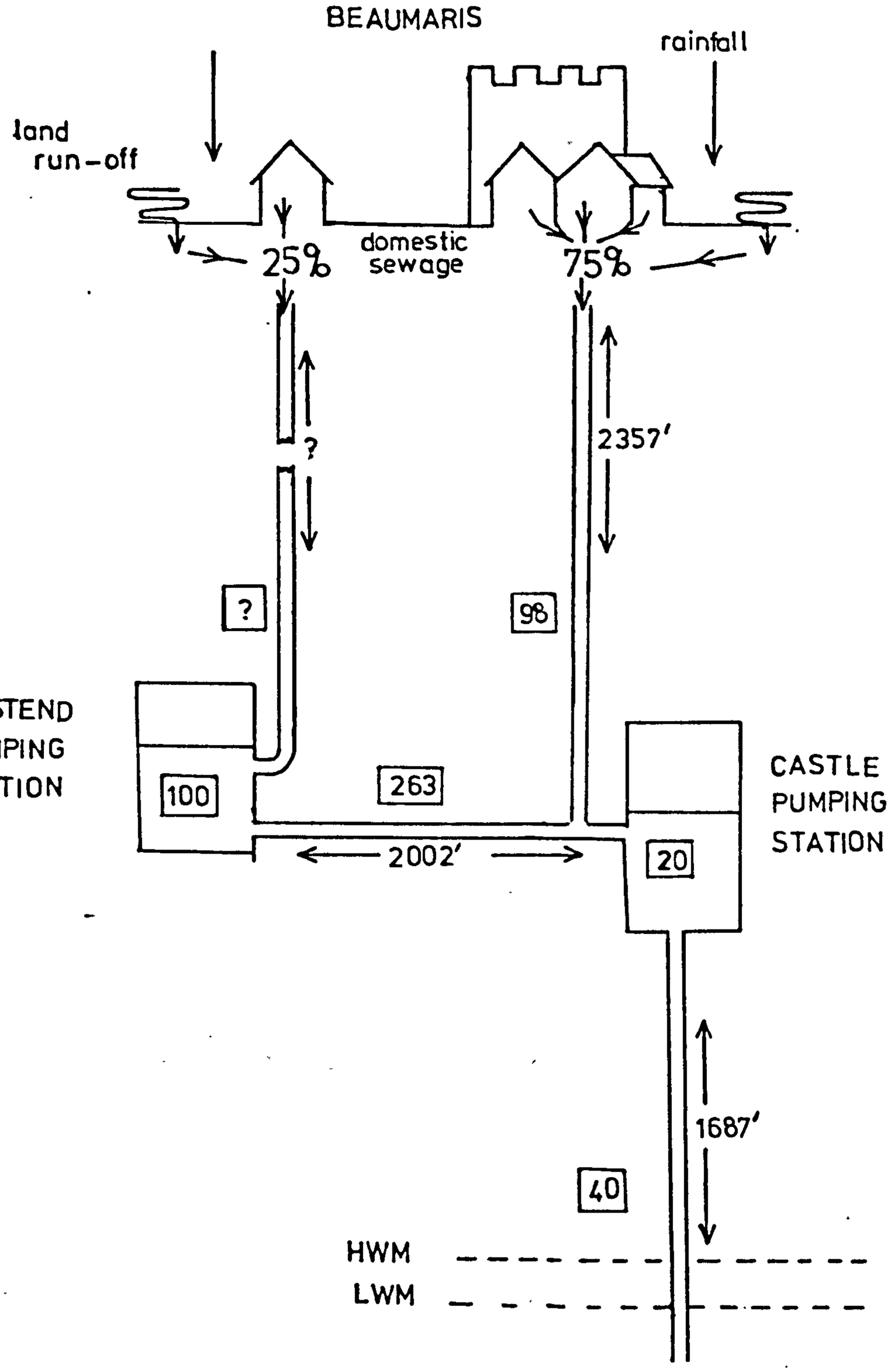

figure 3.3: Schematic representation of the Beaumaris sewer system. Figures in boxes are retension times of sewage in each part of the system in minutes.

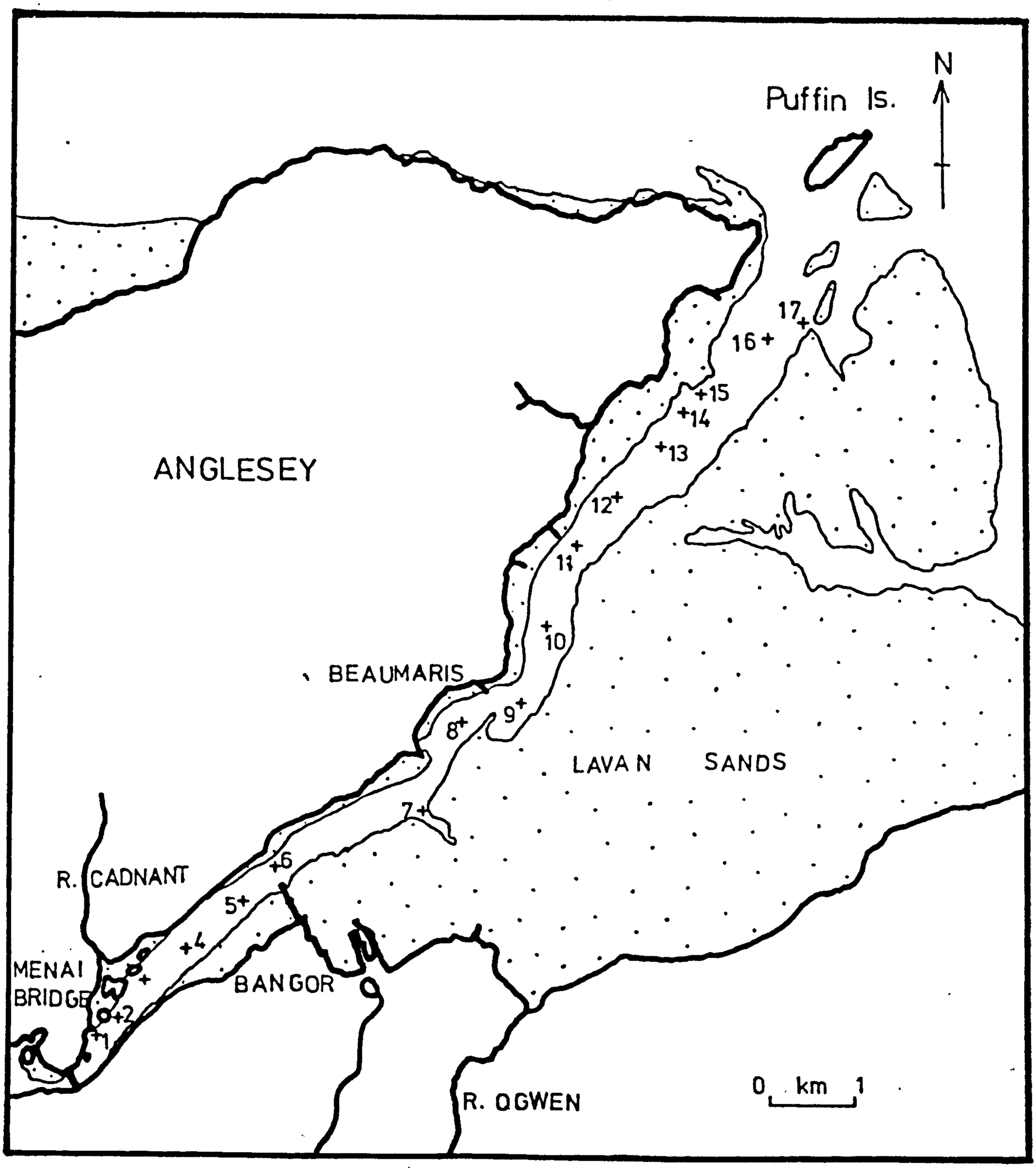

fig. 3·4 : N.E. SECTION OF THE MENAI STRAIT

+ station position

Menai Bridge ——— tidal current ———→ Puffin Is.

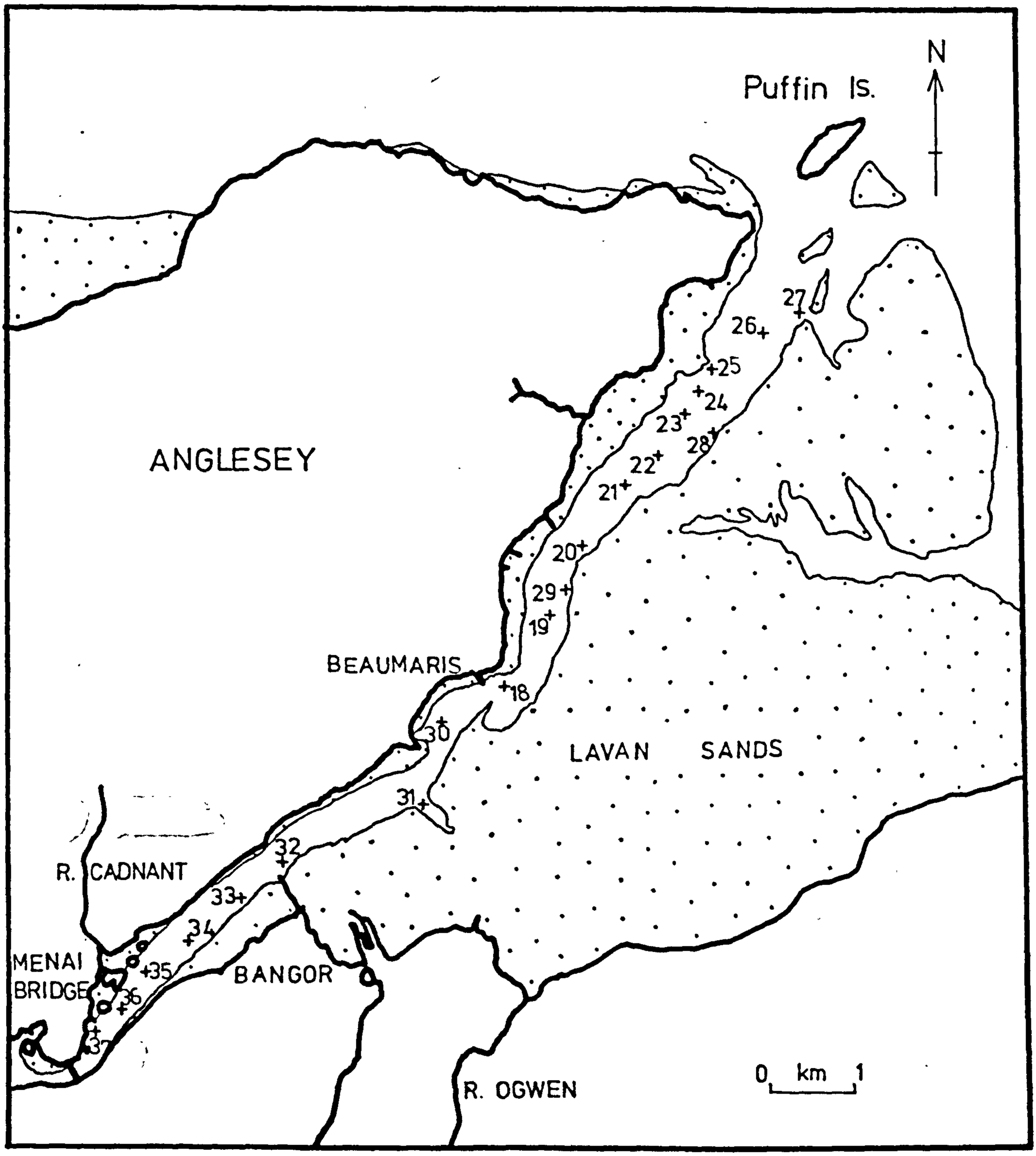

fig. 35 : N.E. SECTION OF THE MENAI STRAIT

+ station position

Menai Bridge ← stns. 28–37 tidal current stns. 18–27 → Puffin Is.

results show that there is an extremely high microbial urease activity within the sewage.

Since neither the velocity of sewage nor the pumping pressure were known as a final substantiation of the idea that most of the urea is taken up in the Beaumaris sewer system the retention times were calculated (Table 3.6 and Fig. 3.3). A 25% portion of the sewage passes through the Westend pumping station and has a minimum retention period of over 7 hrs. The remaining 75% of the sewage flows directly to the Castle pumping station and has a minimum retention period of 2.5 hrs. These retention periods are estimated from the total capacity of pipes and pumping stations, i.e. conditions which are likely to occur only at times of heavy rainfall and are therefore great underestimates.

With an average urea turnover time of 3 hrs. and sewage retention times greater than 2.5 - 7 hrs. it is therefore not surprising to find such low concentrations in the Castle pumping station and discharged sewage. Indeed, the increase of urea concentration away from the sewer may be due to inhibition of urease containing micro organisms in the sewage by sea water or the gradual dilution of urease micro organisms with increased distance from the outfall. It can be concluded that the length of time the crude sewage from the populace of Beaumaris takes from entry into the system to discharge into Beaumaris Bay results in the removal of much if not all of the urea from the system by microbial action.

Urea concentrations were investigated in the N. E. section of the Menai Strait to see if concentrations were as low as those found in Beaumaris Bay. Station positions are marked on Figures 3.4 and 3.5 and results given in Table 3.7. Urea concentrations from the 37 stations again lay between 0 and 1.2 μ mol l^{-1}.

TABLE 3.1: DISCHARGES INTO THE MENAI STRAIT*. SUMMARY OF SELECTED INFORMATION FROM REPORT OF A RIVER POLLUTION SURVEY OF ENGLAND AND WALES, 1973

a) Crude Sewage+

Number of discharges	22
Percentage satisfactory	0
Population served by crude sewage discharges	31,089
DWF** of crude sewage discharged (m^3 day^{-1})	8,751
Percentage DWF to a satisfactory standard	0

b) Sewage Effluent//

Number of discharges	3
Percentage satisfactory	100
Population served by treatment works discharge	3,725
DWF of sewage effluent discharged (m^3 day^{-1})	591
Percentage DWF to a satisfactory standard	100

c) Industrial effluent excluding solely cooling water

Number of discharges	2
Percentage satisfactory	50
DWF of industrial effluent discharge (m^3 day^{-1})	1,473
Percentage satisfactory	91

d) Unsatisfactory storm overflows

Number of discharges	0

** DWF = dry weather flow

* The figures relate only to discharges direct to the Menai Strait and do not take into account any pollution contained in rivers flowing into it.

+ "Foul sewage which is untreated or which is given physical treatment only by screening or maceration or tidal storage"

// "The discharge from a sewage treatment works where foul sewage receives at least settlement, after being screening or macerated"

TABLE 3.2: OBSERVATIONS OF UREA AND AMMONIUM CONCENTRATIONS IN BEAUMARIS BAY

Station Number		Urea (μmol l^{-1})	NH_4^+ (μmol l^{-1})
1	(a)	0.00	2.27
	(b)	0.10	0.11
2	(a)	0.22	0.73
	(b)	0.28	0.43
3	(a)	0.08	0.73
	(b)	0.96	0.94
4	(a)	0.35	0.67
	(b)	0.24	0.69
5	(a)	0.40	0.85
	(b)	0.27	1.13

Surface samples were taken from Station positions marked on Figure 3.1. Stations marked with (a) were sampled when the tidal current was N. W. ward and those marked with (b) when the tidal current was S. E. ward. Station 1 was sited directly above the discharge pipe from Beaumaris Sewer and organic matter indicitive of untreated domestic sewage was easily discernible both in the sample and surrounding water.

TABLE 3.3: OBSERVATIONS OF UREA, NH_4, NO_3 CONCENTRATIONS ABOVE THE BEAUMARIS SEWER DISCHARGE PIPE (STATION 1 ON FIGURE 3.1) OVER A 5 HOUR PERIOD. DEPTH OF WATER COLUMN IS 16 m.

Time of Sampling	Depth (m)	Urea (μmol l^{-1})	NH_4 (μmol l^{-1})	NO_3^+ (μmol l^{-1})
1130	0	0.55	2.20	11.6
1200	0	0.75	2.30	15.2
	7.5	0.05	1.80	15.5
	15.0	0.45	1.30	7.9
1230	0	0.45	1.70	11.9
	7.5	0.35	2.30	6.0
	15.0	0.45	1.70	11.4
1300	0	0.75	1.90	9.3
	7.5	0.75	1.00	11.3
	15.0	0.45	1.40	11.5
1330	0	0.73	2.10	7.0
	7.5	0.00	3.10	6.9
	15.0	0.25	3.10	5.6
1400	0	0.25	2.50	11.5
	7.5	0.25	2.90	6.1
	15.0	0.00	2.60	6.8
1430	0	0.65	4.30	11.4
	7.5	0.25	4.70	14.8
	15.0	1.55	3.40	8.8
1500	0	0.25	1.70	10.5
	7.5	0.55	1.70	10.9
	15.0	0.05	1.70	6.6
1530	0	0.00	2.20	10.8
	7.5	0.35	1.60	6.5
	15.0	0.00	2.50	7.3

TABLE 3.3 CONTINUED

Time of Sampling	Depth (m)	Urea (μmol l^{-1})	NH_4^+ (μmol l^{-1})	NO_3^- (μmol l^{-1})
1600	0	0.00	3.10	8.5
	7.5	0.35	2.40	10.6
	15.0	0.35	2.10	8.8
1630	0	1.15	2.10	11.2
	7.5	0.55	1.90	11.9
	15.0	0.55	2.50	8.0

TABLE 3.4: ASSIMILATION OF UREA IN BEAUMARIS SEWAGE

Incubation*	$^{14}CO_2$ released from whole sewage (dpm)	^{14}C in particulate fraction of whole sewage (dpm)	$^{14}CO_2$ released from sewage filtered through 0.45 /um filter (dpm)
1	6, 674, 984	3,501	35,478
2	5, 017, 791	1,887	86,875
3	6, 856, 685	6,276	70,995
Control	33, 178	1,014	8,495

* 1 /umol urea containing 5 /uCi ^{14}C urea was added to 100 ml sewage and incubated at 20°C for 100 minutes. Formalin was added to the control flasks to prevent biological activity and the dpm taken from the dpm in the experimental incubations.

	Turnover Time (Hours)	Urea Assimilation Rate (/umol l^{-1} hr^{-1})
1	2.78	5.02
2	3.69	3.77
3	2.70	5.15
Mean	3.06	4.65

Percentage urease activity carried out intracellularly 98.96%

Percentage urease activity carried by non biological agents (free urease?) 1.04%

Percentage urea incorporated in cell 0.06%

Percentage urea incorporated on non-living matter 0.01%

Measure of concentration of urea in sewage (/umol l^{-1})** 3.93 (3.98-3.87)

" " NH_4 " " 86.6 (94.8-78.4)

" " NO_3 " " 44.0 (49.0-38.9)

" " NO_2 " " 2.5 (3.0- 2.0)

** Sewage from inlet pipe to Castle pumping station

TABLE 3.4: ASSIMILATION OF UREA IN BEAUMARIS SEWAGE

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** Sewage from inlet pipe to Castle pumping station

TABLE 3.5: CALCULATION OF EXPECTED UREA CONCENTRATIONS IN CASTLE PUMPING STATION, BEAUMARIS

Pumping rate of Castle pumping station	500 gall/min
Number of hours of pumping in dry weather (DWF)	3 hrs/day
Amount of sewage pumped per dry day	90,000 gall/day
Number of hours of pumping in wet weather (WWF)	12 hrs/day
Amount of sewage pumped per wet day	360,000 gall/day
Population of Beaumaris*	2102
Average amount of urea excreted per person	25g/day
'Expected' concentration of urea in pumping station on dry day	2140 μmol l^{-1}
'Expected' concentration of urea in pumping station on wet day	573 μmol l^{-1}

* According to 1971 National Population Census. This refers to the resident population of Beaumaris Urban District. Beaumaris receives a large number of tourists during the summer. The urea concentrations above would therefore be underestimates for the summer months.

TABLE 3.6: CALCULATION OF THE MINIMUM RETENTION TIME (I.E. WWF) OF SEWAGE IN THE BEAUMARIS SEWER SYSTEM

a) Westend pumping station

Pumping rate	23,850 gall/day
Capacity of well	1718 gall.
Retention time of sewage	104 min.

b) Pipe from Westend pumping station to Castle pumping station

Diameter	8"
Length	2002'
Capacity	4368 galls.
Flow rate	23,850 gall/day
Retention time of sewage	264 min.

c) Pipe direct to Castle pumping station from domestic areas

Diameter	8"
Length	2357'
Capacity	5099 galls
Flow rate	75,150 gall/day
Retention time of sewage	98 min.

d) Castle pumping station

Pumping rate	99,000 gall/day
Capacity of well	1413 galls
Retention period	21 min.

e) Pipe from Castle pumping station to sea

Diameter	7"
Length	1687'
Capacity	2818 galls
Flow rate	99,000 gall/day
Retention period of sewage	41 min.

TABLE 3.7: OBSERVATIONS OF UREA, NH_4, NO_3 AND NO_2 CONCENTRATIONS IN THE N.E. MENAI STRAIT

Station No.	Urea (μmol l^{-1})	NH_4 (μmol l^{-1})	NO_3 (μmol l^{-1})	NO_2 (μmol l^{-1})
1	0.64	1.00	2.20	0.03
2	0.50	2.70	2.20	0.05
3	0.41	2.45	2.19	0.04
4	0.00	4.00	2.11	0.12
5	0.20	2.10	2.18	0.12
6	0.36	1.00	2.23	0.07
7	0.56	1.70	2.49	0.06
8	0.70	1.10	2.23	0.07
9	0.24	1.90	2.20	0.10
10	0.34	1.10	2.19	0.11
11	0.40	1.60	2.17	0.06
12	0.82	2.50	2.27	0.23
13	1.11	1.70	2.42	0.135
14	1.05	1.60	2.41	0.09
15	0.82	1.85	2.48	0.07
16	0.56	1.70	2.56	0.04
17	0.55	1.50	2.46	0.04
18	1.21	2.60	2.21	0.19
19	0.05	1.85	2.32	0.08
20	1.14	2.30	2.07	0.11
21	0.46	1.80	2.51	0.04
22	0.00	3.00	2.29	0.11
23	0.25	2.60	2.32	0.08
24	0.00	1.30	5.54	0.06
25	0.60	1.30	1.79	0.11
26	0.01	1.75	2.13	0.07
27	0.00	2.30	2.54	0.06
28	0.38	1.85	2.59	0.06
29	0.00	2.50	1.95	0.05
30	0.44	2.50	1.99	0.06
31	1.23	7.40	2.19	0.31
32	0.34	2.70	2.23	0.17
33	0.44	2.60	3.24	0.06
34	0.00	2.70	2.13	0.07
35	0.37	2.85	2.29	0.06
36	0.10	2.40	2.02	0.03
37	0.30	4.10	3.06	0.04

TABLE 3.8: CALCULATION OF 'EXPECTED' UREA CONCENTRATIONS IN THE MENAI STRAIT

Population served by crude sewage discharges*	31,089
Urea entering the Menai Strait each day ..... (from an average of 25g excreted per day per person)	777,225g
Volume of the Menai Strait at mean water** (pers.comm. J. Hunter, Menai Bridge)	700,000 x 10^3 m^3
Concentration of urea in Menai Strait per day	1·11 mg/m^3
Flushing rate of the Menai Strait (pers.comm. J. Hunter)	8.1 days
'Expected' urea concentration in Menai Strait	0·15 /umol l^{-1}

* from Report of a River Pollution Survey of England and Wales, 1973

** Calculated from a number of cross-sectional areas of the Menai Strait x length of section where area of the cross section (A) is calculated from:

$$A = BO(D) + SLP(D)^2$$

where BO is the bottom width, D is the depth and SLP is the cotangent of the angle supplement to the angle made by the side and the bottom.

SECTION 4

INVESTIGATIONS IN THE SOUTHERN GERMAN BIGHT

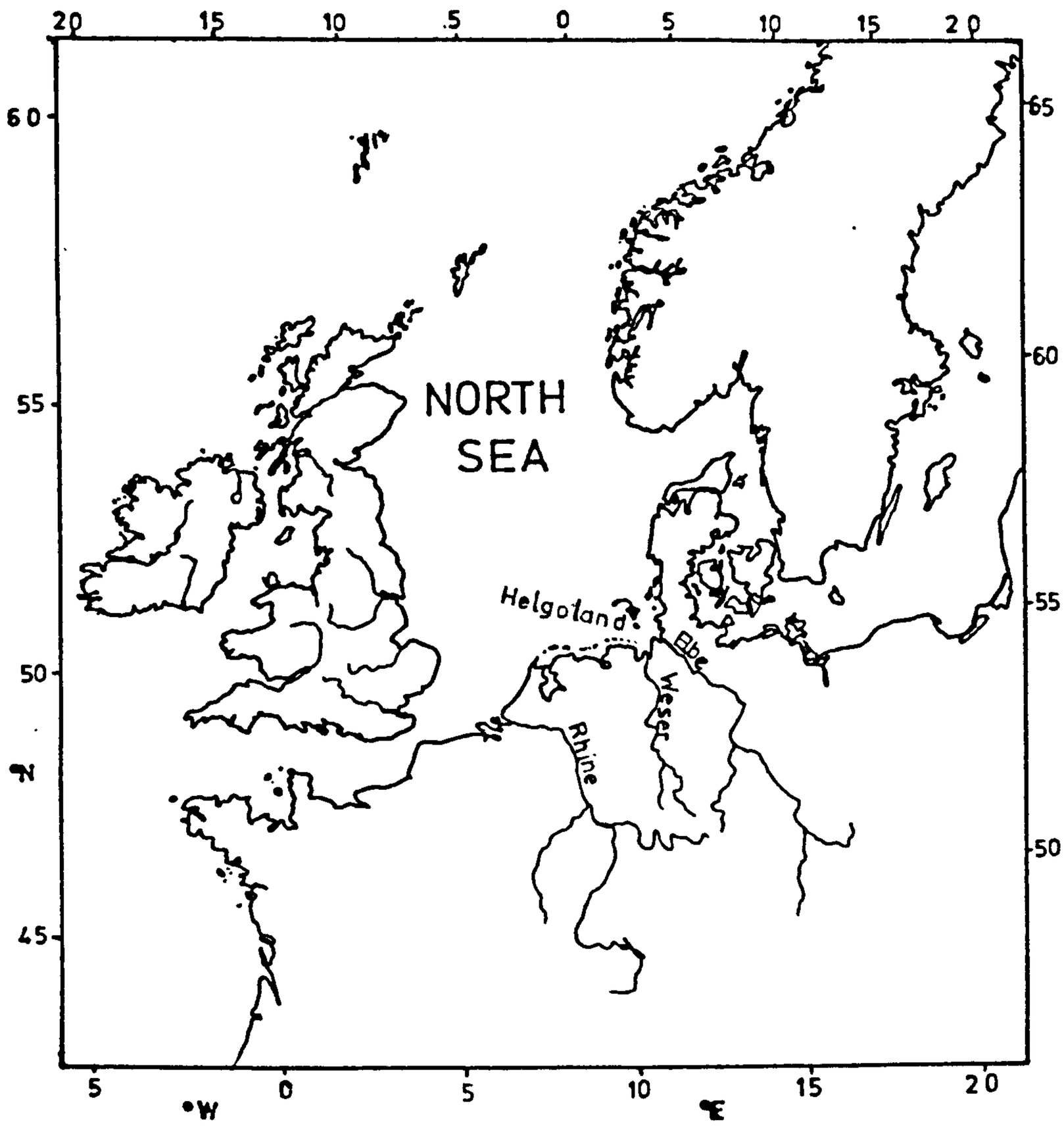


Fig. 4.1 The North Sea and location of Helgoland and the Elbe.

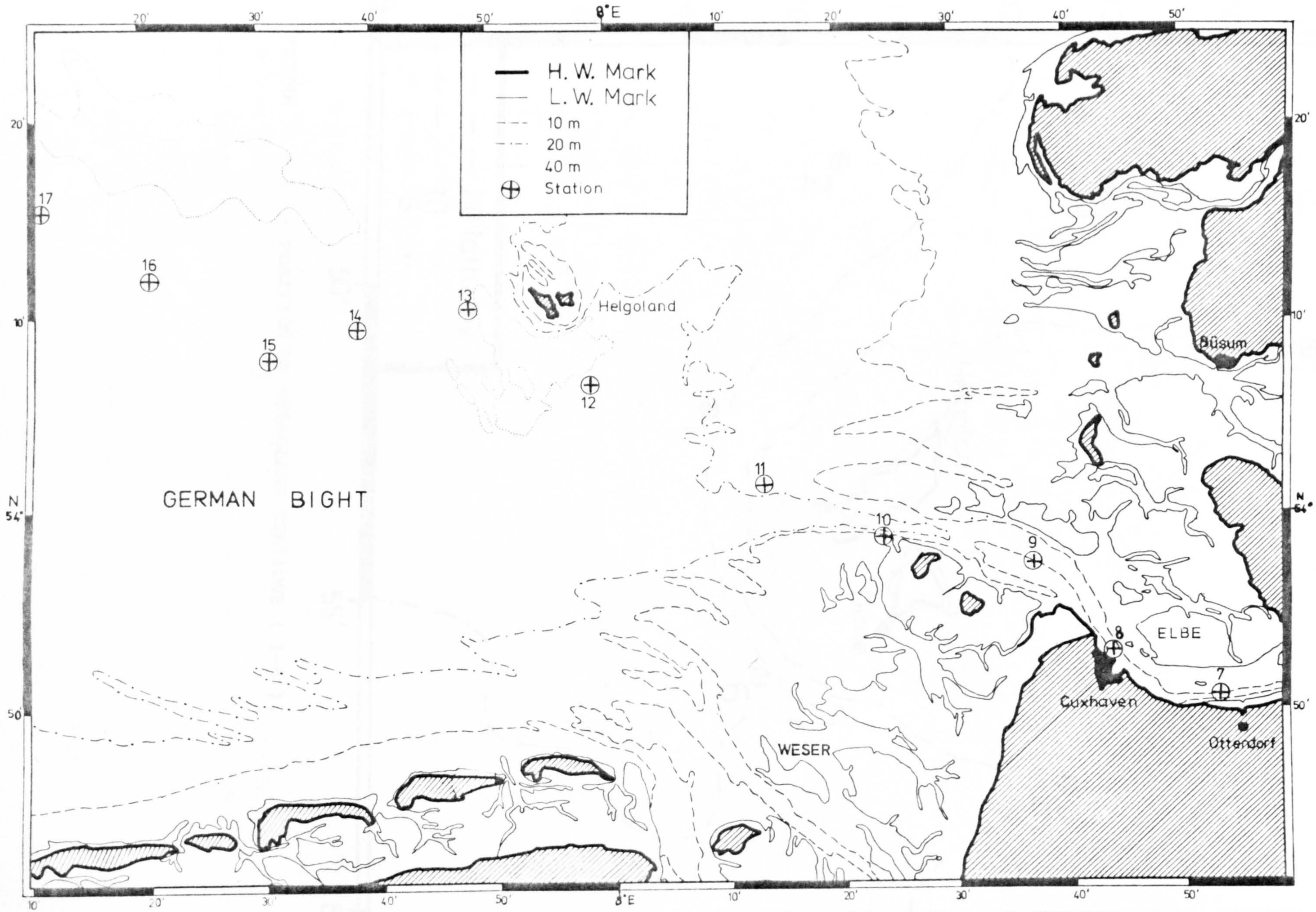


Fig. 4.2 Position of stations in the southern German Bight and Elbe estuary.

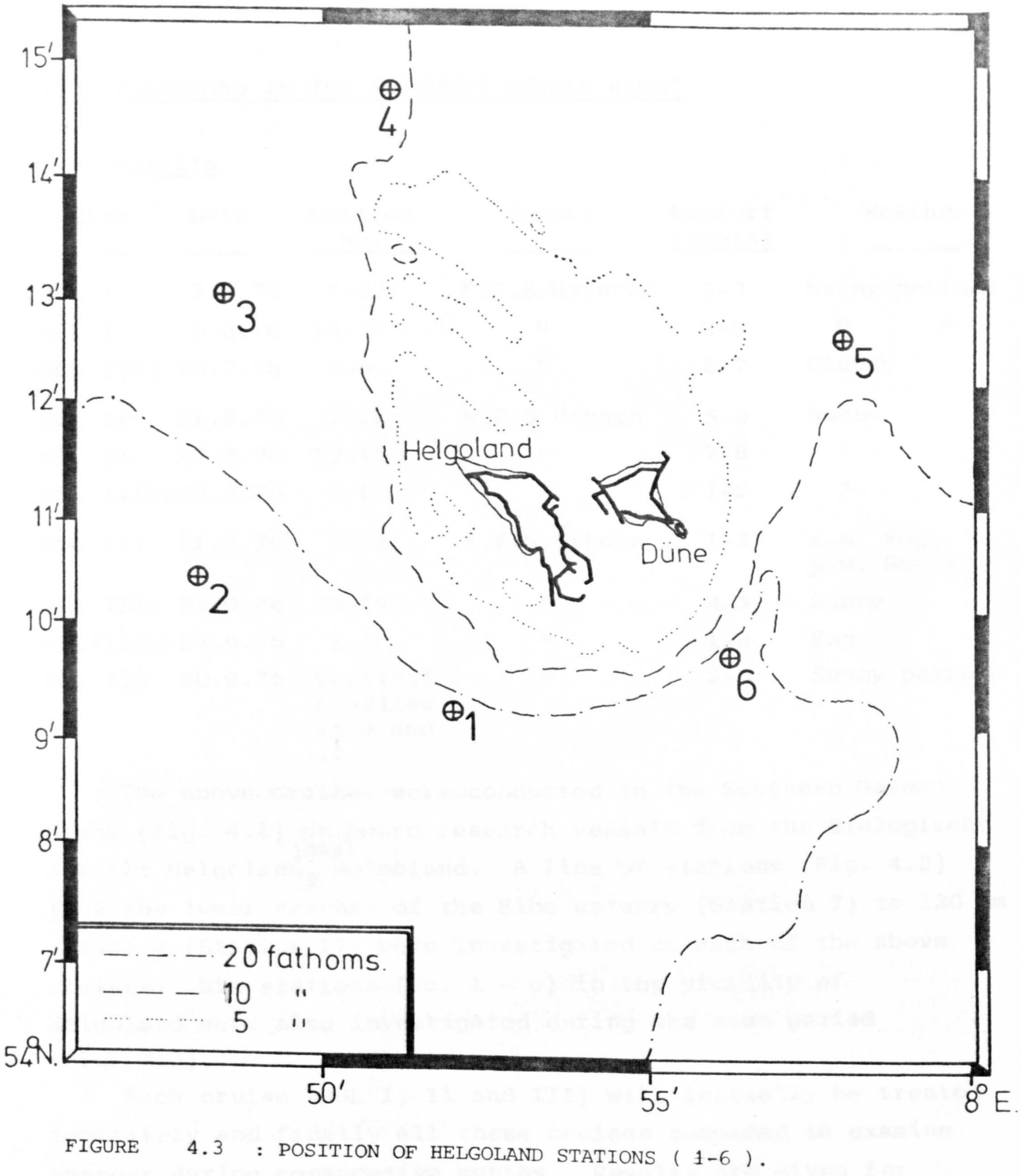


FIGURE 4.3 : POSITION OF HELGOLAND STATIONS (1-6).

SECTION 4

INVESTIGATIONS IN THE SOUTHERN GERMAN BIGHT

4.1 Results

Cruise	Date	Station No.	Vessel	Beafort (knots)	Weather
HGL I	3.8.76	7-12	F.F.S.Heincke	2-3	Sunny periods
HGL I	5.8.76	13-17	"	2-3	" "
HGL I(h)	30.7.76	1-6	"	6-7	Cloudy
HGL II	31.8.76	7-12	F.F.S Üthorn	5-6	Sunny
HGL II	27.8.76	13-17	"	7-8	"
HGL II(h)	25.8.76	1-6	"	1-2	"
HGL III	21.9.76	7-12	F.F.S.Üthorn	1-2	a.m. Fog, p.m. Sunny
HGL III	23.9.76	13-17	"	4-5	Sunny
HGLIII(h)	27.9.76	1-6	"	1-2	Fog
HGL III	20.9.76	Vertical Profiles at 8 and 11.	"	2-3	Sunny periods

The above cruises were conducted in the Southern German Bight (Fig. 4.1) on board research vessels from the Biologische Anstalt Helgoland, (BAH) Helgoland. A line of stations (Fig. 4.2) from the lower reaches of the Elbe estuary (Station 7) to 120 Km offshore (Station 17) were investigated on each of the above cruises. Six stations (No. 1 - 6) in the vicinity of Helgoland were also investigated during the same period (Fig. 4.3).

Each cruise (HGL I, II and III) will initially be treated separately and finally all three cruises compared to examine changes during consecutive months. Results are given for measurements taken at 10 m. depth unless stated otherwise.

4.1.1 Cruise HGL I

4.1.1.1 Physical Measurements

Results for physical measurements are shown in Figure 4.4. An estuarine regime is obvious from the salinity and density (sigma t) distribution at station 7 - 10, showing lower salinity and density at station 7 increasing steadily to station 10. Unfortunately,

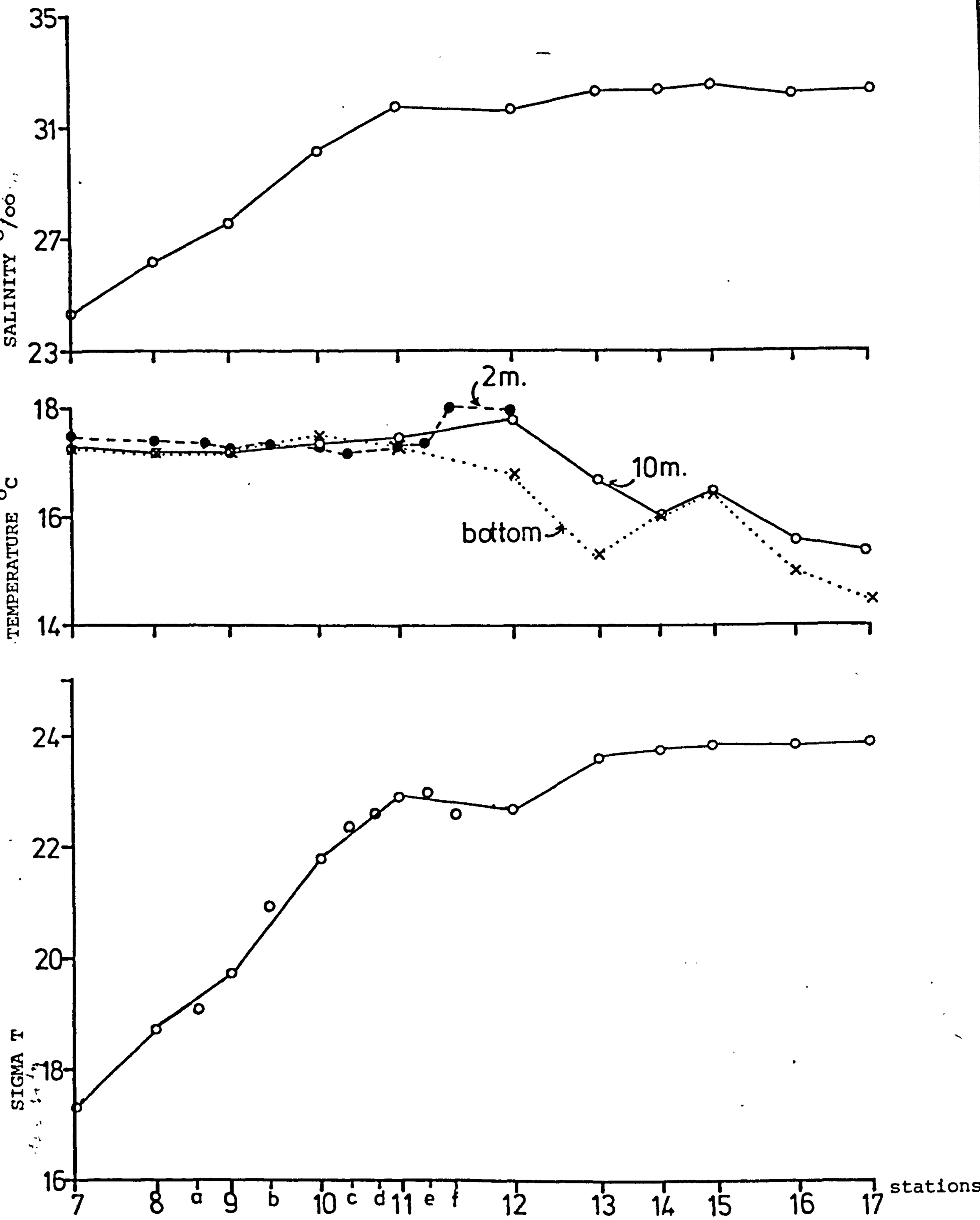


FIGURE 4.4 : CRUISE HGLI. DISTRIBUTION OF PHYSICAL MEASUREMENTS OF SALINITY , TEMPERATURE AND SIGMA T.

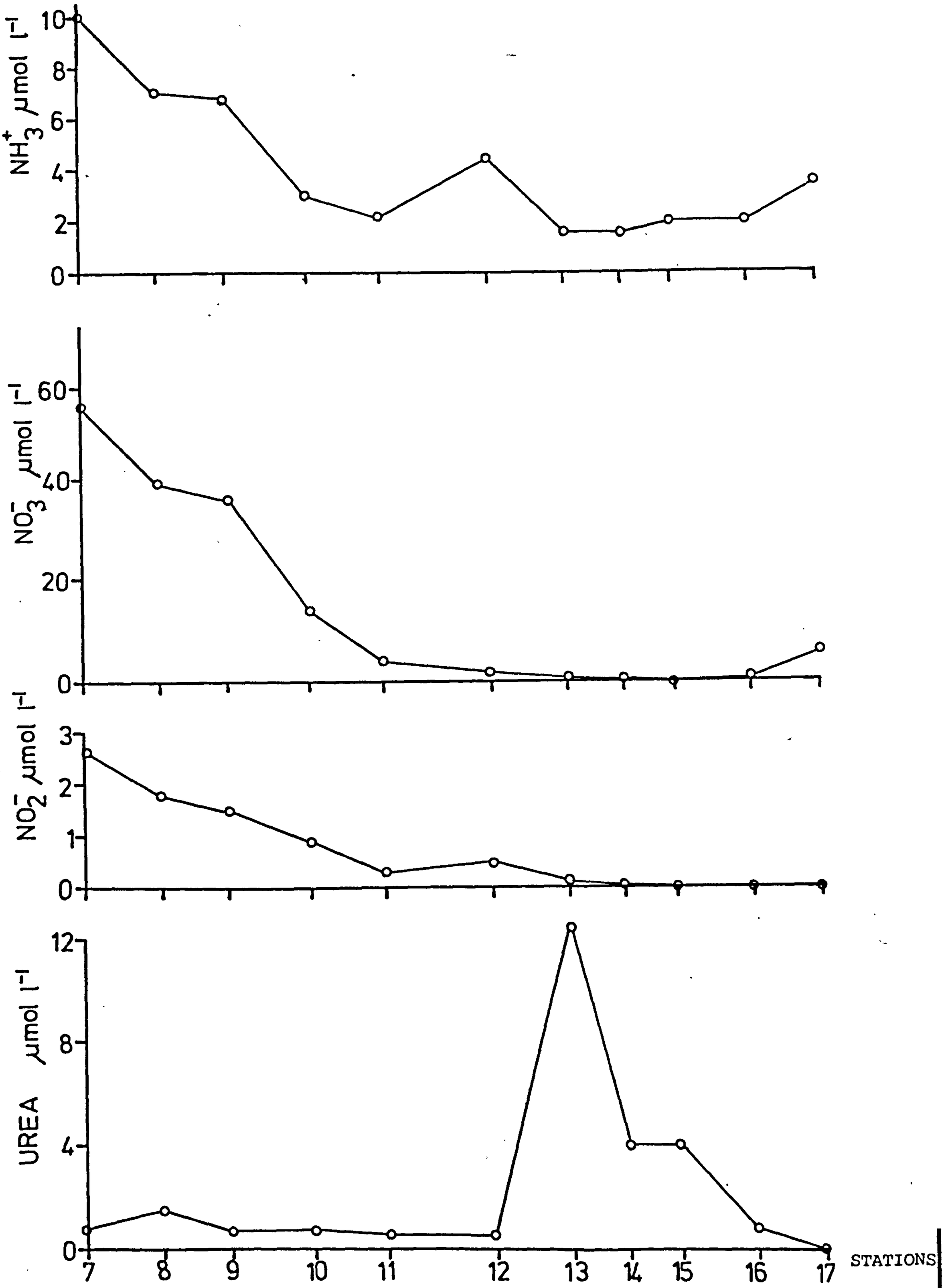


FIGURE 4.5 : CRUISE HGLI. DISTRIBUTION OF AMMONIUM, NITRATE, NITRITE AND UREA.

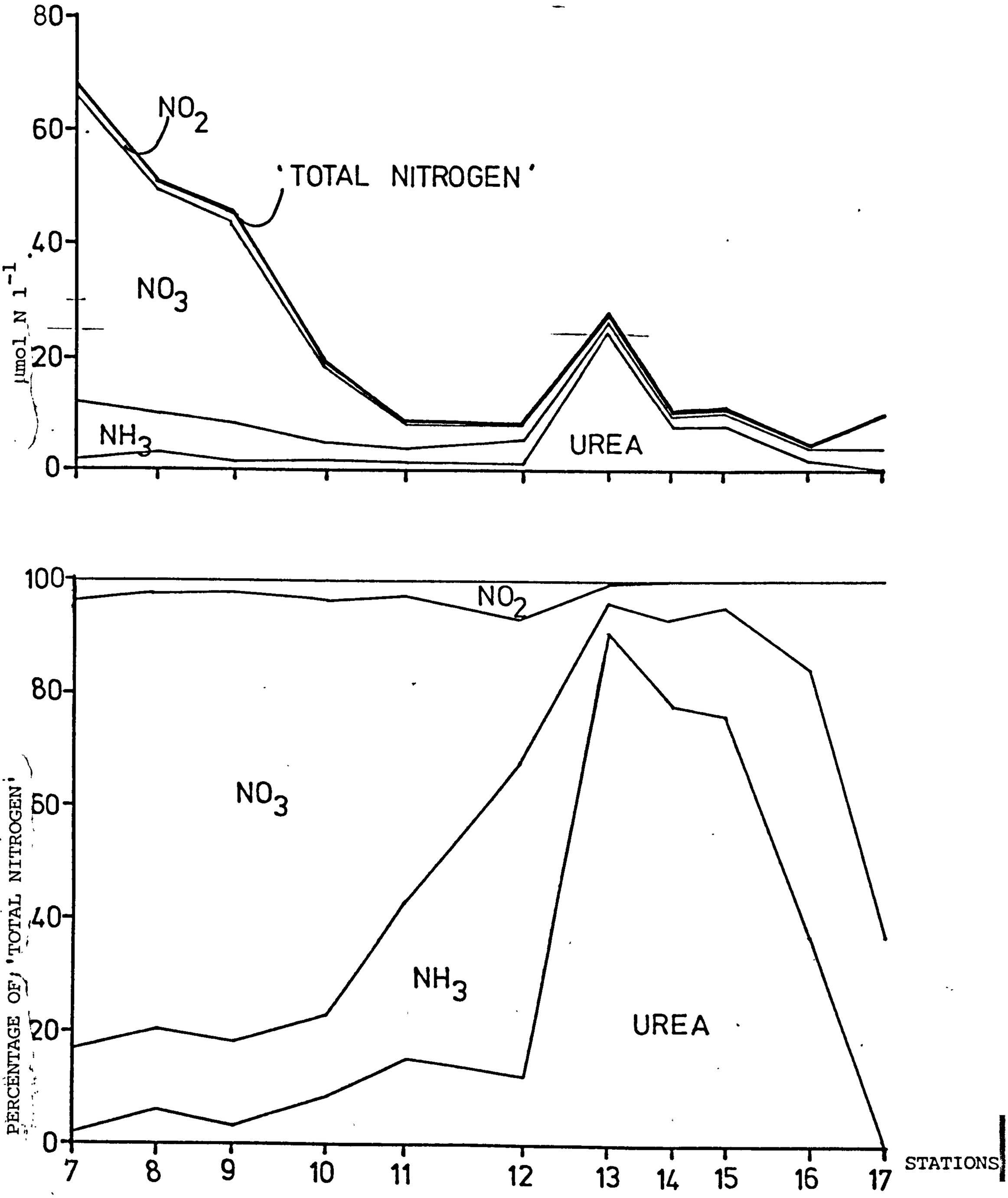


FIGURE : 4.6 : CRUISE HGLI: DISTRIBUTION OF UREA, AMMONIUM, NITRATE and AND NITRITE AS AN ACCUMULATE AND PERCENTAGE OF 'TOTAL NITROGEN'.

values for salinity and sigma t at different depths in the water column are not available so that the degree of stratification at each station cannot be assessed. However, salinity (Fig. 4.4) does not increase at a progressive rate with distance seawards, notably at station 12 which indicate that there is not free mixing and dilution of the inflowing fresh water. The distribution of temperature indicates that there is no temperature stratification from stations 7 -11. However, there are indications of temperature stratification at some of the offshore stations despite temperature data only being available for 10m. and bottom waters. Stations 14 and 15 show no evidence of temperature differences between water at 10m. and bottom water. Stations 12 and f have noticeably higher surface water temperatures than the estuarine water.

4.1.1.2 Nutrient measurements

Distribution of nutrient measurements are presented in Fig. 4.5. Nitrate and nitrite decrease seawards, from high concentrations in the estuary to extremely low concentrations offshore. Ammonium follows a similar distribution but does not decrease by the same proportion as nitrate and nitrite. Conversely, the concentration of urea is low in the estuary, showing no obvious decrease towards the mouth of the estuary as seen for the inorganic nitrogen compounds. Indeed, the highest urea concentrations are found in offshore stations which results in a peak of 'total nitrogen', urea comprising as much as 91% of the 'total nitrogen'. Fig. 4.6 indicates that the inorganic nitrogen compounds, particularly nitrate, are the major source of the 'total nitrogen' at the estuarine and inshore stations whereas urea is generally the major component offshore.

4.1.1.3 Biomass measurements

The results of chlorophyll a and total microbial ATP are presented in figure 4.7. ATP noticeably increases seawards, reaching maxima at stations 16 and 17. Chlorophyll a increases from station 7 to 10 where it reaches a maximum concentration, seawards of

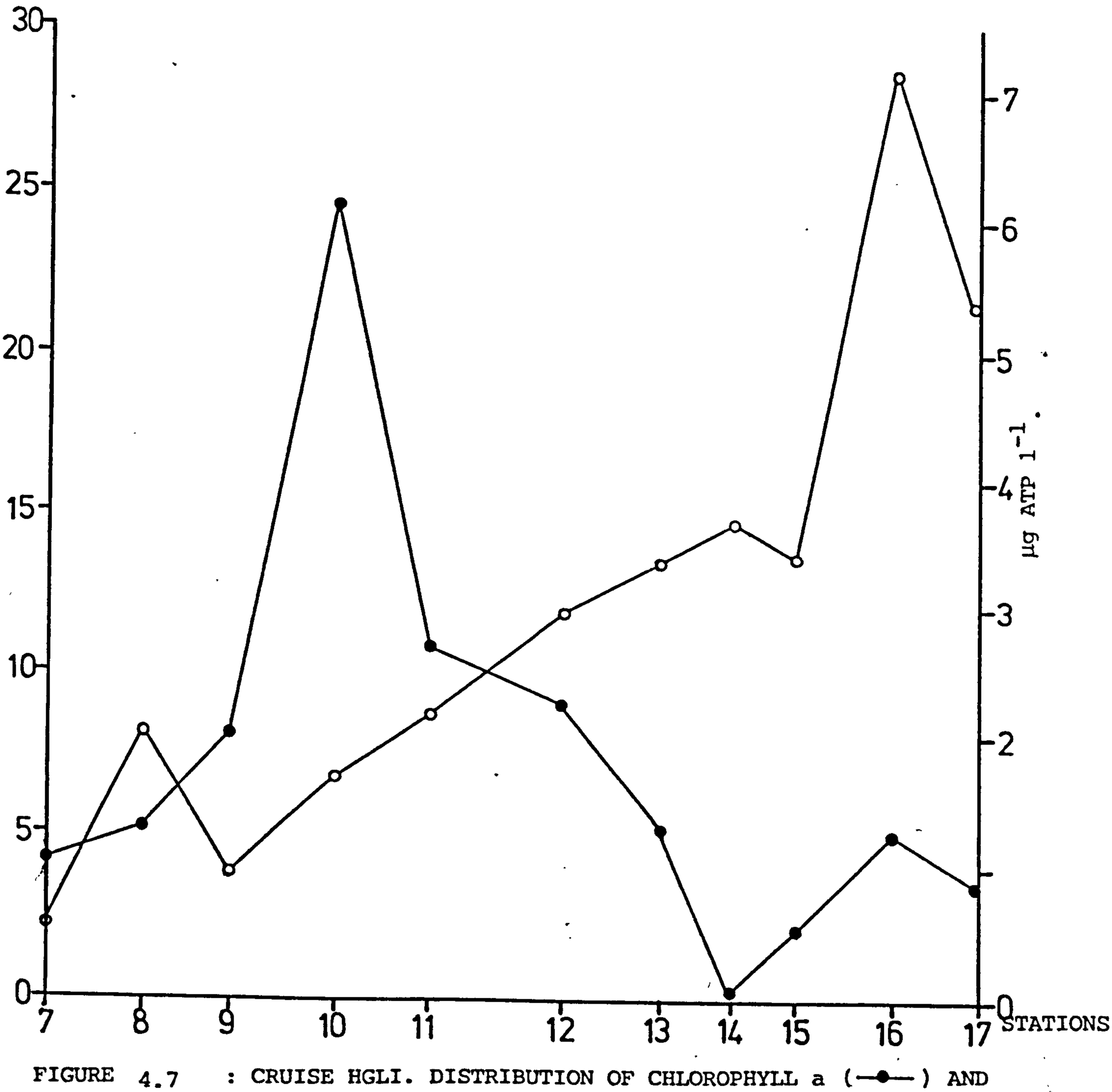


FIGURE 4.7 : CRUISE HGLI. DISTRIBUTION OF CHLOROPHYLL a (—●—) AND TOTAL MICROBIAL ATP (—○—) .

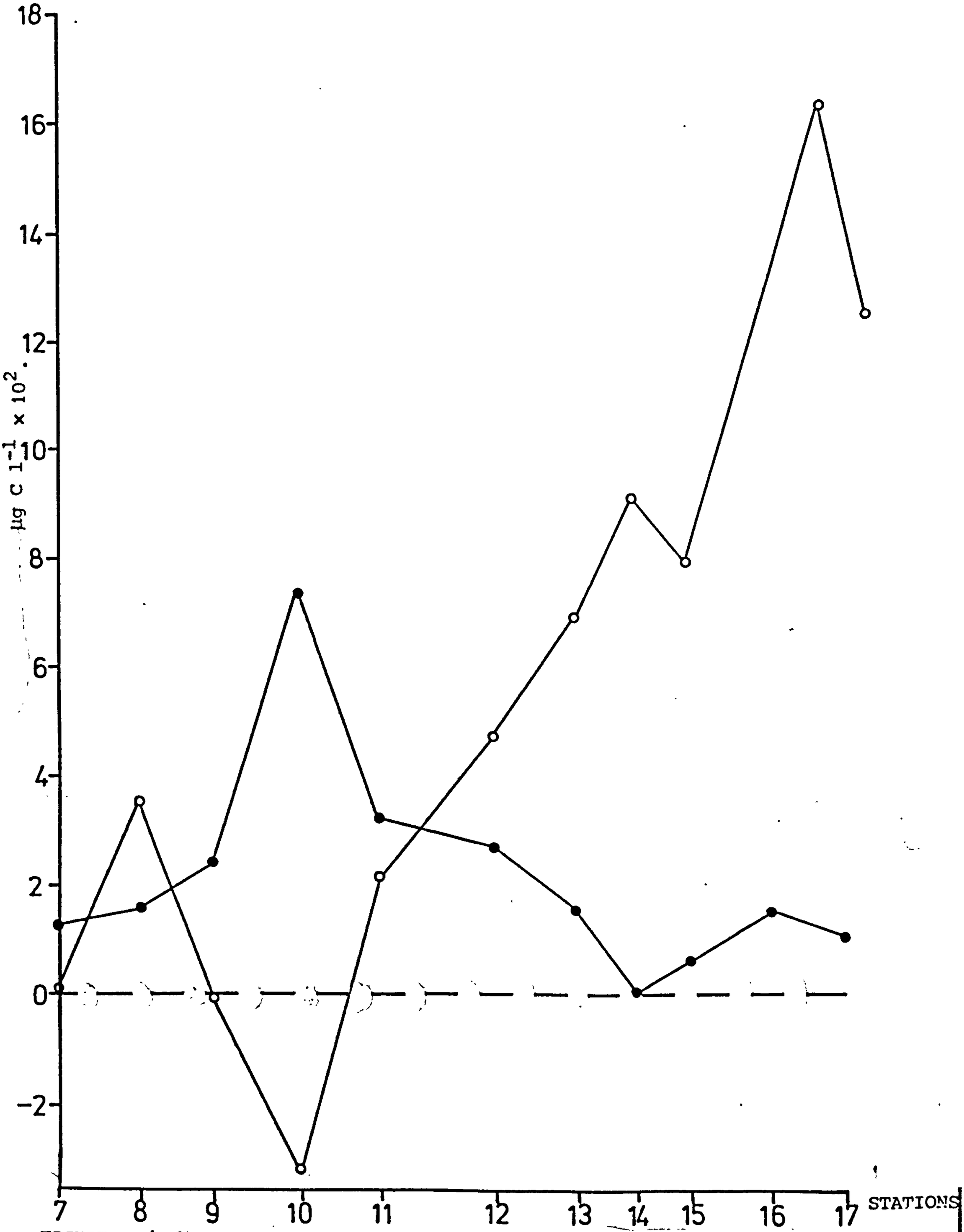


FIGURE 4.8 : CRUISE HGLI. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—○—) CARBON.

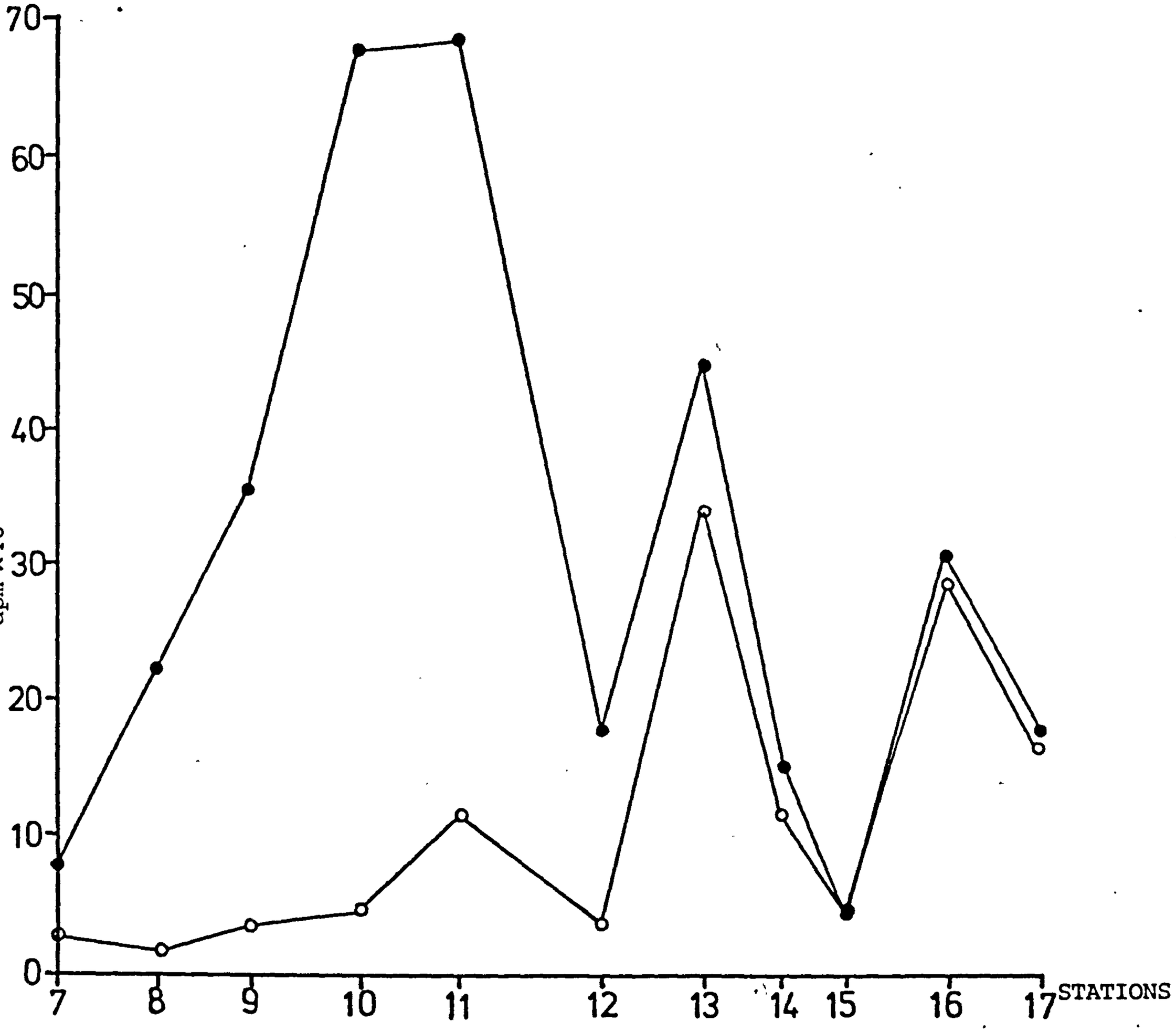


FIGURE 4.9 : CRUISE HGLI. DISTRIBUTION OF UREA UPTAKE IN THE LIGHT (—●—) AND DARK (—○—).

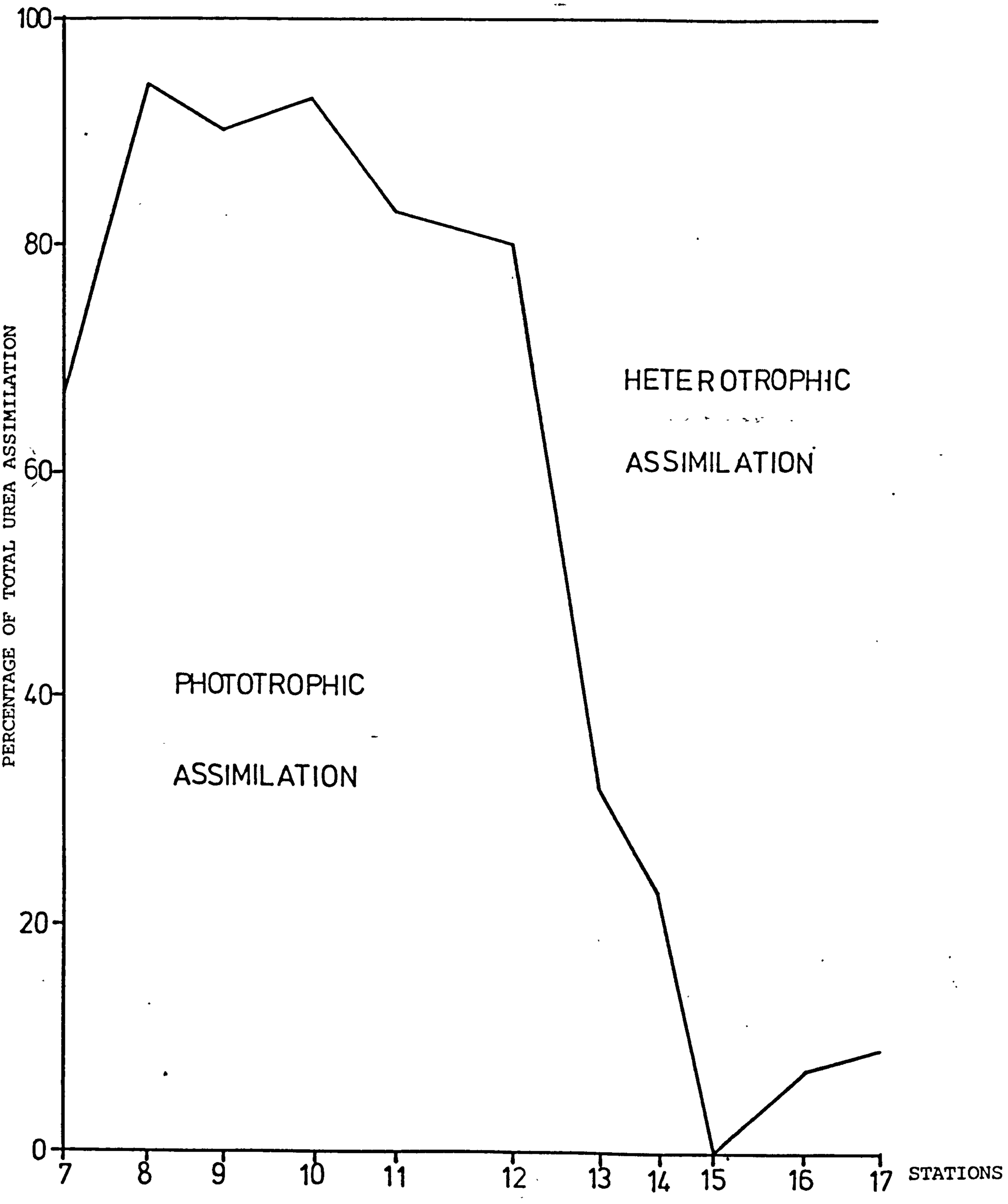


FIGURE 4.10 : CRUISE HGLI. DISTRIBUTION OF PHOTOTROPHIC AND HETEROTROPHIC UREA ASSIMILATION AS A PERCENTAGE OF TOTAL UREA ASSIMILATION.

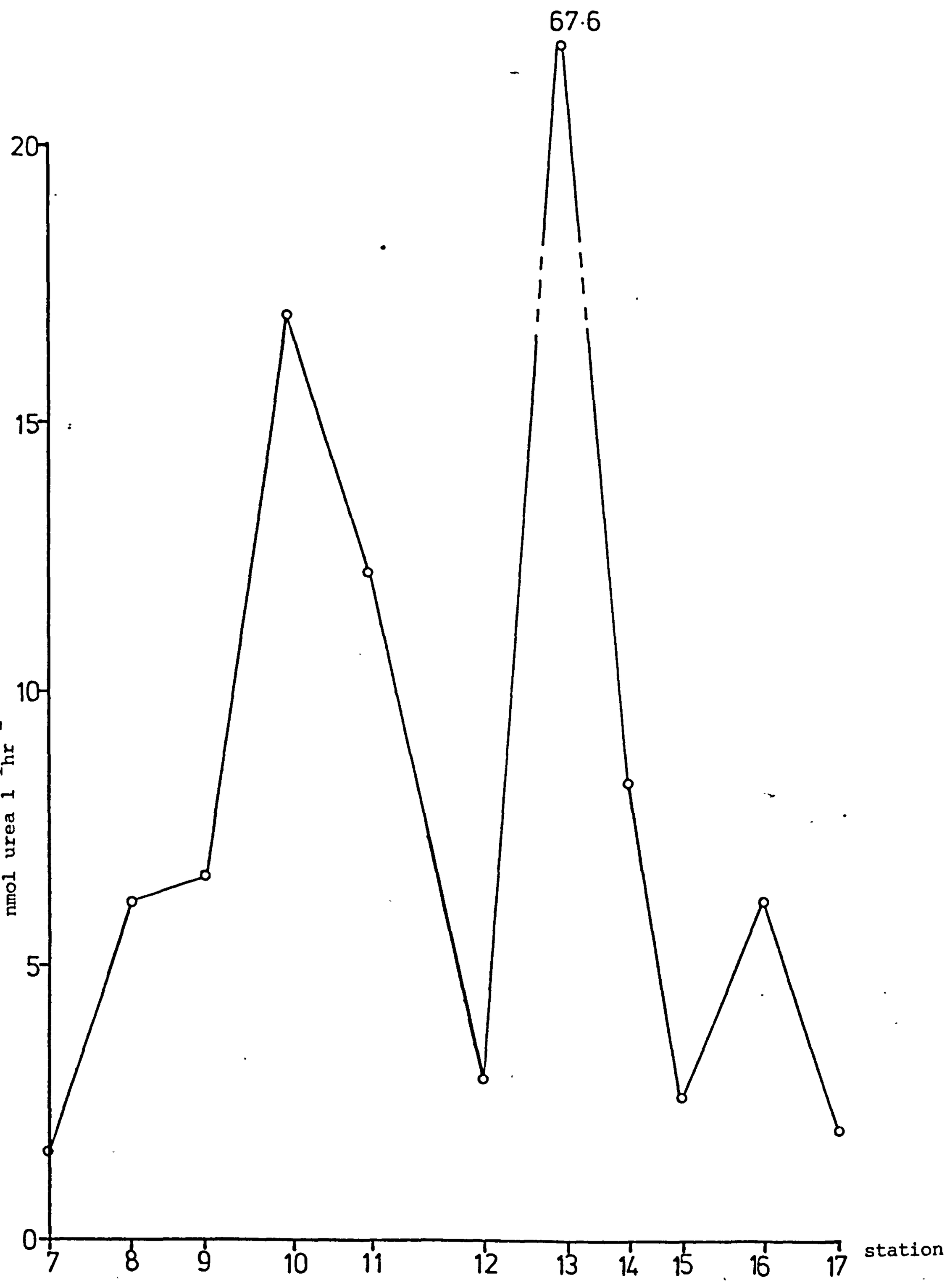


FIGURE 4.11 : CRUISE HGLI. DISTRIBUTION OF TOTAL UREA ASSIMILATION RATES.

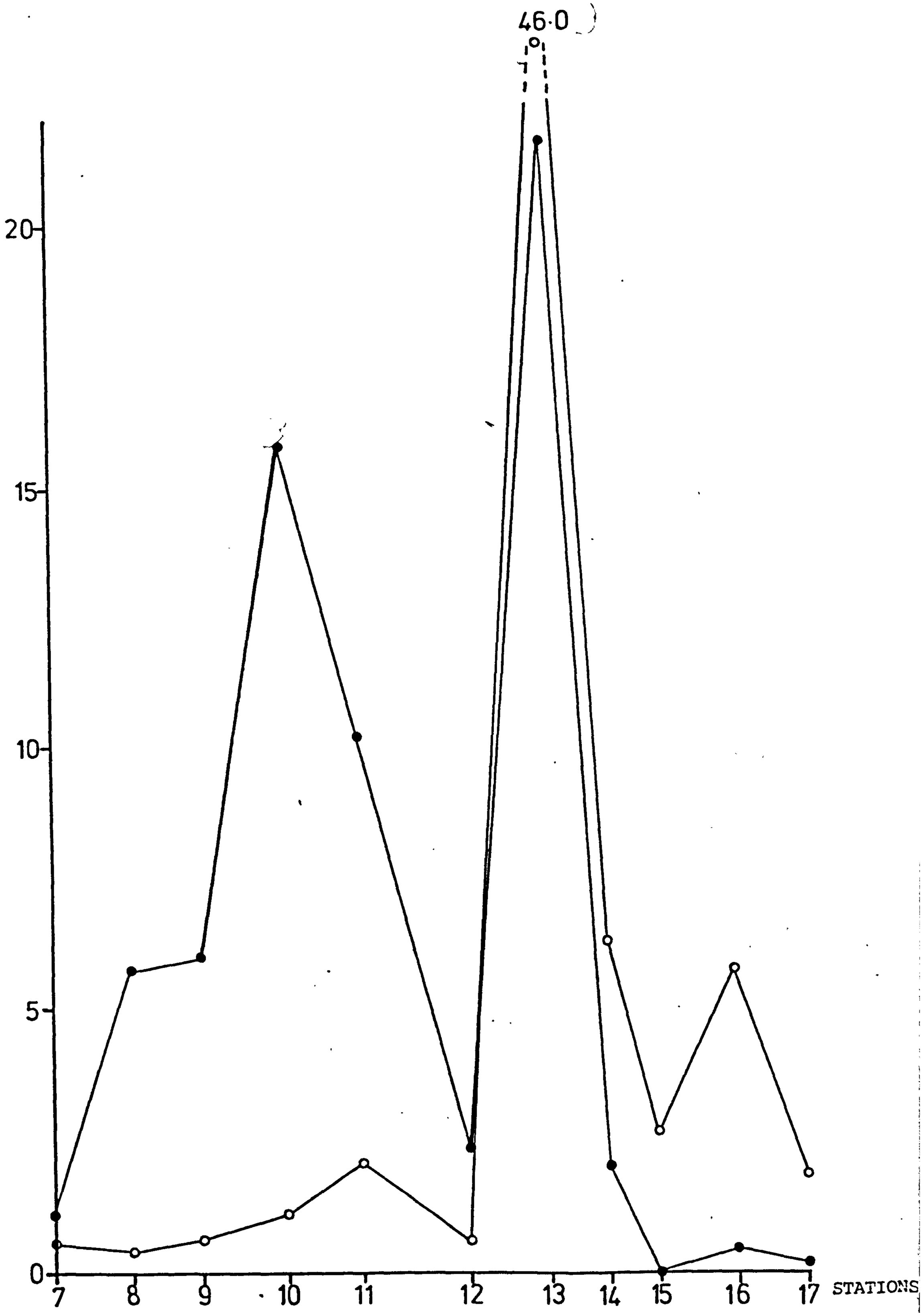


FIGURE 4.12 : DISTRIBUTION OF UREA ASSIMILATION RATES BY PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—○—) MICRORGANISMS.

which there is a general decrease despite the high concentrations of ATP.

Figure 4.8 shows the distribution of 'derived' phototrophic (A) and heterotrophic carbon (C), calculated from chlorophyll a and ATP concentrations as detailed in Section 2.4.4. It is obvious that one or both of the correction factors used in these biomass calculations are unapplicable and this will be discussed in Section 5. However, it is not the absolute values which are important in the present context but rather the distribution trends.

Heterotrophic carbon is highest in the offshore waters (Stations 13 - 17), where phototrophic biomass is relatively low, and reaches a minimum at Station 10 where phototrophic biomass is highest. This indicates that there is a predominantly phototrophic biomass inshore, at Stations 9 and 10, and a predominantly heterotrophic biomass offshore (Stations 13 - 17), while Stations 11 and 12 are intermediate, having similar concentrations of both heterotrophic and phototrophic biomass.

4.1.1.4 Urea assimilation measurements

The uptake (dpm) of ^{14}C-urea in light and dark incubations are given in Figure 4.9 and shows that most of the urea uptake is occurring in the light from stations 7 - 12, and in the dark from stations 13 - 17. Urea uptake increases with distance down the estuary (stations 7 - 10), the highest uptake occurring at stations 10 and 11. Offshore high uptake was found at stations 13 and 16 while minima occurred at stations 12, 14 and 15. Figure 4.10 clearly shows that phototrophic urea uptake predominates inshore while heterotrophic uptake predominates offshore.

Total urea assimilation rates (fig. 4.11) increase from station 7 - 10, where it reaches a maximum, decreases from stations 10 - 12, reaches another maximum at station 13 and thereafter the rates decline. From fig. 4.12 it is evident that the high urea assimilation rates at station 10 are due to phototrophic activity seawards of which, with the exception of station

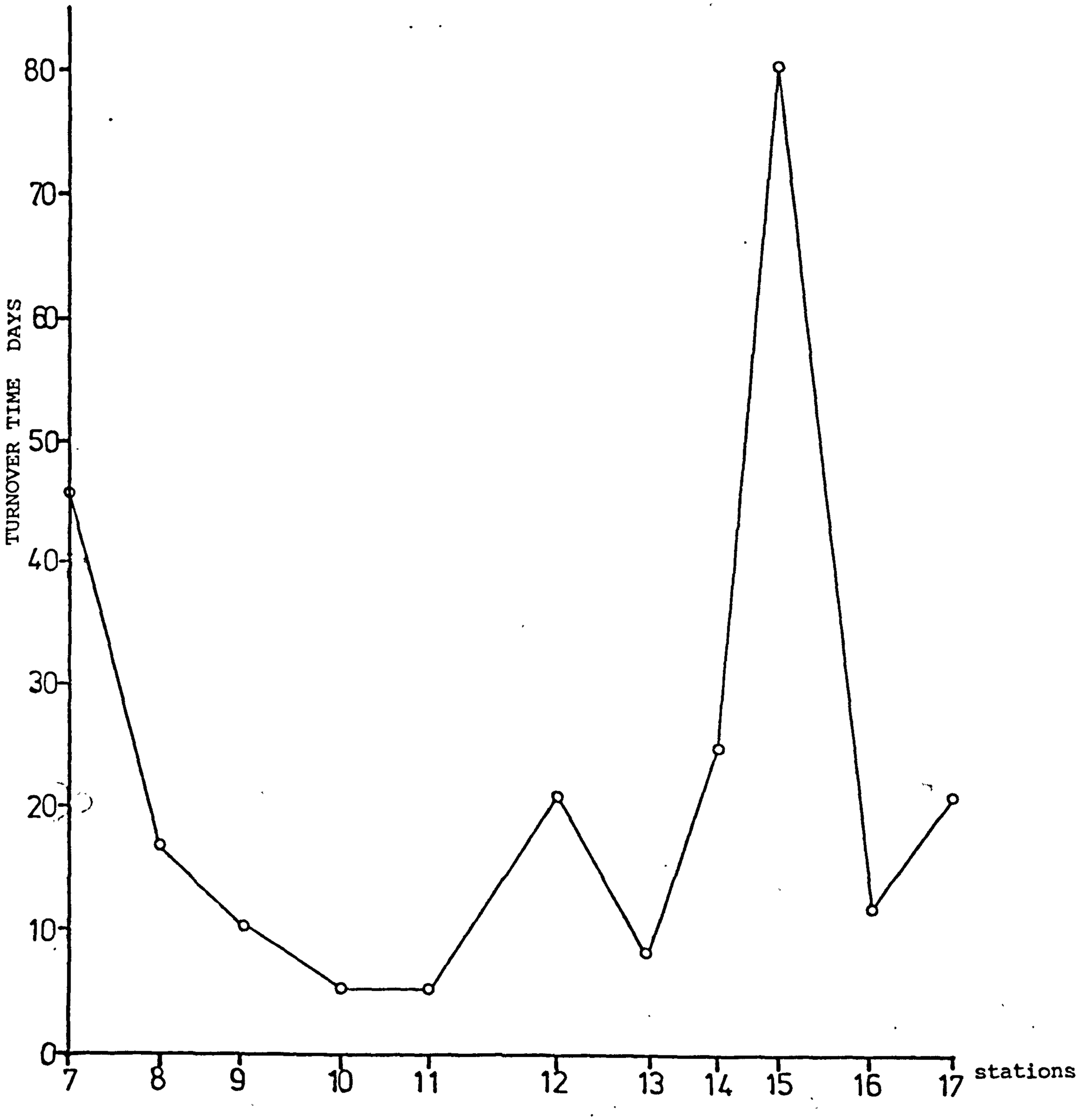


FIGURE 4.13 : CRUISE HGLI·DISTRIBUTION OF TOTAL UREA TURNOVER TIMES.

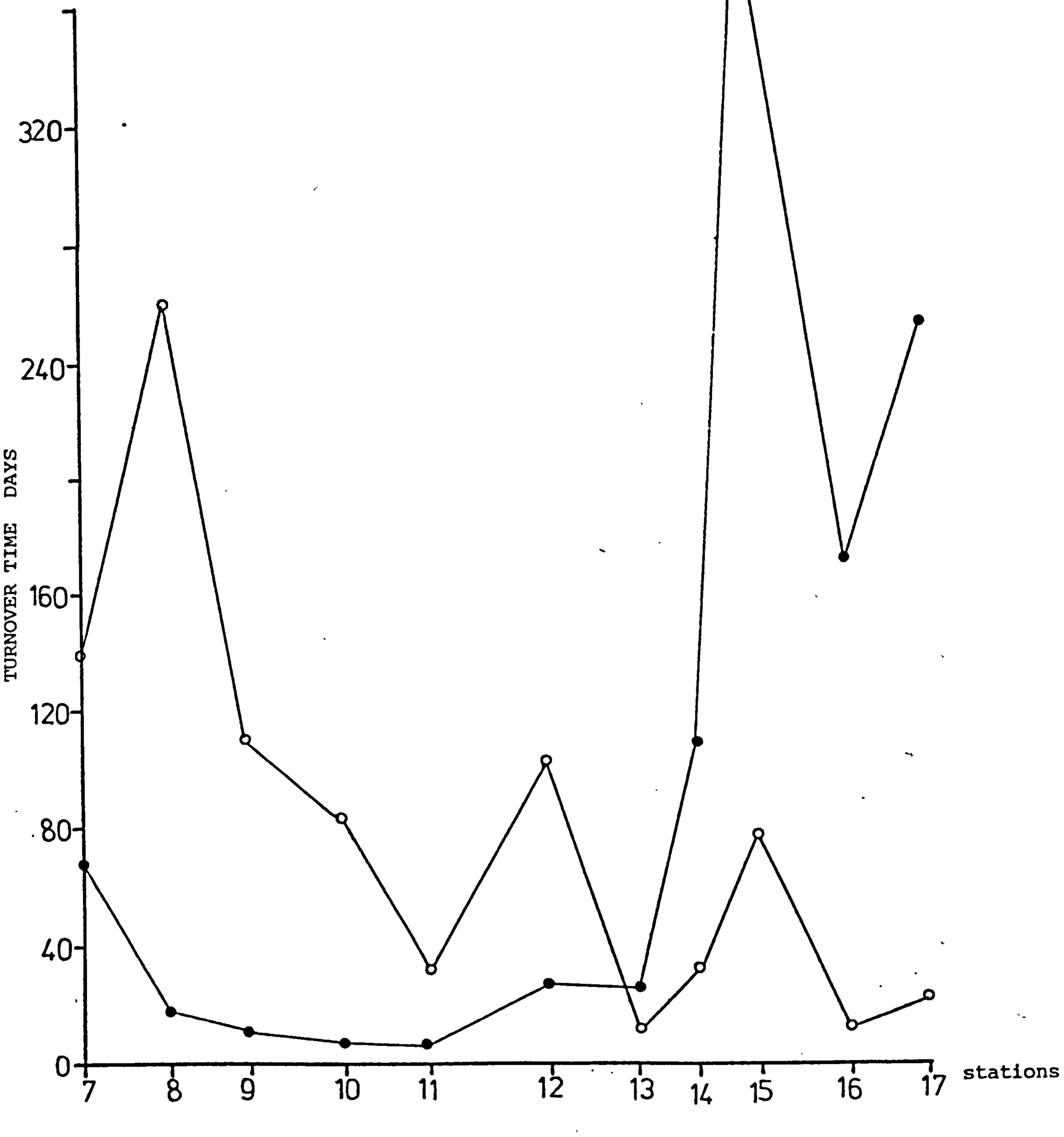


FIGURE 4.14 : CRUISE HGLI. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—o—) UREA TURNOVER TIMES.

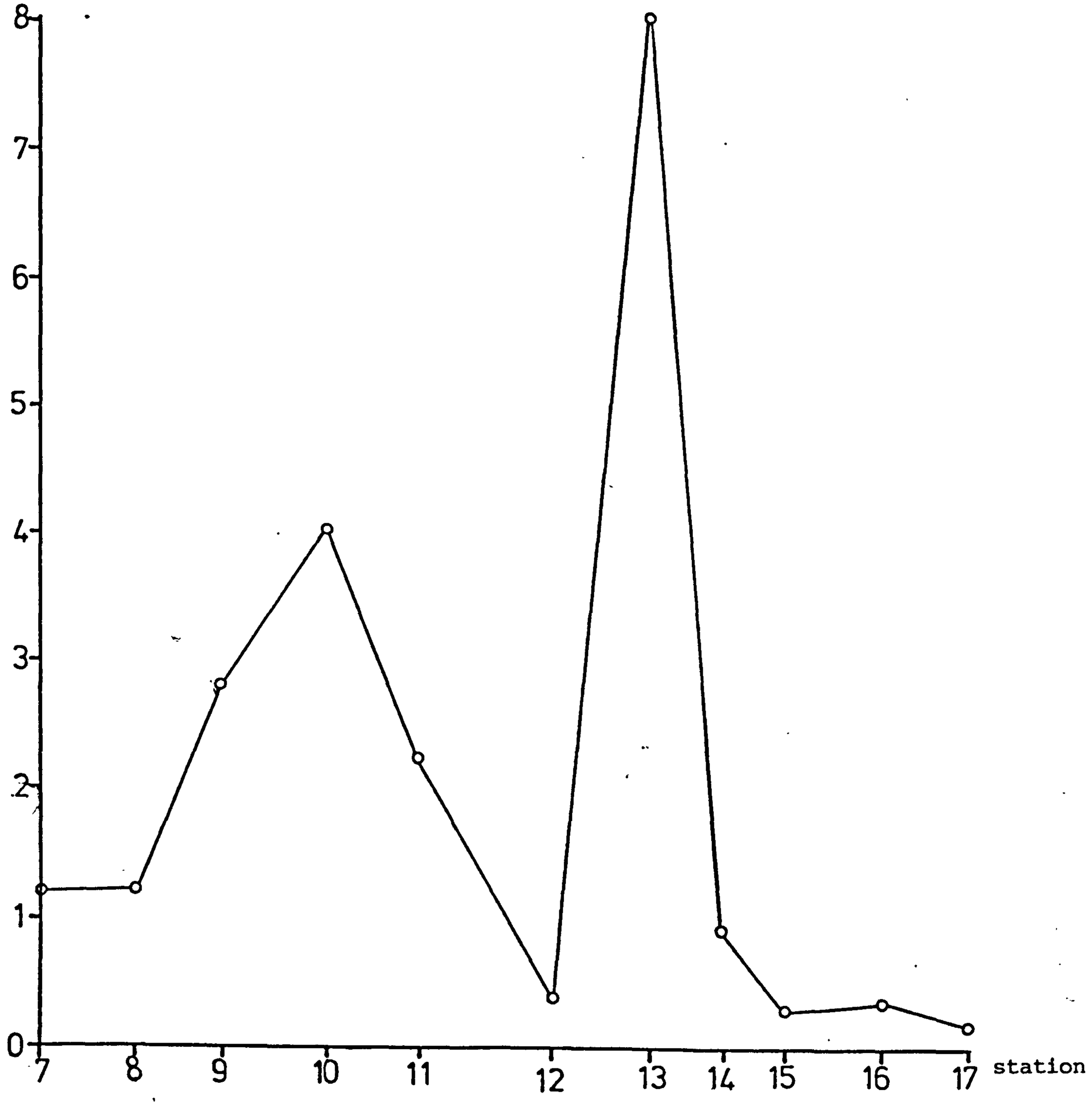


FIGURE 4.15 : CRUISE HLGI. DISTRIBUTION OF TOTAL UREA ASSIMILATION INDICES.

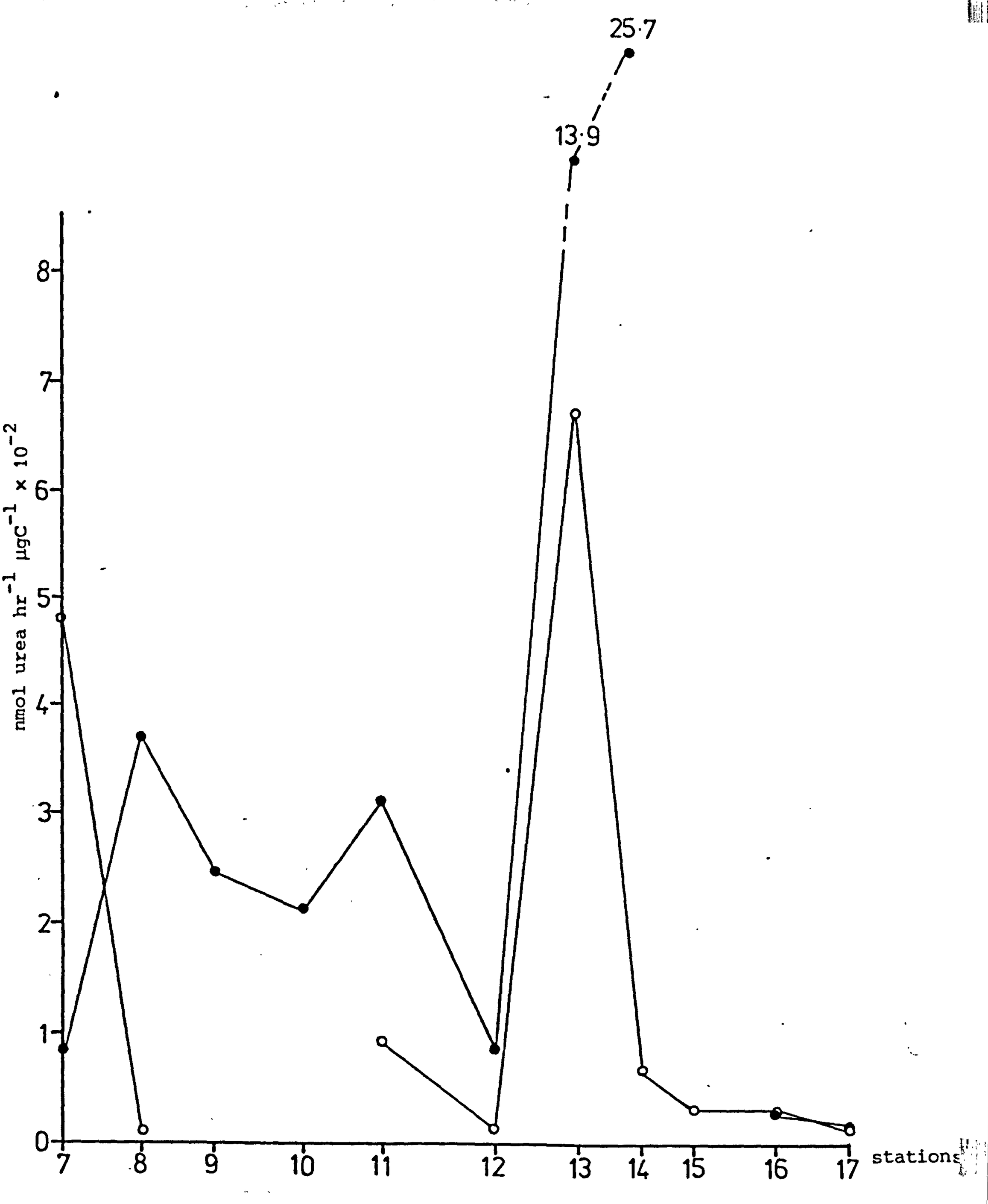


FIGURE 4.16 : CRUISE HGLI. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—o—) UREA ASSIMILATION INDICES.

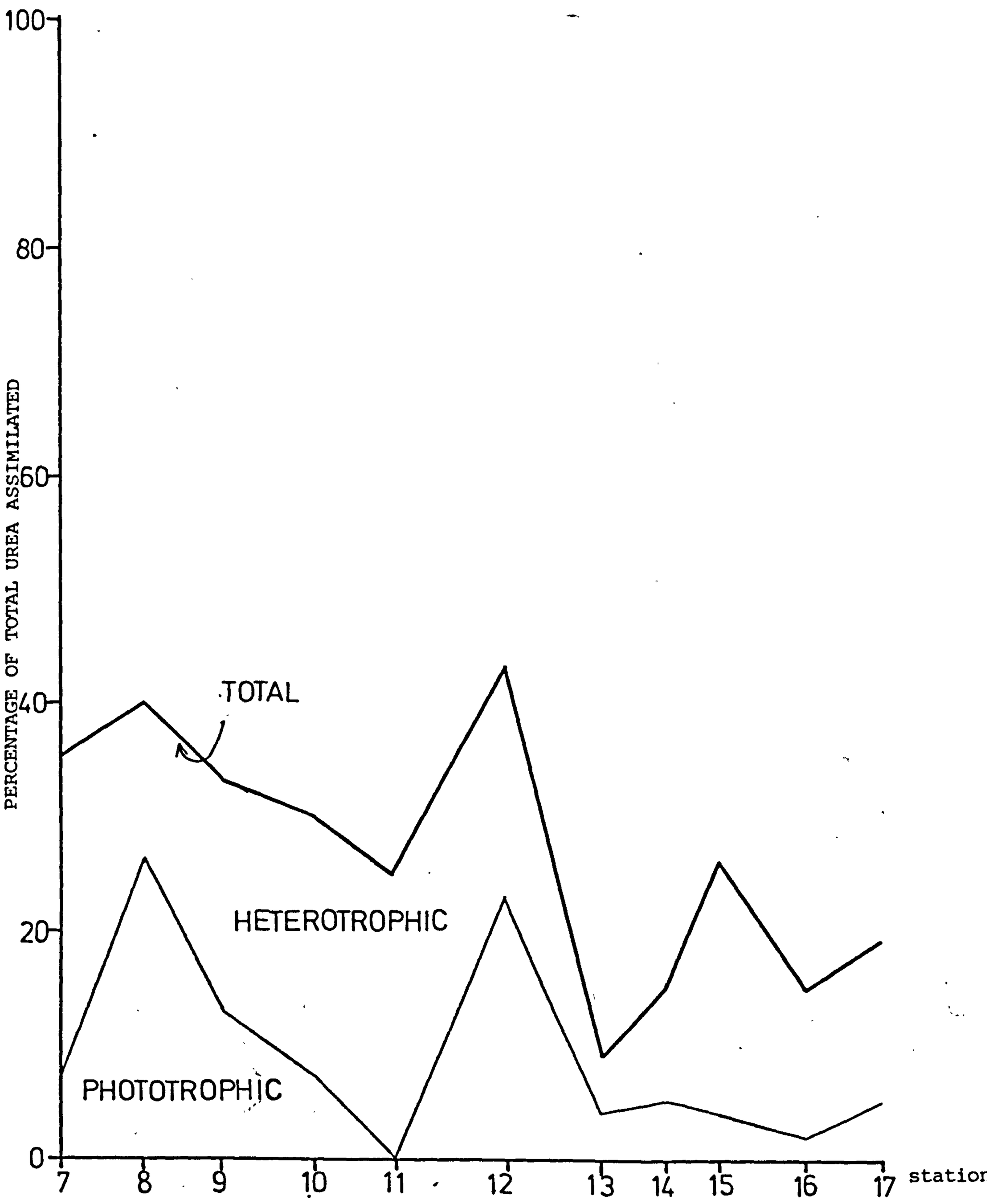


FIGURE 4.17 : CRUISE HGLI. DISTRIBUTION OF ^{14}C-UREA INCORPORATED IN LIVING CELLS (PHOTOTROPHIC AND HETEROTROPHIC) AS A PERCENTAGE OF TOTAL UREA ASSIMILATED.

13 where very high rates occur, the phototrophic urea assimilation rates notably decrease. Conversely, the heterotrophic urea assimilation rates are comparatively higher offshore than those in inshore and estuarine water with an exceptional maxima at station 13. Heterotrophic assimilation rates are faster than phototrophic assimilation rates in offshore waters of stations 13 - 17, whilst the opposite is true for the inshore and estuarine water.

Total urea turnover times decrease from stations 7 - 11 (fig. 4.13) and then show a tendency to increase offshore. The fastest turnover times of urea were measured at stations 9, 10, 11 and 13. Faster phototrophic urea turnover times were recorded in the estuarine and inshore waters whilst the opposite is true for heterotrophic urea turnover times, lower heterotrophic turnover times being recorded in the offshore stations (fig. 4.14).

Total urea assimilation indices (B), that is, urea assimilation rate/Carbon (the latter being derived from ATP) as seen in figure 4.15 are greatest at stations 9, 10, 11 and 13. With the exception of the latter station the total urea assimilation indices are lower in the offshore waters. Phototrophic urea assimilation indices (A) (fig. 4.16), are relatively high at stations 8 and 11 and exceptionally high at stations 13 and 14. Heterotrophic urea assimilation indices (C) are consistently low with the exception of stations 7 and 13,

Figure 4.17 shows the percentage of the ^{14}C urea assimilated which is incorporated in living cells. There is a general decrease from station 7 - 17, and higher proportion of the ^{14}C (either in the form of urea or CO_2) in the cells in the estuarine and inshore water than in the offshore water where the ^{14}C is mainly liberated from the cell in the form of $^{14}CO_2$.

4.1.2 Cruise HGL I (h)

4.1.2.1 Physical measurements

Physical data (table 4.12) is characteristic of that recorded in the offshore waters of stations 12 - 17. Temperatures at different depths indicate

that stations 4, 5 and 6 are mixed while station 3 is temperature stratified. There is not sufficient physical data at stations 1 and 2 to determine whether they are mixed or stratified. In comparison to the other stations in the vicinity of Helgoland station 5 is relatively cold.

4.1.2.2 Nutrient measurements

Urea concentrations (Table 4.13) are relatively high and contribute a major proportion of the 'total nitrogen' (32 - 62%). The concentration of the inorganic nitrogen compounds are low and similar to those found at stations 12 - 17.

4.1.2.3 Biomass measurements

Chlorophyll a (table 4.14) is higher than the offshore stations (14 - 17) but has similar concentrations to those measured at stations 11 - 13. Similarly, total microbial ATP and heterotrophic carbon (C) (table 4.15) have concentrations characteristic of those determined at stations 11 and 12.

4.1.2.4 Urea assimilation measurements

Phototrophic assimilation rates (table 4.18) are consistently higher than heterotrophic assimilation rates as was the case at station 12. Total and phototrophic assimilation rates are also similar to those found at station 12. With the exception of station 1 urea assimilation indices (table 4.20) are consistent with those determined at station 12. Urea turnover times are generally higher than those found in the offshore waters (table 4.19).

4.1.3 Cruise HGL II

4.1.3.1 Physical measurements

Salinity and density (fig. 4.18) indicate estuarine conditions at stations 7 - 10, the river water influence decreasing down the estuary. Salinity and density at different depths in the water column indicate that stations 7 - 11 are well mixed while station 12 is stratified. Since salinity data is not available at different depths for the offshore stations, surface to bottom density differences cannot be

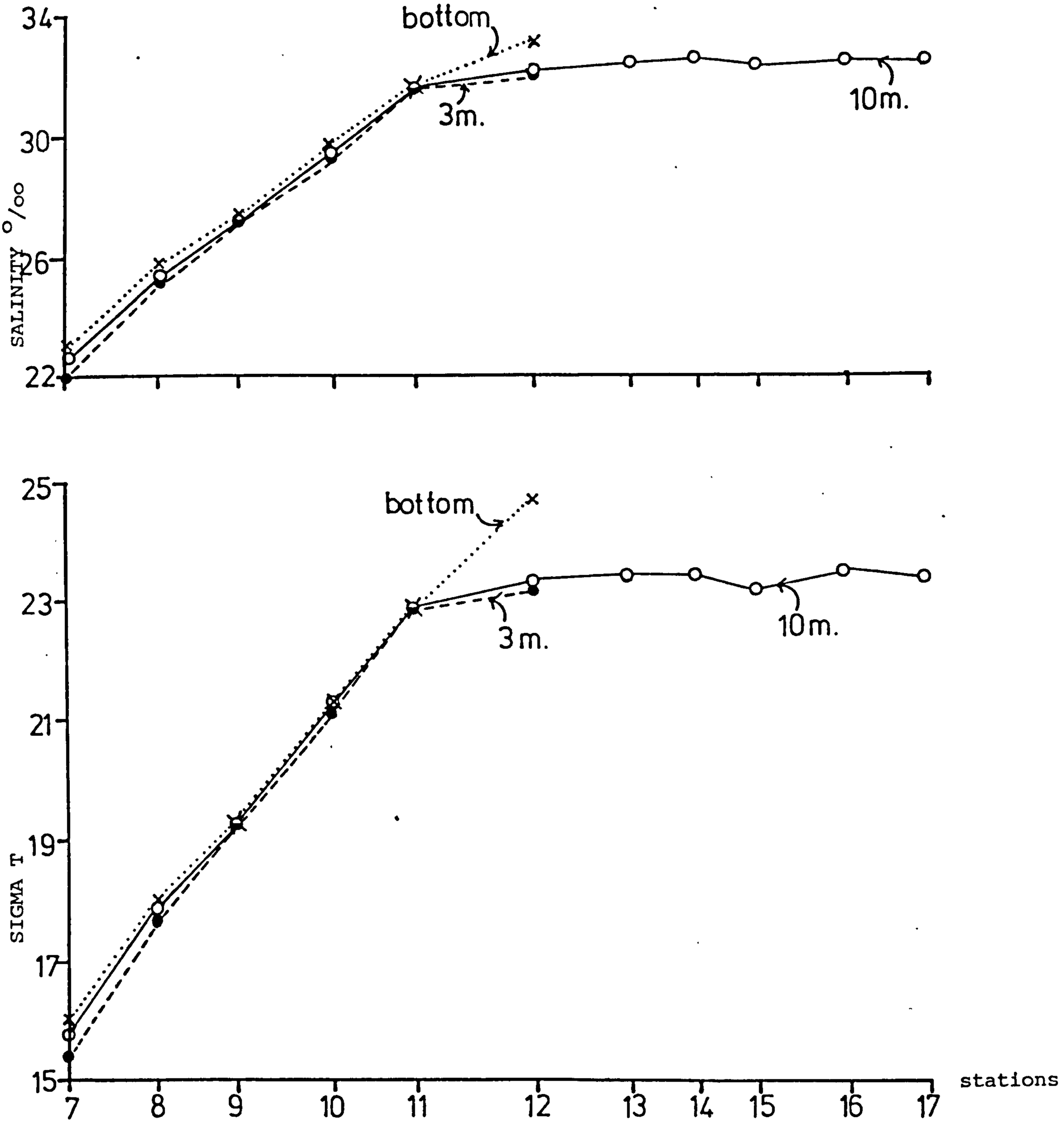


FIGURE 4.18 : CRUISE HGLII. DISTRIBUTION OF PHYSICAL MEASUREMENTS OF SALINITY AND SIGMA T.

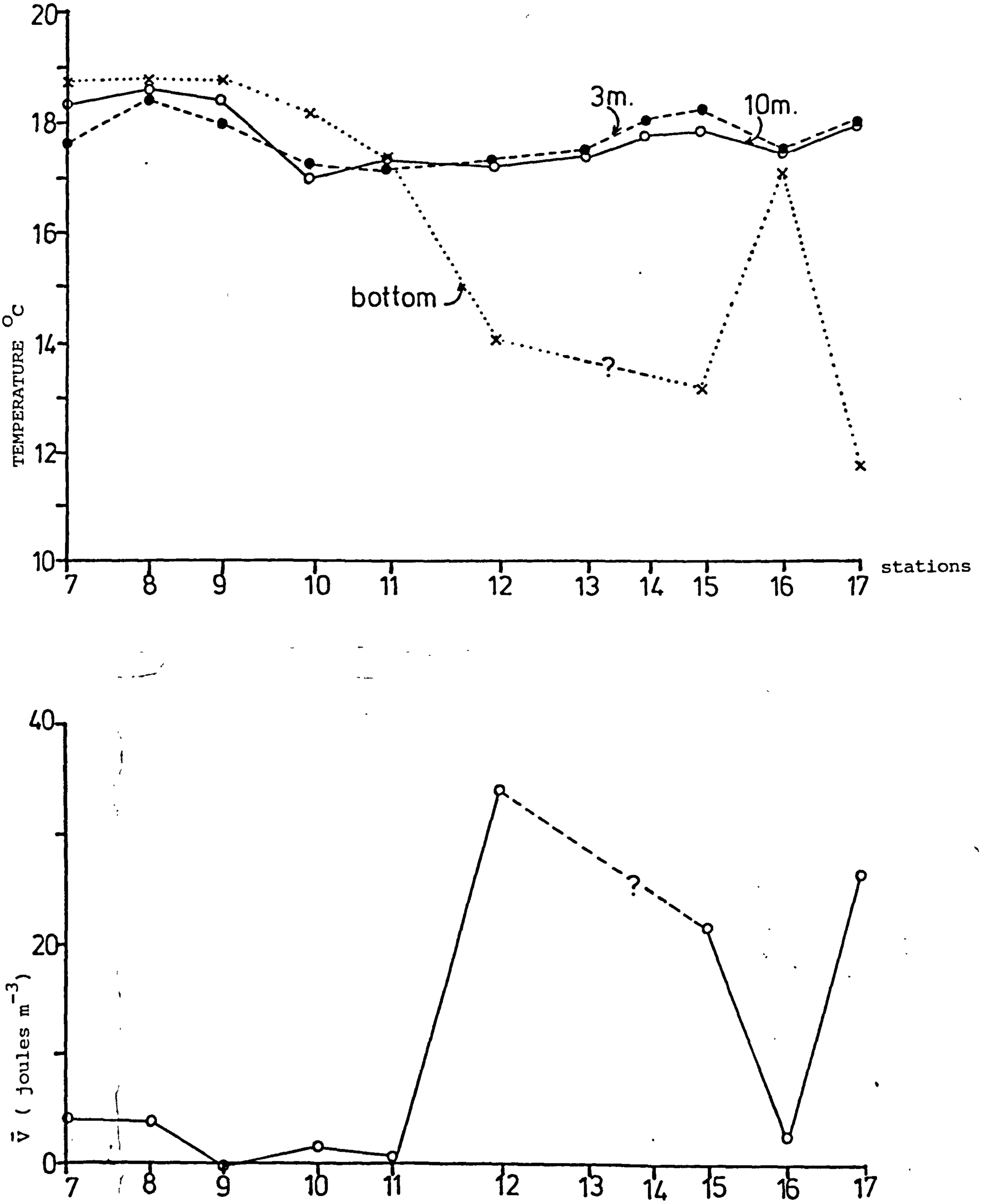


FIGURE 4.19 a : CRUISE HGL II. DISTRIBUTION OF TEMPERATURE AND V

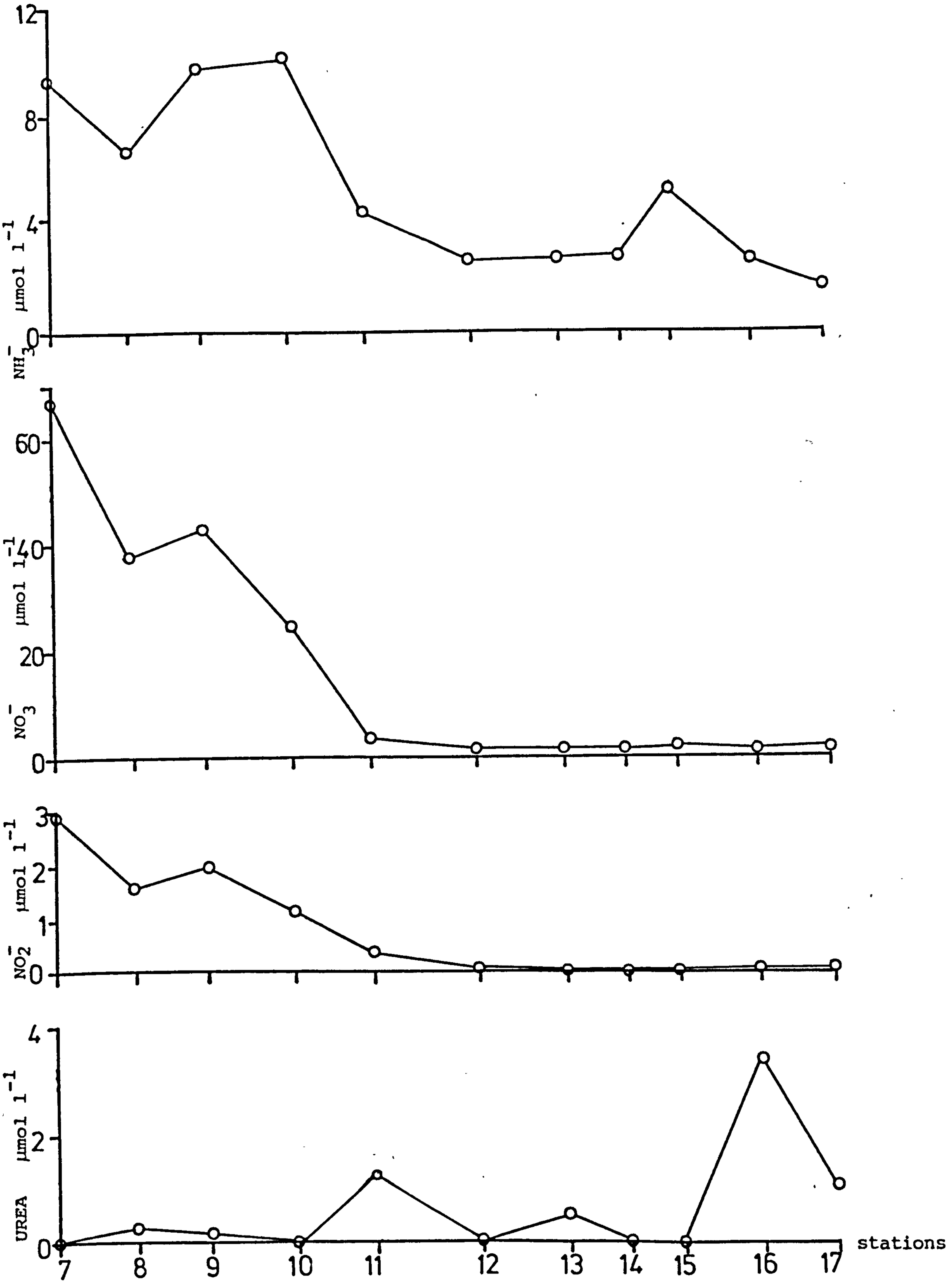


FIGURE 4.19b : CRUISE HGLII. DISTRIBUTION OF AMMONIUM, NITRATE, NITRITE AND UREA.

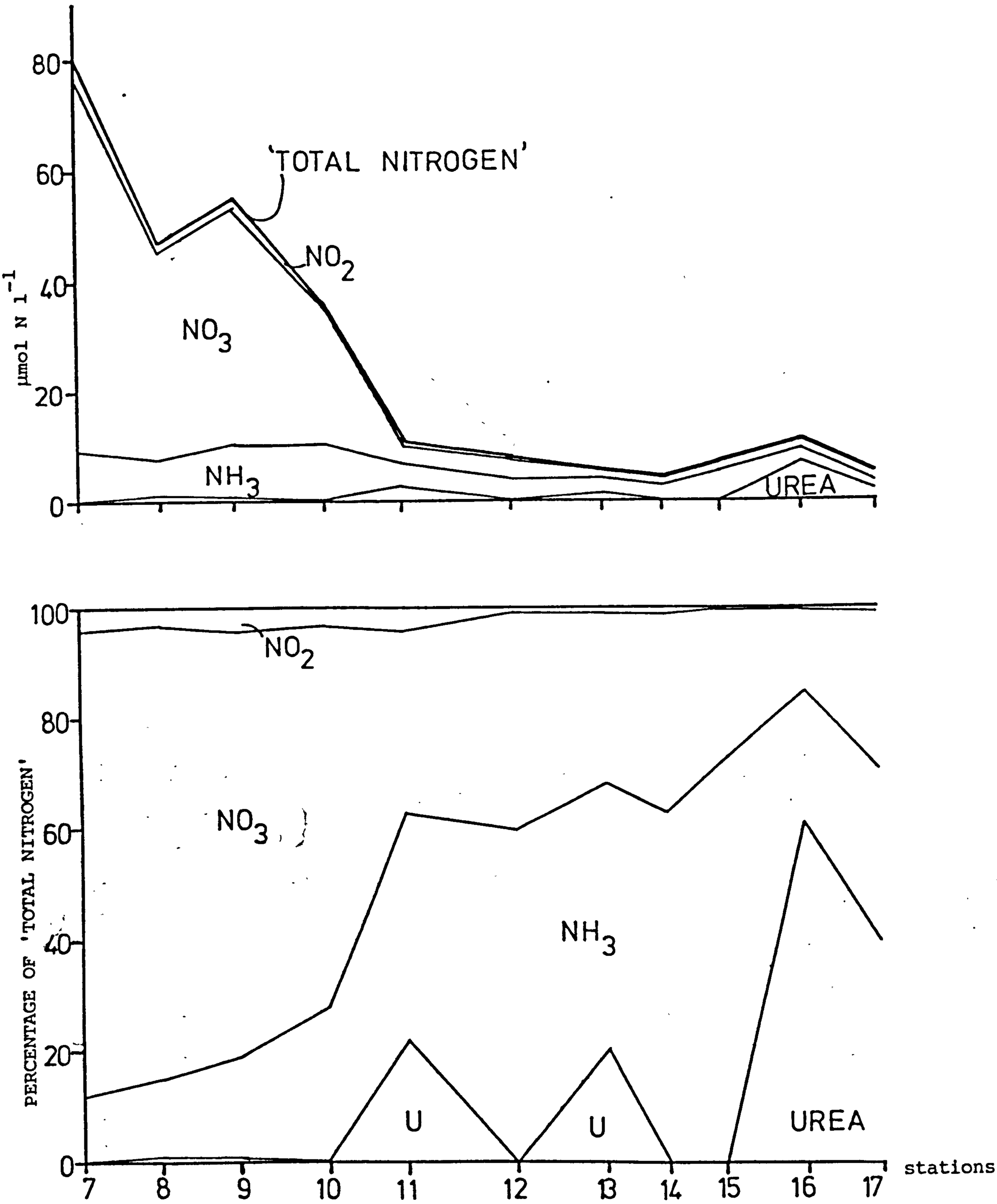


FIGURE 4.20: CRUISE HGLII. DISTRIBUTION OF UREA, AMMONIUM, NITRATE AND NITRITE AS AN ACCUMULATE AND PERCENTAGE OF 'TOTAL NITROGEN'.

calculated and degree of stratification accessed. However, large surface to bottom temperature differences (fig. 4.19) indicate that there is strong thermal stratification, regardless of any salinity stratification, in a number of the offshore stations.

$\bar{V}$ (fig. 4.19a), a stratification parameter (Simpson et.al. 1977), verifies that stations 7 - 11, 16 are well mixed (< 10 joules m^{-3}) while stations 12, 15 and 17 are strongly stratified (>10 joules m^{-3}). Faulty thermometers did not enable temperatures to be recorded in the bottom waters of stations 13 and 14 and hence the degree of stratification cannot be determined.

4.1.3.2 Nutrient measurements

Results for nutrient measurements are given in figures 4.19 and 4.20. Nitrate and nitrite (fig. 4.19b) decrease from high concentrations in the estuarine stations to very low concentrations in the offshore stations. Ammonium concentrations are higher in the estuarine station, generally decreasing with distance offshore but not to the same extent as nitrate and nitrite.

Urea concentrations are low or below the level of detection at stations 7 - 10 whereas higher concentrations are found in offshore waters, although the distribution is somewhat patchy in comparison to the inorganic nitrogen compounds.

The concentration of 'total nitrogen' (fig. 4.20) is high at stations 7 - 10, low at stations 11 - 17. Nitrate is the predominant nitrogen source at stations 7 - 10 (fig. 4.20); nitrate and ammonium have similar concentrations at station 11, and with the exception of stations 16 and 17, where urea predominates, ammonium comprises the highest proportion of 'total nitrogen'.

4.1.3.3 Biomass measurements

Results are presented in figures 4.21 and 4.22. Chlorophyll a (fig. 4.21) increases down the estuary reaching a maximum at station 11, seawards of which relatively low concentrations were measured. Total microbial ATP also increases with distance down the

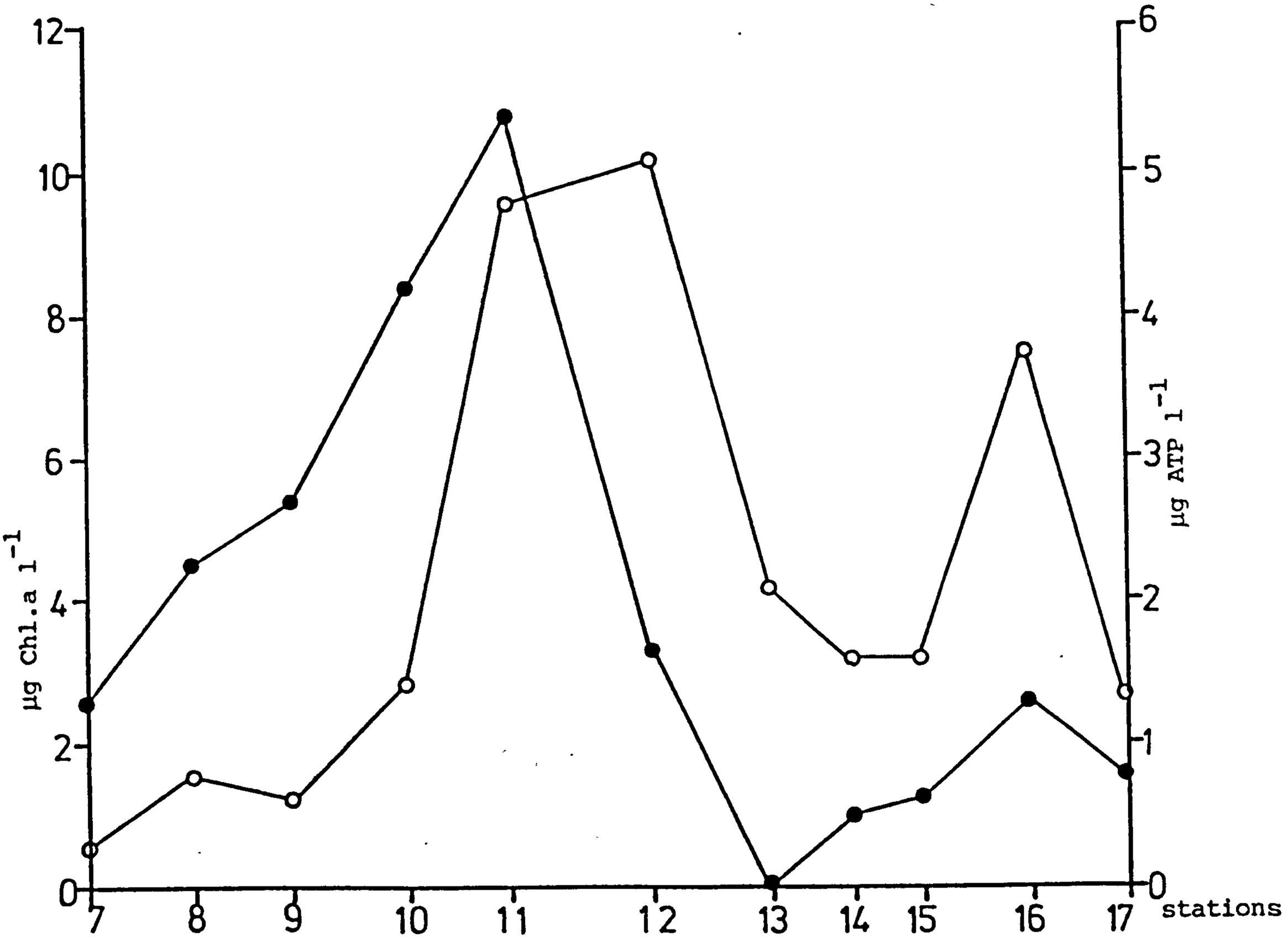


FIGURE 4.21 : CRUISE HGLII. DISTRIBUTION OF CHLOROPHYLL a (—●—) AND TOTAL MICROBIAL ATP (—○—).

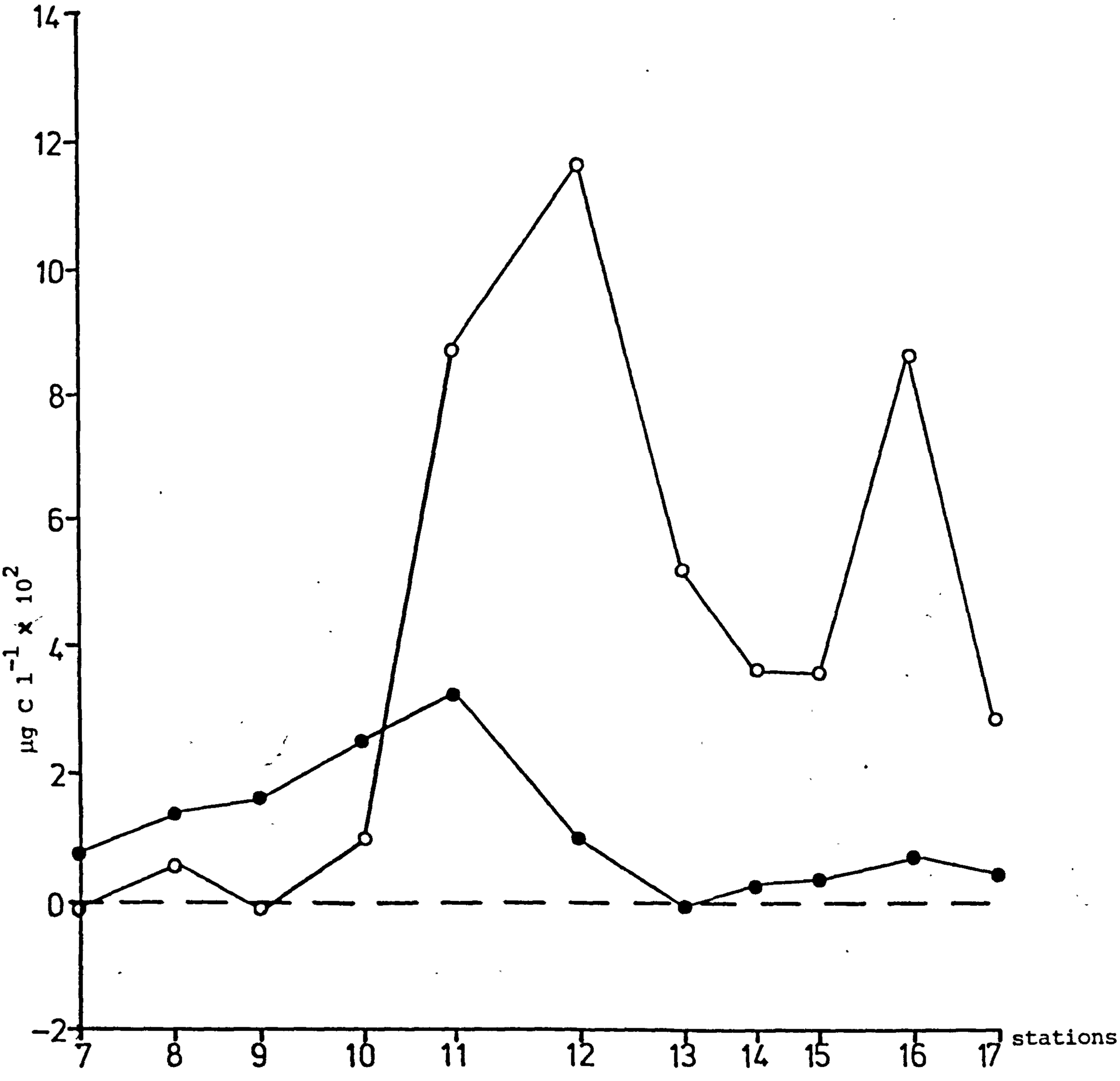


FIGURE 4.22 : CRUISE HGLII. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—o—) CARBON.

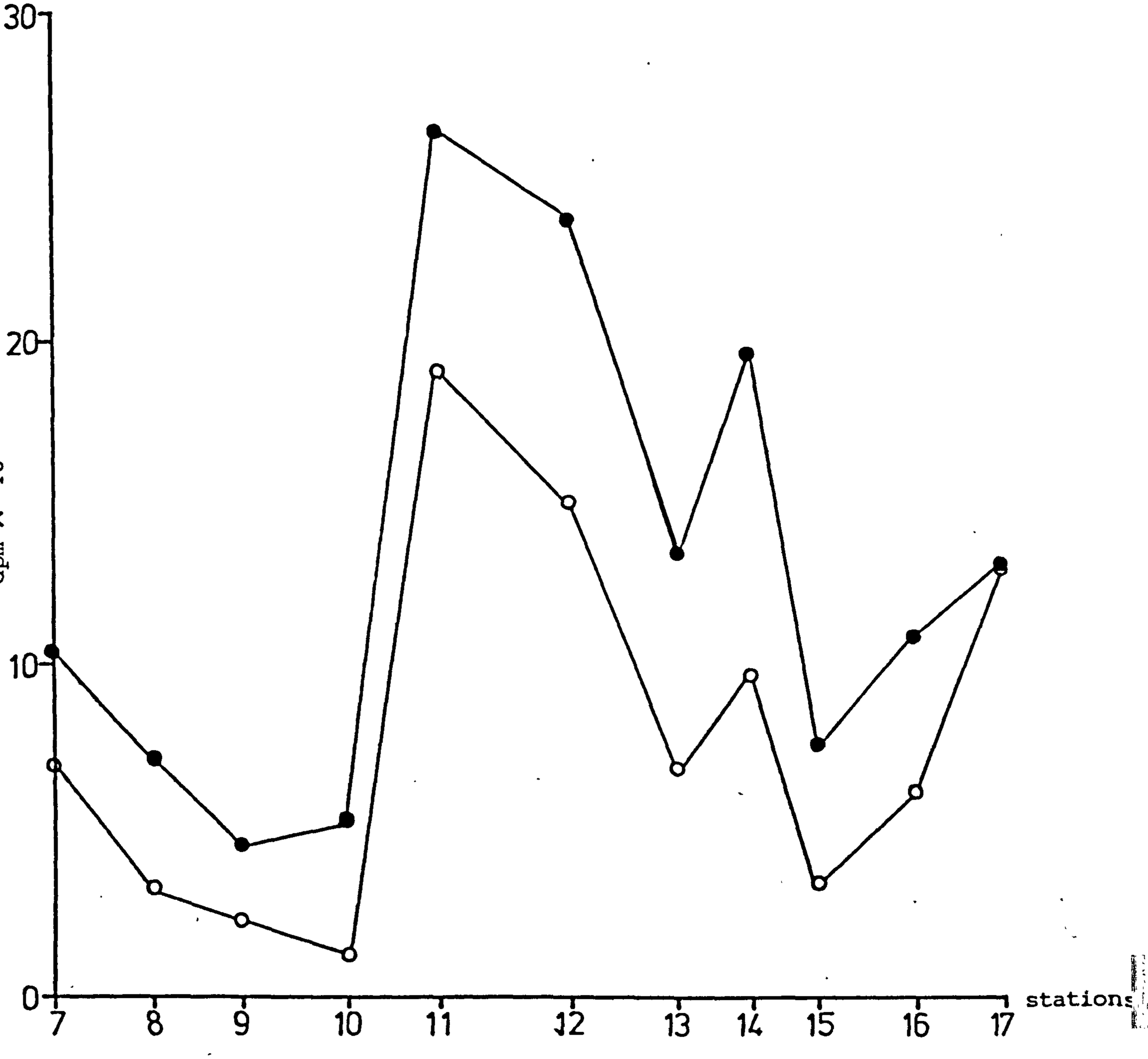


FIGURE 4.23 : CRUISE HGLII. DISTRIBUTION OF UREA UPTAKE IN THE LIGHT (—●—) AND DARK (—○—).

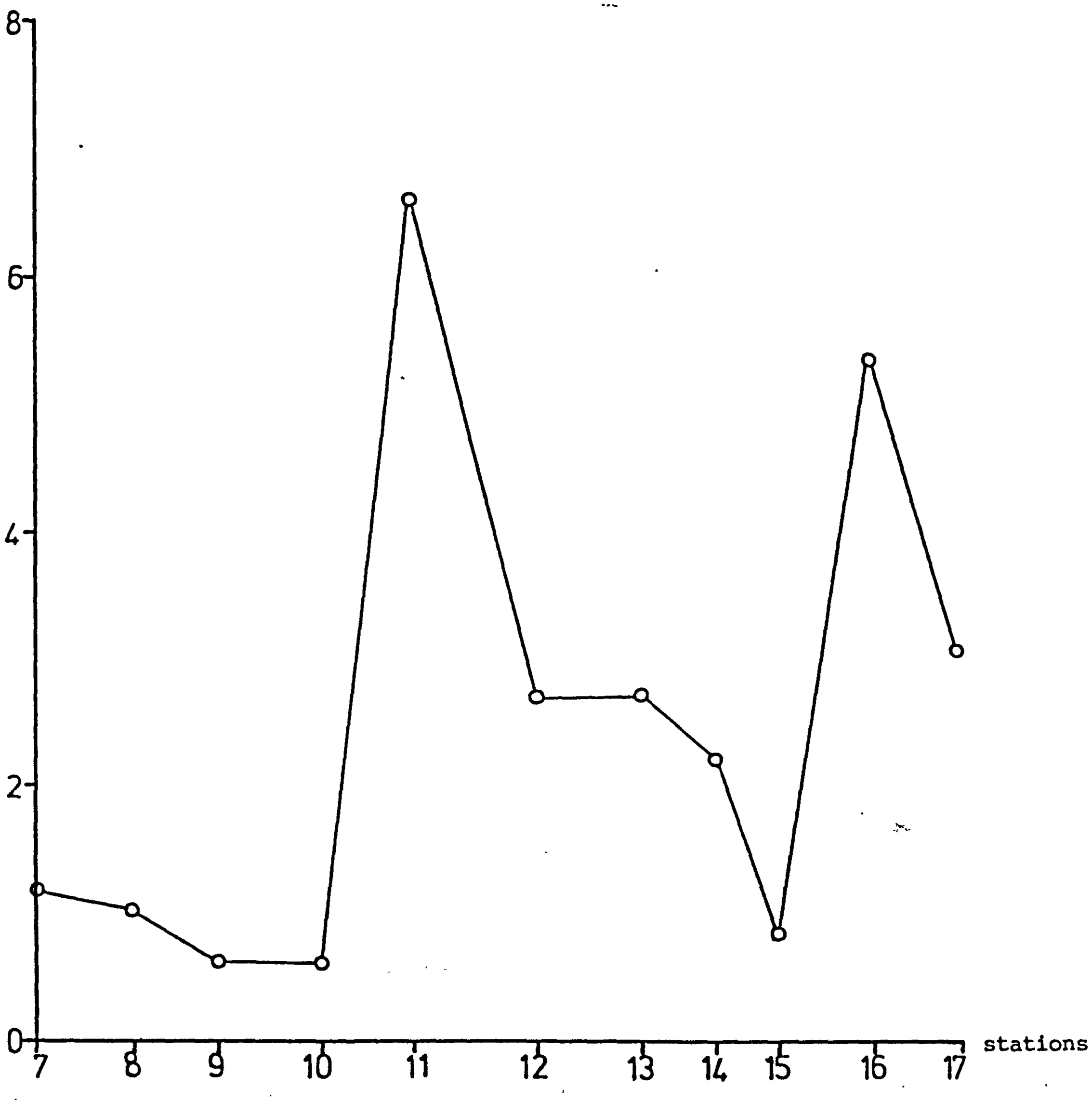


FIGURE 4.24 : CRUISE HGLII. DISTRIBUTION OF TOTAL UREA ASSIMILATION RATES.

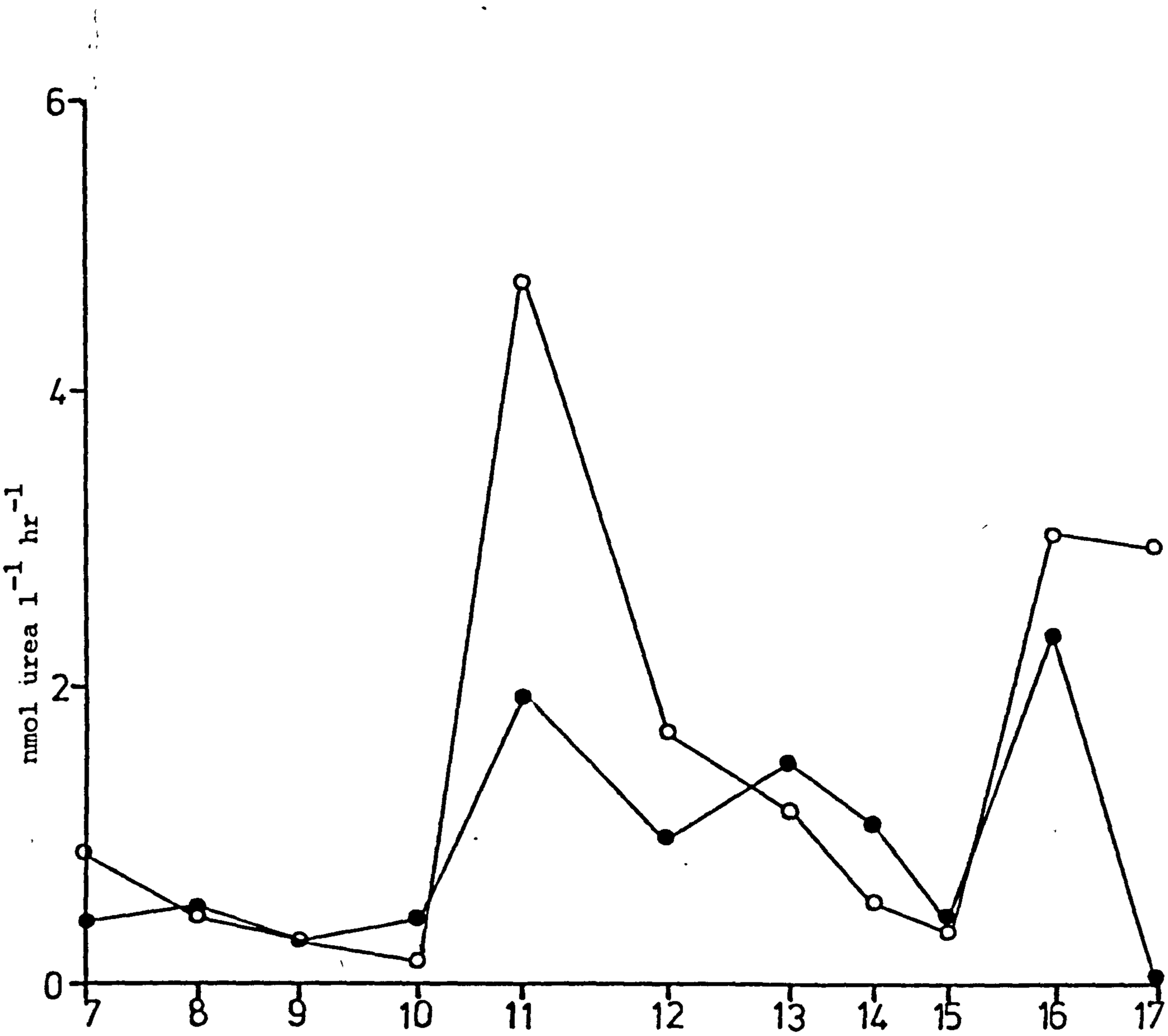


FIGURE 4.2 5 : CRUISE HGLII. DISTRIBUTION OF UREA ASSIMILATION RATES BY PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—o—) MICRORGANISMS.

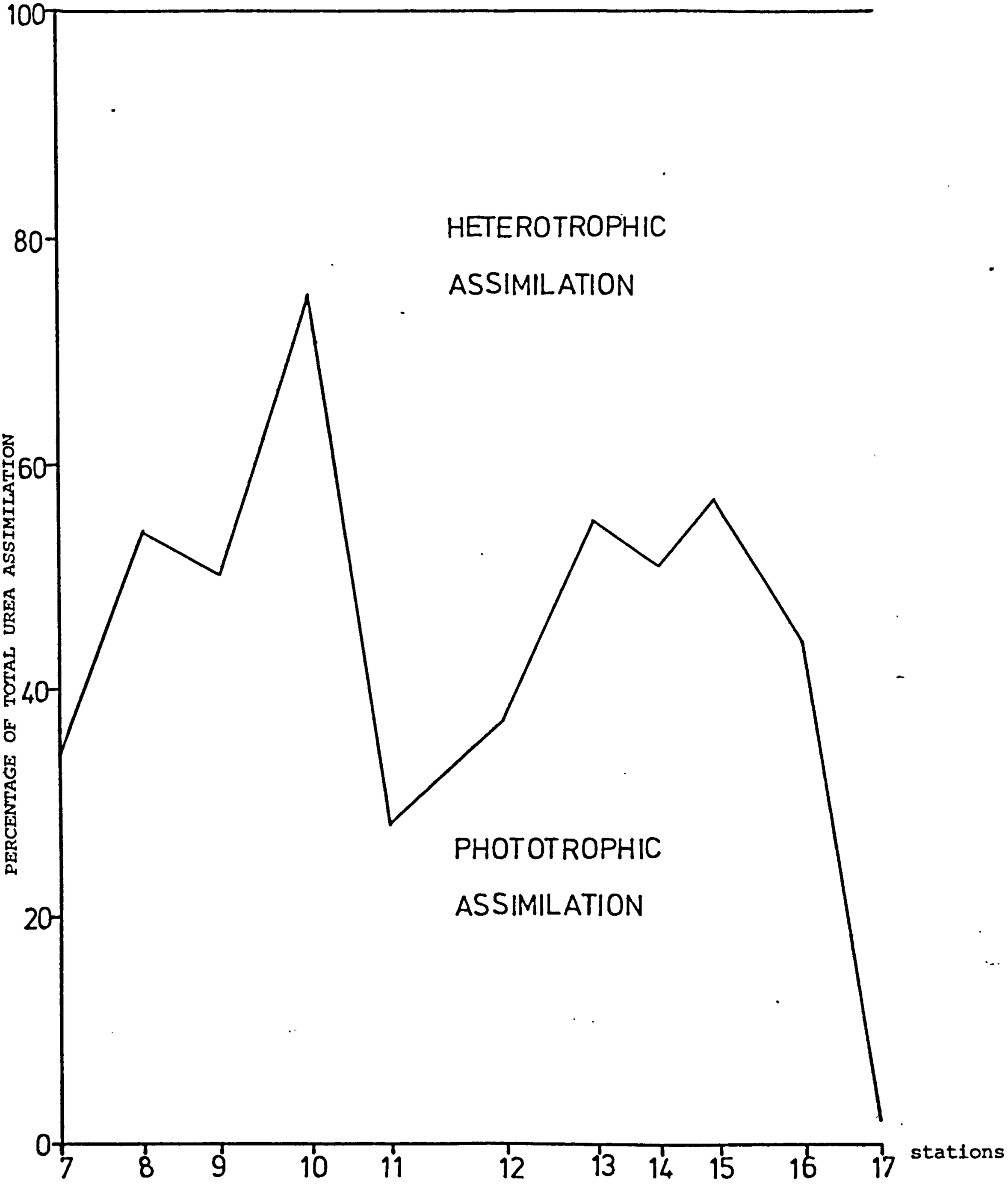


FIGURE 4.26 : CRUISE HGLII. DISTRIBUTION OF PHOTOTROPHIC AND HETEROTROPHIC UREA ASSIMILATION AS A PERCENTAGE OF TOTAL UREA ASSIMILATION.

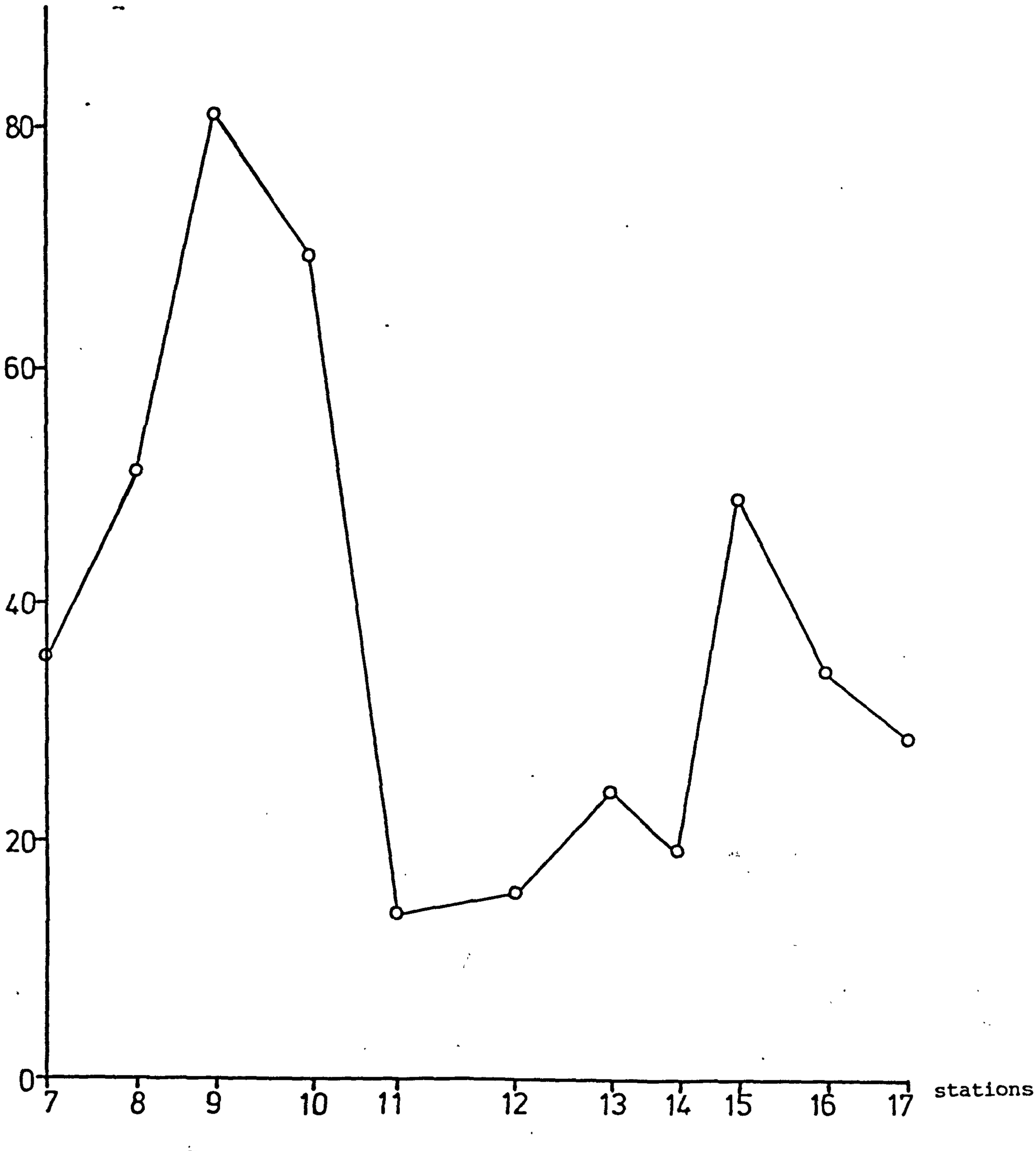


FIGURE 4.2.7 : CRUISE HGLII. DISTRIBUTION OF TOTAL UREA TURNOVER TIMES.

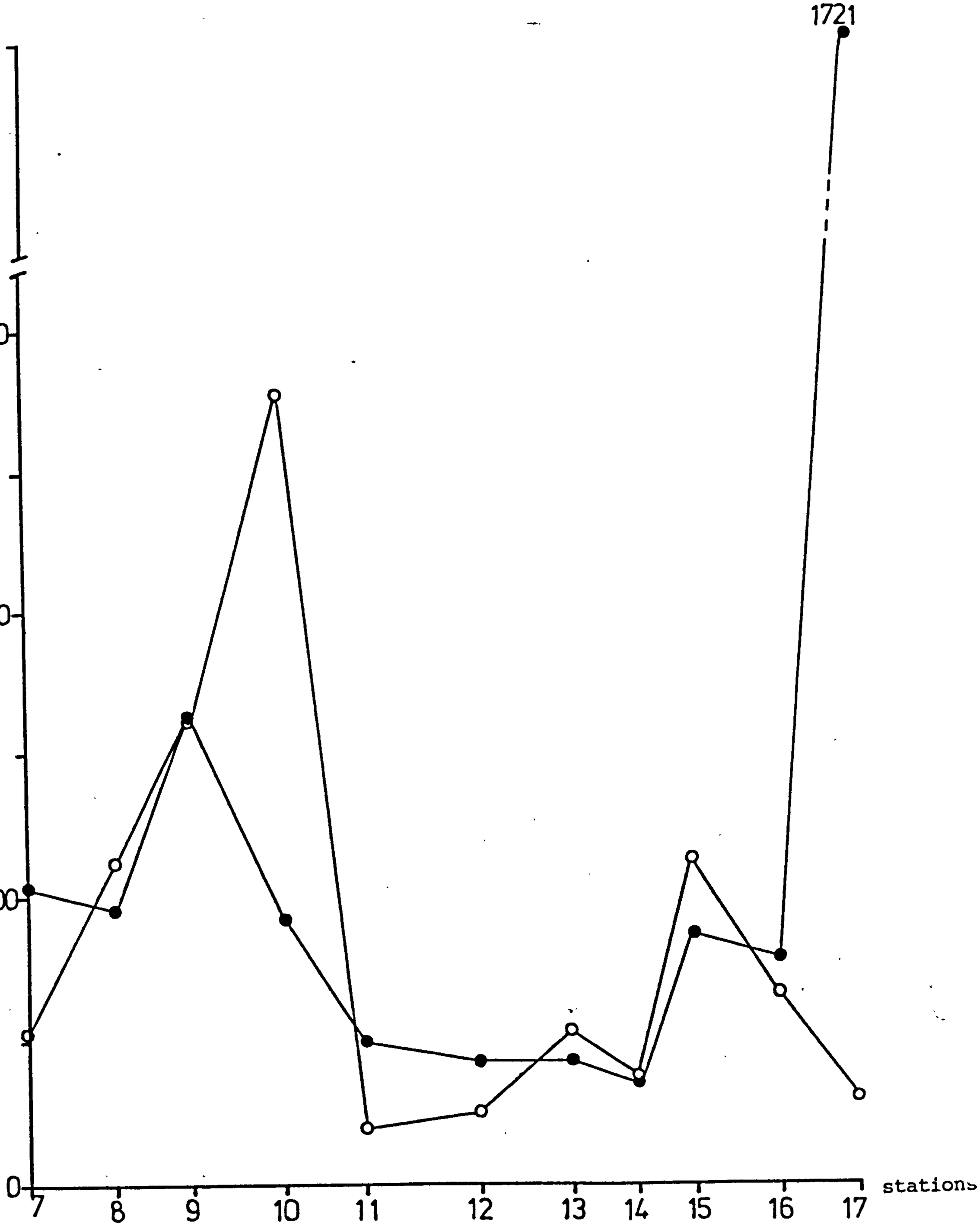


FIGURE 4.2.8 : CRUISE HGLII. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—○—) UREA TURNOVER TIMES.

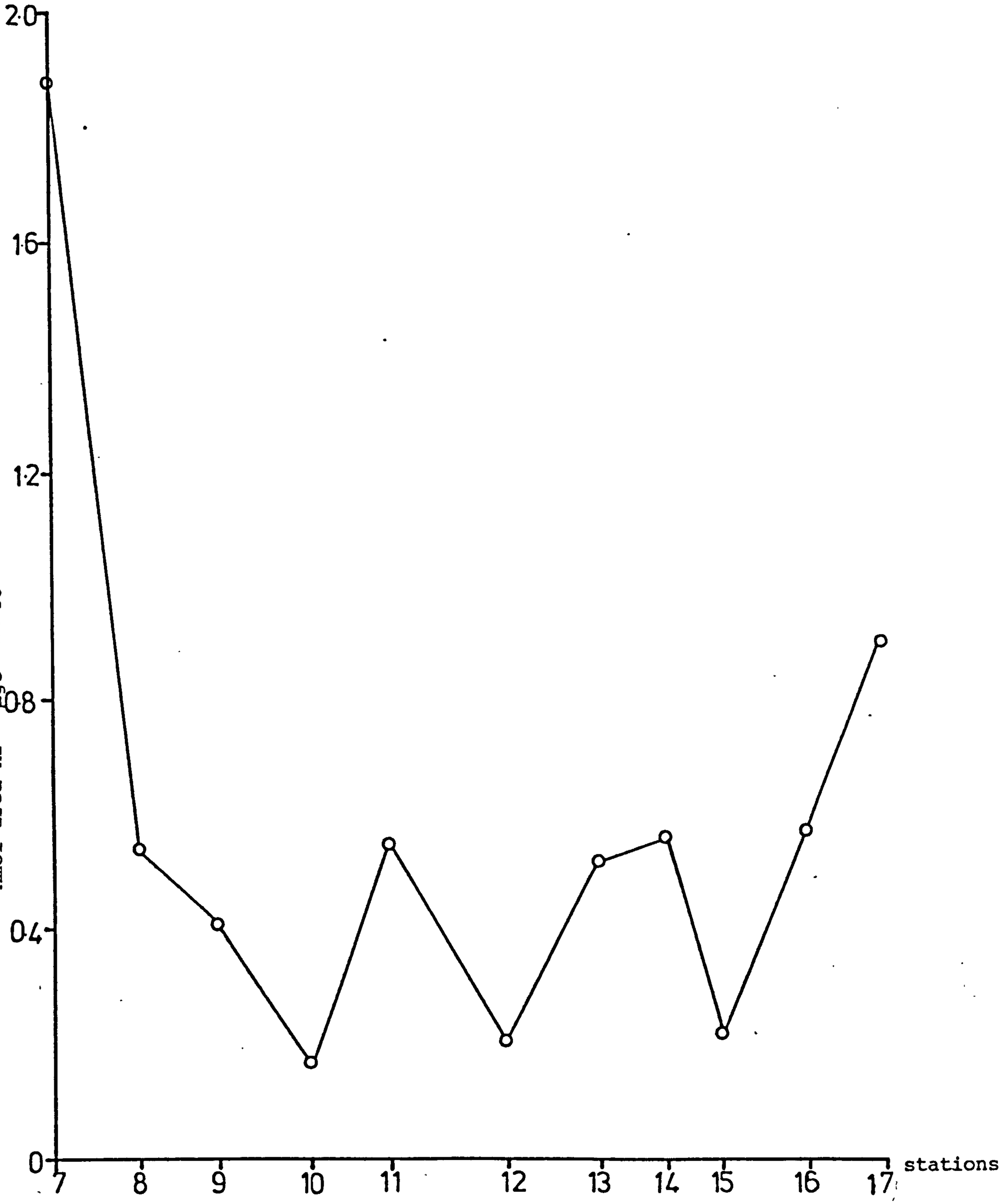


FIGURE 4.29 : CRUISE HGLII. DISTRIBUTION OF TOTAL UREA ASSIMILATION INDICES.

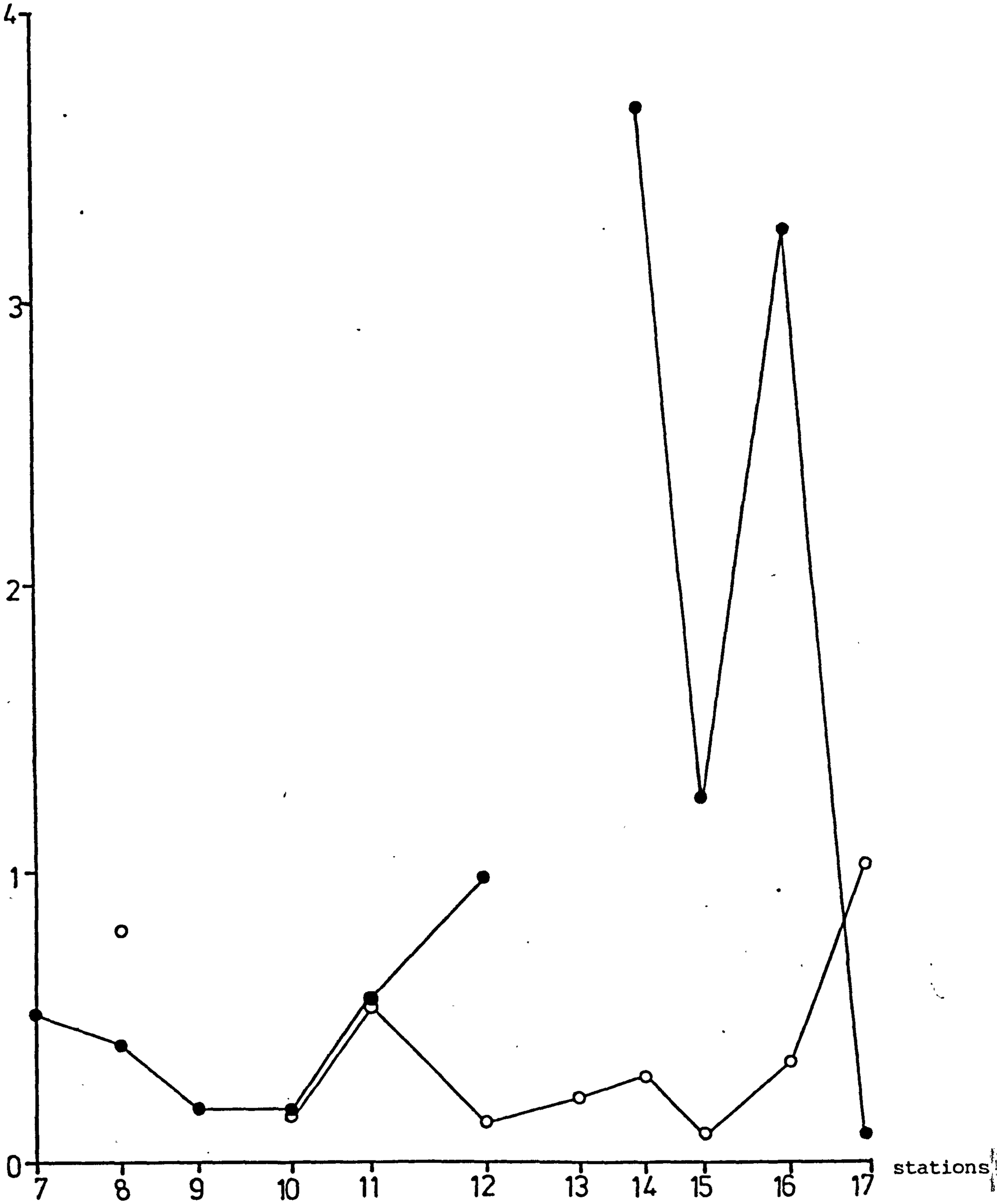


FIGURE 4.30) : CRUISE HGLII. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—o—) UREA ASSIMILATION INDICES.

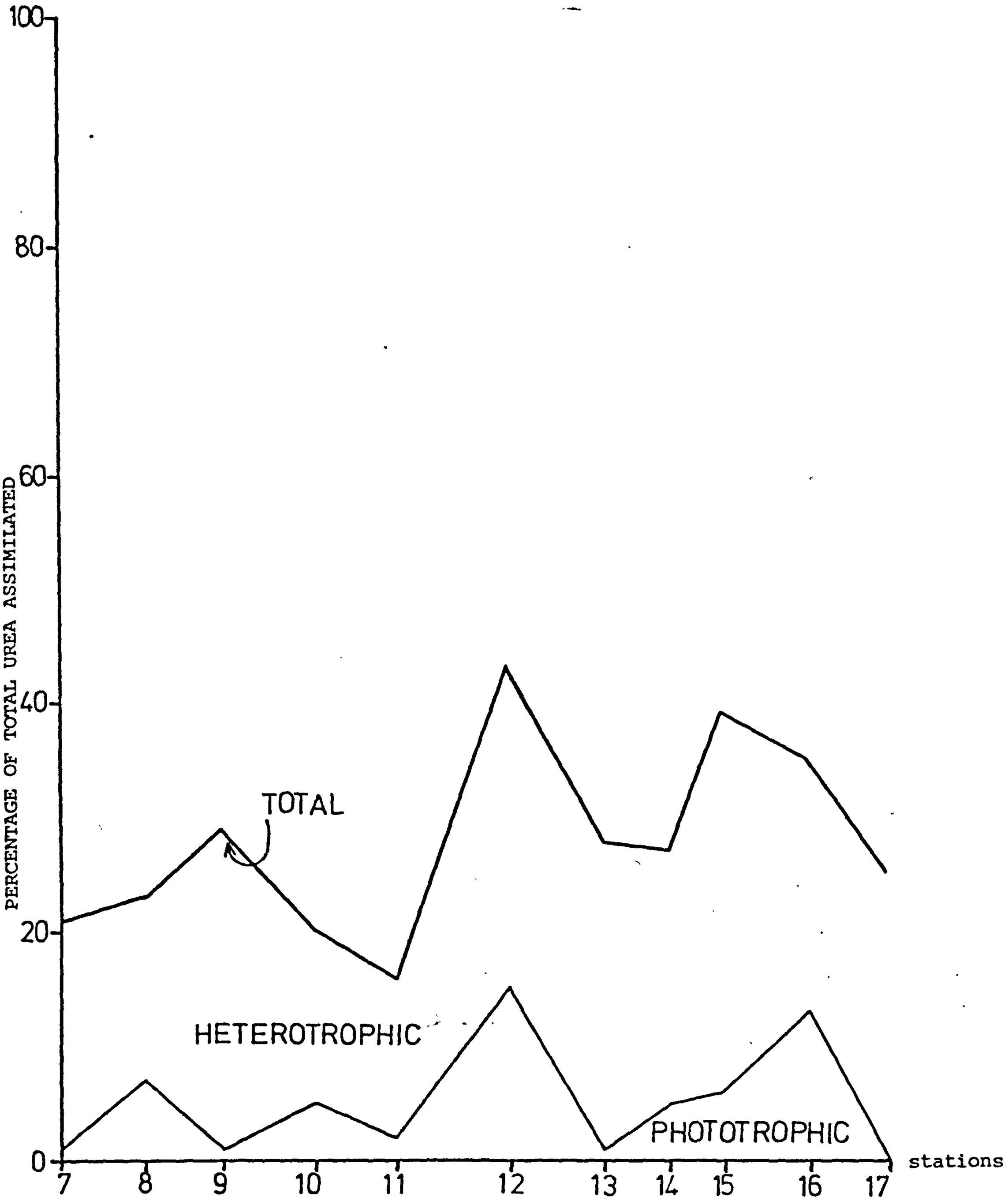


FIGURE 4.3 1 : CRUISE HGLII. DISTRIBUTION OF ^{14}C-UREA INCORPORATED IN LIVING CELLS (PHOTOTROPHIC AND HETEROTROPHIC) AS A PERCENTAGE OF TOTAL UREA ASSIMILATED.

estuary reaching maxima in the inshore waters of stations 11 and 12. ATP concentrations in the offshore stations are higher than those found in the estuary with a second maximum occurring at station 16. Heterotrophic carbon (C) (fig. 4.22) is highest in the inshore and offshore waters (stations 11 - 17) where it greatly exceeds phototrophic carbon (A). In the estuary, however, phototrophic carbon is greater than that for heterotrophs.

4.1.3.4 Urea assimilation measurements

Data concerning urea assimilation is presented in figures 4.23 to 4.31. Urea uptake in dpm (fig. 4.23) is low in the estuary and decreases from station 7 - 10 in both light and dark incubations whereas it is notably higher out of the estuary.

Total phototrophic and heterotrophic urea assimilation rates (figs. 4.24 and 4.25) are low in the estuary and high in the inshore and offshore stations with marked maxima at stations 11 and 16. The rate of heterotrophic urea assimilation is also high at station 17 where phototrophic assimilation rates are negligible.

Total urea turnover times (fig. 4.27) are highest at stations 9 and 10 and lowest at stations 11 - 14. Heterotrophic turnover times (fig. 4.28) increase from stations 7 - 10 and with the exception of station 15, fastest turnover was recorded in the non-estuarine waters, with minima at stations 11 and 12. Phototrophic turnover times were lowest at stations 11 - 14.

Besides a decrease with distance down the estuary (stations 7 - 10) there is no notable pattern in the distribution of urea assimilation indices (fig. 4.29). However, phototrophic assimilation indices (A) (fig.4.30) with the exception of station 17, are lower in the estuarine environment. Heterotrophic indices (C) are generally lower than the phototrophic indices.

A larger percentage of the assimilated urea was incorporated in living cells in the offshore stations (fig. 4.31).

4.1.4 Results of Cruise HGL II (h)

4.1.4.1 Physical measurements

The stations in the vicinity of Helgoland (stations 1 - 6) have similar salinities and densities (table 4.32) as those recorded in the offshore station 12. Temperatures - depth profiles (table 4.32) indicate that there is some degree of temperature stratification at all stations. $\bar{V}$, which has been estimated on temperature surface to bottom differences only and does not take into account any salinity surface to bottom differences and is therefore an underestimate of stratification, indicates some degree of stratification at stations 2, 3, 5 and 6.

4.1.4.2 Nutrient measurements

Concentrations of urea (table 4.33) vary considerably from station to station contributing 0-57% of the 'total nitrogen'. Ammonium concentrations also vary but generally the inorganic nitrogen compounds have similar concentrations to those measured at stations 12 - 17.

4.1.4.3 Biomass measurements

Chlorophyll a concentrations (table 4.34) are low and are comparable to those found at stations 12 - 17 on Cruise HGL II (fig. 4.21). With the exception of station 3 total microbial ATP and heterotrophic carbon concentrations (table 4.35) are again in the same range as those measured in the offshore stations.

4.1.4.4 Urea assimilation measurements

High urea assimilation rates (table 4.38) were measured at stations 1 and 2. Station 1 has low turnover times (table 4.39) and are comparable with those found at stations 11 and 12 on Cruise HGL II (fig. 4.27). Urea turnover times are otherwise higher than those measured at stations 11 - 17.

There is a considerable variation in urea assimilation indices and they show no obvious distribution pattern (table 4.40).

4.1.5 Cruise HGL III

4.1.5.1 Physical measurements

Salinity distribution (fig. 4.32) again depicts an estuarine environment from station 7 - 10, with salinity stratification occurring at stations 9 and 10 and to some extent in the offshore stations 12, 13 and 14. Surface temperatures (fig. 4.32) are consistent at all stations bar the offshore stations 16 and 17. Temperatures at 10m. are colder in the estuary whereas bottom temperatures are similar at all stations. All stations show some degree of temperature stratification. Density distribution (fig. 4.33) basically mirrors that of salinity, increasing from station 7 towards the offshore stations. Large surface - bottom density differences are most marked at station 9, 10, 14 and to some extent 12. This is reflected in the stratification parameter $\bar{V}$ (fig. 4.33) which indicates marginal stratification at station 12 and 13 and relatively strong stratification at stations 9 and 10 at the mouth of the Elbe estuary and in the offshore water of station 14, other stations being well mixed.

Secchi disc extinction depth (fig. 4.32) indicates that stations 7 and 8 are most turbid, stations 12 - 17 being least turbid, while stations 9 - 11 are similar, having intermediate turbidity between the upper estuary and offshore waters. The greatest change in turbidity occurred between stations 11 and 12.

4.1.5.2 Nutrient measurements

Nitrate and nitrite (fig. 4.34) concentrations are highest in the estuarine stations 7 - 9, intermediate concentrations were measured at stations 10 - 12 and comparatively low concentrations measured in the offshore stations 13 - 17. Ammonium, although generally higher in the estuarine stations than those offshore, does not decrease constantly or at the same rate as nitrate with distance. Urea

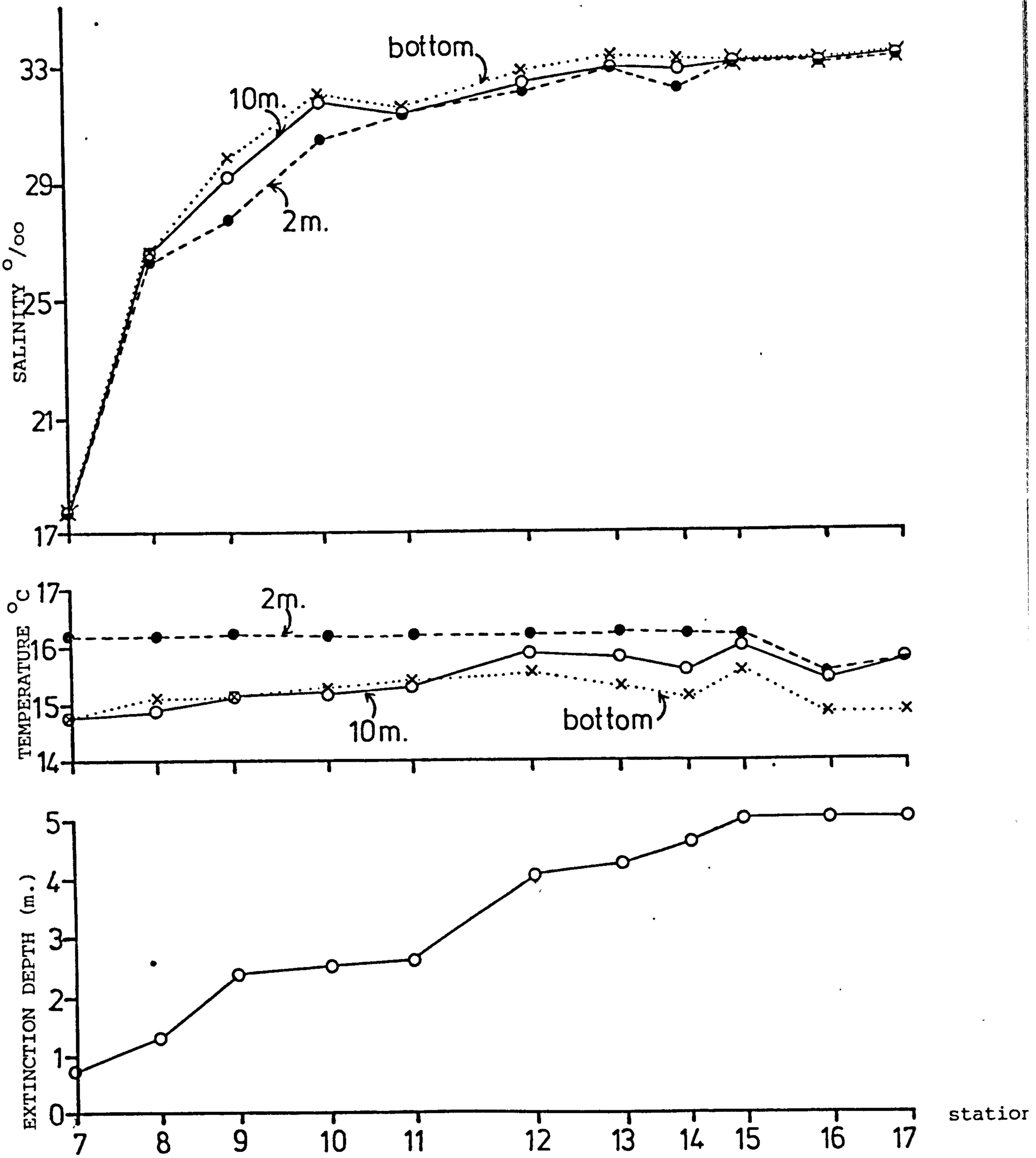


FIGURE 4.32 : CRUISE HGL III. DISTRIBUTION OF PHYSICAL MEASUREMENTS OF SALINITY , TEMPERATURE AND EXTINCTION DEPTH OF SECCHI DISC. (21 & 23·9·76)

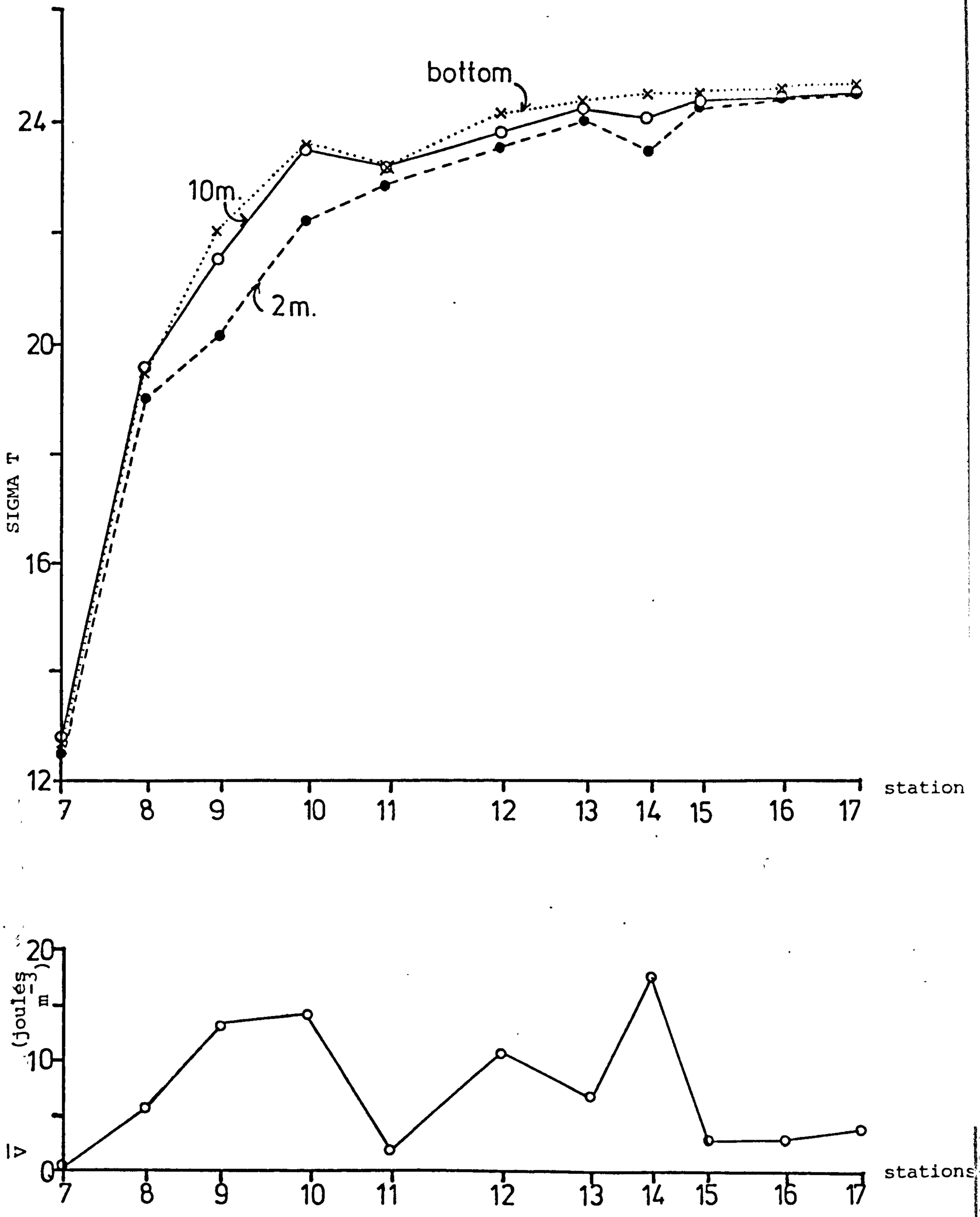


FIGURE 4.33 : CRUISE HGL III. DISTRIBUTION OF SIGMA T AND $\bar{V}$.
(21 & 23.9.76)

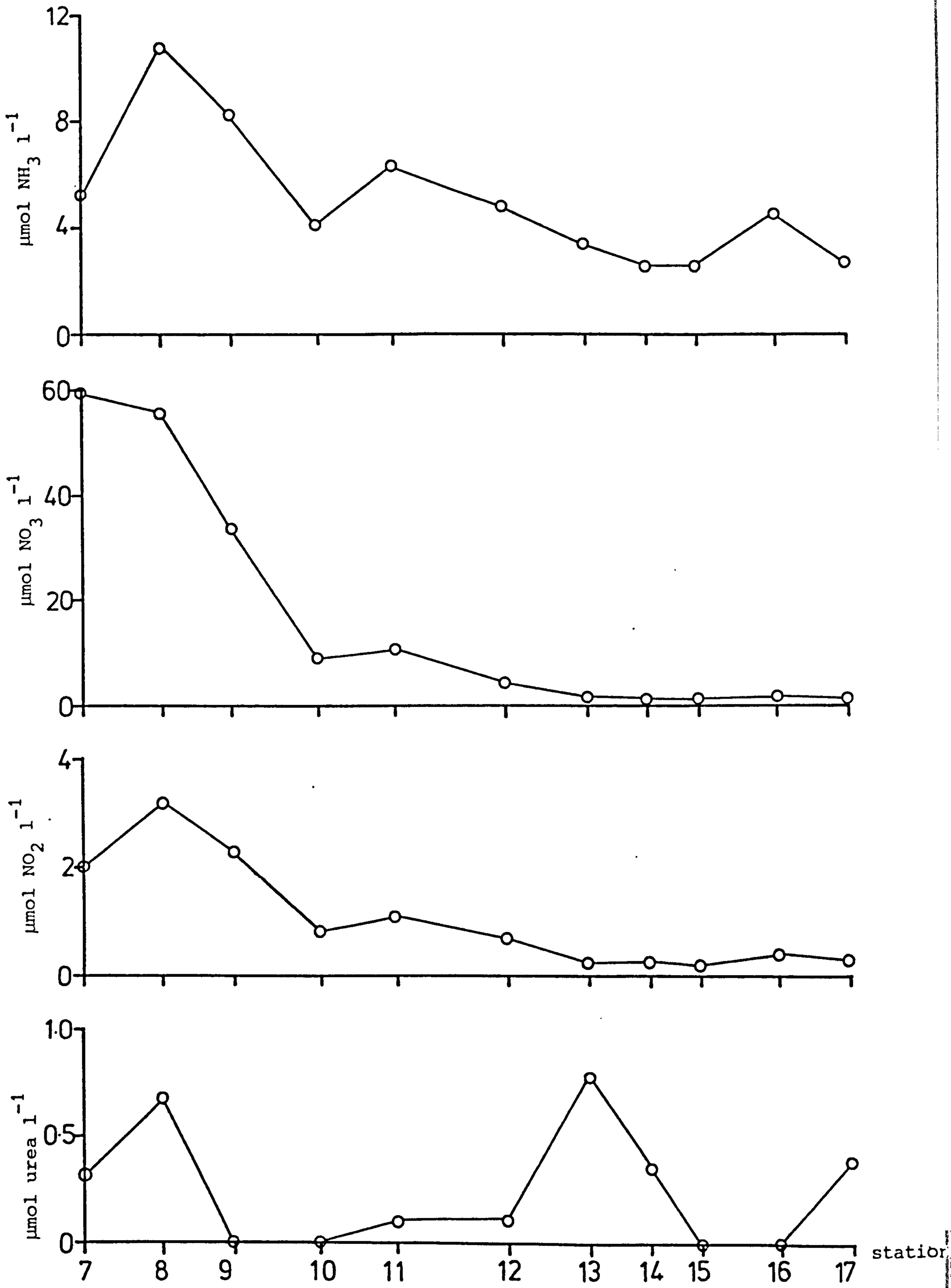


FIGURE 4.34 : CRUISE HGL III. DISTRIBUTION OF AMMONIUM , NITRATE , NITRITE AND UREA. (21 & 23.9.76).

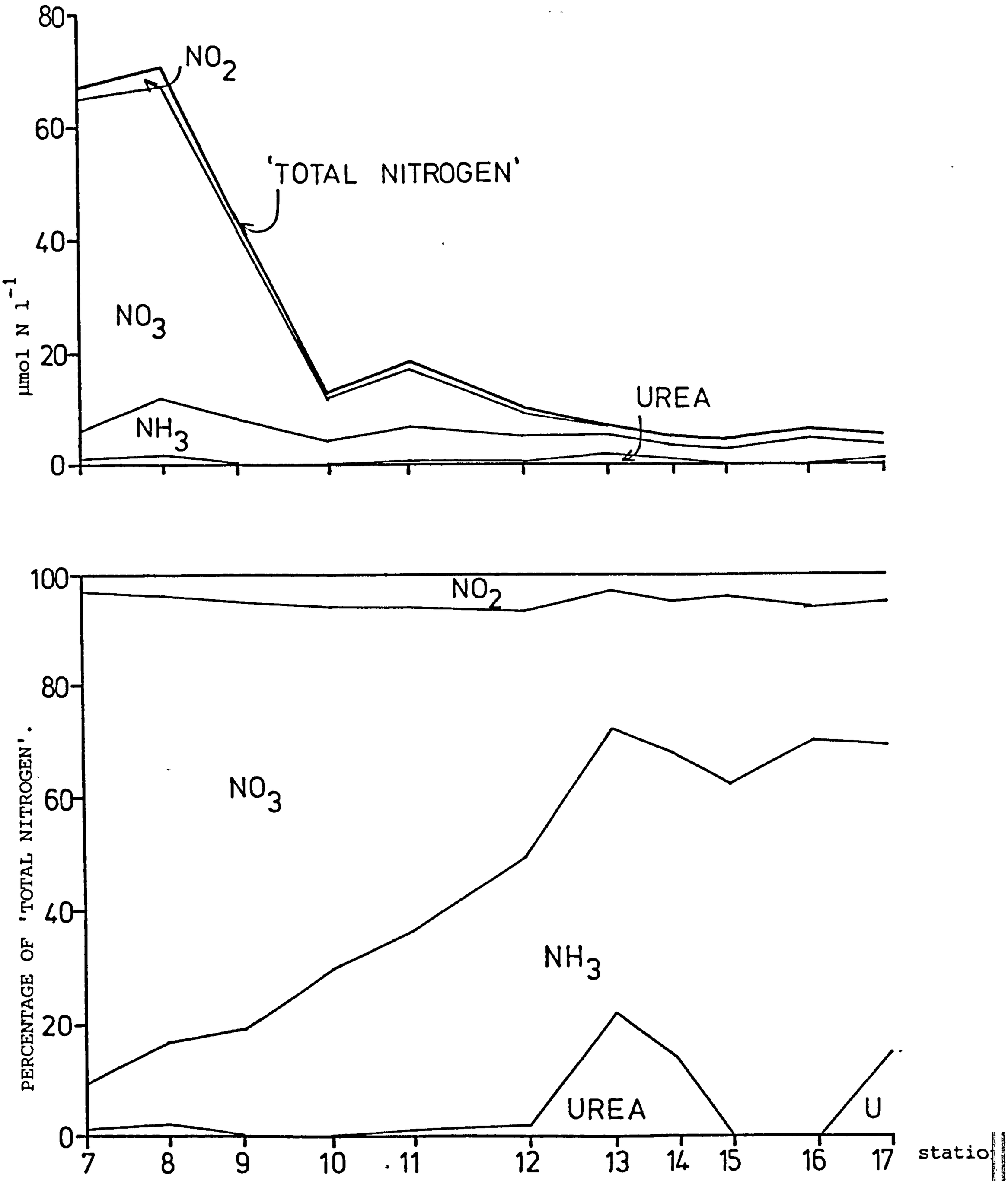


FIGURE 4.35 : CRUISE HGL III. DISTRIBUTION OF UREA AMMONIA , NITRATE AND NITRITE AS AN ACCUMULATE AND PERCENTAGE OF 'TOTAL NITROGEN'. (21 & 23·9·76).

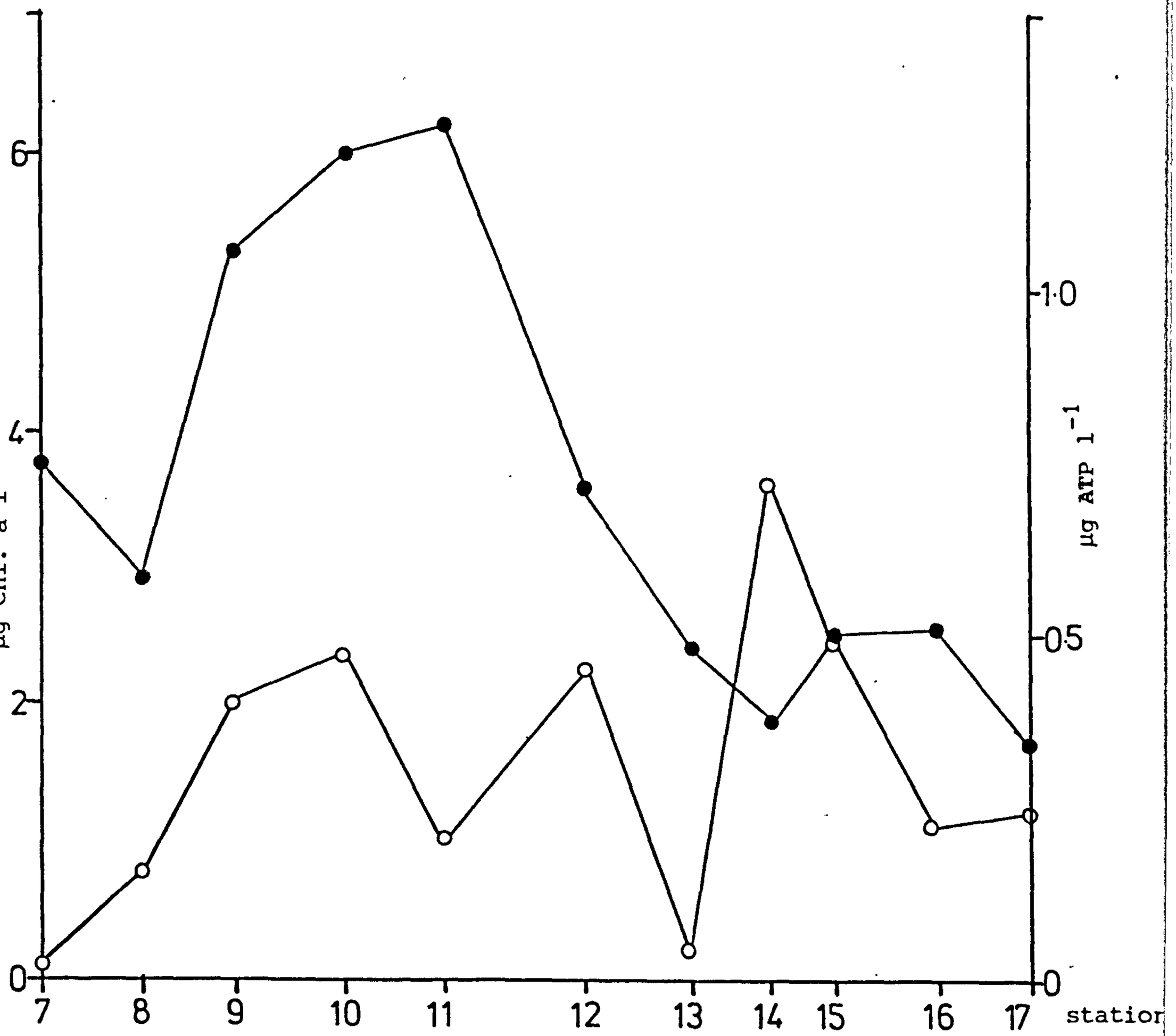


FIGURE 4.36 : CRUISE HGL III. DISTRIBUTION OF CHLOROPHYLL a (—●—) AND TOTAL MICROBIAL A.T.P. (—○—). (21 & 23·9·76).

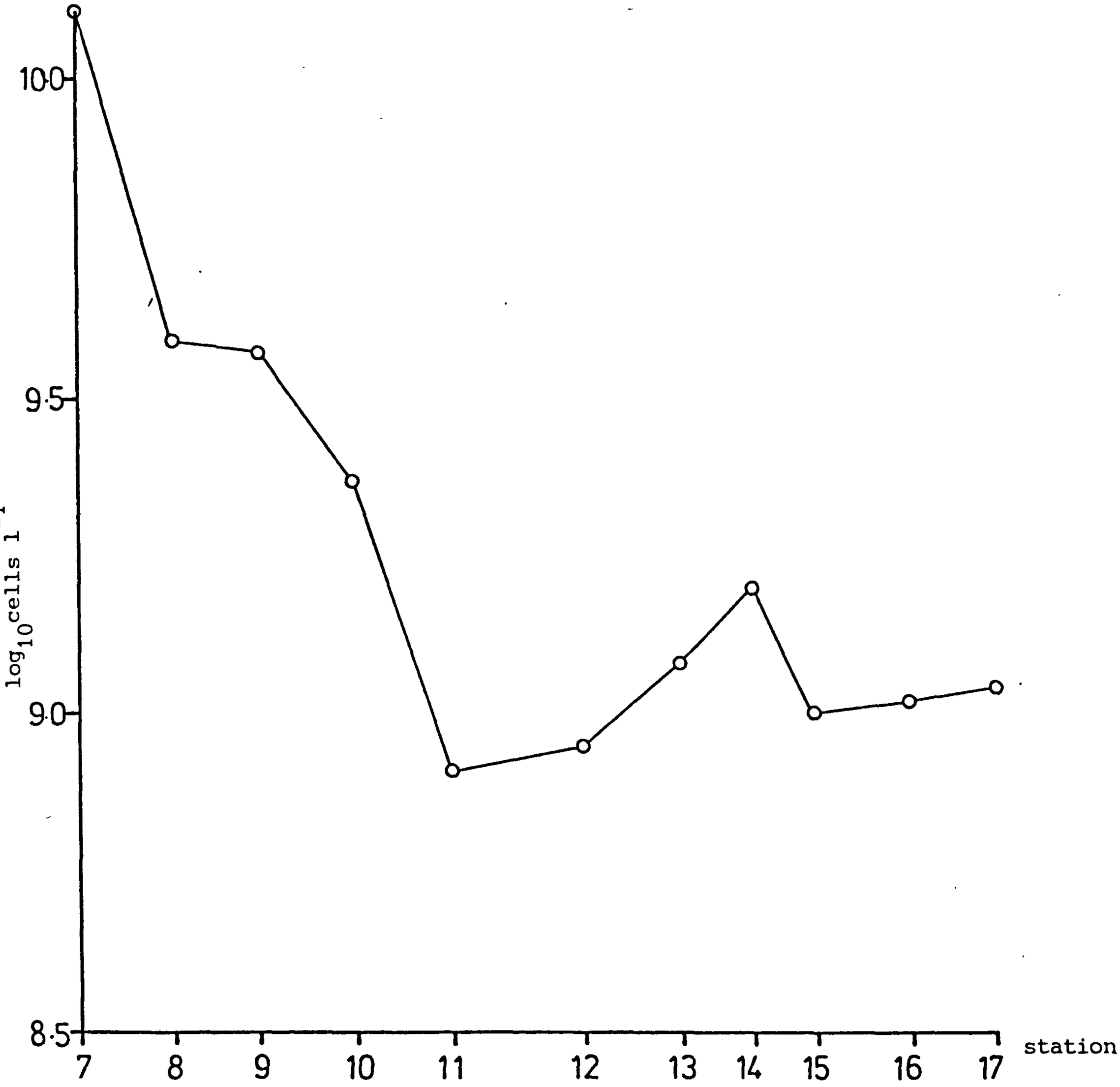


FIGURE 4.37 : CRUISE HGL III. DISTRIBUTION OF BACTERIAL CELL NUMBERS. (21 & 23·9·76).

concentrations are low or undetectable at stations other than 7, 8, 13, 14 and 17.

Nitrate is the major source (fig. 4.35) of nitrogen in the estuarine and inshore (stations 7 - 11) waters while ammonium comprises a greater proportion of 'total nitrogen' in offshore waters. Urea only makes up a significant proportion of the 'total nitrogen' in the offshore stations 13, 14 and 17.

The distribution of 'total nitrogen' (fig. 4.35) generally reflects the inorganic nitrogen compounds, particularly nitrate; high concentrations in the estuary decreasing drastically between station 8 and 10, and comparatively very low concentrations occurring offshore.

4.1.5.3 Biomass measurements

There is an obvious geographical chlorophyll a (fig. 4.36) maxima at station 9, 10 and 11. Total microbial ATP (fig. 4.36) increases from station 7 - 10 seawards of which it follows no obvious distribution pattern, with a minimum concentration at station 13 and a maximum at station 14.

Bacteria cell numbers (fig. 4.37) (AODC method) are highest in the estuarine environment with comparatively low cell concentrations at the offshore stations. A small offshore maximumwas found at station 14. In the estuarine stations bacteria were characteristically large (Table 4.44b), had a great diversity in morphology and a large proportion of which were attached to detritus. Diplococcoid and bacillus were most common cell shape of those bacteria in the estuarine waters whereas in offshore waters very small cocci were most common although the proportion of vibroids were greater than in the estuarine waters. Bacteria in the offshore waters were mainly unassociated with detritus.

Microbial biomass has been calculated by several methods for this cruise. Phototrophic carbon (A), total microbial carbon (B) and heterotrophic carbon (C)

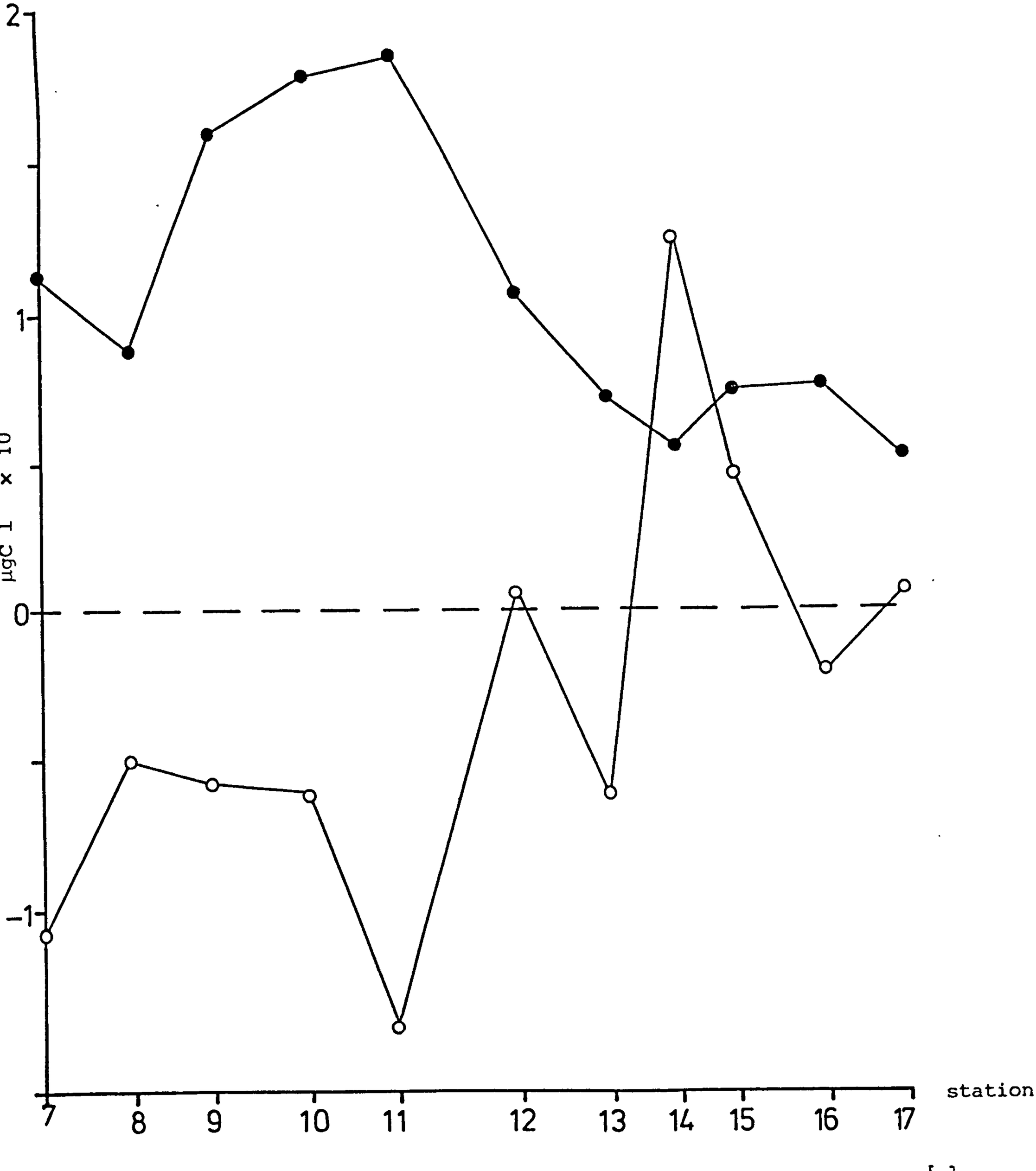


FIGURE 4.38 : CRUISE HGL III. DISTRIBUTION OF PHOTOTROPHIC CARBON [A] (—●—) DERIVED FROM CHLOROPHYLL a AND HETEROTROPHIC CARBON [C] (—○—) DERIVED FROM CARBON FROM ATP MINUS PHOTOTROPHIC CARBON. (21 & 23·9·76).

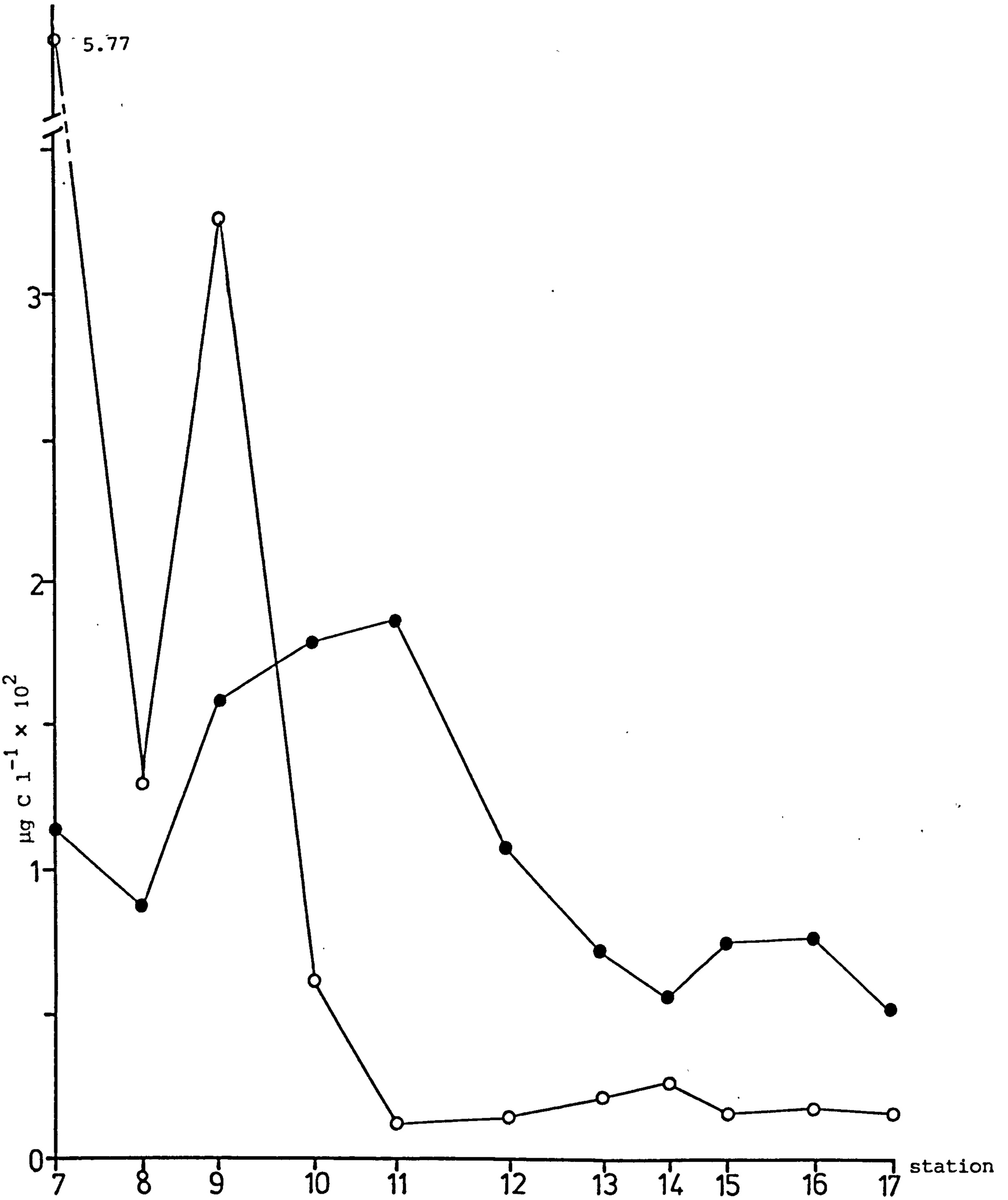


FIGURE 4.39 : CRUISE HGL III. DISTRIBUTION OF PHYTOPLANKTON BIOMASS [A] DERIVED FROM CHLOROPHYLL a (—●—) AND BACTERIAL BIOMASS [D] DERIVED FROM CELL NUMBERS AND VOLUME (—○—). (21 & 23.9.76).

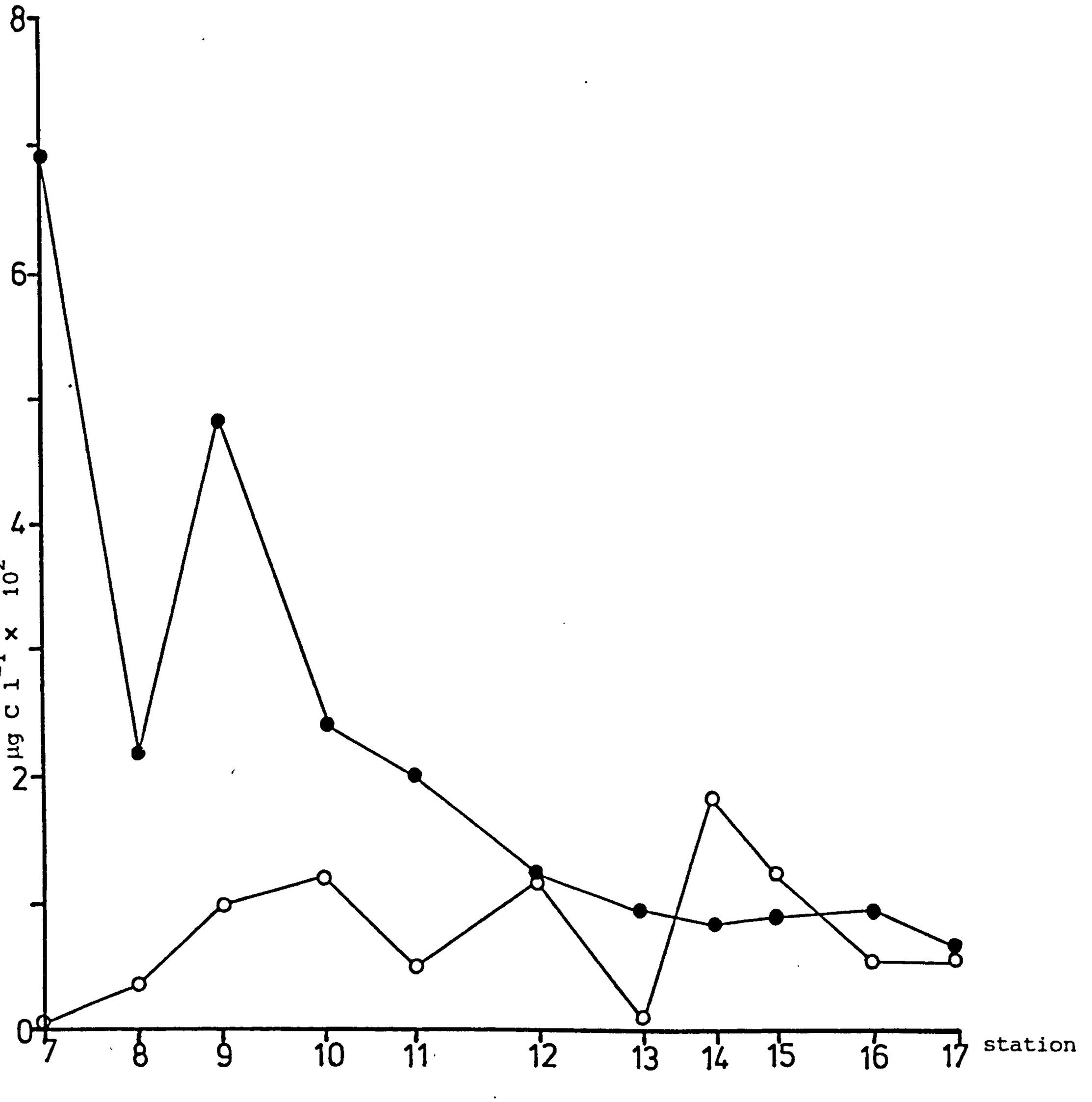


FIGURE 4.40 : CRUISE HGL III. DISTRIBUTION OF TOTAL MICROBIAL BIOMASS DERIVED FROM ATP[B] (—o—) AND FROM CHLOROPHYLL a PLUS BACTERIAL CELL NUMBERS AND VOLUMES (—●—) [E]. (21 & 23·9·76).

have been derived, as in Cruises HGL I and II, from chlorophyll a, total microbial ATP and total microbial carbon (B) minus phototrophic carbon (A) respectively. In addition, heterotrophic (bacterial) biomass (D) has been calculated from bacterial cell numbers and volumes, and total microbial biomass (E) has been derived from bacterial biomass (D) plus phototrophic biomass (A). The associated letters ((A) - (F)) are to prevent confusion regarding the biomass derivation.

Heterotrophic biomass (C) (fig. 4.38) is calculable only at stations 12, 14, 15 and 17 (reaching maxima at station 14. It is obvious that either one or both of the conversion factors used to derive heterotrophic biomass (C) are incorrect and this will be discussed in Section 5.

Bacterial biomass (D) (fig. 4.39) is large in the estuarine water, with maxima at stations 7 and 9, and considerably smaller in offshore waters. The bacterial biomass (D) is less than the phototrophic biomass (A) from stations 10 - 17 whilst the opposite is true for stations 7 - 9.

There is little similarity between the distribution of total microbial biomass (B) and total microbial biomass (E) (fig. 4.40). They do, however, have carbon concentrations in the same range in the offshore stations 12 - 17. Total microbial biomass (B) shows the same distribution as already described for total microbial ATP. Total microbial biomass (E) indicates that there is generally higher biomass in the estuary, and apart from an estuarine minimum at station 8, there is a gradual seawards decrease.

The ratio of microbial ATP:microbial carbon, the latter derived from total microbial carbon (E), is extremely low at the estuarine stations, whilst, with the exception of station 13, the ratio is higher at the offshore stations with a maximum at station 14 (fig. 4.49).

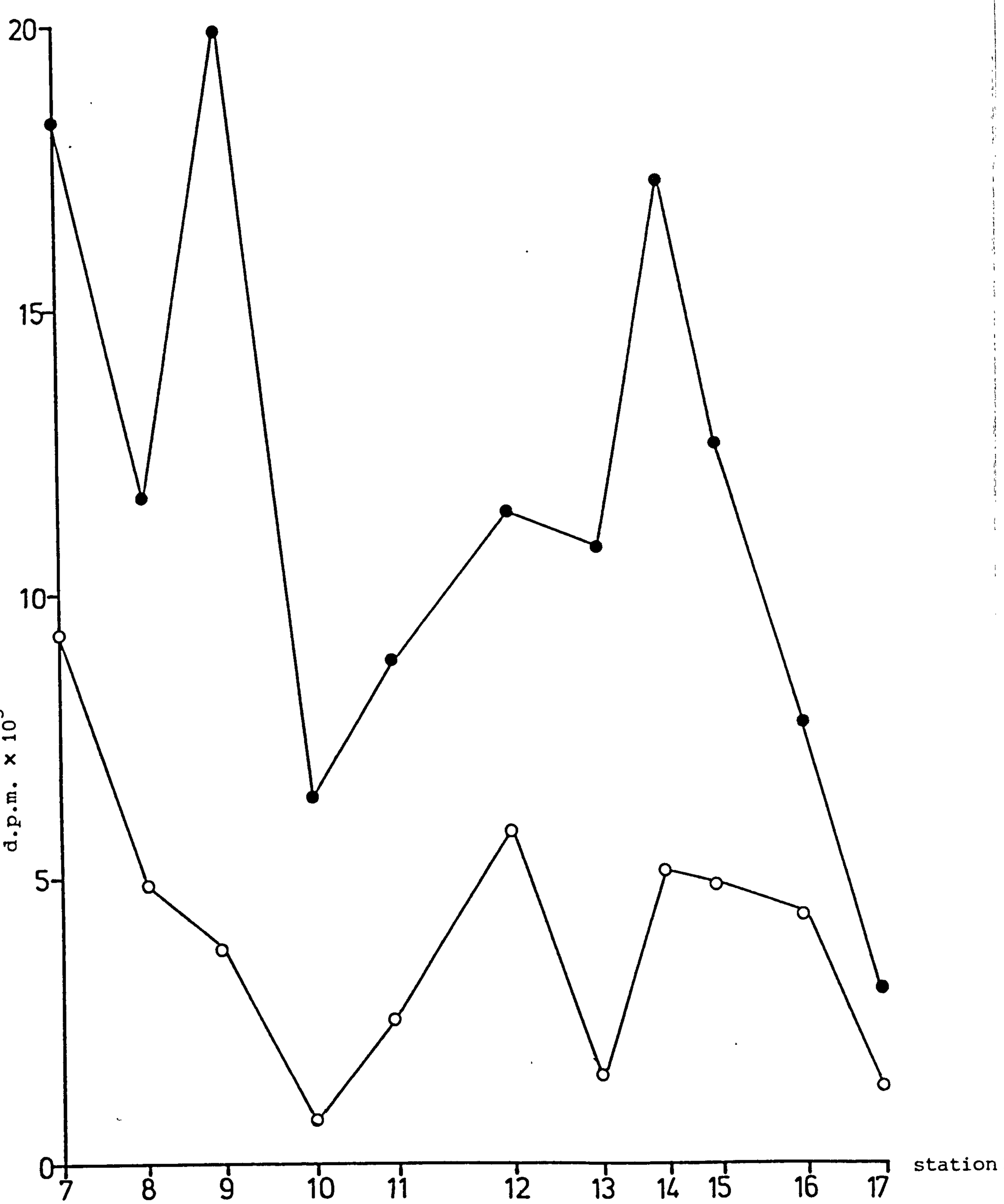


FIGURE 4.41 : CRUISE HGL III. DISTRIBUTION OF UREA UPTAKE IN LIGHT (—●—) AND DARK (—o—). (21 & 23·9·76).

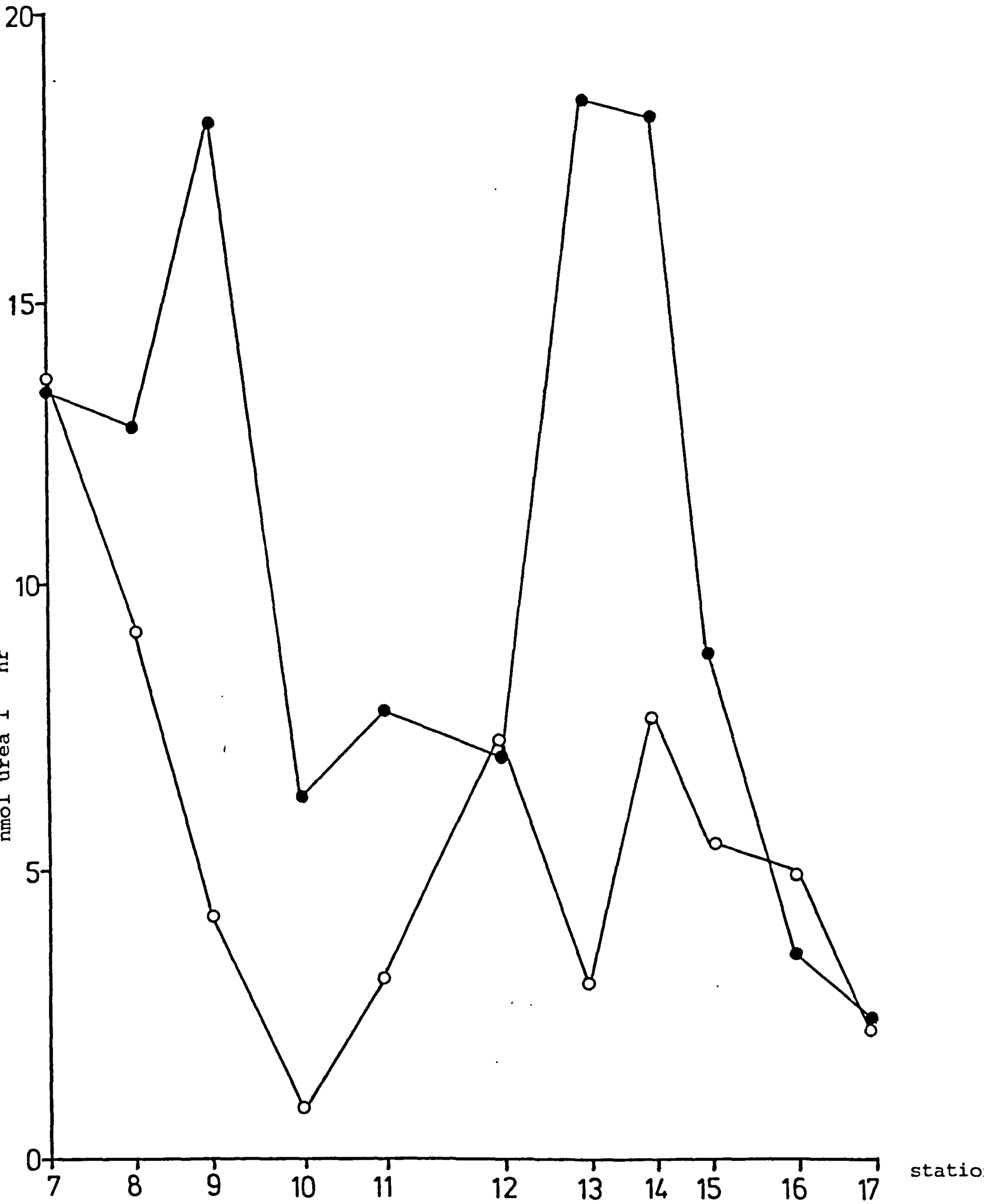


FIGURE 4.43 : CRUISE HGL III. DISTRIBUTION OF UREA ASSIMILATION RATES BY PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—○—) MICRORGANISMS. (21 & 23.9.76).

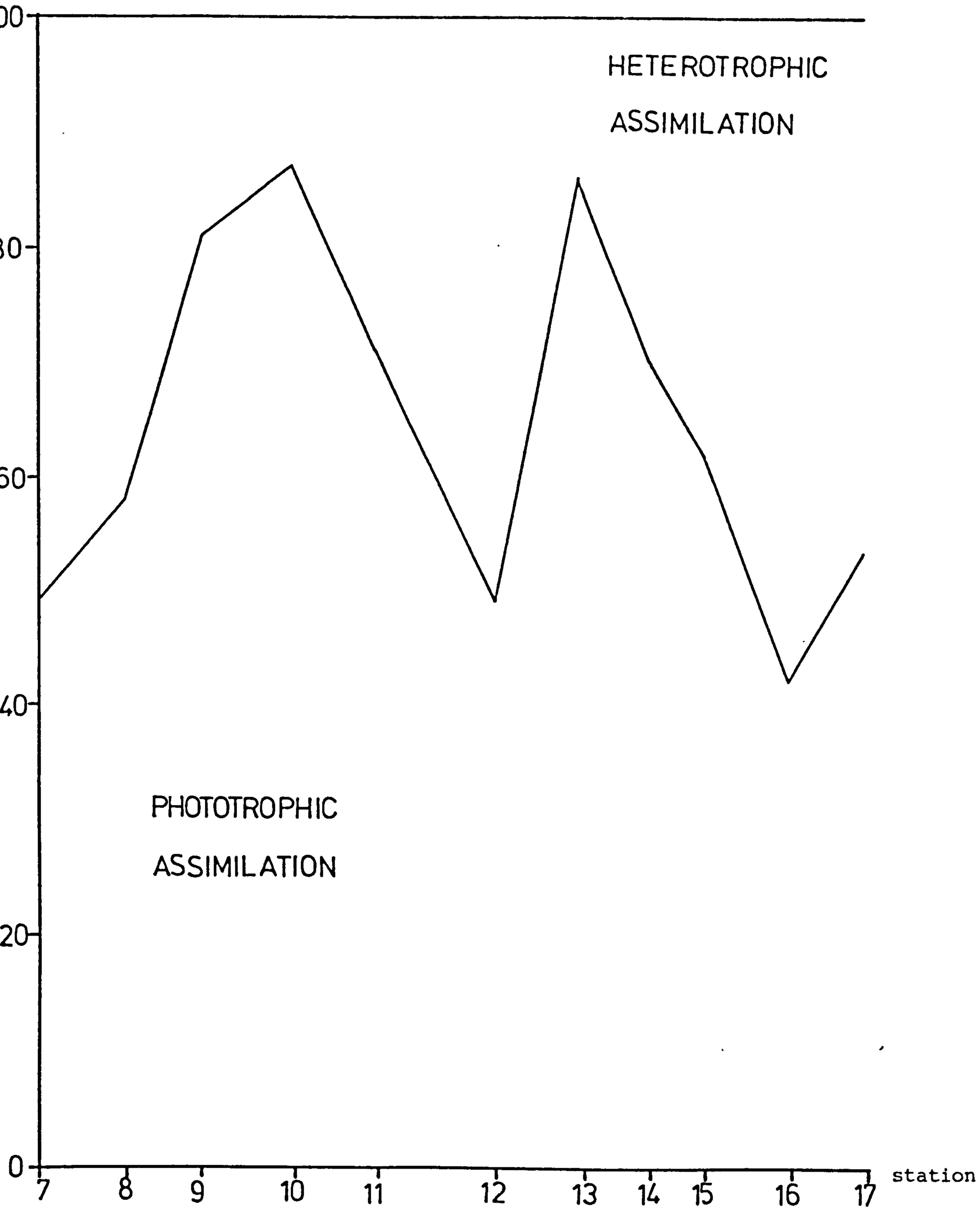


FIGURE 4.44 : CRUISE HGL III. DISTRIBUTION OF PHOTOTROPHIC AND HETEROTROPHIC UREA ASSIMILATION AS A PERCENTAGE OF TOTAL UREA ASSIMILATION. (21 & 23.9.76).

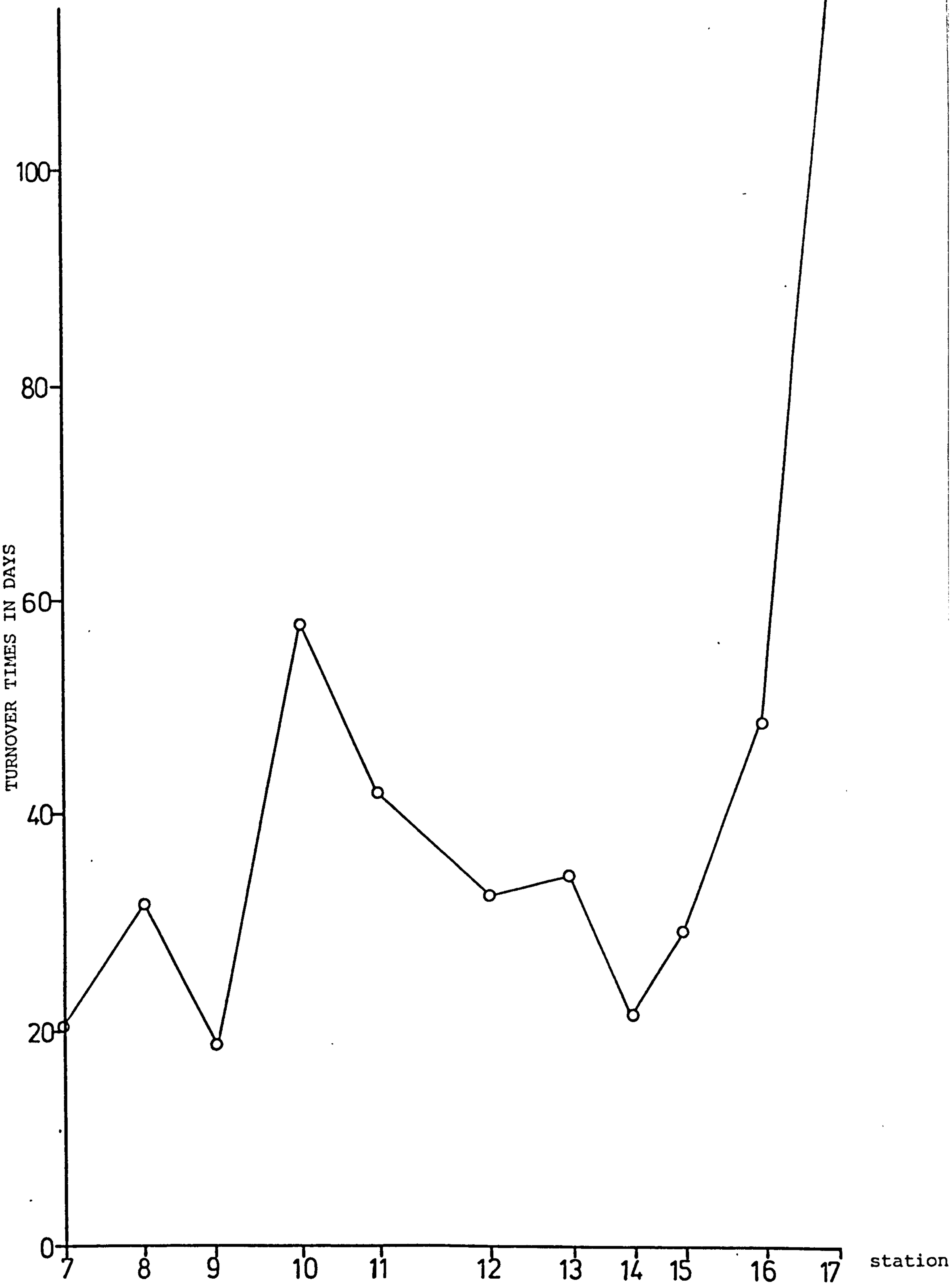


FIGURE 4.45 : CRUISE HGL III: DISTRIBUTION OF TOTAL UREA TURNOVER TIMES. (21 & 23.9.76).

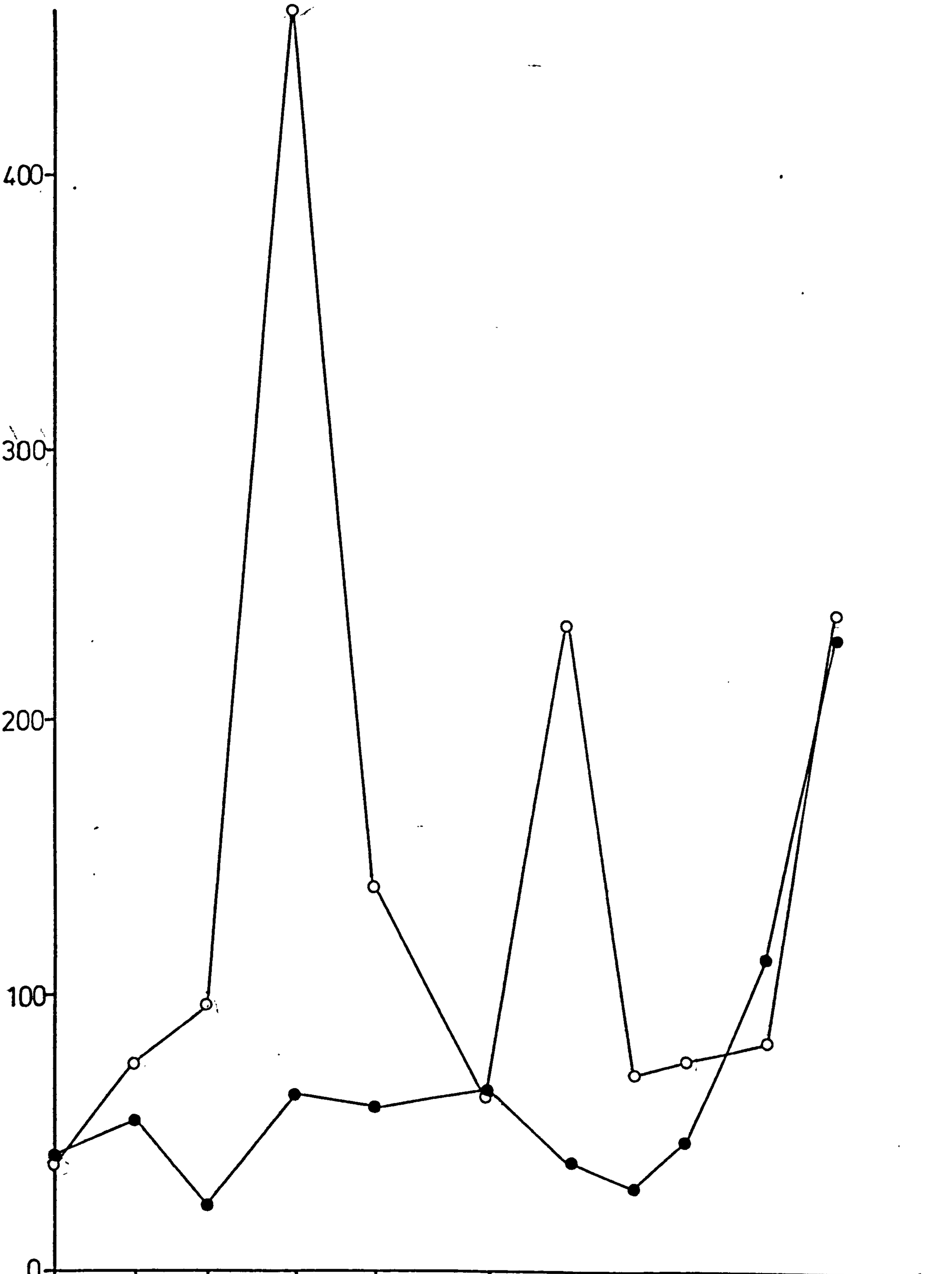


FIGURE 4.46 : CRUISE HGL III. DISTRIBUTION OF PHOTOTROPHIC (—●—) AND HETEROTROPHIC (—○—) UREA TURNOVER TIMES. (21 & 23·9·76).

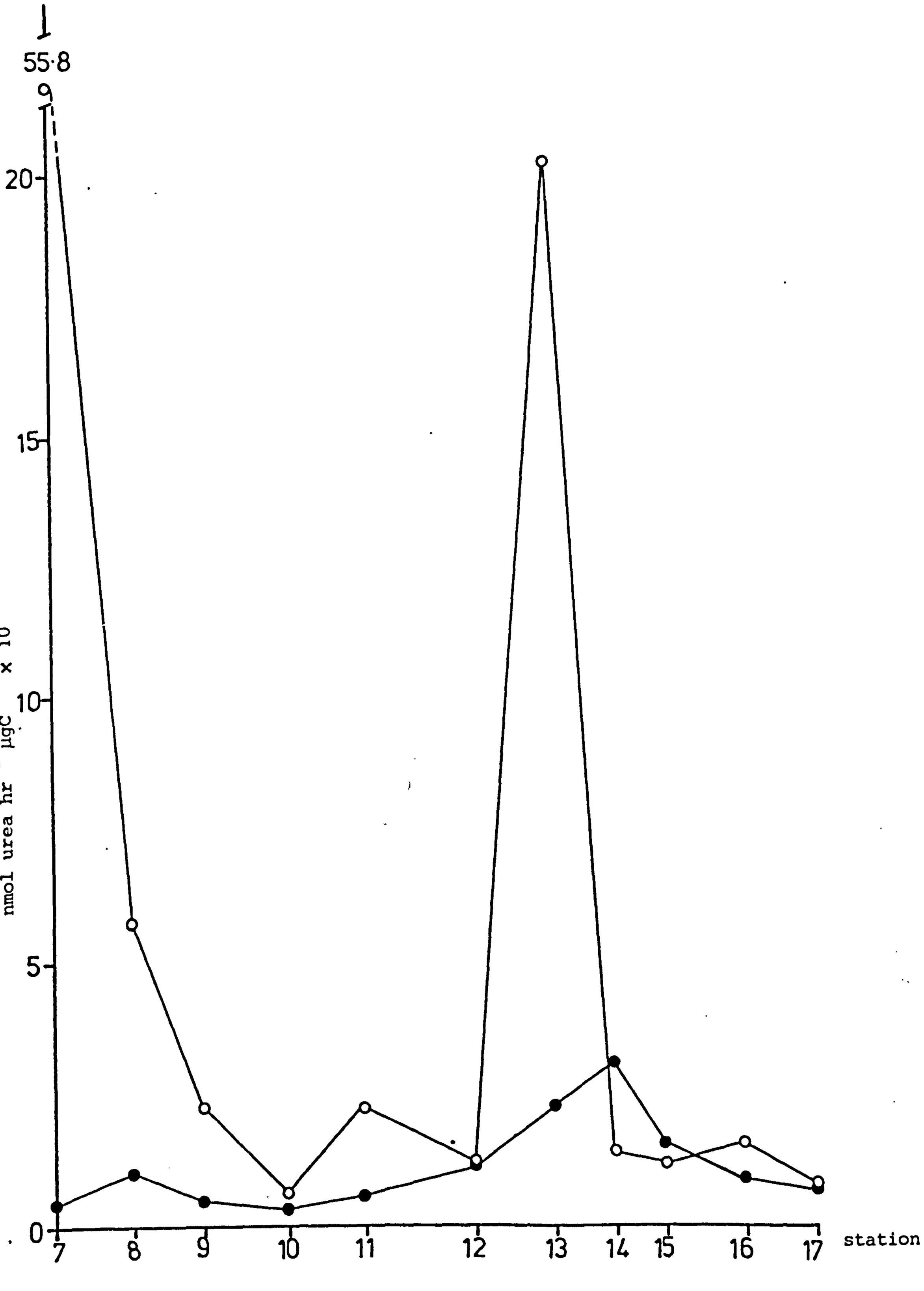


FIGURE 4.47 : CRUISE HGL III. DISTRIBUTION OF TOTAL UREA ASSIMILATION INDICES USING CARBON DERIVED FROM ATP (—o—) [B] AND FROM CHLOROPHYLL a PLUS BACTERIAL NUMBERS AND VOLUME (—●—)[E]. (21 & 23·9·76).

4.1.5.4 Urea assimilation measurements

Urea uptake (fig. 4.41) in the dark gradually decreases from station 7 - 10, rate of uptake at the latter station was the lowest measured on this cruise. Stations 12, 14, 15 and 16 show relatively high dark uptake. Uptake of urea in the light (fig. 4.41), unlike that in the dark, does not decrease with distance down the estuary, maximum uptake occurring at station 9. Light uptake increases from station 10 to 14, thereafter decreasing.

The distribution of total urea assimilation rates (fig. 4.42) shows that there are two regions of high rates of urea assimilation; at estuarine stations 7 - 9 and offshore stations 13 and 14. Similarly, photo-trophic urea assimilation rates (fig. 4.43) are notably high at stations 7 - 9 and 13 - 14. However, hetero-trophic urea assimilation rates decrease from a maximum at station 7 to a minimum at station 10, thereafter increasing seawards with peaks occurring at station 12 and 14.

With the exception of stations 7, 12 and 16 where an equal proportion of urea assimilation (fig. 4.44) is carried out phototrophically and heterotrophically, a greater proportion of urea is assimilated photo-trophically rather than heterotrophically.

Fastest total urea turnover times (fig. 4.45) were measured in the estuarine waters of stations 7 - 9 and also in the offshore waters of stations 12 - 15. Phototrophic turnover times (fig. 4.46) did not vary to the same extent as heterotrophic turnover times, particularly from stations 7 - 15. Lowest phototrophic turnover times were recorded at station 9 and 13 - 15. Heterotrophic turnover times are generally higher than phototrophic turnover times.

Total urea assimilation indices (B) (fig. 4.47) calculated by using microbial carbon (B) derived from microbial ATP, decrease from station 7 - 10, the lowest index occurring at station 10. Offshore the indices remain relatively low and constant with the exception of a high index at station 13.

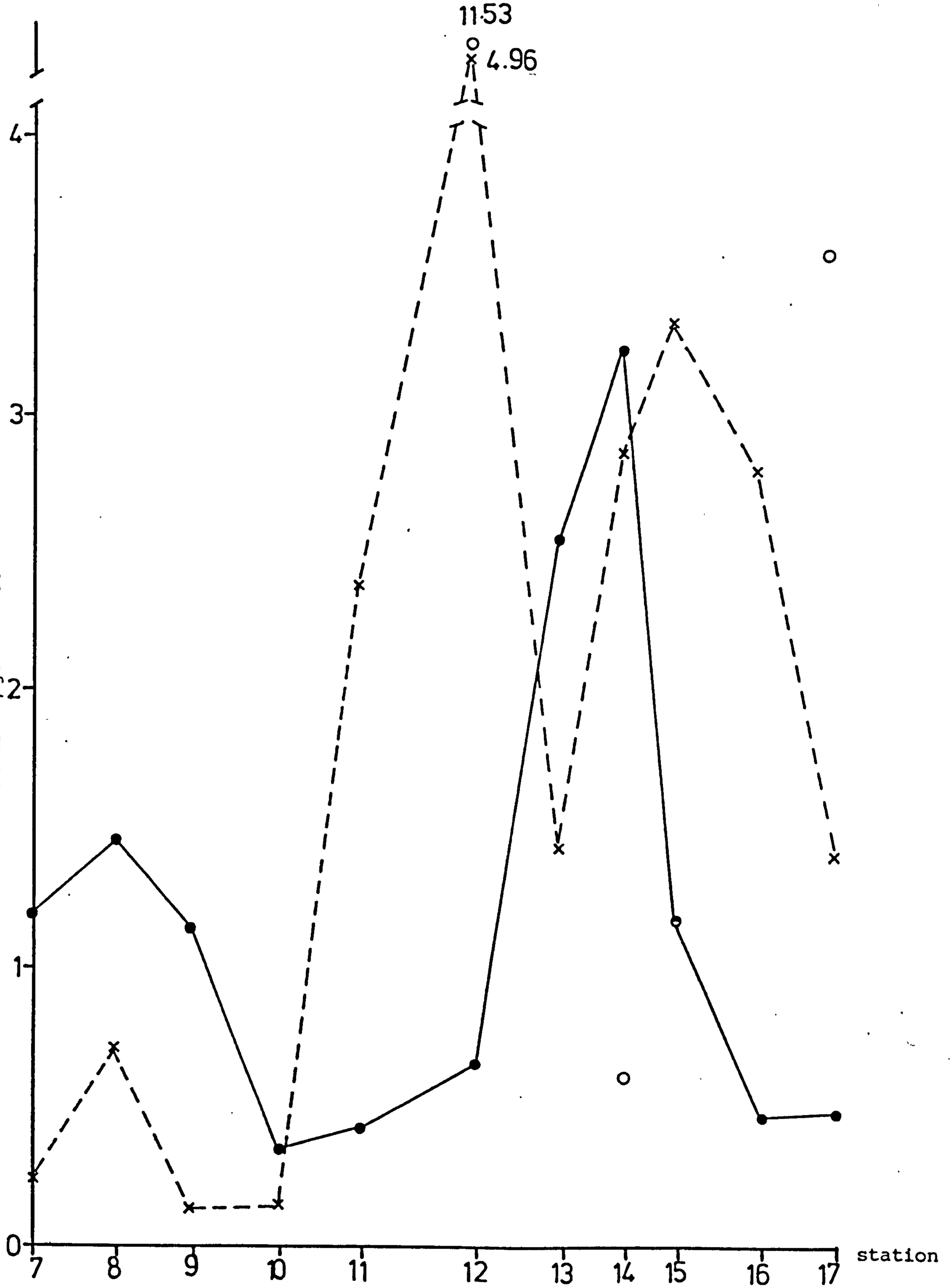


FIGURE 4.48 : CRUISE HGL III. DISTRIBUTION OF PHOTOTROPHIC UREA ASSIMILATION INDICES[A](-●-) AND HETEROTROPHIC UREA ASSIMILATION INDICES USING CARBON DERIVED FROM ATP (O) [C] AND FROM BACTERIAL NUMBERS AND VOLUME (-×--) . [D] . (21 & 23·9·76).

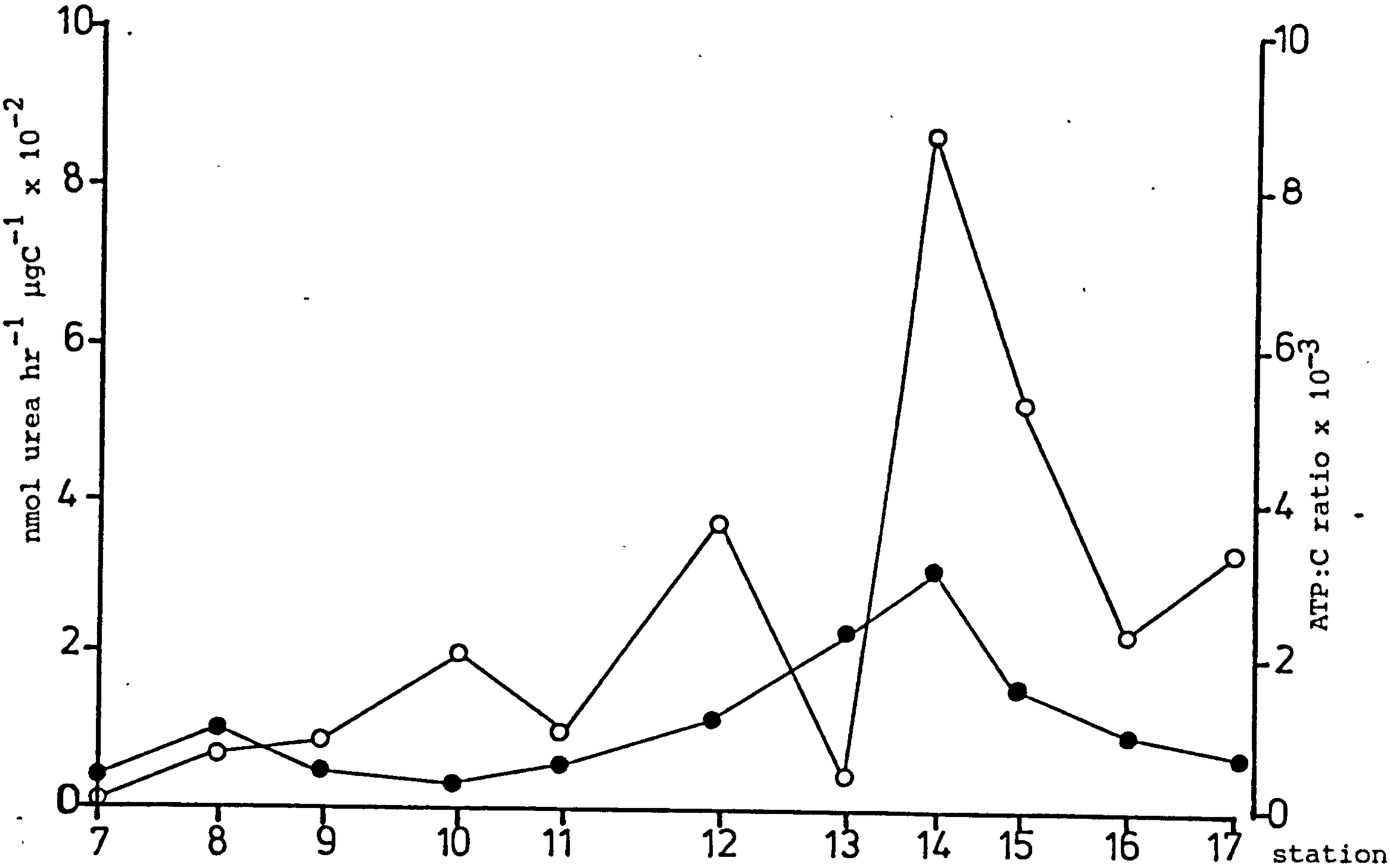


Fig. 4.49 CRUISE HGL III. DISTRIBUTION OF CELLULAR ATP : CELLULAR C RATIOS (—o—) AND TOTAL UREA ASSIMILATION INDICES [E] (—●—). (21 & 23·9·76).

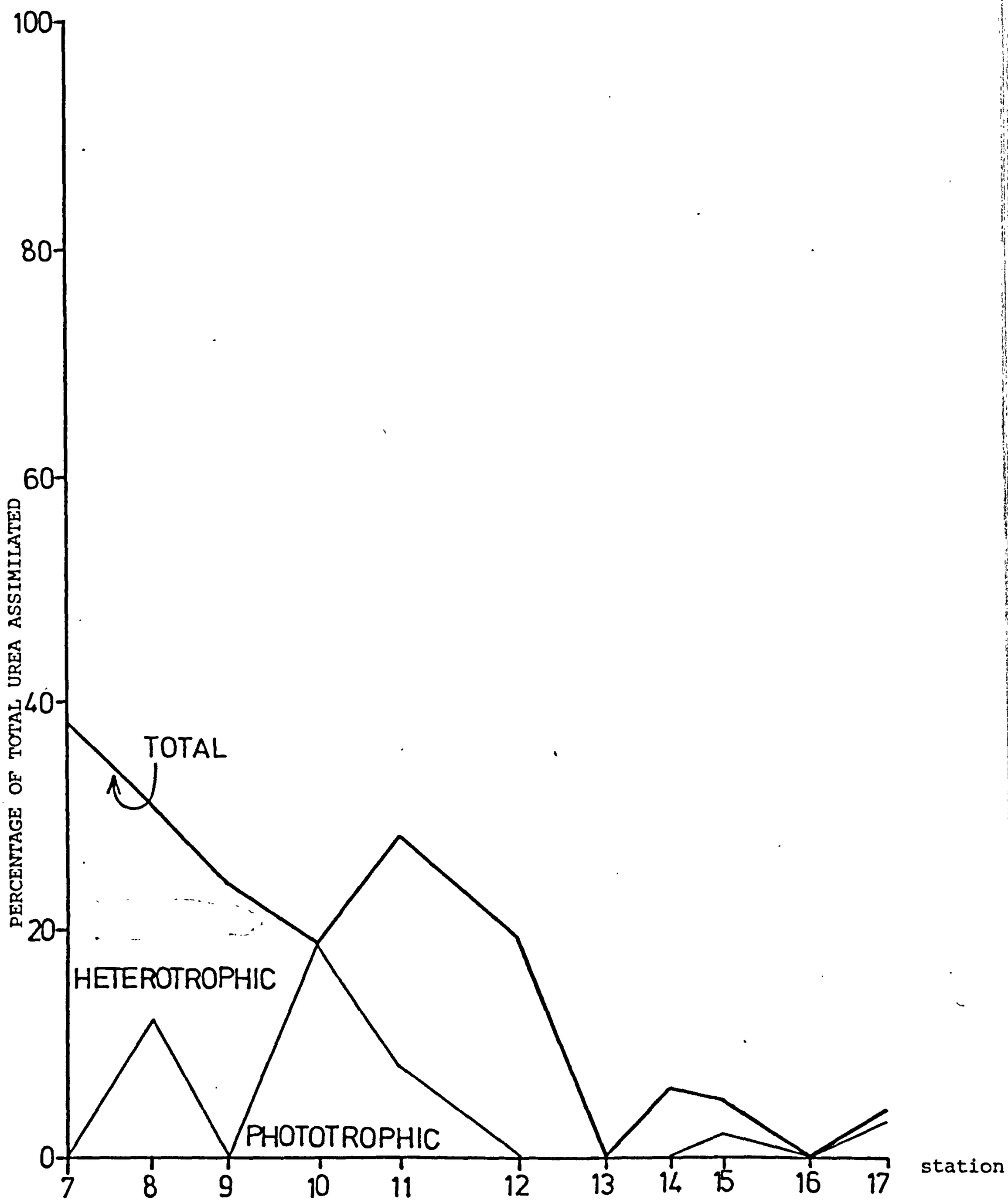


FIGURE 4.50 : CRUISE HGL III. DISTRIBUTION OF ^{14}C - UREA INCORPORATED IN LIVING CELLS (PHOTOTROPHIC AND HETEROTROPHIC) AS A PERCENTAGE OF TOTAL UREA ASSIMILATED. (21 & 23.9.76).

Total urea assimilation indices (E) (fig. 4.47) calculated from microbial carbon (E) derived from chlorophyll a and bacterial numbers and volumes show less variation as index (B) with the highest indices found at stations 13 and 14. The two total urea assimilation indices (E) and (B) bear no relation to each other.

Little can be said about the distribution of heterotrophic urea assimilation indices (C) (fig. 4.48) calculated from carbon derived from microbialATP minus carbon derived from chlorophyll a, as often the carbon derived from the latter was greater than that derived from the former.

Heterotrophic urea assimilation indices (D) (fig.4.48) calculated from carbon derived from bacterial numbers and volumes are lowest in the estuarine stations 7 - 10 with comparatively high indices occurring in the offshore stations.

There are two notable peaks of phototrophic urea assimilation indices (A) (fig. 4.48) calculated using carbon derived from chlorophyll a; a large peak at stations 13 and 14 and a comparatively smaller one at station 7 - 9. Phototrophic urea assimilation indices (A) are substantially higher than heterotrophic indices (D) in the estuary, whilst, with the exception of stations 13 and 14, the opposite can be said for the non-estuarine waters.

It should be noted that the distribution of cellular ATP:cellular carbon ratios and total urea assimilation indices (E) (fig. 4.49) are very similar, both values are low in the estuary and inshore stations whilst both are comparatively high in the more offshore stations.

The percentage of ^{14}C (from the labelled urea) incorporated in living cells (fig. 4.50) shows a general seawards decrease. With the exception of stations 10 and 17 the majority of ^{14}C is incorporated in heterotrophic cells.

4.1.6 Cruise HGL III (h)

4.1.6.1 Physical results

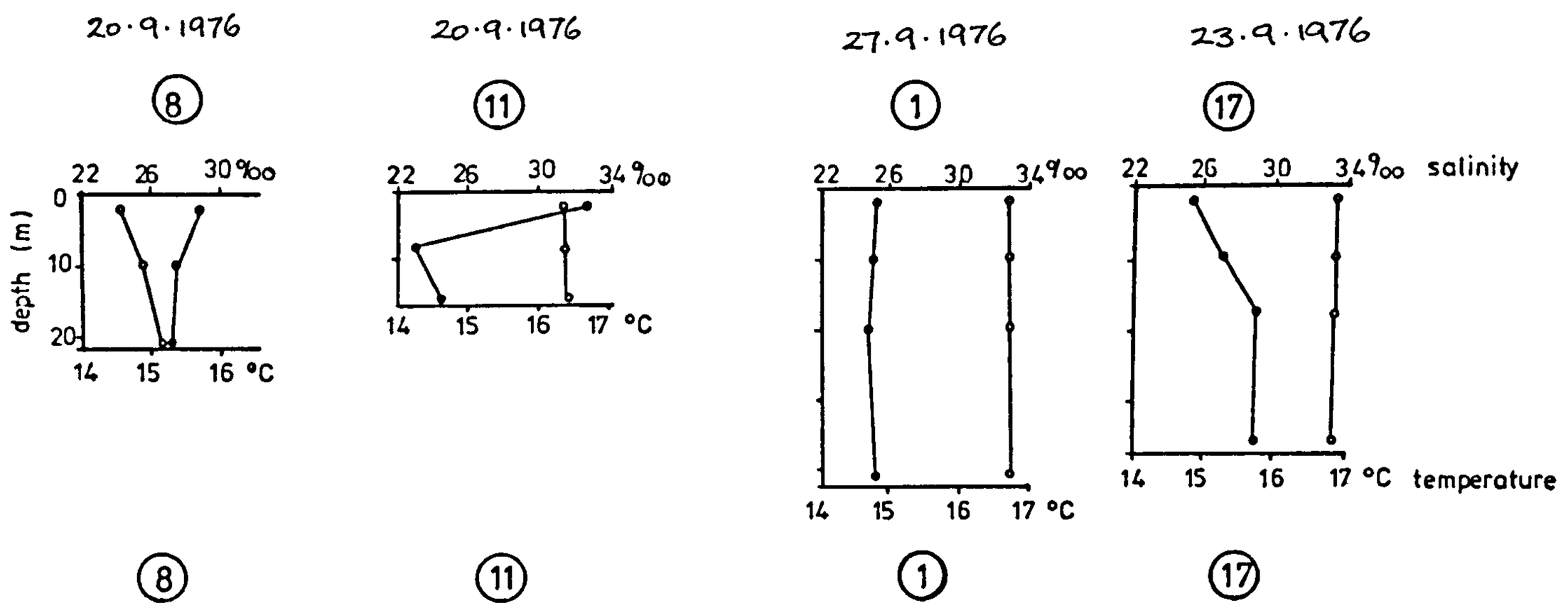
Salinity, density and secchi disc extinction depth

Figure 4.51 : Cruise HGL III. Depth profiles. Station number = ○

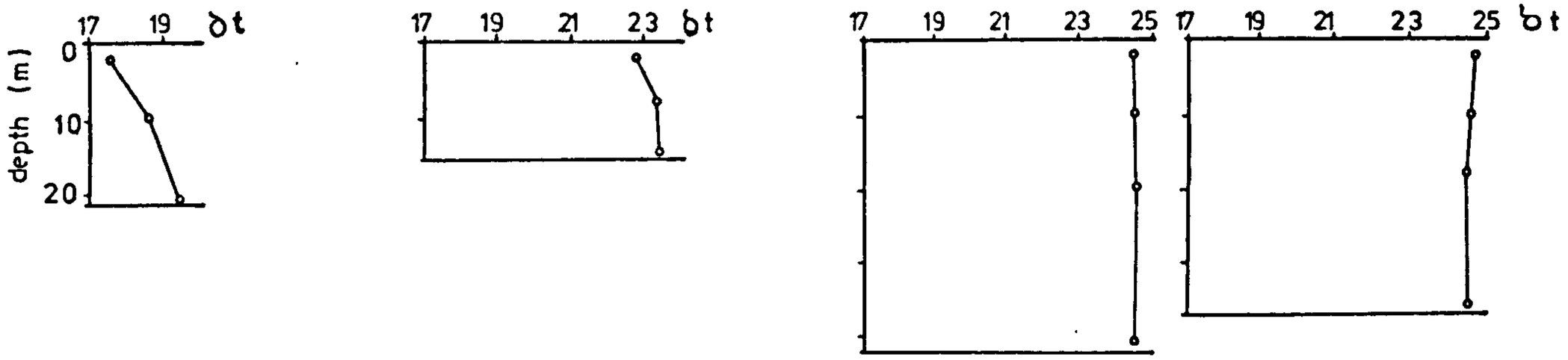
Sampling date :

Temperature —●—

Salinity —○—



Density (sigma t) —○—



Chlorophyll a —●—

Total microbial ATP —○—

Bacteria numbers —□—

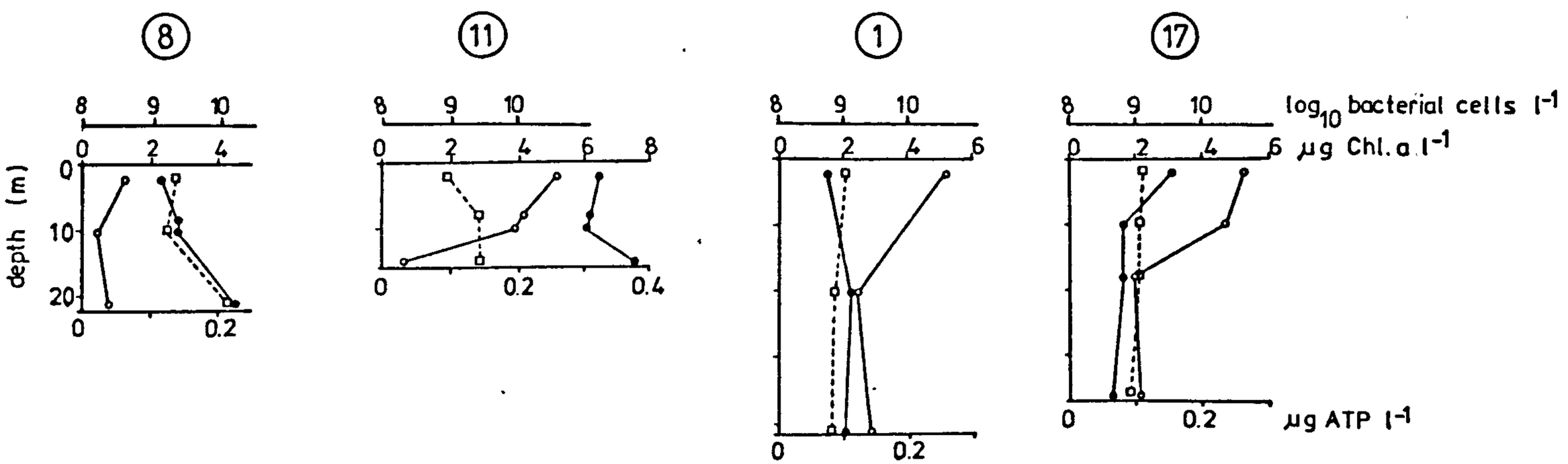
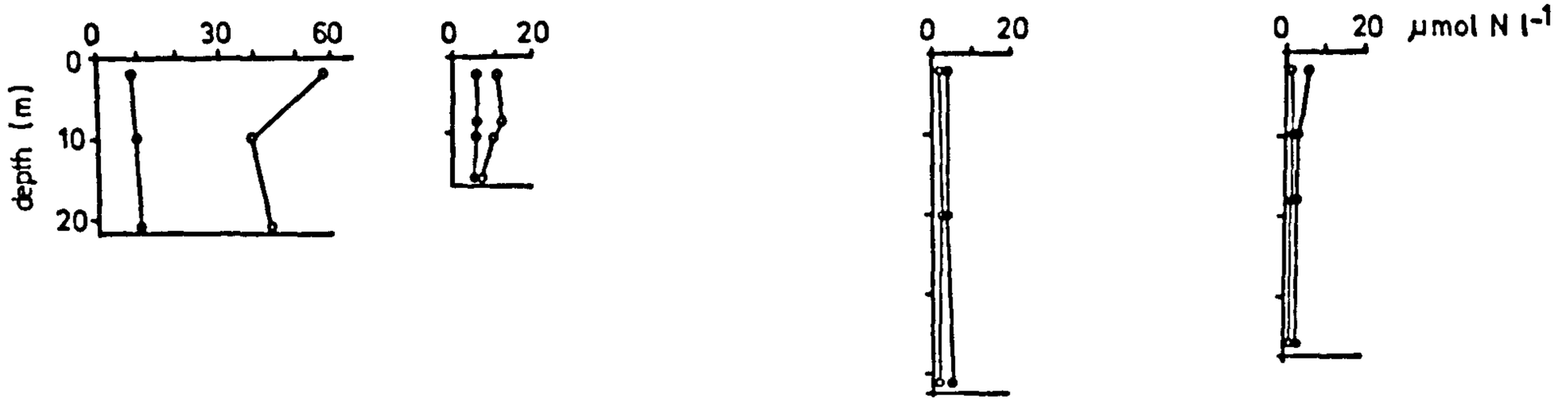


Figure 4.52 : Cruise HGL III. Depth profiles. Station number = ○

Sampling date : 20·9·1976 (⑧), 20·9·1976 (⑪), 27·9·1976 (①), 23·9·1976 (⑰)

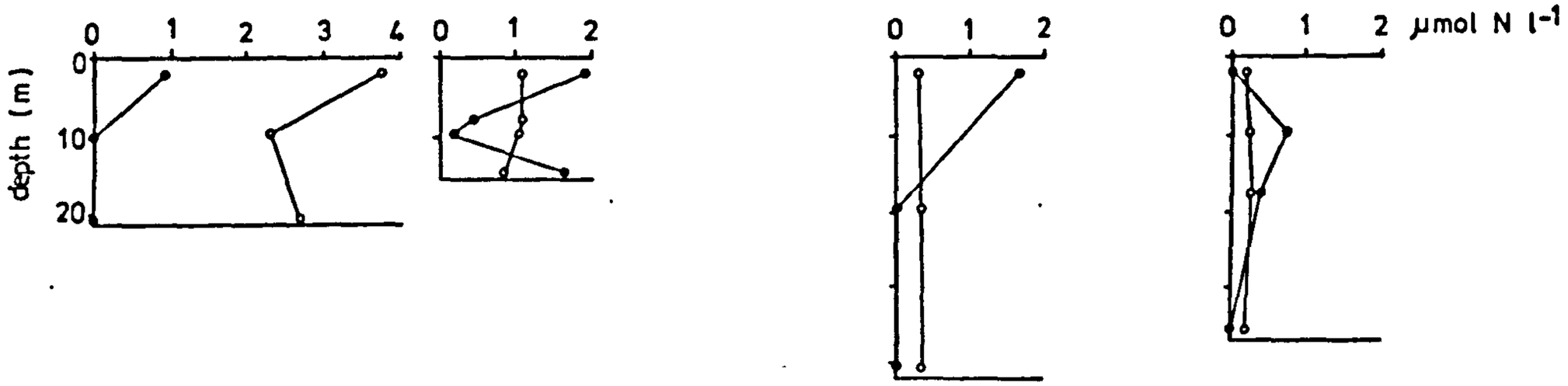
NH_3 —●—

NO_3 —○—



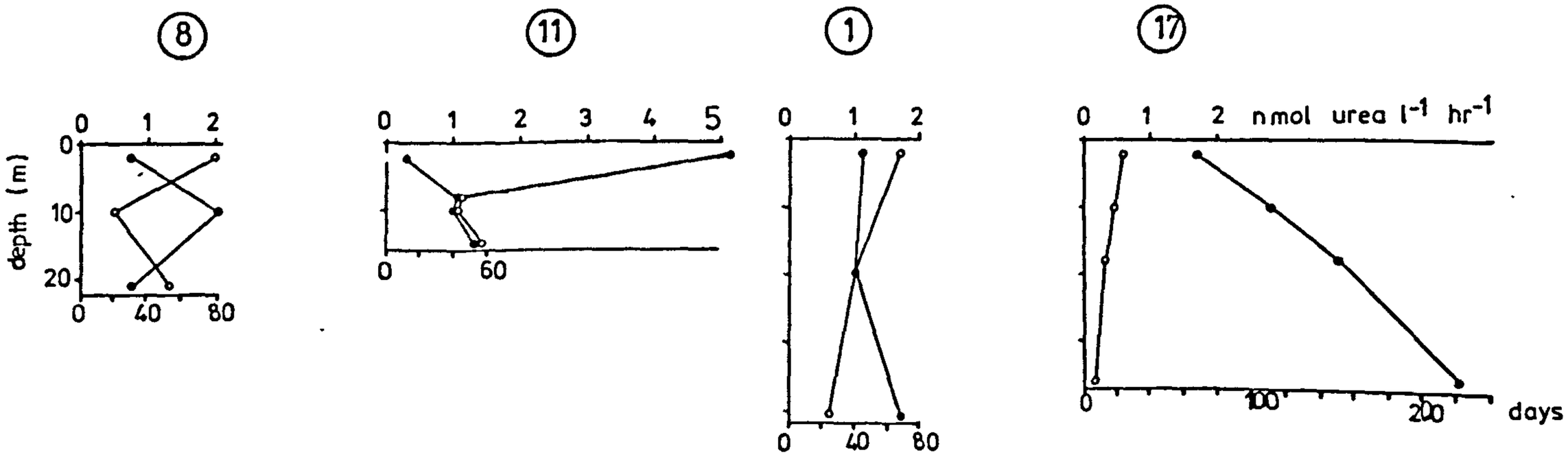
Urea-N —●—

NO_2 —○—



Total urea assimilation rates (nmol l^{-1} hr^{-1}) —○—

Total urea turnover times (days) —●—



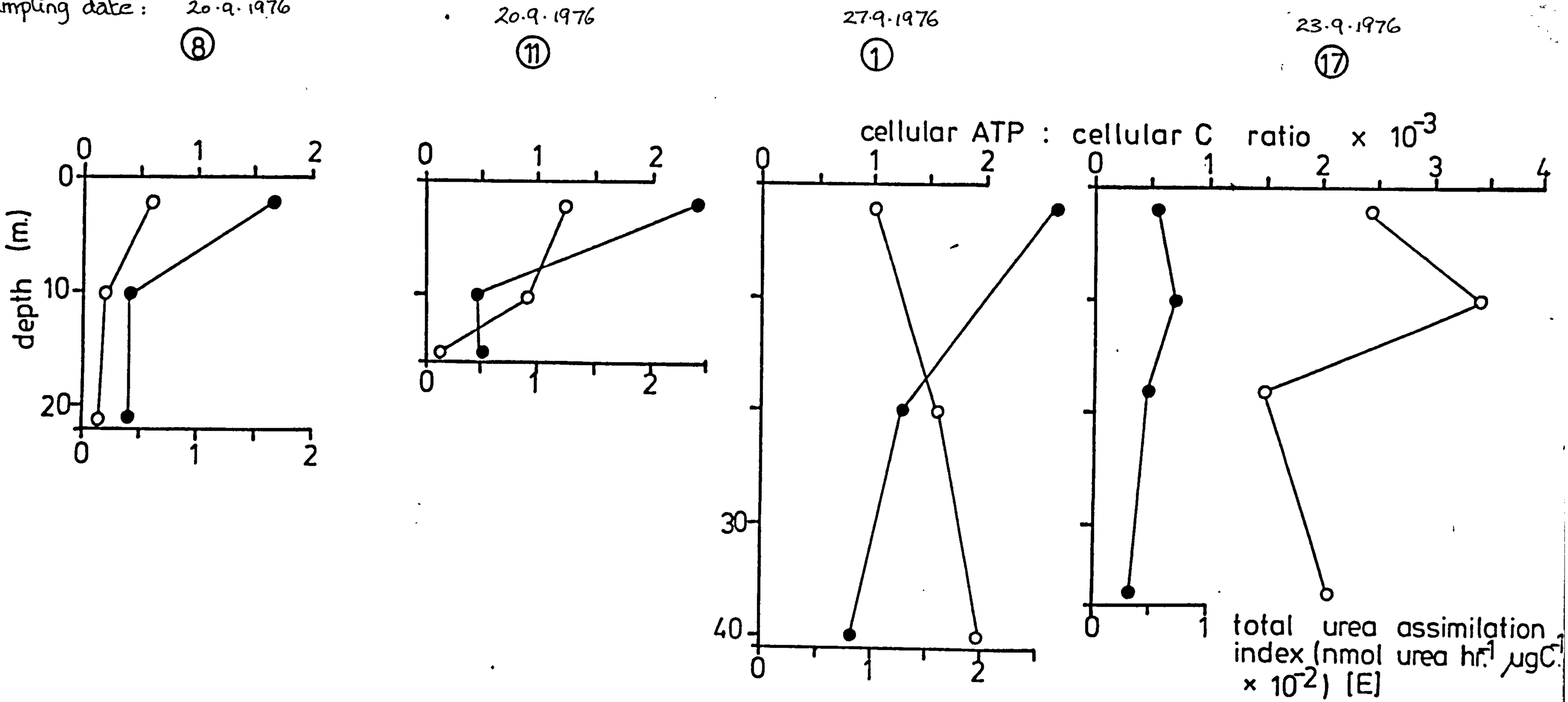


Fig. 4.53 CRUISE HGL III. VERTICAL DISTRIBUTION OF CELLULAR ATP : CELLULAR C RATIOS (—○—) AND TOTAL UREA ASSIMILATION INDEX [E] (—●—).

○ STATION NUMBER.

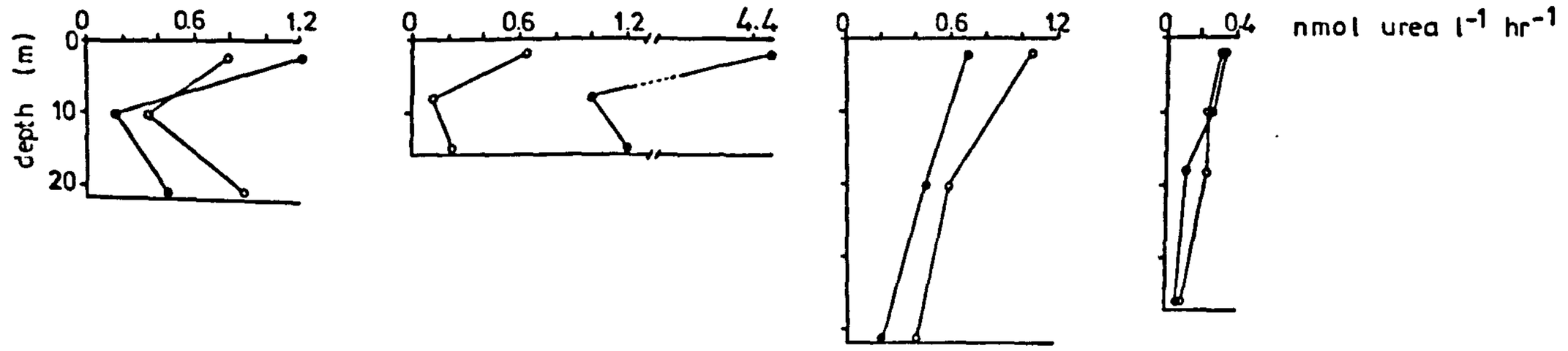
Figure 4.54 : Cruise HGL III. Depth profiles. Station number = ○

Sampling date : 20·9·1976 (8) | 20·9·1976 (11) | 27·9·1976 (1) | 23·9·1976 (17)

Urea assimilation rates (nmol l^{-1} hr^{-1}):

phototrophic —●—

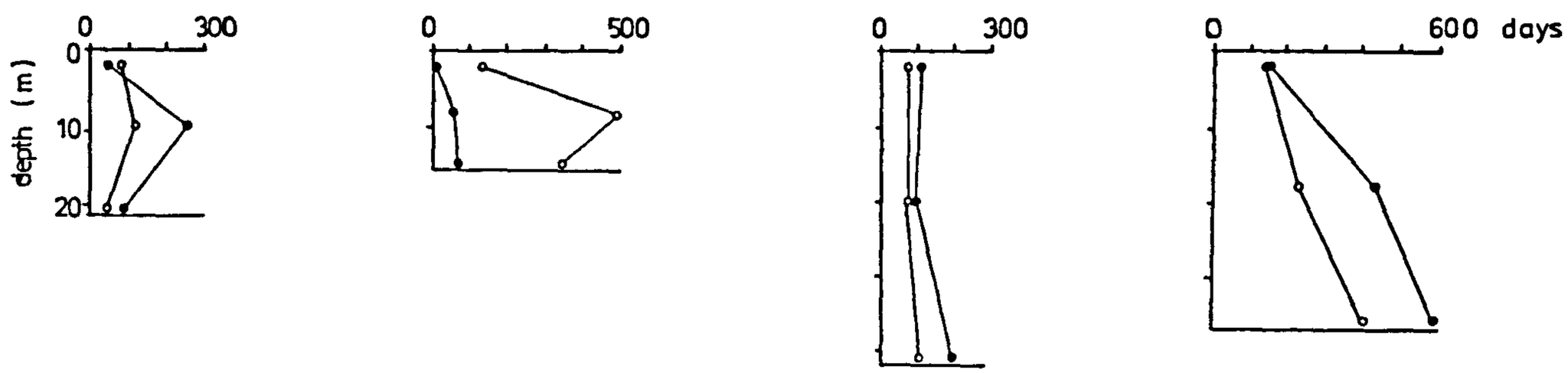
heterotrophic —○—



Urea turnover times (days):

phototrophic —●—

heterotrophic —○—



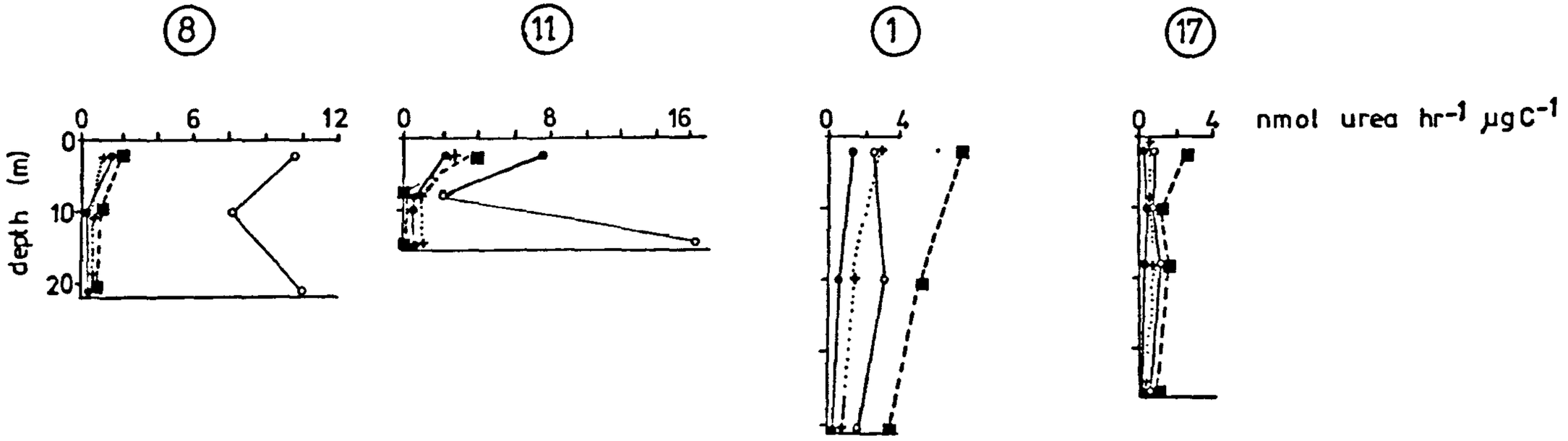
Urea assimilation indices (nmol urea hr^{-1} μgC^{-1} $\times 10^{-2}$):

[A] phototrophic (chl.a)* —●—

[B] total (ATP)* —○—

[E] total (chl.a + bacterial biomass)* ·····+·····

[D] heterotrophic (bacterial biomass)* ---■---



* origin of carbon use to calculate indices.

(table 4.52) indicate that these stations, in the vicinity of Helgoland are not greatly influenced by fresh water. $\bar{V}$ values (table 4.52) show that all of these stations are well mixed. These stations have the same salinity as the water of station 13 and the bottom water of station 14.

4.1.6.2 Nutrient, biomass and urea assimilation measurements

Nutrient and microbial biomass (tables 4.53 - 4.55) measurements are generally characteristic of stations 12 - 17, most particularly stations 12 and 13. Urea assimilation rates and turnover times (tables 4.57 - 4.61), however, show a greater resemblance to those measured at stations 16 and 17.

4.1.7 Cruise HGL III Depth profiles at Stations 8, 11, 1 & 17

4.1.7.1 Physical measurements

Profiles of the physical data (fig. 4.51) indicate that station 8 is both temperature and salinity stratified (having a $\bar{V}$ of 20 joules m^{-3}) while station 11 is only slightly stratified ($\bar{V}$ of 4 joules m^{-3}) which can be attributed mostly to temperature. Stations 1 and 17 have little density surface-bottom difference, indicating mixed waters.

4.1.7.2 Nutrient measurements

Urea concentrations (fig. 4.52) are generally higher in the surface waters, although the bottom water of station 11 has a relatively high concentration. Nitrate and nitrite concentrations are highest in the surface water of stations 8 and 11 whilst homogenous throughout the water column at stations 1 and 17. Concentrations of ammonium do not vary greatly throughout the water column of all four stations.

4.1.7.3 Biomass measurements

The distribution of chlorophyll a (fig. 4.51) throughout the water column varies according to the station; stations 8, 11 and 1 have a high concentration in the bottom waters, while station 17 has a high surface maximum. The highest concentrations of chlorophyll a were measured throughout the water column of station 11.

The highest concentrations of total microbial ATP (fig. 4.51) were found in the surface waters of stations 11, 1 and 17. The concentration of ATP decreased with depth at all four stations.

Bacterial numbers (fig. 4.51) and biomass were highest in the bottom waters of stations 8 and 11, while stations 1 and 17 if any change at all, showed a decrease in numbers and biomass with depth. Table 4.63 indicates that there is considerable differences in the morphology of the cells of surface and bottom waters of station 8. The former has a predominance of rods while the bottom water is mainly composed of coccoid and diploccoid forms. The bottom water of station 17 is composed totally of minute cocci while the surface waters have a large proportion of vibroiS forms.

Total microbial carbon (E) derived from chlorophyll a and bacterial numbers and volumes showed a tendency to increase with depth except at station 17 where it decreased with depth.

Cellular ATP:cellular carbon ratios (fig. 4.53) decreased with depth at stations 8 and 11, increased with depth at station 1 and showed a 10 m. maximum at station 17.

4.1.7.4 Urea Assimilation measurements

Urea assimilation rates (figs. 4.52 and 4.54) are highest in surface waters at all stations, decrease with depth at stations 1 and 17, while stations 8 and 11 have midwater minima. Phototrophic urea assimilation rates are higher than heterotrophic assimilation rates in the surface water of station 8 and throughout the water column of station 11 whereas heterotrophic assimilation rates are higher at station 1 while both rates are similar throughout the water column at station 17.

The vertical distribution of urea turnover times (fig. 4.52) is generally inverse to that of the urea assimilation rates, lowest turnover times usually present in the surface waters.

There is no consistency between total urea

assimilation indices (B) and (E) (fig. 4.54) except perhaps at station 17. Exempting total assimilation index (B) there is a general decrease of assimilation indices with depth. Phototrophic indices (A) are higher than heterotrophic indices (D) in the mid and bottom water of station 11 while the reverse can be said at all other stations and depths, particularly at stations 1 and 17.

4.2 Discussion

4.2.1 Discussion of Hydrography of Southern German Bight

Before discussing the biology and chemistry of the Southern German Bight it is necessary to establish and understand the general hydrographical features of the area. Physical data was not collected in sufficient detail for Cruise HGL I. This was in part because the importance of physical features on the biology and chemistry was not anticipated, and in part due to lack of oceanographic facilities at the B.A.H. It is therefore important to use all means possible to understand the complexity of the hydrography of this area. Infra-red (IR) satellite imagery, hydrographic surveys described in the literature, physical models which predict stratified or mixed waters as well as physical data collected on the HGL Cruises will be amalgamated and models of the water regimes during the times of sampling postulated.

The IR satellite scanner measures temperatures of the top 0.1 mm of the sea surface and not the whole surface layer. When there is no interference from cloud it seems likely that the radiation temperature is representative of the pattern of sea-surface temperatures (Simpson, et.al. 1977). Warm (dark image) water and cooler (light image) water are easily identified and sharp changes in image density have been identified with frontal systems (Simpson et.al. 1977; Simpson & Bowers, 1979).

Serious interference from dense cloud cover during Cruises HGL I and III results in no IR images during that period. However, images are available around the time of

Figure 4.55 : Infra-red satellite image of the Southern German Bight at 0929 (c.1.5hrs before high water) on 24.8.76

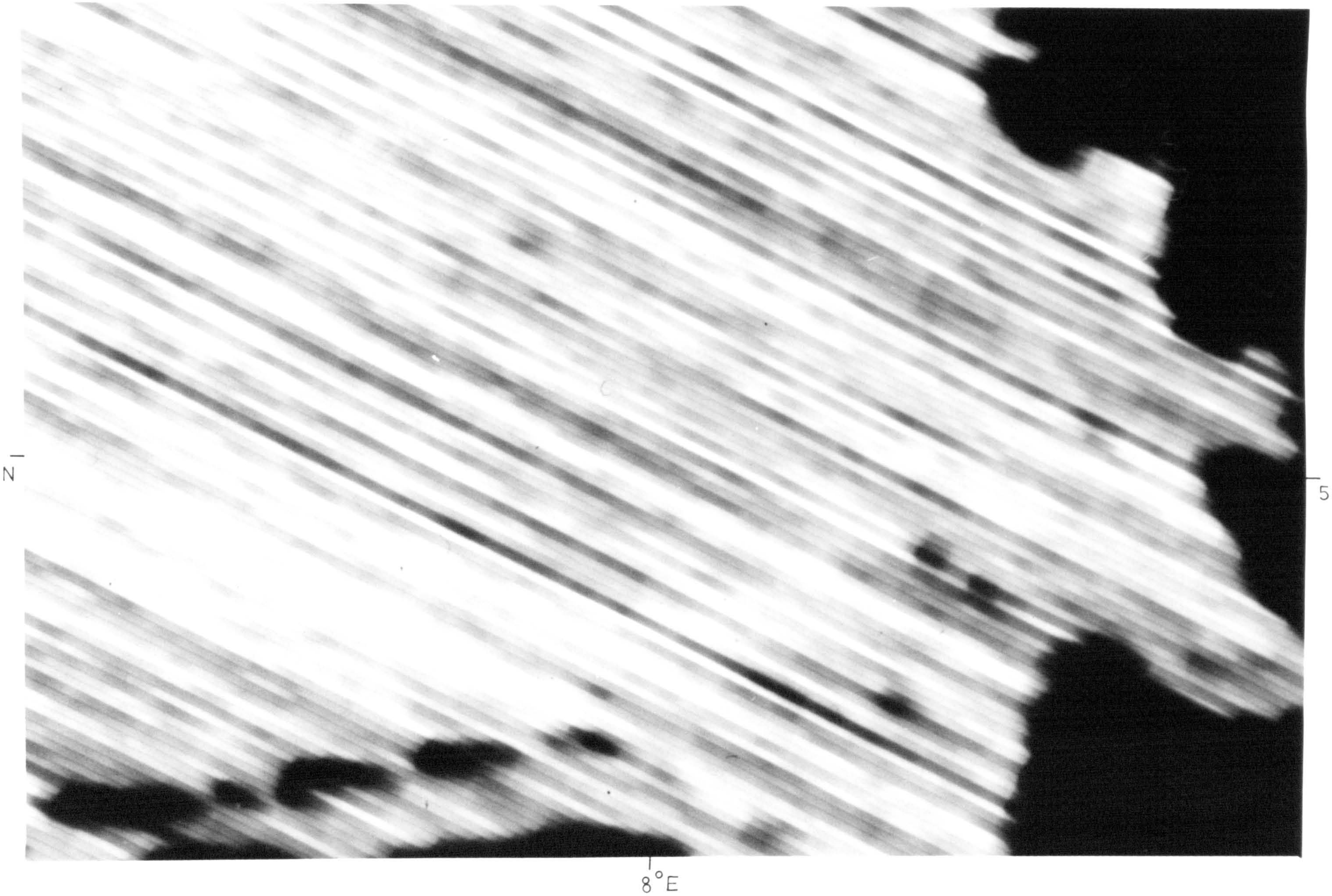


Figure 4.56 : Infra-red satellite image of the Southern German Bight at 1851 hrs (approx. 1 hrs after low water) on 24.8.76

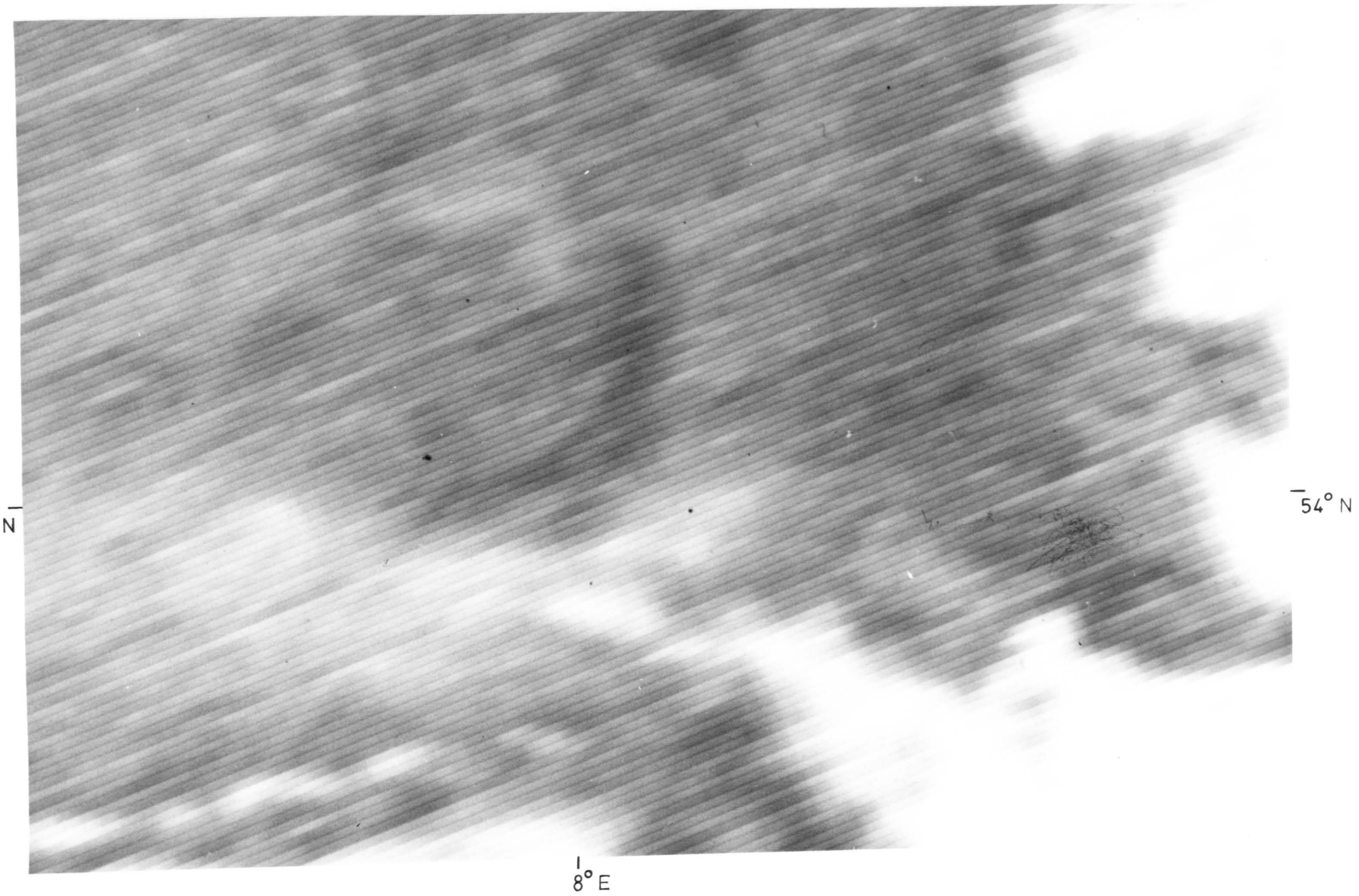


Figure 4.57 : Infra-red satellite image of the Southern German Bight at 1040 hrs (c. 1hr before high water) on 25.8.76

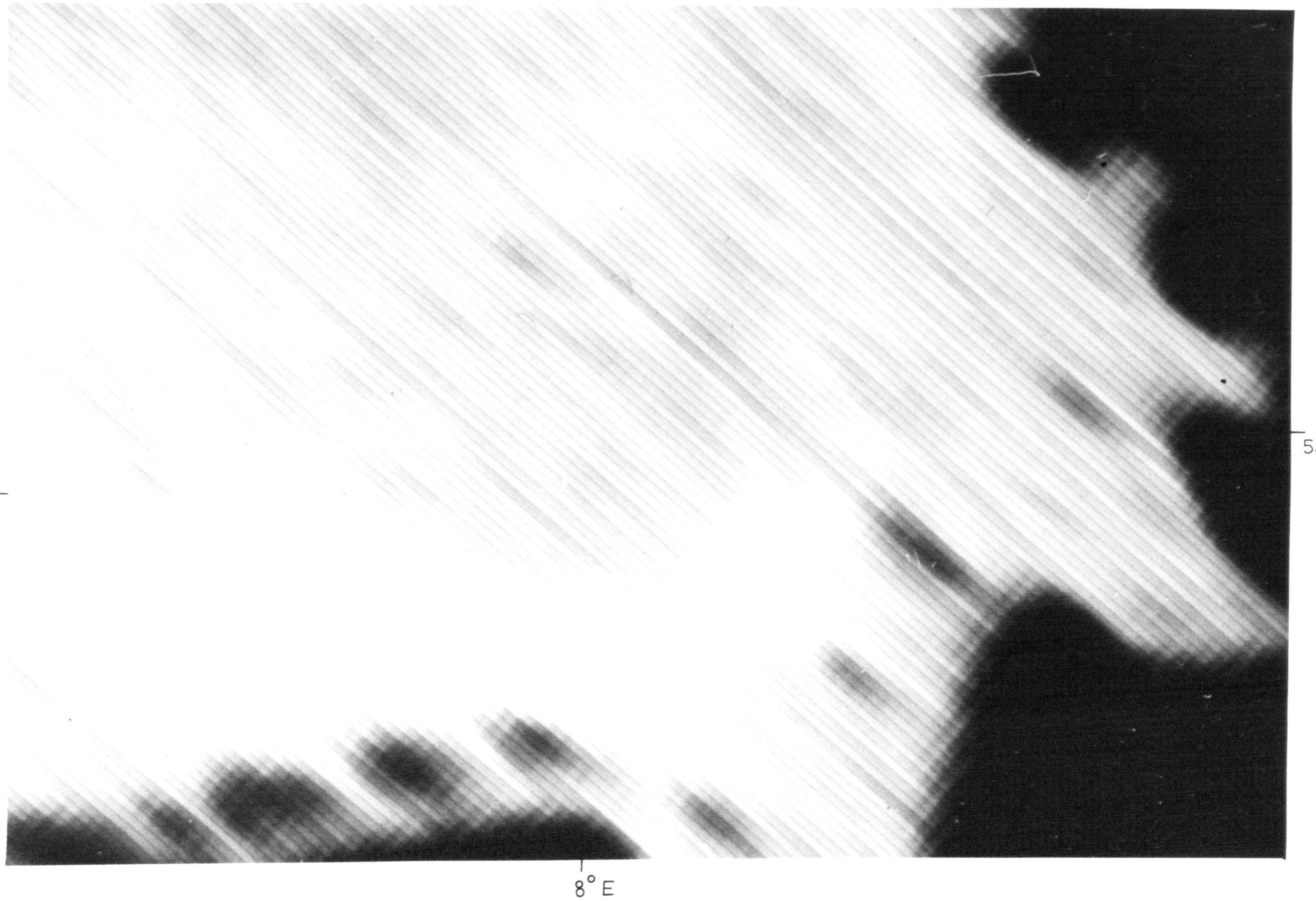


Figure 4.58 : Infra-red satellite image of the Southern German Bight at 2002 hrs (c.1.5hrs after low water) on 25.8.76

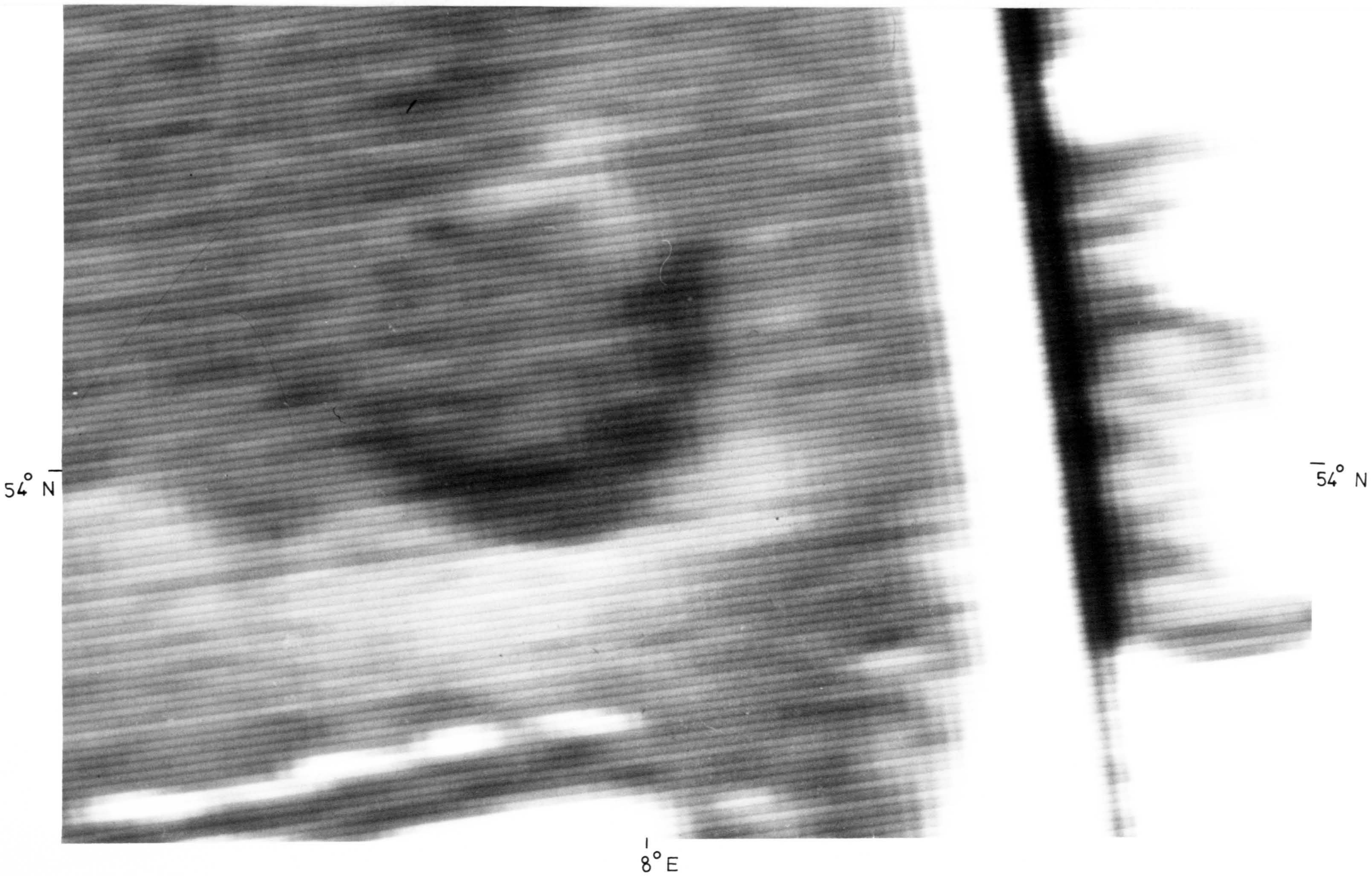
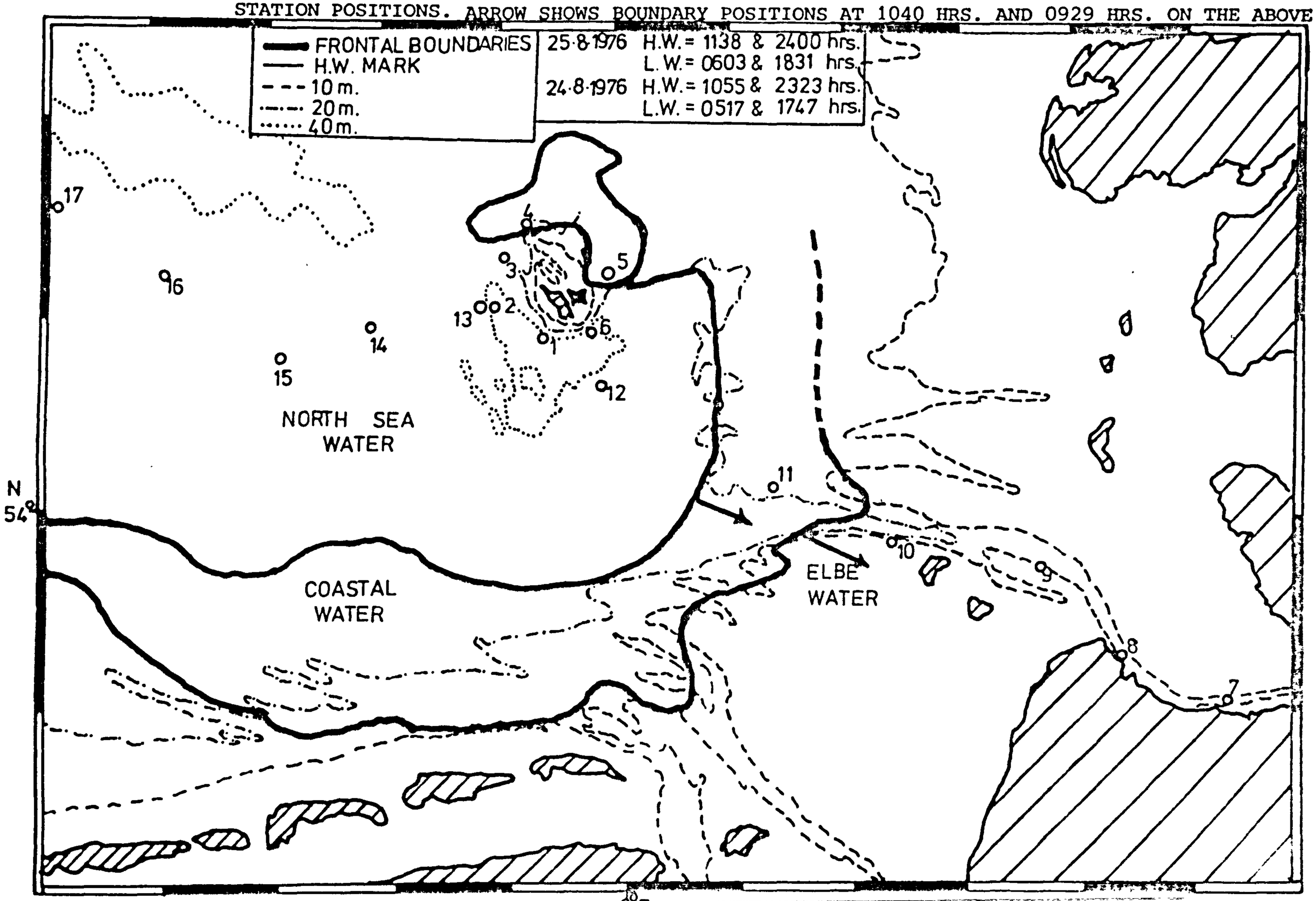


FIGURE 4.59 : POSITION OF THERMAL BOUNDARIES AS SHOWN BY SATELLITE IMAGES TAKEN AT 2002HRS. ON 25.8.1976 AND 1851 HRS. ON 24.8.1976 (PERIOD OF CRUISE HGL II) IN RELATION TO BOTTOM TOPOGRAPHY AND STATION POSITIONS. ARROW SHOWS BOUNDARY POSITIONS AT 1040 HRS. AND 0929 HRS. ON THE ABOVE DAYS.



cruise HGL II, in the morning and evening of 24.8.76 and 25.8.76 (figs. 4.55 - 4.58). Surface features are easily distinguishable on the images taken in the evening after the surface waters have received hours of solar heating during the daylight hours (figs. 4.56 and 4.58). Surface features on the images taken in the morning are not so distinguishable due to surface cooling during the night (figs. 4.55 and 4.57). Figure 4.55 unfortunately is affected by mechanical interference, but despite this 'noise' a cold coastal regime is just discernible.

The satellite images are on approximately the same scale as the maps of the southern German Bight (eg. fig. 4.59) indicating station positions. If we examine the evening images (figs. 4.56 and 4.58) similar surface features are visible which suggests that tidal mixing does not disrupt the features. Three distinct water temperature regimes are easily identified:

a) a warm North Sea regime, its limit marked by the Southern edge of a cresent.
b) a colder coastal regime running parallel to the coast.
c) a warm inshore regime which extends to the coastline and up the Elbe and Weser estuaries and will be called the Elbe regime.

Sharp boundaries between the three regimes are easily distinguishable. Figure 4.59 shows the position of these thermal boundaries in relation to station position and bottom topography. Boundary positions at approximately high and low water are also marked indicating the tidal movement of the water regimes.

A persistent cold patch of water north-northeast of Holgoland coincides with shallower (<15 m.) water associated with a ridge called the Steingrund (Stocks, 1955). The Steingrund could act as a stirring rod mixing water as the tidal streams move back and forth. Due to shallow water in this area less energy is required to bring about mixing.

The boundary between the Coastal and Elbe regime follows the bottom topography (fig. 4.59), notably the 10 m. depth contour, the warmer water occurring in the shallower

FIGURE 4.60

CRUISE HGLI

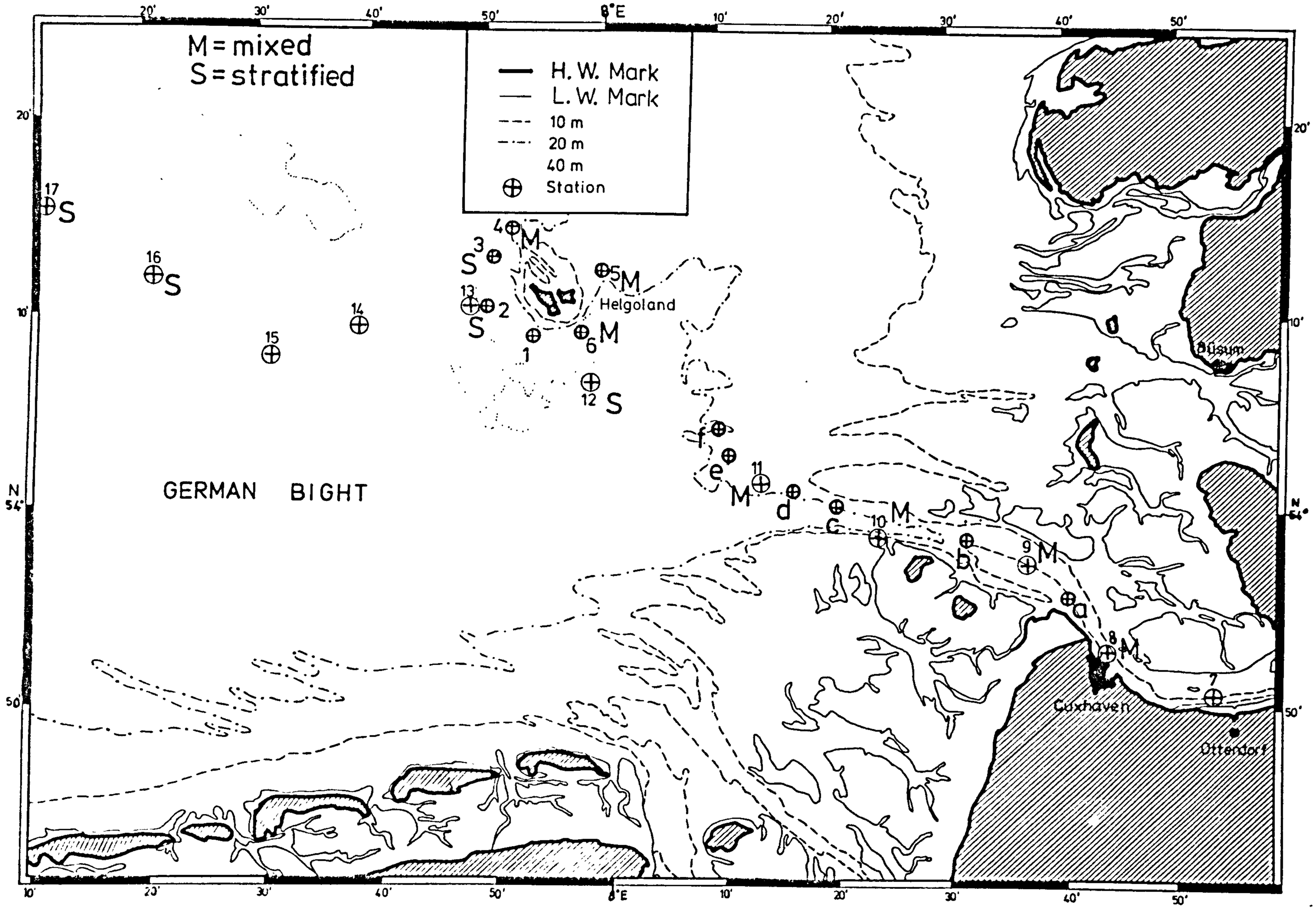


FIGURE 4.61

CRUISE HGL II

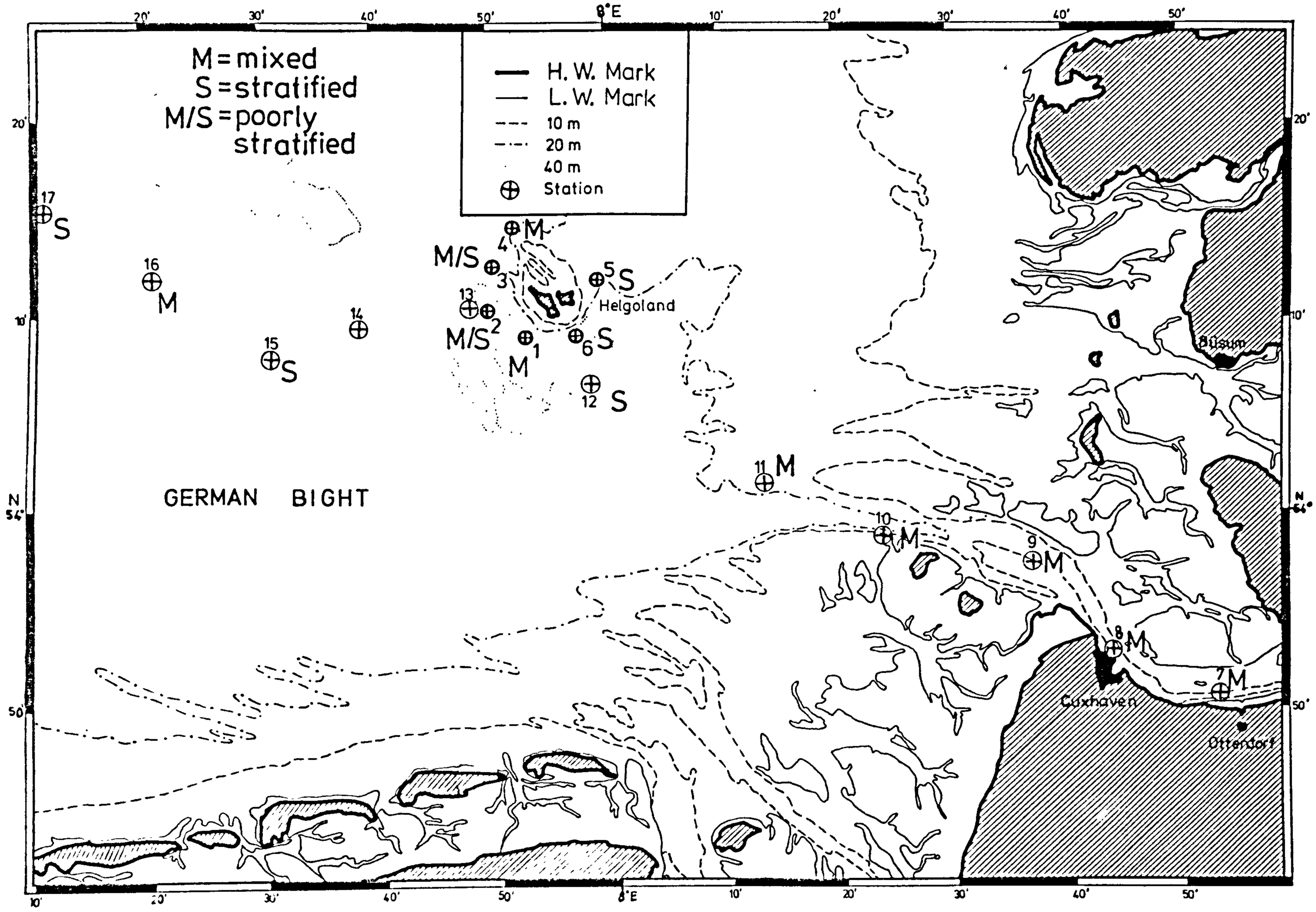
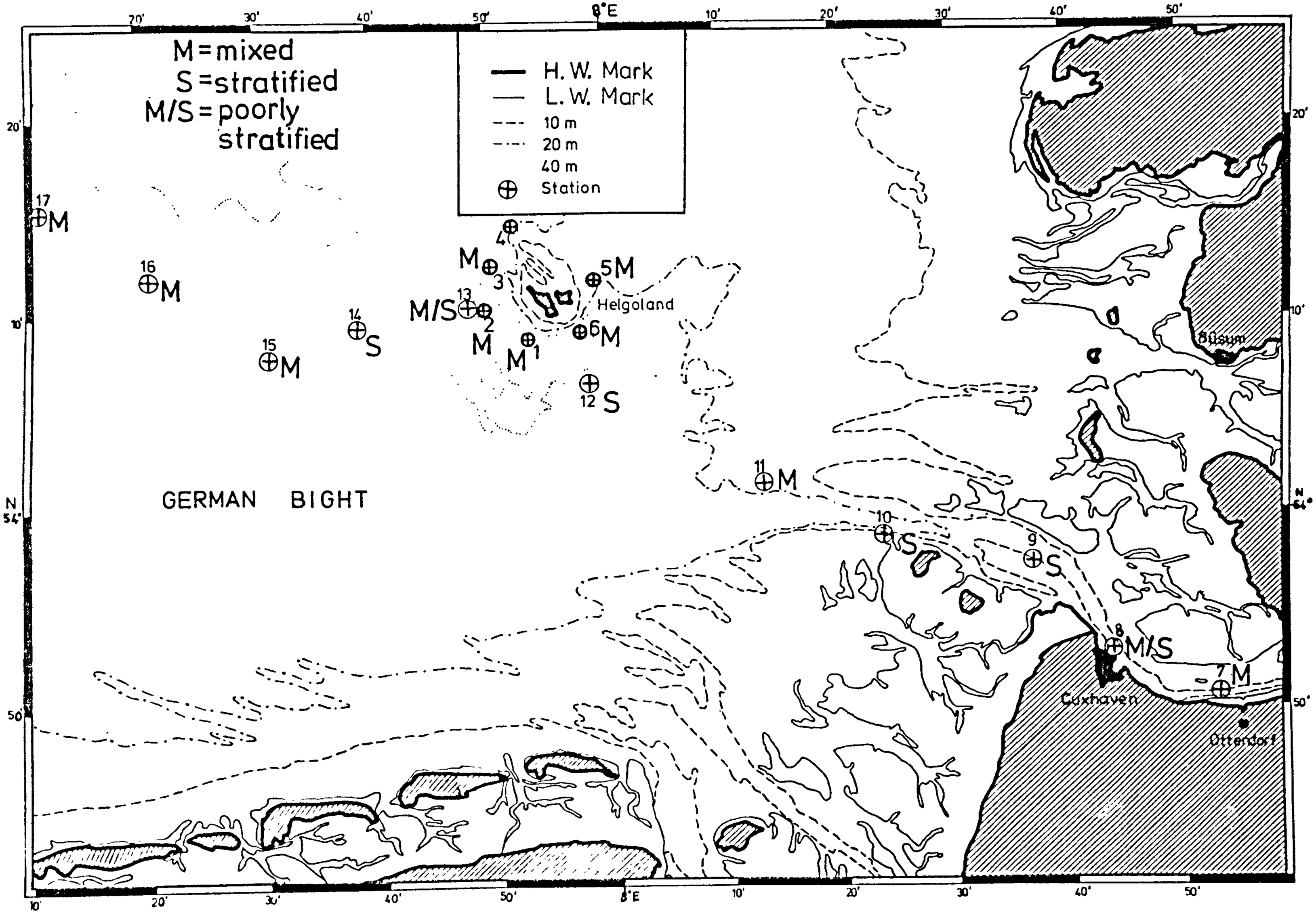


FIGURE 4.62

CRUISE HGL III



Elbe water. Simpson et.al. (1977) found, with a few exceptions, that these areas are not permanently stratified and attributed the higher surface temperatures to increasing surface heat input per unit volume with decreasing depth. Physical data obtained on Cruises HGL I and II (Section 4.1) verify that there is little surface to bottom temperature difference in the Elbe regime and values for $\tilde{V}$ obtained on Cruise HGL II indicate mixed water. The sharp horizontal boundary or discontinuity between the coastal and Elbe regimes could therefore be termed a topographic front.

The coastal regime which is intermediate between the Elbe and North Sea regimes has greater depth than the Elbe regime. The satellite photographs indicate the coastal regime has much colder surface water than either of the two other water regimes which could indicate mixing. Physical data obtained on Cruises HGL I and II also indicate that this water is intensively mixed (figs. 4.60, 4.61 and 4.62).

The warm (dark) waters on the IR images in the deeper (>20 m.) North Sea regime could be indicative of thermal stratification. Indeed, physical data obtained on Cruises HGL I and II also indicate that there is strong temperature and salinity stratification resulting in high $\tilde{V}$ values. The boundary between the stratified North Sea regime and the mixed coastal regime is either termed a "shelf sea front" (Simpson and Bowers, 1979) or a "shallow sea front" (Bowman and Esaias, 1978). These fronts are commonly located in boundary regions between shallow wind and tidally mixed inshore waters and stratified, deeper offshore waters, e.g. Western Irish Sea front (Simpson, 1971; Simpson and Hunter, 1974), Celtic Sea front (Simpson and Hunter, 1974; Simpson, 1976), Ushant front (Pingree et.al., 1978; Simpson and Pingree, 1978). The shelf sea fronts can be located by the parameter h/U_s^3 (Simpson and Hunter, 1974; Simpson et.al., 1977) where h is the water depth in meters and U_s is the tidal stream amplitude at springs in m. sec^{-1}. Simpson and Hunter (1974) found the Irish Sea front was approximately parallel to contours of h/U_s^3 at a value between 65 and 100.

Unfortunately, h/U_s^3 has not been modelled in the Southern German Bight and U_s data was not available to determine h/U_s^3 in conjunction with this investigation and compare its values with the position of the shelf sea front.

However, a large scale model, $E = \log_{10}E$ (Pingree et.al., 1978) did take the Southern German Bight into account, where E is the tidal energy dissipated per unit mass (erg g^{-1} s^{-1}). $E = \log_{10}E$ is a theoretical calculation of summer stratified waters ($E < -2$), mixed waters ($E > -1$) and transitional waters ($E = -1.5$). They predicted mixing in the coastal regime ($E > -1$) and a transitional zone ($-2.0 < E < 1.0$) in the North Sea regime. The distribution of $E = -1.5$, which represents the predicted position of frontal boundaries, corresponds closely to the position of the shallow sea front described above.

Lüneburg (1963) described distinct water bodies in the Southern German Bight; the Weser and Elbe water which influences the coastal water, a tongue of $1^{o}/oo$ more saline Northern water which intrudes into and often runs under the Weser and Elbe water and Westwater which is a residual current flowing west to east along the East Fresian islands. He also describes a convergence zone between the Northern water and the Elbe and Weser water. However, his observations are based on surface water salinities and no data is provided for salinity or temperature stratification or mixing.

A more extensive and lengthy investigation of the hydrography of the German Bight from 1933 to 1967 was conducted by Goedecke (1955 and 1968). He concludes that the South Eastern German Bight is an area where two distinct water bodies, the North Sea water and the coastal water, meet and overlap. The more dense North Sea water penetrates under the less dense coastal water resulting in strong temperature and salinity gradients in the 'convergence zone'. The boundary between the two water bodies is maintained in spite of relatively low water depth and turbulent water movements due to constant input of new water from the two centres of the water bodies resulting in permanent thermohaline stratification. In the 'convergence

FIGURE 4.63: PHOTOGRAPHS OF THE SHALLOW SEA FRONT SEPARATING THE NORTH SEA AND COASTAL REGIMES TAKEN ON 14.5.78 NEAR STATION 12.

zone' a strong halocline occurs at all times of the year with maximum salinity stratification occurring at times of high freshwater input (winter and early spring). He found little thermal stratification during winter in the South Eastern North Sea except when long lasting winds blowing from the land to the sea occurred which resulted in the development of a thermocline between cold surface and warm bottom waters. This winter situation was also found in November 1976 during an investigation into the hydrographical structure of the Eastern German Bight by Martens (1978).

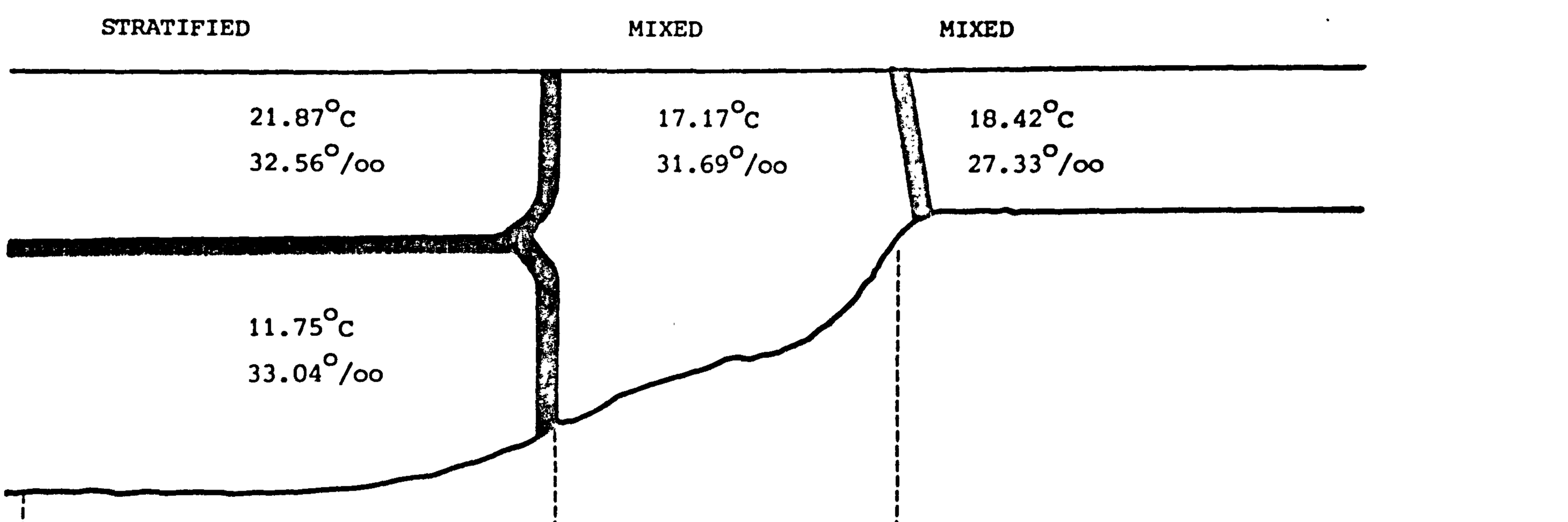
Goedecke (1968) found maximum thermal stratification, with warm surface and cold bottom water, occurring during the summer months in the deeper water, with the 15-20 m. bottom contour acting as the inner limit. No thermal stratification occurred in shallow coastal waters indicating good mixing.

It is therefore evident from the literature (Goedecke 1955 and 1968; Lüneburg 1963; Martens 1978) and from Cruise HGL I - III (figs. 4.4, 4.18, 4.19, 4.32 and 4.33) data that there are distinct, stable water regimes in the German Bight which can be traced year after year. Indeed, photographs (fig. 4.63) taken on 14.5.1978 show a distinct frontal boundary between two converging water masses (Bowman and Iverson, 1978) at approximately the position of the shallow sea front (between Station 11 and 12) thus emphasising its annual occurrence.

The hydrographical situation in the Southern German Bight described by Goedecke (1955 and 1968) and Lüneburg (1963) as summarized above is the same as the hydrographical situation interpreted from data from Cruises HGL I and II and the satellite imagery obtained around the time of Cruise HGL II. Cruise HGL III, however, is intermediate between the summer and winter hydrographic situations. The theoretical model of Pingree et.al. (1978), also described above, predicts the findings of Cruises HGL I and II and the findings of Goedecke's and Lüneburg's investigations.

It is therefore reasonable to present three stylised models of the hydrography of the German Bight: the summer situation on Cruises HGL I and II (fig. 4.64), the

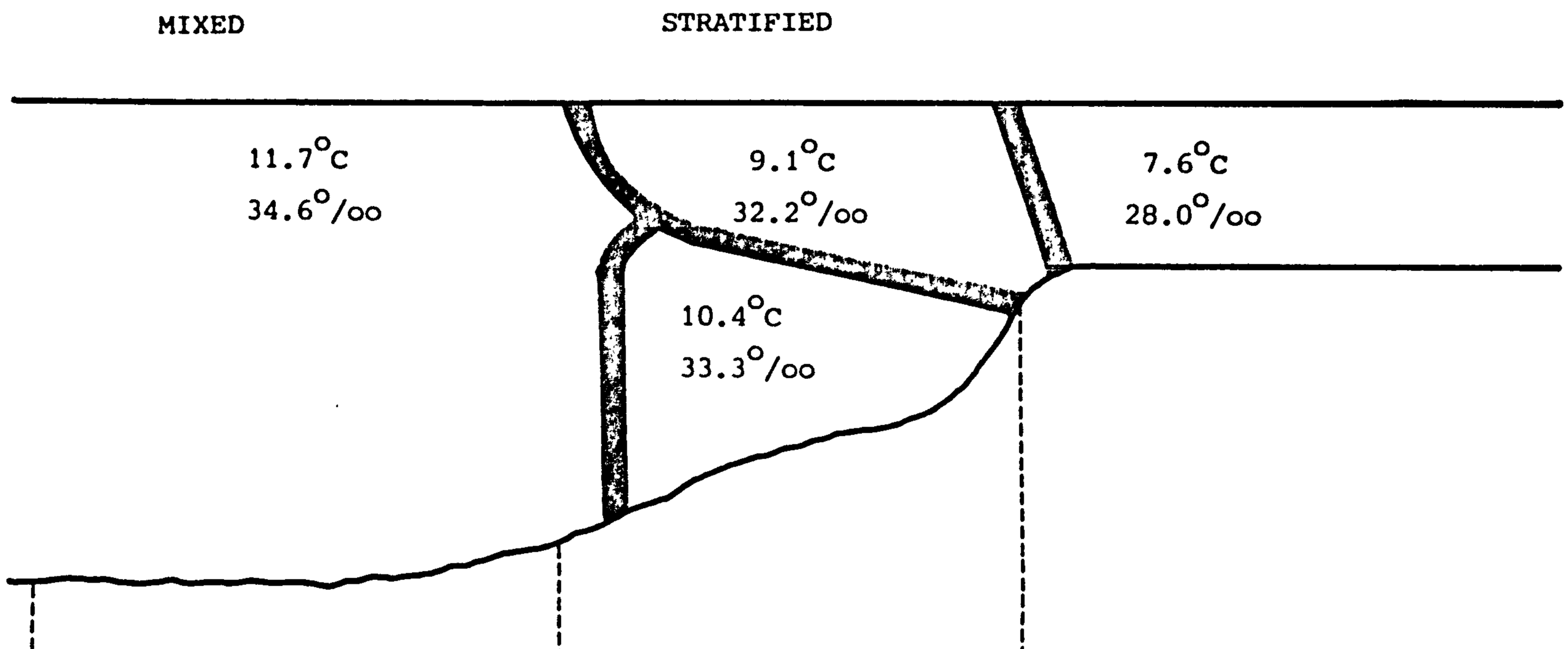
Figure 4.64 : Schematic presentation of water regimes on Cruises HGL I and II.



relative station positions	17 16 15 14 13 12	11	10 9 8 7
	NORTH SEA WATER	COASTAL WATER	ELBE WATER
$\overline{V}$ (joules m^{-3})	34.0	0.5	4.2
Δ temperature (°C)	6.30	0.19	1.05
Δ salinity (°/oo)	0.90	0.14	1.00
Δ sigma T	1.511	0.063	0.596

All values are maxima found in each water type. Δ values refer to maximum surface to bottom differences. These values are derived from figs. 4.4, 4.18 and 4.19.

Figure 4.65 : Schematic presentation of water regimes in November 1976 derived from Martens (1978).

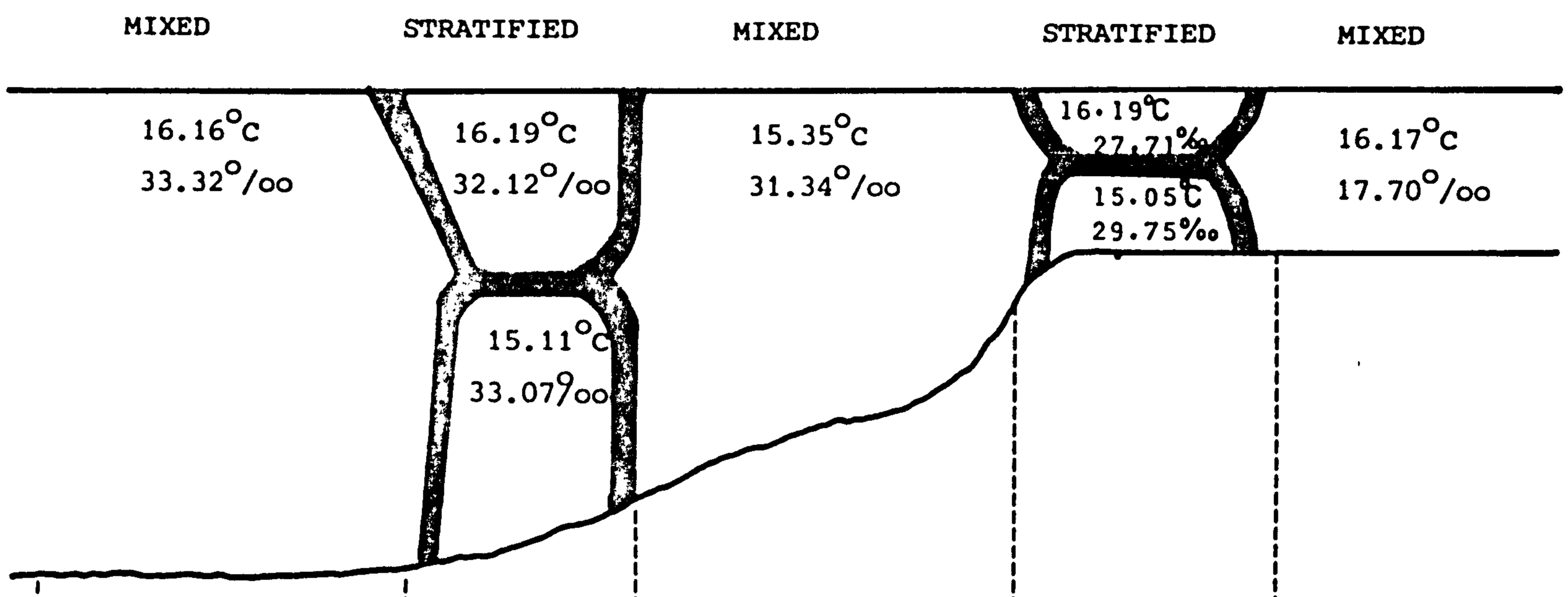


	NORTH SEA WATER	COASTAL WATER	ELBE WATER
$\overline{V}$ (joules m^{-3})	5.9	9.6	N/A
Δ temperature (^{o}C)	0.5	1.3	N/A
Δ salinity ($^{o}/oo$)	0.5	1.1	N/A
Δ sigma T	0.3	0.64	N/A

All values are maxima found in each water type. Δ values refer to maximum surface to bottom differences.

N/A = data unavailable.

Figure 4.66 : Schematic presentation of water regimes on Cruise HGL III.



$\bar{V}$ (joules m^{-3})	2.8			17.4			4.4			20.1	1.4
Δ temperature (°C)	0.64			1.07			0.20			1.07	1.47
Δ salinity (°/oo)	0.02			0.95			0.05			2.40	0.00
Δ sigma T	0.143			0.970			0.005			1.917	0.282

All values are maxima found in each water type. Δ values refer to maximum surface to bottom differences. These values are derived from figs. 4.32 and 4.33.

intermediate or transitional situation on Cruise HGL III (fig. 4.65) and the winter situation (fig. 4.65). It is necessary to include the winter hydrographical situation to understand the intermediate situation found on Cruise HGL III.

4.2.1.1 Summer Model (fig. 4.64): Cruises HGL I (30.7-5.8.76) and HGL II (25-31.8.76).

The stratified North Sea regime described here is equivalent to the 'convergence zone' described by Goedecke (1968). The lighter coastal water flows over the more dense North Sea water resulting in stratification. Heating of the surface water during summer results in increased temperature surface to bottom differences and therefore increased stratification and stability. It should be stressed that the hydrography is dynamic, water from the northern North Sea and coastal water continually flowing towards each other. Despite the dynamics of the hydrography a distinct surface boundary or front occurs between the waters of the North Sea and coastal regimes. In the mixed coastal regime heat input is distributed throughout the water column and not restricted to the surface water, as is the case in the stratified regime resulting in lower temperatures than the North Sea regime.

The Elbe regime shows little thermohaline stratification. The higher water temperature compared to the coastal regime is attributed to increasing surface heat input per unit volume with decreasing depth. A steep sea bottom topographical gradient in the area of station 10 results in a sharp horizontal temperature gradient which forms the boundary between the cool, mixed coastal water and the warmer, mixed Elbe water.

4.2.1.2 Winter Model (fig. 4.65)

This model is based on data collected in November 1976, over a month after Cruise HGL III, by Martens (1978). It is obvious that the influence of river influx on the hydrography of the area is greater in winter. Stratification occurs in the coastal regime with freshwater influenced surface waters of low salinity and low temperature and North Sea influenced water of higher salinity and temperature in the bottom waters. The North Sea regime

shows only slight stratification (surface to bottom temperature and salinity differences of 0.5°C and 0.5°/oo respectively).

4.2.1.3 Intermediate Model (21-27.9.76) (fig.4.66):Cruise HGL III

The physical situation found on Cruise HGL III is obviously transitional between the summer situation when stratification is influenced greatly by water heating and the winter situation when stratification is mainly influenced by freshwater input. This results in two areas of stratification (high $\bar{V}$ values), one in the mouth of the Elbe estuary due to increased freshwater influence and the other in the North Sea regime where thermal stratification occurs but is reduced to a smaller area due to lower heat input. The time and method in which thermal stratification breaks down would not necessarily occur at the same time and in the same manner each year as it would depend on the balance between the factors which set up and retain stratification and those that produce energy and break down stratification. Although stratified waters in the mouth of the Elbe were found on both the 20.9.1976 and 21.9.1976 the stability of this feature is unknown.

The effect of the different water regimes shown in the hydrographical models (figs. 4.64-4.66) on the microbiology and chemistry will now be investigated.

4.2.2 Discussion of the microbiology and nutrient chemistry present during Cruise HGL I in relation to the hydrography

The range of values and mean values of the micro-biological and chemical measurements are summarized for the different water regimes (fig. 4.64) in tables 4.74 and 4.75. Since only one sample was taken in the coastal regime little emphasis can be placed on the characteristics of this area.

Inorganic nitrogen compounds and 'total nitrogen' are higher in the Elbe regime than in the North Sea regime, the Coastal regime seemingly having intermediate concentrations. An inverse correlation ($< 0.1\%$ significance level) between salinity and each of the inorganic nitrogen compounds indicates that river water flowing into the Elbe estuary is rich in inorganic nitrogen and that the North Sea regime has little freshwater influence.

TABLE 4.74: CRUISE HGL I. The median and range of nitrogen concentrations (/umol l^{-1}), microbial biomass (/ug Cl^{-1}), chlorophyll a (/ug l^{-1}) and microbial ATP (/ug l^{-1}) measured at 10 m. depth in the three water regimes (fig. 4.64).

Station Numbers :	ELBE REGIME 7-10	COASTAL REGIME 11	NORTH SEA REGIME 12-17,1,2,4,5
Urea-N	1.83 (1.32-2.98)	1.20	5.45 (0.00-24.85)
Ammonium-N	6.7 (2.95-10.05)	2.10	2.41 (1.15-4.40)
Nitrate-N	35.65 (14.02-53.87)	4.3	1.63 (0.45-6.02)
Nitrite-N	1.71 (0.88-2.66)	0.30	0.14 (0.00-0.515)
'Total N'	45.89 (19.33-68.12)	7.90	9.62 (4.28-27.35)
% N as urea	4.8 (2.0-8.0)	15.0	46.5 (0.0-91.0)
Phototrophic Carbon A	315.5 (125.1-736.5)	324.9	172.5 (7.7-304.5)
Heterotrophic Carbon C	91.0 (0.0-373.0)	218.5	695.5 (114.3-1632.0)
Total microbial Carbon B	325.6 (136.2-509.3)	543.4	868.0 (373.8-1,782.2)
Chlorophyll a	10.52 (4.17-24.55)	10.83	5.75 (0.26-10.15)
Microbial ATP	1.30 (0.54-2.04)	2.17	3.47 (1.50-7.13)

The mean urea concentration is highest in the North Sea regime and composes nearly half of the 'total nitrogen' while composing a much smaller (<5%) proportion of the 'total nitrogen' in the Elbe regime. Unlike the inorganic nitrogen compounds urea does not correlate negatively with salinity. This may indicate that little urea is introduced by freshwater input and that the urea in the North Sea regime is produced in situ. Urea is excreted by many marine animals to smaller and larger degrees and as a microbial degradation product of amino acids, purines and pyrimidines (see Section 1). One therefore might expect to find little or no urea when zooplankton grazing is light or absent whereas during heavy grazing the balance between supply and utilization might allow a greater concentration to accumulate. The high urea concentrations in the North Sea regime may therefore indicate high zooplankton grazing pressure and the wide variation of urea concentrations may mirror the patchiness of the zooplankton.

Concentrations of chlorophyll a are lowest in the North Sea regime. The mean chlorophyll a concentration in the Elbe regime is high, however this is mainly due to the localized 'bloom' concentration at station 10, at the position of the topographic front. The following hypothesis is presented as an explanation of the high phytoplankton concentrations in this area. Due to Coriolis forces residual currents flow anticlockwise in the northern hemisphere. Elbe water would therefore tend to run along the North Freisan coast (Maler-Reimer, 1977; Ramming, 1968) rather than perpendicular to the coast. Mixing would occur between the parallel residual flows of the Elbe and Coastal water to a large extent but uninterrupted, continuous dilution of the Elbe water would not be expected on a transect running perpendicular to the coast. Indeed, salinity, density, ammonium and nitrate show a discontinuity between stations 9 and 10 suggesting that continuous dilution of the Elbe water does not occur. Strong convergence velocities have been associated with fronts between parallel flowing water regimes, often resulting in accumulation of particulate matter, (Bowman and Iverson, 1978). The low degree of stratification in the shallow Elbe water probably indicates that tidally generated bottom turbulent stirring

is sufficiently strong to prevent vertical stratification unlike the plume front situation, which involves stratification in less shallow estuarine waters with less turbulent mixing, described by Bowman and Iverson (1978). They also found distinct colour contrast across fronts associated with estuaries and attributed it to more turbid estuarine water on one side and clearer coastal water on the other.

Enhancement of standing plankton biomass in the frontal region has been attributed to nutrient enrichment of the photic zone followed by local plankton growth (Relevante and Gilmartin, 1976) or through accumulation of plankton due to convergence (Bowman and Iverson, 1978).

The high phytoplankton biomass at station 10 may therefore be due to accumulation or due to growth in optimal conditions provided by complimentary influences from each water regime; relatively high nutrient concentrations due to enrichment from the Elbe water, higher salinities than further up the estuary (indeed chlorophyll a increases with increasing salinity) and better light penetration due to less turbid waters. To what extent is the comparative importance of each of these possibilities is hard to say, but it is possible that both accumulation and growth may be an explanation for the high phytoplankton concentration found at the topographic front.

The highest concentrations of total microbial ATP and heterotrophic biomass were found in the North Sea regime. Indeed both correlate with density at the 1% and 5% significance level respectively. There is also an inverse correlation, at the 5% significance level, between phototrophic and heterotrophic biomass, lowest heterotrophic biomass present at the topographic front (station 10) where there is highest phototrophic biomass. This inverse relationship could be indicative of either (i) the production of antibacterial exudates by phytoplankton as suggested by Droop and Elson (1966) and Sieburth (1963 and 1968), (ii) the environmental stress in the Elbe regime is greater on the microheterotrophs than in the North Sea regime, (iii) the North Sea regime has a naturally occurring large heterotrophic biomass in relation to the Elbe regime. Whatever the

explanation, the North Sea and Elbe regions are distinctly different in regard to microbial ATP and heterotrophic biomass.

Although mean total urea assimilation rates are similar in the three regimes mean phototrophic and heterotrophic urea assimilation rates are different; the Elbe regime having high phototrophic and low heterotrophic assimilation rates while the North Sea regime has high heterotrophic and low phototrophic assimilation rates. That is, phytoplankton are the predominant urea assimilators in the Elbe regime and the heterotrophic micro organisms are the predominant urea assimilators in the North Sea regime. This is probably simply because phototrophs are predominant in the Elbe regime while heterotrophs predominate in the North Sea regime.

It is interesting to note that despite relatively high inorganic nitrogen the rate of phototrophic urea assimilation reaches a maximum at station 10 where peak phytoplankton biomass was measured. This may either indicate preferential uptake of urea rather than nitrate or ammonium by some cells (indeed this has been observed in some algae (McCarthy et.al. 1977; Antia et.al. 1975)) or that there is insufficient inorganic nitrogen to support such a high phytoplankton population. Another maximum of both phototrophic and heterotrophic assimilation rates occur at station 13 where urea comprises of over 90% of the 'total nitrogen'. Since the inorganic nitrogen concentration is low and probably limiting, those organisms which can utilize urea as a nitrogen source would be at an advantage at station 13. It is interesting to speculate whether ureolytic micro organisms have developed in this area of high urea concentrations, particularly as the urea assimilation indices are highest at this station, that is, the raté of urea assimilation per biomass unit is higher than at other stations.

There are correlations between total (0.1% significance level), phototrophic (5% significance level) and heterotrophic (0.1% significance level) urea assimilation rates and <u>in situ</u> urea concentrations. These correlations suggest that first order uptake kinetics are operative. It seems

TABLE 4.75: CRUISE HGL I. The median and range of urea assimilation rates (nmol urea $l^{-1}hr^{-1}$), urea turnover times (days) and urea assimilation indices (nmol $hr^{-1}/ugC^{-1} \times 10^{-2}$) measured at 10 m. depth in the three water regimes (fig. 4.64).

Station Numbers	ELBE REGIME 7-10	COASTAL REGIME 11	NORTH SEA REGIME 12-17,1,2,4,5
Total urea assimilation rate	7.82 (1.61-16.87)	12.19	9.93 (1.77-67.57)
Phototrophic urea assimilation rate	7.13 (1.08-15.76)	10.14	3.38 (0.00-21.55)
Heterotrophic urea assimilation rate	0.67 (0.40-1.11)	2.05	6.55 (0.60-46.02)
Total turnover time	19.6 (5.5-45.6)	5.5	33.9 (8.3-80.4)
Phototrophic turnover time	25.8 (5.9-67.8)	6.6	90.43 (26.0-251.7)
Heterotrophic turnover time	148.8 (84.2-260.0)	32.6	96.6 (12.2-265.4)
Total urea assimilation index	2.30 (1.18-4.02)	2.24	1.21 (0.15-8.02)
Phototrophic urea assimilation index	2.29 (0.86-3.69)	3.12	4.88 (0.16-25.71)
Heterotrophic urea assimilation index	2.45 (0.11-4.79)	0.94	0.96 (0.13-6.71)

likely that there is an association with first order uptake kinetics (that is, the rate of uptake is proportional to the substrate concentration) in heterotrophic urea assimilation rates because of the highly significant correlation between rate of assimilation and substrate concentration. However, the correlation at only the 5% significance level between phototrophic rate of assimilation and substrate concentration may indicate a more complex form of uptake kinetics for the phytoplankton. The in situ urea concentrations (max. found was 1.2×10^{-5}M) are markedly below the K_m value of pure urease (1.9×10^{-3}M); therefore first order uptake kinetic will theoretically be operative.

Heterotrophic biomass and percentage of urea assimilated by the heterotrophs correlate at the 0.1% significance level and phototrophic biomass and percentage of urea assimilated by the phototrophs correlate at the 5% significance level. This again suggests that there is an important inter-relationship between the phototrophs and heterotrophs, although the nature of the relationship is dependent on the biochemistry of urea degrading systems. The above correlations may validate the use of the ATP method of estimating microbial biomass and heterotrophic biomass and indicate that there is a consistency between microbial ATP and heterotrophic and phototrophic carbon in this area at this particular time. However, since 'heterotrophic biomass' originates from ATP measurements it could also be interpreted as 'heterotrophic ATP' and therefore the highly significant correlation between 'heterotrophic biomass' and percentage of heterotrophic urea assimilation may be related to heterotrophic ATP rather than biomass. It is obvious that this dilemma in interpretation will only be solved by estimated heterotrophic biomass by a more direct means. Indeed, this was done in Cruise HGL III by means of direct counts of bacterial numbers and cell volumes.

Total and phototrophic turnover times are lowest in the Elbe and Coastal regimes while heterotrophic turnover times correlate inversely, at the 1% significance level, with density, the lower turnover times present in the North Sea regime. Turnover times are similar to those measured by Remsen et.al.(1974), the values of which ranged between

3.2 and 98.0 days.

Although widely used, the validity of the use of turnover times should be questioned as it assumes a constant rate of uptake and steady state conditions. As mentioned above the rate of urea assimilation is proportional to the substrate concentration. Rate of urea uptake will therefore not remain constant, as the substrate is assimilated and the concentration reduced, unless the rate of urea production is the same as the rate of assimilation. Since this assumption is unsupported by measurements of urea production rates caution should be used in the application of turnover times. Despite this short coming turnover time is still generally accepted as a valuable tool in the study of microbial processes.

Total urea assimilation indices are highest in the Elbe and Coastal regimes with a notable maximum at station 10, the micro organisms taking up urea more efficiently than in the North Sea regime. The exceptionally high index at station 13 has already been discussed above. It is also interesting that mean phototrophic urea assimilation indices are highest in the North Sea regime. Since the ability to use urea as a nitrogen source is not present in all phyto-plankton species (Guillard, 1963) it is possible that the high concentrations of urea associated with relatively low inorganic nitrogen concentrations may exert a considerable influence on phytoplankton species composition. Some species of marine phytoplankton can also grow on urea as a sole nitrogen source (Syrett, 1962; Guillard, 1963; Leftley and Syrett, 1973; Remsen et.al. 1974). It therefore is reasonable to suppose that if inorganic nitrogen concentrations are low, as in the North Sea regime, the presence of urea in sufficient concentration will increase the growth rates of those species which can utilize it while not affecting those that cannot, thus influencing the species composition and phototrophic urea assimilation indices.

The mean heterotrophic urea assimilation index in the North Sea regime is lower than the mean phototrophic index although heterotrophic assimilation rates are higher than

phototrophic rates. This could indicate that either (i) the heterotrophs are more efficient 'scavengers' for the remaining inorganic nitrogen or (ii) the heterotrophs are utilizing other, more complex organic compounds, or (iii) the phytoplankton are better competitors for urea than the heterotrophs. Regarding the latter possibility Remsen et.al. (1974) concluded that "...phytoplankton play a more dominant role than bacteria in the utilization and/or decomposition of urea in coastal waters". They also suggest that urea utilization seems to be an exception to the general rule that "any competition between algae and bacteria for dissolved organic compounds appears to favour the bacteria,at least at the low substrate concentrations found in nature" (Hobbie and Wright, 1965). Mitamura and Saijo (1975) and Herbland (1976) also found that phytoplankton seem to be responsible for the major part of the urea decomposition. The latter author gave the following explanation "urea is an organic compound of low molecular weight; its hydrolysis reaction is weakly exothermic and does not allow ATP synthesis from ADP and phosphate so that urea is then less attractive for sensu stricto heterotrophic organisms than more complex organic compounds. On the other hand, it is a nitrogen component easily hydrolysable for autotrophic organisms which are under nitrogen limiting conditions". It therefore seems possible that the heterotrophs are assimilating other, more complex organic compounds besides urea, which act as both a nitrogen and energy source. Indeed, considering that microbial ATP concentrations are so high in the North Sea regime there may be sufficient organic compounds to support this high metabolic activity. Since urea concentrations are so high in this regime and most likely being produced in situ through animal grazing, excretion and decomposition of cells and faeces it is more than likely that more complex organic compounds are also present in relatively high concentrations.

From the discussion above and tables 4.74 and 4.75 it is possible, at least at the particular time of this cruise, to distinguish between the different water regimes by biological and chemical measurements. In comparison

to the North Sea regime the Elbe regime has higher concentrations of inorganic nitrogen compounds and chlorophyll a; higher phototrophic assimilation rates heterotrophic turnover times and total urea assimilation indices while having lower concentrations of urea, microbial ATP and heterotrophic carbon; lower heterotrophic urea assimilation rates, total and phototrophic turnover times and finally lower phototrophic urea assimilation indices. It is obvious that the phototrophic micro organisms predominate, influence and are more effective in the Elbe regime while the heterotrophic micro organisms do likewise in the North Sea regime. The topographic front, at station 10, is obviously of biological significance (most notably of significance to phytoplankton) having extremely high concentrations of chlorophyll a which is also reflected in high phototrophic urea assimilation rates and low phototrophic turnover times for urea.

4.2.3 Discussion of the microbiology and nutrient chemistry present during Cruise HGL II in relation to the hydrography

The range of values and mean values of the microbiology and chemistry measured on Cruise HGL II are presented for the different water regimes depicted in fig. 4.64 are presented in tables 4.76 and 4.77.

The Elbe regime again contains higher concentrations of the inorganic nitrogen compounds and 'total nitrogen' than either the Coastal or North Sea regimes. Ammonium correlates inversely with salinity at the 1% significance level while 'total nitrogen', nitrate and nitrite correlate inversely with salinity at the 0.1% significance level. As found in Cruise HGL I there is no similar inverse correlation between urea and salinity. Although urea concentrations are generally lower than those found during the previous cruise there is still a notable difference between the Elbe and North Sea regimes; the latter containing a higher mean urea concentration and making up a significant proportion of the 'total nitrogen' in both the Coastal and North Sea regime.

As in the previous cruise the mean chlorophyll a concentration is highest in the Elbe and Coastal regimes. High concentrations are again found at station 10; however

TABLE 4.76: CRUISE HGL II. The median and range of nitrogen concentrations (/umol l^{-1}), microbial biomass (/ug C l^{-1}), chlorophyll a (/ug l^{-1}) and microbial ATP (/ug l^{-1}) measured at 10 m. depth in the three water regimes (fig.4.04).

Station Number	ELBE REGIME 7-10	COASTAL REGIME 11	NORTH SEA REGIME 12-17, 1-5
Urea-N	0.24 (0.00-0.52)	2.45	1.62 (0.00-6.80)
Ammonium-N	9.00 (6.75-10.20)	4.50	3.29 (1.50-7.95)
Nitrate-N	43.04 (24.55-66.86)	3.56	1.80 (1.14-2.67)
Nitrite-N	1.92 (1.20-2.94)	0.43	0.06 (0.01-0.13)
'Total N'	54.20 (35.95-79.05)	10.93	6.77 (2.65-11.43)
% N as urea	0.5 (0.0-1.0)	22.0	18.6 (0.0-61.0)
Phototrophic carbon A	155.72 (76.47-251.28)	322.77	51.16 (0.00-111.12)
Heterotrophic carbon C	38.60 (0.00-96.22)	872.23	440.33 (0.00-1,168.22)
Total microbial carbon B	189.18 (64.23-347.50)	1195.00	488.77 (15.75-1,267.50)
Chlorophyll a	5.19 (2.55-8.38)	10.76	1.72 (0.00-3.70)
Microbial ATP	0.76 (0.26-1.39)	4.78	1.96 (0.06-5.07)

the chlorophyll a maximum occurred at station 11. However, chlorophyll a concentrations in the Elbe and North Sea regime are much lower than those found on the previous cruise and it therefore seems reasonable to suggest that the phytoplankton in these regimes are on the decline due to unsuitable growth conditions. However, the chlorophyll a concentration at station 11, in the mixed Coastal regime is consistent with that measured during Cruise HGL I. Obviously conditions must be suitable for this sustained high phytoplankton biomass despite relatively low concentrations of inorganic nitrogen. Low concentrations do not necessarily indicate waters impoverished in that particular compound and hence indicate limiting growth conditions. High rates of utilization and replenishment, be it through physical mixing or in situ production, may result in low measurable concentrations without limiting but rather optimal conditions for growth. Since the Coastal regime is well mixed there is likely to be a continuous replenishment of nutrients in the photic zone. High heterotrophic biomass at station 11 may be evidence for in situ utilization and remineralization of dissolved organic compounds which would also aid in sustaining the high phytoplankton biomass. Indeed, Wangersky (1977) and Pingree et.al. (1978) produced evidence that heterotrophic in situ regeneration of dissolved organic compounds are of importance in sustaining phytoplankton growth and may even effect the phytoplankton species composition.

Total microbial ATP and heterotrophic biomass correlate positively with density at the 5% significance level, there still being large differences between the Elbe and North Sea regime and is consistent with that found during Cruise HGL I, the latter regime having higher mean values for both measurements. However, the heterotrophic biomass has decreased in the North Sea relative to the previous month while increasing in the Coastal regime. The heterotrophs seem to be reaching their maximum activity during the decline of the phototrophic population as was found by Rheinheimer (1965) and Gunkel (1968). This could be due to a either or a combination of production of antibacterial exudates during healthy phytoplankton growth and bacterial

decomposition of the phytoplankton during their decline. Indeed, phototrophic and heterotrophic biomass are no longer significantly inversely correlated as was the situation during the previous cruise, the phytoplankton possibly, during their decline, having no adverse effect on the heterotrophs.

Mean total urea assimilation rates are notably higher in the North Sea regime than in the Elbe regime, the maximum occurring in the mixed Coastal regime. Total urea assimilation rates correlate positively with microbial ATP at the 1% significance level. Thus high microbial activity as indicated by microbial ATP is related to high urea assimilation rates. The opposite could be the case, that high urea assimilation rates result in high microbial activity, but this seems less probable. However, uptake of urea may be indicative of uptake of other, more complex organic compounds which provide energy for heterotrophic activity and growth, result in high cellular ATP contents.

Mean phototrophic and heterotrophic urea assimilation rates are lowest in the Elbe regime, both mean rates are also similar. This is not surprising as there are high concentrations of other forms of nitrogen available for microbial assimilation. However, the mean heterotrophic assimilation rate is higher than that for the phototrophs in the Coastal and North Sea regime. This is probably because heterotrophic biomass is greater in these regimes. Indeed, heterotrophic biomass correlates positively with heterotrophic urea assimilation rates at the 5% significance level. This correlation indicates that either there is a significant relationship between heterotrophic biomass and heterotrophic urea assimilation or, since 'heterotrophic biomass' was determined from ATP measurements it can be stated to be 'heterotrophic ATP', there is a relationship between heterotrophic ATP and heterotrophic urea assimilation rates. This will be discussed in more detail in Section 5.

As was also observed during Cruise HGL I there are positive correlations between total (1% significance level), phototrophic (2% significance level) and heterotrophic (5% significance level) urea assimilation rates and <u>in situ</u>

TABLE 4.77: CRUISE HGL II: The median and range of urea assimilation rates (nmol urea l^{-1} hr^{-1}), urea turnover times (days) and urea assimilation indices (nmol hr^{-1}/ugC^{-1} x 10^{-2}) measured at 10 m. depth in the three water regimes (fig. 4.64).

Station Numbers	ELBE REGIME 7-10	COASTAL REGIME 11	NORTH SEA REGIME 12-17,1-5
Total urea assimilation rate	0.86 (0.60-1.18)	6.59	2.23 (0.32-5.36)
Phototrophic urea assimilation rate	0.43 (0.31-0.55)	1.84	0.92 (0.03-1.89)
Heterotrophic urea assimilation rate	0.43 (0.15-0.78)	4.75	1.31 (0.29-3.02)
Total turn-over time	59.28 (35.34-81.16)	14.07	50.59 (10.93-129.19)
Phototrophic turnover time	113.62 (92.34-163.00)	50.43	374.94 (30.90-1,720.93)
Heterotrophic turnover time	151.11 (53.44-277.36)	19.51	111.12 (16.91-426.76)
Total urea assimilation index	0.74 (0.17-1.84)	0.55	0.71 (0.12-2.79)
Phototrophic urea assimilation index	0.33 (0.18-0.52)	0.57	1.59 (0.08-4.34)
Heterotrophic urea assimilation index	0.49 (0.16-0.81)	0.54	0.33 (0.10-1.03)

urea concentrations. This could be further evidence of uptake kinetics as suggested in the discussion of Cruise HGL I.

Total urea turnover times are higher than those encountered on the previous cruise, this is obviously due to slower phototrophic turnover times as heterotrophic urea turnover times are consistent with those found on Cruise HGL I. Total urea turnover times are lowest in the Coastal regime and the more inshore stations of the North Sea regime. The higher urea uptake in this region may be associated with the shallow sea frontal region. Increased phytoplankton activity and/or biomass has often been associated with shallow sea fronts (eg. Savidge, 1976 and 1978; Pingree et.al. 1976 and 1978; Holligan and Harbour, 1977) although little work has been carried out from bacteriological aspects. Wangersky (1977) and Pingree et al.(1978) do, however, attribute sustained dinoflagellate growth in nutrient depleted surface waters, where little enrichment occurs through vertical mixing, to <u>in situ</u> heterotrophic regeneration of dissolved organic compounds. This would suggest that bacterial activity and biomass could also be high in frontal regions. Indeed the same arguments and theoretical calculations may be presented to explain high bacterial biomass as those used by Okubo (1978) to explain high phytoplankton concentrations in areas of convergence. According to his theoretical calculations the critical patch size of a growing population within a convergence zone becomes smaller as the convergence velocity increases, resulting in a narrow belt of cells. Whereas a weak divergence of even only a few centimeters per second is capable of dispersing the strongest concentration of cells. It therefore is reasonable to propose that the high heterotrophic biomass with associated low heterotrophic urea turnover time at station 12 is a product of converging waters, particularly as this region is known to be a convergency zone (see Section 4.2.1).

The low heterotrophic and phototrophic urea turnover times at the inshore stations of the North Sea regime may be a result of inorganic nitrogen limitation in the waters above the pycnocline in the stratified waters.

There is no significant difference in mean total and heterotrophic urea assimilation indices in the three regimes. However, in semblance with the previous month, the mean phototrophic urea assimilation index is highest in the North Sea regime and is higher than the mean heterotrophic index. The same interpretation as that discussed in the previous cruise may be appropriate here.

There is a positive correlation, at the 2% probability level, between phototrophic turnover times and heterotrophic urea assimilation indices, i.e. when there is fast phototrophic turnover of urea the concentration of urea assimilated per heterotrophic biomass unit is low and when there is slow phototrophic turnover there is high urea assimilation per heterotrophic carbon. This may indicate that there is strong competition for urea between the phototrophic and heterotrophic micro organisms. Whatever the interpretation of this correlation, it does indicate an interesting relationship between phototrophs, heterotrophs and urea which obviously requires further elaboration to fully understand it.

As with Cruise HGL I, it again is possible to distinguish between the different water regimes by their microbiological and chemical properties. Although not totally consistent with the previous cruise, remarkable similarities in the biological and chemical characteristics of the water regimes exist between those found on either cruise. As was the case in Cruise HGL I, in comparison to the North Sea regime the Elbe regime had higher concentrations of inorganic nitrogen compounds and chlorophyll a; higher heterotrophic turnover times and low concentrations of urea, microbial ATP and heterotrophic carbon; lower heterotrophic assimilation rates, phototrophic turnover times and lower phototrophic urea assimilation indices.

Overall, urea utilization was less than that found during the previous month and this is attributed to decreasing predominance of the phytoplankton. Heterotrophic biomass increased in the mixed coastal regime and in the area of the shallow sea front. That is, heterotrophs were no longer restricted to the stratified North Sea regime

and this was reflected in increased heterotrophic biomass, high heterotrophic urea assimilation rates and low heterotrophic urea turnover times. The stratified North Sea regime and shallow sea front are of microbiological significance, particularly for the heterotrophs during the decline of the phytoplankton in the inorganic nitrogen depleted waters above the pycnoline.

Urea concentrations, although lower than those measured during the last cruise, are still of significance in the North Sea regime while of little significance in the Elbe regime.

4.2.4 Cruise HGL III

Mean and extreme values of the microbiological and chemical parameters for the water regimes encountered on Cruise HGL III, modelled in fig. 4.66, are provided in tables 4.78 - 4.81.

In accordance with the previous cruises the inorganic nitrogen concentration, measured on Cruise HGL III, are high in the Elbe regime relative to the Coastal and North Sea regimes. Again nitrate and nitrite and 'total nitrogen' correlate inversely with salinity at the 0.1%, 2% and 0.1% significance levels respectively. However, unlike the previous cruises, there is not a significant correlation between ammonium and salinity. Lucht (1964) attributed the high inorganic nitrogen concentrations in the Elbe to the input of sewage waters particularly from the city of Hamburg and any change in concentration was attributed to microbiological action. Foster et.al. (1978) in an investigation of ammonium distribution in Liverpool Bay, which also receives large quantities of industrial, agricultural and domestic wastes, attributed a poor correlation between ammonium and salinity, found on some of their cruises, to increased biological influence rather than simply physical mixing processes. It therefore seems plausible that physical mixing processes are responsible for the distribution of nitrate and nitrite whereas microbiological activity may be responsible for the ammonium distribution.

It is interesting to consider the low inorganic nitrogen concentrations at station 10 which also has

TABLE 4.78: CRUISE HGL III. The median and range of nitrogen concentrations (/umol l^{-1}) measured at 10 m. depth in the three water regimes (fig. 4.66) and the mixed and stratified waters within the Elbe and North Sea regimes.

	ELBE REGIME		COASTAL REGIME	NORTH SEA REGIME	
	Mixed	Stratified	Mixed	Stratified	Mixed
Station Nos:	7,8	8*,9,10	11,11*	12,13,14	15-17,2-6
Urea-N	0.39 (0.00-1.34)		0.33 (0.20-0.45)	0.49 (0.00-1.56)	
	0.99 (0.63-1.34)	0.00 -		0.80 (0.21-1.53)	0.35 (0.00-1.56)
Ammonium -N	7.64 (4.10-10.70)		6.40 (6.30-6.50)	3.58 (2.60-4.80)	
	7.95 (5.20-10.70)	7.43 (4.10-10.00)		3.60 (2.60-4.80)	3.56 (2.60-4.50)
Nitrate -N	39.47 (8.88-59.43)		11.45 (10.60-12.70)	1.95 (1.27-4.43)	
	57.54 (55.64-59.43)	27.43 (8.88-40.04)		2.47 (1.29-4.43)	1.73 (1.27-2.23)
Nitrite -N	2.19 (0.79-3.16)		1.10 (1.06-1.13)	0.31 (0.17-0.67)	
	2.57 (1.98-3.16)	1.80 (0.79-2.36)		0.37 (0.22-0.67)	0.29 (0.17-0.40)
'Total N'	49.61 (13.77-70.84)		19.47 (18.15-20.78)	6.32 (4.20-10.11)	
	69.04 (67.23-70.84)	36.66 (13.77-52.40)		7.23 (4.79-10.11)	5.93 (4.2-7.00)
% N as urea	0.04 (0.0 - 2.0)		1.5 (1.0 - 2.0)	7.8 (0.0 - 22.0)	
	1.5 (1.0 - 2.0)	0		12.67 (2.0 - 22.0)	5.71 (0.0 - 22.0)

* Stations sampled on 21.9.76 during vertical profiling.

TABLE 4.79: CRUISE HGL III. The median and range of microbial biomass (μgCl^{-1}), chlorophyll a ($\mu g\ l^{-1}$) and microbial ATP ($\mu g\ l^{-1}$) bacterial numbers (nos. l^{-1}) and cellular ATP:cellular C ratios measured at 10 m. depth in the three water regimes (fig.4.66) and the mixed and stratified waters within the Elbe and North Sea regimes.

	ELBE REGIME		COASTAL REGIME	NORTH SEA REGIME	
	Mixed	Stratified	Mixed	Stratified	Mixed
Station Nos.	7,8	8*,9,10	11,11*	12,13,14	15-17,2-6
Phototrophic carbon A	125.4 (87.9-179.1)		187.8 (186.6-188.7)	76.2 (51.9-84.3)	
	100.8 (88.0-113.5)	141.9 (87.9-179.4)		78.9 (56.4-107.7)	75.0 (51.9-84.3)
Bacterial carbon from D numbers & volume	225.2 (34.2-577.0)		30.36 (13.51-47.2)	16.7 (8.3 - 26.9)	
	353.5 (129.9-577.0)	139.7 (34.2-323.5)		21.2 (14.7-26.9)	14.7 (8.3-17.9)
Total microbial carbon E from A plus D	350.7 (122.2-690.5)		218.0 (200.1-235.8)	92.9 (68.6-122.4)	
	454.2 (217.9-690.5)	281.7 (122.2-482.4)		100.1 (83.4-122.4)	89.8 (68.6-103.3)
Chlorophyll a	4.18 (2.93-5.97)		6.26 (6.22-6.29)	2.54 (1.73-2.81)	
	3.36 (2.93-3.78)	4.73 (2.93-5.97)		2.63 (1.88-3.59)	2.50 (1.73-2.81)
Total microbial ATP	0.21 (0.02-0.48)		0.205 (0.20-0.21)	0.27 (0.04-0.73)	
	0.09 (0.02-0.15)	0.30 (0.02-0.48)		0.41 (0.04-0.73)	0.21 (0.04-0.49)
Bacterial numbers x 10^9	4.93 (2.04-12.70)		1.75 (0.82-2.67)	1.03 (0.52-1.58)	
	8.29 (3.88-12.70)	2.70 (2.04-3.71)		1.23 (0.89-1.58)	0.95 (0.52-1.23)
Cellular ATP: cellular C x 10^{-3}	0.75 (0.03-1.99)		0.95 (0.90-0.99)	2.94 (0.45-8.74)	
	0.37 (0.03-0.70)	1.01 (0.20-1.99)		4.31 (0.45-8.74)	2.35 (0.48-5.34)

* Stations sampled on 21.9.76 during vertical profiling.

relatively high chlorophyll a and microbial ATP concentrations. This may indicate high assimilation of inorganic nitrogen and little replenishment through physical mixing processes since this station is stratified. In contrast the Coastal regime has relatively high concentrations of inorganic nitrogen, in both regard to station 10 and to the previous cruises and this is reflected in high concentrations of chlorophyll a. The high inorganic nitrogen concentrations and high phytoplankton biomass can be attributed to mixing of relatively nutrient rich bottom waters with water in the photic zone.

In comparison with the previous cruises urea concentration during Cruise HGL III is low, although urea still represents a higher proportion of the 'total nitrogen' in the North Sea regime, particularly in the stratified waters, than in either the Elbe or Coastal regimes.

Although concentrations of chlorophyll a are lower than those measured on the previous cruises the general distribution shows a parity with Cruise HGL II; the Elbe regime having higher concentrations than the North Sea regime, while the highest concentration occurred in the Coastal regime.

Microbial ATP concentrations are considerably lower than those measured on the other cruises which indicates less microbial metabolic activity at this time of year. The negative values for heterotrophic biomass (C) (derived from ATP and chlorophyll a) indicate that either one or both of the conversion factors for ATP and chlorophyll a into carbon are incorrect, at least during the period of this cruise. Indeed, further evidence that ATP is not a good indicator of biomass is the disparity between biomass derived from ATP and that derived from chlorophyll a plus bacterial numbers and volumes. The usefulness and reliability of the ATP method of estimating biomass will be discussed in detail in Section 5. However, the ratio between cellular ATP and cellular carbon, the latter derived from chlorophyll a and bacterial numbers and volumes, allows the comparison of the metabolic activity per biomass unit in the different water regimes. The lowest ratios occur in the Elbe regime where there is high

phytoplankton biomass and the highest bacterial biomass (AODC). This may indicate that the micro organisms in this regime are particularly inactive and under great environmental stress when compared to those in the North Sea regime where high cellular ATP:cellular carbon ratios occur in association with low microbial biomass. Indeed Rheinheimer (1965) concluded that the majority of bacteria occurring in the Elbe during summer originate from sewage wastes. One would also expect a terrestrial or freshwater input of bacteria during periods of rainfall during the time of this cruise. If this were the case, an estuarine environment of high salinity and low nutrient concentration, relative to the micro organisms original environment, could be envisaged as being particularly stressful.

It has already been shown from the physical data and discussion that the Elbe and Coastal regimes and the North Sea regimes have different origins and it seems likely that the greater bacterial cell size, more diverse morphology and lower cellular ATP:cellular carbon ratios in the Elbe regime indicate that the micro organisms, particularly the bacteria are also of separate origins and that the river and upper estuary may be a source of bacteria to the lower estuary and Coastal regime. The large proportion of bacteria attached to detritus, in the Elbe regime, may indicate a transportation mechanism from freshwater sediments, soils and sewage wastes to the lower estuary. These results support the findings of other investigations (Oppenheimer and Jannash, 1962; Wiebe and Pomeroy, 1972; Furguson and Rublee, 1976; Wright, 1978 and Lochte, 1979) which have indicated similar changes in bacterial numbers and cell morphology between inshore and offshore waters.

The high cellular ATP:cellular carbon ratios in the North Sea regime indicate that these micro organisms are not under great environmental stress, possibly they are far better adapted to low nutrient conditions to those in the Elbe or Coastal regime.

The uptake of urea is generally much lower than encountered on the previous cruises. Relative to this cruise, notable fast total turnover times and high total assimilation rates are present in the mixed area of the

TABLE 4.80: CRUISE HGL III. Median and range of urea assimilation rates (nmol l^{-1} hr^{-1}) and turnover times (days) measured at 10 m. depth in the three water regimes (fig. 4.66) and the mixed and stratified waters within the Elbe and North Sea regimes.

	ELBE REGIME		COASTAL REGIME	NORTH SEA REGIME	
	Mixed	Stratified	Mixed	Stratified	Mixed
Station Nos:	7,8	8*,9,10	11,11*	12,13,14	15-17, 2-6
Total urea assimilation rate	1.67 (0.50-2.71)		1.12 (1.10-1.14)	1.21 (0.48-2.59)	
	2.46 (2.20-2.71)	1.15 (0.50-2.24)		2.06 (1.43-2.59)	0.85 (0.48-1.43)
Photo-trophic urea assimilation rate	1.04 (0.16-1.81)		0.91 (0.78-1.03)	0.67 (0.09-1.85)	
	1.31 (1.28-1.34)	0.87 (0.16-1.81)		1.46 (0.70-1.85)	0.33 (0.09-0.88)
Hetero-trophic urea assimilation rate	0.63 (0.04-1.37)		0.22 (0.11-0.32)	0.54 (0.19-0.82)	
	1.15 (0.92-1.37)	0.29 (0.04-0.43)		0.60 (0.31-0.77)	0.51 (0.19-0.82)
Total turnover time	42.1 (18.6-82.5)		43.2 (41.7-44.7)	55.0 (21.5-117.2)	
	25.9 (20.3-31.6)	53.0 (18.6-82.5)		29.3 (21.5-34.1)	66.0 (29.2-117.2)
Photo-trophic turnover time	88.2 (23.0-258.7)		54.2 (49.2-59.2)	175.9 (30.6-462.5)	
	47.6 (41.1-54.2)	115.2 (23.0-258.7)		45.5 (30.6-65.9)	231.8 (47.6-462.5)
Hetero-trophic turnover time	159.2 (39.9-461.9)		312.2 (141.3-483.0)	121.9 (54.4-238.4)	
	57.9 (39.9-75.6)	226.7 (97.0-461.9)		123.5 (63.4-235.2)	121.1 (54.4-238.4)

* Stations sampled on 21.9.76 during vertical profiling

Elbe regime and the stratified area of the North Sea regime. The greater uptake of urea in the latter area is apparently because of greater phototrophic action as there is little difference between heterotrophic assimilation rates and turnover times between the mixed and stratified waters, whilst phototrophic assimilation rates are considerably higher in the stratified waters of the North Sea regime. Phototrophic urea assimilation rates are almost invariably greater than that for heterotrophs which would appear to support the conclusions of Mitamura and Saijo (1975), that bacterial decomposition of urea played only a minor role in the decomposition of urea, and Remsen et.al. (1974) that the decomposition of urea is the exception to the general rule of Hobbie and Wright (1965) that 'any competition between algae and bacteria for dissolved organic compounds appear to favor the bacteria, at least at the low substrate concentrations found in nature'. However, a more appropriate examination of urea decomposition in the form of relative assimilation per phototrophic and heterotrophic unit of biomass (the phototrophic and heterotrophic urea assimilation indices, the latter using the AODC method of determining bacterial biomass) indicates that, with the exception of the Elbe regime, the heterotrophs are far more effective urea decomposers than the phototrophs. This brings into question the conclusions of Cruises HGL I and II, Mitamura and Saijo and Remsen et.al. and supports Hobbie and Wrights theory that bacteria are better competitors for dissolved organic compounds than phytoplankton.

The relative unimportance of bacterial activity in the estuary has been discussed above. The low heterotrophic urea assimilation indices supports the argument that the bacteria present in the estuary have originated from a freshwater or terrestrial source, the estuarine environmental condition being particularly stressful, resulting in low metabolic activity and rates of urea assimilation.

The urea assimilation indices give more interpretable values regarding the relative decomposition of urea. Unlike the previous cruises the determination of bacterial biomass from direct bacterial counts allows the determination of

TABLE 4.81: CRUISE HGL III. Median and range of urea assimilation indices (nmol $hr^{-1}/ugC^{-1} \times 10^{-2}$) measured at 10 m. depth in the three water regimes (fig. 4.66) and the mixed and stratified waters within the Elbe and North Sea regimes.

	ELBE REGIME		COASTAL REGIME	NORTH SEA REGIME	
	Mixed	Stratified	Mixed	Stratified	Mixed
Station Nos.	7,8	8*,9,10	11,11*	12,13,14	15-17,2-6
Total urea assimilation index A from carbon derived from ATP	14.53 (0.60-55.76)		2.19 (2.14-2.23)	4.06 (0.82-20.17)	
	30.75 (5.74-55.76)	3.72 (0.60-8.33)		7.61 (1.25-20.17)	2.53 (0.82-5.96)
Total urea assimilation index B from carbon derived from chlorophyll a and bacterial volumes	0.51 (0.30-1.01)		0.52 (0.48-0.55)	1.31 (0.48-3.10)	
	0.70 (0.39-1.01)	0.39 (0.30-0.46)		2.18 (1.17-3.10)	0.94 (0.48-1.56)
Photo-trophic urea assimilation index C from carbon derived from chlorophyll a.	0.86 (0.18-1.45)		0.49 (0.42-0.55)	0.96 (0.12-3.22)	
	1.32 (1.18-1.45)	0.56 (0.18-1.14)		2.14 (0.65-3.22)	0.45 (0.12-1.17)
Bacterial urea assimilation index E from carbon derived from bacterial volumes.	0.44 (0.13-0.99)		1.30 (0.23-2.37)	3.84 (0.98-6.81)	
	0.48 (0.24-0.71)	0.42 (0.13-0.99)		3.08 (1.42-4.96)	4.16 (0.98-6.81)

* Stations sampled on 21.9.76 during vertical profiling.

the rate of urea assimilation per biomass unit by a more reliable, direct method than the much questioned ATP method of estimating biomass.

It is obvious that the relative rate of urea assimilation (total urea assimilation index (E)) is greatest in the North Sea regime and more specifically in the stratified waters of that regime while considerable lower indices are present in the Elbe and Coastal regimes. These high total urea assimilation indices support the argument that the micro organisms in the North Sea regime are particularly adapted to the environmental conditions of these waters, the micro organisms being under less environmental stress than those in the environment of the Elbe and Coastal regimes.

An interesting and important aspect of this research is that two different and novel methods of determining relative microbial activity or assimilation; the cellular ATP:cellular carbon ratios and the total urea assimilation indices, correlate positively at the 1% significance level. This suggests that either or indeed both of these parameters may be a useful tool in future research in microbial ecology.

Vertical profiles of urea assimilation rates, urea assimilation indices, cellular ATP:cellular carbon ratios and <u>in situ</u> urea concentrations almost invariably show surface maxima which may indicate that there is a complex relationship between the bacteria, phytoplankton and zooplankton. It is generally accepted that zooplankton migrate to the surface waters, to graze on the phytoplankton situated in the photic zone, between dusk and dawn. Investigations (Corner et.al. 1965; Hargrave and Geen, 1968 and Harris, 1973) on a number of different species of zooplankton indicate that excretion increases when zooplankton feed. One would also expect defaecation to increase during grazing. Luxury grazing or 'spillage' as well as increased excretion and defaecation may therefore contribute to an increased and to some extent continuous supply of urea, ammonium, inorganic phosphorus and dissolved organic carbon.

High phototrophic urea assimilation indices (A) in surface waters can be attributed to an increase in photosynthetic activity with an increase in light. Mitamura and Saijo (1975) found a positive relationship between photosynthetic activity and phototrophic assimilation of urea. This relationship may be due to the presence of a urea-degrading enzyme which requires ATP for activity: ATP: urea amidolyase (UAL-ase) rather than urease which does not require ATP. That is, the breakdown of urea by UAL-ase is under metabolic control. It may therefore be possible that the phytoplankton sampled during this cruise contain UAL-ase rather than urease, although UAL-ase has only to date been isolated from some yeasts and members of the Chlorophyceae (Roon and Levenberg, 1968; Syrett and Leftley, 1976).

High heterotrophic urea assimilation indices (D) indicate that heterotrophic assimilation activity is also high in the surface waters and may further indicate that the heterotrophic activity is related to the activity of the primary and secondary producers.

As was the situation in the previous cruises, it is again evident that there are microbiological and chemical distinguishing characteristics, not only between the three water regimes but also to some extent, between the mixed and stratified areas of the individual regimes. It is also evident that although microbial biomass is high in the Elbe and Coastal regimes the micro organisms are under considerable physiological stress imposed by environmental conditions. Perhaps the most striking differences between the water regimes are the cellular ATP:cellular carbon ratios and the urea assimilation indices. High cellular ATP:cellular carbon ratios and urea assimilation indices occur in the North Sea regime which indicate that although the inorganic nitrogen concentrations are low the micro organisms do not seem to be under such physiological stress as those present in the Elbe and Coastal regimes.

SECTION 5

FINAL DISCUSSION

SECTION 5

FINAL DISCUSSION

In other investigations on the distribution of urea (eg. Remsen, 1971; Remsen et.al., 1974 and Steinmann, 1976) it has been assumed that terrestrial sources of urea, such as sewage, contribute to the urea concentrations in coastal and estuarine waters. An interesting aspect of this research is that there is no evidence that this assumption is valid; indeed, it seems from the preliminary investigation of the domestic sewage and waters of the Menai Strait that there is little or no terrestrial influence in sea water urea concentration. Similarly, results from the Elbe estuary indicate that although there is an input of inorganic nitrogen from further up the river there is no such indication for urea. Pineda (1973) and Savidge and Hutley (1977) also found that the effect of sewage discharge appeared to be minimal on urea sea water concentration.

However, these investigations were marine orientated and it is only when investigations into waste waters are examined that it becomes more obvious than urea from anthropogenic sources will not reach the sea in significant concentrations; Jones (1932) and Fowler (1934) both state that urea is broken down so rapidly that it seldom reaches the sewer yet alone the treatment plant. A more recent investigation by Sridhar and Pillai (1974) showed that raw sewage contained small amounts of urea but had high urease activity, the effluent from septic tanks had no urea, but had high urease activity and the effluent from activated sludge had no urea and no urease activity (the activated sludge itself having very high urease activity). It therefore seems reasonable to conclude from the literature and this research that sewage discharges have little effect on urea sea water concentration.

This infers that the urea in the sea water is produced in situ by the biota. There is indirect evidence from the HGL cruises to support this as follows:

1. Urea showed greater spatial variability than the inorganic nitrogen compounds. This may reflect the patchiness of the urea producers which are known to occur in patches,

layers and shoals.

2. Urea concentrations were highest in the North Sea regime where low inorganic nitrogen occurred, indicating that there was no external input of urea.
3. In the North Sea the high urea concentrations were associated with waters above the pynocline where little bottom to surface mixing occurs, so urea enrichment by upwelling is unlikely.
4. Surface urea concentrations were almost invariably higher than those deeper in the water column, where zooplankton grazing and excretion would be expected to be greatest.
5. Urea concentrations were highest on Cruise HGL I, the period of highest biological biomass and activity, and decreased with the onset of winter when biological biomass and activity was lowest.
6. High rates of urea assimilation were often associated with high concentrations of urea and as any measured concentration of urea represents the balance between production and assimilation of urea, high urea production rates would be expected where high concentrations and rates of assimilation occur.

Possible contributors of urea are summarized in Section 1 and these include zooplankton. Indeed McCarthy (1970) has postulated that "when zooplankton grazing is absent or relatively light one may expect to find little or no urea in the water whereas during heavy grazing the balance between supply and utilization might allow a greater accumulation". Floodgate et.al. (in press) found high microbial activity associated with high urea utilization and sea water concentration on a front in Liverpool Bay where zooplankton numbers were not only higher than elsewhere but their development seemed more advanced than elsewhere in Liverpool Bay.

The high urea concentrations, high urea assimilation indices by photo-and heterotrophs and high cellular ATP:cellular carbon ratios in the frontal region and stratified waters in the North Sea regime encountered in the HGL cruises indicate high microbial activity. The high concentrations of urea associated with these may also indicate that zooplankton grazing and excretion has contributed to this high microbial activity. To substantiate this a similar investigation including a zoo-

plankton study is required. However, it seems that there is a complex, dynamic relationship between the plankton and that this can be related to the hydrography.

Although Carpenter et.al. (1972b) recovered negligible amounts of ^{14}C in the particulate fraction in a laboratory study of urea utilization by Skeletonema costatum, urea utilization in this present research was determined by measuring the release of $^{14}CO_2$ on acidification plus particulate ^{14}C from the ^{14}C-urea added to the samples. These results (Tables 4.11, 4.30 and 4.50) indicate that between 0 and 43% of the total urea carbon degraded was incorporated into the particulate material. This is similar to the 10-55% incorporation found by Webb and Haas (1976) although values ranging between 38-84% have been found by Mitamura and Saijo (1975). The results of Carpenter et.al. (1972b) mentioned above may indicate that the differences encountered here and by other workers may result from different species composition of the phytoplankton.

Although there is evidence that urea carbon is incorporated into the particulate phase via the photosynthetic assimilation of $^{14}CO_2$ which is liberated from urea (Allison et.al., 1964 and Webster et.al. 1955) there is also evidence which indicates preferential labelling of amino acid pools from urea carbon compared to environmental CO_2, that is, urea may be delivered to the CO_2 dark fixing pathways rather than to the photosynthetic pathways and not mix extensively with the environmental CO_2 pool (Webster et.al., 1955; Webb and Haas, 1976 and Mitamura & Saijo, 1975). The results from the HGL cruises could support this hypothesis particularly as much of the ^{14}C-incorporated into the particulate phase occurs in the dark incubations. On the other hand it should be noted that the ^{14}C in the particulate phase may be in the form of intact urea, and as CO_2 not yet respired as well as ^{14}C incorporated into the cell via one pathway or another. Indeed, Ellner and Steers (1955) found some evidence for a direct incorporation of urea carbon into guanine by Chlorella and Scenedesmus.

It should be noted that if there is dark fixation of $^{14}CO_2$ liberated from ^{14}C-urea by the phytoplankton "heterotrophic urea assimilation" determined in this study may include a small amount of assimilation by phytoplankton although the greater part would be due to bacteria and yeasts.

Evidence in the literature (see Section 1) indicates that urea is an ecologically important nitrogen source for phytoplankton. Results from the HGL cruises support this conclusion particularly in the North Sea regime where the concentration of inorganic nitrogen is low and urea concentration and rate of assimilation high. The positive relationship between sea water urea concentration and urea assimilation rates may indicate that urea is preferred relative to its availability or on the other hand since high urea concentrations were often associated with low ammonium concentrations that there is a secondary preference for urea-N when urea is available as suggested by McCarthy et.al. (1977). That is, in the estuary there could be preference for ammonium which is in sufficient supply to meet the microbial demand for nitrogen, whereas in the North Sea regime there is not sufficient ammonium to meet the demand so urea, which is there in higher concentrations, is taken up in preference to the low concentrations of ammonium.

Both phototrophic and heterotrophic action is important in the breakdown of urea and the distribution of urea assimilation rates by both groups of micro organisms as well as the sea water urea concentration, all of which were related to the hydrography of the water. This makes it difficult to directly compare phototrophic and heterotrophic urea assimilation and in particular to comment on competition between both groups of microorganisms for urea. Past investigations on urea assimilation in sea water have only involved the measurements of rates of assimilation or turnover of urea without measuring the microbial population responsible for the assimilation, that is, they have not related urea degrading activity and microbial biomass. "Urea assimilation indices", proposed in this research, give a quantitative expression of the relationship between urea degrading activity and microbial biomass. Indeed the approach of "urea assimilation indices" is similar to that of "specific activity indices" proposed by Wright (1978, 1979) for bacterial populations.

This index enables a direct comparison of the urea degrading ability of the microbes in different samples of sea water. Furthermore "phototrophic and heterotrophic urea assimilation indices" also enables a direct comparison of urea degrading ability between the two groups of micro organisms.

The conclusions of Herbland (1976), Remsen et.al. (1972) and Mitamura and Saijo (1975) that phytoplankton are more effective competitors for urea than bacteria have also been based on measurements of rates of urea assimilation without taking their numbers or biomass into consideration. When examining the results for the Coastal and North Sea regimes on Cruise HGL III it is apparent that mean phototrophic assimilation rates are similar to or just greater than heterotrophic assimilation rates and it is also tempting to reach the same conclusion as the above authors, that the phototrophs are better competitors for urea than the heterotrophs. The phototrophic and heterotrophic assimilation indices, however, indicate that in these water regimes the heterotrophs are 3-4 times more effective urea degraders than the phototrophs.

In the Elbe regime during this cruise the reverse situation is evident, the mean phototrophic assimilation index is 2 times higher than the heterotrophic assimilation index. It could be concluded that in this estuarine environment phytoplankton are better competitors for urea than heterotrophs. On the other hand the heterotrophs in these inorganic nitrogen rich waters may have sufficient alternative nitrogen sources other than urea and may therefore not be in direct competition with the phototrophs for urea. Another possibility is that the bacteria in the Elbe may not be indigenous, being of a freshwater or terrestrial origin and find the estuarine conditions particularly stressful. This latter explanation is supported by the low cellular ATP:cellular carbon ratios found in the Elbe regime, which is discussed below, and by the findings of Rheinheimer (1965).

It is also interesting to note that despite a general decrease as the year advances, the mean phototrophic assimilation indices on all three cruises are always higher in the stratified North Sea regime than in the Elbe regime although phototrophic assimilation rates are always higher in the latter regime. This could again indicate that either urea is more important in the North Sea waters of low inorganic nitrogen concentration than in the relatively inorganic nitrogen rich Elbe waters, or that the phytoplankton also find the estuarine environment stressful to some degree.

Contrary to the other authors mentioned above, results from this research indicate that in sea water of low inorganic

nitrogen, competition between bacteria and phytoplankton for urea seems to favour the bacteria and therefore supports Hobbie and Wright's (1965) theory of competition between these two groups of micro organisms for dissolved organic compounds.

It should be noted that the above discussion did not involve urea assimilation indices calculated from carbon derived from the questionable ATP method of measuring biomass.

Perhaps it is now expedient to discuss the use and interpretability of ATP measurements and the cellular carbon derived from ATP measurements using laboratory estimated conversion factors, and their applicability to sea water. There seems to be some confusion in the literature regarding the value of ATP as an estimation of biomass in sea water since the heralding of this method in 1966 by Holm-Hansen and Booth.

Although it has been stated that in both unicellular algal (Holm-Hansen, 1970) and bacterial (Hamilton and Holm-Hansen, 1967) cells the cellular content of ATP is fairly constant in exponentially growing cells under normal environmental conditions there is evidence of abrupt changes of cellular ATP in response to physiological stresses such as mercury addition, pH change and limiting nutrient concentrations (Hamilton and Holm-Hansen, 1967; Holm-Hansen, 1970; Brezonik and Patterson, 1972 and Brezonik et.al. 1975).

In the majority of the samples taken on Cruise HGL III the microbial biomass derived from chlorophyll a and direct bacterial counts exceeded the microbial biomass derived from ATP measurements. Similarly Jassby (1975) in 75% of the samples taken from Castle Lake, California, found that there was not sufficient ATP to fulfil the requirements of the conversion factors for phytoplankton biomass let alone take into account other micro organisms which could be expected to be in the lake. This indicates that the conversion factors from cellular ATP into cellular carbon estimated from unstressed laboratory cultures overestimate the cellular ATP in natural populations.

However, this situation rarely occurs in Cruises HGL I and II where there is sufficient microbial carbon left over after phytoplankton carbon has been taken from microbial carbon derived from ATP to account for large amounts of heterotrophic carbon suggesting very high bacterial and/or yeast biomass. Indeed, Jassby (1975) also finds estimates of bacterial biomass,

in this fashion, possible only when heterotrophic biomass is dominant.

Nevertheless, it is now time to view the estimate of ATP as a valuable measurement in its own right rather than a means of determining biomass. If ATP is estimated in addition to phytoplankton and bacterial biomass the resulting cellular ATP:cellular carbon ratios may reveal valuable information of how the micro organisms are responding to the environment. Such a measurement was used by Brezonik and Patterson (1972); Brezonik et.al. (1975; Lochte (1979) and Floodgate et.al. (in press) to assess the physiological state of the micro organisms. Since changes in numbers or biomass can only be a relatively long-term response to changes in the environment biomass does not necessarily reflect the growth conditions of the water when sampling occurs; variations in physiological activity, however, will be the first adaptation to changes in the environment. Cellular ATP:cellular carbon ratios may therefore give some indication of how the micro organisms are responding to the environment whereas microbial biomass or numbers may indicate how they have responded in the recent past.

Although the low cellular ATP:cellular carbon ratios and large bacterial cell size found in the Elbe estuary in Cruise HGL III may be an indication of either high anabolic activity or low catabolic activity. The low urea assimilation indices found in the Elbe estuary can also be interpreted to indicate low catabolic activity and both these may signify that these micro organisms are under stress and therefore adds substance to the conclusion of Rheinheimer (1965) that they are not indigenous to the estuary.

Conversely in the North Sea regime on this cruise, the high cellular ATP:cellular carbon ratios and high urea assimilation indices can be interpreted as indicating high catabolic activity by the micro organisms. The small cell size of the bacteria indicates that, at the present, the anabolic activity is low and that these marine bacteria may have recently experienced exogenous dormancy, a state suggested as a survival mechanism for marine bacteria because of poor growth conditions by Novitsky and Morita (1978) and Stevenson (1978).

One interpretation of the significant correlation between

cellular ATP:cellular carbon ratios and urea assimilation indices may indicate that the cellular ATP:cellular carbon ratios may be an indicator of the catabolic rather than the anabolic state of the micro organisms. A measure of the energy charge with these two measurements may well have shed more light upon this situation but unfortunately it was not available.

The importance of the hydrography on the microbiology has been discussed in detail in Section 4.2 and will therefore not be reiterated again. It should, however, be stressed that the hydrography of the S. German Bight has had considerable influence on the plankton and adds a further complexity to the already complicated relationship between the different planktons and sea water nutrient chemistry. It should also be emphasised that without the hydrographical data, as presented in the physical models in Section 4.2, the distribution and biodegradation of urea and the distribution of the micro organisms concerned with its degradation cannot be properly understood. It is therefore felt that a hydrographical survey is essential and should be an integral part of an investigation such as this.

CONCLUSIONS

CONCLUSIONS

1. There is no evidence to suggest that land derived urea is an important source of urea to the waters of Beaumaris Bay, the Menai Strait, the lower reaches of the Elbe estuary and the S. German Bight. There is some evidence that *in situ* production of urea seems likely to be a major contributor to sea water urea concentration.

2. Urea contributes an ecologically significant amount to the 'total nitrogen' (ammonium + nitrate + nitrite + urea-N) in the Elbe estuary and S. German Bight during the periods investigated.

3. There is considerable variability in the spacial distribution of urea. Urea concentrations were, however, considerably higher in offshore stratified waters of the S. German Bight than in the Elbe estuary where concentrations of inorganic nitrogen compounds were highest. Urea-N concentrations in the former water regime often exceeded the concentrations of inorganic nitrogen.

4. A seasonal distribution was also evident, urea concentrations were highest during periods of greatest biological activity (July-August: Cruise HGL I) and decreased as the year advanced; lowest overall urea concentrations were measured in the October period (Cruise HGL III).

5. Both phototrophic and heterotrophic micro organisms were important in the biodegradation of urea. Phototrophic degradation of urea predominated in the estuary while heterotrophic degradation generally predominated in offshore waters. Like the concentrations, the rate of urea degradation was also highest during the time of highest biological activity (July-August: Cruise HGL I) and decreased as the year advanced. During the Cruises HGL I and II a significant correlation was found between *in situ* urea concentration and rate of urea biodegradation. This relationship did not hold during Cruise HGL III when

microbiological activity was low.

6. Although bacterial biomass and numbers were very high in the Elbe estuary during the October cruise (HGL III), heterotrophic urea assimilation indices and cellular ATP: cellular carbon ratios were extremely low. Conversely, the offshore North Sea regime contained low bacterial biomass and numbers, high heterotrophic urea assimilation indices and high ratios of cellular ATP:cellular carbon. This may indicate that the microbial populations found in the estuary are under greater environmental stress than those in the North Sea regime.

7. From points 4 and 5 it is therefore evident that a complex relationship exists between the urea producers (possibly zooplankton) and urea degraders as well as between the phototrophic and heterotrophic micro organisms. Further investigations including the distribution and enumeration of zooplankton is needed to elucidate these relationships.

8. Distinct water regimes of different physical properties, often separated by frontal regions were evident on the HGL cruises. The distribution of the micro organisms and in situ urea concentrations were related to the hydrography and these in turn affected the distribution of rates of urea bio-degradation. A knowledge of the hydrography in an investigation such as this is therefore concluded to be essential.

9. Urea assimilation indices, when using reliable measurements of microbial biomass, were found to be a useful means of relating phototrophic and heterotrophic urea degradation, particularly when commenting on their competition for urea. These indices indicated that in areas of low inorganic nitrogen bacteria are more effective competitors for urea than phytoplankton.

10. The ATP method of measuring microbial biomass is not

always reliable, however, cellular ATP:cellular carbon ratios may be a useful indicator of physiological activity and environmental stress.

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APPENDIX

Table 4.1 : Cruise HGL I. Physical measurements.

Station number	Depth (m.)	Salinity (°/oo)	Temperature (°C)	Sigma T
7	2	-	17.49	-
7	10	24.33	17.30	17.316
8	2	-	17.38	
8	10	26.14	17.20	18.723
8	15	-	17.18	-
a	2	26.69	17.35	19.108
9	2	-	17.17	-
9	10	27.47	17.17	19.736
b	2	29.10	17.30	20.955
10	2	-	17.29	-
10	10	30.22	17.35	21.797
10	18	-	17.49	-
c	2	30.94	17.20	22.383
d	2	31.36	17.60	22.608
11	2	-	17.31	-
11	10	31.69	17.28	22.895
11	12	-	17.27	-
e	2	31.72	17.40	22.930
f	2	31.46	18.00	22.589
12	2	-	17.88	-
12	10	31.56	17.80	22.713
12	23	-	16.74	-
13	10	32.34	16.71	23.567
13	36	-	15.28	-
14	10	32.35	16.06	23.722
14	31	-	16.00	-
15	10	32.59	16.48	23.808
15	33	-	16.47	-
16	10	32.29	15.60	23.774
16	31	-	14.99	-
17	10	32.36	15.41	23.873
17	33	-	14.50	-

Table 4.2 : Cruise HGLI. Concentrations of nitrogen compounds (µmol l^{-1}).

Station	Urea-N.	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
7	1.53	10.05	53.874	2.660	68.12	2
8	2.98	7.00	38.900	1.800	50.68	6
9	1.32	6.80	35.800	1.500	45.42	3
10	1.48	2.95	14.020	0.880	19.33	8
11	1.20	2.10	4.300	0.300	7.90	15
12	0.95	4.40	2.085	0.515	7.95	12
13	24.85	1.50	0.848	0.152	27.35	91
14	7.90	1.50	0.662	0.039	10.10	78
15	7.95	2.00	0.450	0.000	10.40	76
16	1.58	2.00	0.700	0.000	4.28	37
17	0.00	3.60	6.021	0.009	9.63	0

TABLE 4.3: CRUISE HGL I. Chlorophyll a and total microbial ATP (/ug l^{-1})

Station	Chlorophyll a	Total Microbial ATP
7	4.17	0.54
8	5.21	2.04
9	8.13	0.95
10	24.55	1.68
11	10.83	2.17
12	8.93	2.96
13	5.179	3.36
14	0.258	3.66
15	2.155	3.42
16	5.00	7.13
17	3.49	5.39

TABLE 4.4: CRUISE HGL I. Microbial biomass (/ug C l^{-1})

Station Number	Phototrophic carbon	Total Microbial Carbon	Heterotrophic Carbon
7	125.1	136.2	11.1
8	156.3	509.3	353.0
9	243.9	237.5	- 6.4
10	736.5	419.2	-317.3
11	324.9	543.4	218.5
12	267.9	740.9	473.0
13	155.4	841.1	685.7
14	7.7	914.5	906.7
15	64.7	854.4	789.8
16	150.0	1782.2	1632.2
17	104.7	1348.4	1243.7

TABLE 4.5: CRUISE HGL I. Phytoplankton species composition and enumeration at station 10.

	No.s l^{-1}
Asterionella japonica	300
Biddulphia regia	14,400
Biddulphia sinensis	6,800
Ceratium fusus	700
Chaetoceros curvisetum	172,500
" sociale	551,700
" sp.	2,100
Coscinodiscus sp.	350
Eucampia zoodinacus	64,100
Guinardia flaccida	350
Gyrosigma sp.	1,400
Lithodesmium undulatum	6,000
Peridinium sp. (60-100/u)	1,400
Rhizosolenia shulsolei	200
Triceratium alternaus	4,800
Total	827,100

Table 4.6 : Cruise HGLI. Uptake of ^{14}C-urea in light (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	5,311	2,806	8,117
8	13,076	8,882	21,958
9	23,745	11,714	35,459
10	46,701	20,194	66,894
11	50,864	16,797	67,661
12	10,132	7,491	17,623
13	40,549	4,147	44,696
14	12,638	2,197	14,835
15	3,412	1,193	4,605
16	26,021	4,536	30,557
17	14,274	3,394	17,668

Table 4.7 : Cruise HGLI. Uptake of ^{14}C-urea in dark (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	1,925	733	2,658
8	1,228	198	1,426
9	2,694	667	3,361
10	3,364	1,029	4,393
11	8,560	2,794	11,354
12	2,893	739	3,632
13	29,062	1,378	30,440
14	10,248	1,196	11,444
15	3,738	1,053	4,788
16	24,617	3,786	28,403
17	13,881	2,317	16,198

Table 4.8 : Cruise HGLI. Urea assimilation rates (nmol urea $l^{-1}hr^{-1}$)

Station number	Total assimilation rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
7	1.61	1.08	0.53
8	6.16	5.67	0.40
9	6.63	6.00	0.63
10	16.87	15.76	1.11
11	12.19	10.14	2.05
12	2.93	2.33	0.60
13	67.57	21.55	46.02
14	8.27	1.99	6.28
15	2.58	0.00	2.58
16	6.16	0.43	5.73
17	1.99	0.17	1.82

Table 4.9 : Cruise HGLI. Urea turnover times (days).

Station number	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
7	45.6	67.8	139.2
8	16.9	18.0	259.5
9	10.4	11.5	110.1
10	5.5	5.9	84.2
11	5.5	6.6	32.6
12	21.0	26.5	101.9
13	8.3	26.0	12.2
14	24.9	109.1	32.3
15	80.4	∞	77.3
16	12.1	171.8	13.0
17	20.9	251.7	22.8

TABLE 4.10: CRUISE HGL I. Urea assimilation indices
(nmol urea hr^{-1}/ug C^{-1})

Station Number	Total Assimilation Index	Phototrophic Assimilation Index	Heterotrophic assimilation Index
7	1.18×10^{-2}	0.86×10^{-2}	4.79×10^{-2}
8	1.21×10^{-2}	3.69×10^{-2}	0.11×10^{-2}
9	2.79×10^{-2}	2.46×10^{-2}	-
10	4.02×10^{-2}	2.14×10^{-2}	-
11	2.24×10^{-2}	3.12×10^{-2}	0.94×10^{-2}
12	0.40×10^{-2}	0.87×10^{-2}	0.13×10^{-2}
13	8.02×10^{-2}	13.87×10^{-2}	6.71×10^{-2}
14	0.90×10^{-2}	25.71×10^{-2}	0.69×10^{-2}
15	0.30×10^{-2}	-	0.33×10^{-2}
16	0.35×10^{-2}	0.29×10^{-2}	0.35×10^{-2}
17	0.15×10^{-2}	0.16×10^{-2}	0.15×10^{-2}

TABLE 4.11: CRUISE HGL I. ^{14}C- urea incorporated in living cells as a percentage of total urea assimilation

Station Number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
7	35	7	28
8	40	26	14
9	33	13	20
10	30	7	23
11	25	0	25
12	43	23	20
13	9	4	5
14	15	5	10
15	26	4	22
16	15	2	13
17	19	5	14

Table 4.12 : Cruise HGLI (h). Physical measurements.

Station number	Depth (m.)	Salinity (°/oo)	Temperature (°C)	Sigma T
1	10	32.21	16.07	23.613
2	10	32.32	15.64	23.788
3	2	-	15.80	-
3	10	32.41	15.50	23.890
3	26	-	14.00	-
4	2	-	16.16	-
4	10	32.37	16.16	23.713
4	19	-	16.16	-
5	2	-	14.83	-
5	10	32.59	14.83	24.172
5	11	-	14.80	-
6	2	-	15.82	-
6	10	32.35	15.82	23.771
6	34	-	15.83	-

Table 4.13 : Cruise HGLI(h). Concentrations of nitrogen compounds (µmol l^{-1}).

Station	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
1	4.00	1.15	1.190	0.110	6.45	62
2	2.65	2.50	1.985	0.162	7.30	36
4	2.65	2.50	1.117	0.183	6.45	41
5	2.00	2.90	1.217	0.183	6.30	32

TABLE 4.14: CRUISE HGL I(h). Chlorophyll a and total microbial ATP (/ug l^{-1})

Station	Chlorophyll a	Total Microbial ATP
1	8.650	1.50
2	8.060	1.99
4	10.150	3.11
5	5.620	2.20

TABLE 4.15: CRUISE HGL I(h). Microbial biomass ($\mu g\ C\ l^{-1}$)

Station Number	Phototrophic Carbon	Total Microbial Carbon	Heterotrophic Carbon
1	259.50	373.80	114.30
2	241.80	497.29	255.49
4	304.50	777.64	473.14
5	168.60	550.02	381.42

Table 4.16 : Cruise HGLI(h). Uptake of ^{14}C-urea in light (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
1	8,591	1,732	10,323
2	5,334	1,702	7,036
4	7,858	2,431	10,289
5	5,777	2,091	7,868

Table 4.17 : Cruise HGLI(h). Uptake of ^{14}C-urea in dark (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
1	2,576	275	2,851
2	1,239	155	1,394
4	2,193	214	2,407
5	2,079	265	2,344

Table 4.18 : Cruise HGLI(h). Urea assimilation rates (nmol urea l^{-1} hr^{-1}).

Station number	Total assimilation rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
1	3.49	2.53	0.96
2	1.84	1.48	0.36
4	2.69	2.06	0.63
5	1.77	1.24	0.53

Table 4.19 :Cruise HGLI(h). Urea turnover times (days).

Station number	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
1	35.84	49.52	129.78
2	52.59	65.58	265.42
4	35.96	46.94	153.72
5	47.03	66.98	157.85

Table 4.20 : Cruise HGLI(h). Urea assimilation indices (nmol urea hr^{-1} μg C^{-1}).

Station number	Total assimilation index	Phototrophic assimilation index	Heterotrophic assimilation index
1	0.93 10^{-2}	0.97 10^{-2}	0.84 10^{-2}
2	0.37 10^{-2}	0.61 10^{-2}	0.14 10^{-2}
4	0.35 10^{-2}	0.68 10^{-2}	0.13 10^{-2}
5	0.32 10^{-2}	0.78 10^{-2}	0.14 10^{-2}

Table 4.21 : Cruise HGLI(h). ^{14}C-urea incorporated in living cells as a percentage of total urea assimilated.

Station number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
1	17	7	10
2	24	13	11
4	24	15	9
5	27	16	11

Table 4.22 : Cruise HGL II. Physical measurements.

Station number	Depth (m.)	Salinity (°/oo)	Temperature (°C)	Sigma T	$\bar{V}$ (joules m^{-3})
7	3	21.90	17.65	15.398	4.2
7	10	22.60	18.32	15.778	
7	14	23.00	18.70	15.994	
8	3	25.20	18.42	17.728	3.8
8	10	25.46	18.58	17.888	
8	19	25.80	18.74	18.108	
9	3	27.20	17.99	19.348	0.5
9	10	27.28	18.42	19.308	
9	15	27.33	18.72	19.274	
10	3	29.28	17.26	21.101	1.6
10	10	29.49	17.02	21.317	
10	19	29.76	18.13	21.263	
11	3	31.55	17.17	22.854	0.5
11	10	31.63	17.36	22.871	
11	15	31.69	17.36	22.917	
12	3	32.03	17.32	23.186	34.0
12	10	32.20	17.26	23.330	
12	45	33.04	13.99	24.697	
13	3	-	17.49	-	-
13	10	32.42	17.44	23.455	
13	18.5	-	17.39	-	
13	37	-	-	-	
14	3	-	18.08	-	-
14	10	32.56	17.81	23.474	
14	18.5	-	17.48	-	
14	36	-	-	-	
15	3	-	18.26	-	21.6*
15	10	32.36	17.86	23.309	
15	19	-	17.34	-	
15	38	-	13.12	-	
16	3	-	17.58	-	2.3*
16	10	32.50	17.47	23.509	
16	37	-	17.06	-	
17	3	-	18.04	-	26.2*
17	10	32.51	17.97	23.397	
17	19	-	17.88	-	
17	39	-	11.75	-	

* $\bar{V}$ calculated by assuming salinity is the same throughout the water column, thus only temperature differences are taken into account. Therefore these $\bar{V}$ values are minima.

Table 4.23 : Cruise HGLII. Concentrations of nitrogen compounds ($\mu mol\ l^{-1}$).

Station	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
7	0.00	9.25	66.860	2.940	79.05	0
8	0.52	6.75	37.720	1.580	46.57	1
9	0.42	9.80	43.025	1.975	55.22	1
10	0.00	10.20	24.550	1.200	35.95	0
11	2.45	4.50	3.555	0.425	10.93	22
12	0.00	2.70	1.735	0.065	4.50	0
13	1.10	2.70	1.760	0.040	5.60	20
14	0.00	2.70	1.570	0.030	4.30	0
15	0.00	5.20	2.025	0.025	7.25	0
16	6.80	2.60	1.660	0.040	11.10	61
17	2.10	1.60	1.475	0.065	5.24	40

Table 4.24 : Cruise HGLII. Chlorophyll a and total microbial ATP ($\mu g\ l^{-1}$).

Station	Chlorophyll a	Total microbial ATP
7	2.549	0.2569
8	4.477	0.7700
9	5.360	0.6100
10	8.376	1.3900
11	10.759	4.7800
12	3.306	5.0700
13	0.000	2.0800
14	1.018	1.5700
15	1.273	1.5800
16	2.586	3.7400
17	1.598	1.3400

Table 4.25 : Cruise HGLII. Microbial biomass ($\mu g\ C\ l^{-1}$)

Station number	Phototrophic carbon	Total microbial carbon	Heterotrophic carbon
7	76.47	64.23	-12.24
8	134.31	192.50	58.19
9	160.80	152.50	-8.30
10	251.28	347.50	96.22
11	322.77	1195.00	872.23
12	99.18	1267.50	1168.22
13	0.00	520.00	520.00
14	30.54	392.50	361.96
15	38.19	395.00	356.81
16	72.03	935.00	862.97
17	47.94	335.00	287.06

Table 4.26 : Cruise HGLII. Uptake of ^{14}C-urea in light (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	8,279	2,190	10,469
8	5,544	1,665	7,209
9	3,254	1,305	4,559
10	4,271	1,070	5,341
11	22,203	4,096	26,299
12	13,593	10,102	23,695
13	11,109	4,275	15,384
14	14,251	5,317	19,568
15	4,613	2,978	7,591
16	7,026	3,792	10,818
17	9,746	3,238	12,984

Table 4.27 : Cruise HGLII. Uptake of ^{14}C- urea in dark (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	5,509	1,415	6,924
8	2,778	526	3,304
9	1,644	645	2,289
10	1,140	194	1,334
11	16,392	2,570	18,962
12	10,889	4,134	15,023
13	5,028	1,859	6,887
14	7,441	2,157	9,598
15	2,205	1,092	3,297
16	4,782	1,320	6,102
17	9,335	3,434	12,769

Table 4.28 : Cruise HGLII. Urea assimilation rates (nmol urea $l^{-1}hr^{-1}$).

station number	Total assimilation rates	Phototrophic assimilation rate	Heterotrophic assimilation rate
7	1.18	0.40	0.78
8	1.02	0.55	0.47
9	0.62	0.31	0.31
10	0.60	0.45	0.15
11	6.59	1.84	4.75
12	2.67	0.98	1.69
13	2.69	1.49	1.20
14	2.20	1.12	1.08
15	0.85	0.48	0.37
16	5.36	2.34	3.02
17	3.00	0.05	2.95

Table 4.29 :Cruise HGLII. Urea turnover times (days).

Station number	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
7	35.34	104.37	53.44
8	51.33	94.75	111.99
9	81.16	163.00	161.64
10	69.28	92.34	277.36
11	14.07	50.43	19.51
12	15.62	42.66	24.63
13	24.05	43.55	53.72
14	18.91	37.11	38.55
15	48.74	86.17	112.22
16	34.20	78.46	60.64
17	28.50	1720.93	28.98

TABLE 4.30: CRUISE HGL II. ^{14}C- urea incorporated in living cells as a percentage of total urea assimilation

Station Number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
7	21	1	20
8	23	7	16
9	29	1	28
10	20	5	15
11	16	2	14
12	43	15	28
13	28	1	27
14	27	5	22
15	39	6	33
16	35	13	22
17	25	0	25

TABLE 4.31: CRUISE HGL II. Urea assimilation indices (nmol urea hr^{-1} /ugC^{-1})

Station Number	Total assimilation index		Phototrophic assimilation index		Heterotrophic assimilation index	
7	1.84	10^{-2}	0.52	10^{-2}	-	
8	0.54	10^{-2}	0.41	10^{-2}	0.81	10^{-2}
9	0.41	10^{-2}	0.19	10^{-2}	-	
10	0.17	10^{-2}	0.18	10^{-2}	0.16	10^{-2}
11	0.55	10^{-2}	0.57	10^{-2}	0.54	10^{-2}
12	0.21	10^{-2}	0.99	10^{-2}	0.14	10^{-2}
13	0.52	10^{-2}	-		0.23	10^{-2}
14	0.56	10^{-2}	3.67	10^{-2}	0.30	10^{-2}
15	0.22	10^{-2}	1.26	10^{-2}	0.10	10^{-2}
16	0.57	10^{-2}	3.25	10^{-2}	0.35	10^{-2}
17	0.90	10^{-2}	0.10	10^{-2}	1.03	10^{-2}

Table 4.32 : Cruise HGL II (h). Physical measurements.

Station number	Depth (m.)	Salinity (^{o}/oo)	Temperature (^{o}C)	Sigma T	$\bar{V}$ (joules m^{-3})
1	3	-	18.67	-	2.1*
1	10	31.89	18.55	22.783	
1	23	-	18.34	-	
1	45	-	18.30	-	
2	3	-	20.07	-	6.9*
2	10	32.10	20.02	22.571	
2	22	-	19.93	-	
2	44	-	18.84	-	
3	3	-	21.69	-	7.9*
3	10	32.22	20.33	22.582	
3	15	-	19.85	-	
3	29	-	19.62	-	
4	3	-	19.41	-	3.4*
4	10	32.06	18.26	23.267	
4	24	-	17.07	-	
5	3	-	21.87	-	10.7*
5	7	-	21.25	-	
5	10	32.03	18.90	22.803	
5	14	-	15.74	-	
6	3	-	23.64	-	
6	10	32.01	22.41	21.863	12.22*
6	23	-	21.75	-	
6	45	-	21.71	-	

* $\bar{V}$ calculated by assuming salinity is the same throughout the water column, thus only temperature surface to bottom differences are taken into account. Therefore these $\bar{V}$ values are minima.

Table 4.33 : Cruise HGLII(h). Concentrations of nitrogen compounds (µmol l^{-1}).

Station	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
1	0.00	1.50	1.140	0.010	2.65	0
2	6.50	3.05	1.770	0.110	11.43	57
3	0.00	4.30	2.125	0.125	6.55	0
4	1.35	1.85	1.820	0.060	5.08	27
5	0.00	7.95	2.670	0.100	10.72	0

TABLE 4.34: CRUISE HGL II(h). Chlorophyll a and total microbial ATP ($\mu g\ l^{-1}$)

Station	Chlorophyll a	Total Microbial ATP
1	3.704	2.13
2	1.452	0.94
3	1.508	0.06
4	1.283	1.97
5	1.214	1.03

TABLE 4.35: CRUISE HGL II(h). Microbial biomass (/ug C l^{-1})

Station Number	Phototrophic Carbon	Total Microbial Carbon	Heterotrophic Carbon
1	111.12	531.60	420.48
2	43.56	234.30	190.74
3	45.24	15.75	- 29.49
4	38.49	491.95	453.46
5	36.42	258.33	221.91

Table 4.36 : Cruise HGLII(h). Uptake of ^{14}C-urea in light (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
1	23,645	10,210	33,855
2	3,692	1,119	4,811
3	2,856	1,025	3,881
4	3,707	1,285	4,992
5	2,137	727	2,864

Table 4.37 : Cruise HGLII(h). Uptake of ^{14}C-urea in dark (dpm).

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
1	17,156	4,725	21,881
2	724	143	867
3	1,149	475	1,624
4	3,325	797	4,122
5	1,652	950	2,600

Table 4.38 : Cruise HGLII(h). Urea assimilation rates (nmol urea l^{-1} hr^{-1}).

Station number	Total assimilation rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
1	3.81	1.35	2.46
2	2.30	1.89	0.41
3	0.44	0.26	0.18
4	0.94	0.16	0.78
5	0.32	0.03	0.29

Table 4.39 Cruise HGLII(h). Urea turnover times (days).

Station number	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
1	10.93	30.90	16.91
2	76.91	93.81	426.76
3	95.34	163.93	227.83
4	74.12	425.29	89.76
5	129.19	1,401.52	142.31

Table 4.40 :Cruise HGLII(h). Urea assimilation indices (nmol urea hr^{-1} μg C^{-1}).

Station number	Total assimilation index	Phototrophic assimilation index	Heterotrophic assimilation index
1	0.72 10^{-2}	1.21 10^{-2}	0.59 10^{-2}
2	0.98 10^{-2}	4.34 10^{-2}	0.21 10^{-2}
3	2.79 10^{-2}	0.57 10^{-2}	-
4	0.19 10^{-2}	0.42 10^{-2}	0.17 10^{-2}
5	0.12 10^{-2}	0.08 10^{-2}	0.13 10^{-2}

Table 4.41 : Cruise HGLII(h). ^{14}C-urea incorporated in living cells as a percentage of total urea assimilation.

Station number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
1	30	8	22
2	23	7	16
3	29	0	29
4	26	7	19
5	37	0	37

Table 4.42 : Cruise HGL III. Physical measurements at various depths.

Station number	Depth (m.)	Salinity (^{o}/oo)	Temperature (^{o}C)	Sigma T	$\overline{V}$ (joules m^{-3})
7 (0.7)*	2	17.70	16.17	12.512	1.4
7	6	17.70	14.95	12.747	
7	11	17.70	14.70	12.794	
8 (1.3)*	2	26.20	16.18	18.992	5.4
8	10	26.60	14.89	19.567	
8	21	26.60	15.05	19.535	
9 (2.4)*	2	27.71	16.19	20.143	13.4
9	7	28.83	15.12	21.228	
9	10	29.18	15.12	21.496	
9	15	29.75	15.12	21.933	
10 (2.5)*	2	30.41	16.17	22.211	13.8
10	10	31.77	15.18	23.469	
10	21	31.85	15.20	23.526	
11 (2.6)*	2	31.22	16.17	22.830	2.0
11	6	31.34	15.15	23.146	
11	10	31.37	15.26	23.145	
11	13	31.39	15.35	23.141	
12 (4.0)*	2	32.16	16.17	23.550	11.4
12	10	32.38	15.87	23.786	
12	20	32.66	15.50	24.082	
12	41	32.69	15.50	24.105	
13 (4.2)*	2	32.86	16.19	24.082	6.7
13	10	32.90	15.80	24.200	
13	20	32.95	15.31	24.347	
13	39	33.04	15.26	24.427	
14 (4.6)*	2	32.12	16.18	23.517	17.4
14	10	32.69	15.57	24.090	
14	16	32.85	15.11	24.313	
14	37	33.07	15.11	24.482	
15 (5.0)*	2	33.14	16.16	24.303	2.8
15	10	33.14	16.02	24.335	
15	20	33.14	15.85	24.373	
15	39	33.14	15.52	24.446	

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16	(5.0)*	2	33.17	15.45	24.485	2.7
16		10	33.17	15.41	24.494	
16		19	33.17	15.11	24.559	
16		37	33.18	14.81	24.632	
17	(5.1)*	2	33.31	15.75	24.526	3.8
17		10	33.31	15.75	24.526	
17		18	33.31	15.29	24.627	
17		36	33.31	14.82	24.737	

Station	Depth	Salinity	Temperature	Sigma T	$\overline{V}$

* Secchi disc extinction depth (m.).

Table 4.43 : Cruise HGL III. Concentrations of nitrogen compounds (µmol l^{-1}).at 10m. depth.

Station	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
7	0.63	5.20	59.425	1.975	67.23	1
8	1.34	10.70	55.640	3.160	70.84	2
9	0.00	8.20	33.360	2.240	43.80	0
10	0.00	4.10	8.8780	0.792	13.77	0
11	0.20	6.30	10.595	1.055	18.15	1
12	0.21	4.80	4.430	0.670	10.11	2
13	1.53	3.40	1.685	0.215	6.80	22
14	0.67	2.60	1.290	0.230	4.79	14
15	0.00	2.60	1.4301	0.170	4.20	0
16	0.00	4.50	1.580	0.370	6.45	0
17	0.75	2.70	1.270	0.250	4.97	15

TABLE 4.44a: CRUISE HGL III. Chlorophyll a ($\mu g\ l^{-1}$), total microbial ATP ($\mu g\ l^{-1}$), bacterial numbers (cells l^{-1}), bacterial cell volumes ($\mu m^3 l^{-1}$) and cellular ATP:cellular C ratios at 10 m depth.

Station	Chlorophyll a	Total Microbial ATP	Bacterial Numbers	Bacterial Cell Volumes	Cellular ATP: cellular C
7	3.783	0.0195	1.270×10^{10}	5.77×10^{9}	0.03×10^{-3}
8	2.934	0.1532	3.880×10^{9}	1.25×10^{9}	0.70×10^{-3}
9	5.297	0.4037	3.712×10^{9}	3.24×10^{9}	0.84×10^{-3}
10	5.973	0.4779	2.337×10^{9}	6.13×10^{8}	1.99×10^{-3}
11	6.219	0.1972	8.190×10^{8}	1.35×10^{8}	0.99×10^{-3}
12	3.588	0.4559	8.930×10^{8}	1.47×10^{8}	3.73×10^{-3}
13	2.424	0.0429	1.208×10^{9}	2.19×10^{8}	0.45×10^{-3}
14	1.884	0.7287	1.576×10^{9}	2.69×10^{8}	8.74×10^{-3}
15	2.512	0.4902	1.000×10^{9}	1.65×108	5.34×10^{-3}
16	2.550	0.2183	1.045×10^{9}	1.79×10^{8}	2.31×10^{-3}
17	1.734	0.2339	1.105×10^{9}	1.66×10^{8}	3.41×10^{-3}

TABLE 4.44b : CRUISE HGL III. BACTERIAL CELL MORPHOLOGY AND SIZE (/um) AS A PERCENTAGE OF THE TOTAL CELL NUMBERS

Station No.	Cocci (diameter) 0.2-1.2	1.2-1.8	Rods (width x length) 0.2x0.4-1.2	0.5x1.2-2.4	Vibroids(V) & Spirilla(S) 0.2x0.4-1.8	Comments
7 *	10	20	35	25	10(V)	Diplococci & 6-8 cell filaments common. Diverse morphology & size.
8 *	80	10	5	0	5(V)	Diplococci common
9 *	45	45	10	0	P(V)	" "
10 *	90	0	0	5	5(V)	Diplococci common. Diatoms covered with bacteria also common.
11 *	90	0	5	0	5(V)	Diplococci common
12	90	0	0	0	10(V/S)	Less detritus than above stations and more free cells.
13	95	0	0	0	5(V/S)	Little detritus cells free
14	85	0	5	5	5(V/S)	" " "
15	90	0	0	0	10(V/S)	" " "
16	85	0	0	5	10(V/S)	" " "
17	80	0	0	0	20(V)	" " "

* Bacteria (mainly the cocci) often associated with detritus. Large amounts of detritus in the sample. P = present but less than 5% of the total cell numbers.

TABLE 4.45: CRUISE HGL III. Microbial biomass (/ugC l^{-1}) at 10 m. depth.

Station Number	A Phototrophic carbon (from chl.a.)	B Total microbial carbon (from ATP)	C Heterotrophic carbon (B - A)	D Bacterial Carbon (from numbers and volume)	E Total microbial carbon (A + D)
7	113.49	4.86	-108.63	577.00	690.49
8	88.02	38.31	- 49.71	129.90	217.92
9	158.91	100.93	- 57.98	323.50	482.41
10	179.19	119.46	- 59.73	61.30	240.49
11	186.57	49.30	-137.27	13.51	200.08
12	107.64	113.97	6.33	14.73	122.37
13	72.72	10.71	- 62.01	21.90	94.62
14	56.52	182.18	125.66	26.90	83.42
15	75.36	122.55	47.19	16.50	91.86
16	76.50	54.56	- 21.94	17.90	94.40
17	52.02	58.47	6.45	16.60	68.62

Table 4.46 : Cruise HGL III. Uptake of ^{14}C- urea in light (d.p.m.) at 10m. depth.

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	12,773	5,237	18,268
8	7,890	3,655	11,715
9	14,414	5,467	19,881
10	5,210	1,198	6,408
11	6,348	2,519	8,867
12	9,351	2,105	11,456
13	10,844	0	10,844
14	15,977	1,066	17,217
15	11,865	649	12,657
16	7,664	12	7,676
17	2,948	123	3,071

Table 4.47 : Cruise HGL III. Uptake of ^{14}C- urea in dark (d.p.m.) at 10m. depth.

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
7	5,456	3,553	9,267
8	3,784	929	4,883
9	2,503	1,312	3,815
10	801	0	801
11	2,087	531	2,618
12	4,701	.1,137	5,838
13	1,573	0	1,573
14	4,817	320	5,137
15	4,603	138	4,884
16	4,418	0	4,418
17	1,455	9	1,464

Table 4.48 : Cruise HGL III. Urea assimilation rates (nmol urea l^{-1} hr^{-1}) at 10m. depth.

Station number	Total assimilation rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
7	2.71	1.34	1.37
8	2.20	1.28	0.92
9	2.24	1.81	0.43
10	0.72	0.63	0.09
11	1.10	0.78	0.32
12	1.43	0.70	0.73
13	2.16	1.85	0.31
14	2.59	1.82	0.77
15	1.43	0.88	0.55
16	0.86	0.36	0.50
17	0.48	0.25	0.23

Table 4.49 Cruise HGL III. Urea turnover times (days) at 10m. depth.

Station number	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
7	20.25	41.11	39.93
8	31.58	54.16	75.77
9	18.61	23.03	96.99
10	57.74	63.72	461.92
11	41.73	59.21	141.33
12	32.30	65.86	63.38
13	34.12	39.91	235.22
14	21.49	30.63	72.03
15	29.23	47.60	75.76
16	48.20	113.57	83.75
17	117.16	230.39	238.40

TABLE 4.50: CRUISE HGL III. ^{14}C- urea incorporated in living cells as a percentage of total urea assimilation at 10 m. depth

Station Number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
7	38	0	38
8	31	12	19
9	24	0	24
10	19	19	0
11	28	8	20
12	19	0	19
13	0	0	0
14	6	0	6
15	5	2	3
16	0	0	0
17	4	3	1

TABLE 4.51: CRUISE HGL III. Urea assimilation indices (nmol urea hr^{-1}/ug C^{-1}) at 10 m. depth

Station Number	Total Assimilation Index		Phototrophic Assimilation Index	Heterotrophic Assimilation Index	
	B*	E *	A *	C *	D *
7	55.76×10^{-2}	0.39×10^{-2}	1.18×10^{-2}	-	0.24×10^{-2}
8	5.74×10^{-2}	1.01×10^{-2}	1.45×10^{-2}	-	0.71×10^{-2}
9	2.22×10^{-2}	0.46×10^{-2}	1.14×10^{-2}	-	0.13×10^{-2}
10	0.60×10^{-2}	0.30×10^{-2}	0.35×10^{-2}	-	0.15×10^{-2}
11	2.23×10^{-2}	0.55×10^{-2}	0.42×10^{-2}	-	2.37×10^{-2}
12	1.25×10^{-2}	1.17×10^{-2}	0.65×10^{-2}	11.53×10^{-2}	4.96×10^{-2}
13	20.17×10^{-2}	2.28×10^{-2}	2.54×10^{-2}	-	1.42×10^{-2}
14	1.42×10^{-2}	3.10×10^{-2}	3.22×10^{-2}	0.61×10^{-2}	2.86×10^{-2}
15	1.17×10^{-2}	1.56×10^{-2}	1.17×10^{-2}	1.17×10^{-2}	3.33×10^{-2}
16	1.58×10^{-2}	0.91×10^{-2}	0.47×10^{-2}	-	2.79×10^{-2}
17	0.82×10^{-2}	0.70×10^{-2}	0.48×10^{-2}	3.57×10^{-2}	1.39×10^{-2}

* B Using carbon derived from total microbial ATP

E Using carbon derived from Chlorophyll a plus bacterial numbers and volumes

A Using carbon derived from Chlorophyll a

C Using carbon derived from B minus A

D Using carbon derived from bacterial numbers and volumes

Table 4.52 : Cruise HGL III (h). Physical measurements.

Station number	Depth (m.)	Salinity (^{o}/oo)	Temperature (^{o}C)	Sigma T	$\bar{V}$ (joules m^{-3})
1 (4.0)*	2	32.99	14.82	24.483	0.5
1	10	33.00	14.77	24.502	
1	20	33.01	14.70	24.524	
1	41	33.01	14.78	24.507	
2 (4.8)*	2	32.97	14.97	24.436	0.5
2	10	32.98	14.87	24.465	
2	20	32.98	14.88	24.463	
2	40	32.98	14.87	24.465	
3 (4.8)*	2	32.86	15.49	24.238	1.0
3	10	32.85	15.24	24.285	
3	14	32.86	15.23	24.295	
3	28	32.87	15.20	24.309	
5 (5.0)*	2	32.99	15.17	24.408	0.01
5	6	32.99	15.44	24.414	
5	10	32.98	15.11	24.413	
5	14	32.98	15.07	24.422	
6 (4.3)*	2	32.84	15.10	24.308	3.4
6	10	32.85	15.06	24.324	
6	22	32.90	14.99	24.378	
6	45	33.00	14.96	24.461	

* Secchi disc extinction depth (m.).

Table 4.53 : Cruise HGL III(h). Concentrations of nitrogen compounds ($\mu mol\ l^{-1}$) at 10m. depth.

Station	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	% total nitrogen as urea
2	0.00	4.45	2.000	0.400	6.85	0
3	0.00	4.50	2.225	0.275	7.00	0
5	0.13	3.15	1.577	0.223	5.08	3
6	1.56	3.05	2.003	0.327	6.94	22

TABLE 4.54: CRUISE HGL III(h): Chlorophyll a ($\mu g\ l^{-1}$), total microbial ATP ($\mu g\ l^{-1}$), bacterial numbers (cells l^{-1}), bacterial cell volumes ($\mu m^3 l^{-1}$) and cellular ATP:cellular C ratios at 10 m depth.

Station Number	Chlorophyll a	Total Microbial ATP	Bacterial Numbers	Bacterial Cell Volumes	Cellular ATP: cellular C
2	2.317	0.0396	1.000×10^9	1.28×10^8	0.48×10^{-3}
3	2.797	0.2051	1.230×10^9	1.94×10^8	1.99×10^{-3}
5	2.813	0.1846	5.240×10^8	8.25×10^7	1.99×10^{-3}
6	2.790	0.0872	7.190×10^8	1.16×10^8	0.92×10^{-3}

TABLE 4.55: CRUISE HGL III(h). Microbial biomass ($\mu gC\ l^{-1}$), at 10 m. depth

Station Number	A Phototrophic carbon (from Chl. a)	B Total microbial carbon (from ATP)	C Heterotrophic carbon (B - A)	D Bacterial Carbon (from numbers & volume)	E Total microbial carbon (A + D)
2	69.51	9.90	- 59.61	12.8	82.31
3	83.91	51.28	- 32.63	19.4	103.31
5	84.39	46.14	- 38.25	8.3	92.64
6	83.70	21.79	- 61.91	11.6	95.30

TABLE 4.56: CRUISE HGL III. BACTERIAL CELL MORPHOLOGY AND SIZE (/um) AS A PERCENTAGE OF THE TOTAL CELL NUMBERS

Station No.	Cocci (diameter)		Rods (width x length)		Vibroids (V) & Spirella (S)	Comments
	0.2-1.2	1.2-1.8	0.2x0.4-1.2	0.5x1.2-2.4	0.2x0.4-1.8	
2	65	0	5	0	30(V)	Little detrit cells free
3	85	0	0	0	15(V)	Little detrit cells free
5	85	0	0	0	15(V)	Little detrit cells free
6	70	0	10	10	10(V)	Little detrit cells free

Table 4.57 : Cruise HGL III(h). Uptake of ^{14}C-urea in light (d.p.m.) at 10m. depth.

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
2	4,904	332	5,236
3	4,067	361	4,428
5	6,978	525	7,699
6	4,884	504	5,695

Table 4.58 : Cruise HGL III(h). Uptake of ^{14}C-urea in dark (d.p.m.) at 10m. depth.

Station	$^{14}CO_2$ liberated	^{14}C incorporated	Total uptake
2	3,835	601	4,436
3	1,562	137	1,699
5	5,972	633	6,801
6	3,399	213	3,919

Table 4.59 : Cruise HGL III(h). Urea assimilation rates (nmol urea l^{-1} hr^{-1}) at 10m. depth.

Station number	Total assimilation rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
2	0.59	0.09	0.50
3	0.50	0.31	0.19
5	0.92	0.10	0.82
6	1.14	0.35	0.79

TABLE 4.60: CRUISE HGL III(h). Urea turnover times (days) at 10 m. depth

Station Number	Total Turnover Time	Phototrophic turnover time	Heterotrophic turnover time
2	70.67	462.50	83.41
3	83.56	135.58	217.78
5	48.06	412.03	54.40
6	64.97	220.76	94.41

TABLE 4.61: CRUISE HGL III(h). ^{14}C- urea incorporated in living cells as a percentage of total urea assimilation at 10 m. depth

Station Number	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
2	14	0	14
3	8	0	8
5	9	0	9
6	9	4	5

TABLE 4.62: CRUISE HGL III (h). UREA ASSIMILATION INDICES (nmol urea hr^{-1}/ug C^{-1}) AT 10m. DEPTH

Station No.	Total Assimilation Index B *	E *	Phototrophic Assimilation Index A *	Heterotrophic Assimilation Index C *	D *
2	5.96×10^{-2}	0.72×10^{-2}	0.13×10^{-2}	-	3.91×10^{-2}
3	0.98×10^{-2}	0.48×10^{-2}	0.37×10^{-2}	-	0.98×10^{-2}
5	1.99×10^{-2}	0.99×10^{-2}	0.12×10^{-2}	-	9.94×10^{-2}
6	5.23×10^{-2}	1.20×10^{-2}	0.42×10^{-2}	-	6.81×10^{-2}

* B using carbon derived from total microbial ATP (B)
E using carbon derived from chlorophyll a plus bacterial numbers and volumes (E)
A using carbon derived from chlorophyll a (A)
C using carbon derived from (B) minus (A)
D using carbon derived from bacterial numbers and volumes (D)

TABLE 4.63: CRUISE HGL III. Bacterial cell morphology and size (/um) as a percentage of the total cell numbers

Station Number	Depth (m)	Cocci (diameter) 0.2-1.2	1.2-1.8	Rods (width x length) 0.2x0.4-1.2	0.5x1.2-2.4	Vibroids(V) & Spirilla(S) 0.2 x 0.4-1.8	Comments
8 *	2	80	0	0	10	10 (V)	Diplococci common
8 *	10	90	0	0	5	5 (V)	"
8 *	21	30	0	60	10	0	"
11 *	2	98	0	0	0	2 (V)	"
11 *	8	98	0	0	0	2 (V)	"
11 *	15	95	0	0	0	5 (V)	"
1	2	90	0	0	0	10 (V)	Little detritus,cells free
1	20	90	0	0	0	10 (V)	"
1	41	85	0	0	0	15 (V)	"
17	2	50	0	0	0	50 (V)	"
17	10	80	0	0	0	20 (V)	"
17	18	80	0	0	0	20 (V)	"
17	36	100	0	0	0	0	"

* Bacteria (mainly the cocci) often associated with detritus. Large amounts of detritus in the sample.

Table 4.64 : Cruise HGL III. Physical measurements when biological vertical profiles were made.

Station number	Depth (m.)	Salinity (^{o}/oo)	Temperature (^{o}C)	Sigma T	$\bar{v}$ (joules m^{-3})
8	2	24.20	15.70	17.566	20.13
8	10	25.50	15.37	18.627	
8	21	26.60	15.30	19.483	
11	2	31.28	16.64	22.770	4.4
11	8	31.30	14.23	23.308	
11	10	31.35	14.34	23.324	
11	15	31.47	14.61	23.360	
1	2	32.99	14.82	24.483	0.5
1	10	33.00	14.77	24.502	
1	20	33.01	14.70	24.524	
1	41	33.01	14.78	24.507	
17	2	33.31	15.75	24.526	3.8
17	10	33.31	15.75	24.526	
17	18	33.31	15.29	24.627	
17	36	33.31	14.82	24.737	

Table 4.65 : Cruise HGL III. Concentrations of nitrogen compounds (µmol N l^{-1}) at various depths

Station	depth (m.)	Urea-N	NH_3	NO_3	NO_2	'Total nitrogen'	%total nitrogen as urea
8	2	0.91	8.70	58.200	3.800	71.61	1
8	10	0.00	10.00	40.040	2.360	52.40	0
8	21	0.00	11.30	45.272	2.728	59.30	0
11	2	1.91	6.60	11.655	1.095	21.29	9
11	8	0.45	6.50	12.700	1.130	20.78	2
11	15	1.64	6.10	7.943	0.857	16.54	10
1	2	1.66	3.30	1.750	0.300	7.01	24
1	20	0.00	3.80	2.053	0.347	6.20	0
1	41	0.00	4.90	1.745	0.355	7.00	0
17	2	0.00	5.15	1.270	0.180	6.60	0
17	10	0.75	2.70	1.270	0.250	4.97	15
17	18	0.41	2.70	1.247	0.273	4.63	9
17	36	0.00	3.55	1.520	0.180	5.25	0

TABLE 4.66: CRUISE HGL III. Chlorophyll a ($\mu g\ l^{-1}$), total microbial ATP ($\mu g\ l^{-1}$), bacterial numbers (cells l^{-1}), bacterial cell volumes ($\mu m\ l^{-1}$) and cellular ATP:cellular C ratios at various depths.

Station Number	Depth (m)	Chlorophyll a	Total Microbial ATP	Bacterial Numbers	Bacterial Cell Volumes	Cellular ATP: cellular C
8	2	2.454	0.0679	2.621×10^{9}	4.61×10^{8}	0.57×10^{-3}
8	10	2.934	0.0240	2.036×10^{9}	3.42×10^{8}	0.20×10^{-3}
8	21	4.690	0.0434	1.750×10^{10}	1.77×10^{8}	0.14×10^{-3}
11	2	6.553	0.2627	9.010×10^{8}	1.59×10^{8}	1.24×10^{-3}
11	8	6.288	0.2128	2.672×10^{9}	4.72×10^{8}	0.90×10^{-3}
11	15	7.652	0.0347	2.750×10^{9}	4.75×10^{8}	0.13×10^{-3}
1	2	1.561	0.0628	1.053×10^{9}	1.74×10^{8}	0.98×10^{-3}
1	20	2.262	0.1254	7.180×10^{8}	1.19×10^{8}	1.57×10^{-3}
1	41	2.163	0.1465	6.490×10^{8}	1.02×10^{8}	1.95×10^{-3}
17	2	3.210	0.2668	1.260×10^{9}	1.32×10^{8}	2.43×10^{-3}
17	10	1.734	0.2339	1.105×10^{9}	1.66×10^{8}	3.41×10^{-3}
17	18	1.756	0.1037	1.105×10^{9}	1.66×10^{8}	1.50×10^{-3}
17	36	1.372	0.1128	7.400×10^{8}	1.33×10^{8}	2.07×10^{-3}

TABLE 4.67: CRUISE HGL III. Uptake of ^{14}C- urea in light (d.p.m.) at various depths

Station	Depth (m)	$^{14}CO_2$ liberated	^{14}C incorporated	Total Uptake
8	2	10,655	1,262	12,165
8	10	3,701	606	4,483
8	21	10,099	1,717	11,816
11	2	21,926	1,639	23,374
11	8	6,422	1,864	8,286
11	15	6,615	372	6,987
1	2	7,740	509	8,249
1	20	8,253	685	8,938
1	41	5,262	104	5,366
17	2	4,628	612	5,387
17	10	2,948	123	3,071
17	18	2,094	371	2,465
17	36	1,501	32	1,533

TABLE 4.68: CRUISE HGL III. Uptake of ^{14}C- urea in dark (d.p.m.) at various depths

Station	Depth (m)	$^{14}CO_2$ liberated	^{14}C Incorporated	Total Uptake
8	2	3,965	592	4,805
8	10	2,556	323	3,053
8	21	6,741	1,070	7,881
11	2	2,902	0	2,902
11	8	577	189	766
11	15	1,084	0	1,084
1	2	4,439	522	4,961
1	20	4,604	444	5,048
1	41	3,490	0	3,490
17	2	2,438	200	2,638
17	10	1,455	9	1,464
17	18	1,472	140	1,612
17	36	905	0	905

TABLE 4.69: CRUISE HGL III. Microbial biomass (/ugC l^{-1}) at various depths

Station Number	Depth (m)	A Phototrophic carbon (from chl.a)	B Total microbial carbon (from ATP)	C Heterotrophic carbon (B - A)	D Bacterial carbon (from numbers & volume)	E Total microbial carbon (A + D)
8	2	73.62	16.98	- 56.64	46.1	119.72
8	10	88.02	6.00	- 82.02	34.2	122.22
8	21	140.70	10.86	-129.84	177.0	317.70
11	2	196.59	65.68	-130.91	15.9	212.49
11	8	188.64	53.19	-135.45	47.2	235.84
11	15	229.56	8.67	-220.89	47.2	276.76
1	2	46.83	65.70	18.87	17.4	64.23
1	20	67.86	31.36	- 36.50	11.9	79.71
1	41	64.89	36.63	- 28.26	10.2	75.11
17	2	96.35	66.70	- 29.65	13.2	109.55
17	10	52.02	58.47	6.45	16.6	68.62
17	18	52.68	25.91	- 26.77	16.6	69.28
17	36	41.10	28.20	- 12.90	13.3	54.40

TABLE 4.70: CRUISE HGL III. Urea assimilation rates (nmol urea l^{-1} hr^{-1}) at various depths

Station Number	Depth (m)	Total Assimilation Rate	Phototrophic assimilation rate	Heterotrophic assimilation rate
8	2	1.99	1.20	0.79
8	10	0.50	0.16	0.34
8	21	1.33	0.45	0.88
11	2	5.15	4.51	0.64
11	8	1.14	1.03	0.11
11	15	1.43	1.21	0.22
1	2	1.70	0.68	1.02
1	20	1.01	0.44	0.57
1	41	0.60	0.21	0.39
17	2	0.61	0.31	0.30
17	10	0.48	0.25	0.23
17	18	0.33	0.11	0.22
17	36	0.17	0.07	0.10

TABLE 4.71: CRUISE HGL III. Urea turnover times (days) at various depths

Station Number	Depth (m)	Total turnover time	Phototrophic turnover time	Heterotrophic turnover time
8	2	30.42	44.26	77.00
8	10	82.53	258.74	121.19
8	21	31.31	92.38	47.37
11	2	15.83	18.07	127.50
11	8	44.65	49.20	483.03
11	15	52.96	62.70	341.33
1	2	44.85	112.53	74.58
1	20	41.40	95.12	73.30
1	41	68.95	197.23	106.02
17	2	68.68	142.20	132.86
17	10	117.16	230.39	238.40
17	18	150.10	433.76	229.53
17	36	241.36	589.17	408.84

TABLE 4.72: CRUISE HGL III. Urea Assimilation indices (nmol urea hr^{-1}/ug C^{-1}) at various depths

Station Number	Depth (m)	Total Assimilation Index		Phototrophic Assimilation Index	Heterotrophic Assimilation Index	
		B *	E *	A *	C *	D *
8	2	11.72×10^{-2}	1.66×10^{-2}	1.63×10^{-2}	-	1.71×10^{-2}
8	10	8.33×10^{-2}	0.41×10^{-2}	0.18×10^{-2}	-	0.99×10^{-2}
8	21	12.25×10^{-2}	0.42×10^{-2}	0.32×10^{-2}	-	0.50×10^{-2}
11	2	7.85×10^{-2}	2.42×10^{-2}	2.29×10^{-2}	-	4.03×10^{-2}
11	8	2.14×10^{-2}	0.48×10^{-2}	0.55×10^{-2}	-	0.23×10^{-2}
11	15	16.49×10^{-2}	0.52×10^{-2}	0.53×10^{-2}	-	0.47×10^{-2}
1	2	2.59×10^{-2}	2.65×10^{-2}	1.45×10^{-2}	-	5.86×10^{-2}
1	20	3.22×10^{-2}	1.27×10^{-2}	0.65×10^{-2}	-	4.81×10^{-2}
1	41	1.64×10^{-2}	0.80×10^{-2}	0.32×10^{-2}	-	3.82×10^{-2}
17	2	0.91×10^{-2}	0.56×10^{-2}	0.32×10^{-2}	-	2.27×10^{-2}
17	10	0.82×10^{-2}	0.70×10^{-2}	0.48×10^{-2}	3.57×10^{-2}	1.39×10^{-2}
17	18	1.27×10^{-2}	0.48×10^{-2}	0.21×10^{-2}	-	1.33×10^{-2}
17	36	0.60×10^{-2}	0.31×10^{-2}	0.17×10^{-2}	-	0.75×10^{-2}

* B Using carbon derived from total microbial ATP

E Using carbon derived from chlorophyll a plus bacterial numbers and volume

A Using carbon derived from chlorophyll a

C Using carbon derived from B minus A

D Using carbon derived from bacterial numbers and volume

TABLE 4.73: CRUISE HGL III. ^{14}C- urea incorporated in living cells as a percentage of total urea assimilation at various depths.

Station Number	Depth (m)	Total ^{14}C in cells	^{14}C in phototrophic cells	^{14}C in heterotrophic cells
8	2	12	0	12
8	10	14	3	11
8	21	15	1	14
11	2	7	7	0
11	8	25	0	25
11	15	5	5	0
1	2	11	0	11
1	20	9	0	9
1	41	2	2	0
17	2	11	4	7
17	10	4	3	1
17	18	15	6	9
17	36	2	2	0

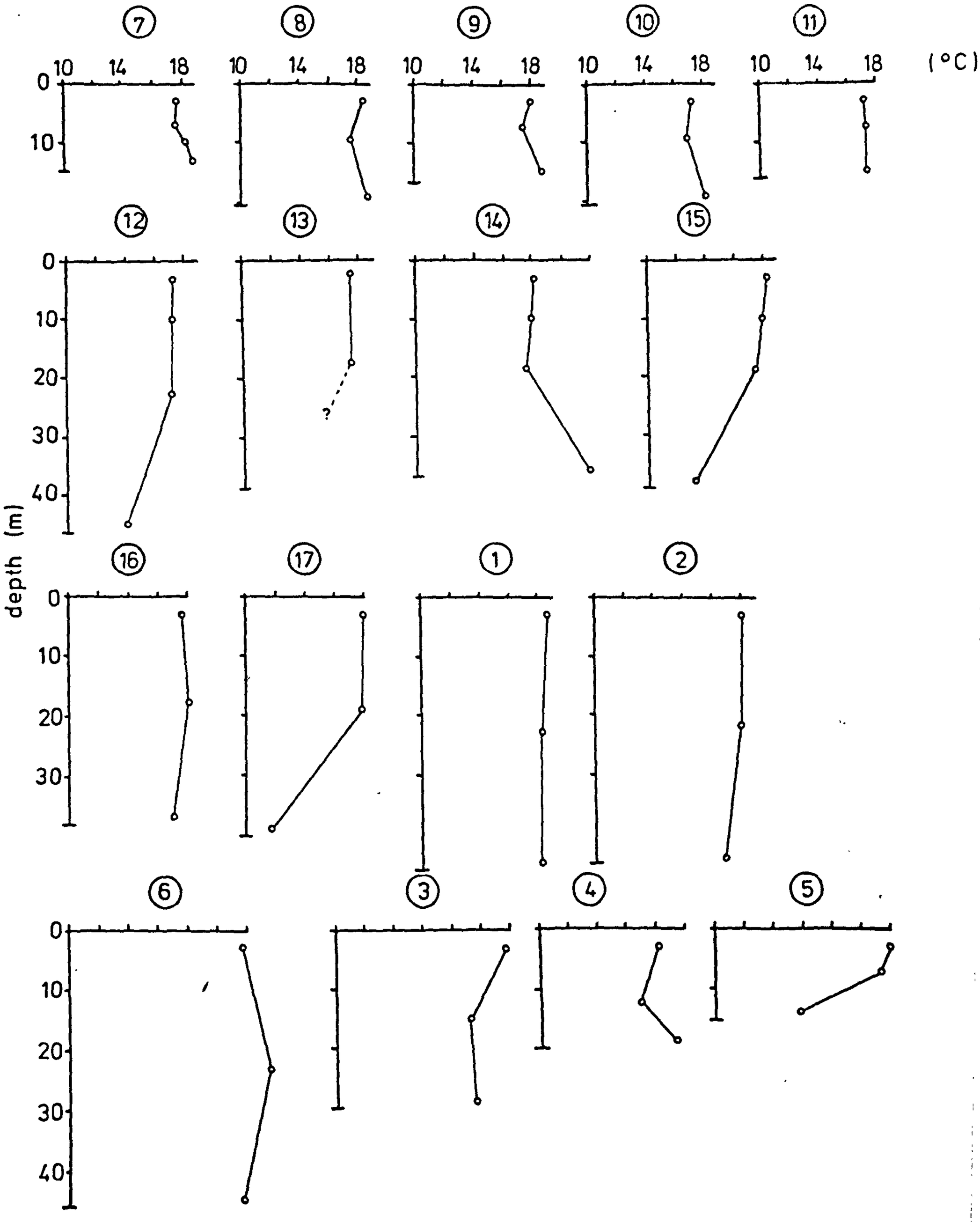

Figure 4.67 :Cruise HGL II. Temperature depth profiles

Station number = ◯

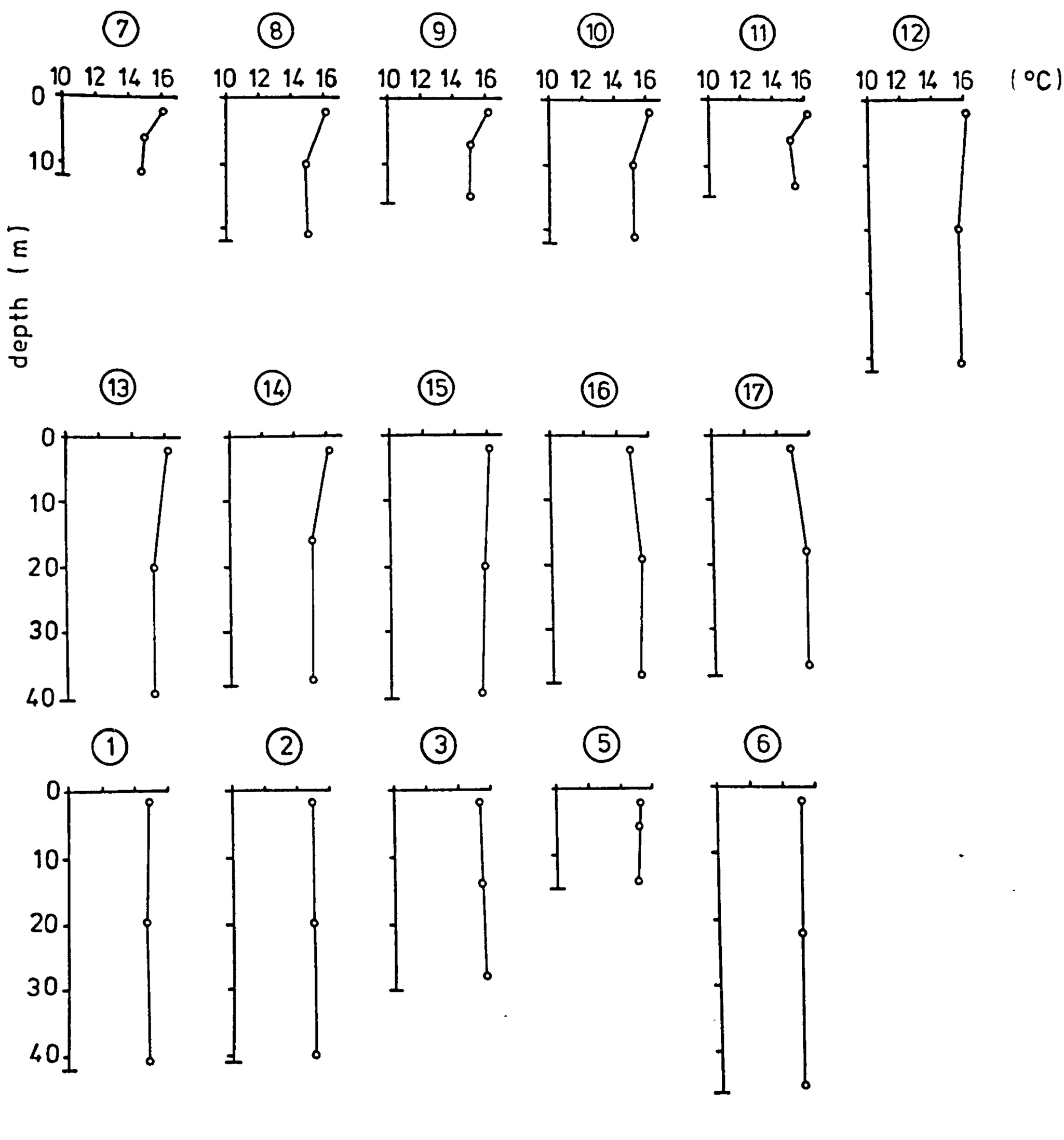

Figure 4.68 : Cruise HGL III . Temperature depth profiles

Station number = ◯